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Host-specificity and Hyperparasitoids of Three New Costa Rican Species of *Microplitis* Foerster (Hymenoptera: Braconidae: Microgastrinae), Parasitoids of Sphingid Caterpillars

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Abstract.—Three new species of parasitoid wasps (Braconidae: Microgastrinae) from Costa Rica are described: ***Microplitis espinachi* Walker, n. sp.**; ***Microplitis figueresi* Walker, n. sp.** and ***Microplitis marini* Whitfield, n. sp.** Two parasitoids of Sphingidae are redescribed for comparison with the three new species: *Microplitis ceratomiae* Riley and ***Microplitis chacoensis* (Cameron) (=*Microplitis ayerzai* Brethes, New Synonymy)**. The ichneumonid wasp ***Acrolyta stroudi* Gauld, n. sp.,** and the chalcidid wasp ***Conura convergea* Delvare, n. sp.** are also described; both are hyperparasitoids of prepupae in newly spun cocoons of *M. espinachi* and *M. figueresi.* The mesochorine ichneumonid hyperparasitoid *Mesoschorus angustistigmatus* Dasch, a hyperparasitoid of *M. espinachi* and *M. espinachi* larvae while still inside the caterpillar, is redescribed. The seasonal biology and host specificity of the *Microplitis* and associated hyperparasitoids is discussed in the context of the extensive caterpillar and parasitoid inventory data for the Area de Conservación Guanacaste (ACG) in northwestern Costa Rica. *M. espinachi* is a dry forest parasitoid of *Agrius cingulata, Sphinx merops* and nine species of *Manduca* (all Sphingidae), all when in the most open and insolated habitats and on a variety of host plants; it does not search for other common species of *Manduca* or other Sphingidae in slightly shadier microhabitats a few meters away. The extremely similar *M. figueresi* parasitizes *Erinnyis ello* and *Erinnyis crameri* (Sphingidae) in slightly shadier older woody succession (only a few meters from the microhabitat occupied by *M. espinachi*), and conspicuously does not parasitize *Erinnyis oenotris* or the tens of other species of sphingid caterpillars in the same habitat. *M. figueresi* finds *E. ello* on seven different species of food plants, and *E. crameri* on two others (but does not parasitize *E. crameri* on an insolated third). Neither species of *Microplitis* extends from the ACG dry forest into the contiguous cloud forest or rain forest, even though their host caterpillars do. While *E. ello* is a common pest in commercial cassava plantations, *M. figueresi* does not appear to have followed this host into this highly insolated habitat. Both species are highly univoltine and pass the last two thirds of the rainy season and six-month dry season in an extremely tough silk cocoon in the litter. In the ACG, *M. marini* is a parasitoid of only *Xylophanes tersa* in very insolated low herbaceous vegetation in mid-elevation rainforest and lower elevation cloud forest, and does not parasitize at least 15 other species of *Xylophanes* in the adjacent forest understory.

The Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica contains 110,000 ha of dry forest and associated wetter ecosystems that are being restored, developed and conserved for their ecosystem services and biodiversity (Janzen 1988a, 1988b, 1993, 1998a, 1998b, 1999a, 1999b, 2000a, 2000b, 2001a, 2001b;

⟨http://www.acguanacaste.ac.cr⟩, ⟨http://janzen.sas.upenn.edu/caterpillars/RR/rincon_rainforest.htm⟩). As part of the biodiversity development of these wildlands, the ACG is conducting, in collaboration with the taxonomic community, a thorough inventory of its biodiversity so as to set up that biodiversity for nondamaging use (e.g., Janzen 1996a, 1996b). Such inventory encounters many undescribed species, and simultaneously reveals a sketchy outline of their natural history and the ecological patterns to which they contribute (e.g., Dangerfield et al. 1996, Gauld and Janzen 1994, Sharkey and Janzen 1995, Woodley and Janzen 1995, Miller et al. 1997, Janzen and Gauld 1997, Janzen et al. 1998, Zitani et al. 1998, Burns and Janzen 1999, Burns and Janzen 2001, Schauff and Janzen 2001, Lachance et al. 2001). Inventory also connects the newly encountered species with other better-known species, thereby allowing increased inferential understanding of all of their natural histories, just as does cladistics.

One of the foci of the ACG biodiversity inventory has been dry forest macrolepidoptera caterpillars (Janzen 1985, 1988a, 1993) and their parasitoids (e.g., Gauld and Janzen 1994, Gauld et al. 1992, Dangerfield et al. 1996, Sharkey and Janzen 1995, Woodley and Janzen 1995, Janzen and Gauld 1997, Janzen et al. 1998, Zitani et al. 1998, Schauff and Janzen 2001, Burns and Janzen 2001; ⟨http://janzen.sas.upenn.edu⟩). Caterpillars of Sphingidae (Janzen 1984, 1986) have been frequently encountered in the inventory process, and then reared in captivity to obtain their parasitoids. In this paper we describe three new species of microgastrine braconid wasp parasitoids, and their ichneumonid and chalcidid hyperparasitoid wasps, that parasitize the ACG dry forest sphingid caterpillars (Figs. 1–5, 8), and compare them with *Microplitis ceratomiae*, a well-known North American sphingid parasitoid (Fig. 6), and with *M. chacoensis* (Fig. 7), a widespread but poorly known South American species with similar biology. We also use natural history information from the ACG inventory to begin to elucidate how these parasitoids interact with their hosts.

NATURAL HISTORY AND METHODS OVERVIEW

The ACG dry forest, lying on the coastal plain and plateaus between the Pacific Ocean and the Cordillera Guanacaste 20–40 km to the east (Janzen 2002a, 2002b, Burns and Janzen 2001), contains about 78 species of Sphingidae that annually have one or more generations during the 6-month rainy season (mid-May to December; Janzen 1993). More than 14,000 caterpillars of all but five of these species have been located in the wild and reared in various numbers (Janzen and Hallwachs 2002). Among these reared caterpillars are four common species of *Erinnyis* (*Erinnyis ello, Erinnyis alope, Erinnyis crameri, Erinnyis oenotrus*), two rare species of *Erinnyis* (*Erinnyis obscura, Erinnyis lassauxi*), eight common species of *Manduca* (*Manduca rustica, Manduca florestan, Manduca lefeburii, Manduca barnesi, Manduca lanuginosa, Manduca dilucida, Manduca muscosa, Manduca occulta*), and two rare species of *Manduca* (*Manduca sexta, Manduca hannibal*). Several of these species, and a few other Sphingidae (*Sphinx merops, Agrius cingulata*) are frequently parasitized by two species (described below) of very host-specific small braconid wasps in the cosmopolitan genus *Microplitis* (Table 1). Another rare sphingid caterpillar, *Xylophanes tersa,* is attacked by a third closely related species of *Microplitis* (also described below) at the mid-elevation interface of dry forest with cloud forest. All three of these *Microplitis* are closely related to *Microplitis ceratomiae,* a widely distributed North American sphingid parasitoid, and to *M. chacoensis* (Cameron), a similarly widespread South American

Table 1. Intensity of attack by *Microplitis figueresi* and *Microplitis espinachi* for 5,853 wild-caught caterpillars of the 19 species for which at least one attack has been recorded in the dry forested Sector Santa Rosa of the Area de Conservación Guanacaste. Neither species of *Microplitis* attcked another 8,159 wild-caught sphingid caterpillars of 54 other species in the same habitat. Another 70,000-plus wild-caught caterpillars of more than 1,650 species in the same habitat did not yield either species of *Microplitis* (source: Janzen and Hallwachs 2002).

Braconid species	Sphingid species	Number reared	Percent attacked by *Microplitis*	% Identified to species
Microplitis figueresi	*Erinnyis crameri* (Schaus)	501	23	74
	Erinnyis ello (Linnaeus)	481	26	76
	Erinnyis lassauxii (Boisduval)	11	9 (n=1)	100
	Xylophanes turbata (Edwards)	1120	0.09 (n=1)	100
Microplitis espinachi	*Agrius cingulata* (Fabricius)	70	9	100
	Cocytius duponchel (Poey)	164	1.3 (n=3)	100
	Erinnyis ello (Linnaeus)	481	1.2 (n=6)	100
	Manduca barnesi (Clark)	87	1.1 (n=1)	100
	Manduca corallina (Druce)	75	8	100
	Manduca dilucida (Edwards)	654	0.7 (n=3)	100
	Manduca florestan (Stoll)	395	2.5	100
	Manduca hannibal (Cramer)	3	100 (n=3)	100
	Manduca lanuginosa (Edwards)	847	0.1 (n=1)	86
	Manduca lefeburii (Guer.-Men.)	143	30	100
	Manduca muscosa (Roth. & Jord.)	74	11	81
	Manduca occulta (Roth & Jord.)	96	10	100
	Manduca rustica (Fabricius)	219	15	100
	Manduca sexta (Linnaeus)	49	2 (n=1)	100
	Perigonia ilus Boisduval	370	1.6 (n=6)	100
	Sphinx merops Boisduval	13	15 (n=2)	100

species that also parasitizes sphingids. The braconids that parasitize *Erinnyis* and *Manduca* in the ACG dry forest are in turn hyperparasitized by a species of *Conura* (Chalcididae, described below) and two species each of *Acrolyta* and *Mesochorus* (Ichneumonidae). These caterpillars are also parasitized by a small fauna of other wasps and parasitic flies (Tachinidae), but they are not treated extensively here.

Microplitis parasitoids of *Manduca* and *Erinnyis* caterpillars in the ACG dry forest are usually first noticed when a full-sized last instar sphingid caterpillar "hangs up" on a branch in its rearing container or on a twig among the foliage of its food plants in the wild. On the following morning (after daybreak) the wasp larvae are encountered wiggling their way through multiple holes they have made in the back of the caterpillar (Fig. 1). The holes close rather than lead to caterpillar blood loss and the caterpillar body remains turgid, physiologically alive (but motionless unless poked, when it violently turns toward the contact) and clinging tightly to the substrate. The caterpillar usually dies and falls from the substrate 1–2 days after the *Microplitis* larvae have emerged.

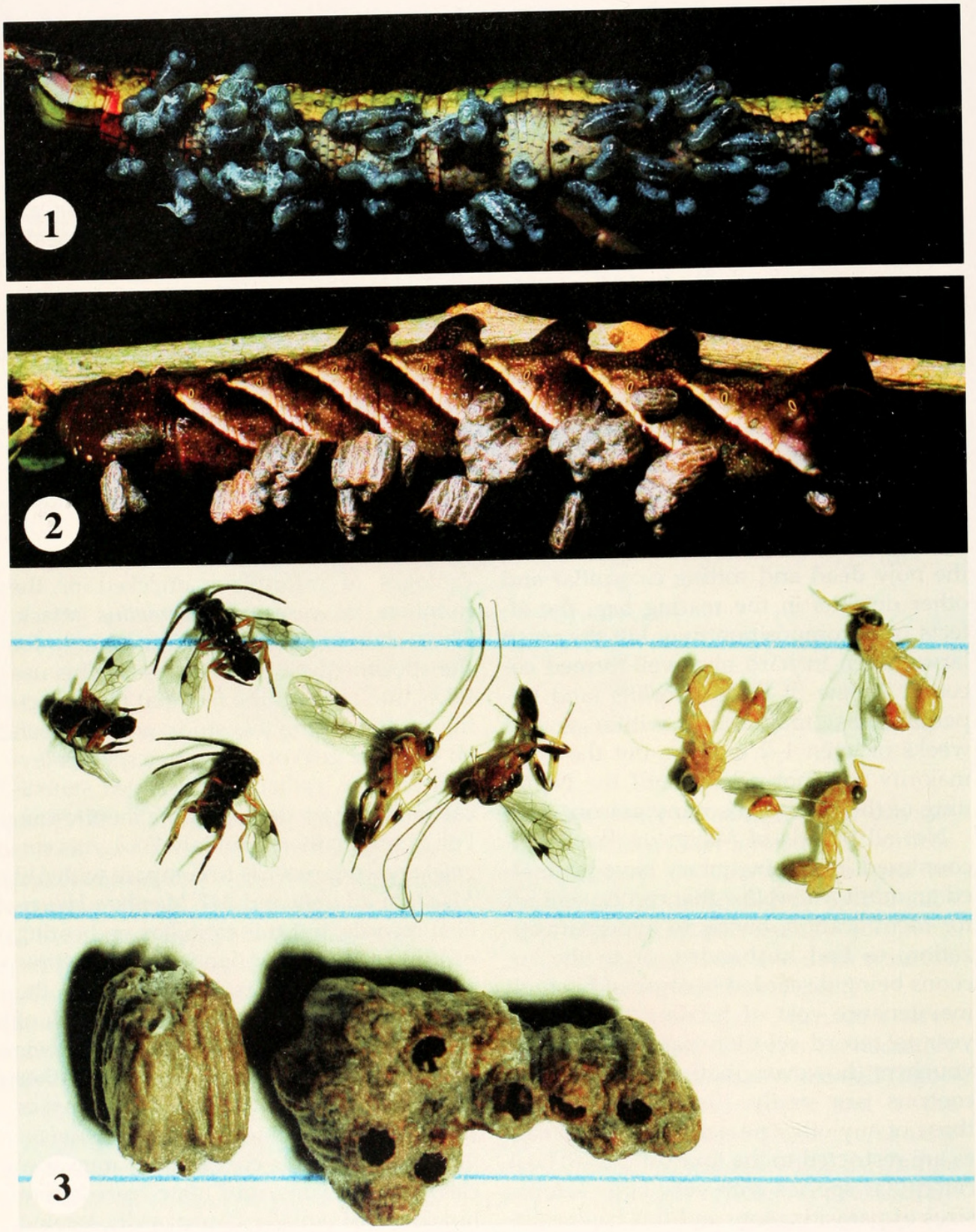
Each newly emerged *Microplitis* larva from *Manduca* and *Erinnyis* immediately begins to spin its cocoon while still (lightly) attached by its posterior end to the back of the caterpillar. There are usually many tens of larvae spinning in clumps over their emergence holes, approximately erect at right angles to the caterpillar cuticle, with the result that any given cocoon is lightly to firmly attached to several other adjacent cocoons by the coincident sticking and drying of their silk glue (Fig. 2). A single larva can, however, spin a normal cocoon without the presence of other larvae, especially if it is still attached to

the caterpillar. On the other hand, the other species of *Microplitis* described here emerge in patches and thus very tightly side-by-side, to form a very distinctive dense solid block of cocoons tightly glued to the caterpillar cuticle, with their long axis at right angles to the caterpillar cuticle (Figs. 4–7).

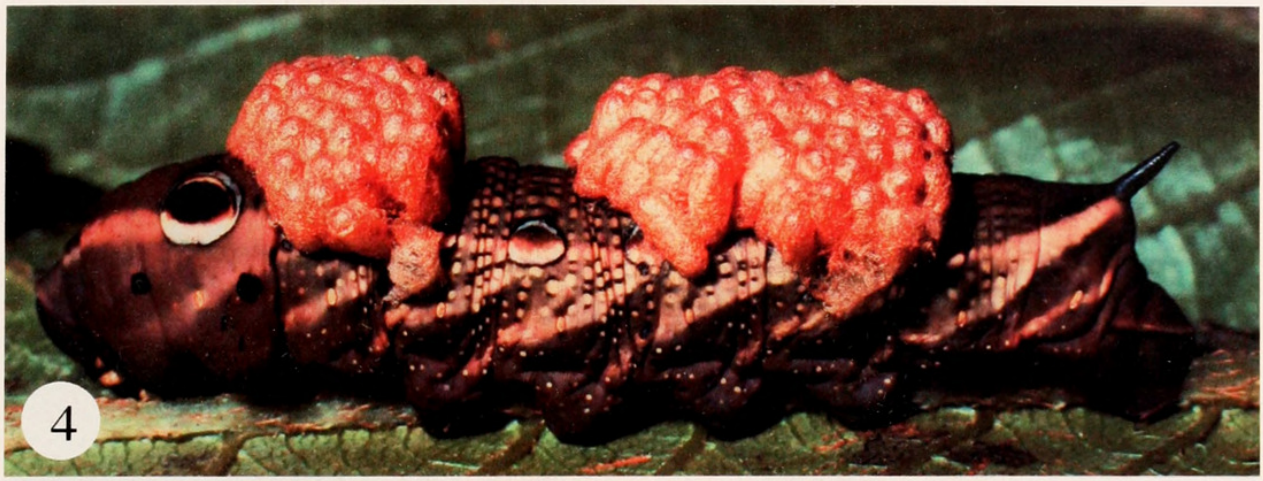
If the caterpillar with its newly emerged wasp larvae is not perturbed during the day of emergence, essentially all of the larvae successfully spin cocoons. In nature, the hard cocoons are incorporated into the litter as the caterpillar decomposes. When rearing in the laboratory, once the cocoons are hard it is best to gently pull them off the back of the caterpillar and put them in a clean dry bottle with their voucher label, and set them aside for eclosion. If left with the now dead and rotting caterpillar and other detritus in the rearing bag, the effects of decomposition may kill the wasp larvae even in hard and well-formed cocoons. A few of the *Microplitis* (and hyperparasites) may eclose within several weeks or even 1–2 months, but the great majority will not eclose until the beginning of the next year's rainy season.

Not all broods of *Microplitis* larvae encountered in this inventory have generated an adult *Microplitis* that can be sent off for identification, owing to hyperparasitization, to bad husbandry, or to the cocoons being discarded because of the high maintenance cost of holding them for a year to record eclosion dates and obtain vouchers (however, their very distinctive cocoons are easily distinguished from those of any other parasites). All such cases are restricted to the four (of the 18) host caterpillar species with very large sample sizes of parasitization, and this has resulted in only 76% to 86% of the wasps being identifiable to species (Table 1). However, in these four cases there is no basis to suspect or assume that those *Microplitis* that did not survive to adults were of any other species than their conspecifics in the same species of host caterpillars, though this remains a remote possibility in the case of the *Microplitis* in *Erinnyis ello* since in 5% of the cases they were indeed *M. espinachi* instead of the usual *M. figueresi* (Table 1). The same ecological conclusions are reached whether just the species-vouchered percent parasitizations are used, or whether those only generically identified are assumed to be the same species as their congenerics reared from the same species of caterpillar. All records of *Microplitis marini* discussed here are based on adults identified by J. B. Whitfield (though its very distinctive cocoons and high host specificity probably render this unnecessary), and all hyperparasite records discussed are based on adults identified by I. D. Gauld or G. Delvare.

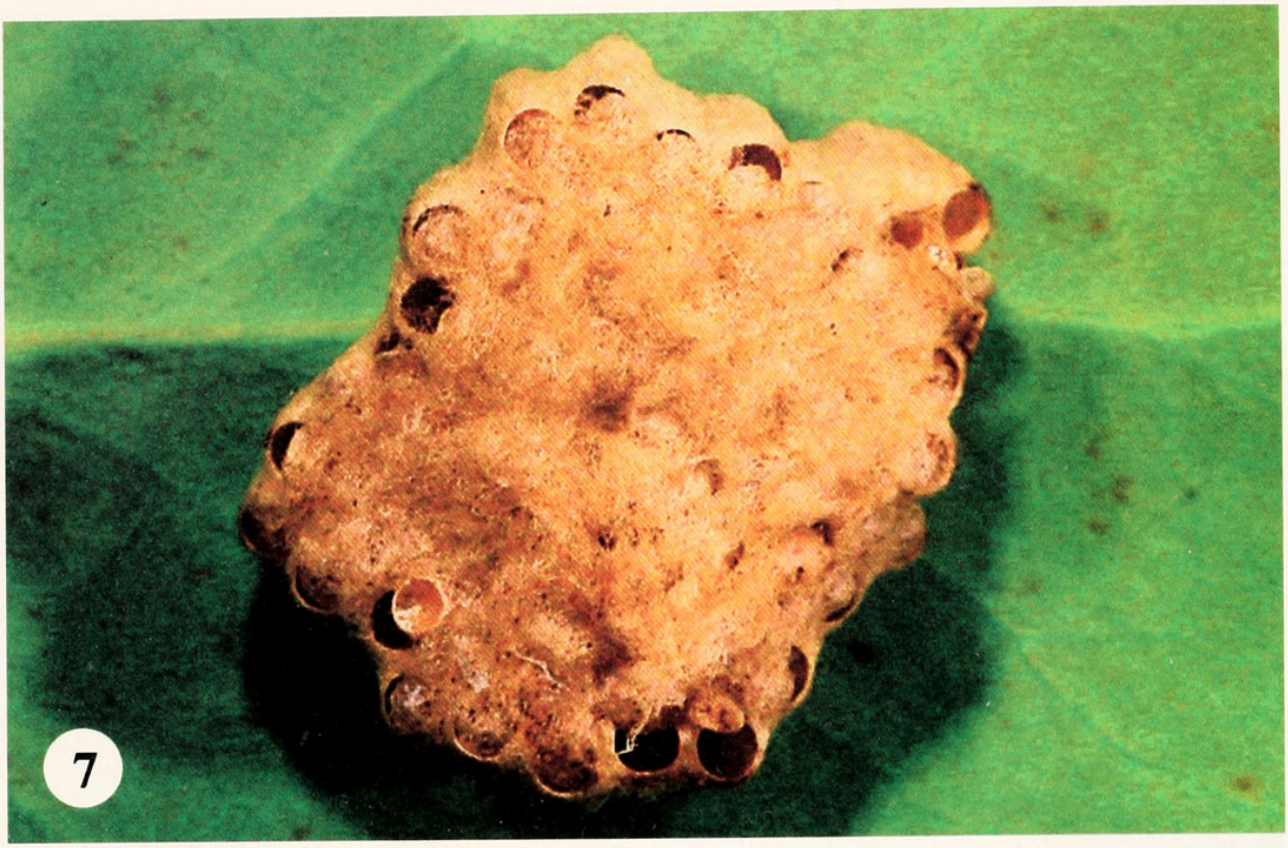
In this paper we make use of the percentages of caterpillars attacked or the numbers of cases of *Microplitis* attack. These data are meant to be used only for the specific questions addressed. This use takes into account the fact that the collecting underpinning this study was conducted with the goal of qualitative species-level inventory, rather than planned statistical sampling or demographic monitoring. For example, there are only 70 *Agrius cingulata* rearing records to compare with 613 *Manduca dilucida* and 847 *Manduca lanuginosa* records, but this ratio has no bearing on the relative abundance of these three species of caterpillars in the wild in the ACG dry forest habitat (but says much of the relative ease of finding them on their respective food plants). On the other hand, the fact that only one *Microplitis* was reared from the hundreds of *Manduca lanuginosa* caterpillars captured on nine species of host plants, and none reared from hundreds of equally haphazardly located *Erinnyis oenotrus* caterpillars on one species of host plant, does allow the robust conclusion that these two species of sphingids are not successfully used by *Microplitis* even though many of their congeners living only a few meters away are often attacked by *Microplitis*.

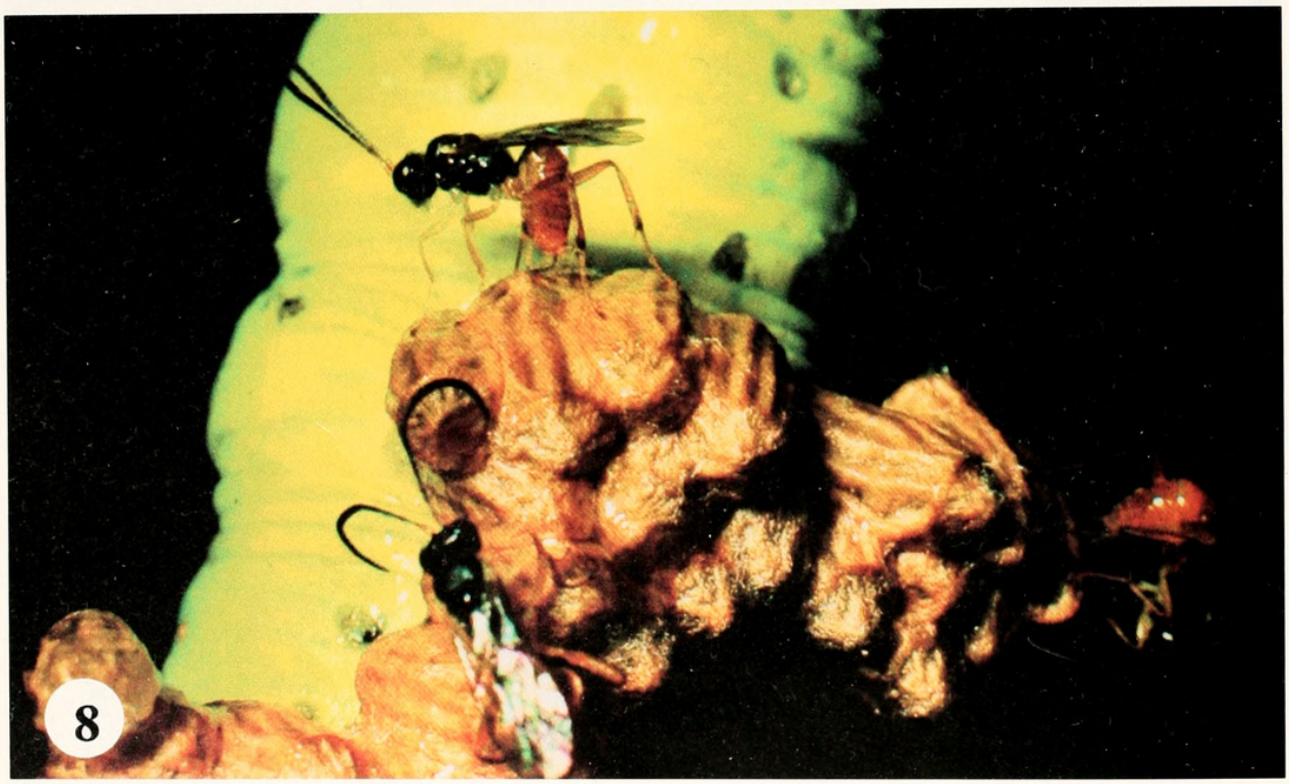


Figs. 1–3. 1, Last instar larva of *Erinnyis ello* with newly emerged prepupal *Microplitis figueresi* larvae, just beginning to spin (84-SRNP-683). 2, Last instar larva of *Manduca occulta* with newly spun cocoons of *Microplitis espinachi* still attached to its back (93-SRNP-1906). 3, *Microplitis espinachi* (upper left), *Mesochorus microstigmatus* (upper center), *Conura convergea* (upper right), and cocoons (lower center) with *Microplitis espinachi* exit holes from *Manduca lefeburiii* (92-SRNP-2496).



Figs. 4–6. 4, *Microplitis marini* hard and tough cocoons firmly stuck to the back of a last instar *Xylophanes tersa* (97-SRNP-1395). 5, *Microplitis marini* cocoons spun on back of *Xylophanes falco* on *Bouvardia glabra,* Box Canyon, Arizona (photo courtesy Jim Tuttle). 6, *Microplitis ceratomiae* cocoons on back of undetermined sphingid larva, Sierra Co., nr. Sierraville, California (photo by David Wagner and Jim Whitfield).





Figs. 7–8. 7, *Microplitis chacoensis* (Cameron) emerged cocoon mass from *Manduca* sp., Villa de Cura, Venezuela (photo by J. Whitfield). 8, *Acrolyta stroudi* ovipositing in cocoons of *Microplitis espinachi* (93-SRNP-2227).

A second methodological complexity is that if a wild-caught caterpillar is brought into captivity and reared in a plastic bag (see methods at http://janzen.sas.upenn.edu), it is protected from further oviposition (or other kinds of attack) by parasitoids and hyperparasitoids. This means that "percent attack" figures for laboratory-reared wild-caught caterpillars will always be lower, and variably lower depending on the caterpillar age at time of capture, than is the case in nature. The major exception to this statement is the case where a caterpillar is captured after the instar in which parasite oviposition occurs but before the stage at which the parasite emerges or ecloses. Our collection methods preclude the discovery of parasitoids that attack sphingid pupae or *Microplitis* cocoons directly rather than ovipisiting into sphingid larvae.

Rearing *Microplitis* (but not its hyperparasites) requires a minimum of a year, since many of the species discussed here pass many months of the rainy and dry seasons as dormant prepupae or pupae. In nature, they are tied to eclosion dates by both internal physiological processes and externally received cues. ACG inventory rearing is done in plastic bags and glass bottles in open-air rearing barns (http://janzen.sas.upenn.edu) but these air temperatures only approximate those in nature, since the temperatures to which the cocoons are subject in nature are also determined by evaporative cooling and heat retention by moist litter. The result is that eclosion dates in captivity are indicators but do not precisely mirror the phenology of free-living siblings.

SPECIES DESCRIPTIONS

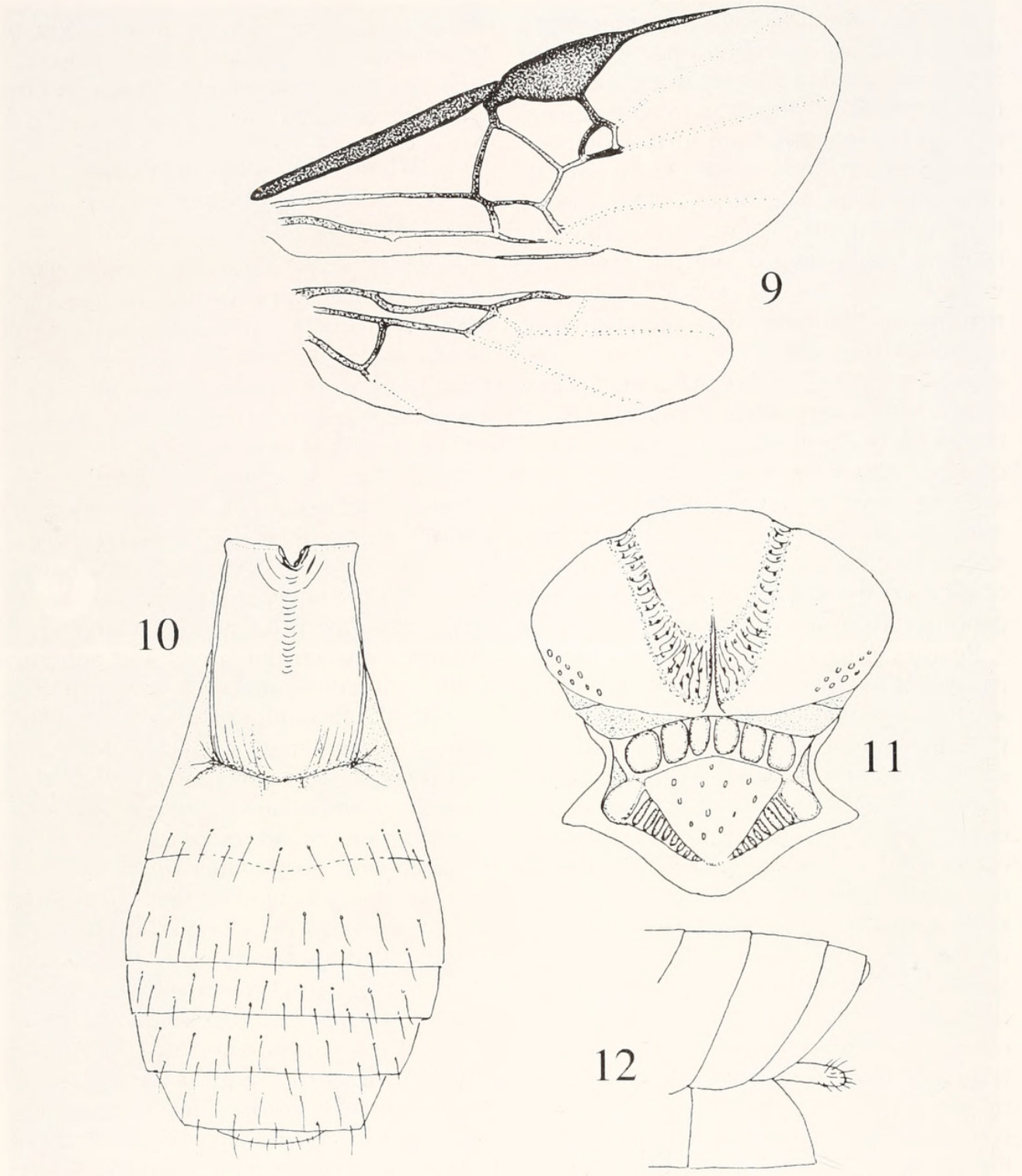
BRACONIDAE

The Microgastrinae is one of the largest subfamilies of Braconidae, with an estimated world fauna of 5,000–10,000 species. Mason (1981) presents the first keys to the currently defined genera from which *Microplitis* can be distinguished; Whitfield (1997) provides a fully illustrated key to the New World genera of Microgastrinae including *Microplitis*.

Microplitis espinachi Walker, new species

(Figs. 2–3, 9–12, 17, 21, 22)

Female.—Color: General body color black except: pedicel and scape brown, legs variable but usually light brown to yellow; hind femora and tibia infuscate on apical third; tarsi dark brown; fore wing veins almost all pigmented; tergite I of metasoma and tergite II medially sometimes dark brown. *Head:* Face rugose punctate; labrum prominent with an apical shelf which forms a lip, the mandibles forming a margin to this labral lobe; eyes hairy; frons shiny and faintly punctate; ocelli large, their diameter about equal to the distance between the lateral and anterior ocellus. Antennae almost as long as body; basal half of flagellum thick, apical half tapering toward apex. *Mesosoma:* Mesonotum (Figs. 11, 17) shiny, finely punctate, rugose on anterolateral margins; notaulices complete, broad and rugose anteriorly; coalescing posteromedially into a rugose area which is often also foveolate, this area divided by a longitudinal carina. Scutellum shiny, faintly punctate. Metanotum with large setose anterolateral lobes (Fig. 19). Propodeum rugose, divided by a prominent median longitudinal carina (Fig. 19). *Metasoma:* Tergite I parallel sided on anterior two thirds, shiny with a shallow depression medially; posterior third raised, faintly punctate laterally, shiny medially and constricted where it joins tergite II. Median field of tergite II faintly indicated by two ill-defined depressions anteromedially, when visible they are directed towards the posterolateral margins; a posterolateral irregular row of hairs present, sometimes formed into two rows. Remaining tergites shiny with scattered hairs. Hypopygium large. Ovipositor sheaths short and just visible beyond the



Figs. 9–12. *Microplitis espinachi* Walker, n. sp. 9, wings. 10, Metasoma in dorsal view. 11, Mesoscutum and scutellum in dorsal view. 12, Apex of female metasoma, lateral view showing hypopygium and ovipositor sheaths.

hypopygium in most dead specimens. Ovipositor (Fig. 21) bearing 4 teeth distally, second valvulae constricted medially. Hind tibia with a few scattered spines on outer margin. Hind tarsi laterally compressed, basal tarsomere the longest, as long as the total length of the following three segments, tibial spurs subequal, less than half the length of the basal tarsal segment. *Wings:* Fore wing (Figs. 9, 22) with stigmal vein R1 thick and about 1.5 times the length of the distance between the

apex of R1 and spurious vein 3Rs. Areolet sometime variable in shape but usually 1Rs is curved and longer than 2Rs which is shorter than r-m and distally angled at their junction, r-m less pigmented and subequal with 2M, 2rs+m often faintly pigmented and subequal with 2M.

Male.—Similar to female except antennal segments longer.

Cocoon.—Figs. 2, 3. Brownish, ribbed, spun in small groups on the back of the host caterpillar.

Material examined.—**Holotype female:** Costa Rica, Guanacaste Pr., Guanacaste Conserv. Area. D.H. Janzen, Voucher Specimen Database, rearing voucher 93-SRNP-1895, host *Manduca occulta* feeding on *Cestrum glanduliferum.* Deposited in U. S. National Museum, Washington, D.C. **Paratypes:** 761 females and 562 males have been deposited in INBio, U. S. National Museum, Washington, The Natural History Museum, London, and Canadian National Collection, Ottawa. REARED SPECIMENS: 7m, 83-SRNP-726; 3f & 7m, 84-SRNP-660.1; 2m, 84-SRNP-931; 2f & 2m, 84-SRNP-1127; 4f & 1m, 84-SRNP-813; 6f & 4m, 86-SRNP-232; 1m, 86-SRNP-321; 1f & 1m, 86-SRNP-330; 1f & 5m, 87-SRNP-529; 6f & 9m, 87-SRNP-556; 12f & 17m; 87-SRNP-557; 22f & 25m, 87-SRNP-558; 19f & 9m, 87-SRNP-559; 16f & 2m, 87-SRNP-566; 46f & 16m, 87-SRNP-573; 7f & 1m, 87-SRNP-677; 1f & 37m, 87-SRNP-582; 5f & 2m, 89-SRNP-489; 8f & 2m, 89-SRNP-575; 1f & 1m, 89-SRNP-617; 1f & 1m, 90-SRNP-771; 1f & 1m, 90-SRNP-1129; 20f & 3m, 91-SRNP-799a; 1f, 91-SRNP-799b; 12f & 19m, 91-SRNP-899; 1f & 2m, 91-SRNP-936; 13f & 1m, 91-SRNP-1007a; 6f & 1m, 91-SRNP-1007b; 2m, 91-SRNP-1007c; 1m, 91-SRNP-1141; 7m, 91-SRNP-1242; 6f & 3m, 91-SRNP-1271a; 12f & 1m, 91-SRNP 1271b; 1f & 1m, 91-SRNP 1273a; 2f, 91-SRNP-1273b; 8f & 1m, 91-SRNP-1273c; 1f & 1m, 91-SRNP-1275a; 6m, 91-SRNP-1275b; 1f & 3m, 91-SRNP-1275c; 7m, 91-SRNP-1275d; 3f & 2m, 91-SRNP-1409; 12f & 14m, 91-SRNP-1706; 5m, 91-SRNP-1848; 10f & 3m, 91-SRNP-1969; 30f & 14m, 92-SRNP-1604; 4f & 4m, 92-SRNP-1607; 29f & 26m, 92-SRNP-2135; 11f & 11m, 92-SRNP-2156; 12f & 3m, 92-SRNP-2333; 3f & 8m, 92-SRNP-2515; 14f & 19m, 92-SRNP-2516; 7f & 7m, 92-SRNP-2518; 5f & 3m, 92-SRNP-2519; 18f & 9m, 92-SRNP-2668; 17f & 3m, 92-SRNP-2699; 21f & 7m, 92-SRNP-2712; 5f & 15m, 92-SRNP-2726; 14f & 4m, 92-SRNP-2740; 11f & 6m, 92-SRNP-2773; 7f & 6m, 92-SRNP-3382; 20f & 38m, 92-SRNP-3414; 14f & 4m, 93-SRNP-1644; 12f & 9m, 93-SRNP-1808; 3f, 93-SRNP-1820; 3f & 1m, 93-SRNP-1891; 12f & 15m, 93-SRNP-1893a; 1f, 93-SRNP-1893b; 5f & 15m, 93-SRNP-1894; 22f & 9m, 93-SRNP-1895; 32f & 9m, 93-SRNP-1896; 10f & 19m, 93-SRNP-1897; 38f & 22m, 93-SRNP-1906; 21f & 1m, 93-SRNP-1939; 17f & 8m, 93-SRNP-1989; 15f & 4m, 93-SRNP-2185; 6f & 1m, 93-SRNP-2228; 5f & 1m, 93-SRNP-2229; 23f & 12m, 93-SRNP-2332; 2f & 3m, 93-SRNP-2445; 15f & 11m, 93-SRNP-2450.

Etymology.—This species is named after Carlos Espinach in recognition of his nine years of tireless efforts to locate major economic resources for the conservation of Costa Rican wildland biodiversity, his long struggle to facilitate former President Jose Maria Figueres Olsen to be elected, and his support of the Area de Conservacion Guanacaste's efforts to incorporate a portion of Finca Pasmompa.

Comments.—This species corresponds to "*Microplitis* n. sp. 1" in the phylogenetic study by Whitfield et al. (2002). Under that name, DNA sequence data for the 16S, COI and 28S genes have been deposited in GenBank with accession numbers AY044197, AY044211 and AY044222, respectively.

Microplitis figueresi Walker, new species

(Figs. 1, 13–16, 18, 20, 23–25)

Similar to *M. espinachi* except: face smoother, narrower between the eyes, shorter distance from antennal sockets to clypeus; mesoscutum with ill-defined no-

taulices (Fig. 18), smooth posteromedially but with a faint longitudinal ridge often present; ovipositor (Fig. 20) bearing only three teeth distally, second valvulae distal to the medial constriction, broader and shorter; fore wing with areolet of different shape (Figs. 23–25) more variable than *M. espinachi* but usually with r-m slightly shorter than 2M; median field of tergite II usually with lateral margins present which are almost parallel sided and directed towards the posterior margin.

Material examined.—**Holotype female:** Costa Rica, Guanacaste Pr., Guanacaste Conserv. Area. D.H. Janzen, Voucher Specimen Database, rearing voucher 92-SRNP-1643, host *Erinnyis ello* feeding on *Sebastiana pavoniana.* Deposited in U. S. National Museum, Washington, D.C. **Paratypes:** 209 females and 175 males have been have been deposited in INBio, U. S. National Museum, Washington, The Natural History Museum, London, and Canadian National Collection, Ottawa. REARED SPECIMENS: 1f & 1m, 84-SRNP-248; 1f & 1m, 84-SRNP-255; 1f & 1m, 84-SRNP-257; 2f, 84-SRNP-292; 1f & 1m, 84-SRNP-344; 71f & 34m, 84-SRNP-687; 1f & 1m, 86-SRNP-62.1; 1f & 1m, 86-SRNP-119.1; 33f & 13m, 88-SRNP-116; 9f & 3m, 88-SRNP-160; 2f, 90-SRNP-160; 1f & 2m, 90-SRNP-166; 10f & 18m, 90-SRNP-170; 2m, 90-SRNP-214; 1f & 1m, 91-SRNP-572; 2f & 1m, 91-SRNP-70; 1f & 6m, 91-SRNP-813a; 1f, 91-SRNP-813b; 3m, 91-SRNP-813c; 4f & 2m, 91-SRNP-900a; 1f & 1m, 91-SRNP-900b; 3f, 91-SRNP-901a; 1f & 1m, 91-SRNP-901b; 1f, 91-SRNP-911; 3f, 92-SRNP-1520; 10f & 11m, 92-SRNP-1522; 14f & 38m, 92-SRNP-1643; 3f & 7m, 92-SRNP-2127; 16f & 11m, 92-SRNP-2155; 2f & 5m, 92-SRNP-2256; 6f & 8m, 93-SRNP-1645; 5f & 1m, 93-SRNP-1834; 1f & 1m, 93-SRNP-1837.

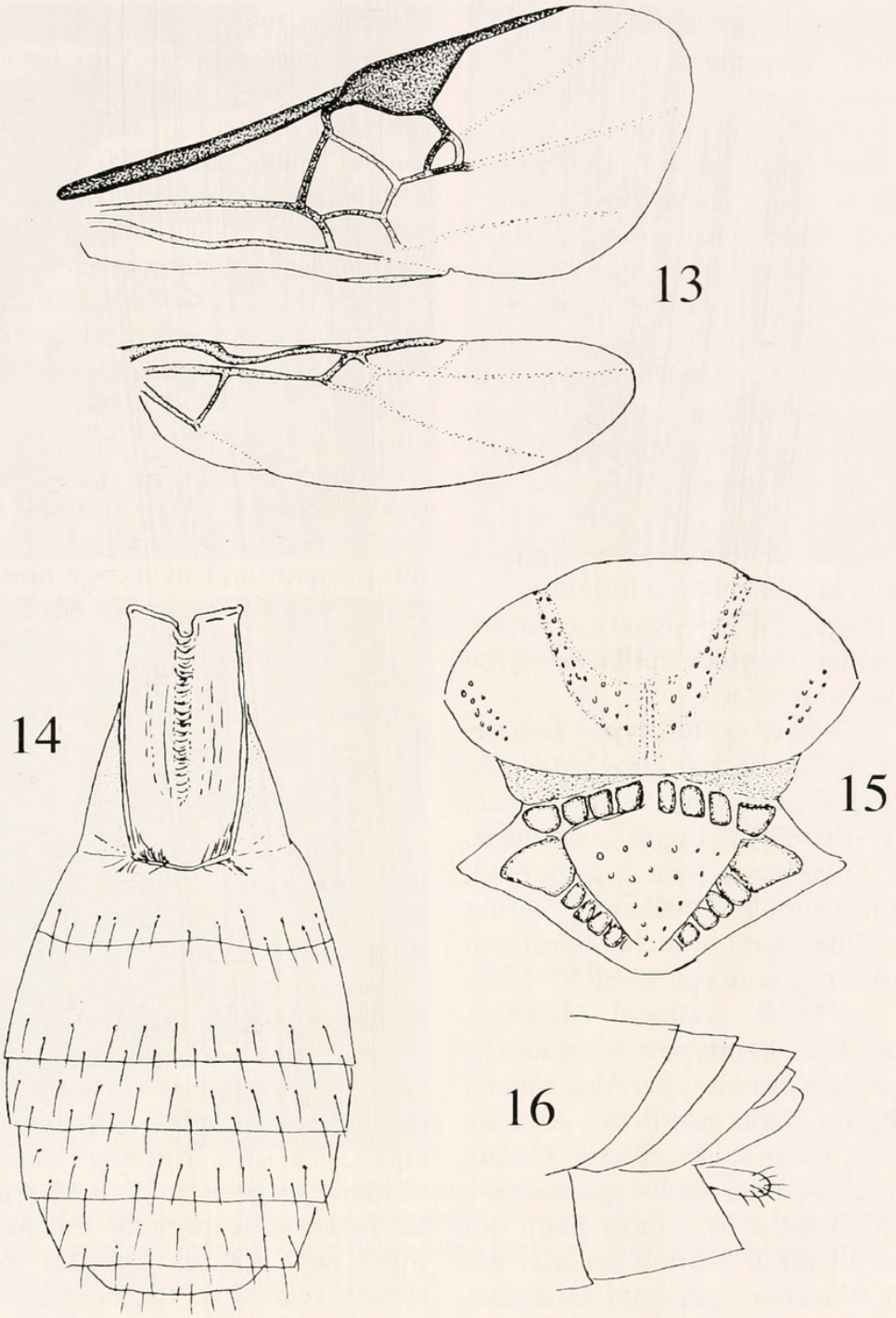
Etymology.—This species is named after former President Jose Maria Figueres Olsen in recognition of his enormous contribution to the survival of wild biodiversity in Costa Rica and his concern for the improvement of the quality of life for the custodians of that biodiversity. It is especially apt that this species is a potential biological control agent of *Erinnyis ello,* the cassava hornworm, since former President Figueres served as Costa Rica's Minister of Agriculture and Ranching before he became president.

Comments.—This species corresponds to "*Microplitis* n. sp. 2" in the phylogenetic study by Whitfield et al. (2002). Under that name, DNA sequence data for the 16S, COI and 28S genes have been deposited in GenBank with accession numbers AY044198, AY044212 and AY044223, respectively.

Microplitis marini Whitfield, new species

(Figs. 5, 28–31)

Female.—Body length 3.5 mm. Fore wing length 3.6 mm. *Color:* General body color black, except lighter brown/yellowish labial and maxillary palps, all femora and tibiae, fore and mid tarsi, hind basitarsi, and lateral semimembranous margins of first metasomal tergum. Wings hyaline to faintly smoky, veins including stigma generally pigmented dark brown, with (RS + M)b and 1m-cu paler. *Head:* Face relatively flat and wider than tall, slightly bulging medially, coarsely punctate to punctulorugose. Vertex with posterior ocelli at posterior edge of weak smoother depression that includes medial ocellus. All ocelli distinctly farther apart from each other than their own diameters. Antennae evenly thick, slightly longer than entire body length. *Mesosoma:* Mesonotum (Fig. 30) coarsely punctate with smoother regions laterally and anteromedially; notaulices complete, foveolate and merging posteriorly into a broad foveolate area nearly bisected by hint of obsolescent medial carina. Scutellum with sparse punctures, separated from mesoscutum by scrobe with four large pits. Metanotum with broad anterolateral setose lobes. Propodeum strongly and evenly rugose, di-



Figs. 13–16. *Microplitis figueresi* Walker, n. sp. 13, Wings. 14, Metasoma in dorsal view. 15, Mesoscutum and scutellum in dorsal view. 16, Apex of female metasoma, lateral view showing hypopygium and ovipositor sheaths.

vided by prominent medial longitudinal carina. *Metasoma:* Tergite I (Fig. 29) relatively parallel-sided up to broadly rounded apex, just slightly less than twice as long as broad, sparsely puncate along anterolateral margins and laterally on rounded apex, with distinct but shallow longitudinal medial groove over anterior 0.6–0.7. Median field of tergite II not obviously indicated except at extreme anterolateral corners. Tergite II and remaining terga with usually 2 irregular rows of setae posteriorly. Hypopygium relatively short but not distinctly truncate apically

(Fig. 31). Ovipositor sheaths short, blunt, apically hairy, projecting only to about end of hypopygium. *Legs:* Hind tibiae slightly thickened, with scattered thicker spines on outer faces. Hind basitarsus approximately as long as next two tarsomeres combined. Hind tibial spurs subequal in length, outer one slightly thicker. *Wings:* Fore wing (Fig. 28) R1 extending about 1.5 times as far beyond stigma as distance from its distal tip to end of 3RS fold. Stigma evenly dark brown, without basal lighter spot. Areolet large and quadrangular, angle between 3RSa and r-m sharp and distinct.

Male.—Similar to female except antennal segments longer relative to body.

Cocoon (Figs. 5, 6).—Rusty-colored, tough, cemented together in blocks on the back of host caterpillar.

Material examined.—**Holotype female:** COSTA RICA: Guanacaste Prov., Area de Conservacion Guanacaste, Sector Cacao, Arenales, 19-VI-1997, Benigno Guadamuz, reared ex *Xylophanes tersa* (Linnaeus), (host plant not known but all other rearing records are Rubiaceae), Voucher Specimen Database, rearing voucher 97-SRNP-1395. Deposited in U. S. National Museum, Washington, D.C. **Paratypes:** 5 females, 2 males, same data as holotype. Also 1 male, COSTA RICA: Guanacaste Prov., Area de Conservacion Guanacaste, Sector Cacao, Est. Cacao, 18-VI-1995, coll. "gusaneros", reared ex *Xylophanes tersa* (host plant not known but all other rearing records are Rubiaceae), Voucher Specimen Database, rearing voucher 95-SRNP-847. Deposited in INBio, U. S. National Museum, Washington, The Natural History Museum, London and Canadian National Collection, Ottawa. **Other material:** COSTA RICA: Malaise trapped, wild caught specimens from Universidad de Costa Rica and INBio.: 1f Fca. Cafrosa. Est. Las Mellizas, P.N. Amistad, 1300m. Prov. Punt. COSTA RICA. M. Ramirez. Mar 1991. L-S-316100, 596100; 3f, Costa Rica: Puntarenas, San Vito, Estac. Biol. Las Alturas, 1500m, ii.1992, Paul Hanson; 1f, Costa Rica: Puntarenas, San Vito, Estac. Biol. Las Alturas, 1500m, i.1992, Paul Hanson. ARIZONA: Pima Co., Box Canyon, 14 females, 1 male, 1-IX-2000, J. P. Tuttle, host fifth instar larva of *Xylophanes falco* on *Bouvardia glabra* Polak., emerged 9-IX-2000.

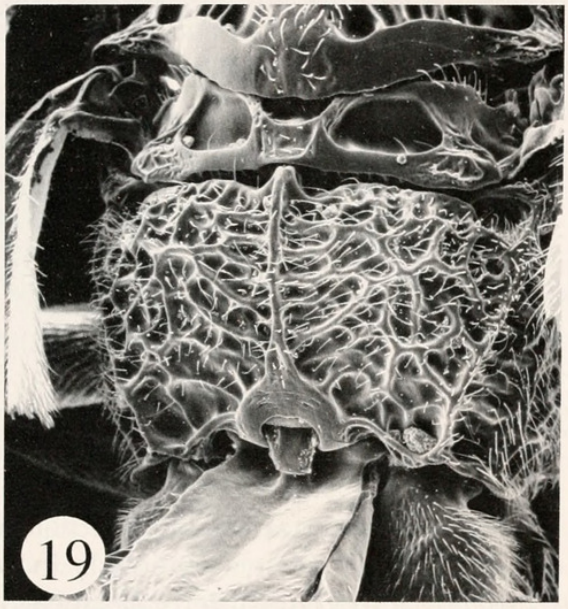
Etymology.—This species is dedicated to Sr. Sigifredo Marín Zuñiga, the former Director of the Area de Conservación Guanacaste (ACG), in recognition of three decades of dedicated service to the ideals and process of the Costa Rican Servicio de Parques Nacionales, in recognition of the guidance of the ACG through rough waters by him and his family from 1987 to the present, and in recognition of his explicit efforts to conserve the medium-elevation tropical habitats in which this species occurs.

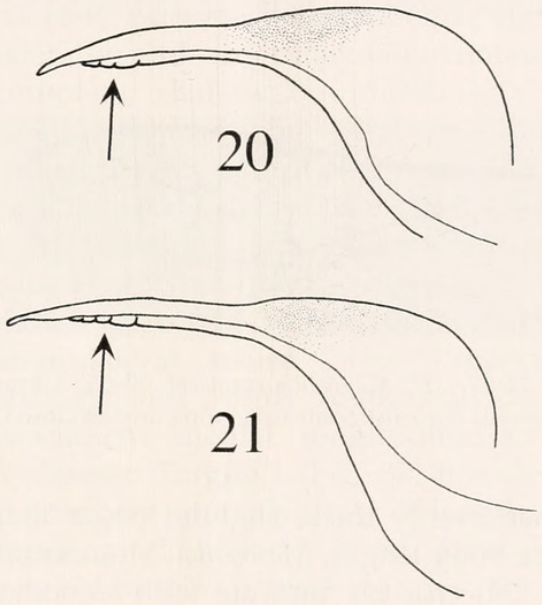
Comments.—This species corresponds to "*Microplitis* n. sp, 3" in the phylogenetic study by Whitfield et al. (2002). Under that name, DNA sequence data for the 16S, COI and 28S genes have been deposited in GenBank with accession numbers AY044199, AY044213 and AY044224, respectively.

The *M. marini* records from Arizona, while appearing geographically disjunct, are from the same subgroup of the host genus—*Xylophanes*—which occurs throughout the regions between Arizona and Costa Rica. Although clearly similar in many respects to both *M. espinachi* and *M. figueresi,* (especially the former), this third new species appears to be most closely related to the nearctic species *M. ceratomiae* Riley and the South American species *M. chacoensis* (Cameron) (see comparisons below). Additionally, the three species spin very similar cocoon masses on the backs of their host caterpillars (see Figs. 4–7). Brief redescriptions of both related species are provided below for comparison.

Microplitis ceratomiae Riley
(Figs. 6, 32–35)

Microplitis ceratomiae Riley, 1881. Type, U.S. National Museum, examined.

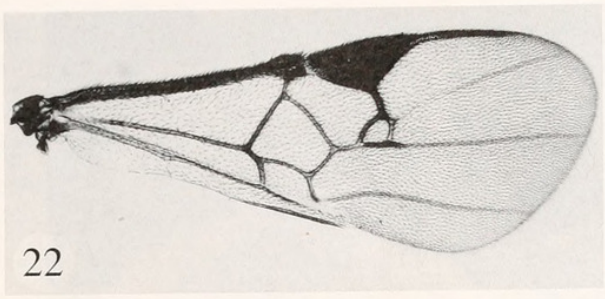


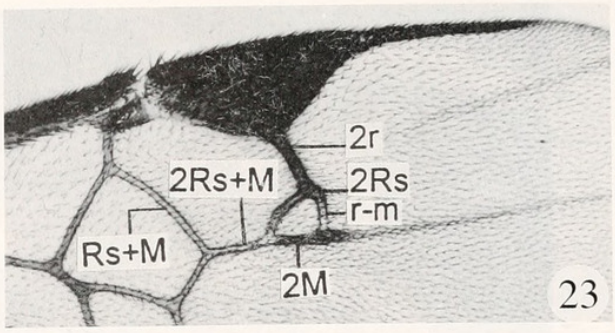


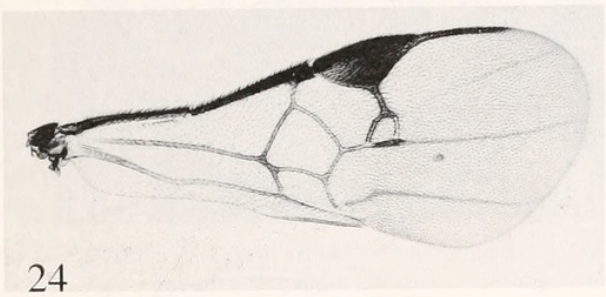
Figs. 17–21. 17, *Microplitis espinachi* mesonotum illustrating complete notaulices. 18, *Microplitis figueresi* mesonotum illustrating ill-defined notaulices. 19, *Microplitis espinachi* thorax illustrating large setose anterolateral lobes on the metanotum and the propodeum divided by a prominent median logitudinal carina. 20, *Microplitis figueresi* ovipositor. 21, *Microplitis espinachi* ovipositor.

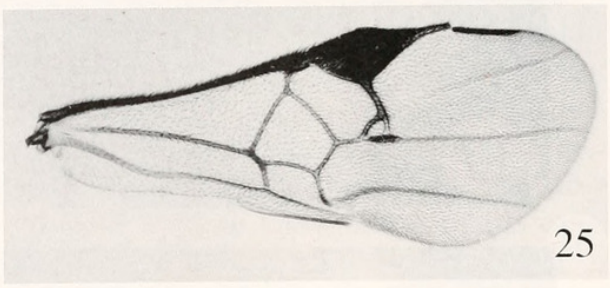
Microplitis waldeni Viereck, 1917. Type Connecticut Agricultural Experiment Station, examined. Synonymized by Muesebeck (1922).

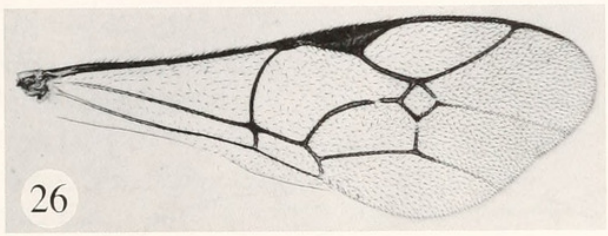
Female.—Body length 3.1–3.6 mm. Fore wing length 3.2–3.6 mm. *Color:* General body color black, except lighter brown/yellowish labial and maxillary palps, scapes and pedicels, all femora and tibiae, fore and mid tarsi, hind proximal portion of basitarsi, and lateral semi-membranous margins of first metasomal tergum. Wings hyaline to very faintly smoky, veins including stigma generally pigmented dark brown, with (RS + M)b, 1m-cu and portions of areolet veins paler. *Head:* Face relatively flat and wider than tall but slightly bulging medially, coarsely punctate to punctulorugose. Vertex with posterior ocelli at the posterior edge of weak faint depression that includes medial ocellus. Posterior ocelli slightly farther from anterior ocellus than their own diameters. An-

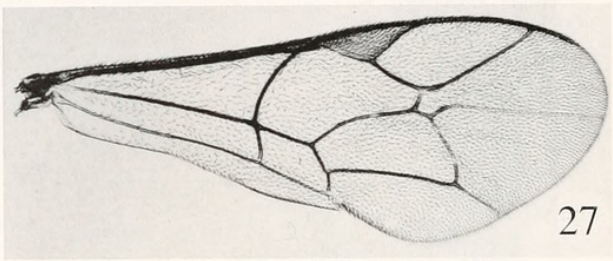












Figs. 22–27. 22, *Microplitis espinachi*. 23–25, *Microplitis figueresi*, showing variation in shape of areolet. 26, *Mesochorus angustistigmatus*, showing areolet closed distally. 27, *Acrlyta stroudi*, showing areolet open distally.

tennae evenly thick, slightly longer than entire body length. *Mesosoma:* Mesonotum (Fig. 34) coarsely puncate with smoother regions laterally and anteromedially; notaulices complete, foveolate and merging posteriorly into broad foveolate area bisected posteriorly by distinct medial carina. Scutellum with sparse punctures, separated from mesoscutum by scrobe with 6–8 large pits. Metanotum with broad anterolateral setose lobes. Propodeum strongly and evenly rugose, divided by prominent medial longitudinal carina. *Metasoma:* Tergite I (Fig. 33) broadening posteriorly up to broadly rounded apex, with bulging lateral margins, just slightly less than 1.33 as long as broad, distinctly puncate near posterolateral margins, with distinct but shallow longitudinal medial groove over anterior 0.4–0.5. Median field of tergite II not always obviously indicated except at extreme anterolateral corners, but if so, this field is suggested by two weak subparallel grooves that would indicate a narrow median field. Tergite II and remaining terga with usually 2 irregular rows of setate posteriorly. Hypopygium relatively long, not especially truncate apically (Fig. 35). Ovipositor sheaths short, blunt, apically hairy, projecting only to near end of hypopygium or often less. *Legs:* Hind tibiae slightly thickened, with scattered thicker spines on outer faces. Hind basitarsus slightly longer than next two tarsomeres combined. Hind tibial spurs subequal in length, outer one slightly thicker. *Wings:* Fore wing (Fig. 32) R1 extending about halfway from stigma to

end of 3RS fold. Stigma evenly dark brown, without basal lighter spot. Areolet large, subtriangular to weakly quadrangular, angle between (usually very short) 3RSa and r-m obtuse, often indistinct.

Male.—Similar to female except antennal segments longer.

Cocoon.—(Fig. 6). Orange-brown to somewhat pinkish brown, tough and stiff and usually closely glued together into clusters on the back of the host corpse as in *M. marini* (and in *M. chacoensis* below).

Material examined.—We have examined material from Arkansas, Missouri, Texas, California, Oregon, and Michigan, reared from *Ceratomia amyntor* (Geyer), *Paonias myops, Sphinx kalmiae, Sphinx canadensis,* and deposited in the Illinois Natural History Survey and the U. S. National Museum. Marsh (1979) also lists *Manduca sexta* (L.) and other species of *Sphinx* as hosts, but we have not been able to confirm these first-hand.

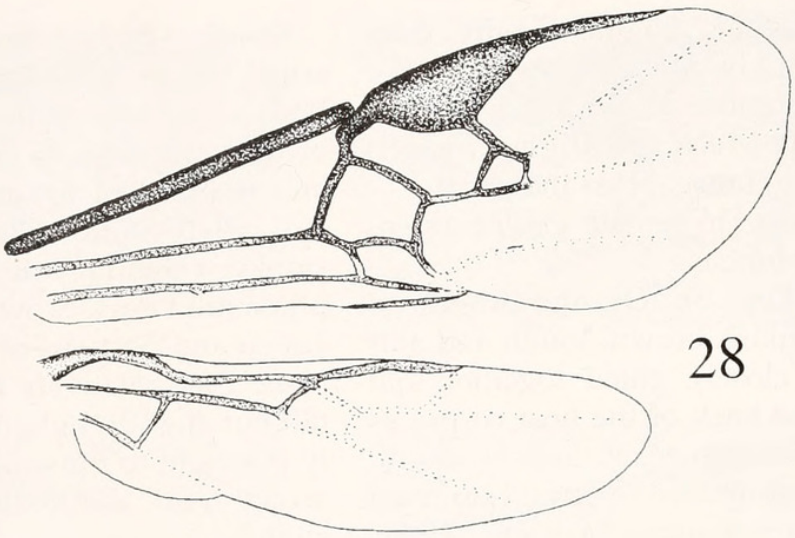
Comments.—This species has the broadest first metasomal tergite in this species complex, and should be easily distinguishable on that basis, in addition to the apparent geographical disjunction to the north of the other species referred to here. In other respects, this species strongly resembles the South American species *M. chacoensis* as well as the new species *M. espinachi* and *M. marini.* It is not yet known how far south the distribution of *M. ceratomiae* extends; the New World fauna is currently being revised by JBW. From the variation in cocoon types reported for this species, it appears at least possible that *M. ceratomiae* could itself ultimately prove to be a complex of morphologically similar but biologically distinct species.

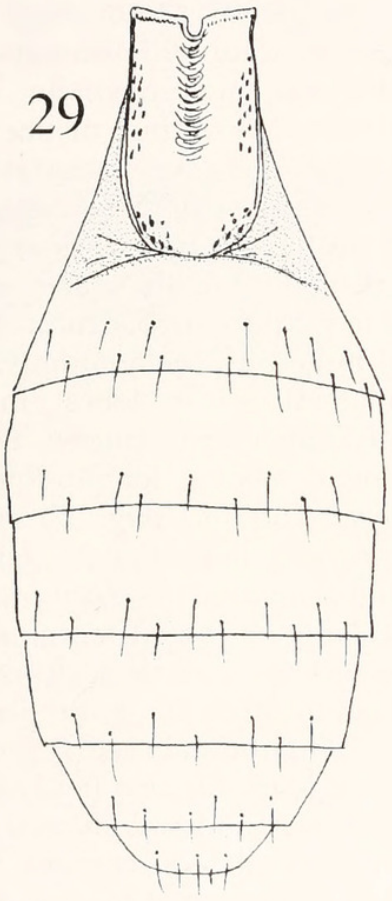
Microplitis chacoensis (Cameron)
(Figs. 7, 36–39)

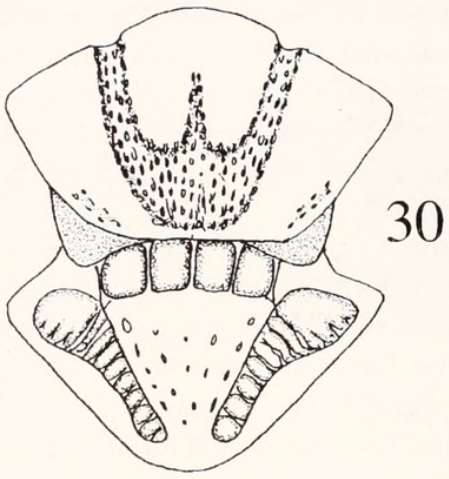
Microgaster chacoensis Cameron, 1908. Type Natural History Museum, London, examined.

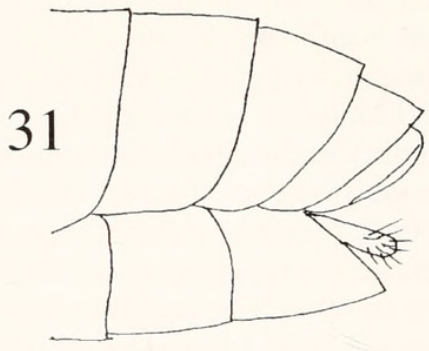
Microplitis ayerzai Brèthes, 1910. Type National Natural History Museum, Buenos Aires, examined. **New Synonymy.**

Female.—Body length 3.1–3.4 mm. Fore wing length 3.2–3.7 mm. *Color:* General body color orange-brown, except darker brown (sometimes nearly black) head and margins of metanotum. Wings (Fig. 36) nearly uniformly but not intensely smoky, veins including stigma generally pigmented dark brown, with (RS + M)b, 1m-cu and portions of areolet veins paler. *Head:* Face relatively flat and wider than tall but slightly bulging medially, coarsely punctate to punctulorugose. Ocelli not set in weak depression. Posterior ocelli slightly farther from anterior ocellus than their diameters. Antennae rather evenly thick, approximately same length as body. *Mesosoma:* Mesonotum (Fig. 38) coarsely puncate with smoother regions laterally and anteromedially; notaulices complete, shallow but distinctly sculptured, and merging posteriorly into a broad, weakly sculptured depression bisected posteriorly by a distinct medial carina. Scutellum with sparse punctures, separated from mesoscutum by scrobe with 4 large pits. Metanotum with broad anterolateral setose lobes. Propodeum strongly and evenly rugose, divided by prominent medial longitudinal carina. *Metasoma:* Tergite I (Fig. 37) broadening posteriorly up to about 0.7 of length, then tapering slightly to blunt apex, with weakly bulging lateral margins, 1.4–1.53 as long as broad, nearly sculptureless and polished throughout, with distinct but shallow longitudinal medial groove over anterior 0.4–0.5. Median field of tergite II not always obviously indicated except at extreme anterolateral corners, but if so, this field is suggested by two weak subparallel grooves that would indicate a narrow median field. Tergite II and remaining terga with usually 2 irregular rows of setae posteriorly. Hypopygium relatively long, not especially truncate apically (Fig. 31). Ovipositor sheaths short, blunt, apically hairy, projecting only to near end of hypopygium or often less. *Legs:* Hind tibiae slightly thickened,



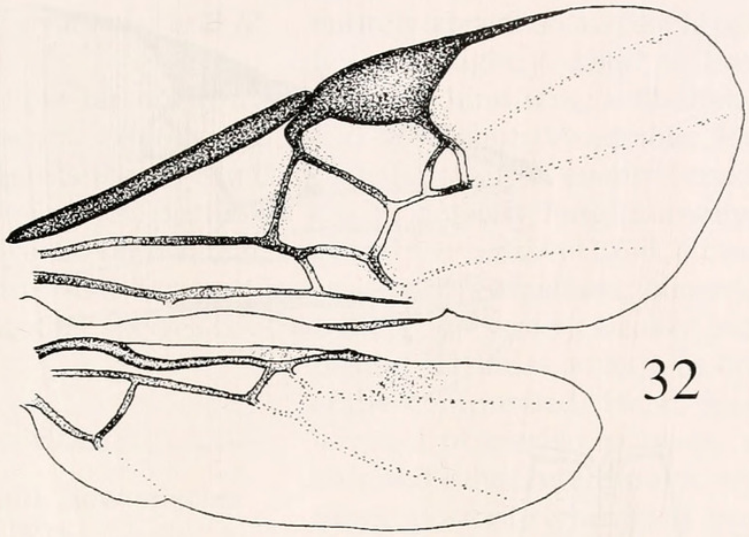


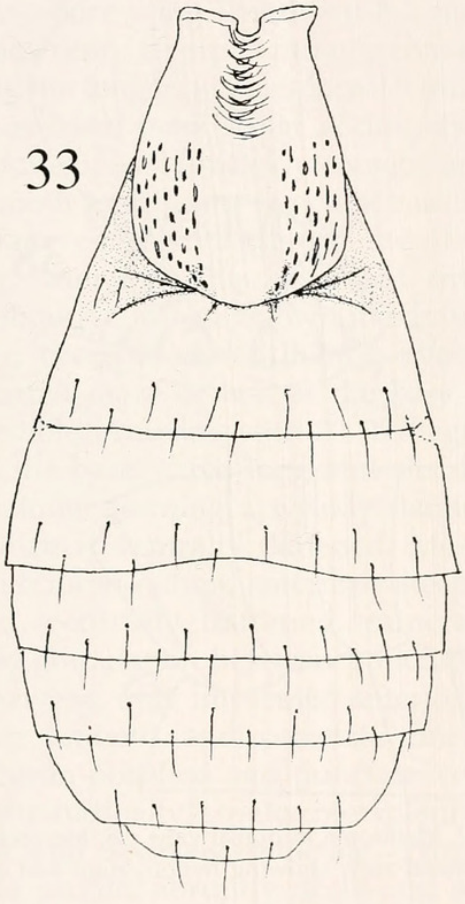


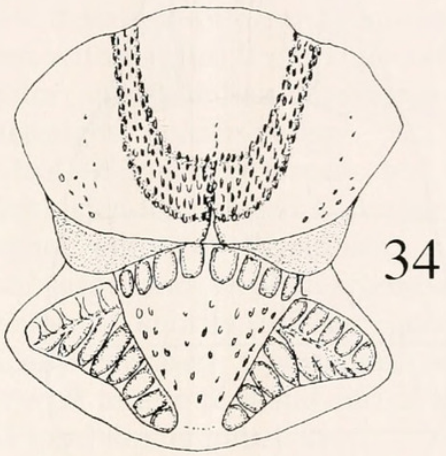


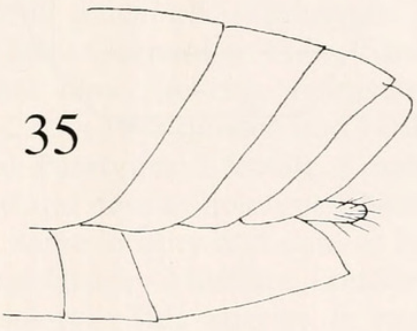
Figs. 28–31. *Microplitis marini* Whitfield, n. sp. 28, wings. 29, metasoma in dorsal view. 30, mesoscutum and scutellum in dorsal view. 31, apex of female metasoma, lateral view showing hypopygium and ovipositor sheaths.

with scattered thicker spines on outer faces. Hind basitarsus slightly longer than next two tarsomeres combined. Hind tibial spurs subequal in length, outer one slightly thicker. *Wings:* Largely infuscate (Fig. 36). Fore wing R1 extending about halfway from stigma to end of 3RS fold. Stigma evenly dark brown, without basal lighter spot. Areolet large, subtriangular to weakly quadrangular, angle between









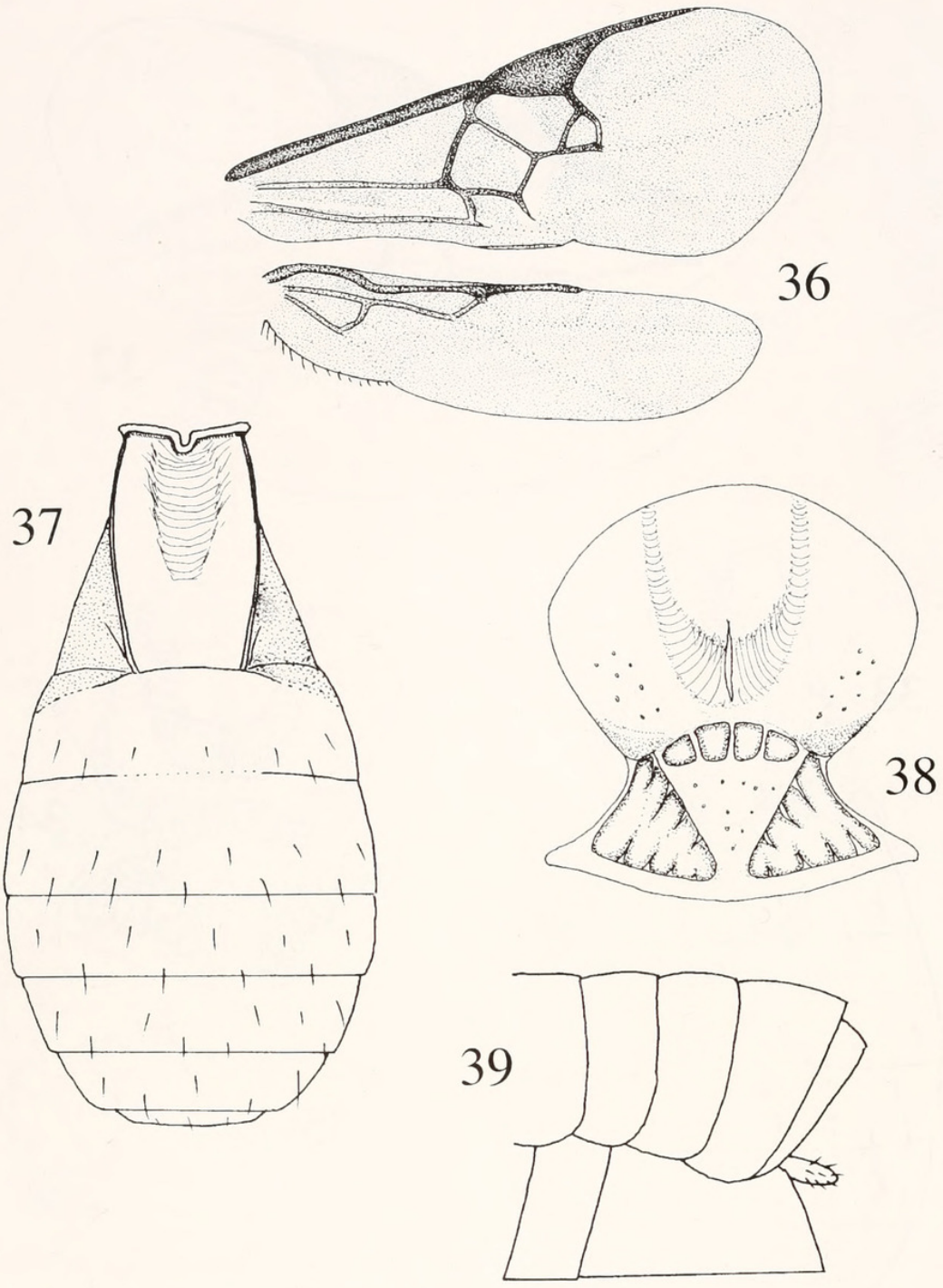
Figs. 32–35. *Microplitis ceratomiae* Riley. 32, Wings. 33, Metasoma in dorsal view. 34, mesoscutum and scutellum in dorsal view. 35, Apex of female metasoma, lateral view showing hypopygium and ovipositor sheaths.

(usually very short) 3RSa and r-m obtuse, often indistinct.

Male.—Similar to female except antennal segments longer.

Cocoon (Fig. 7).—Orange-brown, relative tough and stiff, glued together in tight clusters on the corpse of the host caterpillar as in *M. ceratomiae* and *M. marini.*

Material examined.—In addition to the types, we have examined material from Argentina, Brazil, Paraguay, Uruguay, Trinidad and Venezuela, reared principal-



Figs. 36–39. *Microplitis chacoensis* (Cameron). 36, Wings. 37, Metasoma in dorsal view. 38, Mesoscutum and scutellum in dorsal view. 39, Apex of female metasoma, lateral view showing hypopygium and ovipositor sheaths.

ly from *Manduca sexta* (the tomato hornworm) and *Manduca rustica*, but also with isolated records from *Erinnyis ello* and *Agrius cingulatus* (Fabricius) (the sweet potato hornworm). The cocoons are spun in a tight, pale tan mass nearly identical to that of *M. ceratomiae* (Fig. 6).

Comments.—It is clear from all of the material examined, as well as the identical host records, that *Microplitis ayerzai* Brethes is conspecific with Cameron's *M. chacoensis*. Due to the striking orange-brown coloration and dark wings, this species appears superficially very distinctive, but closer inspection reveals that many of its morphological details strong-

ly resemble those of *M. ceratomiae* and *M. espinachi.*

It is not yet known how far north the distribution of *M. chacoensis* extends; the known distribution suggests that it could be present in the eastern (wetter) portions of Panama and Costa Rica. So far our rearings of the known hosts that far north have produced only the other species covered here.

ICHNEUMONIDAE

Acrolyta stroudi Gauld, new species
(Figs. 8, 27)

Female.—Fore wing length 3.0–3.2 mm. Mandible evenly tapered with upper tooth distinctly the longer; malar space 0.9 times as long as basal mandibular width; clypeus truncate apically, weakly convex, apically smooth grading to punctate basally; lower face centrally slightly swollen, punctate; lateral ocellus separated from eye by about 1.1 times its own maximum diameter; occipital carina joining hypostomal carina more or less at the base of the mandible. Antenna with 20–22 flagellomeres the basal three long and slender the remainder forming a weakly defined club, which is ventrally flattened. Mesosoma with mesoscutum, anteriorly steeply rounded, centrally flattened, punctate with fine granulation between punctures; notaulus weak, only impressed anteriorly; scutellum smooth and punctate finely; mesopleuron polished and punctate, centrally longitudinally striate; metapleuron polished and sparsely punctate. Propodeum, in profile, abruptly declivous, anterior and posterior transverse carinae close together, strong, centrally arched forwards, subparallel with the intervening area longitudinally rugose/striate; posterior part with weak lateral longitudinal carinae, centrally transversely rugose/striate; pleural carina complete, otherwise longitudinal carinae absent. Legs unspecialized; hind femur about 4.5 times as long as deep. Fore wing with vein *3rs-m* entirely absent so areolet is open externally; *cu-a* slightly distal to base of *Rs&M* (Fig. 27); hind wing with distal abscissa of *Cu*1 weak but discernible. Metasoma deplanate; tergite I evenly broadened posteriorly, dorsally longitudinally striate; tergite II posteriorly 1.6–1.7 times as broad as long, punctostriate; succeeding tergites with progressively weaker punctures; ovipositor 1.1 times as long as hind tibia, laterally compressed. Head, mesosoma and tergite I of metasoma black, with mandibles and other mouthparts, tegula and extreme posterior corner of pronotum yellow; antenna yellowish with the swollen flagellomeres (i.e. 4+) infuscate grading to black distally; uniformly yellowish; metasoma with tergites II+ orange-yellow; ovipositor sheath infuscate. Wings hyaline, pterostigma golden yellow.

Male.—Similar to female, but with flagellum slender, setaceous; tergite II with a distinct elliptical thyridium; subgenital plate large and weakly sclerotized, conspicuously shortly hirsute; gonosquama apically rounded. Coloration, as female, but with tergite II, distal end of hind tibia and hind tarsus infuscate.

Material examined.—**Holotype:** female, Costa Rica: Guanacaste Prov., Santa Rosa National Park, (rearing reference # 93-SRNP-2227), 1993 (Janzen and Hallwachs) (INBio). **Paratypes:** 1 female, 1 male, same locality and data as holotype (INBio), 2 females, same locality and data as holotype (Natural History Museum, London).

Etymology.—This species is named in honor of Steven Stroud in recognition of his enormous support for forest conservation in the Rincon Rainforest expansion of the Area de Conservación Guanacaste.

Remarks.—This species runs to *Acrolyta* in Townes (1969) key. However, it is rather distinctive, in having both a swollen female flagellum and in having the strong, close and subparallel transverse propodeal carinae. There are no described species of this genus in the Neotropics, although there are several species described

in the closely related genus *Isdromas*, all of which have the occipital carina joining the hypostomal carina further away from the mandibular base. *Acrolyta*, and species placed in related genera in the acrolytine Phygadeuontini (= Acrolytina *sensu* Townes, 1969) are commonly parasitoids of the cocoons of small ichneumonoids (Carlson, 1979), as is the case with *Acrolyta stroudi* as a parasitoid of cocoons of these small braconids (see below).

Mesochorus angustistigmatus Dasch
(Figs. 3, 26)

Mesochorus angustistigmatus Dasch, 1974: 277. Holotype, Brazil (Canadian National Collection, Ottawa), examined.

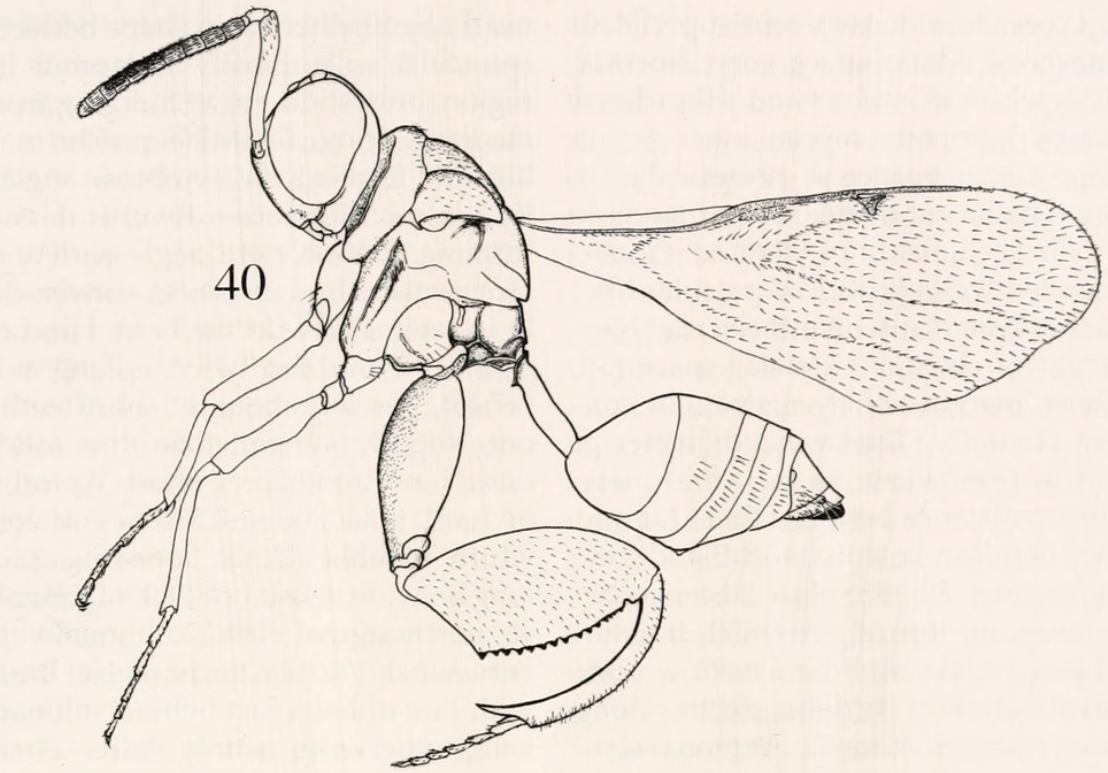
Redescription.—Fore wing length 2.8–3.5 mm; mandible strongly tapered with upper and lower teeth subequal in length; malar space broad, striate, about 1.0 times basal mandibular width; lower face about 1.0 times as broad as high, coarsely and sparsely punctate, with strong median vertical ridge; subantennal ridge weakly dipped medially; frons weakly shagreened, impunctate; ocelli small, lateral one separate from eye by 1.6–1.83 its own maximum diameter; vertex without a groove from lateral ocellus to eye; occipital carina complete, antenna with 30–33 long slender flagellomeres. Mesosoma with mesoscutum polished and finely punctate; mesopleuron similar but more sparsely punctate; scutellum strongly rounded; propodeum polished, completely carinate, with area superomedia hexagonal, about 1.4 times as long as broad. Metasoma polished, tergite I with fine longitudinal striations, remaining tergites smooth; female with ovipositor sheath long and slender, projecting beyond apex of metasoma by 0.7 times length of hind tibia. Yellowish brown species with head and mesosoma dorsally slightly darker; propodeum and tergite I generally blackish brown; tergite II white with anterior and anterolateral margins infuscate; tergite III anteriorly pallid, posteriorly broadly infuscate; tergites IV+ dark. Legs yellowish brown, hind coxa and trochanter slightly darker; distal apex of tibia blackish. Fore wing hyaline, pterostigma reddish brown.

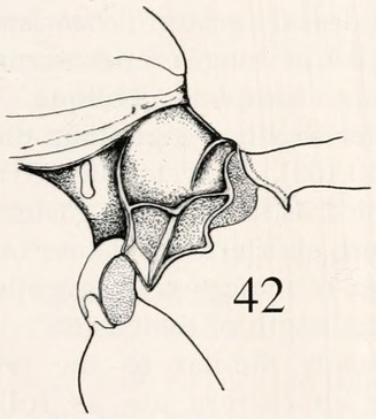
Remarks.—*Mesochorus angustistigmatus* is one of approximately 15 species of *Mesochorus* known to occur in Costa Rican dry forests. It differs from other species in a) having the ocelli small and widely separate from the eye, b) the characteristic shape of the area superomedia, c) having a long slender ovipositor sheath, and d) coloration, particularly the colour pattern of the first three metasomal tergites. This species is easily distinguished in the field from *Acrolyta stroudi* in that the latter has a red-orange gaster and black head and thorax.

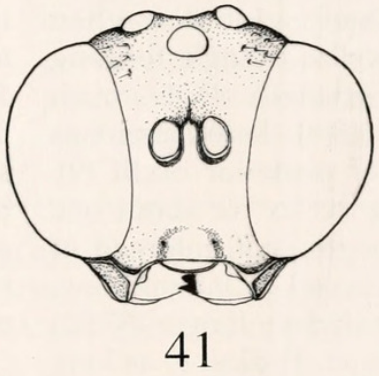
CHALCIDIDAE

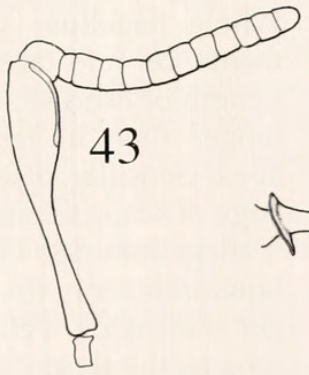
Conura convergea Delvare, new species
(Figs. 3, 40–44)

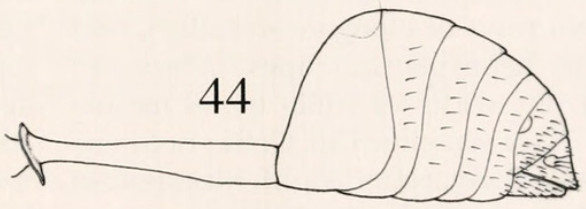
Holotype female.—3.6 mm. Body entirely bright-yellow (note: specimens kept in alcohol and subsequently dried can be pale yellow and even white on pronotal collar, mesoscutum along notauli, most of scutellum, propodeum, meso- and metapleuron, petiole), as well as tegula, legs, scape, pedicel flagellum in part. Last segment of hind tarsi slightly darkened. First 3 funicular segments entirely yellow, funicle 4 darkened dorsally, funicle 5 to 7 blackish dorsally as well as basal part of first segment of clava, remaining part of flagellum yellow. Teeth of mandibles and valvulae of ovipositor black. Veins of forewing pale. Wings hyaline. Pilosity of the body entirely yellow, that of wing black. *Head:* Head slightly wider than thorax (82:75), 1.8 times as wide as long (82:45). Frons regularly convex in lateral outline. Height of head 66, of eyes 50. Oral fossa 29. Mandible formula 2.3. Lower edge of mandibles with translucent flange. Clypeus well delimited through submedian impres-











Figs. 40–44. *Conura convergea* Delvare n. sp. 40, Female habitus. 41, Female head in frontal view. 42, Female propodeum in lateral view. 43, Male antenna. 44, Male petiole and gaster.

sions. Lower face densely and superficially alutaceous. Malar space very short, 10 at sulcus which is evident and ± bordered behind by complete carina; inner carina missing. Gena bordered posteriorly by narrow translucent flange above mandible corner, flange quickly obliterated. Antennae inserted well above lower ocular line, distance between antennal toruli and lower margin of clypeus 33 malar space (30: 10). Inner margins of eyes strongly convergent ventrally. Transverse diameter of eyes 24 in front view, 36 in lateral view. Narrowest distance between them (at mid distance between antennal toruli and lower ocular line) 29. Broadest distance between eyes, on top of vertex 50. Interantennal projection visible as a narrow plate delimited laterally by faint ridges along the inner margins of toruli. Antennal scrobes shallow. Adscrobal area alutaceous with a few and shallow piliferous punctures. Head relatively globular when viewed dorsally. Ocellar triangle forming a slightly obtuse triangle. POL much greater than OOL (13:8), latter about as large as diameter of posterior ocelli (9). Scape 46, exceeding vertex for about one third of its own length, not enlarged at apex and slightly curved in lateral view. Pedicel + flagellum slightly longer (87:82) than the width of head. Pedicel 9, as long as each of the five first funicular segments; following segments very slightly shortened, last one 7.5. Each funicular segment with two rows of elongate sensilla. Clava 13, with hemispherical apex. *Mesosoma:* Length 100, width of collar 65, of mesoscutum 75, of scutellum 40. Collar not margined anteriorly, rounded off. Mesonotum alutaceous, the network delimiting transverse meshes. In addition to mid lobe of the mesoscutum with shallow piliferous punctures, the background sculpture merging to squamose posteriorly. Lateral lobes without punctures, scutellum with very shallow ones, especially laterally. Scutellum about as long as the mesoscutum (37:38), distinctly convex. Propodeum nearly hemispherical in shape between the spiracular sulci, mostly alutaceous in this region, only short rugae merging from the median carina. Costulae nearly in same line and forming a very obtuse angle with the latter. Postero-subventral carinae forming about a right angle with spiracular carinae. Hind coxae 80, convex dorsally in lateral view at the base. Hind femur slightly more than twice as long as wide (97:46), bearing about 20 short teeth, first one slightly longer than the following ones; inner tooth very short. Apical spine of hind tibia about 2.5 times as long as width of tibia (22:9). Forewing 2.5 3 as long as wide. Costal cell 80, marginal vein 46, postmarginal vein 54. Stigmal vein 8.5, very short. Pilosity fairly dense. Basal cell with line of hairs just behind submarginal vein, otherwise mainly bare. Area between marginal vein and Rs+M (latter visible as line of hairs) with only a few hairs on its dorsal surface. *Petiole and gaster.* Petiole 0.4 as long as mesosoma (40: 100), with a complete, oblique, basal flange. Gaster slightly longer than the mesosoma (110:100). First tergite (31) less than one third as long as the gaster. Epipygium short, shorter than its own width (12:17). Apex of hypopygium slightly less than half the length of the gaster.

Male.—Mostly similar to the female. Distinctive characters are as follows. Whole flagellum yellow. Last two segments of mid and hind tarsi blackish. Length of head 48, width 78. Scape 66, yet longer than in female and enlarged at apex. Sensillar plate as a line on ventral edge of scape where it is enlarged. Pedicel + flagellum 68. Funicular segments subquadrate, only first one very slightly longer than wide. Petiole about 0.7 times as long as the thorax (72:100), gaster 80.

Material examined.—**Holotype female:** COSTA RICA: Guanacaste Prov, Area de Conservacion Guanacaste, Sector Santa Rosa, 250 m, ex *Microplitis espinachi* ex *Manduca lefeburii,* adult eclosion on 28.VI.1993 (D. H. Janzen & W. Hallwachs,

ref. 93-SRNP-2445, in U. S. National Museum). **Paratypes:** 36 females, 10 males same data as holotype; 12 females same data as holotype but adult eclosion on 27.VI.1993 (ref. 93-SRNP-2450); 5 females same data as holotype but adult eclosion 08.VII.1993 (ref 93-SRNP-2450); 8 females same locality and collectors, ex *Microplitis figueresi* ex *Erinnyis ello,* adult eclosion on 08.VII.1993 (in U. S. National Museum, American Entomological Institute, Canadian National Collection, Natural History Museum, London, MNHN, CIRAD (Montpellier), INBio). COSTA RICA, Guanacaste, Santa Rosa National Park, San Emilio I–II 1987 (1 female) and XII 1986 (1 female) in INBio (malaise trap, I. D. Gauld, D. H. Janzen and W. Hallwachs, collectors).

Remarks.—This new species belongs to the *immaculata* group as defined by Delvare (1992:213) and more precisely to the *immaculata* subgroup. The closest described species is *Conura* (*Ceratosmicra*) *camescens* Delvare, for a long time known as *Ceratosmicra flavescens* Cameron (Cameron 1913; De Santis 1979). The latter species differs in having a very faint (even absent) malar carina, the shorter scape, only slightly exceeding vertex, POL relatively shorter, absence of piliferous punctures on mesonotum, etc. The body is also orange rather than yellow.

There are also many undescribed species that are similar to *Conura convergea.* Comparison with them shows that the main diagnostic characters for *C. convergea* (apart from those shared with other members of the *immaculata* group and subgroup and already mentioned by Delvare 1992) are: 1) the presence of a malar groove and carina, 2) the converging eyes, 3) the ocellar triangle and relative proportions of OOL and POL, 4) the very long scape which noticeably exceeds the vertex, 5) the special coloration of the flagellum of the female, 6) the pilosity of the fore wing, 7) the dorsal outline of the hind coxa near its base, and 8) the relative proportions of the petiole and gaster. The appearance of the interantennal projection is also unique within the *immaculata* group.

KEY TO *MICROPLITIS* AND ASSOCIATED SPECIES OF PARASITOIDS OF SPHINGID CATERPILLARS IN COSTA RICAN DRY FOREST (ALSO INCLUDES THE NEARCTIC *M. CERATOMIAE* AND SOUTH AMERICAN *M. CHACOENSIS* FOR COMPARISON)

1 Fore wing with no enclosed cells present (Fig. 40) ..... ***Conura convergea* Delvare sp. n.**
– Fore wing with enclosed cells (e.g., Figs. 22–27) 2

2 Fore wing without vein 2m-cu and without distal abscissa of Rs enclosing marginal cell; vein RS + M present separating submarginal and discal cells (Fig. 23) 3
– Fore wing with vein 2m-cu complete; distal abscissa of Rs complete, enclosing a triangular marginal cell; veins Rs + M broadly incomplete so submarginal and discal cells are broadly confluent (Figs. 26, 27) 7

3 Body color, except often head, orangish brown; wings mostly infuscate (Fig. 36) ..... ***Microplitis chacoensis* (Cameron)**
– Body color, especially mesosoma, black; wings mostly hyaline 4

4 Mesonotum with notauli complete, broad and rugose, coalescing posteriorly into a rugose or foveolate area often bisected by posterior medial longitudinal carina (Fig. 17); metasomal tergite I less than twice as long as broad at broadest point (Figs. 10, 33, 37) ... 5
– Mesonotum with notauli indicated strongly only on anterolateral margins, smoother posteriorly (Fig. 18) but often with a faint medial longitudinal carina present; metasomal tergite I usually slightly more than twice as long as broad (Fig. 14) ..... ***Microplitis figueresi* Walker, sp. n.**

5 Metasomal tergite I only about 1.2–1.33 as long as broad, with strongly bulging lateral margins (Fig. 33); areolet in fore wing usually somewhat subtriangular, or at least not sharply quadrangular (Fig. 32) (may not occur in Costa Rica) ..... ***Microplitis ceratomiae*** **Riley**

– Metasomal tergite I approximately 1.53 as long as broad, with weakly bulging or subparallel lateral margins; areolet in fore wing usually clearly quadrangular due to relatively long and angled 3Rsa (Figs. 9, 28) 6

6 Tergite I relatively smooth over posterolateral surface (Fig. 10); posterior confluent region of notauli bisected by strong medial carina (Figs. 11, 17) ..... ***Microplitis espinachi*** **Walker, sp. n.**

– Tergite I punctate posterolaterally and near lateral margins over anterior 0.6 (Fig. 29); posterior confluent region of notauli with only very weak medial carina, although foveolate sculpturing often extends anteromedially where this carina would be (Fig. 30) ..... ***Microplitis marini*** **Whitfield, sp. n.**

7 Fore wing with a completely delineated rhombic areolet; hind wing with distal abscissa of Cu1 entirely absent; female with a large subgenital plate that in side view is triangular; male with distal end of clasper extended as an elongate spine-like process .. ***Mesochorus***

– Fore wing lacking r-m2, thus without a delineated areolet; hind wing with distal abscissa of Cu1 complete; female with a small, rounded subgenital plate; male with distal end of clasper gently rounded ..... ***Acrolyta***

NATURAL HISTORY OF *MICROPLITIS* AND ITS PARASITOIDS IN THE ACG DRY FOREST

Microplitis figueresi.—This 3 mm long black microgastrine braconid (Fig. 3) is unambiguously a specialist at parasitizing the caterpillars of just two species of Sphingidae, *Erinnyis ello* and *Erinnyis oenotrus*, of the many species in ACG dry forest (Table 1) (once there are more rearing records for *Erinnyis lassauxii*, it may be found to also parasitize this species). *Microplitis figueresi* has not been encountered outside of the ACG, despite massive and multi-habitat Malaise trapping in Costa Rica by two decades of intensive Hymenoptera inventory (I. D. Gauld and P. Hanson, personal communication) and sporadic rearing of caterpillars throughout Mesoamerica.

There is no sign of *M. figueresi* in the wetter ACG habitats (cloud forest and rain forest and intergrades), despite that one of its two major hosts, *Erinnyis ello*, is a common pest caterpillar on commercial and feral cassava (*Manihot esculenta* Crantz (Euphorbiaceae)) in these wetter habitats. Since this wasp apparently has not been reared previously from this very widespread neotropical agricultural pest caterpillar, *M. figueresi* might well be found to be endemic to the dry forests of the Costa Rican Pacific coastal plain, once the neotropical Hymenoptera fauna is well known. It may well not even venture out of the dry forest into the agroscape dotted with small scale cassava plantations, though it is a parasite of *E. ello* feeding on cassava growing on the forest edge and abandoned farmsteads in the ACG dry forest.

Nearly all the specimens of *Microplitis figueresi* reared to date from *E. ello* have been from caterpillars feeding on the early rainy season leaves of the dry forest understory tree *Sebastiania pavoniana* Mueller. Arg. (Euphorbiaceae; known in most Costa Rican biodiversity literature as *Sebastiania confusa* Lundell) (Table 2). The other primary host for *M. figueresi*, *Erinnyis crameri* feeding on *Stemmadenia obovata* K. Schum. (Apocynaceae), is very common in the exact same forest, living just a few meters from the *Sebastiania pavoniana* attacked

Table 2. Food plants of the caterpillars that were parasitized by *Microplitis figueresi* in the ACG dry forest Sector Santa Rosa (source: Janzen and Hallwachs 2002).

Sphingidae	Food plant family	Food plant species	Percent parasitized	Number of rearings
Erinnysis ello	Apocynaceae	*Forsteronia spicata*	33	6
	Caricaceae	*Carica papaya*	20	5
	Euphorbiaceae	*Euphorbia colletioides*	50	2
	Euphorbiaceae	*Euphorbia schlechtendalii*	6	136
	Euphorbiaceae	*Manihot aesculifolia*	22	9
	Euphorbiaceae	*Manihot esculenta*	7	76
	Euphorbiaceae	*Sebastiania pavoniana*	51	206
Erinnyis crameri	Apocynaceae	*Rauvolfia tetraphylla*	3	37
	Apocynaceae	*Stemmadenia obovata*	23	377
Erinnyis lassauxii	Asclepiadaceae	six species	9	11

by *M. figueresi.* The host records in Table 2 offer a clue as to why *M. figueresi* does not appear to have moved into the *Erinnyis ello-Manihot*-rich agroscape. The two heavily parasitized hosts live side-by-side in the shady undestory of 10–80-year old secondary successional forest. However, the other three *M. figueresi* host records with a usefully large sample size (*Euphorbia schlectendalii* Boiss., *Manihot esculenta, Rauvolfia tetraphylla* Linnaeus) were all growing in strongly insolated young successional vegetation, much as is a *Manihot esculenta* plantation, and have very low percent attack by *M. figueresi.*

Based on rearing wild-caught first and second instar caterpillars of *Erinnyis ello* and *E. crameri* in captivity, *Microplitis figueresi* can oviposit in first and second instar *Erinnyis* caterpillars, but this observation does not negate the possibility that it may also oviposit in caterpillars in their later instars as well. Irrespective of when oviposition occurs, as few as 40 to as many as 150 *M. figueresi* larvae begin to feed and grow in the middle/late days of the last (fifth) instar of the parasitized caterpillar. Prior to this late last instar stage, crude exploratory dissections did not locate the very small and presumably first instar wasp larvae.

The prepupal wasp larvae emerge from the caterpillar (Fig. 1) by burrowing through the dorsal cuticle during a 1–3 hour period, usually in the first hours of daylight. At this time the caterpillar is often on the underside of its support twig, but need not be for successful emergence. Each larva exits through its own hole. The holes are scattered along the dorsal side of the caterpillar (not clumped as in *Microplitis marini,* Fig. 4–5). The hole seals (or is sealed by the larva), and there is no noticeable loss of fluid by the caterpillar. The larvae exit the caterpillar at the stage in the last larval instar that would be 1–3 days before the caterpillar would become a prepupa if it were not parasitized. Each wasp larva spins a very tough and hard individual beige/gray silk cocoon side-by-side but not perfectly adjacent to other cocoons, while attached to the cuticle by its posterior end (Figs. 2, 3). The glue on the silk of one cocoon often sticks strongly to an adjacent cocoon, leading to a mass of cocoons lightly and irregularily stuck together. The cocoons are very much harder and tougher (and thus characteristic of the cocoons of most *Microplitis*) than are those of other similar-sized microgastrine braconids (e.g., *Apanteles, Cotesia, Parapanteles,* and *Glyptapanteles*), the occupants of which do not remain dormant for many months

A few hours before the wasp larvae exit from the caterpillar, the caterpillar ceases to feed and walks a few decimeters to a few meters from the place of feeding

(which often takes it off the food plant), and perches motionless, usually on the underside of a stem (Fig. 1–2). A consequence is that the wasp cocoons are generally encountered "stuck" to the dorsal side of the upside-down caterpillar (Fig. 2). The finished hard coccons may be knocked off into the litter by movement of the vegetation. Alternatively, when the caterpillar "dies" 1–3 days later and falls to the litter, the cocoons are incorporated into the litter through normal decomposition processes. If the newly emerged larvae are knocked off the caterpillar, sometimes they successfully spin a normal-appearing cocoon in the litter.

The batch of 20–100 or more *Microplitis* larvae that emerge from a single caterpillar may well be from a single ovipositing wasp, but this assumption deserves further testing through genetic fingerprinting. A *Microplitis* wasp has never been observed ovipositing during this inventory, but then again, an explicit effort has not been made to observe oviposition. In all of the hundreds of cases of parasitism by *Microplitis figueresi* (or *Microplitis espinachi* or *Microplitis marini*) found in this inventory, in no case has the caterpillar produced small numbers (e.g., 1–10) of larvae. However, other species of *Microplitis* in the ACG dry forest habitat have one larva per caterpillar, but their hosts are small Noctuidae such as *Coenipita bibitrix* Huebner (Janzen and Hallwachs 2002).

While a few of the wasps in the batch of cocoons from a single caterpillar may eclose 2–6 weeks after cocoon spinning, the great majority of *M. figueresi* larvae remain as dormant prepupae in their very hard and thick-walled cocoons for 11–13 months until shortly before and during the beginning of the next rainy season (May–June, see records in http://janzen.sas.upenn.edu for actual eclosion dates in the ACG dry forest). This timing of eclosion places the adult wasps in the habitat during the month (May–June) when their host species of *Erinnyis* caterpillars, as well as the non-host species of *Erinnyis*, initiate the first, and usually only, generation of the year in this dry forest. For the most part, *M. figueresi* is univoltine in the ACG dry forest, just as is its host caterpillar.

Wasp eclosion is apparently triggered by the drop in temperature that is generated by the oncoming rain at the end of the long dry season, a change that the wasp prepupae do perceive through a closed glass bottle exposed to ambient temperatures in the rearing barns. This temperature drop is also used by many other insects in this forest as an activity cue (Janzen 1987a, 1993). Newly-eclosed (and unfed) wasps survive only 1–2 days in a clean dry bottle, but presumably live for weeks when circulating freely in the habitat in search of mates and hosts, with access to food. Since there appears to be only one major generation per year, it appears as though the wasps must die within a few weeks of eclosion. While the few *Microplitis* individuals that eclose a few weeks after spinning may have a second generation on the laggard tail of the host caterpillar population's primary annual generation, none of the very few sphingid larvae encountered after July have been parasitized by *Microplitis*.

In 1978–2001 the ACG dry forest inventory (Sector Santa Rosa) reared 14,012 wild-caught sphingid caterpillars in 73 species. Of these, 26% of *Erinnyis ello* (n = 481) and 23% of *Erinnyis crameri* (n = 501) caterpillars were parasitized by *M. figueresi* (except for one case of the very rare sphingid *Erinnyis lassauxii*, and one naturally occurring "error" among 1,120 *Xylophanes turbata* rearings; Table 1). *M. figueresi* is unambiguously a specialist parasite whose population survives primarily on just these two species of *Erinnyis* out of the potentially available 73 other species of sphingid caterpillars in the ACG dry forest. (When a larger sample of *Erinnyis lassauxii* has been inventoried, it may well be found that it is a third host for *M. fi-*

gueresi). While not enough caterpillars of three other *Erinnyis* have been reared to comment on (*Erinnyis yucatana* (Druce), *Erinnyis obscura* (Fabricius), *Erinnyis domingonus* (Butler), *Erinnyis alope* (Drury)), the 92 rearing records of *Erinnyis oenotrus* have produced no *Microplitis* records. This is an outstanding result because *E. crameri* feeds on *Stemmadenia obovata* growing within a few meters of *E. oenotrus* (and even *Erinnyis ello*) feeding on *Forsteronia spicata* G. F. W. Mey. There is no way to determine at this stage whether *M. figueresi* simply does not oviposit in or notice *Erinnyis oenotrus*, or whether *E. oenotrus* is resistant to *M. figueresi*. The ACG dry forest caterpillar inventory rears all species of wild-encountered macrocaterpillars and there is no suggestion that *Microplitis figueresi* parasitizes caterpillars in other families (more than 70,000 wild-caught rearing records of more than 1,650 species in http://janzen.sas.upenn.edu).

Erinnyis ello and *Erinnyis crameri* share habitat and season but do not share food plants. In this dry forest, free-ranging *Erinnyis ello* caterpillars are found feeding on the leaves of the species in Table 2 and on leaves of *Hippomane mancinella* Linnaeus, *Sapium thelocarpum* K. Schum and Pittier, *Euphorbia tirucali* Linnaeus, and *Mabea occidentalis* Benth. (Euphorbiaceae), *Forsteronia spicata* (Apocynaceae), *Manilkara chicle* (Pittier) Gilly and *Chrysophyllum brenesii* Cronquist (Sapotaceae), and *Licania arborea* Seem. (Chrysobalanaceae). All but the last species are latex-producers. However, to date only *Erinnyis ello* caterpillars feeding on those food plants in Table 2 have been parasitized by *M. figueresi*, all of which are latex-producing plant families. Caterpillars of *Erinnyis ello* found on their other food plants may also be found to be attacked by *M. figueresi* in years to come, since the inventory sample to date contains less than 10 records of caterpillars for each of these other food plants. *Erinnys crameri*, however, does appear to have one regular food plant on which it is not attacked by *M. figueresi*. There are 85 records of *E. crameri* from *Rauvolfia ligustrina* R. and S. (Apocynaceae), a rare shrub occurring in one small patch in a heavily insolated site; no *E. crameri* caterpillar feeding on this plant was attacked. It is also significant that there is only a single record of *M. figueresi* from *Erinnyis crameri* on *Rauvolfia tetraphylla*. This does demonstrate that *M. figueresi* larvae can survive in the microhabitat of *Erinnyis crameri* feeding on *Rauvolfia* (very toxic to vertebrates), and therefore the strikingly low percent attack of caterpillars feeding on *Rauvolfia* is probably due to some ecological factor (as mentioned above in reference to *Erinnyis ello*). Both species of *Rauvolfia* live in very insolated early stages of secondary succession.

The single record of *Microplitis figueresi* from a *Xylophanes turbata* caterpillar feeding on *Hamelia patens* Jacq. (Rubiaceae) (in the same forest that is the source of all the other records reported here) is probably an ovipositional "error". The inventory through 2001 has reared 1,120 wild caught *Xylophanes turbata* caterpillars in the ACG dry forest. We feel comfortable with the conclusion that *Microplitis figueresi* is not a normal parasite for this species of caterpillar and that this record does not reflect any "generalist tendencies" by *M. figueresi*. However, this ovipositional "error" makes it clear that this braconid can, at least occasionally, develop in the tissues of this caterpillar (as can a number of other species of hymenopteran and dipteran parasites) and we suspect in other species as well. Were the wasp to find itself in a habitat lacking its usual hosts, a jump to another species of sphingid might require little more genetic change than becoming able to smell it or at least recognize it as a potential host when encountered.

In the ACG dry forest, *Microplitis figueresi* "shares" *Erinnyis ello* with 3 species of Tachinidae (*Drino piceiventris* (Walker), *Blepharipa fimbriata* (Wulp), *Belvosia* sp. 7), one species of Ichneumonidae (*Crypto-*

phion espinozai Gauld), and another microgastrine braconid (*Cotesia* sp.) (http://janzen.sas.upenn.edu). However, out of 481 caterpillars, only 5% had these other parasites (all of which are found much more frequently in a short list of other species of caterpillars, species that should be viewed as their "usual" hosts) while 26% were parasitized by *M. figueresi*. *M. figueresi* is unambiguously the primary specialist killer of *Erinnyis ello* caterpillars in the ACG forest.

In like manner, *M. figueresi* "shares" *Erinnyis crameri* with three species of Tachinidae (*Drino piceiventris, Belvosia* sp. 7, Mystery genus 1, sp. 1) and one species of Ichneumonidae (*Cryptophion espinozai*). Again, as was the case with *Erinnyis ello*, out of 501 *Erinnyis crameri* caterpillars only 10% had these other parasites (all of which, except for Mystery genus 1, sp. 1, are found more frequently in a short list of other species of caterpillars) while 17% were parasitized by *M. figueresi*. Furthermore, almost all of these were in caterpillars feeding on *Stemadenia obovata*. Again, when the caterpillar is feeding on *Stemadenia obovata, M. figueresi* is the primary specialist killer of *Erinnyis crameri* in the ACG dry forest.

Seen from the other side of the interaction, the *M. figueresi* population in the ACG dry forest is entirely sustained by the population of the caterpillars of *Erinnyis ello* (primarily on *Sebastiana pavoniana*) and *Erinnyis crameri* (on *Stemadenia obovata*). The absence of *M. figueresi* from the rearings of *Erinnyis oenotrus* (n = 92) is particularily striking since it lives only a few meters from larvae of *E. ello* and *E. crameri*.

No *Microplitis figueresi* (or *Microplitis espinachi* for that matter) have been encountered to date in more than 3,400 rearings of wild-caught Sphingidae caterpillars collected from the rain forests and cloud forests in the wetter eastern end of the ACG (including 130 *Erinnyis* and 117 *Manduca* rearing records), from which we conclude that it (and *Microplitis espinachi*) is entirely a "dry forest" wasp. The largely univoltine seasonality of its breeding biology is compatible with this conclusion.

In ACG dry forest, *Erinnyis crameri* is even more thorougly univoltine than is *E. ello*, and has only one generation per year (and this occurs during the first half of the rainy season). Just as does *E. ello*, it migrates out of the ACG dry forests after eclosing from its pupae in July and early August. Its pupae never become dormant under open-air ambient temperature conditions in the ACG. It has other generations in the lowland to mid-elevation rain forests in other parts of Costa Rica, before returning to the ACG dry forests with the first rains of the following year. It is unknown if *Microplitis figueresi* occurs in or parasitizes *Erinnyis crameri* in its wetter rainforest haunts, but it is unlikely since this wasp has not been found there during any of the extensive Malaise trapping done in these other areas (I.D. Gauld and P. Hanson, personal communication). The dormancy biology of *Microplitis figueresi* also suggests that this wasp does not migrate to other habitats when its host does.

Erinnyis ello also has only one large generation a year in the ACG dry forests (in the first half of the rainy season). However, very rarely a caterpillar of this species is found in the second half of the rainy season, probably the offspring of a few adults that did not migrate away at this time. The few *Microplitis figueresi* wasps (less than 2%) that eclose 2–6 weeks after spinning may represent a phenological polymorphism and have a second generation on these few *Erinnyis ello* caterpillars (however, there are no records of such to date) or may simply be "phenological accidents" that die without further reproduction, or both.

The *M. figueresi* larvae in *E. ello* and *E. crameri* are parasitized by *Mesochorus angustistigmatus* (Ichneumonidae) (Figure 3) wasps while the braconid larvae are still inside the caterpillar. Since such hyperparasitization cannot occur once the cat-

erpillar is in captivity, and may well not occur until the *M. figueresi* larvae have grown to a large size during a few days in the middle of the last instar, the low frequency of *M. angustistigmatus* hyperparasitization (5 out of 250 rearings of *M. figueresi*) may be a severe underestimate of the frequency in nature. In all cases the hyperparasitoid wasps emerged from the braconid cocoons 2–3 weeks after *M. figueresi* spun their cocoons. Given this lack of larval dormancy by *M. angustistigmatus*, this species probably hyperparasitizes other species of ichneumonoids in other species of caterpillars as well. *M. angustistigmatus* is also a parasitoid of *Microplitis espinachi* in *Manduca* caterpillars, again with the same low frequency as encountered with *M. figueresi.*

Microplitis figueresi larvae usually emerge from their host caterpillars during mid-morning hours and by dusk have spun a hard strong cocoon. From noon to dusk, these newly spun cocoons are located by *Conura convergea* (Chalcididae), a small stocky yellow wasp (Fig. 3). The wasp oviposits directly into the newly spun cocoons, presumably ovipositing into or on the prepupa inside. *C. convergea* never emerges from cocoons produced from caterpillars that have been in captivity until the time that the *Microplitis* larvae have emerged, from which we conclude that the chalcidid never oviposits into the braconid larvae inside the caterpillar. *Microplitis* cocoons produced in captivity and placed out in the forest the second day after spinning do not attract *C. convergea*, while fresh ones do. The behavior of ovipositing (or arriving to oviposit) only at the time of its host's cocoon spinning or new molt from the prepupa to pupa (in non-cocooning species) is commonplace among similar species of Chalcididae encountered during the ACG caterpillar inventory.

C. convergea emerge from the *Microplitis* cocoons in late June or July, in the first half of the rainy season and within 2–4 weeks of spinning by *Microplitis.* There is no indication of prepupal or pupal dormancy. While there are *Microplitis* cocoons in the litter throughout the remaining rainy season and dry season, they presumably lack the odor cues that would allow them to be used for multiple generations of *C. convergea.* Presumably *C. convergea* locates the newly spun cocoons of other species of braconids for subsequent generations during the remainder of the year. That none have been reared from other cocoons in the inventory is probably due to having collected almost no wild-spun braconid cocoons (the very large number of braconids reared from the caterpillar inventory are spun in captivity by larvae emerging from wild-caught caterpillars). *C. convergea* parasitizes *Microplitis espinachi* cocoons in exactly the same manner as it does those of *M. figueresi.*

Microplitis espinachi.—This 3 mm long black microgastrine braconid (Fig. 3) is unambiguously a specialist at parasitizing the caterpillars of six species of *Manduca* (*M. corallina, M. rustica, M. lefeburii, M. muscosa, M. occulta, M. hannibal*), and *Agrius cingulata* and *Sphinx merops* (Table 1), among the many species of Sphingidae in ACG dry forest. As with *Microplitis figueresi*, which it resembles very closely, *Microplitis espinachi* has not been encountered outside the ACG dry forest, despite massive and multi-habitat Malaise trapping in Costa Rica by two decades of intensive Hymenoptera inventory (I. D. Gauld and P. Hanson, personal communication) and sporadic rearing of caterpillars throughout Mesoamerica.

The breeding biology of *Microplitis espinachi* is essentially identical to that described above for *Microplitis figueresi* above, except for the species of caterpillars that it parasitizes, and that it appears to frequent caterpillars in slightly more open and insolated places. Also, the cocoons of the two species (Fig. 2–3, 8) are not morphologically distinguishable in color,

shape, size or the pattern of the way they stick together.

As mentioned above, the 1978–2000 ACG dry forest inventory has reared 12,994 wild-caught sphingid caterpillars of 73 species through the end of 2000. Of these, only 6 species of *Manduca* (out of 2,644 *Manduca* caterpillar rearings of 11 species), *Sphinx merops* (13 rearings), and *Agrius cingulata* (70 rearings) are frequently parasitized by *Microplitis espinachi.* The 6 *Microplitis espinachi* records from *Erinnyis ello,* the 3 from *Cocytius duponchel,* and the 6 records from *Perigonia ilus* (Table 1) are natural "errors" in the same sense as is the single record of *Microplitis figueresi* reared from *Xylophanes turbata.* We conclude that *Microplitis espinachi* is a specialist dry forest parasite on certain species of *Manduca* and species in the two genera *Sphinx* and *Agrius* (which are monospecific in the ACG).

The species of *Manduca, Agrius* and *Sphinx* that are parasitized by *Microplitis espinachi* share habitat (old fields, very young secondary succession, pasture edges) but only occasionally overlap on species of food plants. They live in the more insolated and drier part of the overall habitat, in contrast to the hosts of *Microplitis figueresi* parasitizing the *Erinnyis* species feeding on foliage of *Sebastiana pavoniana* and *Stemmadenia obovata* in the more shady understory of older secondary succession. However, it is commonplace to find all five of these genera of sphingid caterpillars living within a few meters of each other in essentially the same habitat.

In the ACG dry forest, many rearings of *Manduca rustica, M. muscosa, M. corallina, M. lefeburii, M. occulta* and *M. hannibal* have generated *Microplitis espinachi* records in significant numbers. However, *Manduca lanuginosa* (n = 847, one *Microplitis*), *M. dilucida* (n = 654, three *Microplitis*), and *M. florestan* (n = 395, ten *Microplitis*) are conspicuously under-used despite their food plants and caterpillar locations being thoroughly intertwined with those of the six *Manduca* species that are most heavily used by *M. espinachi.* This may be due to extreme habitat specialization by *M. espinachi.* All ten records of *M. espinachi* on *Manduca florestan,* and all 31 records for parasitized *Manduca rustica*—the caterpillars of both may be found from deep shade to fully insolated sites—were from individual plants less than 2 meters tall and with fully insolated crowns. *Manduca lanuginosa* caterpillars are virtually always on plants growing in light shade on forest edges rather than in full sun, and they have no *M. espinachi* records at all.

The 9–15% parasitization of *Agrius cingulata* and *Sphinx merops*—the former feeding on insolated Convovulaceae crowns and the latter on insolated herbaceous mints (Lamiaceae) and *Lantana camara* Linnaeus (Verbenaceae) bushes—reinforces our perception of this pattern of host choice. All three of the natural "errors" recorded in Table 1 (*Cocytius duponchel, Erinnyis ello, Perigonia ilus*) were individual caterpillars in very insolated circumstances. The five records from *E. ello* were all from caterpillars on the crowns of *Manihot* and *Carica* growing in full sun less than two meters above the ground. However, this needs to be counterbalanced by the observation that there are at least 10 other species of sphingid caterpillars that also occur in insolated ACG dry forest habitats and have not (yet) been found attacked by *M. espinachi.* Also, the records of *M. espinachi* on *Manduca lefeburii* on *Casearia corymbosa* Kunth., *Casearia arguta* H. B. and K. and *Casearia sylvestris* Sw. (Flacourtiaceae) are all from caterpillars living within crowns of plants on forest edge or even in the forest edge understory.

While *M. figueresi* parasitizes caterpillars feeding on plants with milky latex (Table 2), the hosts of *M. espinachi* appear to have nothing in common: Annonaceae, Asteraceae, Bignoniaceae, Caricaceae, Convolvulaceae, Euphorbiaceae, Flacour-

tiaceae, Rubiaceae, Solanaceae, Verbenaceae (http://janzen.sas.upenn.edu).

The two "errors" of parasitization of *Cocytius duponchel* caterpillars (feeding on Annonaceae) are instructive. In both cases, the *M. espinachi* larvae emerged over a period of 48 hours and each individual larva struggled for nearly a half hour to get through the thick cuticle. Many of the wasp larvae failed to spin normal tightly closed and strong-walled cocoons.

The suite of caterpillars regularily attacked by *Microplitis espinachi* is also attacked by a small zoo of Tachinidae (*Drino rhoeo* (Walker), *Drino piceiventris, Metavoria* spp., *Leschenaultia* sp. 12, *Chetogena scutellaris* (Townsend), *Belvosia* sp. 6), Ichneumonidae (*Tricyphus respinozai* Ward and Gauld, *Cryptophion manueli* Gauld) and Eulophidae (*Euplectrus walteri* Schauff). However, there is only one braconid record (*Glyptapanteles* sp.) other than *Microplitis espinachi.* This record is probably in itself a "natural error". None of these species of tachinids is highly host-specific, while the parasitic Hymenoptera are.

Conura convergea (Fig. 3) chalcidids attack the cocoons of *Microplitis espinachi* just as they do the cocoons of *Microplitis figueresi. Mesochorus angustistigmatus* likewise attacks *Microplitis espinachi* just as it does *Microplitis figueresi.* There is also one record of a tiny perilampid wasp that emerged from the cocoons of *M. espinachi* from a *Manduca rustica* brought into captivity long before its *Microplitis* larvae emerged from the caterpillar. This single record out of hundreds of *Microplitis* records may suggest that this is a generalist hyperparasite, or at least that this host is not part of its normal host range.

Newly spun *Microplitis espinachi* cocoons are sought at night by females of *Acrolyta stroudi* (Ichneumonidae), while the caterpillar is still "alive" and hanging motionless on a twig (Fig. 8). It is not known if older cocoons can be located by this wasp. The cluster of *Microplitis espinachi* cocoons in Fig. 8 had eleven female *Acrolyta* wasps walking over its surface. Each wasp was territorial about its set of 5–10 cocoons and did not permit the others to walk onto them. The wasps remained in place, walking and ovipositing, throughout the perturbations of capturing the caterpillar, breaking off its branch, and carrying it in a plastic bag for an hour bouncing on a belt loop, and through an hour of photography in the laboratory. Oviposition was directly into the end or side of the cocoon. The daughter wasps eclosed 16–24 days later. There was no suggestion of dormancy. This wasp probably parasitizes other species of ACG dry forest Braconidae in the cocoon stage. This wasp has been seen on only three occasions, but it is a candidate to be a parasite of *Microplitis figueresi* as well.

Microplitis marini.—Only one other species of gregarious *Microplitis* has been encountered among parasite rearings from more than 162,000 wild-caught caterpillars in the ACG dry forest, rain forest, cloud forest, and intergrades. Of 71 rearing records of *Xylophanes tersa* (Sphingidae), only 7 last instar larvae produced *Microplitis marini* (http://janzen.sas.upenn.edu). The rearing records range from 500–1000 m rainforest to cloud forest, but always in early stages of succession (*Xylophanes tersa* feeds on herbaceous Rubiaceae in insolated sites). *M. marini* has been reared from no other species of caterpillar in Costa Rica; in Arizona it has been reported from *X. falco* (Fig. 5), a close congener of *X. tersa.* The single other Costa Rican rearing record of *M. marini* is from a last instar *Xylophanes tersa* caterpillar from near the town of Las Alturas at 1,000 m elevation on the Pacific side of Costa Rica (Marianella Segura, personal communication). This habitat is identical to that of 5 of the 7 ACG *M. marini* records, and the same habitat from which came the three single Malaise trap records of *M. marini* cited under its description above.

Microplitis marini cocoons are distinctive

for their rust red color and for being spun in a tightly packed solid clump (Fig. 5). The clumps result from the larvae emerging through the caterpillar cuticle in 1–3 patches, rather than scattered along the back of the caterpillar as is the case with *M. figueresi* and *M. espinachi.* This clump of cocoons is "glued" very tightly to the back of the caterpillar as well as to each other, and cannot be pulled off without tearing the cuticle of the caterpillar. They are formed on the caterpillar when it is standing upright (rather than hanging below the branch as is normal for *M. figueresi* and *M. espinachi*), *X. tersa* caterpillars often perch upright on the ground and on very low vegetation, both when unparasitized and when the *M. marini* larvae are emerging.

Fifty-four of the 71 ACG rearing records for *Xylophanes tersa* are from dry forest. Since *M. marini* parasitized none of them, it is likely that it is not a dry forest wasp. It has never been collected in more than 30 Malaise trap-years of ACG dry forest. It may, however, be significant that the habitat of its host in the rain forest, cloud forest, and intergrades—very early secondary succession—is the driest, sunniest and warmest microhabitat available. There is no suggestion that it parasitizes any of the other 15-plus species of *Xylophanes* (from more than 1,300 wild-caught rearings) and many tens of other species of Sphingidae that occupy the ACG rainforest and cloud forest. It is hyperparasitized by a single unidentified species of *Mesochorus* (Ichneumonidae).

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