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BIODIVERSITY OF PYRRHOPYGINE SKIPPER BUTTERFLIES (HESPERIIDAE) IN THE AREA DE CONSERVACIÓN GUANACASTE, COSTA RICA

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ABSTRACT. Twenty-two years of rearing 2192 pyrrhopygine caterpillars (and collecting far fewer adults) show that the Area de Conservación Guanacaste (ACG) supports at least 15 species, or some 60% of the Costa Rican pyrrhopygine fauna: 3 in (lowest elevation) dry forest—*Elbella scylla* (Ménétriés) [of which *E. dulcinea* (Plötz) is a **synonym**], *Mysoria ambigua* (Mabille & Boullet), and *Myscelus amystis hages* Godman & Salvin; 4 in (highest elevation) cloud forest—*Pyrrhopyge creon* H. Druce, *P. aesculapus* Staudinger, *P. cosyra* H. Druce, and *Passova gellias* (Godman & Salvin); and 10 in (middle elevation) rainforest—*Pyrrhopyge zenodorus* Godman & Salvin, *P. crida* (Hewitson), *P. cosyra, P. erythrosticta* (Godman & Salvin) [**lectotype** designated], *Parelbella macleannani* (Godman & Salvin), *Jemadia pseudognetus* (Mabille) [**reinstated status**], another *Jemadia* belonging to a *J. hewitsonii* species complex, *Myscelus belti* Godman & Salvin, *M. perissodora* Dyar [**reinstated status**], and *Passova gellias.* No species spans all three ecosystems, and none occurs in both dry forest and rainforest. The caterpillars are mostly 0.1–3 m above the ground, even when individuals of their foodplants rise 20–40 m. Except for *Myscelus* and *Passova,* the caterpillars are showy because they are ringed, barred, or spotted (with a row of large round dots) in contrasting colors. Pyrrhopygine caterpillars and pupae differ sharply from those of all other hesperiids in being long-haired.

ACG pyrrhopygines are strongly host specific, like other dicot-eating skippers (pyrgines) and certain butterfly and moth families in the ACG. (However, pyrrhopygines are more ecosystem-specialized than pyrgines.) Although ACG pyrrhopygine foodplants are dotted across the botanical taxonomic landscape (in the families Lauraceae, Clusiaceae, Flacourtiaceae, Cunoniaceae, Myrtaceae, Combretaceae, Meliaceae, Malpighiaceae, and Araliaceae), some patterns emerge. The three species of *Myscelus* plus *Passova gellias,* which are morphologically similar, all focus on Meliaceae (mainly *Guarea glabra* Vahl). Two-thirds of the reared species currently in the large genus *Pyrrhopyge* are monophagous to oligophagous on members of the Clusiaceae. At the same time, ACG pyrrhopygine caterpillars are specialists at levels far below that of the plant family: for each species of caterpillar, there are many ACG species of plants within the plant family fed upon that are not used. Moreover, within an oligophagous species, percentages of records among its few foodplants do not reflect the relative abundances of those plants. Host specificity seems to be geographically conservative: relatives of half of the ACG pyrrhopygine species were reared by Moss (1949) in Pará, Brazil, on plants that are usually in the same genera, and always in the same families, as those of their Costa Rican counterparts. The only pyrrhopygine to enter the USA, *Pyrrhopyge arizonae* Godman & Salvin [**reinstated status**], has an unusually drab adult but a gaudily ringed caterpillar, whose foodplant (*Quercus*) is in yet another unrelated family (Fagaceae).

Though attacked at times by ichneumonids, braconids, and tachinids, ACG pyrrhopygines are remarkably free of parasitoids. Despite slow larval growth rates (among the longest within the ACG hesperiids), pyrrhopygines are at the low end of the spread of larval parasitization frequencies—not just among skippers but among ACG macrolepidoptera generally: only 7.1% of all wild-caught pyrrhopygine caterpillars were parasitized. Most notably, not one of 295 caterpillars in the closely related genera *Myscelus* and *Passova* (the Meliaceae eaters) has yielded parasitoids.

Additional key words: caterpillars, foodplants, pupae, parasitoids, ecology, taxonomy.

Not once upon a time, but every day, a protected tropical wildland such as the Area de Conservación Guanacaste (ACG) in northwestern Costa Rica (Fig. 1) becomes more of an ecological island in an agrarian sea. Its biodiversity, derived mostly from what was there before the advent of European agriculture, keeps dwindling to a new equilibrium density of species. Some additional species may immigrate to the ACG or—given enough time—even evolve in situ, owing to the increasing insularization of the site. An inventory of its present biodiversity offers a baseline against which these changes can be measured.

Skipper butterflies (Hesperiidae)—along with the moth families Saturniidae, Sphingidae, and Notodontidae—have had special attention in the early years of the macrocaterpillar inventory of the ACG (Janzen & Hallwachs 2001). Here we treat the distinctive skipper subfamily Pyrrhopyginae, after rearing 2192 pyrrhopygine caterpillars of 15 species found over a 22-year period in ACG dry forest, cloud forest, and rainforest. Though the inventory will not have turned up every last pyrrhopygine species in the ACG, we think it has almost all of them by now.

Pyrrhopygines, whatever their taxonomic rank, are a monophyletic group (Ackery et al. 1999) of basically neotropical Hesperiidae ranging from the southwestern USA (southeastern Arizona and adjacent southwestern New Mexico, plus the Big Bend area of Texas) to northern Argentina (especially Misiones, but also Salta, Formosa, Chaco, Tucumán, La Rioja, Corrientes, Entre Ríos, and Buenos Aires [Hayward 1948]). While only one species extends northward to the USA,

TABLE 1. Foodplants and parasitization frequency of wild-caught pyrrhopygine caterpillars in the Area de Conservación Guanacaste (data source: Janzen & Hallwachs 2001).

Caterpillar species Plant family *Plant species*	Rearing records n	Rearing records %	% caterpillars attacked by Ichneumonidae	Braconidae	Tachinidae	Total % parasitized
Pyrrhopyge zenodorus	541		0	3.7	3.0	6.7
Clusiaceae						
Vismia baccifera		99				
Vismia ferruginea		1				
Pyrrhopyge crida	14		0	0	0	0
Clusiaceae						
Vismia billbergiana		100				
Pyrrhopyge creon (1 found as pupa, 2 found as larvae not reared out but presumed to belong to this species)	3		0	0	0	0
Araliaceae						
Dendropanax gonatopodus		50				
Dendropanax querceti		50				
Pyrrhopyge aesculapus	4		0	0	0	0
Cunoniaceae						
Weinmannia wercklei		100				
Pyrrhopyge cosyra	353		12.1	0.2	5.4	17.7
Clusiaceae						
Chrysochlamys glauca		81				
Chrysochlamys psychotriifolia		1				
Clusia cylindrica		2				
Clusia minor		9				
Clusia rosea		1				
Clusia 13877		1				
Clusia 14104		5				
Pyrrhopyge erythrosticta	3		0	0	0	0
Clusiaceae						
Marila laxiflora		100				
Elbella scylla	137		0	8.0	0	8.0
Malpighiaceae						
Banisteriopsis muricata		7				
Byrsonima crassifolia		66				
Heteropterys laurifolia		2				
Hiraea reclinata		13				
Combretaceae						
Combretum farinosum		12				
Terminalia catappa		1				
Parelbella macleannani	59		0	0	2.0	2.0
Myrtaceae						
Eugenia basilaris		29				
Eugenia aff. *basilaris*		1				
Eugenia 13782		1				
Eugenia 14017		69				
Jemadia pseudognetus	31		0	0	0	0
Lauraceae						
Nectandra hihua		45				
Nectandra aff. *latifolia*		16				
Nectandra membranacea		16				
Ocotea cernua		7				
Ocotea insularis		3				
Persea povedae		13				
Jemadia sp. X	16		0	0	0	0
Flacourtiaceae						
Casearia arborea		100				
Mysoria ambigua	736		0	0.3	5.4	5.7
Flacourtiaceae						
Casearia arguta		4				
Casearia corymbosa		67				
Casearia sylvestris		11				
Zuelania guidonia		18				

TABLE 1. (continued).

Caterpillar species Plant family *Plant species*	Rearing records n	Rearing records %	% caterpillars attacked by Ichneumonidae	Braconidae	Tachinidae	Total % parasitized
Myscelus amystis hages	54		0	0	0	0
Meliaceae						
Trichilia americana		91				
Trichilia glabra		1				
Trichilia trifolia		8				
Myscelus belti	106		0	0	0	0
Meliaceae						
Guarea bullata		2				
Guarea glabra		37				
Guarea rhopalocarpa		14				
Guarea 14097		47				
Myscelus perissodora	1		0	0	0	0
Meliaceae						
Guarea glabra		100				
Passova gellias	134		0	0	0	0
Meliaceae						
Guarea glabra		88				
Guarea rhopalocarpa		1				
Guarea 13856		2				
Guarea 13860		1				
Guarea 14097		7				
Guarea 14137		1				

many extend southward into Argentina. Pyrrhopygines occur from sea level to upper elevation forests. Owing to their diurnal flight, flower visitation, large size, and showy patterns, plus the puddling and hilltopping behaviors of males, adult pyrrhopygines have been rather extensively collected; but their early stages are poorly known. Adults of these robust skippers are distinctive in having most to all of the antennal club reflexed. Both their dicot-eating caterpillars and the resulting pupae are the hippies of the skipper world; they are well endowed with long hairs—not just on the head but over the body as well (Figs. 2–28). We hope that this exposure of the pyrrhopygine caterpillars of the ACG, and this demonstration of their foodplant specificity, will stimulate further rearing in other areas.

MATERIALS AND METHODS

The inventory site. The macrocaterpillar inventory of the ACG (Janzen 1988a, 1993, in press; Janzen & Hallwachs 2001) began in the dry forest in 1978 and has gradually intensified and spread to adjacent rainforest and cloud forest (and all intergrades) (Fig. 1). ACG dry forest (about 60,000 ha) ranges from sea level to about 600 m across the Pacific coastal plain on volcanic, marine alluvial, and serpentine soils, and receives about 1.5 m of rain during the May–December 6-month rainy season, but essentially none during the dry season. It is a fine-scale mosaic of different successional stages (5–400 years of age) and scattered bits of old-growth forest (Janzen 1988b, http://www.acguanacaste.ac.cr). The cloud forest (about 10,000 ha) ranges from about 800 to 2000 m on three recent volcanos (Orosí, Cacao, Rincón de la Vieja) and receives 3–5 m of rain and frequent ground-level clouds, with distinct seasonality. It is mostly old-growth forest with some abandoned farms, ranches, and logging sites on both the Pacific and Caribbean sides of the volcanos. The rainforest (about 40,000 ha) ranges from about 400 to 800 m on the eastern and northern foothills of the three volcanos, even extending in a narrow band at about 800 to 1000 m around the western sides of the volcanos, and receives 3–4 m of rain, with a 1- to 3-month semi-dry season (February–May). It is a large-scale mosaic of old-growth forest, lightly logged forest, secondary succession, and abandoned farms and ranches (see http://janzen.sas.upenn.edu/caterpillars/RR/rincon_rainforest.htm for photographs of the cloud forest and rainforest).

Collection and rearing process. We report records through 1999 (along with a few critical recent records) from this ongoing inventory. Many methods of haphazard and patterned search by highly experienced resident paraecologists and parataxonomists have been used to locate caterpillars in all ACG habitats and ecosystems. The 2192 pyrrhopygine rearing records summarized here are part of some 120,000 wild-caught caterpillar rearings. Except in a few recent cases, pyrrhopygines were not explicitly sought but were found through general search for all macrocaterpillars on all species of plants. Wild-caught caterpillars

were brought to rearing barns and reared individually, in foliage-filled plastic bags, at ambient temperatures (see photographs in Janzen & Hallwachs 2001). Pyrrhopygines were segregated for this analysis after completion of the rearing process. Each caterpillar rearing was recorded, and each species of caterpillar was usually photographed when first encountered (as well as later). These individual rearing records and some of these photographs are in the web site database (Janzen & Hallwachs 2001).

Parasitoid frequency (Table 1) comes from rearing wild-caught pyrrhopygine caterpillars of any instar in captivity. It is an underestimate of what occurs in nature because, once caterpillars are captured, they are protected from parasitoids. Parasitoids that oviposit in eggs or pupae are not considered here.

Adult pyrrhopygines were identified by Burns, who studied and compared genitalia of both sexes. This involved not only our reared individuals but also other museum material of the same species as well as similar, related taxa. Arriving at the best names for reared Costa Rican species sometimes required taxonomic minirevision. Caterpillars that failed to produce adults were identified by Janzen and an experienced team of 13 resident paraecologists and parataxonomists. In each case the identifier is specified in the database (Janzen & Hallwachs 2001). Species of ACG pyrrhopygines reared to date can be identified from their larvae and pupae (Figs. 2–25).

Series of conspecific adults reared by the macrocaterpillar inventory are pinned and spread, and many of the Hesperiidae are deposited as voucher specimens in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA. Representative series are also being deposited in INBio (Instituto Nacional de Biodiversidad), Santo Domingo de Heredia, Costa Rica, and elsewhere.

Adult hesperiids were rather thoroughly but haphazardly collected throughout the ACG by Janzen and W. Hallwachs from 1978 to the present and, in a total of about 20 person-years of effort, by INBio and ACG parataxonomists from 1989 to the present. Furthermore, adult skippers were intensively collected by Dan L. Lindsley in 1998 and by Paul A. Opler and Evi Buckner in 2000. All this collecting has yielded no pyrrhopygine species that we have not reared. On the other hand, six of our 15 reared pyrrhopygine species have yet to be found as wild adults in the ACG.

PYRRHOPYGINE CATERPILLARS

Feeding behavior and growth rate. Pyrrhopygine eggs are laid singly near the margins of mature leaves, on the upper sides. If the foodplant grows in a sun/shade mix, the leaves chosen are usually fully insolated.

The first instar cuts a 5–7 mm diameter disc nearly all the way out of the leaf interior, or in from the margin, and silks the disc initially so as to fold it over on its hinge, and then so as to form a shallow cup tightly pressed to the leaf surface. As the caterpillar grows, it builds and abandons successive nests (or shelters), each larger than the last.

All instars live solitarily in their leaf/silk nests, venturing out at night to feed. In later instars the nest varies from a couple of overlapping leaves to several leaves silked together. The leaf nests of pyrrhopygines are among the most heavily silked of all ACG hesperiids. Of the ACG pyrrhopygines examined, *Pyrrhopyge cosyra* H. Druce and *Passova gellias* (Godman & Salvin) make the strongest and densest nests.

Pupation occurs in a leaf/silk nest, which is usually on the host plant and is usually the nest of the last instar. Occasionally a caterpillar makes its feeding and/or pupation nest with the foliage of a plant other than its host, generally when the foliage of the two plant species is interleaved.

Each species of ACG pyrrhopygine caterpillar is monophagous to oligophagous within a single plant family—or, in one case, two plant families (Table 1). (No laboratory trials were conducted to determine if the caterpillars can feed and develop on species other than those on which they are found in nature.) Because the ACG inventory of macrocaterpillars searches all species of foodplants and has been going on for 22 years, further search probably will not expand the plant lists for the caterpillar species in Table 1 except to add a few more closely related species within the genera or families already listed.

Pyrrhopyginae caterpillars are among the slowest growing of the ACG Hesperiidae (Table 2). As a group, they are conspicuously slower than Pyrginae and Hesperiinae. Their prepupal stage lasts 3–5 days, also among the longest in the ACG Hesperiidae. In no instance has a reared pyrrhopygine prepupa become quiescent or dormant in response to the dry season or some other inimical time of year (other large ACG hesperiids, such as the pyrgines *Epargyreus* and *Typhedanus ampyx* [Godman & Salvin], do so as one of their behaviors for passing part of the dry season). Once pupation has occurred, their rate of development (Table 2) is about the same as that of other hesperiids of similar body weight. In no instance has a pyrrhopygine pupa become seasonally dormant, though there are several cases where the pupal stage has lasted a few weeks more than expected. The cooler

TABLE 2. Life table traits for wild-caught pyrrhopygine caterpillars reared at ambient temperatures on the species of foodplants on which they were found, Area de Conservación Guanacaste (data source: Janzen & Hallwachs 2001). The prepupal stage lasts about 3 days, but the prepupa is not always located on its first day. A close approximation to pupal duration may be obtained by subtracting two days from the mean number of days between prepupa and eclosion. Extreme values are not included in the means.

	First instar to prepupa (days)			Prepupa to eclosion (days)			
Species	Mean	Range	n	Mean	Range	n	Extremes
Pyrrhopyge zenodorus	78	61–93	13	20.8	15–33	106	none
Pyrrhopyge crida	n/a	n/a	n/a	23.5	23–24	2	none
Pyrrhopyge aesculapus	n/a	n/a	n/a	33.7	31–36	3	none
Pyrrhopyge cosyra							
in Sector Cacao	104	92–137	21	31.1	24–37	91	52 (n = 1)
in Sector San Cristobal	125	106–160	8	23.9	19–27	59	none
Pyrrhopyge erythrosticta	n/a	n/a	n/a	18.0	18.0	1	none
Elbella scylla	89	82–96	2	19.1	17–22	35	none
Parelbella macleannani	141	139–144	3	20.4	17–28	21	none
Jemadia pseudognetus	133	127–139	2	25.4	22–28	11	none
Mysoria ambigua	45	41–47	3	19.7	17–28	129	34–48 (n = 4)
Myscelus amystis hages	51	51	1	16.6	15–21	5	none
Myscelus belti	81	64–117	5	22.9	16–26	67	35–51 (n = 3)
Myscelus perissodora	n/a	n/a	n/a	24.0	24.0	1	none
Passova gellias	68	51–95	10	21.1	15–34	50	none

the weather, the longer the pupal duration, as evidenced by *Pyrrhopyge cosyra* (Table 2).

Color pattern and hairiness. ACG pyrrhopygine caterpillars have one of two color patterns. The first is basically dark with strongly contrasting yellow to orange-yellow "rings" that are ventrally incomplete (Figs. 2, 3, 7, 8, 9, 12) or lateral, vertical bars (Figs. 5, 6, 10, 11) or, in one case, large, orange lateral discs (Fig. 4)—sometimes with red on the head and rump (Figs. 2, 3, 8, 9) and ventrally as well (Fig. 12). These pyrrhopygine caterpillars are thus part of an array of presumably aposematic, mimetic ACG caterpillars that involves hundreds of species, scores of genera, and virtually all families (see photographs in Janzen & Hallwachs 2001). The second pattern is dull green/pink with black to brown/red heads (Figs. 13–15), a seemingly cryptic color pattern shared with hundreds of other species of ACG macrocaterpillars. In contrast to many other ACG hesperiids (see Janzen & Hallwachs 2001), none of the pyrrhopygine caterpillars has false eye markings on the head.

All ACG pyrrhopygines in all instars have notably long hairs on both the body and the head. They are the only ACG skippers with long head hairs—except for the pyrgine *Astraptes fulgerator azul* (Reakirt) whose polymorphic caterpillars include one morph that superficially resembles the yellow-ringed pyrrhopygine caterpillars figured here (but *A. f. azul* lacks long body hairs). Pyrrhopygine pupae are hairy over much of the body and are often brightly colored (Figs. 16–25). Unlike the caterpillars, the pupae of several pyrrhopygines have conspicuous false eye markings, which will be treated in a future study of this phenomenon across all Hesperiidae (see Janzen & Hallwachs 2001).

SPECIES COMMENTARY ON PYRRHOPYGINES OF THE ACG

In the course of reviewing the skipper fauna of the world using the matchless holdings of the British Museum (Natural History), Evans became overly enamored of the polytypic species concept and applied it far too freely. In the brief introduction to his treatment of the skippers of Europe, Asia, and Australia, Evans (1949:xi) observed that

> In accordance with modern ideas, as expressed in books such as Mayr's [1942] *Systematics and the Origin of Species*, as wide a view as is possible has been taken of a species. Whenever a form in one area can be considered as replacing a form in another area, the two are presumed to be conspecific, even though the differences in facies, structure and genitalia appear considerable. The bringing together of subspecies in this manner presents no great difficulty through the Malay Archipelago and the South Sea islands; for instance, the variations of *Tagiades japetus* [(Stoll)] can be traced all the way from Ceylon to the Solomons and compared with those of other similar species flying with it. In continental areas, such as China and Malaya, it is not always easy to decide whether two forms flying together are species or overlapping sub-species of the same species. There are difficulties also in the islands. For instance, in Borneo there seem to be unduly numerous forms of the genus *Telicota*, due perhaps to migrations or infiltration from Java, Timor or the Philippines, and it is difficult to decide whether a particular series, differing slightly in genitalia and facies from another series, represents a species or a sub-species or perhaps a migration, which will become submerged in due course by the dominant form in the island.

Evans used the same philosophy in his subsequent treatments of pyrrhopygines (Evans 1951) and the rest of the New World skippers. Although Evans's distributional data were incomparably rich, they were incom-

plete. Because of this, because of his cavalier tolerance of sympatry between subspecies, and because he pushed to finish cataloging all the skippers on earth before he died, he frequently lumped separate species as subspecies of a single species. On finer analysis, his polytypic species often turn out to comprise one or more superspecies (e.g., Burns 1964) or species groups—or even a distinct genus (Mielke 1995). We know that allopatry, parapatry, or slight sympatry of closely related species is frequent. What Evans called subspecies are sometimes nothing more; but, for the reasons given above, they should be reexamined whenever possible.

Pyrrhopyge zenodorus Godman & Salvin

According to Evans (1951), *Pyrrhopyge zenodorus* is one of 10 subspecies of *P. phidias* (Linnaeus). However, especially on the basis of genitalic comparison (Godman & Salvin 1893:pl. 73, fig. 3, Bell 1931:fig. 10, Evans 1951:fig. A.1.2), *P. zenodorus* is a species in its own right, ranging from central Mexico to Costa Rica, at least.

While the caterpillars of *P. zenodorus* are moderately common in the ACG rainforest, neither caterpillars nor adults have been found in the dry forest, even though patches of the food plant, *Vismia baccifera* (L.) Triana & Planch. (Clusiaceae), are scattered through it in moist places. This apparent absence from dry forest is supported by the fact that the conspicuous caterpillar nests have not been found there either. A *V. baccifera* leaf is dark green above and bright rusty beige below so that, when the caterpillar cuts a section and folds it up and over, the resulting nest is a bold fingerprint that lasts for many months. Even where caterpillars are found, adults are not usually seen. They rarely have been encountered visiting flowers of *Stachytarpheta jamaicensis* (L.) Vahl (Verbenaceae) at the intersection of ACG dry forest and rainforest (in the Río Gongora region).

The adult of *Pyrrhopyge zenodorus* (Fig. 2), which is blue-black, white-fringed, and red-orange on both its head and rump, looks enough like the unrelated *Passova gellias* (Fig. 15) to be indistinguishable from it in flight (unless one can detect the marginal pale blue on the dorsal hindwing of *P. gellias*). In flight, *Pyrrhopyge zenodorus* superficially resembles one other ACG rainforest skipper, the pyrgine *Phocides palemon lilea* (Reakirt) (which, however, has a small red bar at mid-costa of the forewing both above and below and lacks the red-orange rump that gives *Pyrrhopyge* its name).

The caterpillar of *P. zenodorus,* which is ringed brightly with orange-yellow (Fig. 2), superficially resembles those of at least 12 other ACG rainforest skippers (Janzen & Hallwachs 2001), but none of these feeds on *Vismia baccifera: Pyrrhopyge crida* (Hewitson) (Fig. 3), *P. cosyra* (Fig. 6), *P. erythrosticta* (Godman & Salvin) (Fig. 7), *Parelbella macleannani* (Godman & Salvin) (Fig. 9), *Jemadia pseudognetus* (Mabille) (Fig. 10), another *Jemadia* belonging to a *J. hewitsonii* species complex (Fig. 11), *Phocides palemon lilea* (penultimate instar), *Polythrix caunus* (Herrich-Schäffer), *Astraptes fulgerator azul, Nascus broteas* (Cramer), one of two species currently going under the one name *Nascus phocus* (Cramer), and *Achlyodes busirus heros* Ehrmann. The highly similar caterpillars of *Pyrrhopyge zenodorus* and *P. crida* are most readily distinguished by knowing what they were found on (*Vismia baccifera* and the foodplant of *P. crida, V. billbergiana* Beurl., grow within a few meters of each other, with the former in the sun and the latter more on the forest edge). Then, too, the purplish-red hairs on the head and body of the caterpillar are not as brilliant in *P. zenodorus* (Fig. 2) as they are in *P. crida* (Fig. 3).

Caterpillars of *P. zenodorus* are oligophagous on mature leaves of the shrubby treelets *V. baccifera* and *V. ferruginea* Kunth (Table 1). *Vismia baccifera* is widespread and common in the early successional stages of old ACG rainforest pastures returning to forest. When the area was entirely old-growth forest, *V. baccifera* was probably a much rarer plant restricted to the early stages of tree-fall succession and continually disturbed sites such as watercourse edges and landslides. A few hours' search can usually produce at least a few old nests of *P. zenodorus* caterpillars on *V. baccifera,* and currently this plant supports the vast bulk of the population. *Vismia ferruginea* is very rare, occurring just in the interface between dry forest and rainforest (Estación Biológica Maritza area). Despite intensive search, only five caterpillars have been found on it.

Moss (1949:33) reared other members of the *Pyrrhopyge phidias* species complex (to which *P. zenodorus* belongs) without knowing exactly what they were: "Amongst the commonest of the *Pyrrhopyge* in Pará [Brazil], were a number of species closely resembling in their underside coloration [*P. phidias hyperici* (Hübner)]. Unfortunately I took them for one single species and in consequence did not make detailed observations on their separate larvae and pupae. Their tent-like shelters are found on the upper side of the leaves of *Lacre* bushes (*Vismia guianensis* (Aubl.) Choisy., [Clusiaceae]). They also frequently occur[r]ed on *Guava* and *Aracá* (*Myrtaceae*)."

In later instars, *P. zenodorus,* like *P. crida* and *P. aesculapus* Staudinger, only lightly silks a pair of leaves to-

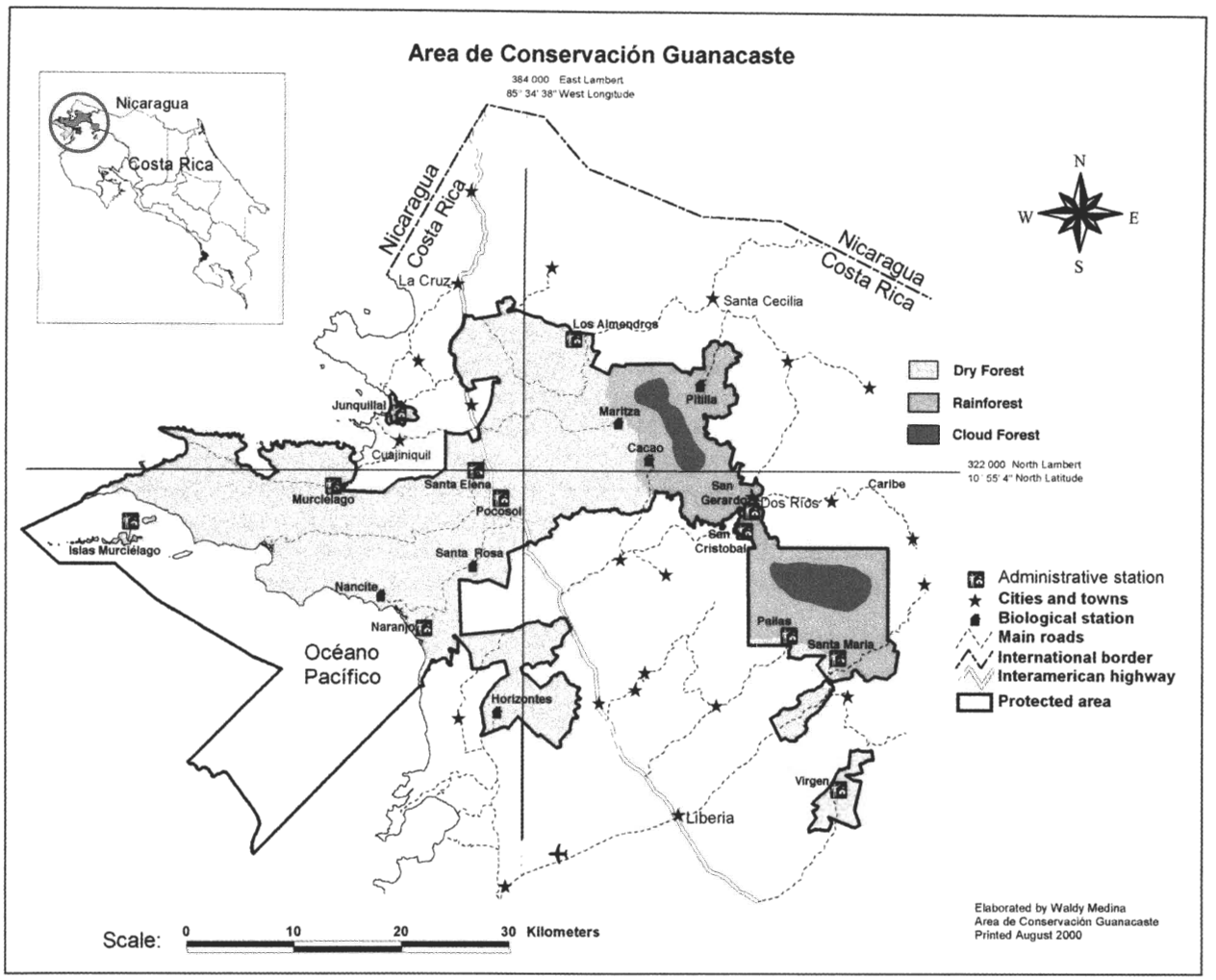


FIG. 1. Area de Conservación Guanacaste (ACG) in northwestern Costa Rica and the locations of its three major ecosystems.

gether to make its nest, in striking contrast to the other pyrrhopygines, most of which make nests with much more extensive and dense silk linings.

Pyrrhopyge zenodorus is one of the three pyrrhopygine caterpillars with more or less host-specific tachinid fly parasites. Eleven of the records of *Houghia* sp. 9 are from this skipper (the other record is from *Phocides nigrescens* Bell); and all three records of *Pseudosturmia* sp. 1 are from *Pyrrhopyge zenodorus*. The distinctive *Apanteles* wasp (Braconidae) that attacks *P. zenodorus* (n = 20) may also turn out to be host-specific.

Pyrrhopyge crida (Hewitson)

Superficially, the adult of *Pyrrhopyge crida* (Fig. 3) does not closely resemble other pyrrhopygines or other ACG hesperiids. The combination of uniform black (both dorsally and ventrally) with an oblique, wide, bright white, hyaline slash tapering across the forewing from below the mid-costa to above the tornus—along with a narrow, off-white fringe on the hindwing and an orange head and rump—is unique (though a number of ACG pyrgines are very dark with a row of white hyaline spots angling across the forewing).

Pyrrhopyge crida is a rainforest skipper in the ACG. Knowledge of its presence comes from 14 rearings, and the capture of a single wild female, by P. Ríos and C. Moraga, parataxonomists at Estación Biológica Pitilla in the northeastern ACG. Though clearly a wide-ranging species, *P. crida* is rare in collections. For example, there are only 8 specimens in the BMNH (from Nicaragua, Colombia, and Ecuador) and 5 in the USNM (from Costa Rica, Panama, and Colombia). It extends north to southern Mexico (Hoffmann 1941).

The caterpillar of *P. crida*, unlike that of *P. zeno-*

dorus (which occurs throughout the rainforest on the widespread *Vismia baccifera*), is apparently restricted to *V. billbergiana* (Table 1), found to date only in the understory of old secondary successional rainforest at about 600 m along the entrance road to Estación Biológica Pitilla. The caterpillar of *P. crida* (Fig. 3) looks very like that of *P. zenodorus* (Fig. 2). However, the hairs on the head and the shorter hairs on the body of *P. crida* are more brilliantly purplish-red than they are in *P. zenodorus*.

Although Evans (1951) included *P. zenodorus* in his second species of *Pyrrhopyge* and treated *P. crida* as his thirty-fifth species (five species groups removed from *P. zenodorus*), the two seem closer. This is suggested by similarities not only in the caterpillars, their foodplants, and how lightly they silk leaves of those plants together when making a nest, but also in basic genitalic form of the adults (Godman & Salvin 1893:pl. 73, fig. 3 & pl. 74, fig. 3, Evans 1951:figs. A.1.2 & A.1.35).

Pyrrhopyge creon H. Druce

The wings of this stunning skipper are iridescent blue, with black edges and fringes and a red-orange spot above the tornus of the hindwing (in space 1c); this prominent spot is expressed on both surfaces, but is a little smaller dorsally than ventrally. Evans (1951) treated *Pyrrhopyge creon* as a monotypic species, represented in the BMNH by specimens from Costa Rica and Panama (plus a pair from Colombia). Much later, Nicolay and Small (1969, 1981) described two subspecies—superficially quite distinct from each other and from *P. creon creon*—from cloud forest on isolated mountains of Panama and Costa Rica, respectively: *Pyrrhopyge creon lilliana,* in which the red-orange subtornal spot of the hindwing is not only enlarged but also expanded into a series of three to five submarginal spots (in spaces 1b to 4); and *P. c. taylori,* in which the iridescent blue of both pairs of wings is replaced by iridescent purple, while the subtornal spot remains unchanged.

Pyrrhopyge c. creon ranges along the continental divide from Guanacaste, Costa Rica, to Coclé, Panama; because it was never found farther east in suitable Panamanian habitat, despite intensive efforts, records from Colombia seem doubtful (Nicolay & Small 1981). Both *P. c. taylori* (at 1150 m in the Fila Cruces, Puntarenas, Costa Rica) and *P. c. lilliana* (at 800 m at Cerro Campana and La Mesa in a disjunct massif in the provinces of Panamá and Coclé, Panama) are separated from typical *P. c. creon* by relatively low-elevation gaps of just 30–40 km. Since intergrades are unknown, these skippers, though strong fliers, are presumably sedentary (Nicolay & Small 1981).

Male genitalia, which are moderately asymmetric in the distal part of the valvae (Godman & Salvin 1893:pl. 73, fig. 11, Bell 1931:fig. 45), are identical in all three subspecies (Nicolay & Small 1969:fig. 3, 1981:fig. 2). In comparing the genitalia of 14 ♂ and 3 ♀ that represent these taxa, we, too, found no significant differences.

Pyrrhopyge c. creon is the epitome of cloud forest hesperiids. Adults are occasionally seen flying and perching on leaves 2–10 m above the ground in the upper parts of tree falls on sunny/warm to foggy/cool days on the peak of Volcán Cacao (1200–1500 m). Their presence in this elevated habitat mirrors their presence at 1600–2000 m—flying even in heavy fog—on Volcán Barba and Volcán Poás, further south in Costa Rica. *Pyrrhopyge c. creon* flies in fog so heavy that its wings may be covered with fine beads of moisture. No other diurnal ACG butterflies have been seen on the wing under these conditions.

In flight in the ACG cloud forest, this large blue-black skipper can be confounded with *P. aesculapus.* When *P. c. creon* perches, the red-orange subtornal spot of the hindwing sets it apart.

A pupa found at 1550 m, on the summit of Volcán Cacao, produced our only reared adult of *P. c. creon.* However, two pyrrhopygine caterpillars whose dark bodies sported large orange dots (Fig. 4)—instead of bars or rings—were found somewhat lower (at about 1200 and 1000 m) on *Dendropanax querceti* Donn. Sm. and *D. gonatopodus* (Donn. Sm.) A. C. Sm. (Araliaceae). The first died of apparent disease in the penultimate instar while the second pupated, only to sprout a mass of white fungus. Though we have yet to rear the adult we need for positive identification of these odd caterpillars, we strongly suspect—from their elevation and habitat—that they are those of *P. c. creon.* But, because we cannot be certain, we have deliberately omitted photographs of the presumed adult from Fig. 4.

Pyrrhopyge aesculapus Staudinger

Pyrrhopyge aesculapus presents no taxonomic problems at the species level. The adult has iridescent purplish-blue wings with a wide, strongly contrasting, orange fringe on the hindwing but not on the forewing (Fig. 5) (except for traces in space 1b in some individuals). The hindwing is purpler and darker, whereas the forewing is bluer. The body is dull because it lacks the orange or red hot tail for which many pyrrhopygines are famous; nor is it "hotheaded." One feature of the distinctive male genitalia—the elongate caudal projection comprising the distal half of the valva—can be exposed relatively easily with dry dissection. In lateral view, this projection looks peculiar because it is almost

uniformly wide, marginally dentate, terminally blunt, and evenly curved upward from its horizontal beginning to its vertical end (Godman & Salvin 1893:pl. 73, fig. 9, Bell 1931:fig. 43, Evans 1951:fig. A.1.46). Known mainly from Costa Rica and Panama, *P. aesculapus* apparently ranges south to Colombia and Ecuador.

In flight in the ACG cloud forest, the large blue-black *P. aesculapus* resembles only *P. c. creon.* At rest, these species are readily distinguished by their hindwings: orange-fringed in the former (Fig. 5), spotted red-orange above the tornus in the latter.

In this cloud-forest habitat, the caterpillar of *P. aesculapus,* with bright yellow, lateral, vertical bars on a black background (Fig. 5), resembles the barred caterpillar of *P. cosyra* (Fig. 6) and, to a lesser extent, the ringed caterpillars of *Ridens mephitis* (Hewitson), *Astraptes fulgerator azul,* and a species of *Venada.* However, none of these caterpillars feeds on *Weinmannia wercklei* Standl. (Cunoniaceae), the sole known foodplant of *P. aesculapus* (Table 1). *Weinmannia wercklei* is a shrubby treelet characteristic of high elevations in Costa Rica. *Pyrrhopyge aesculapus* spins its nest lightly and conspicuously among the thin, flimsy leaves of this plant. Tearing at the nest easily exposes the boldly patterned caterpillar which does not try to stay hidden in the nest but actively crawls away, as if to flaunt its colors.

Too few examples of *P. aesculapus* have been reared to draw conclusions about its lack of parasitoids (Table 1). In the habitat, and at the elevations, where *P. aesculapus* occurs, caterpillars of *P. cosyra* are attacked by a host-specific tachinid fly.

Pyrrhopyge cosyra H. Druce

Of the many species currently in *Pyrrhopyge,* this is one of at least 15 in which the valvae of the male genitalia are asymmetric (Godman & Salvin 1893:pl. 74, fig. 2, Evans 1951:fig. A.1.55) (others include *P. creon* and members of the *P. maculosa* species complex). Superficially, *P. cosyra* is extremely distinct: both pairs of wings are iridescent dark blue, but dorsally they sport a huge, bold, proximal, orange splotch; the forewing has three distal bands that are white and hyaline (hence ventral as well as dorsal); and the body, except for the dorsally orange thorax, is banded black and white (Fig. 6). In the only other pyrrhopygine that resembles it—a South American species, *P. spatiosa* (Hewitson)—the splotch is a redder orange. *Pyrrhopyge erythrosticta* (whose ground color is black instead of iridescent dark blue) presents a color pattern basically like that of *P. cosyra,* except that the huge, central, orange splotch is ventral instead of dorsal (Fig. 7). *Pyrrhopyge cosyra* ranges from Guatemala through Central America to Colombia and Ecuador.

In Costa Rica *P. cosyra* occurs from lowland rainforest (sea level on the Osa Peninsula in the southwest) to ACG rainforest at 400–800 m and extends up into cloud forest at 1400 m. Neither adults nor caterpillars have been found in ACG dry forest, even though one of its foodplants, *Clusia rosea* Jacq. (Clusiaceae), is sporadic in wet sites there. In ACG cloud forest and rainforest, adults have been seen only when they descended from the tree canopy for brief exploration of potential foodplants. The relatively common caterpillars of *P. cosyra* are found less than 3 m above the ground.

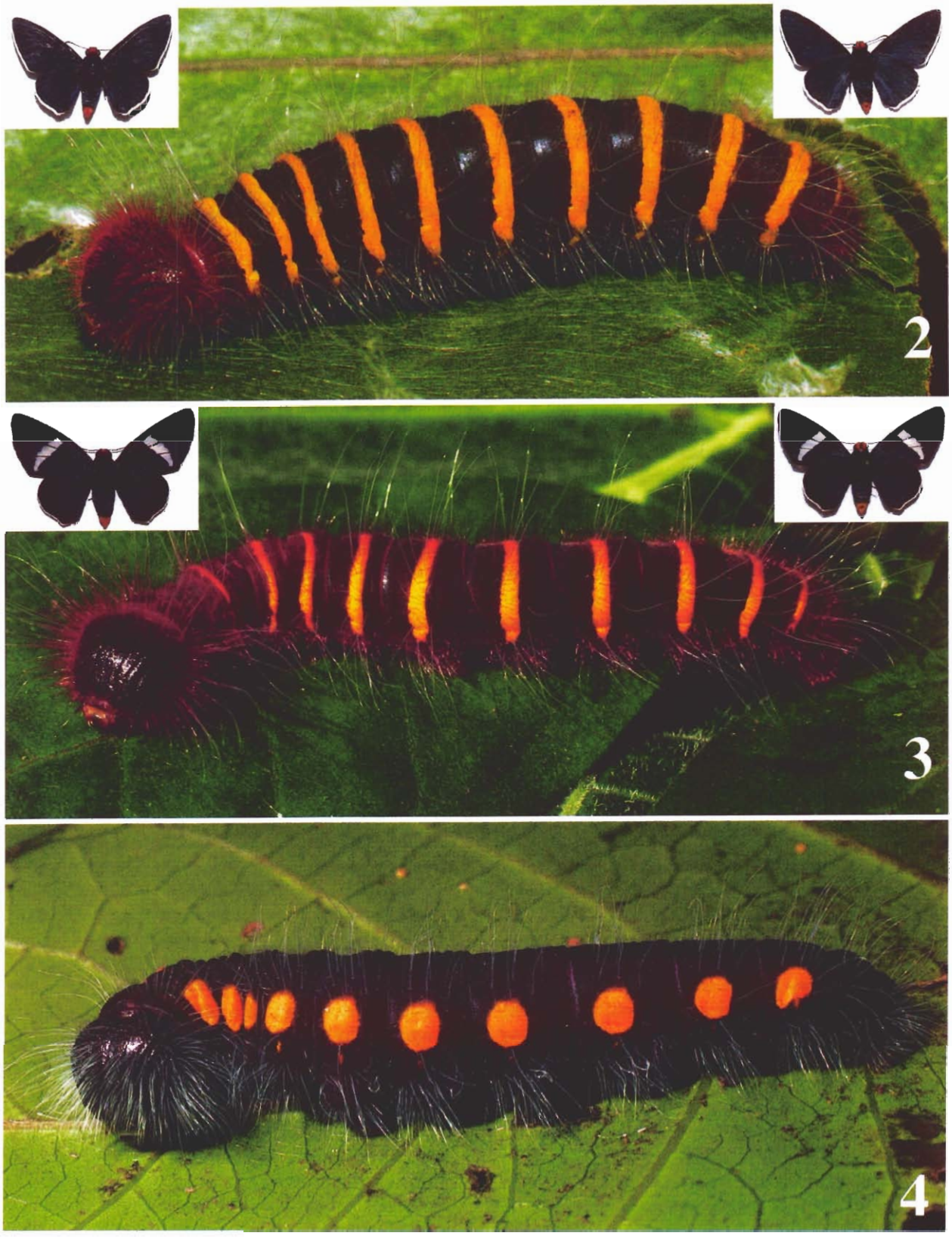
The caterpillar of *P. cosyra,* which is black with orange-yellow, lateral, vertical bars (Fig. 6), looks superficially a lot like the larvae of both *Jemadia* species (Figs. 10, 11) and much like those of *Pyrrhopyge zenodorus* (Fig. 2) and several other rainforest skippers listed in our account of that pyrrhopygine. However, none of these species feeds on *Chrysochlamys* (=*Tovomitopsis*) or *Clusia,* the only foodplants of *P. cosyra* (Table 1).

On small-leaved plants such as *Chrysochlamys* and *Clusia minor* L., the caterpillar of *P. cosyra* spins an extraordinarily tough and baglike silk nest. It is hard to tear open; and when one does, the caterpillar retreats inside in an apparent effort to stay out of sight. When feeding on the other species of *Clusia* with their massive thick leaves, the caterpillar silks a couple of leaves very tightly together into an equally strong nest.

Pyrrhopyge cosyra is the most heavily parasitized of all the pyrrhopygines reared, and the only one attacked by Tachinidae, Ichneumonidae, and Braconidae (Table 1). The tachinid *Chlorohystricia* sp. 1 appears to use it almost exclusively (18 records on *P. cosyra* plus one on *Venada* sp. in the same habitat) and occurs throughout the caterpillar's range in the ACG (400–1400 m). *Pyrrhopyge cosyra* is the sole known host for the ichneumonid genus "MCAM" sp. 1 (n = 10); and it is heavily used by *Casinaria* sp. 9, an ichneumonid wasp that also attacks a few species of pyrgines. The lone braconid individual reared from this skipper has yet to be placed to genus.

Pyrrhopyge erythrosticta (Godman & Salvin)

For their original description of *Pyrrhopyge erythrosticta,* Godman and Salvin (1879) used very few words, no illustrations, and an unspecified number of specimens (from Chontales, Nicaragua, and Veragua [part of central Panama]) without designating a type. Even in the Biologia Centrali-Americana, Godman and Salvin (1893) did not picture an adult; but they did



FIGS. 2–4. Last instars, plus adults in dorsal (L) and ventral (R) view, of ACG pyrrhopygines. **2,** *Pyrrhopyge zenodorus* (rainforest) 94-SRNP-707, L/R ♀ 94-SRNP-6631. **3,** *Pyrrhopyge crida* (rainforest) 97-Rios-491, L/R ♂ 97-Cali-188. **4,** *Pyrrhopyge creon* presumably (cloud forest) 00-SRNP-20314.

FIGS. 5–7. Last instars, plus adults in dorsal (L) and ventral (R) view, of ACG pyrrhopygines. **5,** *Pyrrhopyge aesculapus* (cloud forest) 97-SRNP-513, L/R♂ 97-SRNP-514. **6,** *Pyrrhopyge cosyra* (rainforest to cloud forest) 98-SRNP-2767, L♀ 97-SRNP-1805, R♀ 97-SRNP-6531. **7,** *Pyrrhopyge erythrosticta* (rainforest) 00-SRNP-15831, L/R♂ 00-SRNP-15831.

what was much better in the end by clearly figuring (vol. 3, pl. 73, fig. 13) and verbally describing (vol. 2, p. 252) the "very peculiar" male genitalia of *P. erythrosticta.* Having found that their type series includes more than one genitalically divergent species, Burns hereby chooses as lectotype (BMNH) the male whose genitalia were shown. This action fixes the taxonomic concept of the name and ensures its future consistent interpretation. The lectotype bears a distinctive Godman-Salvin miniature genitalia slide (numbered 369) plus three labels: (1) Chontales, / Nicaragua. / T.Belt. (2) B.C.A. Lep. Rhop. / Pyrrhopyge / erythrosticta, / G. & S. (3) Godman-Salvin / Coll.1912.–23. Its left wings have been bleached for study of venation. This is the species that we have reared in the ACG. At present we know it only from Nicaragua and Costa Rica. The more wide-ranging entity that has been confused with it will be described separately, in the context of the entire *P. maculosa* complex.

While we were writing the paper you hold, ACG parataxonomists Petrona Ríos and Calixto Moraga reported that twice in 1996 they had seen yellow-ringed, black pyrrhopygine caterpillars on *Marila laxiflora* Rusby (Clusiaceae) at Estación Biológica Pitilla (in rainforest at 700 m on the northeast side of Volcán Orosí) but had been unable to rear them. Asked now to try for more, Ríos found a single last instar (Fig. 7) in its nest on a non-host plant—i.e., a plant that the caterpillar was not eating in the field and would not eat in captivity. It fed normally on *M. laxiflora* until pupation (Fig. 19) and produced our lone reared adult (Fig. 7). Two wild adults of *P. erythrosticta* have been caught in the rainforest at 600–800 m in the pass between Volcán Cacao and Volcán Rincón de la Vieja. This species has not been seen anywhere else in the ACG.

Pyrrhopyge erythrosticta gets its specific name from the small, dull red spot near the base of the dorsal forewing between veins 1 and 2 (Fig. 7); but the forewing also bears nine, more conspicuous, small, white hyaline spots in fixed positions. It is important that in true *P. erythrosticta,* the lowest hyaline spot, which is in space 1b, is directly under the spot in space 2 (Fig. 7). The spot in space 1b is likewise under the spot in space 2 in a more northern species, *P. hoffmanni* Freeman, to which *P. erythrosticta* is also genitalically related. However, *P. hoffmanni* is much more closely related to the still more northern *P. mulleri* (Bell): this pair has essentially the same genitalia in both sexes (for males, cf. Bell 1934:fig. 5 and Freeman 1977:fig. 17), but *P. mulleri* has lost all hyaline spots. The members of the *P. mulleri-P. hoffmanni* / *P. erythrosticta* trio appear to replace each other geographically. Their apparent parapatry independently supports their grouping on morphological grounds. On the other hand, both *P. hoffmanni* and *P. erythrosticta* coexist with the species that is currently confounded with the latter. In this unnamed species, the spot in space 1b is not under the spot in space 2 but, instead, displaced outward so that the spots in spaces 1b, 2, and the cell form a straight line—as they also do in its more southern (and closer) relative, *P. maculosa* Hewitson.

Elbella scylla (Ménétriés)

Elbella scylla amounts to much more than the latest taxonomic revision implies. Mielke (1995) treats *E. dulcinea* (Plötz) as a different species, occurring in Mexico with *E. scylla* and extending farther south than *E. scylla* into northern South America (see map plotting both in Mielke 1995:fig. 44); but all this is one species ranging from central Mexico to Colombia, Venezuela, and Ecuador. Its genitalia (Godman & Salvin 1893:pl. 73, fig. 6, Bell 1931:fig. 35, Evans 1951:fig. A.2.1, Mielke 1995:figs. 15, 16) look the same (within normal limits of individual variation) everywhere (41 closely compared KOH-dissections: Mexico 3 ♂, Guatemala 1 ♂ 1 ♀, Honduras 1 ♂ 1 ♀, Costa Rica 14 ♂ 14 ♀, and Panama 3 ♂ 3 ♀). *Elbella scylla* (described in 1855 from Nicaragua) and *E. dulcinea* (described in 1879 from the part of Colombia that, in 1903, became Panama) were considered synonymous in the 1940s. However, Evans (1951) called *dulcinea* a subspecies of *scylla;* and Freeman (1966:227)—who claimed, without specifics, that the two "differ somewhat genitalically and morphologically" and "occur together in the same areas of Veracruz," Mexico—raised *dulcinea* back to the level of species (for complete references, see Mielke 1995:460).

The main color character that "distinguishes" *dulcinea* from *scylla*—i.e., inward expansion of white from the white hindwing fringe into the outer margin of the black hindwing proper—is variably expressed by most of the ACG specimens of *E. scylla.* Since this "white expansion" is more pronounced and more uniformly expressed in specimens from Panama, and since it is still more pronounced in Venezuela (see Mielke 1995:fig. 87), it is apparently a clinally varying trait in southern portions of *E. scylla's* range. (The "white expansion" is better expressed ventrally than dorsally in every individual showing it; furthermore, it is sexually dimorphic and better expressed by females than by coexisting males.) Geographic variation in fringe-whitening, and in the extent to which white invades the dark hindwing itself, has been well documented in the pyrgine genus *Erynnis* in which a white fringe has evolved eight times independently, always in

those populations occurring in the southwestern USA and Mexico plus points south (Burns 1964). In *Elbella scylla* a color character of the tegulae—whether their longitudinal stripe is yellowish, reddish-orange, or bluish-white (it is occasionally unexpressed)—also varies geographically, but not in concordance with the clinal variation noted above. In ACG material the stripe is reddish-orange.

Adults of *E. scylla* are occasionally encountered visiting flowers (e.g., *Trigonia rugosa* Benth. [Trigoniaceae], *Cordia* spp. [Boraginaceae]) in the ACG dry forest and on the dry side of the intergrades between dry forest on the one hand and rainforests and cloud forests on the other in the eastern ACG. Neither adults nor caterpillars have ever been encountered in rainforest or cloud forest.

Although the adult of *E. scylla* does not closely resemble adults of other ACG dry-forest hesperiids, it can—in flight—be confused with two other large and generally black skippers, *Mysoria ambigua* (Mabille & Boullet) and *Phocides palemon lilea.* The former species has yellow and magenta along the outer and costal margins, respectively, of the underside of the hindwing (Fig. 12), while the latter species has a small red bar at mid-costa of the forewing both above and below.

The brightly yellow-ringed caterpillar of *E. scylla* (Fig. 8) superficially resembles those of at least 13 other ACG dry-forest skippers (Janzen & Hallwachs 2001): *Mysoria ambigua* (Fig. 12), *Phocides palemon lilea, Drephalys alcmon* (Cramer) and *D. kidonoi* Burns (see Burns & Janzen 2000:figs. 21–25), *Polythrix caunus, Chrysoplectrum pervivax* (Hübner), *Ridens mephitis, Astraptes fulgerator azul, Nascus solon corilla* Evans, two species currently going under the one name *Nascus phocus, Pellicia dimidiata* Herrich-Schäffer, and *Achlyodes busirus heros,* all of which appear to be involved in an as yet undescribed, multi-familial, aposematic, caterpillar mimicry complex.

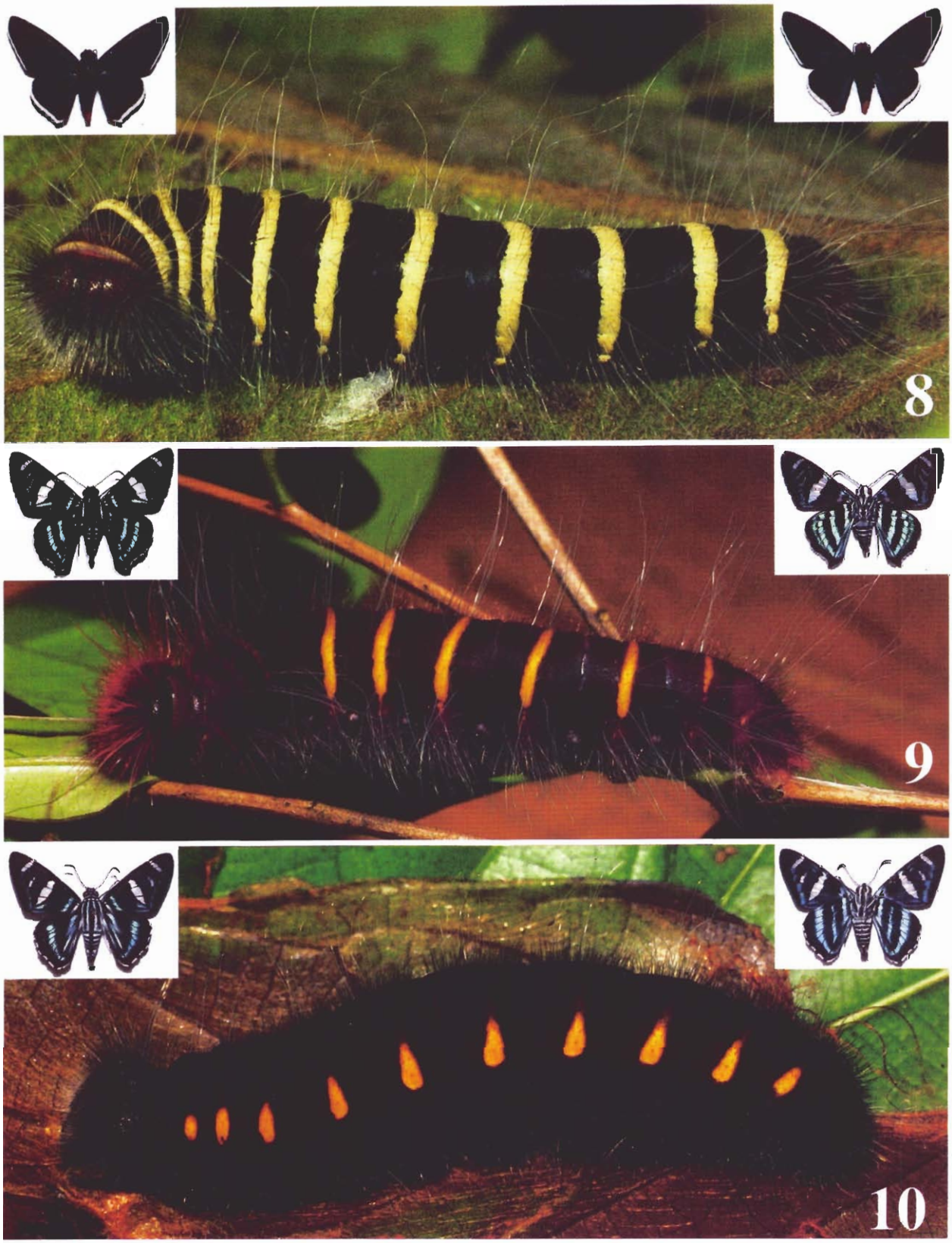
Caterpillars of *E. scylla* are oligophagous on mature leaves of a small subset of the species of ACG Malpighiaceae plus two species of Combretaceae (Table 1). Most caterpillars eat *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae), a shrubby tree that is common in the old and frequently burned pastures cut out of ACG dry forest, but that also persists in many kinds of old-growth forest ranging from exposed sea cliffs to deep soils on the volcanic foothills. The other three malpighiaceous foodplants are woody perennial vines occurring commonly on forest edges and in understory of secondary succession. All four of these foodplants probably will be rarer and more locally distributed when the ACG dry forest has returned to full old-growth status. Other common dry-forest Malpighiaceae (*Heteropterys obovata* [Small] Cuatrec. & Croat, *Gaudichaudia hexandra* Chodat, *Stigmaphyllon ellipticum* A. Juss., *S. lindenianum* A. Juss., *Mascagnia sinemariensis* Griseb., *Bunchosia biocellata* Schlecht., *Malpighia glabra* L., *Banisteriopsis cornifolia* C. B. Rob.), which occur both on edges and in heavily-shaded understory of deep forest, have never yielded *E. scylla* caterpillars. Neither have any of the other five or so species of malpighiaceous treelets and shrubs (e.g., *Tetrapterys discolor* G. Mey., *Hiraea* sp., *Bunchosia* sp.) in the wetter portions of the ACG produced these caterpillars, despite intensive search.

Combretum farinosum H. B. & K. is an occasional woody vine and scandent shrub that grows along ravines and watercourses, and *E. scylla* apparently eats its semi-evergreen foliage primarily in the dry season. This is the only native species of Combretaceae in the ACG dry forest. The others are in the mangroves or in local riparian wet sites, and we do not know whether they, too, would be acceptable. *Terminalia catappa* L. is an introduced beach-edge and garden evergreen combretaceous tree that is very rarely used by *E. scylla.* Inclusion of Combretaceae in the diet of a malpig-eater is mirrored by the pyrgine genus *Cephise:* caterpillars of the tailless species *Cephise nuspesez* Burns as well as the tailed species *C. auginulus* (Godman & Salvin)—which now is considered a synonym of *C. aelius* (Plötz) (Austin & Mielke 2000)—feed heavily on Malpighiaceae and also use Combretaceae (Burns 1996, Janzen & Hallwachs 2001). There is no hint that *E. scylla* caterpillars feed on any plants in the ACG besides the four Malpighiaceae and the two Combretaceae in Table 1.

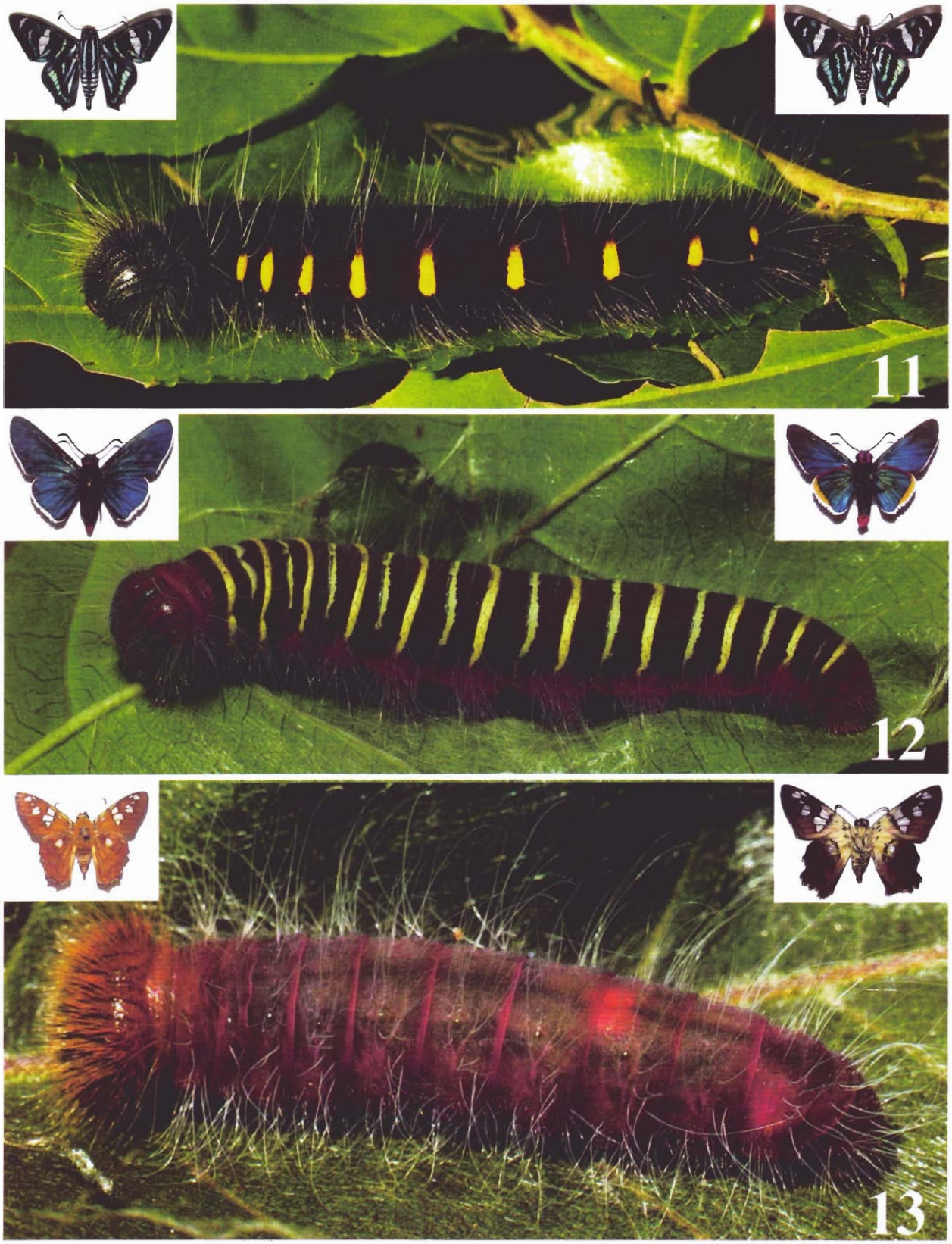
For *E. dulcinea*—which is synonymous with *E. scylla*—Mielke (1995) reported that, in Maracay, Aragua, Venezuela, the caterpillar was reared by F. F. Yépez on *Terminalia catappa.* This Asian introduction was recorded once as a foodplant in the ACG.

In Pará, Brazil, Moss (1949) reared larvae of *E. intersecta* (Herrich-Schäffer) on at least three unspecified species of Malpighiaceae. *Elbella scylla* and *E. intersecta* are very closely related and, since the latter is primarily South American in distribution, mostly allopatric. For *E. intersecta intersecta,* Mielke (1995) stated that larvae are very common on *Vismia guianensis* (Clusiaceae) in Imperatriz, Pará; and for *E. i. peter* Evans, he simply listed *Vismia guianensis* and *Banisteria mossii* Morton (Malpighiaceae) as foodplants.

Elbella scylla appears to be attacked by only one species of parasitoid, a microgastrine braconid (*Cotesia*) (Table 1). A single individual was found with tachi-



FIGS. 8–10. Last instars, plus adults in dorsal (L) and ventral (R) view, of ACG pyrrhopygines. **8,** *Elbella scylla* (dry forest) 96-SRNP-224, L/R ♀ 93-SRNP-6852. **9,** *Parelbella macleannani* (rainforest) 01-SRNP-113, L/R ♀ 98-SRNP-6468. **10,** *Jemadia pseudognetus* (rainforest) 00-SRNP-21908, L/R ♂ 98-SRNP-6196.



FIGS. 11–13. Last instars, plus adults in dorsal (L) and ventral (R) view, of ACG pyrrhopygines. **11,** *Jemadia* sp. X of a *J. hewitsonii* species complex (rainforest) 01-SRNP-9029, L/R ♂ 00-SRNP-4482. **12,** *Mysoria ambigua* (dry forest) 80-SRNP-272, L ♀ 87-SRNP-1162, R ♂ 95-SRNP-8409. **13,** *Myscelus amystis hages* (dry forest) 93-SRNP-8387, L ♂ 96-SRNP-12399, R ♀ 96-SRNP-365.

nid eggs glued on the front of the head, but neither flies nor caterpillar survived the rearing process.

Parelbella macleannani (Godman & Salvin)

Evans (1951) grouped five subspecies in his polytypic species *Elbella polyzona* (Latreille). Mielke (1995) regards this assemblage as a new genus, *Parelbella;* treats four of the subspecies as three distinct species (one that is polytypic includes not only two of those four subspecies but also the fifth as a synonym); and adds a new species. One of *Parelbella*'s four species extends north of South America.

Parelbella macleannani ranges from northern Ecuador (Imbabura) to southern Mexico (Veracruz, Oaxaca), with intervening records from Colombia, Panama, Costa Rica (ours), Nicaragua, and Guatemala (Mielke 1995:fig. 51, 561-562). In the ACG, its caterpillars have been found only in the rainforest from 400–800 m—never in the dry forest—and free-flying adults have not been seen or collected.

Parelbella and *Jemadia* (the genus we consider next) are among those distinctive pyrrhopygines in which adults with a more or less black ground color are striped and banded pastel blue over the body and on both pairs of wings and, in addition, are banded hyaline white on the forewings (Figs. 9–11). (Some species of the pyrgine genus *Phocides* have independently evolved this striking color pattern; but their stout antennal club—in sharp contrast to that of pyrrhopygines—ends in a long, delicate, reflexed apiculus. Nevertheless, in life these pyrgines fold the apiculus back so tightly against the body of the club that even the club suggests that of a pyrrhopygine.)

Though at first glance *Parelbella macleannani* and ACG species of *Jemadia* look much the same, they do differ—not just in major genitalic ways (cf. Mielke 1995:figs. 32–36 and Evans 1951:figs. A.5.1–A.5.7) but in wing pattern and shape (cf. Figs. 9–11). In *P. macleannani* the slender hyaline spots in spaces 3 and 4 of the forewing (which, at times, are barely or not expressed) are widely disjunct, whereas in *Jemadia* these two spots are in contact and aligned. *Parelbella macleannani* has a fine blue line (expressed much better ventrally than dorsally) at the distal end of the forewing cell, but *Jemadia* does not. In *P. macleannani* the inner (basal) blue band on the dorsal hindwing is single; in *Jemadia* it is double. The submarginal blue band on the ventral hindwing of *P. macleannani* (which is not as well-developed as the three more proximal blue bands) is lacking in *Jemadia.* And there is a small lobe at the hindwing tornus in *P. macleannani* but not in *Jemadia.*

Caterpillars of *P. macleannani* are monophagous to oligophagous on mature leaves of one to three species (some determinations pending) of *Eugenia* (Table 1). These Myrtaceae are forest-understory-to-edge scandent shrubs, on which the caterpillars were all found within 2 m of the ground. Given that there are more than 30 species of Myrtaceae in the ACG and that *P. macleannani* has been found on only one to three congeneric species, it may eat just it or those. On the other hand, the caterpillar of this skipper occurs at such low density that, with more years of search, its list of myrtaceous foodplants may increase.

In Pará, Brazil, Moss (1949) found caterpillars of what Mielke (1995) treats as *Parelbella ahira ahira* (Hewitson) on an undetermined species of *Eugenia* (and once also on *Virola sebifera* Aubl. [Myristicaceae]). He described both larvae and pupae as strongly crimson and indicated that the larvae have transverse yellow belts.

The caterpillar of *Parelbella macleannani* is reddish-black with orange-yellow rings (Fig. 9). This color pattern basically resembles those of various other ACG rainforest skippers such as *Pyrrhopyge zenodorus,* as listed in the account of that species. Except for the pyrgine *Phocides palemon lilea,* these other skippers do not feed on Myrtaceae.

Our only parasitized caterpillar of *Parelbella macleannani* (Table 1) was attacked by *Hyphantrophaga virilis* (Aldrich & Webber), which is the most extreme generalist of all ACG tachinids reared.

Jemadia pseudognetus (Mabille), **reinstated status**

Evans's (1951:50) polytypic species *Jemadia hospita,* ranging from Guatemala to Peru, Bolivia, and Brazil, includes four subspecies. The two subspecies that are widely distributed are also the first to have been described (originally as species): *Jemadia hospita hospita* (Butler, 1877) and *J. hospita pseudognetus* (Mabille, 1878). Repeated comparison of the genitalia of 20 ♂ shows that these two taxa are indeed separate species, with *J. pseudognetus* ranging from southern Mexico to Colombia, at least, and with *J. hospita* strictly South American (like the other taxa in this complex). The characters given by Evans (1951:50–51) for superficially distinguishing between *pseudognetus* and *hospita* are good. Differences in the male genitalia (not noted by Evans) are subtle and involve a narrow, pointed, finely dentate projection that sweeps anterodorsally from the posterior half of the valva: this projection is shorter and a little less dentate in *J. pseudognetus* (Godman & Salvin 1893:pl. 74, fig. 6) than it is in *J. hospita* (Bell 1933:fig. 24, Evans 1951:fig. A.5.1).

Caterpillars of *J. pseudognetus* have been found

only in the rainforest from 400–800 m, and free-flying adults have never been seen or collected in the ACG. Since no caterpillars have been found in the dry forest, *J. pseudognetus* is clearly a rainforest skipper within the ACG.

Several differences in external appearance between adults of ACG species of *Jemadia* and those of *Parelbella macleannani* are listed under the latter species. But *J. pseudognetus* specifically differs from *P. macleannani* in another respect: the dorsal hindwing has only two pastel blue bands (inner and outer), instead of three (inner, central, and outer) as in *P. macleannani.*

Caterpillars of *J. pseudognetus* are oligophagous on mature leaves of Lauraceae (Table 1). Although there are more than 30 species of Lauraceae in the ACG, *J. pseudognetus* has been found on only six and may be limited to them. But, because the density of caterpillars is low, the list of lauraceous foodplants may, in time, increase. All known foodplants are forest-understory-to-edge saplings and treelets, and all caterpillars have been found within 2 m of the ground.

The caterpillar of *J. pseudognetus* is black with short, lateral, vertical bars of orange-yellow (Fig. 10). More or less similar barred color patterns occur in *Pyrrhopyge aesculapus* (Fig. 5), *P. cosyra* (Fig. 6), and another species of *Jemadia* (Fig. 11) to be treated next. However, each of these ACG wet-forest pyrrhopygines eats plants in a different family (Table 1).

New member of a *Jemadia hewitsonii* species complex

Evans's (1951:53) polytypic species *Jemadia hewitsonii,* which is essentially South American, contains five subspecies: *Jemadia h. pater* Evans, 1951, *J. h. ovid* Evans, 1951, *J. h. albescens* Röber, 1925, *J. h. hewitsonii* (Mabille, 1878), and *J. h. brevipennis* Schaus, 1902. Consideration of the color-pattern characters used by Evans to distinguish among these taxa, coupled with comparison of their genitalia (from a total of 30 ♂—including the holotype of *J. brevipennis*—in the USNM), suggests that several closely related species, rather than subspecies, comprise a *J. hewitsonii* species complex. Genitalic differences among these taxa are modest: for example, the dorsally dentate distal portion of the valva is relatively long, finely dentate, and lower distally than proximally in *J. hewitsonii* (Bell 1933:fig. 27) but relatively short, coarsely dentate, and fully as high distally as proximally in *J. pater,* **new status** (Godman & Salvin 1893:pl. 74, fig. 9). Genitalic study further shows that *J. brevipennis* is not what Evans had in mind but, instead, a species well-removed from the rest and closely allied with *J. gnetus* (Fabricius).

Although Evans recorded *J. pater* from Venezuela (3 ♂ 2 ♀), Colombia (65 ♂ 1 ♀), and Panama (1 ♂ 1 ♀), it is not the northernmost member of the *J. hewitsonii* species complex. What is, is something deep in the rainforest of the ACG known from 16 caterpillars found eating *Casearia arborea* Urb. (Flacourtiaceae) (Table 1) and from the three adults (1 ♂ 2 ♀) they produced. More adults (especially males) are desired before formal description of this apparent differentiate. Here we simply call it *Jemadia* sp. X. Its caterpillar is black with short, lateral, vertical bars of bright, clear yellow (Fig. 11). These short, lateral bars are orange-yellow in *J. pseudognetus* (Fig. 10).

At both Óbidos and Santarém, Pará, Brazil, Moss (1949) found caterpillars of *J. gnetus* feeding on a different flacourtiaceous plant, *Laetia corymbulosa* Spruce.

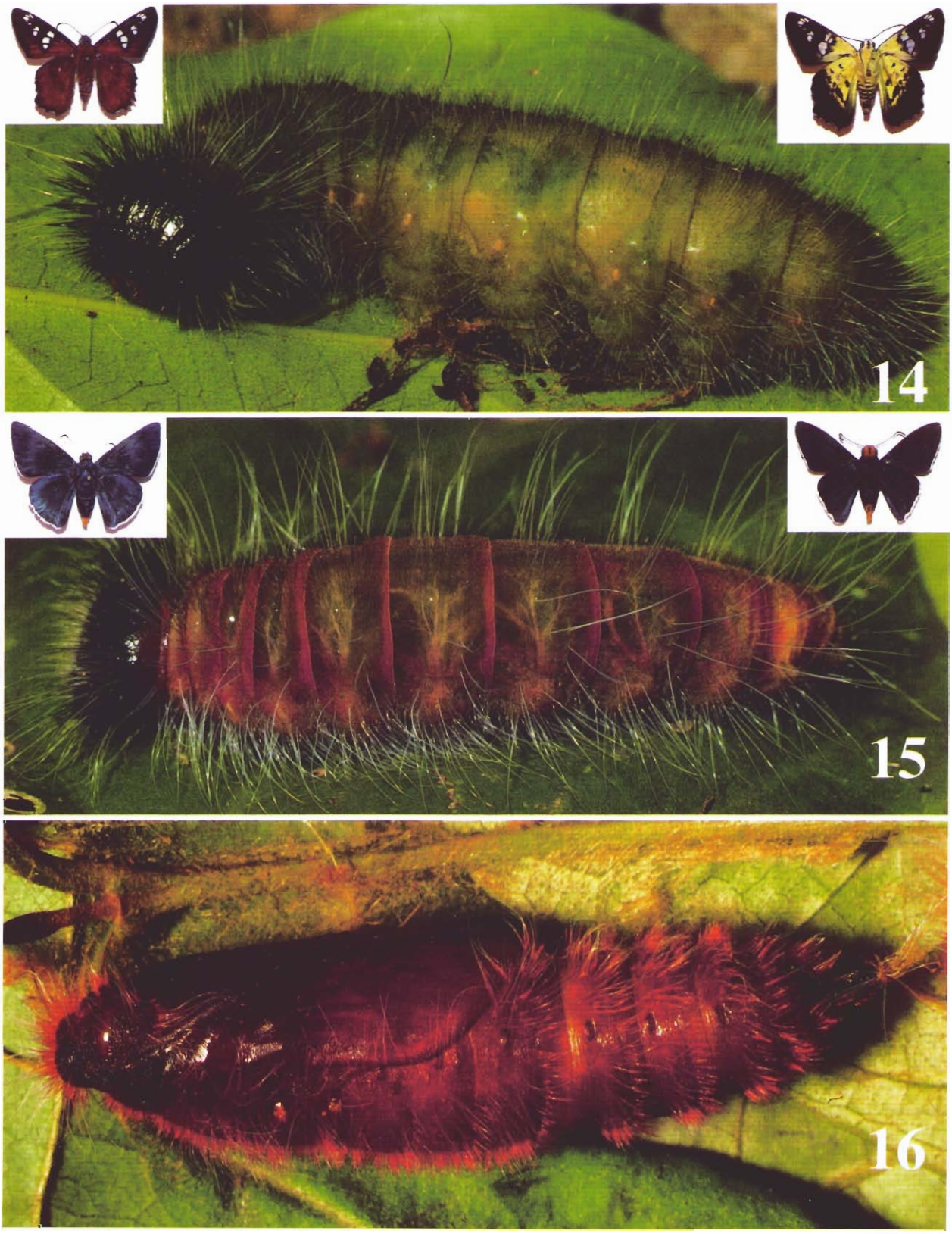
Adults of *Jemadia* sp. X look like those of its ACG congener, except that, on the dorsal hindwing, between the inner and outer pastel blue bands, there is a short, blue, central band (running only from veins 3 to 7), which is absent in *J. pseudognetus* (cf. Figs. 10 and 11).

Mysoria ambigua (Mabille & Boullet)

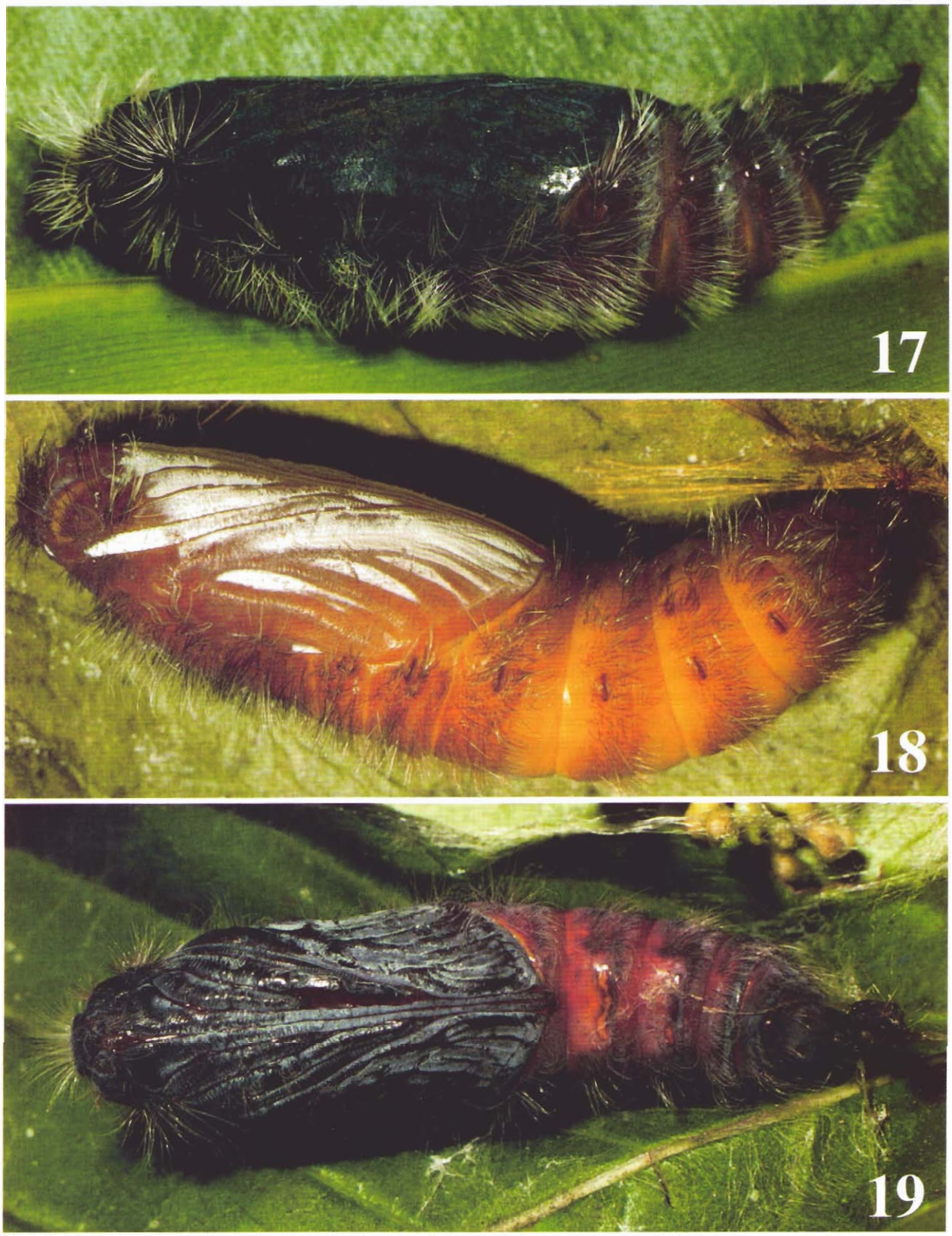
Although Evans (1951) saw *Mysoria ambigua* as the most northern of six subspecies comprising polytypic species *M. barcastus* (Sepp), comparative study—particularly of genitalia (note major valval differences depicted in Evans 1951:fig. A.12.1)—shows that *M. ambigua* is a separate species, occurring from Mexico to Costa Rica.

In the ACG, *M. ambigua* frequents dry forest and the dry side of the intergrades between dry forest and wetter forests to the east. Neither adults nor caterpillars have ever been encountered in rainforest or cloud forest itself. When flying in the ACG dry forest, *M. ambigua* can be confused with two other large and generally black skippers, *Elbella scylla* and *Phocides palemon lilea*—but neither of them has a yellow outer margin and purplish-red costal margin on the ventral hindwing (Fig. 12).

In the ACG, the caterpillars of *M. ambigua* (Fig. 12) are oligophagous on mature leaves of a subset of the resident species of Flacourtiaceae (Table 1). *Casearia corymbosa* Kunth, which is unambiguously the foodplant for the great majority of the caterpillars, is a common forest-edge treelet in secondary succession (both anthropogenic and naturally occurring). *Casearia sylvestris* Sw., though an equally common forest-understory treelet, is rarely used by *M. ambigua* caterpillars. *Casearia arguta* Kunth is a somewhat scarcer secondary successional treelet that likewise is rarely used. *Zuelania guidonia* Britton & Millsp.,



FIGS. 14–16. Last instars, plus adults in dorsal (L) and ventral (R) view, and pupa of ACG pyrrhopygines. **14,** *Myscelus belti* (rainforest) 95-SRNP-8435, L ♀ 99-SRNP-12882, R ♀ 99-SRNP-12671. **15,** *Passova gellias* (rainforest to cloud forest) 95-SRNP-8758, L ♀ 99-SRNP-8542, R ♂ 99-SRNP-4972. **16,** *Pyrrhopyge crida* (rainforest) 00-Cali-013.



FIGS. 17–19. Pupae of ACG pyrrhopygines. **17,** *Pyrrhopyge aesculapus* (cloud forest) 97-SRNP-513. **18,** *Pyrrhopyge cosyra* (rainforest to cloud forest) 95-SRNP-539. **19,** *Pyrrhopyge erythrosticta* (rainforest) 00-SRNP-15831.

though a common tree, is not commonly used (and caterpillars occur only on the foliage of saplings, 1–3 m from the ground). The other four species of ACG dry forest Flacourtiaceae—*Casearia tremula* Griseb. and *C. praecox* Griseb. (both locally common, but with very small distributions) and *Xylosma horrida* Rose and *X. flexuosa* (Kunth) Hemsl.—have never yielded caterpillars of *M. ambigua;* nor have any of the other 10+ species of flacourtiaceous treelets and shrubs in the wetter portions of the ACG, despite intensive search.

At Santarém, Pará, Brazil, Moss (1949) found caterpillars (described as mauve, belted with lemon-yellow) of the *M. barcastus* species complex on small bushes of *Casearia.*

The yellow-ringed caterpillar of *M. ambigua* is superficially similar to at least 13 other ACG dry forest hesperiid caterpillars: *Elbella scylla* plus the 12 pyrgine species listed in our account of that pyrrhopygine. The caterpillar of *M. ambigua* (Fig. 12) has twice as many rings as does that of *E. scylla* (Fig. 8), and they are narrower.

Parasitization frequency of *M. ambigua* caterpillars is very low (Table 1). *Mysoria ambigua* is used by three generalist tachinids—*Hyphantrophaga virilis* (Aldrich & Webber), *Chaetogena scutellaris* (Wulp), and *Lespesia aletiae* (Riley)—as well as by two still unidentified species of *Winthemia,* both of which will probably turn out to be essentially specialists on this pyrrhopygine. The only two cases of parasitization by Hymenoptera (microgastrine braconids) appear to be by species that attack a number of skipper species.

Myscelus amystis hages Godman & Salvin

This taxon ranges from about the Tropic of Cancer in Mexico to Panama (and probably also Colombia). In the ACG dry forest, and on the dry side of the intergrades between dry forest and wetter forests to the east, adults of *Myscelus amystis hages* are very rarely seen visiting flowers such as *Trigonia rugosa* (Trigoniaceae) and *Cordia* spp. (Boraginaceae). Neither adults nor caterpillars have ever been found in ACG rainforest or cloud forest.

Myscelus amystis hages, which looks like no other skipper in the ACG dry forest, most resembles its rust-red congeners *M. belti* Godman & Salvin (Fig. 14) and *M. perissodora* Dyar of the ACG rainforest. Owing to the pronounced sexual dimorphism in color pattern in *M. a. hages,* which is not expressed in the other two species, the females of *M. a. hages* (Fig. 13) approach those species in general appearance, while the more yellow-orange males (Fig. 13) do not.

In the ACG, the caterpillars of *M. a. hages* are apparently oligophagous on mature leaves of three species of *Trichilia* (Meliaceae) and nothing else (Table 1). (*Trichilia* is rarely eaten by other caterpillars of any kind.) *Trichilia americana* (Sessé & Moc.) T. D. Penn., the heavily favored foodplant, is a common forest-edge medium-sized tree in all kinds of secondary succession; the caterpillars (and newly laid eggs) are most often encountered on branches with fully insolated mature leaves. The other four species of ACG dry forest Meliaceae—*Trichilia martiana* C. DC., *Swietenia macrophylla* King, *Cedrela odorata* L., and *Guarea excelsa* H. B. & K.—have never produced these caterpillars; and neither have any of the other five or so species of meliaceous trees in the wetter portions of the ACG, despite intensive search.

The pink/dull green, shaggy caterpillar of *M. a. hages* (Fig. 13) does not resemble any other species of ACG dry-forest hesperiid caterpillar. But it strongly resembles the dull green, shaggy caterpillars of *M. belti* (Fig. 14) and *M. perissodora* and the pink/dull green, shaggy caterpillar of *Passova gellias* (Fig. 15), all found in the wetter forests on the eastern side of the ACG. It can easily be distinguished from *M. belti* and *P. gellias* by the reddish long hairs on its head (which, itself, becomes red posteriorly instead of remaining black).

Myscelus belti Godman & Salvin

Although *Myscelus belti,* like *M. a. hages,* ranges from Mexico to Panama (and perhaps also Venezuela), *M. belti* is a rainforest skipper instead of a dry-forest one. While the caterpillars of *M. belti* are found in the ACG rainforest and in intergrades with dry forest from 400–700 m, no caterpillars have ever been found in dry forest or cloud forest (and free-flying adults have not been seen or collected anywhere).

Myscelus belti, with its brick-red dorsal surface and bright yellow central splotch ventrally (Fig. 14), can be confused with only one ACG rainforest skipper—*M. perissodora.* However, *M. belti* has a small hyaline spot in the cell of the hindwing and, ventrally, a small black spot on the hindwing costa at the angle near its base, both of which *M. perissodora* lacks. Moreover, the three hyaline spots (in spaces 1b, 2, and the cell) that form the innermost band on the forewing are less well aligned and less even along their proximal margin in *M. belti* than they are in *M. perissodora.* The dark, diffuse discal band of the dorsal hindwing is a little less continuous, but at the same time a little darker in spaces 5 and 6, in the former than in the latter. Finally, the dorsal ground color of both wings is a bit redder in *M. belti* than it is in *M. perissodora.*

In the ACG, the caterpillars of *M. belti* are oligophagous on mature leaves of three species of

Guarea (Meliaceae)—*G. glabra* Vahl, *G. rhopalocarpa* Radlk., and *G. bullata* Radlk.—the first of which is also eaten by both *M. perissodora* and *Passova gellias,* and the second, by *P. gellias* (Table 1). *Guarea glabra,* which is certainly the principal foodplant, is a common forest understory and edge treelet in all sorts of secondary succession. Our efforts notwithstanding, *M. belti* caterpillars have never been found feeding on any of some 15 other species of ACG Meliaceae: *Trichilia* spp., *Swietenia macrophylla, Cedrela odorata, Guarea* spp., and various other rainforest Meliaceae.

The dull green, shaggy caterpillar of *M. belti* (Fig. 14) does not resemble any species of ACG dry forest hesperiid caterpillar except the pink/dull green, shaggy caterpillar of *M. a. hages* (Fig. 13) which, however, has reddish hairs on its head. But in the ACG rainforest and cloud forest, it strongly resembles the pink/dull green, shaggy caterpillar of *Passova gellias* (Fig. 15), with which it is easily confused because they feed on the same plants in the same place, and because *P. gellias* varies from pink (usual) to dull green. We know it must also closely resemble the caterpillar of *M. perissodora* (of which we have no photo) because our only reared adult of that species was mistaken, as a caterpillar, for *M. belti.*

In Pará, Brazil, Moss (1949) reared three species that soon (Evans 1951) came to be called *Myscelus pardalina guarea* Evans, *Passova gazera* (Hewitson), and *Passova passova gortyna* (Hewitson), all on *Guarea trichilioides* L.; in addition, he found nests of the *Myscelus* on a second species of *Guarea.* Moss (1949:34) noted not only that the larvae of these three skipper species "are scarcely distinguishable" from one another but also that they are very distinct from those of other pyrrhopygines he had reared because "they do not possess belts or patches of lighter colour. The general tone is olive brown to greenish, ventrally pink with pinkish extremities and the head is warm brown . . . ." Although Evans (1951) viewed *Myscelus* and his new genus *Passova* as separate genera, they are closely related. For those two genera, Evans (1951:72, 79) explicitly stated that "All males have dense brushes on the inside of the femora and tibiae of the hind legs"; and he had already pointed out (Evans 1951:5) that this is "the only secondary sexual character in the subfamily" Pyrrhopyginae. Close similarities in the male genitalia of *Myscelus* and *Passova* are evident in plates 8 and 9 of Evans (1951).

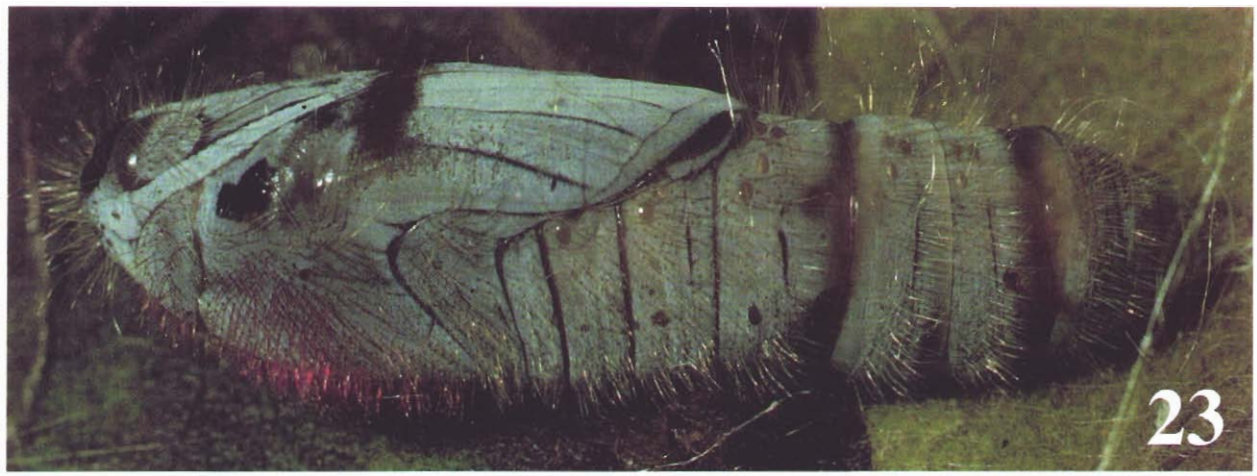
Myscelus perissodora Dyar, **reinstated status**

Evans (1951)—whose material (except from the Colombian department of Cauca) was both limited and variable—treated *Myscelus pegasus* as a polytypic species comprising a pair of subspecies: *Myscelus p. perissodora* ranging from Mexico to Colombia and *Myscelus p. pegasus* Mabille occurring in Venezuela, French Guiana, and Ecuador. Although we lacked males of the latter, we had enough females of both taxa to allow critical comparison, which led to the conclusion that they represent different species. We studied 5 ♀ of *M. perissodora* (1 from Mexico [holotype, USNM], 2 Costa Rica, 2 Panama) and 4 ♀ of *M. pegasus* (Venezuela). Evans (1951) saw even fewer females: 4 ♀ of the former (1 Costa Rica, 1 Panama, 2 Colombia) and 2 ♀ of the latter (1 Venezuela, 1 Ecuador).

Comparison of KOH-dissected genitalia of the holotype, 3 other ♀ of *M. perissodora,* and 2 ♀ of *M. pegasus* showed nothing but slight individual variation on a single theme. However, absence of genitalic differentiation in a group whose genitalia are generally conservative does not argue strongly for conspecificity.

What is more important here is that species of *Myscelus* are also conservative in superficial appearance and that a number of independent superficial features distinguish our females of the taxa in question. The three large, white hyaline spots (in spaces 1b, 2, and the cell) that form the innermost band on the forewing are much smaller in *M. perissodora* than they are in *M. pegasus* and, moreover, they are broadly, rather than narrowly, edged in black. With respect to the four contiguous, subapical hyaline spots on the forewing, which run from the upper part of space 5 through space 8, the spot in space 6 is half again to twice as high as those in spaces 7 and 8 in *M. perissodora,* but only slightly higher than those in spaces 7 and 8 in *M. pegasus;* the subapical spots are not as elongate in *M. perissodora* as they are in *M. pegasus;* and the spot in the top of space 5 is only a point in *M. perissodora* but a short dash in *M. pegasus.* The dark, diffuse discal band of the dorsal hindwing is offset distad at vein 4 more conspicuously in *M. pegasus* than it is in *M. perissodora.* The lobe in the outer margin of the hindwing at the end of vein 4 is a little more pronounced in *M. pegasus* than it is in *M. perissodora.* The rusty-red ground color of the wings dorsally looks slightly paler in *M. pegasus* than it does in *M. perissodora.* The dark central band in the proximal yellow area of the ventral hindwing extends to vein 7 in *M. pegasus* but limits itself to a dash in space 1c in *M. perissodora.* The dark discal band (which extends at least to vein 6 or, more often, to vein 7, with sometimes a detached spot in space 7) is separated from the dark distal half of the ventral hindwing by a strip of yellow in *M. perissodora* (except in the type where just traces of

FIGS. 20–22. Pupae of ACG pyrrhopygines. **20,** *Elbella scylla* (dry forest) 94-SRNP-192. **21,** *Parelbella macleannani* (rainforest) 99-SRNP-13309. **22,** *Mysoria ambigua* (dry forest) 85-SRNP-80.



FIGS. 23–25. Pupae of ACG pyrrhopygines. **23,** *Myscelus amystis hages* (dry forest) 93-SRNP-8387 **24, 25,** *Passova gellias* (rainforest to cloud forest) 94-SRNP-7815.

yellow remain) but is fused with the dark distal half in *M. pegasus.*

Because the caterpillar that produced our lone adult of *M. perissodora* was identified in the field by its finder as *M. belti,* the larvae of these two skippers must look about the same. The look-alike *M. perissodora* caterpillar was likewise feeding on *Guarea glabra,* the usual foodplant of *M. belti.* However, the caterpillar came from the upper Río Mena (700 m) in the intergrade between dry forest and rainforest on the north slope of Volcán Orosí. No examples of *M. belti* have been reared from there, although the habitat looks similar to that on the southeast side of the Volcán Orosí-Volcán Cacao complex where caterpillars of *M. belti* have commonly been found.

Passova gellias (Godman & Salvin)

Passova gellias (Fig. 15) is definitely known from Honduras, Costa Rica, and Panama. While its caterpillars are found in the ACG rainforest, cloud forest, and intergrades with dry forest from 400–700 m, they have not been found in the dry forest proper; and no free-flying adults have been seen or collected in the ACG.

In the wetter forests of the ACG, the caterpillars of *P. gellias* (Fig. 15) are oligophagous on mature leaves of two of the three species of *Guarea* (Meliaceae) that *Myscelus belti* eats (one of which is also eaten by *M. perissodora*); and *G. glabra* is almost always the foodplant of choice (Table 1). See the account of *M. belti* for (1) a list of some 15 other ACG rainforest species of Meliaceae that, despite repeated search, have never yielded caterpillars of *M. belti, M. perissodora,* or *P. gellias* and (2) comments on basic similarities not only in the foodplants and the caterpillars but also in certain critical morphological features of the adults of the genera *Myscelus* and *Passova.*

THE ONLY PYRRHOPYGINE THAT ENTERS THE USA

Pyrrhopyge arizonae Godman & Salvin,
reinstated status

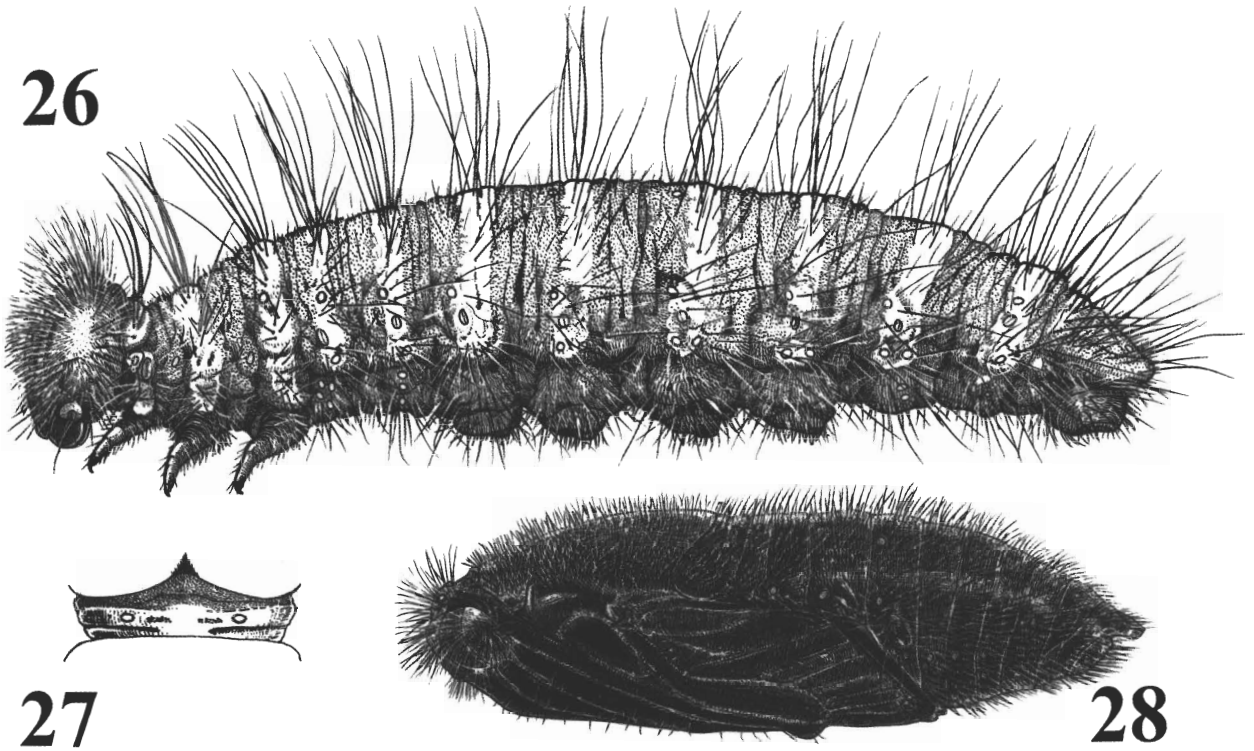
Because this taxon has been considered a northern subspecies of the Mexican *Pyrrhopyge araxes* (Hewitson), it has generally been called either *Pyrrhopyge araxes arizonae* (also, for a time, *Apyrrothrix araxes arizonae*) or—by those who have chosen to downplay subspecies—simply *P. araxes.* Godman and Salvin's (1893:253) original description of *P. arizonae* was both minimal (because this Arizonan skipper was outside the fauna that they were treating) and incidental to their account of *P. araxes* (which belonged to that fauna):

> Hewitson's description of this species [*P. araxes*] was based upon a Mexican specimen now in the British Museum. Our Mexican series of examples agrees generally with the type, though there is a considerable amount of variation as regards the definition of the markings of the underside of the secondaries. In Arizona specimens these marks are evanescent, and the dark outer border is not clearly defined on its inner edge. The difference is sufficient to constitute a distinct race. Plötz also recognized two forms, but unfortunately gave a new name, *cyrillus,* to the true *araxes,* the Arizona form being his *araxes.* To rectify this we propose to call the northern insect *Pyrrhopyge arizonae,* specimens of both sexes being in our collection, sent us by Morrison from the neighbourhood of Fort Grant [which almost certainly means from the Pinaleño Mountains].

It is worth noting that, even though they wrote "*Pyrrhopyge arizonae*," Godman and Salvin used the term "race" rather than "species" in referring to it. Apparently, they themselves saw this taxon as equivalent to a subspecies.

But *P. arizonae* and *P. araxes* are separate (albeit extremely close) species. Superficially—besides the pair of differences noted by Godman and Salvin—the brown ground color of *P. arizonae* is not nearly so dark as that of *P. araxes;* the white wing fringes of *P. arizonae* are more prominent and more heavily checkered than those of its sister; and, ventrally, the proximal yellow of the (mainly hind-) wings is not as intense, not as orangy, in *P. arizonae* as in *P. araxes.* On an average, *P. arizonae* is a little smaller than *P. araxes.*

Genitalically, in males, there are several subtle differences which are not evident when comparing published genitalia figures of *P. araxes* (Godman & Salvin 1893:pl. 73, fig. 16, Bell 1931:fig. 51, Evans 1951:fig. A.1.58) and *P. arizonae* (Skinner & Williams 1922:fig. 1, reprinted in Lindsey et al. 1931:pl. 2, fig. 1). These differences are described here in strict lateral view. Immediately anterior to the uncus, at the posterodorsolateral corners of the tegumen (where in many pyrrhopygines paired, long, caudally-projecting prongs originate), there are very short, dorsally-projecting lobes in *P. araxes* but not in *P. arizonae.* The proximal (massive) portion of the valva is longer in *P. araxes* than it is in *P. arizonae;* and its dorsal edge, as it changes (anterior to posterior) from roughly horizontal to nearly vertical, is somewhat angled in *P. araxes* but more evenly curved in *P. arizonae.* Although the dentate, distal projections of the valvae are variable (and slightly asymmetric) in both species, the ventral ones are wider in *P. araxes* than they are in *P. arizonae.* In the female genitalia of both species, the posteriormost end of the ductus bursae is closely surrounded by heavy sclerotization that forms a long, caudally-extending tube which brings the ostium bursae far back beneath the proximal ends of the ovipositor lobes. Originating from the posterior end of the sclerotized



FIGS. 26–28. Last instar and pupa of *Pyrrhopyge arizonae* (oak eater) in summer 1959; collected as larvae along the Swift Trail, 1615 m, Pinaleño Mountains, Graham County, Arizona, USA, on 5 June 1959. **26,** Larva in left lateral view. **27,** Prothoracic segment (enlarged) in dorsal view. **28,** Pupa in left lateral view.

tube (i.e., at the ostium bursae), a midventral, long, narrow, delicate, terminally-pointed prong and a middorsal, equally long, but wide (and progressively widening) projection, which, in its distal half, is middorsally divided so as to suggest a pair of terminally-blunt paddles, all extend back to the level of the distal ends of the ovipositor lobes. Compared genitalic dissections include 7 ♂ 4 ♀ of *P. arizonae* from the Chiricahua and Huachuca mountains, Cochise Co., plus Peña Blanca Lake, Santa Cruz Co., Arizona, USA, and 30 mi (48 km) N of Mante, Tamaulipas, Mexico; and 4 ♂ 3 ♀ of *P. araxes* from Mexico City, Cuernavaca, and Tizapán, Mexico.

Pyrrhopyge arizonae occurs in the southwestern USA (in the montane oak belt of southeastern Arizona, adjacent southwestern New Mexico, and also the Big Bend region of Texas) and in northern Mexico (from Sonora, Chihuahua, and Tamaulipas southward to uncertain limits). *Pyrrhopyge araxes* occurs in central and southern Mexico (at least from Jalisco through the Distrito Federal and Morelos to Veracruz, south to at least Guerrero and Oaxaca).

In southeastern Arizona (Cochise and Graham counties), Comstock (1956) collected a single caterpillar of *P. arizonae* on oak at 1860 m in Miller Canyon, Huachuca Mountains, on 27 July 1955; and Burns (1964:109, unpubl.) collected three caterpillars on *Quercus arizonica* Sarg. and another on *Quercus* sp. at 1615 m in the South Fork of Cave Creek Canyon, Chiricahua Mountains, on 22, 23, 24 April 1959, plus two, on *Q. arizonica* and *Q. emoryi* Torr., respectively, at 1615 m along the Swift Trail, Pinaleño Mountains, on 5 June 1959 (*Quercus* is in the Fagaceae). After further growth, these last two specimens posed for Figs. 26 to 28. This skipper has also been reported on *Q. oblongifolia* Torr. (Bailowitz & Brock 1991).

Although the adult of *P. arizonae* is a classic "skipper-brown"—with the "usual" hyaline spots on the forewing—and is in no way a flashy pyrrhopygine, the caterpillar (Fig. 26) ranks with the best of them. Its head is black (clypeus tan), densely clothed with (for the most part, relatively short) white hairs—paired ventrolateral patches of which are rusty-orange; and its body is a rich, deep maroon crossed by brilliant yellow bands (one per segment), with long white hairs springing mainly from the yellow bands, but also from a pale, creamy-yellow prothoracic shield. This pale shield bears a very thin, black band dorsolaterally (but not

medially) about two-thirds of the way from its anterior to its posterior margin (Fig. 25).

The pupa (Fig. 26) is dark and heavily clothed with hairs, which are mostly white, but brilliant orange-yellow on the prothorax. The wing covers, the thorax dorsally, plus the proboscis, legs, antennae, the greater part of the eyes, and a few other head plates are all a dark (purplish) black with a whitish blue-gray bloom. The thoracic spiracles, part of the eyes, the anterior head region, and the paired plates anterior to the prothorax are all a rich chestnut-brown. The abdomen looks dirty yellowish-brown, with alternating yellower and browner zones, the latter coated with blue-gray bloom. The terminal segment is mostly brown and blackish-brown, and the cremaster is brown. Although descriptions of the last instar and pupa provided by Comstock (1956) variously supplement, support, and depart from those above, both his and our pupal descriptions clearly fit the subfamily mold (Figs. 16–25).

DISCUSSION

Ecology. Twenty-two years of rearing 2192 pyrrhopygine caterpillars and collecting far fewer adults show that the ACG supports at least 15 species of pyrrhopygine hesperiids: 3 in (lowest elevation) dry forest (*Elbella scylla, Mysoria ambigua,* and *Myscelus amystis hages*); 4 in (highest elevation) cloud forest (*Pyrrhopyge creon, P. aesculapus, P. cosyra,* and *Passova gellias*); and 10 in (middle elevation) rainforest (*Pyrrhopyge zenodorus, P. crida, P. cosyra, P. erythrosticta, Parelbella macleannani, Jemadia pseudognetus, Jemadia* sp. X (an unnamed *Jemadia* belonging to a *J. hewitsonii* species complex), *Myscelus belti, M. perissodora,* and *Passova gellias*). Although caterpillars of some of these species are occasionally found in the intergrades between their "usual" ecosystem and an adjacent one, no pyrrhopygine species spans all three ecosystems; and none occurs in both dry forest and rainforest. Only two range from rainforest to cloud forest: *Pyrrhopyge cosyra,* which occurs from hot lowland rainforest to high, cold cloud forest; and *Passova gellias,* which generally goes less far up into the cloud forest.

ACG pyrrhopygines seem not to migrate seasonally between major ecosystems. Even in the dry season, sexually dormant adults of the three dry-forest species appear in local moist areas of the dry forest rather than in the adjacent rainforest. (Note that these adults do not break reproductive dormancy and oviposit on their respective foodplants when those plants—responding to, say, the clearing of right-of-ways and firebreaks—produce new, leafy, sucker shoots from fresh stumps in the middle of the dry season.)

Ecosystem-level specificity of ACG pyrrhopygines does not stem entirely from the ecology of their foodplants. On the one hand, dry-forest pyrrhopygine foodplants do not occur in rainforest and cloud forest (although congeners do). On the other hand, some wet-forest pyrrhopygine foodplants do occur in dry forest as well (along with congeners), while the pyrrhopygines that eat them do not. For example, *Vismia baccifera* and *Clusia rosea* occur in both ACG dry forest and rainforest; but *Pyrrhopyge zenodorus* and *P. cosyra,* their respective grazers, stick to the wetter forest. However, many other ACG skipper species do occur in both dry forest and rainforest. The plant families Lauraceae, Flacourtiaceae, Myrtaceae, Combretaceae, and Malpighiaceae—which are used by ecosystem-specialist pyrrhopygines—all contain species that occur in both dry forest and rainforest where they support larval pyrgines that likewise range across both ecosystems.

Costa Rica has about 25 species of pyrrhopygines, or about one-eighth of our estimated total of all pyrrhopygine species. This estimate of 200 may still be too low, but it far exceeds the number ("almost 150") offered by Ackery et al. (1999). Since we now have reared 15 species (and anticipate only one to three more), the ACG is home to at least 60% of the Costa Rican pyrrhopygine fauna. Though an ecological island, the ACG seems to offer enough habitat, with abundant foodplants, to sustain these skippers. However, substantial global warming, with a concomitant rise in the elevation of the cloud layer (e.g., Pounds et al. 1999), could seriously reduce the area of cloud-forest habitat for *Pyrrhopyge creon* and *P. aesculapus.* Moreover, the gradual return of large areas of ACG secondary successional forest to old-growth forest over the coming centuries will substantially reduce the sizes and ubiquity of populations of important rainforest foodplants such as *Vismia baccifera* and dry-forest foodplants such as *Byrsonima crassifolia* and *Casearia corymbosa.*

Pyrrhopygine caterpillars, like those of other ACG skippers that feed on broadleaf plants, are concentrated primarily in the zone between 10 cm and 3 m above the ground, even when individuals of their foodplants rise as much as 20–40 m. Although further inventory exploration of the ACG canopy may turn up exceptions, they are not yet evident. While adult skippers can be seen visiting flowers in the crowns of the tallest trees, they do not seem to be ovipositing at these heights.

Foodplants. ACG pyrrhopygine larvae have exclusive tastes. The caterpillars of *Myscelus belti, M. perissodora,* and *Passova gellias* are the only ones that share

their foodplants with other pyrrhopygines—in these cases, each other (Table 1). The caterpillars of *Elbella scylla, Parelbella macleannani,* and *Jemadia pseudognetus* are the only ones that share their foodplants with non-pyrrhopygine hesperiid larvae.

The strong host specificity shown by pyrrhopygine caterpillars is frequent among ACG butterflies and certain families of moths (e.g., host records in Janzen & Hallwachs 2001), and especially among dicot-eating skippers. Even though the foodplant records for our pyrrhopygines (Table 1) are dotted across the botanical taxonomic landscape (i.e., in the families Lauraceae, Clusiaceae, Flacourtiaceae, Cunoniaceae, Myrtaceae, Combretaceae, Meliaceae, Malpighiaceae, and Araliaceae), some patterns emerge. *Myscelus amystis hages, M. belti, M. perissodora,* and *Passova gellias,* which (aside from their adult color patterns) are similar, all focus on Meliaceae—mainly *Guarea glabra.* Several species currently in the large genus *Pyrrhopyge* (*P. zenodorus, P. crida, P. cosyra,* and *P. erythrosticta*) are monophagous to oligophagous on members of the Clusiaceae. A female of another Costa Rican species of *Pyrrhopyge, P. haemon* Godman & Salvin, was found and reared (in 1995 at 1600 m in Tapantí National Park by R. Delgado) on a clusiaceous plant in the genus *Vismia,* species of which are the foodplants of *P. zenodorus* and *P. crida.*

In this connection, it is also clear that ACG pyrrhopygine caterpillars are specialists at levels far below that of the plant family. For each species of caterpillar, there are many ACG species of plants within the plant family fed upon that are not used. It is particularly striking, for example, that *Pyrrhopyge zenodorus* eats the common *Vismia baccifera* (occurring from dry forest to rainforest) and the rare *V. ferruginea,* while *P. crida* eats neither, restricting its diet to the low density and local rainforest *V. billbergiana.*

Within an oligophagous species, percentages of caterpillar records among its small set of foodplants (Table 1) do not reflect the relative abundances of those plants. For example, *Mysoria ambigua* uses *Casearia corymbosa* most of the time, even though its other three foodplants are common in the same dry-forest habitats.

More or less close relatives of half of the pyrrhopygine species that we have reared in the ACG were reared previously in Pará, Brazil, by Moss (1949). The plants he found them eating are usually in the same genera as the foodplants of their Costa Rican counterparts, and are always in the same families. Not surprisingly, the strong host specificity shown by ACG pyrrhopygine caterpillars seems to be geographically conservative.

In also rearing a few pyrrhopygines most of which were well removed from the species we have reared, Moss (1949) recorded foodplants in some other families: Annonaceae, Myristicaceae, Sterculiaceae, and Sapindaceae (although he questioned the accuracy of the identification of the last). In revising both *Elbella* and its near relatives (most of whose diets remain unknown), Mielke (1995) added one foodplant genus (*Quiina* and *Miconia*) from each of the families Quiinaceae and Melastomataceae. While the total taxonomic spread of pyrrhopygine foodplant families becomes a little wider, there is also a little clustering. The Annonaceae may relate to the Myristicaceae; the Quiinaceae, to the Clusiaceae; and the Melastomataceae, to the Combretaceae or Myrtaceae (Heywood 1993).

The only pyrrhopygine to enter the USA, *Pyrrhopyge arizonae,* puts another isolated genus and family (*Quercus,* Fagaceae) on the list of disparate foodplants.

Biogeography. To judge from current distributions, the Pyrrhopyginae (a strictly New World group) probably arose in tropical South America. Most of the existing species are there. Nearly half of the ACG pyrrhopygines we have reared (*Pyrrhopyge zenodorus, Elbella scylla, Parelbella macleannani, Jemadia pseudognetus, Jemadia* sp. X, *Mysoria ambigua,* and *Myscelus amystis hages*) appear to be northern extensions of species complexes that are better represented and more widely distributed in South America. Four more (*Pyrrhopyge crida, P. aesculapus, P. cosyra,* and *Myscelus perissodora*) are species with significant South American ranges (usually Colombia and Ecuador) as well as Middle American ones. Only four (*Pyrrhopyge creon, P. erythrosticta, Myscelus belti,* and *Passova gellias*) seem to be confined to Middle America. There are no pyrrhopygines in the West Indies.

Parasitoids. ACG pyrrhopygines are notably free of parasitoids. Despite their slow larval growth rates (among the longest within the ACG hesperiids), pyrrhopygines are at the low end of the spread of larval parasitization frequencies—and not just among skippers but among ACG macrolepidoptera generally. Only 7.1% of the total wild-caught pyrrhopygine caterpillars were parasitized. Ten of the 15 species reared from wild-caught caterpillars produced no parasitoids whatsoever, even when samples were large (Table 1). It is especially noteworthy that none of our many caterpillars (n = 295) belonging to the closely related genera *Myscelus* and *Passova* has yielded parasitoids (Table 1).

Ichneumonids have been reared only from *Pyrrhopyge cosyra* caterpillars. However, *Casinaria* sp. 9, which frequently attacks *P. cosyra* (31 records),

also attacks the pyrgines *Phocides nigrescens* (2 records) as well as *Achlyodes thraso* (Hübner) (1 record), *A. selva* Evans (2 records), and *A. busirus heros* (6 records) in the same habitat (but has not yet been found to attack tens of other hesperiid species in this habitat). To date, the ichneumonid genus "MCAM" sp. 1 (10 records) has been found parasitizing only *Pyrrhopyge cosyra.* Only *Elbella scylla* is attacked by a braconid with enough frequency to suggest that the relationship might be host-specific. Parasitization by tachinid flies is light, and only four of the 15 species reared from wild-caught caterpillars had any at all. Whether the slow growth rate of pyrrhopygine caterpillars is evolutionarily "permitted" by the low parasitization frequency, or the low parasitization frequency stems from traits of the caterpillars, will be the subject of family-wide analysis at a later time.

Taxonomy. It is hardly surprising that most of the parasitoids attacking ACG pyrrhopygines are undescribed whereas their large and ostentatious hosts are not. Nevertheless, when it came to identifying these Costa Rican skipper butterflies (which led to examining them in a much broader geographic and taxonomic context), fully half of them posed biological questions. The recurring one involved the status of an ACG entity vis-à-vis its nearest relative: Are those perceptible (but closely similar) differentiates species or subspecies? In general, taxa that Evans (1951) treated as subspecies are here granted species rank. Other biological problems bearing on accurate application of names involved (1) something currently passing as a single species that actually comprises a pair of sympatric species, (2) the reverse of this—a supposed pair of sympatric species that actually are one and the same thing, and (3) an entity that belongs to an essentially South American species complex not previously recorded from Costa Rica. Pyrrhopygines are a flashy tip of a taxonomic iceberg. If some of *their* identities were this uncertain, what about those of all the rest of the ACG skipper butterflies (which reflect the world's uniquely rich neotropical hesperiid fauna)? And then, by extension, what about the placement of all the rest of ACG invertebrate biodiversity? Taxonomists and time are of the essence.

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LITERATURE CITED

ACKERY, P. R., R. DE JONG & R. I. VANE-WRIGHT. 1999. The butterflies: Hedyloidea, Hesperioidea and Papilionoidea, pp. 263–300. *In* Kristensen, N. P. (ed.), Handbook of zoology. Vol. IV. Arthropoda: Insecta, part 35, Lepidoptera, moths and butterflies. Vol. 1. Evolution, systematics, and biogeography. Walter de Gruyter, Berlin & New York.

AUSTIN, G. T. & O. H. H. MIELKE. 2000. Hesperiidae of Rondônia, Brazil: *Cephise* Evans (Pyrginae), with descriptions of new species from Mexico and Brazil. Revta bras. Zool. 17:757–788.

BAILOWITZ, R. A. & J. P. BROCK. 1991. Butterflies of southeastern Arizona. Sonoran Arthropod Studies, Inc., Tucson, Arizona. ix + 342 pp.

BELL, E. L. 1931. Studies in the Pyrrhopyginae, with descriptions of several new species (Lepidoptera, Rhopalocera, Hesperiidae). J. New York Entomol. Soc. 39:417–491.

———. 1933. Studies in the Pyrrhopyginae, with descriptions of new species (Lepidoptera, Rhopalocera, Hesperiidae). J. New York Entomol. Soc. 41:265–295, 481–529.

———. 1934. New American Hesperiidae (Lepidoptera, Rhopalocera). Bull. Brooklyn Entomol. Soc. 29:89–96.

BURNS, J. M. 1964. Evolution in skipper butterflies of the genus *Erynnis.* Univ. Calif. Publ. Entomol. 37:1–217.

———. 1996. Genitalia and the proper genus: *Codatractus* gets *mysie* and *uvydixa*— a compact *cyda* group—as well as a *hyster*ectomy, while *Cephise* gets part of *Polythrix* (Hesperiidae: Pyrginae). J. Lepid. Soc. 50:173–216.

BURNS, J. M. & D. H. JANZEN. [2000] "1999." *Drephalys:* Division of this showy neotropical genus, plus a new species and the immatures and food plants of two species from Costa Rican dry forest (Hesperiidae: Pyrginae). J. Lepid. Soc. 53:77–89.

COMSTOCK, J. A. 1956. Notes on the life histories of two southern Arizona butterflies. Bull. South. Calif. Acad. Sci. 55:171–179.

EVANS, W. H. 1949. A catalogue of the Hesperiidae from Europe, Asia and Australia in the British Museum (Natural History). British Museum, London. xix + 502 pp., 53 pls.

———. 1951. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part I. Introduction and Group A, Pyrrhopyginae. British Museum, London. 92 pp., pls. 1–9.

FREEMAN, H. A. 1966. New Hesperiidae records for Mexico. J. Lepid. Soc. 20:226–228.

———. 1977. Six new species of Hesperiidae from Mexico. J. Lepid. Soc. 31:89–99.

GODMAN, F. D. & O. SALVIN. 1879. Descriptions of new species of Rhopalocera from Central and South America. Proc. Zool. Soc. London 1879(1):150–155, pl. 14.

———. 1879–1901. Biologia Centrali-Americana; Insecta; Lepidoptera-Rhopalocera. Vol. 2, 782 pp. Vol. 3, 113 pls.

HAYWARD, K. J. 1948. Genera et species animalium argentinorum. Vol. 1. Insecta., Lepidoptera, Hesperiidae, Pyrrhopyginae and

Pyrginae. Guillermo Kraft Ltda., Buenos Aries. 389 pp., 27 pls.
HEYWOOD, V. H. 1993. Flowering plants of the world. Oxford Univ. Press, New York. 336 pp.
HOFFMANN, C. C. 1941. Catalogo sistematico y zoogeografico de los Lepidopteros Mexicanos. Segunda parte. Hesperioidea. An. Inst. Biol. Mex. 12:237–294.
JANZEN, D. H. 1988a. Guanacaste National Park: Tropical ecological and biocultural restoration, pp. 143–192. *In* Cairns, J. J. (ed.), Rehabilitating damaged ecosystems. Vol. II. CRC Press, Boca Raton, Florida.
———. 1988b. Ecological characterization of a Costa Rican dry forest caterpillar fauna. Biotropica 20:120–135.
———. 1993. Caterpillar seasonality in a Costa Rican dry forest, pp. 448–477. *In* Stamp, N. E. & T. M. Casey (eds.), Caterpillars. Ecological and evolutionary constraints on foraging. Chapman & Hall, New York, New York.
———. In press. Ecology of dry forest wildland insects in the Area de Conservación Guanacaste, northwestern Costa Rica. *In* Frankie, G. W., A. Mata & S. B. Vinson (eds.), Biodiversity conservation in Costa Rica: learning the lessons in seasonal dry forest. Univ. Calif. Press, Berkeley.
JANZEN, D. H. & W. HALLWACHS. 2001. Event-based database of caterpillars, their host plants, and their parasitoids in the Area de Conservación Guanacaste, northwestern Costa Rica. (http://janzen.sas.upenn.edu).
LINDSEY, A. W., E. L. BELL & R. C. WILLIAMS JR. 1931. The Hesperioidea of North America. Denison Univ. Bull., J. Sci. Lab. 26:1–142.
MAYR, E. 1942. Systematics and the origin of species. Columbia Univ. Press, New York, New York. xiv + 334 pp.
MIELKE, O. H. H. 1995. Revisão de *Elbella* Evans e gêneros afins (Lepidoptera, Hesperiidae, Pyrrhopyginae). Revta. bras. Zool. 11:395–586.
MOSS, A. M. 1949. Biological notes on some "Hesperiidae" of Para and the Amazon (Lep. Rhop.). Acta Zool. Lilloana 7:27–79, pls. I–V.
NICOLAY, S. S. & G. B. SMALL JR. 1969. A new subspecies of *Pyrrhopyge creon* (Hesperiidae) from Panama. J. Lepid. Soc. 23:127–130.
———. 1981. Illustrations and descriptions of some species of *Pyrrhopyginae* from Costa Rica, Panama and Colombia (Hesperiidae). J. Res. Lepid. 19:230–239.
POUNDS, J. A., M. P. L. FOGDEN & J. H. CAMPBELL. 1999. Biological response to climate change on a tropical mountain. Nature 398:611–615.
SKINNER, H. & R. C. WILLIAMS JR. 1922. On the male genitalia of the larger Hesperiidae of North America. Trans. Am. Entomol. Soc. 48:109–127.

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