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Hymenopteran parasitoids on fruit-infesting Tephritidae (Diptera) in Latin America and the southern United States: Diversity, distribution, taxonomic status and their use in fruit fly biological control

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Abstract

We first discuss the diversity of fruit fly (Diptera: Tephritidae) parasitoids (Hymenoptera) of the Neotropics. Even though the emphasis is on *Anastrepha* parasitoids, we also review all the information available on parasitoids attacking flies in the genera *Ceratitis*, *Rhagoletis*, *Rhagoletotrypeta*, *Toxotrypana* and *Zonosemata*. We center our analysis in parasitoid guilds, parasitoid assemblage size and fly host profiles. We also discuss distribution patterns and the taxonomic status of all known *Anastrepha* parasitoids. We follow by providing a historical overview of biological control of pestiferous tephritids in Latin American and Florida (U.S.A.) and by analyzing the success or failure of classical and augmentative biological control programs implemented to date in these regions. We also discuss the lack of success of introductions of exotic fruit fly parasitoids in various Latin American countries. We finish by discussing the most pressing needs related to fruit fly biological control (classical, augmentative, and conservation modalities) in areas of the Neotropics where fruit fly populations severely restrict the development of commercial fruit growing. We also address the need for much more intensive research on the bioecology of native fruit fly parasitoids.

Introduction

During the last two decades, there has been a notable resurgence in the use of biological control in various American countries where the production and commercialization of fruits and orchards are affected by the presence of tephritid pests. Costa Rica, Guatemala, El Salvador, Mexico, and the U.S.A. (Florida and Hawaii) have major programs for the liberation of parasitic Hymenoptera in areas with high infestations of tephritid species of quarantine importance such as *Ceratitis capitata* (Wiedemann), *Anastrepha suspensa* (Loew), *A. obliqua* (Macquart), and *A. ludens* (Loew). Similarly, in Argentina and Brazil where the pests of economic interest include *C. capitata*, *A. fraterculus* (Wiedemann), and (in Brazil only) *A. sororcula* (Zucchi), biological control has recently been incorporated as a valid alternative within fruit fly management programs.

The growing acknowledgment of the importance of fruit fly biological control is related to three events: (1) the perfection of mass rearing techniques for exotic and native parasitoids that allow the development of new control strategies involving inundative releases of these natural enemies; (2) the growing world rejection of the use of agrochemicals in fruit orchards due to their negative effects on the environment and human health; and (3) the present drive towards conservation of biodiversity in agroecosystems, through ecologically acceptable tactics such as the habitat manipulation in combination with the employment of natural enemies.

Natural enemies used in the biological control of tephritid pests include parasitic Hymenoptera and staphylinid predators. Predators have been used only rarely [28, 101], and to our knowledge have never been liberated in the Neotropics even though they have been collected there [30]. Most of the available information thus pertains to the relatively more host specific parasitic Hymenoptera that have been used against these plagues. Several reviews have recently been published that highlight various aspects of the role of parasitic Hymenoptera in the biological control of tephritids [29, 55, 66, 86, 126, 157, 162, 163]. However, there is still very little known about the importance of native Neotropical species as potential control agents.

The purpose of this work, therefore, is to: (1) provide information on the diversity, bioecology, distribution and taxonomic status of parasitoid species associated with tephritid fruit flies of the Neotropical region, (2) present detailed commentaries on results of prior classical biological control programs and the more recent augmentative release programs in tropical and subtropical America; and, in light of these last two points, (3) discuss future needs relative to fostering both classical and augmentative biological control of Neotropical tephritid pests as well as the conservation of their natural enemies.

Methods

Source of data

Major sources for this study are cited in Tables 1, 2, 5, and 6. There is an extensive body of literature on tephritid parasitoids of the Neotropical Region. The vast majority of these publications are of an applied nature, however, treating parasitoids of economically important pests of fruits. Data on parasitoids attacking hosts of no economic importance is minimal. But even for the relatively well studied parasitoids specifically used in biological control programs, we lack adequate data on host associations, particularly the range of non-pest flies they attack and non-commerical host plants on which they are found. Moreover, few parasitoids have actually been reared from isolated puparia to ensure true identity of the host [169]. Most of our records come from bulk samples of fruit, from which several species of flies and parasitoids emerge. Parasitoids reared under these conditions are often labelled as coming from the dominant tephritid in the samples. Hence, there are a number of published records as well as specimen data labels with erroneous host data. One of the most common problems in this regard results from the diverse array of drosophilid and other acalypterate dipterans that can occur in tephritid-infested fruit, particularly when samples of heavily-infested, fallen fruit are collected [169]. Without isolation of puparia (fortunately, tephritid puparia are fairly distinct), it is difficult to verify the correct host of parasitoids emerging from such samples. Most records of *Dicerataspis* Ashmead from tephritids, for example, actually refer to drosophilids, and all such records are excluded from the present study. Yet recently, Guimarães [62] and Guimarães *et al*. [63] reported *Dicerataspis flavipes* (Kieffer) from *Anastrepha amita* Zucchi, emphasizing how little we know about host family specificity of some of these parasitoid genera, and how careful we must be in generalizing about their host associations.

In addition to the emphasis on sampling of major pests on commerical fruits, there is a methodological bias in the way samples are processed that further limits our knowledge of parasitoid diversity [118]. Fruits are generally collected from the field and held over containers until full grown larvae have emerged. Emerging larvae fall to the bottom of the container, where they pupate in sand or other suitable substrate. Puparia are then sifted from the substrate and held in cages until flies and parasitoids emerge. Not surprisingly, therefore, most of our records pertain to koinobiont endoparasitoids that oviposit in the host larva and emerge from the puparium. Most sampling programs (including approximately 90% of those in our literature cited sections) thus have a built-in bias against detection of ectoparasitoids, egg parasitoids, and pupal parasitoids.

Data used for assessment of biological control programs in Latin America were obtained from numerous reviews and recent articles (listed in Tables 5 and 6). Several colleagues also provided information on current projects in their respective countries. The terms ‘direct’ and ‘indirect’ releases [53] have been adopted, and refer to the source of the imported, exotic parasitoid. Countries that first imported a particular species

Table 1. List and distribution of hymenopteran parasitoid on fruit-infesting Tephritidae (*Anastrepha* genus is not included) in Neotropical region.

Fruit-infesting Tephritidae species	Parasitoid species	Countries[1]	References
Ceratitis capitata	*Aceratoneuromyia indica*	AR	[114]
	Aganaspis pelleranoi	AR, CR	[121, 169]
	A. nordlanderi	CR	[169]
	Diachasmimorpha longicaudata	GU	[42]
	D. tryoni	GU	[75, 140]
	Doryctobracon crawfordi	GU, VE	[42, 84]
	D. areolatus	AR, VE, BR	[43, 84, 92]
	Fopius arisanus	CR	[169]
	Lopheucoila anastrephae	VE	[148]
	Odontosema anastrephae	CR	[169]
	Opius bellus	VE, BR	[61, 91]
	O. hirtus	CR	[159]
	Opius sp.	GU	[42]
	Pachycrepoideus vindemmiae	AR	[119]
	Pachyneuron sp.	AR	[151]
	Psyttalia concolor	CR	[152]
	Trichopria anastrephae	AR	[151]
	Utetes anastrephae	AR	[113]
Ragholetis ferruginea	*Opius bellus*	BR	[91]
Ragholetis turpiniae	*Aganaspis pelleranoi*	MX	[69]
	Biosteres near *sublaevis*	MX	[69]
	Dicerataspis spp.[2]	MX	[69]
	Opius hirtus	MX	[69]
Ragholetotrypeta pastranai	*Doryctobracon areolatus*	BR	[91, 92]
	D. brasiliensis	BR	[91, 92]
	Opius bellus	BR	[91, 92]
Toxotrypana curvicauda	*Doryctobracon toxtrypanae*	MX, CR, ES	[4, 170] (Ovruski and Zúñiga, unpublished data)
Zonosemata vittigera	*Diachasmimorpha sanguinea*	USA	[166]

[1]Countries: AR, Argentina; BR, Brazil; CR, Costa Rica; ES, El Salvador; GU, Guatemala; MX, Mexico; USA, United States of America; VE, Venezuela.
[2]Normal hosts are likely to be small Diptera as Drosophilidae [169].

from its aboriginal home participated in direct releases. Those that subsequently obtained species from a country to which it had previously been imported engaged in indirect releases.

The data on hosts and parasitoids presented here cover tropical and subtropical America, from southern Texas and Florida to northern Argentina. This area coincides with the native distribution of species in the genus *Anastrepha* Schiner [70]. *Anastrepha* is endemic to the New World, with approximately 180 described species. The plant hosts for many of these species are unknown, and parasitoids have been reared from even fewer of these species. For those species of *Anastrepha* from which parasitoids have been reared, data on host plants and larval feeding sites were extracted from publications by Norrbom and Kim [116], Hernandez-Ortiz [68] and Hernandez-Ortiz and Aluja [70]. The number of families, genera, and species of hosts attacked by all known *Anastrepha* parasitoids was obtained from Bouček [16, 17], DeSantis [36–38], Krombein *et al*. [88], Duan *et al*. [39], and the literature cited in Tables 2, 4, and 5.

Nomenclature for parasitoids follows Johnson [83], Wharton [164, 165], Ronquist [129], Gibson *et al*. [54] and Wharton *et al*. [168, 169]. To facilitate use of older literature on Neotropical parasitoids, some information is also provided on nomenclatural changes and some of the more obvious misidentifications are noted. Reports of *Opius trimaculatus* Spinola [34–36, 89], for example, have been excluded because these records probably represent a misidentification of either *Opius bellus* Gahan or *Utetes anastrephae* (Viereck) [167].

Analysis of data

Following Mills [107] and Ehler [41], we believe the guild should be considered the building block for the community of parasitoids attacking a particular host.

Table 2. List and distribution by country of *Anastrepha*'s parasitoid species.

Parasitoid family	Parasitoid species	Countries[1]	References
Braconidae	*Asobara anastrephae*	CO, BR	[6, 20, 21, 91, 92, 94]
	Fopius arisanus	CR	[170]
	Diachasmimorpha longicaudata	GU, MX, CR, USA , TR, BR, NI, ES, AR	[4, 14, 23, 42, 82, 139]
	Doryctobracon anastrephilus	USA	[8, 10]
	D. areolatus	USA, CR, AR, GU, BR, MX, TR, CO, VE, ES	[6, 9, 14, 20, 42, 58, 59, 71, 82, 84, 87, 113, 114, 118, 119, 121, 123, 132, 170, 171]
	D. auripennis	PA	[166]
	D. brasiliensis	BR, AR	[43, 58, 87, 91, 132]
	D. capsicola	PA	[166]
	D. crawfordi	GU, CO, VE, MX, CR, ES	[4, 42, 71, 82, 84, 85, 121, 166, 171]
	D. fluminensis	BR, VE	[31, 32, 34, 59, 166]
	D. trinidadensis	TR	[166]
	D. zeteki	CR, VE, PA	[84, 166, 170]
	Doryctobracon sp.	VE	[84]
	Doryctobracon n. sp.	BR	[22, 153]
	Idiasta sp.	VE	[84]
	Microcrasis n. sp.	MX	[71]
	Microcrasis sp.	CO	[171]
	Nealiolus n. sp.	MX	[71]
	Opius bellus	CR, BR, AR, VE, PA, BE, TR	[20, 21, 43, 84, 132, 151, 167, 170]
	O. hirtus	MX, CR, DR	[69, 71, 166]
	Opius sp. near *bellus*	BR	[20, 21, 91, 92]
	Opius sp. 1 (from Venezuela)	VE	[84]
	Opius sp. 2 (from Venezuela)	VE	[84]
	Opius sp. 3 (from México)	MX	[59]
	Psyttalia concolor	USA, BO	[10, 152]
	Utetes anastrephae	MX, CO, VE, BR, AR, PR, ES, USA, GU, CR	[4, 10, 11, 20, 21, 42, 58, 71, 84, 87, 92, 113, 170, 171]
	U. vierecki	MX, PA	[166]
Diapriidae	*Coptera haywardi*	AR, MX	[36, 94, 142]
	Coptera sp.	MX	[104]
	Trichopria anastrephae	BR, AR	[33, 34, 151]
	Trichopria sp. 1	CR	[82]
	Trichopria sp. 2	USA	[8]
Figitidae	*Aganaspis daci*	USA	[10]
	A. pelleranoi	MX, CO, VE, BR, AR, CR, PE, ES, PA, BE, BO, GU	[4, 84, 87, 113, 119, 121, 132, 169–171]
	A. nordlanderi	CR, BR	[62, 169]
	Dicerataspis grenadensis	BR	[62]
	Lopheucoila anastrephae	TR, PA, MX, AR, BR	[62, 128, 158, 169]
	Lopheucoila sp.	MX	[71]
	Odontosema anastrephae	BR, CR, MX	[15, 95, 170]
	Odontosema n. sp.	MX	[71]
	Odontosema sp.	BR	[132]
Eulophidae	*Aceratoneuromyia indica*	CR, MX, CO, VE, AR, BO, NI, USA	[4, 78, 82, 84, 113, 152, 171]
Pteromalidae	*Pachycrepoideus vindemmiae*	BR, MX, USA , AR, CR, PR, ES, BO	[8, 11, 81, 119, 121, 132]
	Pachyneuron sp.	AR	[36]
	Spalangia cameroni	USA	[8]
	S. endius	USA	[8]

[1]Countries: AR, Argentina; BE, Belize; BO, Bolivia; BR, Brazil; CO, Colombia; CR, Costa Rica; ES, El Salvador; GU, Guatemala; MX, Mexico; NI, Nicaragua; PA, Panama; PE, Peru; PR, Puerto Rico; DR, Dominican Republic; TR, Trinidad; USA, United States of America (Florida); VE, Venezuela.

Table 3. Guilds and host range of *Anastrepha*'s parasitoid species.

Parasitoid guild				Host range (Diptera)[1] (mean ± SEM)			Parasitoid species represented	
No.	Host stage attacked	Feeder types	Parasitism modes	Family	Genera	Species	Family	Species
1	Egg	Endo	Koino	1	4	7	Braconidae	*Fopius arisanus*
2	Larva	Endo	Koino	1.1 ± 0.1a	2.2 ± 0.3a	5.7 ± 1.2a	Braconidae	*Asobara anastrephae*, *Diachasmimorpha longicaudata*, *Doryctobracon anastrephilus*, *D. areolatus*, *D. brasiliensis*, *D. crawfordi*, *D. trinidadensis*, *D. zeteki*, *Opius bellus*, *O. hirtus*, *Opius* sp. near *bellus*, *Psyttalia concolor*, *Utetes anastrephae*
							Figitidae	*Aganaspis daci*, *A. pelleranoi*, *A. nordlanderi*, *Lopheucoila* sp., *L. anastrephae*, *Odontosema* n. sp., *Odontosema* sp., *O. anastrephae*, *D. flavipes*
							Eulophidae	*Aceratoneuromyia indica*
3	Pupa	Endo	Idio	1.2 ± 0.2a	1.3 ± 0.3a	2.0 ± 0.6a	Diapriidae	*Coptera* sp., *C. haywardi*, *Trichopria* sp. 1, *Trichopria* sp. 2, *T. anastrephae*
4	Pupa	Ecto	Idio	6.0 ± 1.0b	13.0 ± 2.5b	18.0 ± 7.0b	Pteromalidae	*Pachycrepoideus vindemiae*, *Spalangia cameroni*, *S. endius.*

[1]Means in the same column followed by the same letter are not significantly different (Kruskal–Wallis test, $\alpha = 0.05$).

Our characterizarion of tephritid parasitoid guilds, however, is not entirely consistent with either Ehler's [41] definition of parasitoid guilds or the original definition given by Root [130]. Our inclusion of one of the exotic parasitoids now established in the Neotropics, *Fopius arisanus* (Sonan), results in a single species guild. Yet, parasitoid guilds are more reasonably defined as two or more sympatric species exploiting a given developmental stage of the host [41] or a group of species that exploit the same class of environmental resources in a similar way [130].

Known parasitoids of *Anastrepha*, whether native or introduced, were grouped by various biological attributes to facilitate discussion of tephritid parasitoid guilds. Characteristics that were most amenable for comparison with previous works [74, 107] included host stage attacked (egg, larval, pupal) and mode of parasitism (idiobiont, koinobiont, ectoparasitic, endoparasitic). Though information is incomplete for several species, most species could be scored because traits are often applicable to an entire genus or subfamily. Thus, all known eucoiline Figitidae are koinobiont endoparasitoids of larval cyclorrhaphous Diptera, emerging from the puparium. Similarly, the known species of the diapriine genera *Trichopria* Ashmead and *Coptera* Say are idiobiont endoparasitoids of pupae.

Means for the number of families, genera, and species of hosts attacked by all known *Anastrepha* parasitoids were calculated for each parasitoid guild, and compared across guilds (Table 3). Data were analyzed through a non-parametric Kruskal–Wallis test. All questionable host records were excluded from the analysis. These data, though relatively incomplete, nevertheless enable us to discuss the relevance of past generalizations that have been made about parasitoid guilds. They also highlight the major gaps in our knowledge of tephritid parasitoid guilds.

Where appropriate, means and standard errors are used as summary statistics for the discussion of parasitoid assemblage sizes associated with various *Anastrepha* species.

Diversity, distribution, and taxonomic status of parasitoids of fruit-infesting Tephritidae in the Neotropical region

Parasitoids of Tephritidae

The diversity of fruit-infesting tephritids in the Neotropics is high [50], but biological information on most species is lacking. Parasitoids have been reared from relatively few of these species, with most of the published records for parasitoids pertaining either to the Medfly, *C. capitata*, or to species in the genus *Anastrepha* [71, 91, 166, 169]. The data reported here (Tables 1 and 2) are thus highly biased towards *Anastrepha* and Medfly. Medfly is an exotic species, introduced to Latin America at least as far back as 1905. *Anastrepha* is endemic to the New World, with a few widespread species ranging throughout much of the Neotropics, and a large number of other species with more restricted distributions [70, 146, 147, 172]. Parasitoids have been associated with 26 different species of *Anastrepha*, and there are seven records from '*Anastrepha* sp.' that may represent additional species (Table 4).

From the Neotropical Region, 46 parasitic Hymenoptera have been recorded from members of the genus *Anastrepha* (Table 2), and 18 have been recorded from Medfly (Table 1). Parasitoids have been reared from five other native, fruit-infesting tephritids, namely *Rhagoletis ferruginea* Hendel, *R. turpiniae* Hernandez-Ortiz, *Rhagoletotrypeta pastranai* Aczél, *Toxotrypana*

Table 4. List of *Anastrepha* species associated with parasitoid guilds.

Anastrepha species	Larval feeding sites	Host plant range	Parasitoid assemblage size	Number of species in each parasitoid guild				References
				1	2	3	4	
A. alveata Stone	PU	M	1	—	1	—	—	[123]
A. amita Zucchi	PU	M	3	—	3	—	—	[62]
A. bahiensis Lima	PU	P	4	—	3	—	—	[20, 21, 62]
A. bistrigata Bezzi	PU	M	1	—	1	—	—	[92]
A. cordata Aldrich	PU	M	1	—	1	—	—	[71]
A. crebra Stone	SE	M	4	—	3	—	—	[71]
A. distincta Greene	PU	P	3	—	3	—	—	[20, 21, 82, 84]
A. fraterculus (Wiedemann)	PU	P	22	—	15	2	1	[15, 20, 32, 34, 42, 58, 71, 84, 87, 94, 113, 119, 128, 132, 151, 158, 166, 169, 171]
A. interrupta Stone	PU	M	2	—	2	—	—	[10]
A. leptozona Hendel	PU	O	2	—	2	—	—	[20, 21]
A. ludens (Loew)	PU	P	9	—	5	2	1	[4, 23, 42, 59, 71, 78, 81, 104]
A. obliqua (Macquart)	PU	P	14	—	10	1	—	[4, 20, 23, 42, 59, 71, 84, 87, 92]
A. ornata Aldrich	PU	O	2	—	2	—	—	[42, 171]
A. manihoti Lima	ST	M	1	—	1	—	—	[20, 21]
A. montei Lima	SE	M	1	—	1	—	—	[58]
A. parallela (Wiedemann)[1]	PU	M	1	—	—	—	—	[34]
A. pickeli Lima[1]	SE	M	1	—	—	—	—	[84]
A. pseudoparallela (Loew)	PU	M	3	—	2	—	—	[58, 62, 91]
A. rheediae Stone[1]	PU	M	1	—	—	—	—	[166]
A. schultzi Blanchard	PU	M	1	—	—	1	—	[94]
A. serpentina (Wiedemann)	PU	P	9	—	7	1	—	[32, 33, 42, 58, 82, 84, 166]
A. sororcula Zucchi	PU	O	3	—	3	—	—	[91, 92]
A. striata Schiner	PU	P	16	—	11	1	—	[4, 20, 42, 71, 77, 81, 84, 166, 169, 171]
A. suspensa (Loew)	PU	P	11	—	7	1	3	[8–10, 139, 166]
A. zenildae Zucchi	PU	M	2	—	2	—	—	[6]
Anastrepha n. sp. (from Venezuela)	PU	M	2	—	2	—	—	[84]
Anastrepha sp. (from Argentina)	PU	M	1	—	1	—	—	[119]
Anastrepha sp. (from Brazil)[1]	PU	M	1	—	—	—	—	[33]
Anastrepha sp. (from Colombia)	PU	M	1	—	1	—	—	[171]
Anastrepha sp. (from Costa Rica)	PU	M	1	—	1	—	—	[166]
Anastrepha sp. (from Mexico)	PU	M	1	—	1	—	—	[71]
Anastrepha sp. (from Panama)[1]	PU	M	1	—	—	—	—	[166]
Anastrepha sp. (from Trinidad)	PU	M	1	—	1	—	—	[128]

Larval feeding sites: PU, fruit pulp, SE, seed; ST, stem.
Host plant range: M, momophagous; O, olygophagous; P, polyphagous.
[1]*Anastrepha* species could not be associated with a guild due to lack of information on biology of parasitoids found.

curvicauda Gerstaecker, and *Zonosemata vittigera* (Coquillett) (Table 1). Six of the nine parasitoids reared from these other tephritid genera also attack various species of *Anastrepha*, but at least two of the parasitoid species, *Doryctobracon toxotrypanae* (Muesebeck) and *Diachasmimorpha sanguinea* (Ashmead), are more host specific. *D. toxotrypanae* is restricted to *T. curvicauda*, a tephritid of economic importance in the cultivation of papaya, and *D. sanguinea* is found only on hosts in the genus *Zonosemata* Benjamin. Parasitoids not known to attack *Anastrepha* have also been recorded from *Myoleja limata* (Coquillett), *Rhagoletis completa* Cresson, and *R. juglandis* Cresson in the southern portions of Arizona, Florida, and Texas [166]. The two walnut husk flies, *completa* and *juglandis*, extend well into Mexico, and it is quite likely that their parasitoids do as well. In addition to these records, we have seen several parasitoids reared from cucurbit-infesting species of *Blepharoneura* Loew collected by M. Condon, but specifics on these have not yet been published.

Of the 18 species of parasitoids recorded to date from Medfly, only six represent species introduced for biological control of various tephritid pests. One of these (*Pachycrepoideus vindemiae* (Rondani)) already occurred in this region prior to its introduction, and thus the source of records from Medfly is uncertain. The remaining 12 species are endemic to the New World, and although a few of these records still need verification (e.g. *Pachyneuron* sp.), rearings from isolated puparia clearly demonstrate that at least some of the New World species are capable of successfully attacking Medfly. As noted below in the section on biological control, however, Medfly is not heavily parasitized by either the introduced or the native species. With the possible exception of the eucoilines, the native parasitoids appear to be poorly adapted to Medfly.

Parasitoids of Anastrepha

Approximately 59% of the 46 parasitoid species recorded from *Anastrepha* belong to the family Braconidae, 19.5% to the eucoiline Figitidae, 10.8% to the Diapriidae, 8.6% to the Pteromalidae, and 2.1% to the Eulophidae. There are also some unpublished records from Eurytomidae. There are no confirmed records for Chalcididae, Ichneumonidae, and Eupelmidae, though these have been recorded from fruit-infesting tephritids in other regions [73, 136]. Within the Braconidae, 81.5% of the species belong in the Opiinae, 14.8% in the Alysiinae and 3.7% in the Helconinae.

Distribution patterns

Based on roughly equal frequency of sampling efforts reported to date, it is possible to make preliminary comparisons of the parasitoids of *Anastrepha* from four distinct regions. Of the species thus far recorded, 24% are known from Florida [8–10, 143, 144], 39% from Mexico [4, 5, 7, 59, 71, 77, 81, 95, 96, 104, 141, 142], 41% from Central America and the Caribbean [42, 82, 121, 166, 169, 170], and 65% from South America [1, 21, 22, 34, 36, 62, 63, 84, 91, 119, 132, 152, 153, 169, 171]. This is similar to the pattern for *Anastrepha*, with a few species native to Florida and Texas, and the greatest number of species occurring in South America [70, 147].

The only records of *Anastrepha* parasitoids from the U.S. are from Florida, where biological control programs against the introduced pest *A. suspensa* have been on-going since the 1970's. Not surprisingly, therefore, Florida has a 0.6 : 1 ratio of endemic species of the Neotropical region to introduced species. By contrast, South America has a 7.5 : 1 ratio, Mexico has a 5 : 1 ratio, and Central America/Caribbean a 3.8 : 1 ratio. All four areas include the cosmopolitan species *P. vindemiae* and two exotic species introduced for biological control: *Diachasmimorpha longicaudata* (Ashmead) and *Aceratoneuromyia indica* (Silvestri). *Spalangia endius* Walker and *S. cameroni* Perkins, both recorded from *Anastrepha* in Florida, are also virtually cosmopolitan, though rarely reared from tephritids.

Of the 37 native species listed in Table 2, 24% are widely distributed in the Neotropical region, 22% are more regionally distributed, and 53% are thus far known only from a single country. Widely distributed species include the braconids *Doryctobracon areolatus* (Szépligeti) and *Utetes anastrephae* ranging from southern United States to Argentina, *Doryctobracon crawfordi* (Viereck) from central Mexico to northern South America, *O. bellus* from Costa Rica to Argentina, and the eucoilines *Odontosema anastrephae* Borgmeier, *Aganaspis pelleranoi* (Brèthes), and *Lopheucoila anastrephae* (Rohwer) from Mexico to the middle of South America. *Coptera haywardi* (Ogloblin) originally described from Argentina, was recently recorded from central Mexico, and *Aganaspis nordlanderi*

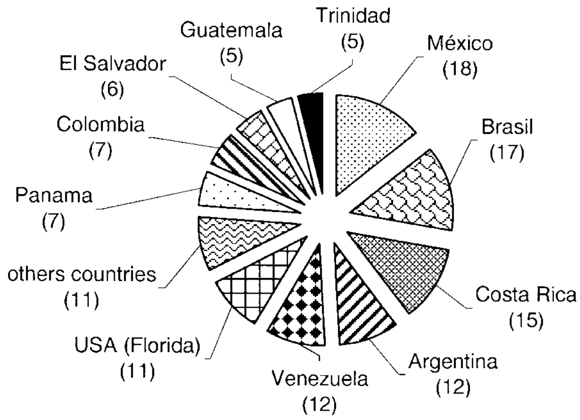

Figure 1. Actual number of *Anastrepha* parasitoid species in each neotropical country. Other countries: Bolivia (4 spp.), Puerto Rico (2 spp.), Belize (2 spp.) Peru (1 sp.), Nicaragua (1 sp.), and Dominician Republic (1 sp.).

(Wharton) is known from Costa Rica and Brasil. Species with a more regional distribution pattern include the braconids *Doryctobracon brasiliensis* (Szépligeti), *D. fluminensis* (Costa Lima), *D. zeteki* (Muesebeck), *Opius hirtus*, *Utetes vierecki* (Gahan), and *Asobara anastrephae* (Muesebeck), the diapriid *Trichopria anastrephae*, and one of the eucoilines in the genus *Dicerataspis*. Of those parasitoids recorded from a single country, only four species of *Doryctobracon* Enderlein have been identified with any certainty (Table 2). The remainder have been identified only to genus, and may either represent undescribed species or regional variants of more widespread species.

The actual number of all *Anastrepha* parasitoid species by country is illustrated in Figure 1. Mexico has the greatest representation with 18 species and Brazil has 17. The availability of results of the intensive sampling efforts in Costa Rica relative to other Central American countries is reflected in the total of 15 parasitoid species recorded from this country vs. five for Guatemala and two for Nicaragua. We were unable to discover any records of *Anastrepha* parasitoids from Chile.

Parasitoid guilds

The 32 *Anastrepha* parasitoids for which data could be scored were categorized into four parasitoid guilds (Table 3). All pupal parasitoids are by definition idiobionts. Two pupal parasitoid guilds were identified: pupal endoparasitoids and pupal ectoparasitoids. No egg parasitoids (ovipositing in and emerging from the host egg) are known. For all other stages attacked by tephritid parasitoids, idiobionts are ectoparasitic and koinobionts are endoparasitic. However, we know of no larval ectoparasitoids from the Neotropical region, though they are sometimes common elsewhere. Thus all remaining species treated here are koinobionts, attacking either the egg (Table 3, guild 1) or larval (guild 2) stage and emerging from the puparium. While parasitoids of guild 1, complete development in the same manner as guild 2 species, that is in the host pupae, there are sufficient differences in their oviposition behaviors to significantly effect their competitive interactions. Based on this niche difference we feel justified to separate the opiines into two guilds.

Guild 1 contains only a single species, *F. arisanus*, which oviposits in the host egg and emerges from the puparium. It has thus far been reared primarily from Medfly and *Anastrepha* especies, with *A. striata* Schiner representing 99% of all emerged *Anastrepha* adults [170]. From an evolutionary standpoint, this guild could be defined as synthetic [40] because the association of *arisanus* with both Neotropical hosts and with Medfly is a result of human activity. This species was introduced from Southeast Asia to Hawaii for control of Oriental fruit fly and then from Hawaii to Costa Rica for control of Medfly (Table 5). Nevertheless, there are indications that other parasitoids may have this same mode of attack [124, 160, 165], and we therefore predict that some of such species will be found in the Neotropical region.

Guild 2 comprises a large group of mostly braconid and eucoiline solitary parasitoids that oviposit in the host larva and emerge from the puparium. The only gregarious parasitoids in this guild are the introduced eulophids *A. indica* and *Tetrastichus giffardianus* Silvestri. We have not listed *T. giffardianus* in Table 3, however, because reports of its establishment in the Neotropics [49] need confirmation. Largely contrary to the findings of Hawkins [64], koinobionts are clearly the more typical parasitoids of these concealed hosts, rather than idiobionts, even when sampling bias is taken into account.

From a co-evolutionary standpoint, guild 2 can be defined as a restructured guild [40], containing both native and exotic species. Currently, most of the parasitoids in guild 2 are native to the Neotropics. Some of these, including members of the genus *Doryctobracon*, which represent 27% of all species in this guild, share a close evolutionary history with *Anastrepha*. Over the last 60 years, however, there has been a continuous introduction of exotic species for biological control of tephritid pests, and 18% of the species belonging to this guild are now exotic. These, obviously, do not share a co-evolutionary history with *Anastrepha*. The most commonly encountered and widely established exotic species are *D. longicaudata* and *A. indica*. Recent introductions for augmentation programs, however, may soon change this picture. Most of the exotic parasitoids introduced to Latin America were either cultured on Medfly or directly field released. Several of those not currently believed to be established, however, were shown to be capable of developing on *Anastrepha* under laboratory conditions. For example, at least three of the species sent to Puerto Rico from Hawaii, *Dirhinus giffardii* (Silvestri), *Psyttalia humilis* (Silvestri), and *Doryctobracon tryoni* (Cameron) were successfully reared in the laboratory on *Anastrepha*.

The idiobiont pupal parasitoids belonging to guilds 3 and 4 (Table 3) all attack the host after pupation in the soil. Guild 3 consists of up to five endoparasitic diapriids belonging to the genera *Coptera* and *Trichopria*. Both *Coptera* and *Trichopria* are large, poorly studied genera (as noted below), and the exact number of species reared to date from *Anastrepha* is thus somewhat uncertain. This is a natural guild, as it consists of native species from the Neotropical region attacking a single developmental stage of *Anastrepha* in the host's native home. Guild 4 is comprised of three polyphagous, ectoparasitic pteromalids, and shows significant differences ($\alpha = 0.05$, Kruskal–Wallis test) from guild 1 and 2 in the three levels of host range (family, genus, and species) (Table 3). Guild 4 is not a 'natural guild' since these cosmopolitan species are not endemic to the Neotropics and lack a co-evolutionary history with *Anastrepha*. This group cannot be readily classified as a restructured guild, either, since the members appear to be cosmopolitan despite the fact that they have been purposefully bred and released for various biological control programs. All three species, *P. vindemiae*, *S. endius*, and *S. cameroni*, are known primarily as parasitoids of synanthropic flies, e.g. in poultry sheds [16, 17, 57, 110]. Hence, they might best be considered as a synthetic or anthropogenic guild [40], associated in this case with increased availability of puparia under certain cultivated conditions, even though we do not know if their presence in the Neotropical region is due to man's interference.

Parasitoid assemblage size

Data on parasitoid assemblage size is summarized in Table 4 for the various *Anastrepha* hosts. Assemblage size varies from 1 to 22 parasitoid species per host fly species (mean $= 3.8 \pm 0.9$), with obvious differences between the major pest species (*A. fraterculus*, *A. ludens*, *A. obliqua*, *A. serpentina* (Wiedemann), *A. striata*, and *A. suspensa*: range = 9–22) and the remainder (range = 1–4). Assemblage size for Medfly (18 species: Table 1) is comparable to that for *Anastrepha* pests. When the species of *Anastrepha* are categorized by host plant range (Table 4), there is a remarkable difference in assemblage size between polyphagous species (mean $= 10.8 \pm 2.34$) and both oligophagous (mean $= 2.3 \pm 0.33$) and monophagous species (mean $= 1.5 \pm 0.24$). Assemblage sizes for parasitoids of the more poorly sampled oligophagous and monophagous species of *Anastrepha* correspond favorably with what Hawkins [65] reported for tephritids with endophytic, non-galling larvae.

Records for idiobionts are confined almost exclusively to the six well-studied, polyphagous pest species. The sole exception is the record by Loiácono [94] for a diapriid on the monophagous *A. schultzi* Blanchard. The six pest species have an average of 9.2 ± 3.3 koinobionts and 2.2 ± 1.2 idiobionts. These data thus suggest that *Anastrepha* is attacked mainly by the koinobiont members of guild 2, with relatively few records from the idiobionts of guilds 3 and 4 (and only one species in guild 1). The disparity between koinobionts and idiobionts may be due to sampling bias since, as noted above, puparia are rarely field collected in sampling programs for tephritid parasitoids. However, regardless of whether they fall into our guild 3 or 4, the number of the pupal parasitoids thus far recorded for the Neotropical region is considerably less than the number known from the Palaearctic region [73]. The disparity between regions may also represent a sampling bias, since pupal parasitoids have been more thoroughly sampled in the Palaearctic region. Increased sampling effort should therefore uncover more of such species in the Neotropics, decreasing the disparity between regions. A less likely, alternative hypothesis that remains to be tested is that pupal parastioids (especially the polyphagous ones) are less speciose in the tropics than in the north temperate regions. As noted by Hoffmeister [73] and others, at least for the Palaearctic region, most of the parasitoid species that attack the pupal stage are more habitat than host specific, and thus can parasitize a wide array of cyclorrhaphous Diptera. Our guild 4 fits this pattern nicely. Guild 4 is made up exclusively of polyphagous species only rarely associated with tephritids. *P. vindemiae*, for example, has been reared from the pupae of 32 species in eight families of Diptera

Table 5. Chronological summary of introduced exotic parasitoid species into American countries to *Anastrepha* spp. and *Ceratitis capitata* biological control.

Introduction years	Parasitoid[1]	Exporting country	Importing country	Target fruit fly species	Parasitoid status			References
					Released	Recovered	Established	
1935–1937	*Diachasmimorpha fullawayi*	Hawaii, USA	Puerto Rico	*A. suspensa* and *A. obliqua*	Yes	Yes	?	[11]
	D. tryoni		Puerto Rico	*A. suspensa* and *A. obliqua*	Yes	No	No	[11]
	Dirhinus giffardii		Puerto Rico	*A. suspensa* and *A. obliqua*	Yes	No	No	[11]
	Psyttalia fletcheri		Puerto Rico	*A. suspensa* and *A. obliqua*	Yes	No	No	[11]
	P. concolor		Puerto Rico	*A. suspensa* and *A. obliqua*	Yes	No	No	[11]
	Tetrastichus giffardianus		Puerto Rico	*A. suspensa* and *A. obliqua*	Yes	No	No	[11]
1937	*Diachasmimorpha tryoni*	Hawaii, USA	Brazil	*Anastrepha* spp. and *C. capitata*	?	?	?	[29]
	Psyttalia fletcheri		Brazil	*Anastrepha* spp. and *C. capitata*	?	?	?	[29]
	Tetrastichus giffardianus		Brazil	*Anastrepha* spp. and *C. capitata*	Yes	?	?	[29, 47]
1947	*Tetrastichus giffardianus*	Brazil	Argentina	*Anastrepha* spp. and *C. capitata*	Yes	No	No	[118]
1954	*Fopius arisanus*	Hawaii, USA	Mexico	*A. ludens*	Yes	No	No	[77]
1954–1955	*Fopius vandenboschi*	Hawaii, USA	Mexico	*A. ludens* and *A. obliqua*	Yes	?	?	[77]
	Diachasmimorpha longicaudata		Mexico	*A. ludens* and *A. obliqua*	Yes	Yes	Yes	[77]
	Psyttalia incisi		Mexico	*A. ludens* and *A. obliqua*	Yes	No	No	[77, 167]
1955	*Aganaspis daci*[2]	Hawaii, USA	Costa Rica	*C. capitata*	Yes	Yes	?	[72, 169]
	A. daci		Mexico	*A. ludens* and *A. obliqua*	Yes	?	?	[79, 81]
	Aceratoneuromyia indica		Mexico	*A. ludens* and *A. obliqua*	Yes	Yes	Yes	[29, 79, 80]
	A. indica		Costa Rica	*C. capitata*	Yes	Yes	?	[152, 162, 170]
	Fopius arisanus		Costa Rica	*C. capitata*	Yes	Yes	Yes	[75, 170]
	F. vandenboschi		Costa Rica	*C. capitata*	Yes	Yes	?	[170]
	Diachasmimorpha longicaudata		Costa Rica	*C. capitata*	Yes	Yes	Yes	[162, 170]
	D. tryoni		Costa Rica	*C. capitata*	Yes	?	?	[29]
	Dirhinus giffardii		Mexico	*A. ludens* and *A. obliqua*	Yes	Yes	No	[77]
	D. giffardii		Costa Rica	*C. capitata*	Yes	No	No	[72]
	Psyttalia incisi		Costa Rica	*C. capitata*	Yes	No	No	[72, 79]
1956	*Psyttalia concolor*	Italy	Costa Rica	*C. capitata*	Yes	Yes	?	[72, 170]
1957	*Aceratoneuromyia indica*	Mexico	Guatemala	*C. capitata*	?	?	?	[78]
1958	*Aceratoneuromyia indica*	Mexico	Nicaragua	*Anastrepha* spp. and *C. capitata*	Yes	Yes	Yes	[152]
	Diachasmimorpha longicaudata	Costa Rica	Nicaragua	*Anastrepha* spp. and *C. capitata*	Yes	Yes	Yes	[152]
1960	*Fopius arisanus*	Hawaii, USA	Peru	*C. capitata*	?	?	?	[13]
	Diachasmimorpha longicaudata		Peru	*C. capitata*	?	?	?	[13]
	Dirhinus giffardii		Peru	*C. capitata*	?	?	?	[13]
	Tetrastichus giffardianus		Peru	*C. capitata*	?	?	?	[13]
1961	*Aceratoneuromyia indica*	Mexico	Argentina	*C. capitata* and *A. fraterculus*	Yes	Yes	Yes	[3, 118, 150]
	Fopius arisanus		Argentina	*C. capitata*	Yes	No	No	[118]
	Diachasmimorpha longicaudata		Argentina	*C. capitata* and *A. fraterculus*	Yes	Yes	Yes	[118, 150]
1969	*Aceratoneuromyia indica*	Costa Rica	Bolivia	*C. capitata* and *Anastrepha* spp.	Yes	Yes	Yes	[3, 12, 125, 152]
	Diachasmimorpha longicaudata		Bolivia	*C. capitata and Anastrepha* spp.	Yes	?	?	[12, 67, 125]
	Psyttalia concolor[3]		Bolivia	*C. capitata* and *Anastrepha* spp.	Yes	Yes	Yes	[3, 12, 152]
1970	*Aganaspis daci*	?, USA	Colombia	*Anastrepha* spp.	?	?	?	[152]
	Aceratoneuromyia indica		Colombia	*Anastrepha* spp.	?	?	?	[152]

	Dirhinus giffardii		Colombia	*Anastrepha* spp.	?	?	?	[152]
	Psyttalia concolor		Colombia	*Anastrepha* spp.	?	?	?	[152]
1971	*Aceratoneuromyia indica*	Costa Rica	Nicaragua	*C. capitata*	Yes	?	?	[170]
	A. indica		Panama	*Anastrepha* spp. and *C. capitata*	Yes	?	?	[170]
	Diachasmimorpha longicaudata		Panama	*Anastrepha* spp. and *C. capitata*	Yes	?	?	[170]
	D. longicaudata		El Salvador	*Anastrepha* spp. and *C. capitata*	Yes	Yes	Yes	[121, 127, 170]
	Dirhinus giffardii		Bolivia	*C. capitata*	Yes	?	?	[12, 67, 125]
	Psyttalia concolor		Panama	*C. capitata* and *Anastrepha* spp.	Yes	?	?	[170]
	P. concolor		El Salvador	*C. capitata* and *Anastrepha* spp.	Yes	?	?	[67, 170]
	P. concolor		Guatemala	*C. capitata* and *Anastrepha* spp.	?	?	?	[67]
1972	*Diachasmimorpha longicaudata*	Hawaii, USA	Florida, USA	*A. suspensa*	?	Yes	Yes	[10]
1974	*Diachasmimorpha longicaudata*	Hawaii, USA	Trinidad	*Anastrepha* spp.	Yes	Yes	Yes	[14]
1974–1975	*Fopius arisanus*	Hawaii, USA	Florida, USA	*A. suspensa*	Yes	No	No	[10]
1977–1979	*Dirhinus giffardii*	France	Florida, USA	*A. suspensa*	Yes	No	No	[10]
	Aganaspis daci		Florida, USA	*A. suspensa*	Yes	Yes	Yes	[10]
	Psyttalia concolor		Florida, USA	*A. suspensa*	Yes	Yes	?	[10]
1978	*Psyttalia concolor*	Costa Rica	Peru	*C. capitata* and *Anastrepha* spp.	?	?	?	[13]
1981–1982	*Diachasmimorpha fullawayi*	Camerron	Costa Rica	*C. capitata*	Yes	?	?	[145]
	Psyttalia perproximus		Costa Rica	*C. capitata*	Yes	?	?	[145]
	Fopius caudatus		Costa Rica	*C. capitata*	Yes	?	?	[145]
	F. silvestrii[4]		Costa Rica	*C. capitata*	Yes	?	?	[145]
1984	*Diachasmimorpha longicaudata*	El Salvador	Guatemala	*C. capitata*	Yes	Yes	Yes	[42]
1986	*Aceratoneuromyia indica*	Costa Rica	Argentina	*C. capitata*	Yes	Yes	Yes	[3, 118]
	A. indica	Mexico	Peru	*C. capitata*	?	?	?	[3, 13]
	Diachasmimorpha longicaudata	Costa Rica	Argentina	*C. capitata*	Yes	Yes	Yes	[118, 152]
1988	*Diachasmimorpha tryoni*	Hawaii, USA	Mexico	*A. ludens*	Yes	Yes	No	Cancino, pers. com.
1994	*Diachasmimorpha longicaudata*	Florida, USA	Brazil	*A. fraterculus*	Yes	Yes	Yes	[25, 26]
	D. tryoni	Hawaii, USA	Mexico	*C. capitata*	No	No	No	[24, 128]
1995	*Diachasmimorpha tryoni*	Mexico	Guatemala	*C. capitata*	Yes	Yes	?	[131] [131]
?	*Aceratoneuromyia indica*	Costa Rica	Peru	*Anastrepha* spp.	?	?	?	[67]
	A. indica		Venezuela	*Anastrepha* spp.	Yes	Yes	Yes	[67]
	A. indica		Trinidad	*Anastrepha* spp.	?	?	?	[67]
?	*Fopius persulcatus*	Hawaii, USA	Florida, USA	*A. suspensa*	No	No	No	[10]
	F. vandenboschi		Florida, USA	*A. suspensa*	Yes	Yes	?	[10]
?	*Diachasmimorpha tryoni*	Hawaii, USA	Florida, USA	*A. suspensa*	Yes	Yes	?	[10]
	D. longicaudata	Costa Rica	Venezuela	*Anastrepha* spp. and *C. capitata*	?	?	?	[67]
	Psyttalia fletcheri	Hawaii, USA	Florida, USA	*A. suspensa*	Yes	No	No	[10]
	P. incisi		Florida, USA	*A. suspensa*	Yes	Yes	?	[10]

[1]This table does not include the cosmopolitan species *P. vindemiae* due to uncertainty about its presence being due to deliberate introduction into Neotropical region.
[2]Although this parasitoid was reported as established in Costa Rica by Hernandez [72], its establishment is doubtful.
[3]Pending verification.
[4]This species was previously misidentified as *Fopius caudatus* (Szepligeti) [160].

[17, 88], and also as a hyperparasitoid [2, 122]. We are less certain about the five species in guild 3. With the exception of the very recently studied *C. haywardi* [142], little is known about their host ranges. One report [151] suggests that *T. anastrephae* can reproduce more easily on drosophilid than tephritid puparia, and some species of *Trichopria* have been recorded as hyperparasitoids [76].

The koinobiont specialists of guild 2 attack on average one family, two genera, and six species of hosts (Table 3). Potential alternate hosts in fleshy fruits include species in the other tephritid genera discussed above as well as drosophilids and lonchaeids. The parasitoid fauna of drosophilids and lonchaeids is very rich [154, 169], but unlike the situation for idiobionts, there is little or no cross-over of koinobiont parasitoids from drosophilids to tephritids. At least three of the *Anastrepha* parasitoids in guild 2 (*A. pelleranoi*, *O. anastrephae*, and *L. anastrephae*) can develop on Lonchaeidae, although the first two of these only rarely do so [170].

Anastrepha *host plant profile*

The majority (97%) of the *Anastrepha* species from which parasitoids have been reared breed in fleshy fruits (Table 4). The larvae of most species (88%) apparently develop in the pulp of the fruit and only 9% feed on the seeds. Assemblage sizes for pulp feeders is nearly identical to that for seed feeders when the six major pest species are excluded (all six are pulp feeders). Only one parasitoid species has been reared from *A. manihoti* Costa Lima the sole stem-infesting species of *Anastrepha* known to us.

Of the 25 described species of *Anastrepha* listed in Table 4, 32% are polyphagous, 56% monophagous (limited to fruit-bearing trees of a single genus), and the remaining 12% are oligophagous (confined mostly on one family of native host plants, such as *A. leptozona* Hendel on Sapotaceae and *A. ornata* Aldrich on Myrtaceae). Polyphagous species (the six pest species mentioned above plus *A. bahiensis* Costa Lima and *A. distincta* Greene) are found on a wide range of hosts from diverse families, and are especially abundant on plants introduced to the American continent such as *Mangifera indica* (L.) (Anacardiaceae), *Citrus* spp. (Rutaceae), *Coffea arabica* (L.) (Rubiaceae), and *Eriobotrya japonica* (Lindl.) and *Prunus* spp. (Rosaceae). Polyphagous species attack fruit from an average of 10.0 ± 1.3 host plant families, in addition to maintaining the large parasitoid assemblages noted above.

Parasitoids that are more broadly distributed in the Neotropical region are, not surprisingly, associated with a greater variety of hosts (both flies and plants). These include *D. areolatus* reared from 17 species of *Anastrepha* and from fruits representing 13 plant families, *U. anastrephae* from eight fly species and eight plant families, *D. crawfordi* from seven fly species and six plant families and *A. pelleranoi* from seven fly species and nine plant families. Conversely, parasitoids of limited distribution are often restricted to few plant species, and often one or two host flies. In the genus *Doryctobracon*, *D. capsicola* (Muesebeck) is known only from Panama, from a species of *Anastrepha* that feeds in the seed capsules of *Manihot esculenta* (Crantz) [112]. The Florida endemic *D. anastrephilus* (Marsh) is a native parasitoid of *A. interrupta* Stone on fruit of *Schoepfia chrysophylloides* ((Rich.) Planch.), but has also been reared on the introduced pest *A. suspensa* [10, 99]. Similarly, *D. zeteki* appears to have coevolved with *A. striata* on *Psidium* (L.) and possibly other Myrtaceae, but has also been reared from *A. fraterculus* [84, 166, 170]. *D. brasiliensis* also shows a strong preference for Myrtaceae, having been reared from the fruits of seven species in this family. It has been reared most frequently from *A. fraterculus* but also attacks *A. serpentina* and *A. sororcula*.

Three of the exotic species that were introduced for biological control of tephritid pests in the neotropics, *A. indica*, *D. longicaudata*, and *F. arisanus*, are well established. They have been reared from Medfly as well as most of the *Anastrepha* pests. There is no evidence for host plant fidelity for these species, as they have been reared from a wide variety of host plant families.

There are a number of fruit characteristics that may enhance parasitoid success, either by increasing attractiveness to the parasitoids or by facilitating detection of and oviposition in the host. Among factors believed responsible for this attraction (or success of attack irrespective of 'attraction') are thin pericarp, fleshy endocarp, specific aromas, and size [21, 60, 92, 93, 105, 115, 137]. Leyva *et al*. [93], for example, demonstrated experimentally that volatiles of certain citrus species were highly attractive to parasitoids but that this was not correlated with oviposition success. In grapefruit, however, a thick pericarp and large pulp to seed ratio may reduce effectiveness by inhibiting the parasitoid's ability to detect and successfully oviposit in all of the host larvae. Native Rutaceae, such as *Sargentia gregii* (Coult.) and *Casimiroa edulis* (Llave & Lex.), have more favorable characteristics, and this may be why they are able to maintain large and diverse associations of Neotropical parasitoids, such as those noted by Gonzalez-Hernandez and Tejada [59] on *A. ludens* from these host plants. Coffee, an exotic, heavily sampled plant in the Rubiaceae with seemingly favorable fruit characteristics for parasitoids, is only rarely attacked by *Anastrepha*.

Families such as Myrtaceae and Anacardiaceae also harbor large parasitoid assemblages. Each species of *Anastrepha* recorded from fruits of these families is attacked by 7.3 ± 2.2 and 6.2 ± 1.9 parasitoid species, respectively. In part, this high diversity reflects the fact that these families contain some of the most commonly sampled fruits, such as guavas and mangoes. Parasitoids have been reared from 22 species in the Myrtaceae, including the genera *Eugenia*, *Jambosa*, *Psidium*, *Feijoa*, *Campomanesia*, *Myrciaria*, and *Blepharocalyx*, whereas parasitoids reared from Anacardiaceae come almost exclusively from five species of *Spondias* (L.) (*S. mombin*, (L.) *S. dulcis* (Parkinson), *S. purpurea* (L.), *S. radkoferi* (J.D. Smith), and *S. venulosa*) (Mart.), and to a lesser extent *Mangifera* (L). Surprisingly, native Sapotaceae, which are also heavily sampled, have yielded significantly fewer parasitoids to date (an average of 2.7 ± 1.2 parasitoid species per *Anastrepha* host). Given these potential differences, direct comparison of native Sapotaceae, Myrtaceae, and Anacardiaceae in a controlled experimental setting should provide excellent opportunities for comparison of the effect of specific fruit characteristics on parasitoid attractiveness and oviposition success.

Only one species of parasitoid has been reared from fruit in the families Apocynaceae, Caricaceae, Guttiferae, Icacinaceae, Passifloraceae, and Rhamnaceae in the Neotropics. For at least some of these, secondary plant compounds may be responsible for decreased diversity, and this is certainly well documented for other insect groups such as Lepidoptera. Toxic plant compounds may decrease insect species richness on a given host plant by eliminating generalists, but at the same time may increase overall diversity by promoting specialists. In Apocynaceae and Caricaceae, toxins are associated with latex production, which may also provide physical inhibition. *Toxotrypana* Gerstaecker provides an excellent example of selection pressure for further specialization leading to successful attack on papaya (Caricaceae).

Taxonomic status of Anastrepha *parasitoids*

The known parasitoids of *Anastrepha* belong to five families of parasitic Hymenoptera: Braconidae, Figitidae (Eucoilinae), Diapriidae, Eulophidae, and Pteromalidae (Table 2). General information on braconid classification can be found in Wharton *et al*. [168], and specific information on the major parasitoids of fruit-infesting tephritids in Wharton [165]. Eucoiline parasitoids of tephritids were recently reviewed by Wharton *et al*. [169], and although there are no recent treatments of Diapriidae [83, 102], Masner and Garcia are preparing a synopsis of the Latin American fauna of Proctotrupoidea. Both *Coptera* and *Trichopria*, the two diapriid genera reported from tephritids, are exceptionally speciose and badly in need of revision. Eulophid parasitoids of Tephritidae belong to the Tetrastichinae, and the most relevant general review of this subfamily is by LaSalle [90]. The name *Pachycrepoideus vindemiae* is often used in its emended form (as *P. vindemmiae*) because Rondani changed the name a year after he proposed it. There appears to be some disagreement as to whether the emendation was justified or unjustified. Additional useful information on Eulophidae and Pteromalidae, including an excellent introduction to the literature on these groups, can be found in Gibson *et al*. [54] and the World Chalcidoidea Database compiled by Noyes [117]. Aside from a short paragraph of the Eucoilinae, the remainder of this section is devoted to the Braconidae.

Within the family Braconidae, parasitoids of Neotropical fruit-infesting Tephritidae are restricted to the subfamilies Opiinae, Alysiinae, and Helconinae. The Opiinae include exotic species in the genera *Fopius* Wharton and *Psyttalia* Walker, and native species in the genera *Doryctobracon*, *Utetes* Foerster, and *Opius* Wesmael. The genus *Diachasmimorpha* Ashmead contains one species group of introduced species and another species group that extends from the Nearctic into the northern part of the Neotropical region [165]. The Alysiinae include the endemic Neotropical genus *Microcrasis* Fischer and the cosmopolitan *Asobara* Foerster. *Microcrasis* has never been revised and most of the species (including at least one that has been reared from Tephritidae) are apparently undescribed. The genus *Asobara* is also badly in need of revision. Most species of *Asobara* are parasitoids of Drosophilidae [155], and are farily well studied biologically, but there is one species group of large-bodied individuals, endemic to the Neotropics [164], that contains at least some tephritid parasitoids (Table 2). Reports of other Alysiinae from Tephritidae need verification, though recently [149] a species of *Phaenocarpa* Foerster was reared from *A. distincta*. Members of the helconine tribe Brachistini normally attack Coleoptera [134, 135], but there are a few records from Tephritidae [71, 136]. The tropical brachistines have never been revised. Since there has been considerable taxonomic work on the Opiinae in recent years, some explanation of the resulting nomenclatural changes will be useful in matching names in older reports with those in newer ones.

O. bellus and *O. hirtus* belong to a complex of closely related species recently accorded separate subgeneric status [165]. The members of this group, *Opius* (*Bellopius*), are difficult to distinguish from one another, and it is likely that several more species within this group will eventually be reared from tephritid hosts. Fischer [45] placed these species in the genus *Desmiostoma* Foerster, but this generic name is more appropriately applied to a group of small agromyzid parasitoids [159].

O. bellus is a widespread species recorded from Belize to Argentina as well as Trinidad [166]. It is abundant in South America, and has been recorded from four species of *Anastrepha* on five families of host plants. This species has been interpreted fairly broadly in the past [166], in part because of color variation noted in the original description [52]. Recent studies in Brazil suggest that *O. bellus* may represent a complex of species, with some populations in northern Brazil (Amazonas) more specific to *Anastrepha* in *S. mombin* (Anacardiaceae) [20, 21, 91], while populations in central Brazil have a greater affinity for *A. fraterculus* in Myrtaceae [87] and *Anastrepha* spp. in *Prunus persica* (Rosaceae) [92]. Because of these differences, some recent reports refer to these parasitoids as *Opius* species near *bellus* or *Opius* sp. (Table 2). The situation is somewhat complicated by two additional available names for this species or group of species that are currently treated as synonyms of *bellus* [166]. Resolution of these problems is not possible with morphological studies alone, and may require crossing tests and/or analysis of genetic structure of the various populations.

A similar problem occurs in the genus *Utetes*. In the Nearctic, the tephritid genus *Rhagoletis* Loew, for example, has a complex of closely related species of *Utetes* that are very difficult to separate from one another [165, 166], and some of the proposed synonymies will almost certainly have to be revisited. It is possible that these parasitoids may eventually be shown to be as host specific as the *Rhagoletis*. Within the Neotropics, one widespread species, *U. anastrephae*, may similarly consist of a complex of sibling species, each relatively restricted in its distribution and host preferences. Widely cultivated host plants, however, provide opportunities for gene flow that complicate assessment of species status of individual populations.

The nomenclatural history of the name *Utetes* is also somewhat complicated, and most of the species have been treated in the applied literature as either *Opius* or *Bracanastrepha* Brethes. *Utetes* was first described by Foërster [46]. It was later treated as a synonym of *Opius* by Marshall [100] and this synonymy was accepted for almost 100 years. Fischer [44] subsequently recognized it as distinct by treating *Utetes* as a valid subgenus, but still retained it in the genus *Opius*. Wharton [161] eventually restored it as a separate genus. Wharton [161, 165] also noted that the Neotropical endemic group called *Bracanastrepha* was a derived species group within *Utetes*, and therefore treated *Bracanastrepha* as a synonym of *Utetes*. Wharton [161] also noted that *Bracanastrepha* could still be recognized as a distinct group within *Utetes* by treating it as a subgenus, but more work still needs to be done on the rest of the genus before a stable subgeneric classification can be proposed.

The history of the name *Psyttalia* is similar. Following its description by Walker [156], the name was essentially forgotten until Muesebeck [111] synonymized it with *Opius*. As with *Utetes*, Fischer [44] initially recognized it as a subgenus of *Opius* and Wharton [160] eventually restored it to full generic rank. The vast majority of the biological work on the included species is consequently published under the generic name *Opius*. For the purpose of this report, we recognize *P. humilis* and *P. perproxima* (Silvestri) as distinct species [167]. The two are very difficult to separate, however, and both have sometimes been synonymized with *P. concolor* (Szépligeti). Though this problem has received some attention in the past, further investigations are warranted.

The name *Doryctobracon* has been in widespread use since about 1980, following the works of Fischer [44, 45] and Wharton and Marsh [166]. Prior to that time, species were placed either in *Opius*, *Parachasma* Fischer, *Biosteres* Foerster, or (rarely) *Diachasma* Foerster. *Doryctobracon* is known almost exclusively from *Anastrepha*, and the species are separated largely on the basis of color. There has not been a good study of the effect of different hosts on color pattern, and as a consequence, slightly different color forms pose identification problems. This situation applies, for example, to *D. crawfordi* and *D. toxotrypanae*, which are very similar to one another, and both are also fairly similar to

D. trinidadensis (Gahan). One of the most widespread and frequently encountered species is *D. areolatus*. Some of the biological work on this species has been published under the names *cereus/cerea* Gahan and *tucumanus* Blanchard, now treated as synonyms of *areolatus* [120, 166].

For the tephritid parasitoids that have relatively recently been placed in *Fopius* and *Diachasmimorpha*, most of the available biological information is published under the generic names *Opius* or *Biosteres*. An important exception is some of the classical work on *D. tryoni* [122], in which the generic name *Diachasma* was used. A recent list of these species and their current combinations can be found in Wharton [165]. Particularly extensive biological data are available for the southeast Asian species *D. longicaudata* and *F. arisanus*, both now established in the Neotropics. A discussion of the extensive synonymy for *longicaudata* is provided by Wharton and Gilstrap [167]. Most of the early literature on *arisanus* was published under the name *oophilus* Fullaway, but prior to the description of *oophilus* [51], there was considerable confusion as to its identity relative to *F. persulcatus* (Silvestri) and *F. vandenboschi* (Fullaway). The name *persulcatus* applies to a species from India that to our knowledge has never been knowingly introduced to the New World. The record of an introduction of *persulcatus* to Florida [10] is quite possibly a result of the confusion over the application of this name to the species introduced to Hawaii.

The Eucoilinae are sometimes treated as a subfamily of the Cynipidae, but are often accorded separate family status. Recently, however, Ronquist [129] has offered compelling evidence that they should be treated as a subfamily of the Figitidae, and we have accepted that classification here. Within the Eucoilinae, genera such as *Dicerataspis*, *Lopheucoila* Weld, and *Odontosema* Kieffer are quite distinct and thus easily recognized, even though the species are still in need of some revision. Available data suggest that all three genera are Neotropical endemics. The remaining eucoiline parasitoids reported from Neotropical tephritid hosts are more problematic, as discussed by Wharton *et al*. [169]. Most of them cannot be satisfactorily placed to genus because many of the eucoiline genera have not been sufficiently well defined to permit placement of Neotropical species. *Ganaspis* Foerster is particularly problematic in this regard, as it affects the classification of the tephritid parasitoids currently placed in *Aganaspis* Lin.

Biological control of fruit flies in Latin America and the southern United States

Introduction

The history of biological control of fruit-infesting Tephritidae in Latin America began with the explorations of George Compere in 1904 [30]. Compere, hired by the state governments of California and Western Australia to collect natural enemies of insect pests, introduced braconid parasitoids and staphylinid predators from Brazil to Western Australia in 1904 to control Medfly. These failed to establish due to seasonal unavailability of hosts, and Compere returned to Brazil in 1905, where he collected more staphylinids. The beetles were successfully transported to Western Australia, but failed to establish due to negligence on the part of the person hired to maintain cultures in Compere's absence. Based on Compere's report of his 1904 collections, the South African entomologists Charles Lounsbury and Claude Fuller travelled to South America in 1905 to collect natural enemies of Medfly [35]. Fuller collected exclusively in Brazil, but Lounsbury also visited the areas around Buenos Aires and Montevideo on his return voyage. Lounsbury [97] concluded that Medfly had probably been introduced to Brazil relatively recently (the origin of Medfly was unknown at the time), and he was somewhat pessimistic about the value of the parasitoids and predators alone to control this pest. Lounsbury also noted that parasitism in larger, fleshy fruit was distinctly lower than in smaller fruits with large seeds. Lounsbury, Fuller, and Compere apparently collected either *D. areolatus* or *O. bellus*, but their parasitoids were misidentified as *O. trimaculatus*, a Chilean species with a similar color pattern.

These earlier explorations used South America as a source of natural enemies for other parts of the world. However, with the exception of Bermuda (which is not covered here), serious efforts to conduct biological control against tephritids within tropical and subtropical America did not begin until the 1930's. Many attempts at classical biocontrol of Medfly and various species of *Anastrepha* were made between the 1930's and 1980's. These were generally sporadic, and in nearly all cases, results still need to be verified. Nonetheless, these efforts led to the successful rearing and subsequent establishment of certain species. These programs were almost exclusively based on the use of hymenopterous parasitoids that had first been established in Hawaii, and which in turn served as the main source of supply for Latin America and Florida. The distribution of these species in at least 15 countries, as well as the development of classical tephritid biocontrol programs worldwide, was documented by Clausen [27, 29], Clausen *et al*. [28], Gilstrap and Hart [55], and Wharton [162, 163]. Additionally, several pilot programs have been developed in Costa Rica, Mexico, Guatemala, and the United States (Florida) to examine the effectiveness of augmentative releases of mass-reared parasitoids against tephritid pest populations. These programs began in the 1970's and are presently spreading to other Central and South American countries. The importance and evolution of augmentative biocontrol of fruit flies has been documented by Gingrich [56], Sivinski [138], Messing [106], Malavasi [98] and Purcell [126].

Historical overview

Introductions of Old World parasitoids for fruit fly biocontrol into Latin America and the southern United States are summarized chronologically in Table 5. Puerto Rico took the initiative in the 1930's, introducing about 18 parasitoid species to combat *A. obliqua* and *A. suspensa* [11, 29]. Six species were received from Hawaii, one from West Africa, and the remainder from Central and South American countries (Tables 5 and 6). The introductions from Hawaii represented indirect releases. The direct shipments from West Africa and Brazil resulted from a larger, USDA-sponsored foreign exploration effort targeting Medfly populations in Hawaii.

The next notable introduction was of *T. giffardianus* from Hawaii to Brazil in 1937 [47–49]. Though the intial shipment from Hawaii could be categorized as a classical biological control introduction, the program quickly developed into a mass rearing effort, perhaps the first of its kind for tephritid parasitoids in South America. As a result of the mass rearing program, *T. giffardianus* was released in large numbers in the state of São Paulo against Medfly and various *Anastrepha* pests over at least a 10 year period, and was also released in smaller numbers throughout Brazil as well as Argentina, Colombia, and Uruguay. During this period, there were also a few additional attempts to move Neotropical parasitoids between various countries, most notably from Argentina to Peru (Table 6).

The well-documented campaign against Oriental fruit fly in Hawaii [28] resulted in an extensive redistribution effort during which a number of parasitoids cultured in Hawaii were shipped to various localities in the U.S.A. and Latin America. The largest of these programs were in Mexico, Costa Rica, and Florida [10, 55, 77, 79–81]. The first shipments of parasitoids were sent from Hawaii to Mexico and Costa Rica in 1954 and 1955. Mexico's Secretary of Agriculture introduced seven species in eight states for the control of *A. ludens* and *A. obliqua* between 1954 and 1955. The most successful of the parasitoids were the braconid *D. longicaudata* and the eulophid *A. indica*, both larval parasitoids. The program in Costa Rica was a direct response to the establishment of *C. capitata* in Costa Rica and its subsequent expansion to the rest of Central America. Costa Rica's Ministry of Agriculture and Cattle, together with OIRSA, introduced nine parasitoid species in 1955: eight from Hawaii and one from Italy (Table 5). Laboratory colonies were established for five of these species, and beginning in 1960, Costa Rica provided these five species for release in 11 American countries. Most of the efforts were for the control of *C. capitata* and *Anastrepha* spp. in Central America (Nicaragua, Panama, El Salvador, Guatemala, and Trinidad), and for the control of *C. capitata* and *A. fraterculus* in South America (Argentina, Bolivia, Peru, and Venezuela). The species primarily released were *D. longicaudata*, *A. indica*, and the pupal parasitoid *P. vindemiae*. Between 1957 and 1961, Mexico also sent parasitoids to Nicaragua, Guatemala, and Argentina (Table 5). Shipments from Hawaii to Florida took place somewhat later (Tables 5 and 6), following the introduction of *A. suspensa* to Florida in 1965. Ultimately, 11 species were imported from Hawaii, France, and South and Central America between 1972 and 1979 [10].

A separate program for classical biocontrol of Medfly was undertaken in Costa Rica between 1981 and 1982 [55]. In an effort to obtain parasitoids that might be more host specific to Medfly, collections of tephritid natural enemies were made in Togo and Cameroon in West Africa [145]. Several species were introduced and directly released. This program also included the indirect introduction of *D. tryoni* from samples that were field-collected in Hawaii. The culturing and periodic releases of tephritid parasitoids, initiated in the 1960's, were still ongoing during this time. Thus, in conjunction with the classical biological control program, augmentative releases of *D. longicaudata*, *A. indica*, *P. concolor*, and *P. vindemiae* were also being made.

Most of the above programs, as noted, involved production and release of substantial numbers of insects. It

Table 6. Neotropical parasitoid species introduced in American countries for fruit fly biocontrol.

Parasitoid species	Country or region of origin	Exporting country	Importing country	Year of parasitoid introductions	Target fruit fly species	Status			References
						Released	Recovered	Established	
Aganaspis pelleranoi	Neotropical	Argentina	Peru	1942	*Anastrepha* spp.	Yes	Yes	Yes	[29, 118]
Doryctobracon areolatus	Neotropical	Panama	Puerto Rico	1935–1937	*Anastrepha* spp.	Yes	No	No	[11]
		Brazil	Peru	1942	*Anastrepha* spp.	Yes	No	No	[152]
		Argentina Trinidad	Florida, USA	1967	*A. suspensa*	Yes	Yes	Yes	[10]
Doryctobracon crawfordi	Neotropical	Ecuador	Florida, USA	?	*A. suspensa*	No	No	No	[10]
		Mexico	Puerto Rico	1935–1937	*Anastrepha* spp.	Yes	No	No	[11]
		Mexico	Argentina	1961	*Anastrepha* spp.	Yes	No	No	[118]
Doryctobracon trinidadensis	Trinidad	Trinidad	Florida, USA	1985	*A. suspensa*	Yes	Yes	?	[10]
Opius bellus	Neotropical	Trinidad	Florida, USA	?	*A. suspensa*	No	No	No	[10]
		Panama	Puerto Rico	1935–1937	*Anastrepha* spp.	Yes	No	No	
Trybliographa brasiliensis[1]	Brazil	Panama	Puerto Rico	1935–1937	*Anastrepha* spp.	Yes	No	No	[11]
Utetes anastrephae	Neotropical	Argentina	Peru	1942	*Anastrepha* spp.	Yes	No	No	[152]

[1]More than likely this species is not a tephritid parasitoid [169].

was not until the late 1980's, however, that truly large scale rearing programs began to be fully developed. Examples of these programs, involving the release of hundreds of thousands to millions of parasitoids, are those developed at Mazapa de Madero, Chiapas, Mexico [23], Costa Rica's Acosta region [19], the southern border between Mexico and Guatemala [24], urban and suburban areas of Florida in the United States [18, 139], the Soconusco region in Chiapas, Mexico [108, 109], and the coffee growing regions of Guatemala [140]. These programs are discussed in more detail below. Initial shipments for these programs often originated in Hawaii. Hawaii has thus provided parasitoids to Latin America, at least on an irregular basis, for at least 60 years.

To date, attempts have been made to introduce 17 Old World species of tephritid parasitoids into Latin America and the southern United States (Table 7). Four of the West African species were involved in direct introductions [11, 145]. The remainder were indirect releases of material shipped from Hawaii, France, and Italy. Eight of the species involved in indirect releases were originally collected in Southeast Asia, one in Australia, two in West Africa, one in South Africa, and one in North Africa. Once introduced to the New World, these exotic parasitoids were redistributed on at least 40 occasions, primarily from Costa Rica (61%), Mexico (24%), and Florida (5%), to at least 11 American countries (Table 5).

It is much more difficult to assess the results of native American parasitoids that have been moved from one country to another within the New World. At least one such species, *D. areolatus*, has been successfully introduced to Florida [8–10]. Most, however, apparently have not become established in places where they did not already occur.

Successful parasitoid introductions

Exotic, Old World tephritid parasitoids have been successfully introduced to at least nine countries (Table 5). Three of the species, *A. indica*, *D. longicaudata*, and *F. arisanus* are well established. The status of three others that were recovered immediately after release (*A. daci*, *P. concolor*, and *T. giffardianus*) is discussed below. A seventh species, *D. tryoni*, may also be established, largely as a result of recent inundative releases. It was recovered shortly after release in Puerto Rico [11], Costa Rica, and Guatemala [140] but permanent establishment has yet to be verified. When taken

Table 7. Fate of exotic parasitoid species introduced to the Neotropical region.

Parasitoid family species	Country or region of origin	Species established		
		Yes	No	Uncertain
Braconidae				
Diachasmimorpha fullawayi	West Africa		+	
D. longicaudata	Southeast Asia via Hawaii	+		
D. tryoni	Australia via Hawaii			?
Fopius arisanus	Southeast Asia via Hawaii	+		
F. persulcatus	Southeast Asia via Hawaii		+	
F. vandenboschi	Southeast Asia via Hawaii			?
F. caudatus	West Africa			??
F. silvestrii	West Africa			??
Psyttalia humilis	Southern Africa via Hawaii		+	
P. fletcheri	Southeast Asia via Hawaii		+	
P. incisi	Southeast Asia via Hawaii		+	
P. concolor	North Africa via France & Italy	+		
P. perproxima	West Africa			??
Chalcididae				
Dirhinus giffardii	West Africa via Hawaii			??
Figitidae; Eucoilinae				
Aganaspis daci	Southeast Asia via France	+		
Eulophidae				
Aceratoneuromyia indica	Southeast Asia via Hawaii	+		
Tetrastichus giffardianus	West Africa via Hawaii			?
Total		5 (29%)	5 (29%)	7 (42%)

? = recovered immediately following release, establishment uncertain.
?? = sampling inadequate for determining whether species became established.

together, 47% of all introduced species were recovered and 7.6% unquestionably became established. About 80% of all indirect introductions were of *D. longicaudata* and *A. indica*. Based on the successful establishment of these two species in most of the importing countries (82%, Table 5), it is not surprising that they are now widely distributed in the Americas [4, 10, 170]. By contrast, *F. arisanus*, introduced to Costa Rica from Hawaii in 1955, is difficult to culture and was thus not widely redistributed. It was first recovered 24 years after its first release, but only in smaller numbers (3% parasitism of *C. capitata*, [170]), and is thus far recorded only from Costa Rica.

Aganaspis daci and *P. concolor* were reported as established on *A. suspensa* in Florida, but were recovered only in very low numbers [10]. The establishment of *A. daci* in Costa Rica on *Anastrepha* sp. [72, 103] is doubtful [169] and similarly requires verification. *Psyttalia concolor* was reportedly established in Bolivia [3, 152], but this parasitoid has not been recovered since its release. Finally, *T. giffardianus* was reportedly established in Brazil [48], but we know of no recent documentation of its occurrence there. Initial reports on *T. giffardianus* were focused primarily on the rearing and release of this species rather than its permanent establishment or impact. Baranowski *et al*. [10] also noted the recovery of *F. vandenboschi* shortly after its release.

We must stress here that the pupal parasitoid *P. vindemiae* is not recognized as part of the complex of exotic species introduced to the American continent. This parasitoid is a cosmopolitan species but was also extensively cultured and widely released against various tephritid pests. Its occurrence in 11 American countries can potentially be attributed to three factors: (1) as a direct result of these purposeful introductions, (2) a synanthropic association; or (3) simply a reflection of its natural distribution. For example, *P. vindemiae* was introduced into Argentina for biocontrol of *C. capitata* and *A. fraterculus* in the 1960's, but this species had already been recorded 30 years before under a different scientific name [119].

Unsuccessful parasitoid introductions

None of the species involved in direct releases from the Old World are known to be established in the New World. The main reason is lack of studies following release. For example, many parasitoid species from West Africa were released in Costa Rica between 1981 and 1982 [145], and although some were trapped soon thereafter, their establishment was not later verified [162]. Of the parasitoids introduced indirectly by way of either Hawaii or Europe, 76.9% have not become permanently established (though some may do so eventually). Of the five species redistributed from cultures established in Costa Rica, Mexico, or Florida, only one (*P. concolor*) has apparently failed to become permanently established.

Failure of the exotic parasitoids may be attributed to one or more of the following reasons: (a) insufficient number of specimens released (for example, only about 200 *F. vandeboschi* and *P. incisi* (Silvestri) were released in Mexico); (b) inappropriate methods of release, such as a small release site with few available hosts; (c) lack of adaptation of the species to new ecological conditions; (d) prolonged laboratory rearing resulting in reduced genetic variability; and (e) parasitoid specificity: e.g. *P. incisi* and *P. fletcheri* (Silvestri) are more specific to *Bactrocera* Macquart and could not be effectively lab reared on *Anastrepha* or Medfly [10, 28 and references therein]. In several cases, difficulties in laboratory rearing were directly responsible for the low numbers released.

Results of classical biocontrol programs

Only *D. longicaudata* and *A. indica* can be considered successfully established in countries such as Costa Rica, Mexico, Nicaragua, Guatemala, El Salvador, Trinidad, Colombia, and Venezuela, but their efficacy when viewed in terms of classical biological control is debatable. The fundamental problem in analyzing most classical biocontrol programs implemented in Latin America is the lack of evaluation of impact in terms of reduction of infestation, and the lack of cost/benefit analysis. Generally, very few studies are done following release of exotic species, and most of these focus on ascertaining whether or not the released organisms have become established. Partial results based on collection of infested fruits and resulting calculations of percent parasitism are available for some programs. Among the most useful of these are Jimenez-Jimenez [77], Aluja *et al.* [4] and López *et al.* [96] for Mexico, Baranowski and Swanson [9] for Florida, Bennett *et al.* [14] for Trinidad, and Wharton *et al.* [170] and Jiron and Mexzon [82] for Costa Rica. Although there is some evidence of substantial impact (notably in the work by Jimenez-Jimenez for Mexico) data on long-term efficacy are lacking. In all other cases where at least some data do exist, classical programs alone have not achieved success. In Puerto Rico, for example, only one of the released species (*D. tryoni*) was ever recovered, and Bartlett [11] considered it doubtfully established. In Florida, *A. suspensa* was still considered a serious pest following establishment of several introduced species [10].

The diverse factors limiting the capacity of classically released parasitoids to keep pests at desirable population levels have been discussed by Wharton [162, 163], Gingrich [56], and Sivinski [138]. Reduction of pest populations below economically damaging levels is rarely a practical goal in a classical biological control program against tephritid pests. Nevertheless, some measure of benefit can be derived by lowering source populations that pose a threat for accidental introductions to countries where these pests do not occur. Also, as demonstrated by the work in Hawaii, reduction of dense populations of introduced pests can limit these pests to preferred hosts, thus providing a potential export market for non-preferred but susceptible hosts.

Results of augmentative biocontrol programs using inundative releases

Documentation of the results of mass releases of parasitoids is somewhat better than that for classical biological control programs, largely because most of these augmentation programs are very recent or still on-going. Although most reports are partial, they demonstrate that this strategy can sometimes be an effective means for suppression of tephritid pest populations. Most of the programs discussed below have relied heavily on *D. longicaudata*, primarily because it is easily mass-reared and it adapts readily to different fruit fly species of economic importance (Table 8). There is, however, increasing interest in *D. tryoni*, which is also easily cultured and readily available from mass rearing programs in Hawaii.

Augmentative releases against *C. capitata* in Costa Rica in the 1970's and 1980's were ineffective, with parasitism rates below 6%. This was due, among other factors, to a low release rate of only 500 *D. longicaudata* and 5000 *A. indica* per week [72]. More recent reports, however, indicate that mass releases of *D. longicaudata* and *P. vindemiae* in isolated areas of Costa Rica have reduced the number of both *C. capitata* and *Anastrepha* spp. [19].

In Florida, where the release program was accompanied by the concurrent development of an effective mass rearing program, populations of *A. suspensa* were greatly decreased in both urban and suburban areas [18, 139].

In Mazapa de Madero Canyon in Chiapas, Mexico, *D. longicaudata* and *D. tryoni* were mass released between 1987 and 1989, substantially reducing infestation in mangos and oranges and greatly decreasing populations of adult *A. ludens* and *A. obliqua* relative to population levels in years prior to releases [23]. For example, parasitism in *Citrus sinensis*, 'sweet orange,' infested with *A. ludens*, due mostly to *D. longicaudata*, varied from 48% to 100% between 1987 and 1988, and resulted in zero infestation during the first two months of 1989. This is in dramatic contrast to 29% parasitism in the same fruit species in the four years prior to mass releases [4].

Results of inundative releases using *D. tryoni* have been inconsistent. For example, mass releases of *D. tryoni* in the early 1990's along the Guatemala–Mexico border resulted in a four-fold reduction of *C. capitata* larvae in coffee fields and a two-fold reduction in adult populations of *C. capitata*

Table 8. Exotic parasitoid species and fruit flies of economic importance in Latin America and the southern United States.

Parasitoids	Fruit flies								References
	Primary pests							Potential	
	A. fraterculus	*A. ludens*	*A. obliqua*	*A. serpentina*	*A. striata*	*A. suspensa*	*C. capitata*	*A. sororcula*	
Aceratoneuromyia indica	+	+	+	+	+	+			[4, 11, 67, 78, 82, 84, 113]
Aganaspis daci	+	+	+	+	+	+	+		[10]
Diachasmimorpha longicaudata	+	+	+	+	+	+	+	+	[4, 10, 26, 42, 81, 82]
Fopius arisanus[1]							+		[170]
Psyttalia concolor						+	?[2]		[10, 152]

[1]Obtained from combined *Anastrepha* spp. pupae.
[2]Records of *P. concolor* on *C. capitata* pending verification.

compared to control zones [24]. Current testing of mass releases of *D. tryoni* against *C. capitata* in coffee fields in Guatemala [75, 140] have yielded up to 80% parasitism [140]. In direct contrast to these programs, *D. tryoni* was not recovered in significant numbers in the Mazapa de Madero program noted in the previous paragraph [23]. Measurable impact was also absent in the Soconusco region of Chiapas, Mexico, where mass releases of *D. tryoni* were made in mango orchards to suppress populations of *A. ludens* and *A. obliqua* [108]. These releases did not result in a decrease in adult fly captures relative to previous years, despite parasitism rates of nearly 92% [108]. While the latter result might be explained by significant migration of adult flies into the release zone, it also highlights the need to be very cautious about reporting and interpreting percent parasitism. Ideally, rates of parasitism need to be presented with corresponding data that provide some measure of host population size, since 92% parasitism, for example, will be much more meaningful at low population densities than at high population densities. In this regard, it would be helpful to develop consistent measures of impact on tephritid pests that can be compared across programs in Latin America.

Augmentative programs that have yet to be evaluated are currently being conducted in El Salvador against *C. capitata*, *A. ludens*, and *A. obliqua* (Gilberto Granados Zuniga, personal communication), against *A. fraterculus* in Brazil [26] and *C. capitata* in Perú [133].

Discussion

Biological control is a viable strategy for the suppression and management of tephritid pests. Preliminary results of pilot studies on augmentative releases of parasitoids in Florida and Mexico, motivated by earlier work in Hawaii, have demonstrated the potential of this strategy for the suppression of tephritid pest populations. Yet there is also a need for a classical approach to this problem since few parasitoids are currently available for augmentation programs, and some of these are almost certainly inappropriate. *P. vindemiae*, for example, has been released for decades without any evidence of efficacy. It thus seems reasonable to abandon use of this species in augmentation programs, particularly in light of its potential preference for non-target hosts. Aside from the cosmopolitan *P. vindemiae*, the most widely employed parasitoids now in use for inundative releases against Medfly and *Anastrepha* in the New World all originated from the Indo-Pacific region. These include *D. longicaudata*, *D. tryoni*, and *A. indica*, as well as *F. arisanus* (whose availability until recently has been limited due to rearing problems).

Therefore, in addition to developing more effective release strategies for augmentative programs, it is highly desirable to search for new parasitoid species for potential use as biological controls. For example, for the control of *C. capitata*, native to subsaharan Africa, it would be fundamental to collect, introduce, and propagate Afrotropical parasitoid species. Excellent candidates can be found in the older works of Silvestri [136] and Clausen *et al.* [28], and in the more recent study by Steck *et al.* [145]. At least three species of parasitoids can be regularly collected from Medfly and related ceratitines in coffee in West Africa. The seasonally abundant *P. perproxima* would probably be easiest of the three to rear, and thus the most logical candidate to mass culture for inundative releases. The two species of *Fopius* would be more suitable for direct releases in a classical program.

The employment of Neotropical parasitoids for the control of *Anastrepha* spp. is another valid and applicable alternative to the use of exotic species such as *D. longicaudata*. Though frequently reared from fruit samples, relatively little is known about even the most commonly encountered species, and exhaustive biological studies are therefore needed. Species in the genus *Doryctobracon*, such as *D. areolatus* and *D. crawfordi*, eucoilines like *A. pelleranoi*, and the diapriid pupal parasitoid *C. haywardi* have considerable potential and need to be examined from a mass rearing standpoint to determine which would be most suitable for augmentative programs.

The Neotropical region undoubtedly represents an important source of additional parasitoid species with possibilities for their employment in the reduction of populations of native tephritid pests. However, there are still many areas of Central and South America where the native tephritid fauna has not yet been studied, and their parasitoids are consequently unknown. There is some urgency to these studies as many of these areas have suffered from a notable reduction in their native flora as a consequence of the growing agricultural frontier and indiscrete logging for commercial markets. Inventories for the recognition of new species that could act as agents of biological control should focus on these areas.

In addition to direct benefits to on-going biological control programs, detailed examination of the parasitoid communities associated with Neotropical tephritids will also provide data that can be used to address theoretical considerations in biological control and community ecology. Issues of host specificity, in particular, can be examined through comparisons of attack rates and developmental capabilites on Medfly and various species of *Anastrepha*. Opportunities abound for examination of the effects of different host fruits, exotic vs. native parasitoids, and koinobionts vs. idiobionts. Using the community of tephritid parasitoids as a model system, predictions regarding the relative contributions of idiobionts and koinobionts to parasitism of concealed hosts can also be tested. Important needs in this regard are detailed surveys for pupal parasitoids and other idiobionts that are missed by the most commonly used sampling methods.

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