

Toward a better understanding of host use and biodiversity in riordinid butterflies (Lepidoptera)

P. J. DeVries

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 01238

I. A. Chacon

Museo Nacional, Apartado 749, San Jose, Costa Rica

and

Debra Murray

Estacion Biologica Jatun Sacha, Casilla 1501-218, Tena, Ecuador

Abstract. Over one hundred-eighty observations on the host use and ant association of ninety-eight riordinid butterflies are presented — a substantial addition to our understanding of this distinctly neotropical group. These observations are contrasted to previous work, and discussed with respect to apparent patterns of phytophagy, aphytophagy, caterpillar sociality, and ant association. The majority of riordinid species have unknown life histories, and thus we conclude that much more fieldwork is need before a phylogenetic approach to host use and ant association can be established.

INTRODUCTION

The fact that there are more species of bats than elephants, more little bats than large ones, more species of insects than mammals, and so on vividly demonstrates one of the best known axioms of biodiversity — there is an inverse relationship between body size and number of species (Hutchinson & MacArthur 1959; May 1978; Van Valen 1973). In other words, the species-number game is not for giants. Add to this that the taxonomy of small-bodied organisms is typically less well known than that of larger ones (Mayr 1969), and it is easy to appreciate how crude our understanding of biodiversity really is. However, the importance of biodiversity lies not simply in numbers but in how organisms live and interact within habitats. Thus another general axiom may be added, namely, that within a particular group the basic natural history of small-bodied species will always be less well known than that of larger ones. For example, among butterflies the host relationships and early stages of the papilionids, pierids and nymphalids are more completely known than are those of the lycaenoid butterflies — the Riordinidae and Lycaenidae. In other words, on average less is known about the lycaenoid butterflies mainly because they are small.

The riordinids are a diverse group of small-bodied butterflies that show an almost entirely neotropical distribution. Starting with Hinton (1951), general reviews of lycaenoid biology have typically treated the riordinid butterflies in passing as peculiar neotropical members of the Lycaenidae (Cottrell 1984; Ehrlich 1958; Pierce 1987; Vane-Wright 1978). Whatever their relationships eventually prove to be, in the absence of solid data and an overall lycaenoid

phylogeny, the fact remains that our perception about the biology and evolution of riodinids has been typically inferred from what we know of lycaenids (DeVries 1991a&c). Recent work with riodinids has increased our understanding of them in two complimentary areas. First, modern systematic studies have lent strong support to the idea that the riodinids are monophyletic (Harvey 1987; see also Martin & Pashley 1992; Robbins 1988). Secondly, experimental and morphological studies have pointed to differences between riodinids and lycaenids with respect to their early stage morphology and the evolution of myrmecophily (e.g., Brevignon 1992; Callaghan 1977, 1982, 1986a&b, 1989; DeVries 1988 a & b, 1991b&c; Harvey 1987; Ross 1964, 1966). Even with the advent of this recent interest in the riodinids, our overall grasp of their early-stage biology can be summarized by a historical quote from Scudder (1887, p. 111) who wrote,

“... Our knowledge of the Lemoniinae [Riodinidae] is exceedingly meagre, so that we can here draw no decided conclusions. There is, indeed, no greater desideratum in the study of butterflies than a knowledge of the transformation of the principal genera of this subfamily....”

More than a century since Scudder penned these words we still know less about the life histories of riodinids than of any other major group of butterflies.

For a number of years one of us (PJD) has been preparing a treatment of the Costa Rican riodinid fauna. This project has provided an impetus for the authors to make field observations on the early stages of riodinid butterflies in an array of tropical areas. Given the unparalleled destruction of tropical habitats within the last century and the scarcity of such basic information on riodinids, we feel some urgency in making our observations available to other researchers. Accordingly we here summarize some of our riodinid host records gathered during the last 8 years. We also briefly discuss our observations within the context of the review provided in Harvey's (1987) tribal classification, and highlight some aspects of riodinid biology that we feel may be useful for future studies. A more detailed analysis of these and other observations will appear elsewhere.

METHODS

The records presented here include cases where field-collected eggs were reared to adults, or where caterpillars of various instar were found in the field and subsequently reared to adults, as well as oviposition records where the female was collected and/or positively identified. The records and information pertinent to them is presented in a telescopic format (Table 1). The complete nomenclature of the butterfly taxa treated in this study is found in Table 2 and follows the higher classification of Harvey (1987). Field observations by DeVries originate from Belize, Costa Rica, Panama, Ecuador, Argentina, Madagascar and Hainan Island, China. Those of Chacon are from Costa Rica only, and those of Murray are from Jatun Sacha, Ecuador only. Coded abbreviations for the geographic locality of each rearing record are listed in Table 3, and those of the families of hosts are found in Table 4. The identity of symbiotic ant taxa found in association with certain caterpillar taxa are listed in Table 5, and

information relevant to these records is found within bold, square brackets [] under 'Notes' in Table 1.

Information regarding eggs and caterpillars is placed within parentheses () under 'Notes' in Table 1, and the coded information is as follows:

- eggs — 1 = laid singly, 2 = small clusters of two to six eggs, 3 = clusters from seven to sixty eggs, and *amo* = probable ant mediated oviposition.
- caterpillars — *s* = solitary, *sg* = semi-gregarious (tolerant of other individuals, including other instars), and *g* = gregarious (synchronous in feeding and molting). As in many other groups of butterflies, riodinid caterpillars typically feed on young leaves or shoots. Unless specified otherwise the abbreviation *lvs* in Table 1 refers to young leaves and *flrs* refers to flowers. Under 'Notes' in Table 1 voucher numbers for Chacon's records are found within brackets {}, the records of Murray are abbreviated DM, and all others are those of DeVries. Voucher material from this study has been deposited in the Museo Nacional de Costa Rica, Museum of Comparative Zoology (Harvard University), and the collections of PJD and DM.

RESULTS AND DISCUSSION

In all, over 180 original natural history observations for 98 species of riodinid butterflies are presented here, including host associations with 37 plant families and one order of insects (Table 1). Many of these records are new, and others corroborate those published previously. We further provide a substantial number of observations on the identity of the ant taxa that associate with some riodinid caterpillars. Although our observations add considerably to the available body of information on riodinids, within the context of their total species richness the sum total of riodinid host records now known remains small. Nevertheless, highlighting some aspects of host relationships and early stage biology may be useful to future workers. Accordingly we discuss the patterns of host use within the context of a tribal level classification (Harvey 1987), and point to various relationships that relate to clutch size, caterpillar behavior, and aphytophagy. Secondly, we discuss some patterns relevant to understanding those taxa that form symbiotic interactions with ants. Finally, we ask what contribution does the information here make to our understanding of the riodinids as a group, and to our understanding of tropical biodiversity in general.

New Host Records at the Tribal Level

The first summary of hostplant information aimed specifically at understanding the riodinids at the tribal level was compiled by Harvey (1987). With that work as a reference point we may now add a significant number of new hostplant families to seven riodinid tribes. These are as follows: 1) **Euselasiinae** — (*Euselasia*) Melastomataceae; 2) "**incertae sedis**" — (*Eunogyra*) Araceae; 3) **Riodinini** — (*Ancyluris*) Euphorbiaceae; (*Necyria* and *Lyropteryx*) Vochysiaceae, Gesneriaceae; (*Rhetus*) Combretaceae; (*Chorinaea*) Hippocrateaceae; (*Ithomeis* and *Metacharis*) Olacaceae; (*Themone*) Quinaceae; (*Lepricornis*) Malpighiaceae; (*Chalodeta*) Passifloraceae; 4) **Symmachiini** — (*Mesene*) Fabaceae, Violaceae; (*Mesenopsis* and *Symmachia*) Melastomataceae; (*Symmachia*) Ulmaceae; 5) **Charitini** — (*Anteros*) Melastomataceae, Vochysiaceae; (*Sarota*) Lejuniaceae;

Table 1. Information on riodinid biodiversity

Genus	Species	Host	Locality	plant part	stage	Notes
<i>Saribea</i>						
	<i>perroti</i>	undetermined genus (23)	R	lvs	el	N=3 (1, s)
<i>Abisara</i>						
	<i>echerius</i>	undetermined genus (23)	H	lvs	e	N=1 (1)
<i>Euselasia</i>						
	<i>rhodogyne</i>	<i>Clusia odorata</i> (7)	B	lvs	lp	N >50 (g) * Zotz
	<i>mystica</i>	<i>Psidium</i> spp (24)	SJ, M	lvs	elp	N=>50 (3, g)
	<i>chrysippe</i>	<i>Miconia elata</i> (21)	CH, L	old lvs	e	N= 1 (3) died as second instars
	<i>nr. cafusa</i>	<i>Eugenia</i> sp. (24)	CV	old lvs	lp	N=15 (g)
	<i>eulione</i>	<i>Psidium</i> sp. (24)	GC	lvs	lp	N>100 (g)
		<i>Psidium guajava</i> (24)	JS	lvs	elp	N>50 (3, g) DM
<i>Mesosemia</i>						
	<i>asa</i>	<i>Psychotria macrophylla</i> (32)	A	lvs	elp	N=10 (1, s)
	<i>carissima</i>	<i>Psychotria luxurians</i> (32)	PL	lvs	lp	N=5 (s) {91-HNP-147; 92-HNP-176}
	<i>nr. tenebricosa</i>	undetermined genus (32)	JS	lvs	elp	N=2 (1, s) DM
	<i>nr. ephyne</i>	undetermined genus (32)	JS	lvs	elp	N=1 (1, s) DM
	<i>telegone</i>	<i>Psychotria</i> sp. (32)	P	lvs	lp	N=2 (s)
		<i>Aphelandra</i> sp. (1)	P	lvs	lp	N=1 (s) * Aiello
		<i>Palicourea guianensis</i> (32)	C	lvs	el	N=1 (s)
	<i>nr. judicialis</i>	<i>Faramea</i> sp. (32)	JS	lvs	lp	N=1 (s)
		<i>Faramea eurycarpa</i> (32)	JS	lvs	elp	N=1 (1, s) DM
<i>Leucochimona</i>						
	<i>lagora</i>	<i>Diodia</i> sp. (32)	L, CH	lvs	elp	N=5 (1, s)
		<i>Borreria</i> sp. (32)	PL	lvs	lp	N=1 (s) {92-HNP-70}
		<i>Coccocypselum herbaceum</i> (32)	PL	lvs	elp	N= 1 (1, s) {92-HNP-70}
		<i>Hemidiodia ocimifolia</i> (32)	PL	lvs	elp	N=7 (1, s) {92-HNP-78; 78.2}
	<i>nr. philemon</i>	undetermined genus (32)	JS	lvs	elp	N=1 (1, s) DM
	<i>nr. molina</i>	undetermined genus (32)	CA	lvs	elp	N=6 (1, s)
<i>Eurybia</i>						
	<i>patrona</i>	<i>Calathea inocephala</i> (20)	CV	flrs	lp	N=6 (1, sg) [3, 10]
	<i>elvina</i>	<i>Calathea</i> spp (20)	L, SJ,	flrs	elp	N>10 (1, s) [3, 17]
		<i>Calathea</i> spp (20)	B	flrs	elp	N=3 (1, s) [1, 2, 3, 17]
		<i>Ischnosiphon pruniosus</i> (20)	B	flrs	lp	N=2 (s) [9, 17]

Genus	Species	Host	Locality	plant part	stage	Notes
	<i>lycisca</i>	<i>Calathea</i> spp (20)	SJ,L,CH	flrs	elp	N>20 (1,s or sg) [1, 2, 3, 9, 16]
		<i>Calathea marantifolia</i> (20)	CV	flrs	elp	N= 4 (1, s) [3, 4, 13]
		<i>Calathea lutea</i> (20)	CV	flrs	elp	N= 2 (1, s) [13]
		<i>Calathea crotalifera</i> (20)	SV	flrs	elp	N =5 (1, s) [5]
		<i>Calathea cleistantha</i> (20)	PL	flrs	elp	N>20 (1, s) [?] {91-HNP-38; 139;140}
		<i>Calathea latifolia</i> (20)	B	flrs	elp	N=2 (1, s) [1]
		<i>Ischnosiphon pruniosus</i> (20)	CV	flrs	elp	N>20 (1, s) [2, 10]
	<i>sp. unknown</i>	<i>Renalmia</i> sp. (37)	GC	flrs	l	N=4 (s) [6]
	<i>nr nicaeus</i>	<i>Calathea nr inocephala</i> (20)	GC	flrs	lp	N=4 (sg) [12]
	<i>nr hyacinthina</i>	<i>Renalmia</i> sp. (37)	JS	flrs	lp	N=1 (2, s) [2, 3]
<i>Napaea</i>						
	<i>eucharilla</i>	<i>Ananas comosus</i> (5)	B	lvs	lp	N=1 (s)
		<i>Ananas comosus</i> (5)	CV	lvs	lp	N=1 (s)
		<i>Achmaea magdalenae</i> (5)s	B	lv	lp	N=1 (s)
		undetermined genus (5)	PL	lvs	lp	N= 24 (s) {91-HNP-196, 92-HNP-177; 163}
	<i>theages</i>	<i>Vriesia</i> sp. (5)	L	lvs	e	N=1 (1)
		<i>Scaphyglottis</i> sp. (27)	Pan	lvs	lp	N=1 (s) *Aiello
<i>Cremna</i>						
	<i>actoris</i>	<i>Maxillaria</i> sp. (27)	JS	lvs	lp	N>10 (1) DM
	<i>thasus</i>	<i>Catasetum viridiflavum</i> (27)	B	lvs	elp	N=5 (1, s)
		<i>Catasetum viridiflavum</i> (27)	CH	lvs	e	N=2 (1)
		<i>Oncidium</i> sp. (27)	B	lvs	lp	N=4 (s)
		<i>Brassavola nodosa</i> (27)	Pan	lvs	lp	N=4 (s) *Aiello
		<i>Mormodeus igneum</i> (27)	Pan	lvs	lp	N=1 (s) *Aiello
<i>Eunogyra</i>						
	<i>satyrus</i>	undetermined (0)	GC	lvs	e	N=2 (1)
<i>Hermathena</i>						
	<i>candidata</i>	<i>Vriesia</i> sp. (5)	CA	flrs	e	N=2 (1)
<i>Ancyluris</i>						
	<i>inca</i>	<i>Miconia argentea</i> (21)	C, L, SV	lvs	elp	N>20 (2, sg)
		<i>Miconia</i> sp. (21)	R	lvs	lp	N = 8 (sg)
		<i>Miconia argentea</i> (21)	B, G	lvs	lp	N=6 (sg)
		<i>Miconia elata</i> (21)	G	lvs	lp	N=5 (sg)
	<i>jurgensenii</i>	<i>Hyeronima</i> sp. (11)	C	lvs	e	N=5 (1)
		<i>Hyeronima oblonga</i> (11)	PL	lvs	lp	N=1 (s) {92-HNP-89}
		<i>Hyeronima</i> sp. (11)	P	lvs	el	N=3 (1)

Genus	Species	Host	Locality	plant part	stage	Notes
<i>Necyria</i>						
	<i>beltiana</i>	<i>Conostegia xalapensis</i> (21)	PL	lvs	lp	N=1 (1, s) {92-HNP- 75}
		<i>Vochysia guatemalensis</i> (36)	PL	lvs	elp	N=11 (1, s) {92-HNP- 72; 74.1; 74.2; 95}
		<i>Drymonia warscewicziana</i> (14)	PL	lvs	lp	N=1 (s) {92-HNP- 116}
<i>Lyropteryx</i>						
	<i>lyra</i>	<i>Vochysia guatemalensis</i> (36)	PL	lvs	lp	N=1 (s) {92-HNP-173}
<i>Rhetus</i>						
	<i>arcius</i>	<i>Terminalia catapa</i> (8)	Pan	lvs	lp	N=1 (s)
<i>Chorinaea</i>						
	<i>faunus</i>	<i>Prionostemma aspera</i> (15)	B	lvs	lp	N=1 (s)
<i>Ithomeis</i>						
	<i>eulaema</i>	<i>Heisteria</i> sp. (26)	SV	lvs	e	N=1 (3)
<i>Melanis</i>						
	<i>pixie</i>	<i>Albizzia caribaea</i> (12)	SJ, SA	lvs	elp	N>100 (3,g)
<i>Themone</i>						
	<i>pais</i>	<i>Quiina</i> sp. (30)	JS	lvs	e	N=1 (1) DM
<i>Lepricornis</i>						
	<i>strigosa</i>	<i>Heteropterus laurifolia</i> (18)	B	lvs	lp	N=1 (s)
<i>Metacharis</i>						
	<i>cuparina</i>	<i>Heisteria coccinna</i> (26)	SV	old lvs	lp	N=1 (s)
<i>Charis</i>						
	<i>nr. anius</i>	unknown canopy vine	JS	lvs	elp	N=2 (1, s) DM
		<i>Mikania</i> sp. (2)	JS	lvs	elp	N=2 (1, s) DM
	<i>gynaea</i>	dead leaves	B, G	dead lvs	el	N=2, (1, s) died as 4th instars
	<i>cleonus</i>	dead leaves	JS	dead lvs	el	N=4 (1, s) died as 2d instars DM
	<i>cleonus</i>	dead leaves	GC	dead lvs	el	N=4, (1, s) died as 2d instars
<i>Caria</i>						
	<i>rhacotis</i>	<i>Celtis iguanae</i> (34)	SV	lvs	el	N=3 (s)
<i>Chalodeta</i>						
	<i>chaonitis</i>	<i>Miconia longifolia</i> (21)	L	flrs	lp	N=1 (s)
	<i>lypera</i>	undetermined (28)	JS	lvs	lp	N=2 (sg) DM
<i>Lasaia</i>						
	<i>agesilaus</i>	<i>Albizzia caribaea</i> (12)	SA	lvs	lp	N=1 (s)
<i>Mesene</i>						
	<i>phareus</i>	<i>Inga</i> sp. (12)	B	old lvs	lp	N=1 (s)
	<i>silaris</i>	<i>Rinorea</i> sp. (35)	P	lvs	e	N=3 (1)

Genus	Species	Host	Locality	plant part	stage	Notes
<i>Mesenopsis</i>						
	<i>bryaxis</i>	<i>Miconia argentea</i> (21)	B,G, P	lvs	lp	N=4 (s)
<i>Symmachia</i>						
	<i>tricolor</i>	<i>Miconia argentea</i> (21)	B,G,P	lvs	elp	N=5 (1, s)
	<i>rubina</i>	<i>Trema micrantha</i> (34)	L	lvs	lp	N=1 (s)
<i>Helicopsis</i>						
	<i>cupido</i>	<i>Monatr理查dia</i> sp. (0)	GC	lvs	lp	N >20 (sg, inside rolled leaf)
<i>Anteros</i>						
	<i>formosus</i>	<i>Miconia impediolaris</i> (21)	L, CH	lvs	lp	N=5 (s)
		<i>Miconia impediolaris</i> (21)	G	lvs	lp	N=2 (s)
		<i>Conostegia micrantha</i> (21)	PL	lvs	lp	N=1 (s) {92-HNP-119}
		<i>Vochysia guatemalensis</i> (36)	PL	lvs	lp	N=1 (s) {92-HNP-98}
	<i>aechus</i>	<i>Miconia</i> sp. (21)	GC, JS	lvs	lp	N=5 (s)
<i>Sarota</i>						
	<i>gyas</i>	<i>epiphylls</i> (17)	B	epiphylls	lp	N=2 (s)
	<i>chrysus</i>	old leaves with epiphylls	B	epiphylls?	e	N=3 (1)
		old leaves with epiphylls	L	epiphylls?	e	N=1 (1)
<i>Argyrogrammana</i>						
	<i>trochilia</i>	<i>Tovomitopsis</i> sp. (7)	JS	lvs	elp	N=1 (1, s) DM
		<i>Garcinia</i> sp. (7)	JS	lvs	elp	N=3 (1, s) DM
<i>Emesis</i>						
	<i>fatima</i>	<i>Heisteria</i> sp. (26)	Cacao	lvs	lp	N=1 (s) {67-HN-89}
	<i>lucinda</i>	<i>Neea</i> spp (25)	L, CH	lvs	elp	N>50 (2 or 3, g)
		<i>Neea</i> sp. (25)	PL	lvs	lp	N=24 (g) {91-HNP-188}
	<i>mandana</i>	<i>Conceveiba pleiostemona</i> (11)	PL	lvs	lp	N=1 (s) {92-HNP-101}
	<i>lacrines</i>	<i>Hyeronima oblonga</i> (11)	PL	lvs	lp	N=2 (s) {92-HNP-39; 122}
		<i>Casearia arborea</i> (13)	PL	lvs	lp	N=2 (s) {92-HNP-188; 189}
	<i>tenedia</i>	<i>Clematis haenkeana</i> (31)	A	lvs	elp	N=6 (1, s)
<i>Lemonias</i>						
	<i>zygia</i>	<i>Croton</i> sp. (11)	GC	lvs	elp	N=>10 (2, sg, amo) [21]
<i>Thisbe</i>						
	<i>irenea</i>	<i>Croton billbergianus</i> (11)	B, G	lvs	elp	N>500 (1, s or sg) [1, 2, 3, 9, 15, 22, 24]

Genus	Species	Host	Locality	plant part	stage	Notes
		<i>Croton billbergianus</i> (11)	PL	lvs	lp	N=6 (s) [?] {92-HNP-101}
		<i>Croton</i> sp. (11)	ER	lvs	lp	N=2 (s) [3]
		<i>Croton</i> spp (11)	L, CH	lvs	lp	N>20 (s or sg) [1, 2, 3, 15, 20]
		<i>Croton</i> sp. (11)	C	lvs	lp	N=3 (sg) [8]
		<i>Croton</i> sp. (11)	Belize	lvs	lp	N=3 (s) [2, 20]
		<i>Croton</i> sp. (11)	GC	lvs	lp	N=4 (s) [2, 22]
	<i>lycorias</i>	<i>Cassia alata</i> (12)	Cañas	lvs	lp	N=1 (s) [?]
<i>Juditha</i>						
	<i>molpe</i>	<i>Inga pezizifera</i> (12)	C	lvs	lp	N=5 (s) [27]
		<i>Inga</i> spp (12)	B	lvs	lp	N=2 (s) [27]
		<i>Cassia biflora</i> (12)	P	lvs	elp	N=8 (1, s, amo) [27]
		<i>Passiflora vitafolia</i> (28)	P	lvs	elp	N=4 (1, s, amo) [27]
		<i>Passiflora adenopoda</i> (28)	C	lvs	lp	N=2 (s) [27]
		<i>Doliocarpus</i> sp. (10)	B	lvs	lp	N=6 (s) [27]
		<i>Stigmaphyllon</i> sp. (18)	P	lvs	lp	N>10 (s) [27]
		<i>Tetracera</i> sp. (10)	B	lvs	lp	N=2 (s) [27]
		<i>Cardiospermum</i> sp. (33)	Bel	lvs	elp	N=3 (1, s, amo) [27]
		<i>Paullinia bracteosa</i> (33)	B	lvs	lp	N=2 (s) [27]
		<i>Serjania mexicana</i> (33)	B	lvs	lp	N=1 (s) [27]
	<i>dorilis</i>	<i>Ochroma lagopus</i> (4)	T	mem?	e	N=4 (1 on or near membr- acids) [28]
<i>Synargis</i>						
	<i>mycone</i>	<i>Cassia fruticosa</i> (12)	L, B	lvs	elp	N=6 (1, s) [2]
		<i>Pithecellobium</i> sp. (12)	B	lvs	lp	N=3 (s) [1]
		<i>Gustavia superba</i> (16)	P	flrs	lp	N=7 (s) [22]
		<i>Paullinia fibrigera</i> (33)	P	lvs	lp	N=1 (s) [1]
		<i>Heteropteris laurifolia</i> (18)	B	lvs	lp	N=4 (s) [22]
		<i>Securidaca diversifolia</i> (29)	B	lvs	lp	N=2 (s) [1]
		<i>Phryganocydia corymbosa</i> (2)	B	lvs	lp	N=2 (s) [1, 18, 20]
		<i>Pachyptera kere</i> (2)	B	lvs	lp	N=1 (s) [1]
		<i>Doliocarpus</i> sp. (10)	B	lvs	elp	N=6 (1, s) [1]
		<i>Tetracera</i> sp. (10)	B	lvs	lp	N=2 (s) [1, 2]
		<i>Omphalea diandra</i> (11)	FS	lvs	lp	N=7 (s) [2]
	<i>phylleus</i>	<i>Heisteria cocinna</i> (26)	B	mem?	el	N=9 (1 on membracids, died as first instars) [27]

Genus	Species	Host	Locality	plant part	stage	Notes
		<i>Ficus</i> sp. (22)	P	mem?	e	N=4 (1 on or near membr-acids) [27]
		<i>Pseudobombax septenatum</i> (4)	P	mem?	e	N=3 (1 on or near membr-acids) [27]
	<i>gela</i>	<i>Inga</i> sp. (12)	JS	lvs	lp	N=3 (s) [2]
	<i>abaris</i>	<i>Acalypha</i> sp. (11)	JS	lvs	lp	N=1 (s) [2]
		<i>Bauhinia</i> sp. (12)	JS	lvs	lp	N=4 (sg) [7] DM
<i>Audre</i>	<i>nr aurinia</i>	unknown	V	unknown	lp	N=7 (sg inside ant nests) [21]
	<i>undetermined sp.</i>	unknown	V	unknown	lp	N≥40 (sg inside ant nests) [21]
<i>Calospila</i>	<i>cilissa</i>	<i>Stigmaphyllon</i> spp (18)	L, C, CH	lvs	elp	N=15 (1, s) [1, 14, 17, 26]
	<i>emylius</i>	<i>Stigmaphyllon</i> sp. (18)	JS	lvs	elp	N=6 (1, s) [2]
		<i>Stigmaphyllon</i> sp. (18)	JS	lvs	lp	N>10 (s) [17] DM
<i>Adelotypa</i>	<i>senta</i>	<i>Bauhinia</i> sp. (12)	JS	lvs	lp	N=6 (sg) [7] DM
<i>Menander</i>	<i>menander</i>	<i>Marcgravia</i> sp. (19)	B	lvs	lp	N=2 (s) [17]
		<i>Sourubea</i> sp. (19)	GC	lvs	elp	N=6 (1, s) [20]
	<i>laobotas</i>	<i>Marcgravia</i> sp. (19)	C	lvs	e	N=2 (1)
	<i>pretus</i>	<i>Marcgravia</i> sp. (19)	L	lvs	lp	N=2 (s) [17]
		<i>Sourubea</i> sp. (19)	PL	lvs	lp	N=8 (s) [?] [92-HNP-97; 100;145]
<i>Setabis</i>	<i>lagus</i>	Scale insects (coc)	PL	scales	elp	N=24 (1, s) [3] [92-HNP-124; 127]
<i>Theope</i>	<i>virgilius</i>	<i>Omphalea diandra</i> (11)	F, Pan	lvs	elp	N=7 (1, s, amo) [25]
	<i>eleutho</i>	<i>Inga</i> sp. (12)	C	lvs	lp	N=1 (s) [25]
	<i>nr decorata</i>	<i>Cecropia insignis</i> (6)	L	lvs	lp	N>15 (g) [9, but see text]
	<i>nr thestias</i>	<i>Maripa panamensis</i> (9)	B	lvs	elp	N=9 (1, s, amo) [25]
		<i>Gustavia superba</i> (16)	P	flrs	lp	N=3 (s) [25]
	<i>nr matuta</i>	<i>Pseudobombax septenatum</i> (4)	P	lvs	elp	N=6 (2, sg, amo) [27]

Genus	Species	Host	Locality	plant part	stage	Notes
<i>Nymphidium</i>						
	<i>mantus</i>	<i>Maripa panamensis</i> (9)	B, P	lvs	elp	N>10 (1, s, amo) [25]
		<i>Inga</i> sp. (12)	B	lvs	elp	N=2 (1, s, amo) [25]
		<i>Serjania</i> sp. (33)	B	lvs	elp	N=1 (1, s, amo) [25]
		<i>Gustavia superba</i> (16)	P	flrs	lp	N=3 (s) [25]
	<i>haematostictum</i>	<i>Inga</i> sp. (12)	B	lvs	elp	N= 6 (1, s) [17]
	<i>cachrus</i>	<i>Inga</i> spp (12)	SV	lvs	elp	N=6 (2, sg) [3, 11, 24]
		<i>Inga</i> sp. (12)	A	lvs	elp	N=5 (2, sg) [3]
		<i>Inga</i> sp. (12)	C	lvs	elp	N= 3 (2, sg) [10]
		<i>Inga ruiziana</i> (12)	B	lvs	lp	N = 3 [17]
	<i>onaenum</i>	<i>Inga</i> sp. (12)	CA	lvs	lp	N=10 (s) [3]
		<i>Cassia fruticosa</i> (12)	H	lvs	el	N=2 (1, s) [?]
		<i>Heteropteris laurifolia</i> (18)	F	lvs	lp	N=8 (sg) [10]
	<i>azanoides</i>	<i>Inga</i> spp (12)	L, B	lvs	e	N= 3 (1) [3, 14]
	<i>nr ninias</i>	<i>Inga</i> sp. (12)	GC	lvs	e	N=1 (2)
	<i>baoetia</i>	<i>Passiflora</i> sp. (28)	JS	lvs	lp	N=1 (s) [?] DM
	<i>nr. derufata</i>	<i>Inga</i> sp. (12)	JS	lvs	lp	N=2 (s) [12] DM
	<i>nr. lisimon</i>	<i>Inga</i> sp. (12)	JS	lvs	lp	N=3 (s) [?] DM
	<i>leucosia</i>	<i>Inga</i> sp. (12)	JS	lvs	lp	N=7 (sg) [19] DM
		<i>Gustavia longifolia</i> (16)	JS	flr bracts	lp	N=5 (sg) [19] DM
	<i>ascolia</i>	<i>Senna</i> sp (12)	JS	lvs	lp	N=4 (s) [?] DM
	<i>caricae</i>	<i>Inga</i> sp. (12)	JS	lvs	lp	N=4 (sg) [3]
		<i>Inga</i> spp (12)	GC	lvs	elp	N=4 (2, sg) [5, 11]
		<i>Inga</i> sp. (12)	JS	lvs	lp	N=5 (sg) [7] DM

Table 2. List of riodinid taxa treated in this study

Hamearinae	
Saribea	perroti Riley, 1932
Abisara	echerius lisa Bennett, 1950
Euselasiinae	
Euselasia	rhodogyne patella Stichel, 1927
	mystica (Schaus, 1913)
	chrysippe (Bates, 1866)
	eulione (Hewitson, 1856)
	nr cafusa (Bates, 1866)
Riodininae	
	tribe: Mesosemiini
Mesosemia	asa asa Hewitson, 1869
	carissima Bates, 1866
	telegone telegone (Boisduval, 1836)
	nr. ephyne (Cramer, 1776)
	nr. tenebricosa Hewitson, 1877
	nr. judicialis Butler, 1874
Leucochimona	lagora (Herrich-Schaffer, 1853)
	nr. philemon (Cramer, 1775)
	nr. molina (Godman & Salvin, 1855)
	tribe: Eurybiini
Eurybia	patrona persona Staudinger, 1875
	elvina elvina Stichel, 1910
	lycisca Westwood, 1851
	nr nicaeus (Fabricius, 1775)
	nr hyacinthina Stichel, 1910
	tribe: incertae sedis
Napaea	eucharilla (Bates, 1867)
	theages theages Godman & Salvin, 1878
Cremna	thasus subrutillia Stichel, 1910
	actoris (Cramer, 1776)
Eunogyra	satyrus Westwood, 1851
Hermathena	candidata (Hewitson, 1874)

tribe: **Riodinini**

Ancyluris

inca inca (Saunders, 1850)

jurgensenii jurgensenii (Saunders, 1850)

Necyria

beltiana Hewitson, 1870

Lyropteryx

lyra cleadas Druce, 1875

Rhetus

arcus castigatus Stichel, 1909

Chorinaea

faunus bogota (Saunders, 1858)

Ithomeis

eulaema imatrix (Godman & Salvin, 1878)

Themone

pais (Hübner, 1820)

Melanis

pixie sanguinea Stichel, 1910

Lepricornis

strigosa strigosa (Staudinger, 1876)

Metacharis

cuparina Bates, 1868

Charis

nr anius (Cramer, 1776)

gynaea (Godart, 1824)

cleonus (Stoll, 1782)

Caria

rhacotis (Godman & Salvin, 1878)

Lasaia

agesilaus (Iatzielle, 1813)

Chalodeta

lypera (Bates, 1868)

chaonitis (Hewitson, 1866)

tribe: **Symmachiini**

Mesene

phareus rubella Bates, 1865

silaris (Godman & Salvin, 1878)

Mesenopsis

bryaxis melanochlora Godman & Salvin, 1878

Symmachia

tricolor hedemanni (Felder & Felder, 1869)

rubina Bates, 1866

tribe: **Helicopini**

Helicopis

cupido (Linnaeus, 1758)

tribe: **Charitini**

Anteros

formosus micon Druce, 1875
 aechus (Stoll, 1781)

Sarota

gyas (Cramer, 1775)
 chrysus (Stoll, 1782)
 tribe: **Emesini**

Argyrogrammana

trochilia (Westwood, 1851)

Emesis

fatima nobilata Stichel, 1910
 lucinda aurimna (Boisduval, 1870)
 mandana (Cramer, 1780)
 lacrines Hewitson, 1870
 tenedia tenedia Felder & Felder, 1861
 tribe: **Lemoniini**

Lemonias

zygia egaensis (Butler, 1867)

Thisbe

irenea (Stoll, 1870)
 lycorias (Hewitson, 1853)

Juditha

molpe (Hübner, 1803)
 dorilis dorilis (Bates, 1866)

Synargis

mycone (Hewitson, 1865)
 phylleus praeclara (Bates, 1866)
 gela (Hewitson, 1853)
 abaris (Cramer, 1776)

Audre

nr aurina (Hewitson, 1863)
 undetermined species
 tribe: **Nymphidiini**

Calospila

cilissa (Hewitson, 1863)
 emylius (Cramer, 1775)

Menander

menander menander (Stoll, 1780)
 menander thallus (Stichel, 1910)
 laobotas (Hewitson, 1875)
 pretus picta (Godman & Salvin, 1886)

Adelotypa

senta (Hewitson, 1853)

Setabis

lagus jansoni (Butler, 1870)

Theope

virgilius virgilius (Fabricius, 1793)
 eleutho Godman & Salvin, 1897
 nr decorata Godman & Salvin, 1878
 nr thestias (Hewitson, 1860)
 nr matuta Godman & Salvin, 1897

Nymphidium

mantus (Cramer, 1775)
 baoetia Hewitson, 1852
 nr. derufata Lathy, 1932
 nr lisimon (Stoll, 1790)
 haematostictum Godman & Salvin, 1878)
 cachrus ascolides (Boisduval, 1870)
 onaeum Hewitson, 1869
 azanoides occidentalis Callaghan, 1986
 ascolia (Hewitson, 1853)
 leucosia (Hübner, 1806)
 nr ninias (Hewitson, 1865)
 caricae (Linnaeus, 1758)

Table 3. Abbreviations for localities

Country	Locality
Costa Rica	A = Las Alturas (Puntarenas)
	C = Parque Nacional Corcovado (Puntarenas)
	SV = Las Cruces (Puntarenas)
	L = La Selva (Heredia)
	CH = Chilamate (Heredia)
	PL = Plastico (Heredia)
	SA = San Antonio de Belen (Heredia)
	T = Turrialba (Cartago)
	M = Rio Macho de Cartago (Cartago)
	SJ = Meseta Central of San Jose (San Jose)
	R = Finca EL Rodeo (San Jose)
	CA = Cañas (Guanacaste)
	H = Hacienda Santa Maria (Guanacaste)
	Belize
Panama	
	G = Gamboa
	P = Pipeline Road
	CA = Cerro Azul
	Pan = near Panama City
	ER = El Real, Darien Province
	F = Fort Clayton nr Colon
Ecuador	JS = Jatun Sacha (Napo)
	GC = Garza Cocha (Sucumbios)
Argentina	V = Volcan (Jujuy)
Madagascar	R = Ranamofauna National Park
China	H = 100 s of Haikou City (Hainan)

Table 4. Abbreviations of host families for riodinid butterflies.

code	host family
0	— Araceae
1	— Acanthaceae
2	— Asteraceae
3	— Bignoniaceae
4	— Bombacaceae
5	— Bromeliaceae
6	— Cecropiaceae
7	— Clusiaceae
8	— Combretaceae
9	— Convolvulaceae
10	— Dilleniaceae
11	— Euphorbiaceae
12	— Fabaceae
13	— Flacourtiaceae
14	— Gesneriaceae
15	— Hippocrateaceae
16	— Lecythidaceae
17	— Lejuniaceae
18	— Malpighiaceae
19	— Marcgraviaceae
20	— Marantaceae
21	— Melastomataceae
22	— Moraceae
23	— Myrsinaceae
24	— Myrtaceae
25	— Nyctaginaceae
26	— Olacaceae
27	— Orchidaceae
28	— Passifloraceae
29	— Polygalaceae
30	— Quiinaceae
31	— Ranunculaceae
32	— Rubiaceae
33	— Sapindaceae
34	— Ulmaceae
35	— Violaceae
36	— Vochysiaceae
37	— Zingiberaceae
mem	— Homoptera: Membracidae
coc	— Homoptera: Coccidae

Table 5: Numerical codes of ant taxa found in association with riodinid caterpillars. Codes are found with square brackets in Table 1.

code	Taxon	subfamily
?	= ants not collected	
1	= <i>Ectatomma ruidum</i>	(Ponerinae)
2	= <i>Ectatomma tuberculatum</i>	(Ponerinae)
3	= <i>Pheidole</i> sp.	(Myrmicinae)
4	= <i>Pheidole biconstricta</i>	(Myrmicinae)
5	= <i>Pheidole</i> nr <i>biconstricta</i> - no. 1	(Myrmicinae)
6	= <i>Pheidole</i> nr <i>biconstricta</i> - no. 2	(Myrmicinae)
7	= <i>Pheidole</i> nr <i>biconstricta</i> - no. 3	(Myrmicinae)
8	= <i>Solenopsis geminata</i>	(Myrmicinae)
9	= <i>Solenopsis</i> (<i>Diplorhoptrum</i> grp) sp.	(Myrmicinae)
10	= <i>Solenopsis</i> sp.	(Myrmicinae)
11	= <i>Megalomyrmex foreli</i>	(Myrmicinae)
12	= <i>Megalomyrmex</i> sp.	(Myrmicinae)
13	= <i>Wasmannia auropunctata</i>	(Myrmicinae)
14	= <i>Wasmannia</i> sp.	(Myrmicinae)
15	= <i>Aphaenogaster araneoides</i>	(Myrmicinae)
16	= <i>Crematogaster brevispinosa</i>	(Myrmicinae)
17	= <i>Crematogaster</i> sp.	(Myrmicinae)
18	= <i>Cephalotes atratus</i>	(Myrmicinae)
19	= <i>Ochetomyrmex</i> sp.	(Myrmicinae)
20	= <i>Camponotus</i> sp.	(Formicinae)
21	= <i>Camponotus distinguendus</i>	(Formicinae)
22	= <i>Camponotus sericeiventris</i>	(Formicinae)
23	= <i>Dendromyrmex</i> sp.	(Formicinae)
24	= <i>Paratrechina</i> sp.	(Formicinae)
25	= <i>Azteca</i> sp.	(Dolichoderinae)
26	= <i>Tapinoma</i> sp.	(Dolichoderinae)
27	= <i>Dolichoderus bispinosus</i>	(Dolichoderinae)
28	= <i>Dolichoderus validus</i>	(Dolichoderinae)

6) **Emesini** — (*Emesis*) Olacaceae, Flacourtiaceae, Ranunculaceae; 6) **Lemoniini** — (*Juditha* and *Synargis*) Dilleniaceae, Sapindaceae, Polygalaceae, Lecythidaceae, Bignoniaceae, and potentially Homoptera; and 7) **Nymphidiini** — (*Theope* and *Nymphidium*) Euphorbiaceae, Moraceae, Convolvulaceae, Lecythidaceae, Sapindaceae, and Bombacaceae.

The host records reported here (Table 1) agree broadly with the monophagous patterns of host use pointed out by Harvey (1987) for the Mesosemiini, and add further support for polyphagy among members of the Emesini. On the other hand, our observations amplify considerably the host records known from the Riodinini, Symmachiini, and Charitini, and suggest that diet

breadth for members of these tribes will eventually include an even greater diversity of host plant families than is currently recognized. Our host records are also completely agree with those noted in Harvey (1987) for the Eurybiini. However, our records amplify the patterns noted for members of the Lemoniini by indicating that some taxa may be a great deal more polyphagous than thought previously, while others seem strictly monophagous. For example, we found that some taxa (e.g., *Juditha molpe* and *Synargis mycone*) may use a suite of plant genera and even families as hosts all at the same site. On the other hand, observations on *Thisbe irenea* indicate that this taxon is monophagous on trees in the genus *Croton* from Belize to Ecuador — most of its geographical range.

Oviposition Patterns and Caterpillar Behavior

Recent work suggests that caterpillar social behavior derives from factors enhancing survivorship and resource utilization. The benefits accrued by aggregated caterpillars have probably led to oviposition patterns facilitating aggregation and social interactions (Fitzgerald 1993; Costa & Pierce 1994). However, we know almost nothing about the relationship between oviposition patterns, clutch size, and degree of social interaction for most groups of butterflies, especially the riodinids. Three points arise from our records. First, the majority of riodinid taxa have caterpillars that feed as solitary individuals, and it is almost certain that the females of all of these taxa lay single eggs. Second, gregarious caterpillars are found within the Euselasiinae (*Euselasia*), Riodinini (*Melanis*) and Emesini (*Emesis*), and as in other Lepidoptera, appears linked to laying clusters of eggs. Available evidence from *Euselasia* and *Hades* suggests this trait may be widespread among members of the Euselasiinae. In contrast, the trait appears labile within *Emesis*, as this genus includes species with both gregarious and solitary caterpillars. Finally, semi-gregarious caterpillars occur in the Eurybiini, Riodinini, Helicopini, Emesini, Lemoniini and Nymphidiini. This trait may occur in both taxa that lay single eggs (*Eurybia*, *Ancyluris*, *Helicopis*, *Thisbe*) and those that lay several eggs in a loose cluster (*Theope*, *Nymphidium*). In those that lay single eggs, gregariousness suggests a non-cannibalistic tolerance of other individuals when caterpillar densities increase on the host. In *Theope* and *Nymphidium* there is some indication that small egg clusters and semi-gregarious caterpillars are traits that may be widespread within these genera.

Aphytophagy

The habit of feeding on non-vegetable hosts, termed aphytophagy, is well known within the Lycaenidae (Ackery 1990; Cottrell 1984; Fiedler 1991). Several observations point to the possibility that utilization of non-vegetable hosts may occur in more riodinid genera than suspected previously. First, the only real suggestion of aphytophagy in riodinids derives from an exiguous communication by Urich (in Kaye 1921), who stated that *Setabis lagus* caterpillars were predaceous on homopterous nymphs (*Horiola*) infesting

Trinidadian cacao plantations. As this record has gone without verification for over 70 years, it was gratifying to demonstrate that *Setabis lagus* in Costa Rica is carnivorous on scale insects, and thereby provide further impetus for examining other members of the genus for the carnivorous habit. Second, although we were unable to verify the diet of *Audre* nr *aurina* and *Audre* sp. found inside ant nests (details will appear elsewhere, DeVries & Martinez, in prep.), two lines of evidence point to the possibility that their diet may include regurgitations provided by their host ants. At no time in the field or in captivity could we induce *Audre* caterpillars to feed on an array of plant matter, and microscopic examination of the frass of both species determined that it contained no fragments of plant material. Furthermore, despite close observations over several months, we found no evidence that caterpillars fed on ant larvae or pupae. Finally, although decidedly inconclusive, we note that direct oviposition on Homoptera by *Synargis phylleus* and *Juditha dorilas* may indicate a aphytophagous habit in these taxa — an oviposition behavior typically observed in *Setabis lagus* females. On the whole, even the few observations here suggest that future work may reveal aphytophagy as a trait in a variety of riordinid taxa.

Symbioses with Ants

Available evidence suggests that butterfly myrmecophily evolved within the context of associations involving secretion-harvesting ant taxa, and that caterpillars, secretion-producing Homoptera, and plants bearing extrafloral nectaries share ant symbionts (DeVries 1991a&b). Overall, most myrmecophilous butterfly taxa appear to be facultative with respect to their ant symbionts, but a few taxa have evolved species specific associations (DeVries 1991b; DeVries et al. 1993; Fiedler 1991; Thomas et al. 1989). The observations here (Table 1) both support these general ideas and provide a more accurate picture of the variation found among riordinid-ant symbioses. Depending on the taxon, members of the tribes Nymphidiini and Lemoniini show associations with a variety of common secretion-foraging ant species in the subfamilies Ponerinae, Myrmicinae, Formicinae and Dolichoderinae. In contrast, our records and those published previously (Horvitz et al. 1987) provide no indication that members of the Eurybiini (*Eurybia* only) form associations with ants in the Dolichoderinae. However, in this case sampling error cannot be ruled out, and this should be investigated in greater detail.

The Interaction between Ant Taxa and Caterpillar Diet

Even the few observations here suggest that eventual understanding of host use patterns by riordinids will require accounting for the interactions between both ants and plants. A number of contrasting examples illustrate this (Table 1). First, the polyphagous species *Synargis mycone* may associate with a variety of ant taxa encompassed by four subfamilies, whereas *Thisbe irenea*, which may associate with members of at least three ant subfamilies, is monophagous on *Croton* throughout its geographical range. Second, the polyphagous species

Juditha molpe appears to have obligate associations with *Dolichoderus bispinosus* ants in Central America, whereas the polyphagous species *Nymphidium mantus* in Panama shows an apparently obligate relationship with the ant genus *Azteca*. Third, the various *Theope* species noted here appear to show a trend toward monophagy (although many more records are needed), but these butterflies appear to have intimate associations with ants in the Dolichoderinae. The one exception of which we are aware is *T. nr decorata*. Although caterpillars of this species fed on a plant inhabited by *Azteca* ants, they were tended entirely by *Solenopsis* ants that had small, open air colonies on the large leaves of the plant. Finally, our field observations indicate that *Lemonias nr zygia*, *Juditha molpe*, *Theope virgilius*, *T. nr thestias*, *T. nr matuta*, and *Nymphidium mantus* all represent cases where the choice of host plant by ovipositing female butterflies is mediated by the presence of particular ant taxa, a trait known from some members of the Lycaenidae (Atsatt 1981; Pierce & Elgar 1985).

Extrafloral Nectaries and Myrmecophiles

The compilation of host records plus demonstration that caterpillars may benefit from drinking extrafloral nectar provided the basis for the idea that plant taxa bearing extrafloral nectaries are important in the diets of myrmecophilous riodinids (DeVries & Baker 1989; DeVries 1991a). The records presented here also support this pattern (e.g., *Synargis*, *Juditha*, *Nymphidium*), but several cases are of particular interest. First, members of the genus *Eurybia* are known to feed only on flowers of the Marantaceae and Zingiberaceae (Harvey 1987; Horvitz et al. 1987). In the latter group, the inflorescence structure may prevent caterpillars from burrowing into the inflorescence as they do in the Marantaceae. Our field observations showed that caterpillars using Zingiberaceae as hosts position their heads over the extrafloral nectaries located on the outside of the cone-like inflorescence bracts, and they are tended by ants that are also feeding at these nectaries (e.g., Schemske 1980). These observations provide the first direct indication that caterpillars in the Eurybiini also drink extrafloral nectar. Secondly, we have found cases where caterpillars were feeding on plants whose shoots were occupied by Homoptera. In cases where the hostplant did not have extrafloral nectaries (e.g., *Synargis gela*, *S. abaris*, some *Juditha molpe*), we observed caterpillars drinking honeydew secretions directly from the resident Homoptera. In cases where the plants had both extrafloral nectaries and membracids (e.g., *Lemonias zygia*, *Synargis gela*, *S. mycone*, *Juditha molpe*, *Theope nr matuta*, and *Nymphidium caricae*), we observed caterpillars drinking both extrafloral nectar and Homoptera honeydew. Together these observations further highlight the apparent importance of drinking secretions in the diet of myrmecophilous riodinid caterpillars, in addition to their regular fare of leaf tissue.

Conclusions and Future Considerations

At the time of their classic paper, Ehrlich & Raven (1964) concluded that

there were insufficient records available on lycaenoid butterflies (almost none on riodinids) to provide predictive patterns of their host use. Pierce (1985), and more recently Fiedler (1991) brought together a large and diffuse literature that provides the best available synthesis of host use patterns to date on the Lycaenidae. Their studies further elaborate the complex nature of lycaenid life histories, but suggest that patterns of host use are in fact emerging for the Lycaenidae. At the present time there remain two major hurdles to cross before we can resolve lycaenid host evolution in greater detail: the lack of a phylogeny for the Lycaenidae in which to frame host associations, and the absence of host records for most neotropical taxa.

The hurdles for riodinids are different. In his synthesis of riodinid host records, Harvey (1987) indicated that patterns of host use were evident in a few higher taxa (i.e., Hamaerinae, Eurybiini, and *incertae sedis*), but there were insufficient records available for most groups. Since that time, the number of known host records has increased (Brown 1993; Brevignon 1992; Callaghan 1989; DeVries 1988, 1991a, 1992, and those reported here). Considering all available records together indicates that riodinid life histories display a diversity of traits including monophagy and polyphagy, caterpillar growth benefits gained by drinking secretions, caterpillar-ant associations ranging from facultative to obligate species specific, and possibly a modicum of aphytophagy. These traits parallel those known from within the Lycaenidae (Cottrell 1984; Fiedler 1991; Pierce 1987). However, even with the inclusion of this new information and the framework of a higher classification to interpret patterns of host use, our understanding of riodinid host use is conjectural — the host records for at least three quarters of the riodinid species are unknown.

An important aspect to the study of myrmecophilous riodinids concerns identification of ant symbionts. However, most studies of myrmecophilous butterflies (including the present one) are guilty of listing ant symbionts without complete identifications. In part this reflects the small number of qualified ant taxonomists in the world, and the negligence of many butterfly biologists in making proper collections of ants. The positive identification to species in some ant groups (e.g., *Pheidole*, *Solenopsis*, *Aphaenogaster*, *Camponotus*, and *Azteca*, among others) is difficult or impossible without specimens of the reproductive castes (S. Cover, pers. comm.). Nevertheless, understanding the phylogenetic and ecological patterns of why some riodinid taxa form symbioses with only a particular subgroup within a genus or even with a particular species of ant (e.g., *Juditha molpe*), while others are apparently ant generalists (e.g., *Synargis mycone*) will depend upon correct identification of their ant symbionts. Thus, we urge future workers to take special care to collect strong series of ant symbionts when rearing myrmecophilous species, and to have them properly identified.

As we stressed previously, biodiversity is a suite of different organisms and their often complex interactions within habitats. Why our understanding of

riodinid biodiversity is so poor is likely the result of many interacting factors. Such factors may include their small size, their almost exclusive occurrence in neotropical forest habitats, fundamental characteristics of their biology and interactions with other organisms that make them difficult to observe, or combinations of these and other factors. Whatever the ultimate reasons may be, it seems to us that Scudder's (1887) counsel regarding the importance of knowing more about the early stages of the riodinids has lost none of its resonance a century later. To fortify our grasp of riodinid evolution and biodiversity many more rearing records from virtually all of the neotropical subfamilies and tribes are required.

Despite the media's apparent concern over the world-wide devastation of biodiversity, we presently live in a time when grant giving and receiving institutions of science seem concerned almost exclusively with the technology of molecular biology and other types of so called 'big science.' Because technology is often equated with science, this trend will continue to reduce interest in whole-organism biology and natural history in both institutions of higher learning and in the students they produce (e.g., see Erzinclioglu 1993). However, without data from the real world, no matter how sophisticated laboratory techniques or models become, in the absence of natural history they are unlikely to broaden our understanding of the myriad interactions among organisms. The message is simple: future insights into tropical biodiversity in general, and riodinid early stage biology specifically will demand a great deal more field work. It is our hope that this paper will encourage more people to study riodinids than have done so in the past century. One thing is inescapable — technology will not stem the destruction of tropical habitats nor will wishful rhetoric save those riodinid taxa and their interactions with other organisms that will be extirpated during the next hundred years. Now is the time for deeds, not words.

Acknowledgments. We wish to acknowledge T. M. Aide, R. Foster, N. Garwood, J. Gomez-Laurito, M. Grayum, N. Greig, B. Hammel, D. Neil, L. Poveda, P. Sanchez and N. Zamora for plant determinations, and S. Cover, J. Longino and R. Snelling for determining some of the ants. Thanks to P. Ackery, C. Callaghan, D. Harvey and I. J. Kitching with help on some of the butterfly determinations and nomenclature. For logistical support we thank Servicios Parques Nacionales de Costa Rica, the Museo Nacional de Costa Rica, Center for Conservation Biology, Fundacion Jatun Sacha, the Smithsonian Tropical Research Institute, Organization for Tropical Studies, A. Bien, and E. Schwartz. We wish to acknowledge B. Bock, R. Brown, W. Camacho, J. Clark, S. Collins, M. Cummings, O. Diorio, E. Foster, M. deGoulain, Y. Gamara, N. Garwood, H. Greeney, N. Greig, P. Knudsen, J. Longino, J. May, D. Promislow, E. Quinter, C. Sierra, the late G. B. Small, N. G. Smith, A. Suarez, C.D. Thomas, T. Walla, D. Windsor, and D. Yeates for assistance in the field, plus A. Aiello and G. Zotz for their host records. We thank J. Costa, S. Cover, N. Greig, and N. Pierce for commenting on drafts of this manuscript. Chacon wishes to acknowledge the support of the Plastico Biodiversity Support Program (WWF grant #7537), La Selva

Tica S.A., R. Bell, J. Richardson, and S. Salas. A substantial portion of the work presented here would have been impossible without the funding to DeVries provided by a MacArthur Foundation fellowship, and the Geraldine Dodge Foundation. The paper is dedicated to Ken Hope, Steve Lacy, and Cecil Taylor whose individual work has pioneered and promoted some astonishingly diverse interactions.

LITERATURE CITED

- ACKERY, P. R. 1990. Biocontrol potential of African lycaenid butterflies entomophagous on Homoptera. *J. African Zool.* 104: 581-591.
- ATSATT, P. R. 1981. Ant dependent food selection by the mistletoe butterfly *Ogyris amaryllis* (Lycaenidae). *Oecologia* 48: 60-63.
- BREVIGNON, C. 1992. Elevage de deux Riodininae guyanais *Napaea beltiana* Bates et *Cremna thasus* Stoll. *Alexanor* 17: 403-4134.
- BROWN, K.S. JR. 1993. Neotropical Lycaenidae: an overview. In T. R. New (ed.) *Conservation biology of Lycaenidae (butterflies)*. pp. 45-61. ICUN, Gland, Switzerland.
- CALLAGHAN, C. J. 1977. Studies on Restinga butterflies I. Life cycle and immature biology of *Menander felsina* (Riodinidae), a myrmecophilous metalmark. *J. Lep. Soc.* 20: 36-42.
- . 1982. Notes on immature biology of two myrmecophilous Lycaenidae: *Juditha molpe* (Riodininae) and *Panthiades bitias* (Lycaeninae). *J. Res. Lep.* 20: 36-46.
- . 1986a. Notes of the biology of *Stalachtis susanna* (Lycaenidae: Riodininae) with a discussion of riodinine larval strategies. *J. Res. Lep.* 24: 258-263.
- . 1986b. Studies on Restinga butterflies: the biology of *Synargis brennus* (Stichel) (Riodinidae). *J. Lep. Soc.* 40: 93-96.
- . 1989. Notes on the biology of three riodinine species: *Nymphidium lisimon attenuatum*, *Phaenochitonia sagaris satinus*, and *Metacharis ptolomaeus* (Lycaenidae: Riodininae). *J. Res. Lep.* 27: 109-114.
- COSTA, J. T. & N. E. PIERCE 1994. Social evolution in the Lepidoptera: ecological context and the role of signal enhancement. in J. C. Choe and B. J. Crespi (eds.) *Social competition and cooperation in insects and arachnids: vol. 2, evolution of sociality*. Princeton University Press, Princeton, New Jersey. (in press)
- COTTRELL, C.B. 1984. Aphytophagy in butterflies: its relationship to myrmecophily. *Zool. J. Linn. Soc.* 80: 1-57.
- DEVRIES, P.J. 1988a. The use of epiphylls as larval hostplants by the neotropical riodinid butterfly *Sarota gyas*. *J. Nat. Hist.* 22: 1447-1450.
- . 1988b. The larval organs of *Thisbe irenea* (Riodinidae) and their effects upon attending ants. *Zool. J. Linn. Soc.* 94: 379-393.
- . 1991a. Ecological and evolutionary patterns in riodinid butterflies. In *Ant-Plant Interactions*, C. Huxley and D. F. Cutler (eds.) p. 142-156 Oxford Univ. Press, Oxford
- . 1991b. The mutualism between *Thisbe irenea* and ants, and the role of ant ecology in the evolution of larval-ant associations. *Biol. J. Linn. Soc.* 43: 179-195.
- . 1991c. Call production by myrmecophilous riodinid and lycaenid butterfly caterpillars (Lepidoptera): morphological, acoustical, functional, and evolutionary patterns. *American Mus. Nov.* 3025: 1-23.
- DEVRIES, P. J., J. A. THOMAS & R. COCROFT. 1993. A comparison of acoustical signals between *Maculinea* butterfly caterpillars and their obligate host ant species. *Biol. J. Linn. Soc.* 49: 229-238.

- DEVRIES, P.J. & BAKER, I. 1989. Butterfly exploitation of a plant-ant mutualism: adding insult to herbivory. *J. N.Y. Ent. Soc.* 97: 332-340.
- EHRlich, P. R. 1958. The comparative morphology, phylogeny, and higher classification of the butterflies (Lepidoptera: Papilionoidea). *Univ. Kansas Sci. Bull.* 39: 305-370.
- EHRlich, P. R. & RAVEN, P. 1965. Butterflies and plants: a study in coevolution. *Evol.* 18: 596-604.
- ENZINCIOGLU, Y. Z. 1993. On the failure of the natural history museum. *J. Nat. Hist.* 27: 989-992.
- FIEDLER, K. 1991. Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). *Bonner Zoologische Monographien* 31: 1-210.
- FITZGERALD, T.D. 1993. Sociality in caterpillars. pp. 372-403 in N.E. Stamp and T. E. Casey (eds.) *Caterpillars*. Routledge, Chapman and Hall, Inc., New York.
- HARVEY, D. J. 1987. The higher classification of the Riodinidae (Lepidoptera). Ph. D. thesis, University of Texas, Austin, Tx.
- HINTON, H.E. 1951. Myrmecophilous Lycaenidae and other Lepidoptera—a summary. *Proc. Trans. S. Lond. Entom. and Nat. Hist. Soc.* 1949-1950: 111-175.
- HORVITZ, C.C., TURNBULL, C. & HARVEY, D. J. 1987. Biology of immature *Eurybia elvina* (Lepidoptera: Riodinidae), a myrmecophilous metalmark butterfly. *Ann. Ent. Soc. Am.* 80: 513-519.
- HUTCHINSON, G. E. & R. H. MACARTHUR. 1959. A theoretical ecological model of size distributions among species of animals. *Am. Nat.* 93: 117-125.
- KAYE, W. J. 1921. A Catalogue of the Trinidad Lepidoptera Rhopalocera (Butterflies) Government Printing office, Trinidad, B.W.I.
- MARTIN, J. A. & PASHLEY, D. P. 1992. Molecular systematic analysis of butterfly family and some subfamily relationships (Lepidoptera: Papilionoidea). *Annals Ent. Soc. Amer.* 85: 127-139.
- MAY, R. M. 1978. The dynamics and diversity of insect faunas. *Symp. Royal Ent Soc* 9: 188-204.
- MAYR, E. 1969. *Principles of Systematic Zoology*. McGraw-Hill, New York, N.Y.
- PIERCE, N. E. 1985. Lycaenid butterflies and ants: selection for nitrogen-fixing and other protein rich food plants. *Am. Nat.* 125: 888-895.
- . 1987. The evolution and biogeography of associations between lycaenid butterflies and ants. *Oxford Sur. Evol. Biol.* 4: 89-116.
- PIERCE, N. E. & ELGAR, M. A. 1985. The influence of ants on host selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. *Behav. Ecol. Sociobiol.* 16: 209-222.
- ROBBINS, R. K. 1988. Comparative morphology of the butterfly foreleg coxa and trochanter (Lepidoptera) and its systematic implications. *Proc. Ent. Soc. Washington* 90: 133-154.
- ROSS, G. N. 1964. Life history on Mexican butterflies III. The early stages of *Anatole rossi*, a new myrmecophilous metalmark. *J. Res. Lep.* 3: 81-94.
- . 1966. Life history studies of a Mexican butterfly. IV. The ecology and ethology of *Anatole rossi*, a myrmecophilous metalmark. *Ann. ent. Soc. Amer.* 59: 985-1004.
- SCHEMSKE, D. W. 1980. The evolutionary significance of extrafloral nectar production by *Costus woodsonii* (Zingiberaceae): an experimental analysis of ant protection. *J. Animal Ecol.* 68: 959-967.

- SCUDDER, S. H. 1887. Note on the group Eumaeidi. In Godman, F. D. and O. Salvin 1879-1901 (eds.) pp.110-112. *Biologia Centrali Americana. Insecta, Lepidoptera, Rhopalocera. Vol. II*, London.
- THOMAS J.A., G. W. ELMES, J.C. WARDLAW, & M. WOYCIECHOWSKI. 1989. Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. *Oecologia* 79: 452-457.
- VAN VALEN, L. 1973. Body size and numbers of plants and animals. *Evolution* 27: 27-35.
- VANE-WRIGHT, R.I. 1978. Ecological and behavioural origins of diversity in butterflies. *Symp. Roy. Ent. Soc. Lond.* 9: 56-70.