Chapter 16 In and Out of Africa: Parasitoids Used for Biological Control of Fruit Flies

Samira A. Mohamed, Mohsen M. Ramadan, and Sunday Ekesi

Abstract This chapter is a demonstration of the wealth of African natural resources and their contribution to biological control of tephritid fruit flies (Diptera: Tephritidae). Africa is the native region of more than 900 species of fruit flies, many of which are significant agricultural pests. Highly diverse assemblages of indigenous hymenopteran parasitoid species have evolved with these fruit flies, which makes Africa a valuable source of parasitoids for use in classical biological control of fruit flies around the world. Interest in the use of parasitoids for biological control has recently increased due to advances in mass rearing techniques for exotic and native parasitoid species alongside the need to reduce synthetic insecticide use. Here we review the diversity of indigenous African parasitoid species and their role in classical biological control of fruit flies in other parts of the world; we also discuss their contribution to the management of native fruit flies in Africa. Likewise, the prospects and potential for using exotic parasitoids for management of newlyestablished invasive fruit flies in Africa is discussed, particularly for Batrocera zonata (Saunders), Bactrocera dorsalis (Hendel), Bactrocera latifrons (Hendel) and Zeugodacus cucurbitae (Coquillett). We cover the introduction and spread of exotic parasitoid species released in Africa for biological control of invasive fruit flies. The rich diversity of indigenous parasitoids of African fruit flies continues to be unraveled as more new species are discovered and recognized as potential biological control agents for fruit fly management.

Keywords Indigenous parasitoids • Exotic parasitoids • Exploration • Introduction

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1 Introduction

Management of tephritid fruit flies requires an holistic IPM approach of which biological control is one of the essential components. Hymenopteran parasitoids are considered to be well suited to biological control of fruit flies because they are generally more host specific compared with predators and entomopathogens. For successful development endoparasitoids must deal with the host immune response and ectoparasitoids must deal with host mobility; for these reasons they are highly co-evolved with their particular hosts. Moreover, parasitoids are able to locate and attack the concealed immature stages of fruit flies inside fruits of both wild and cultivated plants.

Although the history of fruit fly biological control dates back to the beginning of the last century (Silvestri 1914a, b; Clausen 1978), it has recently received increasing attention (Wharton 1989; Knipling 1992; Headrick and Goeden 1996; Sivinski 1996; Purcell 1998). This has been facilitated by technological advances and ease in transportation of parasitoid consignments across the globe. Ovruski et al. (2000) attributed the renewed interest in using parasitoids for fruit fly biological control to the advances made in mass rearing techniques for exotic and native parasitoid species and their tephritid hosts. Increasing pressure to reduce the use of synthetic insecticides and the current drive towards conservation of biodiversity through the use of ecologically acceptable pest management tactics have made classical and augmentative biological control a desirable method to reduce fruit fly populations.

In almost all the published literature on biological control of fruit flies, Africa is highlighted as a source of parasitoids for use in classical biological control of fruit flies that are invasive pests elsewhere in the world; there is also a high species richness of fruit fly parasitoids in Africa (Silvestri 1914a, b, 1915; Clausen et al. 1965; Greathead 1976; Clausen 1978; Neuenschwander 1982; Wharton 1989 and reference there in; Waterhouse 1993; Mkize et al. 2008). In this chapter, we have compiled information on the diversity of indigenous African parasitoid species that attack fruit flies and their role in classical biological control in other parts of the world. Additionally, we highlight the contribution of these parasitoids in management of native fruit flies in Africa. Parasitoid species used for classical biological control of alien fruit flies that have invaded and become established in Africa are also reviewed in this chapter including four newly established Asian fruit flies: the peach fruit fly, *Batrocera zonata* (Saunders); the oriental fruit fly, *Bactrocera dorsalis* (Hendel); the solanaceous fruit fly, *Bactrocera latifrons* (Hendel); and the melon fly, *Zeugodacus cucurbitae* (Coquillett).

2 Diversity of the Indigenous Parasitoids of African Fruit Flies

Africa is the native range of several genera and more than 1000 species of fruit flies in the subfamily Dacinae (Diptera: Tephritidae), many of which are of significant agricultural importance as pests of commercial fruits and vegetables in sub-Saharan and Afrotropical regions (White and Elson-Harris 1992; Thompson 1998; De Meyer and Ekesi 2016). It is not surprising that a highly diverse assemblage of native hymenopteran parasitoid species have evolved with these fruit flies. However, much of our knowledge on the species composition of indigenous African parasitoids of tephritids is derived from the information generated during foreign explorations for natural enemies of African fruit flies that had invaded and become pests in other parts of the world, namely the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), and the olive fruit fly, *Bactrocera oleae* (Rossi) (White and Elson-Harris 1992; CABI 2016).

A comprehensive record of indigenous African fruit fly parasitoids was first documented as early as 1912 by the prominent Italian entomologist Filippo Silvestri during his exploration for natural enemies in the West Coast of Africa (between 1912 and 1913) and Australia for use in biological control in the State of Hawaii (Territory of Hawaii at that time; Silvestri (1914a, b, 1915). He reported a high diversity of hymenopteran parasitoid species attacking fruit flies (Ceratitis species were attacked by ten species of parasitoids and Dacus species were attacked by seven parasitoid species) in the families Braconidae, Eulophidae, Chalcididae and Diapriidae from West Africa and South Africa (Table 16.1). However, the members of the family Braconidae (14 species), particularly in the subfamily Opiinae, were the most numerous in his collection. Additional information on the African parasitoid fauna is also reported from surveys by the earlier Hawaiian explorers e.g. D.T. Fullaway 1914; J.C. Bridwell 1914; F.A. Bianchi and N.L.H. Krauss 1936-1937 (reported in Bianchi and Krauss 1936) in Kenya; R.H. Van Zwaluwenburg in West Africa 1936; J.M. McGough 1949 in Kenya, Congo, Uganda and South Africa; F.E. Skinner 1948 in Kenya, Congo and South Africa; D.W. Clancy 1951 in Congo (reported by Clausen et al. 1965; Greathead 1976; Clausen 1978; Wharton 1989; Waterhouse 1993; Ovruski and Fidalgo 1994). In Hawaii the parasitoids collected were mass reared and introduced into many countries around the world for biological control of invasive fruit flies, where they subsequently became established (Table 16.1).

In contrast, invasions of the African continent by exotic fruit flies in the genus *Bactrocera* prompted many scientists in Africa to carry out inventories of the indigenous parasitoid species as a prerequisite prior to introduction of coevolved natural enemies from the native region of the exotic pest. Records from the indigenous parasitoid species inventories can be found in Appiah (2012) and Vayssières et al. (2011, 2012). Also Fischer and Madl (2008) provided a review for the Opiinae parasitoids of the Malagasy sub-region, most of which are of unknown biology or attack other non-tephritid hosts.

Table 16.1 Hymenopteran parasitoids (grouped by taxon family, subfamily and known biology) originating from Africa and reported to attack frugivorous African Tephritidae

Valid names of parasitoids ^a	Family and subfamily	Mode of parasitism	Country and region of origin	Host records	Distribution outside Africa when used in tephritid biological control programmes	References for distribution and host association
Dirhinus giffardii Silvestri	Chalcididae, Dirhininae	Idiobiont solitary ectophagous pupal parasitoid	Cape Verde, Bgypt, Kenya, Nigeria, West Africa	Ceratitis capitata Ceratitis rosa Dacus demmerezi Dacus frontalis Trirhithromyia cyanescens	Australia 1956 for Bactrocera tryoni via Hawaii. Bolivia 1971 for C. capitata. China released for Tephritidae. Greece 1962 for C. capitata via Israel. Hawaiian Islands 1913 for C. capitata, 1950 for Bactrocera dorsalis. Israel 1956 for C. capitata. Italy 1913 for B. oleae. Mexico 1955 for Anastrepha ludens via Hawaii. Puerto Rico 1935 for Anastrepha suspensa via Hawaii. Samoa 1935 for Bactrocera passiflorae via Fiji.	3, 5, 10, 19, 24, 27, 31, 35
Dirhinus ehrhorni Silvestri	3	Idiobiont solitary ectophagous pupal parasitoid	Nigeria	Ceratitis capitata Ceratitis giffardi Ceratitis sp.	Hawaiian Islands for C. capitata	27, 31
Dirhinus sp.	3	Idiobiont solitary ectophagous pupal parasitoid	Africa	Dacus bivittatus		19
Coptera magnificus (Nixon)	Diapriidae, Diapriinae	unknown	Kenya	Ceratitis contramedia	Hawaii 1947–1952 for <i>B. dorsalis</i> , imported but not released.	41

4, 12, 13, 19, 22, 27, 31, 37														34, 37		34	27		30, 41		31
Hawaiian Islands 1913 for C. capitata. Hawaii 1947–1952 for B.	dorsalis, imported but not released.		Italy 1913 for Bactrocera oleae.														Hawaii 1913 for C. capitata	Israel 1951 for C. capitata	Hawaii 1947–1952 for B. dorsalis,	imported but not released.	
Bactrocera oleae Ceratitis anonae	Ceratitis capitata	Ceratitis colae	Ceratitis contramedia	Ceratitis cosyra	Ceratitis giffardi	Ceratitis punctata	Ceratitis rosa	Ceratitis simi	Dacus bivittatus	Dacus ciliatus	Dacus sp.	Trirhithrum coffeae	Trirhithrum nigerrimum	Ceratitis capitata	Ceratitis punctata	Ceratitis capitata	Ceratitis capitata		Ceratitis anonae	Dacus ciliatus	Bactrocera oleae
Benin, Ghana, Guinea, Kenya,	Mozambique,	Niger, Nigeria,	Africa, Zululand,	Uganda, West	Africa									Guinea, Kenya,	Nigeria, South Africa	Kenya	South Africa		Congo		Ethiopia
Idiobiont solitary ectophagous	pupal parasitoid													Pupal parasitoid		Idiobiont pupal endophagous parasitoid	Pupal parasitoid				Pupal parasitoid
33														"		"	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,		"		Pteromalidae, Pteromalinae
Coptera silvestrii (Kieffer)														Coptera robustior	Silvestri	Coptera sp.	Trichopria capensis	Kieffer	Trichopria sp.		Meraporus graminicola Walker

Table 16.1 (continued)

Valid names of					Distribution outside Africa when	References for
norocitoide ⁸	Family and	Mode of	Country and		used in tephritid biological control	distribution and
parasitorus	subfamily	parasitism	region of origin	Host records	programmes	host association
Pachycrepoideus	,,	Idiobiont solitary	Congo, Kenya,	Bactrocera oleae	Argentina 1960 for Anastrepha	9, 19, 31
vindemmiae		ectophagous	Morocco	Ceratitis capitata	fraterculus and C. capitata via	
(Rondani)		pupal parasitoid		Ceratitis rosa	Hawaii, 1961 via Mexico and 1986	
				Ceratitis sp.	Via Cost Kica. Bolivia Ior Anastronha sp. Brazil for	
				Dacus ciliatus	Anastrepha sp. Costa Rica 1955 for	
				Dacus demmerezi	C. capitata and Anastrepha sp. El	
				Trirhithromyia	Salvador for Anastrepha sp. France,	
				cyanescens	Italy, Spain, and USA for	
					Drosophila suzukii. Florida for	
					Anastrepha sp. via Hawaii.	
					Hawaiian Islands 1947–1952 for C.	
					capitata and B. dorsalis. Mexico	
					for Anastrepha sp. Nicaragua 1955	
					for C. capitata via Hawaii. New	
					Zealand released, not established.	
					Peru for Anastrepha sp. Puerto Rico	
					1935 for Anastrepha suspensa via	
					Hawaii. La Réunion. Syria 2014 for	
					C. capitata (inadvertently)	
Cyrtoptyx latipes	,,	Pupal parasitoid	Egypt, Eritrea	Bactrocera oleae	Crete, Cyprus, Greece, India	8, 20
(Rondani)		(also attack			(inadvertently). Italy for C. capitata	
		larvae)			and B. oleae.	

Subsaiaaster en	3	Punal paracitoid	Tanzania	Coratitie rosa		10 31
Spiregignsier sp			ranzania	Celainis 103a		17, 31
				Ceratitis sp.		
Cyrtoptyx latipes Rondani	23	Unknown	Egypt, Eritrea	Bactrocera oleae	Greece 1975–1980 for <i>B. oleae</i>	8
Mesopolobus modestus (Silvestri)	"	Unknown	Eritrea, Ethiopia	Bactrocera oleae	Italy (inadvertently)	26, 28
Pteromalus semotus Walker	3	Idiobiont solitary ectophagous larval parasitoid	Egypt, Canary Islands, Cape Verde, South Africa	Bactrocera oleae	Cosmopolitan (inadvertently)	20
Halticoptera daci Silvestri	Pteromalidae, Miscogastrinae	Koinobiont endophagous larval parasitoid	Eritrea, Ethiopia, South Africa	Bactrocera oleae	Italy 1914 for B. oleae	19, 20, 21, 26, 28
Spalangia afra Silvestri.	Pteromalidae, Spalangiinae	Idiobiont solitary ectophagous pupal parasitoid	East Africa, Kenya, Nigeria, Tanzania, West Africa	Ceratitis anonae Ceratitis soleae Ceratitis sp. Dacus bivitatus Dacus ciliatus Pardalaspis cyanescens	Hawaii 1947–1952 for <i>B. dorsalis</i> , imported but not released	1, 19, 27, 41
						(commune)

Table 16.1 (continued)

Valid names of	Family and	Mode of	Country and		Distribution outside Africa when used in tephritid biological control	References for distribution and
parasitoids ^a	subfamily	parasitism	region of origin	Host records	programmes	host association
Spalangia cameroni	"	"	Canary Islands,	Ceratitis capitata	Cosmopolitan (inadvertently).	42
Perkins			Malawi, Mauritius, Dacus sp. Madagascar, Morocco, Senegal, Somalia, South Africa, Tanzania	Dacus sp.	Fiji 1935 for <i>B. passiflorae</i> and <i>B. xanthodes</i> via Hawaii.	
Spalangia simplex	"	"	Congo, Mali,	Ceratitis anonae?		45
Perkins			South Africa,	Ceratitis cosyra		
			Uganda	Ceratitis ditissima?		
				Ceratitis fasciventris?		
				Ceratitis quinaria?		
				Ceratitis silvestrii?		
Tachinaephagus	Encyrtidae,	Pupal parasitoid	Congo, South	Tephritidae		20, 30
zealandicus Ashmead Encyrtinae	Encyrtinae	(also reported on larvae)	Africa, Uganda	Bactrocera oleae		
Pnigalio agraules	Eulophidae,	Larval and pupal	Egypt	Bactrocera oleae	Austria. England. France.	&
(Walker)	Eulophinae	parasitoid			Greece 1975–1980 for B. oleae.	
					Italy. Spain. Turkey	
Eulophus sp.	"	Larval	Libya	Bactrocera oleae		31
		ectophagous parasitoid (?)				

Table 16.1 (continued)

Valid names of	Family and	Mode of	Country and	H	Distribution outside Africa when used in tephritid biological control	References for distribution and
	subfamily	parasitism	region of origin	Host records	programmes	host association
Tetrastichus giffardianus Silvestri	3	Koinobiont gregarious	Benin, Cameroon, Egypt, Kenya,	Ceratitis anonae	Australia 1932, 1956 for Bactrocera tryoni via Hawaii.	4, 5, 19, 31, 42
		endophagous	Nigeria, Reunion	Ceratitis rosa	Argentina 1947 for C. capitata via	
		larval parasitoid	Sierra Leone,	Ceratitis cosyra	Brazil. Brazil 1937 for C. capitata	
			Africa	Dacus bivittatus	and Anastrepha sp. via Hawaii.	
				Dacus ciliatus	Cook Island 1938 for <i>B. melanotus</i> via Fiii Costa Rica and Nicarama	
				Dacus demmerezi	1955 for C. capitata via Hawaii.	
				Trirhithromyia	Fiji 1935, 1959, 1960 for	
				cyanescens, Trirhithrum	Bactrocera xanthodes and B.	
				queritum	passiflorae via Hawaii. Hawaiian	
					Islands 1914 for C. capitata, and	
					1947-1952 for B. dorsalis. Greece	
					for B. oleae. Italy 1916 for C.	
					capitata via Hawaii. New	
					Caledonia 1936 for Bactrocera	
					umbrosa and Bactrocera psidii via	
					Fiji.	
					La Réunion. Western Samoa 1935,	
					1938 for B. passiflorae via Fiji.	
					USA 1931 for Rhagoletis sp. via	
					Hawaii. Puerto Rico 1935 for A.	
					suspensa via Hawaii. Spain.	
					Vanuatu.	
	,,	Larval parasitoid	Eritrea, Ethiopia	Bactrocera oleae		26, 28, 31
macutifer Silvestri		(;)				

Tetrastichus oxyurus Silvestri	77	Larval endophagous parasitoid	Kenya, Nigeria, West Africa	Carpophthoromyia tritea Hawaiian Islands	Hawaiian Islands	27
Tetrastichus sp.	3 9	larval gregarious endophagous parasitoid	South Africa, West Africa	Ceratitis anonae Bactrocera oleae	Hawaiian Islands 1936 for C. capitata and Bactrocera cucurbitae.	20, 21, 43
Syntomosphyrum sp.	"	Larval parasitoid	Uganda	Trirhithrum coffeae		12, 13
Macroneura sp.	Eupelmidae, Eupelminae	Unknown	Egypt	Bactrocera oleae		&
Eupelmus urozonus Dalman	3	Idiobiont solitary ectophagous larval and pupal parasitoid	Algeria, Egypt, Libya, South Africa	Bactrocera oleae	Greece 1975–1980 for <i>B. oleue</i>	8, 20, 21, 31
Eupelmus afer Silvestri	3	Idiobiont solitary ectophagous larval or pupal parasitoid.	Eritrea, Ethiopia, South Africa	Bactrocera oleae	Italy 1915 for <i>B. oleae.</i>	20, 21, 26, 28
Eupelmus spermophilus Silvestri	"	Idiobiont solitary ectophagous larval or pupal parasitoid	Eritrea, Ethiopia, South Africa	Bactrocera oleae		28
Eupelmus sp.	,,	Unknown	Tanzania	Ceratitis sp.		31
Eurytoma martelli Domenichini	Eurytomidae, Eurytomiae	larval or pupal ectophagous parasitoid	Egypt, North Africa	Bactrocera oleae	Greece 1975–1980 for <i>B. oleae</i>	8, 19
Eurytoma sp.	3	larval or pupal ectophagous parasitoid	Libya, Egypt	Bactrocera oleae		8, 31

(continued)

Table 16.1 (continued)

					Distribution outside Africa when	References for
Valid names of	Family and	Mode of	Country and		used in tephritid biological control	distribution and
parasitoids ^a	subfamily	parasitism	region of origin	Host records	programmes	host association
Allocerellus inquirendus Silvestri	Encyrtidae, Tetracneminae	Unknown	Eritrea, Ethiopia	Bactrocera oleae		
Microdontomerus sp.		3	South Africa	Bactrocera oleae		20, 21
Aganaspis sp.	Figitidae, Eucoilinae	3	Central African Republic, Congo, Kenya, Reunion, South Africa, Tanzania	Fruit-infesting Tephritidae		04
Eucoila sp.	27	"	Mauritius	Ceratitis capitata		23
Ealata clava Quinlan	"	,,	Cameroon, Congo, Kenya, Mauritius, Principe, South Africa, Uganda	Fruit-infesting Tephritidae	Taiwan (inadvertently)	40
Ealata marica Quinlan	"	"	Congo			40
Ealata saba Quinlan	»	3	Congo, Nigeria, South Africa, Uganda, Zimbabwe			40
Ganaspis kilimandjaroi (Kieffer)	"	"	Tanzania			40
Ganaspis mahensis Kieffer	"	"	Seychelles			40
Ganaspis ruandana (Benoit)	3	3	Rwanda			40

4 1.		TT1	N. 61:			4
p.	braconidae,	Chkhown	Mall	Ceranns cosyra?		c
	Alysiinae			Ceratitis fasciventris?		
				Ceratitis silvestrii?		
Triaspis daci (Szépligeti)	Braconidae, Brachistinae	3	Congo, Ethiopia, South Africa	Bactrocera oleae		19, 26, 28, 31
Bracon celer Szénligeti	Braconinae,	Idiobiont solitary ectophagous	Cape Verde Island, Bactrocera oleae Erifrea. Ethiopia.	Bactrocera oleae	Hawaii 1947–1952 for <i>B. dorsalis</i> , imported but not released.	19, 20, 21, 26, 27, 28, 34, 41
		larval parasitoid	Kenya Namibia,	Trirhithrum ni gerrimum	B. oleae.	(((
			South Africa		Israel 2011 on B. oleae	
					(inadvertently).	
					Italy 1915 for B. oleae.	
Microbracon sp.	"	Unknown	Tanzania	Ceratitis sp.		31
Diachasmimorpha	Braconidae,	Koinobiont	Somalia	Dacus ciliatus		31
brevistyli (Paoli)	Opiinae	solitary				
		endophagous				
		larval parasitoid				
Diachasmimorpha	,,	Koinobiont	Cameroon, Cape	Ceratitis anonae	Hawaiian Islands 1936 for C.	11, 19, 27, 35,
carinata (Szépligeti)		solitary	Verde, Congo,	Ceratitis contramedia	capitata and Bactrocera cucurbitae, 39, 41	39, 41
		endophagous	Guinea, Kenya,	Ceratitis ditissima	released as Hedylus giffardii	
		iarvai parasitoid	Senegal, Sierra Leone Tanzania	Ceratitis giffardi	(Silvesur): Hawaii 1947–1952 101 <i>B. dorsolis</i> imported but not	
			Zaire	Ceratitis punctate	released.	
				Dacus bivittatus		
				Dacus ciliatus		

Table 16.1 (continued)

Valid names of Family and parasitoids ^a subfamily Diachasmimorpha "fullawayi (Silvistri)		Mode of	Country and		used in tenheitid biological control	TOT COUNTY
						distribution and
		parasitism	region of origin	Host records	programmes	host association
vistri)		Koinobiont	Cameroons,	Bactrocera amplexa	Australia 1932 for B. tryoni via	3, 19, 27, 29,
		solitary	Congo, Guinea,	Carpophthoromyia tritea	Hawaii. Brazil for C. capitata.	35, 39, 41, 44
		endophagous	Kenya, Nigeria,	Ceratitis anonae	Fiji for C. capitata.	
		iarvai parasitoid	Senegal, west Africa Rennion	Ceratitis capitata	Hawaiian Islands 1914 for C.	
			Sierra Leone.	Ceratitis cosyrae	capitata. Hawaii 1947-1952 for B.	
			South Africa,	Ceratitis giffardi	dorsalis, imported but not released.	
			Togo, Uganda,	Ceratitis punctata	Maurinus on <i>Ceranns</i> spp (new to fama) Puerto Rico for Tenhritidae	
			Zaire	Ceratitis tritea	1941. La Réunion. Spain.	
				Ceratitus sp.	•	
				Dacus bivittatus		
				Dacus sp.		
				Trirhithrum coffeae		
rpha "		Koinobiont	Madagascar	Ceratitis sp.		35
insignis (Granger)		solitary				
		endophagous				
	_	larval parasitoid				
Fopius bevisi (Brues) "		Koinobiont	Kenya, South	Ceratitis capitata	Hawaiian Islands 1949 for C.	6, 35
	-	solitary	Africa	Dacus ciliatus	capitata and B. dorsalis, imported	
		endophagous Jarval narasitoid		Trirhithrum queritum	but not released.	

19, 27, 27, 29,	33, 34, 35, 39,	41										33, 34, 35			2, 12, 13, 19,	29, 31, 35, 39,	41			
Guatemala for C. capitata.	Hawaiian Islands 1936 for C.	capitata. Hawaii 1947–1952 for B.	dorsalis, imported but not released.	Hawaii (quarantine facility via Kenya 1996–2004 for <i>C. canitata</i>)	ixii) a 1770 - 2004 101 C. Capitata)							Australia. Guatemala 2003 for C.	capitata. Hawaii (2004 cultured for	release on <i>C. capitata</i> via Kenya and Guatemala, pending release). Spain. Puerto Rico. Israel 2011 for <i>C. capitata</i> and <i>B. oleae.</i>	Hawaii 1947–1952 for B. dorsalis,	imported but not released.				
Carpophthoromyi atritea	Ceratitis anonae	Ceratitis antistictica	Ceratitis capitata	Ceratitis giffardi	Ceratitis tritea	Dacus bivittatus	Dacus ciliatus	Dacus humeralis	Dacus momordicae	Trirhithrum coffeae	Trirhithrum nigerrimum	Ceratitis capitata	Ceratitis rosa	Trirhithrum coffeae	Ceratitis anonae	Ceratitis capitata	Ceratitis sp.	Dacus bivittatus	Dacus sp.	Trirhithrum coffeae
Benin, Cameroon,	Congo, Mali,	Guinea, Kenya,	Nigeria, Senegal,	Victoria, West	Africa, Zaire							Kenya			Cameroon, Congo, Ceratitis anonae	Nigeria, Senegal,	Togo, Uganda			
Koinobiont	solitary	endophagous	egg-larval parasitoid	parasitora								Koinobiont	solitary	endophagous egg-larval parasitoid	Koinobiont	solitary	endophagous	Iarval (? eoo-larval)	parasitoid	4
3												,,			3					
Fopius caudatus	(Szépligeti)											Fopius ceratitivorus	Wharton		Fopius desideratus	(Bridwell)				

Table 16.1 (continued)

					Distribution outside Africa when	References for
Valid names of	Family and	Mode of	Country and		used in tephritid biological control	distribution and
parasitoids ^a	subfamily	parasitism	region of origin	Host records	programmes	host association
Fopius niger	3	Koinobiont	Cameroon, Kenya, Dacus humeralis	Dacus humeralis		35
(Szépligeti)		solitary	Tanzania			
		endophagous				
		larval parasitoid				
Fopius okekai	3	Koinobiont	Kenya	Trirhithrum inscriptum		16
Kimani-Njogu &		solitary		Trirhithrum nigrum		
		larval parasitoid				
Fopius ottotomoanus	3	Koinobiont	Cameroon	Dacus sp.		35
(Fullaway)		solitary				
		endophagous larval parasitoid				
Fopius silvestrii	"	Koinobiont	Cameroon,	Ceratitis anonae		39, 43
(Wharton)		solitary	Senegal, Western	Ceratitis capitata		
		endophagous	Kenya	Ceratitis cosyra,		
		iarvai parasiioid		Ceratitis fasciventris		
				Ceratitis flexuosa		
				Dacus bivittatus		
Opius sp.	3	Unknown	Cameroon, West	Ceratitis cosyra		30
			Africa	Trirhithrum coffeae		
Opius sp.	,,	"	Tanzania	Ceratitis sp.	Hawaii 1947–1953 for B. dorsalis	4, 31
Pseudorhinoplus	3	Koinobiont	Cameroon, Congo, Ceratitis anonae	Ceratitis anonae	Hawaii 1947–1952 for B. dorsalis,	40
fuscipennis		solitary	Uganda	Ceratitis ditissima	imported but not released.	
(Szépligeti)		endophagous larval parasitoid		Trirhithrum coffeae		
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3, 7, 8, 10, 14, 17, 19, 21, 27, 31, 35, 39, 41, 42	
	Funland (Inadvertently on Euphrania connexa). France 1919, 1931, 1958 for B. oleare. Greece 1954 for B. oleare via France. Hawaii 1947–1952 for B. dorsalis, imported but not released. Hawaii (quarantine facility 1996–2004 for C. capitata). Greece 1968 for B. oleare via France. Guam. Guatemala mass reared. Italy 1914, 1917 from Libya, 1918, 1923, 1934, for B. oleare. Israel. Jordan. Lebanon. New Caledonia 1966 for B. psidii, and B. frenchi via France. Pakistan. Peru. Puerto Rico 1935, 1936, 1941 for A. suspensa.and A. obliqua. La Réunion. Spain 1923 for C. capitata and B. oleare. Turkey. Yugoslavia.
Bactrocera oleae Capparimyia savastani Carpomya incompleta Ceratitis capitata Ceratitis cosyra, Ceratitis colae, Dacus brevistylus Dacus frontalis Trirhithromyia cyanescens Trirhithrum nigrum	
Algeria, Benin, Cape Verde, Congo, Eritrea, Kenya, Libya, Madagascar, Morocco, Senegal, South Africa, Tunisia	
Koinobiont solitary endophagous larval parasitoid	
3	
Psyttalia concolor (Szépligeti)	

Table 16.1 (continued)

rance tour (commune)	(1)					
					Distribution outside Africa when	References for
Valid names of	Family and	Mode of	Country and	,	used in tephritid biological control	distribution and
parasitoids ^a	subfamily	parasitism	region of origin	Host records	programmes	host association
Psyttalia cosyrae	"	Koinobiont	Congo, Kenya,	Ceratitis capitata		13, 19, 31, 35,
(Wilkinson)		solitary	Nigeria, North	Ceratitis cosyra		39
		endophagous	Africa, Reunion,	Trirhithrum coffeae		
		larval parasitoid	Senegal, Sierra	3		
			Leone, South			
			Alfica, Tanzania, Uganda, Zaire			
Psyttalia dacicida	"	Koinobiont	Eritrea, Ethiopia,	Bactrocera oleae	Italy (inadvertently)	19, 20, 21, 26,
(Silvestri)		solitary	Kenya, South	Tephritidae		28, 31, 35
		endophagous	Africa	7		
		larval parasitoid				
Psyttalia dexter		Koinobiont	Senegal	Dacus longistylus		35
(Silvestri)		solitary				
		endophagous				
		larval parasitoid				
Psyttalia	3	Koinobiont	Madagascar,	Ceratitis capitata		33, 34
distinguenda		solitary	Mascarenes,	Ceratitis rosa		
(Granger)		endophagous	Mauritius,			
		larval parasitoid	Reunion			
Psyttalia halidayi	3	Koinobiont	Kenya	Ceratitis rosa		36
Wharton		solitary				
		endophagous				
		larval parasitoid				
					_	

3, 18, 19, 27, 31, 35, 41, 42	27	23, 33	20, 21, 26, 27, 28, 35, 41
Australia 1932 for <i>B. tryoni</i> . Bermuda 1926 for <i>C. capitata</i> via Hawaii. California 1932 for <i>Rhagoletis</i> sp. via Hawaii. California 2003–2007 for <i>B. oleae</i> via France. Cook Islands. Fiji 1935 for <i>B. xanthodes</i> and <i>B. passiflorae</i> via Hawaii. Guatemala. Hawaiian Islands (Oahu and Maui Islands 1913 for <i>C. capitata</i>). Hawaii 1947–1952 for <i>B. dorsalis</i> , imported but not released. Israel 1926 for <i>C. capitata</i> . Puerto Rico for Tephritidae 1940. Spain 1932 for <i>C. capitata</i> via Hawaii.	Hawaiian Islands		California 2003–2007 for <i>B. oleae</i> via France. France 2007 for <i>B. oleae</i> . Hawaii 1947–1952 for <i>B. dorsalis</i> , imported but not released. Hawaii (quarantine facility 1996 via Kenya for <i>C. capitata</i>)
Bactrocera oleae Ceratitis capitata	Carpophthoromyia tritea Hawaiian Islands	Ceratitis capitata Ceratitis catoirii Neoceratitis cyanescens Trirhithromyia cyanescens	Ceratitis capitata Bactrocera oleae
Egypt, Kenya, Namibia, South Africa	Nigeria	Madagascar, Mauritius, Reunion	Kenya, Namibia, South Africa, Transvaal
Koinobiont solitary endophagous larval parasitoid	Koinobiont solitary endophagous larval parasitoid	Koinobiont solitary endophagous larval parasitoid	Koinobiont solitary endophagous larval parasitoid
3	3	3	2
Psyttalia humilis (Silvestri)	Psyttalia inconsueta (Silvestri)	Psyttalia insignipennis (Granger)	Psyttalia lounsburyi (Silvestri)

Table 16.1 (continued)

					Distribution outside Africa when	References for
Valid names of parasitoids ^a	Family and subfamily	Mode of parasitism	Country and region of origin	Host records	used in tephritid biological control programmes	distribution and host association
Psyttalia masneri Wharton	3	Koinobiont solitary endophagous larval parasitoid	Kenya	Taomyia marshalli		36
Psyttalia	3	Koinobiont	Benin, Cameroon,	Ceratitis capitata	Hawaiian Islands 1913, 1936 for C.	19, 27, 30, 31,
perproximus		solitary	Ghana, Kenya,	Ceratitis colae	capitata. Hawaii 1947–1952 for B.	35, 41
(Silvestri).		endophagous	Mali, Nigeria,	Ceratitis cosyra	dorsalis, imported but not released.	
		iaivai parasitoru	South Africa	Ceratitis flexuosa		
			Tanzania, Togo	Ceratitis giffardi		
				Ceratitis pedestris		
				Ceratitis punctata		
				Dacus bivittatus		
				Dacus ciliatus		
				Dacus sp.		
				Trirhithrum nigerrimum		
				Trirhithrum nigrum		
				Trirhithrum senex		
				Trirhithrum teres		
Psyttalia	3	Koinobiont	Cameroon, Congo, Ceratitis anonae	Ceratitis anonae	Hawaiian Islands 1951 for	19, 31, 35, 38
phaeostigma		solitary	East Africa,	Ceratitis capitata	Bactrocera dorsalis. Hawaii 1996	
(Wilkinson)		endophagous	Kenya,	Ceratitis catoirii	quarantine facility for B.	
		ıarvaı parasıtoru	Mauritius,	Dacus ciliatus	Cucuronae, Mauninas 101 Tephritidae 1934.	
			ınion,	Dacus bivittatus	Mayotte (new to fauna).	
			South Africa	Dacus demmerezi	Madagascar (new to fauna).	
				Trirhithrum queritum	La Réunion.	

Psyttalia ponerophaga (Silvestri)	3	Koinobiont solitary endophagous larval parasitoid	Reunion (Pakistan Bactrocera oleae origin?)		California 2003–2007 for <i>B. oleae</i> via Pakistan.	15
Psyttalia sanctamariana (Fischer)	3	Unknown	Madagascar, Mauritius, Reunion	Spathulina acroleuca (Schiner)		38
Psyttalia subsulcata (Granger)	"	33	Madagascar, Reunion	Spathulina acroleuca (Schiner		38
Psyttalia sp.	3	3	Kenya	Ceratitis anonae Ceraritis lexuosa Ceratitis fasciventris		43
				Ceratitis rosa		
Rhynchosteres mandibularis Kimani-Njogu and Wharton	3	Larval parasitoid	Kenya	Trirhithrum sp.		16
Rhynchosteres clypeatus (Bridwell)	3	Koinobiont solitary endophagous larval parasitoid	Africa, Nigeria	Ceratitis sp.		19
Sternaulopius	"	Unknown	Cameroon, Congo, Ceratitis sp.	Ceratitis sp.		44
<i>bisternaulicus</i> Fischer			Kenya	Trirhithrum sp.		
Sternaulopius sp.	"	"	Kenya	Ceratitis flexuosa		43
				Ceratitis fasciventris		

Table 16.1 (continued)

					Distribution outside Africa when	References for
/alid names of	Family and	Mode of	Country and		used in tephritid biological control	distribution and
asitoids ^a	subfamily	parasitism	region of origin	Host records	programmes	host association
Utetes africanus	"	Koinobiont	Eritrea, Ethiopia,	Bactrocera oleae	California 1990s, 2006 for B. oleae. 19, 20, 21, 26,	19, 20, 21, 26,
.épligeti)		solitary	a,	Ceratitis capitata	Hawaii 1996–2004 for C. capitata	27, 28, 31, 35,
		endophagous	Senegal, South	Ceratitis rosa	and $1947-1952$ for B. dorsalis,	41
		iarvai parasitolu	Апіса	Trirhithrum coffeae	1910, 1915, 1917 for <i>B. oleae</i> .	
Isurgus sp.	Ichneumonidae, Unknown (?	Unknown (?	Tanzania	Ceratitis capitata		19, 31
	Tersilochinae	ectophagous)		Ceratitis sp.		
				Ceratitis. rosa		
				Trirhithrum nigerrimum		

'Accepted names of Chalcidoids and Braconids were revised according to Noyes, J.S. 2012, Chalcidoidea Universal Database, World Wide Web electronic publication http://www.nhm.ac.uk/chalcidoids van Noort, S. 2015. Afrotropical Waspweb Database of Braconidae http://www.waspweb.org/Ichneumonoidea/Braconidae/; and Wharton Lab Database http:// (2) Indicates uncertain interpretation or host information not based on rearing or experiments, e.g. when parasitoids emerged from fruit infested by more than one mx.speciesfile.org/projects/8/public/public_content/show/13189?content_template_id=88

tephritid species

References cited in table: (1) Boucek 1963; (2) Bridwell 1918; (3) Clausen 1956; (4) Clausen et al. 1965; (5) Cochereau 1970; (6) Daiber 1966; (7) Delucchi 1957; (8) El-Heneidy et al. 2001; (9) Etienne 1973; (10) Fry 1987; (11) Ghani 1972; (12) Greathead 1976; (13) Greathead 1972; (14) Kapatos et al. 1977; (15) Hoelmer 21) Neuenschwander et al. 1983; (22) Nixon 1930; (23) Orian and Moutia 1960; (24) Rivnay 1968; (25) Rogg and Camacho 2000; (26) Silvestri 1914a; (27) Silvestri Wharton and Gilstrap 1983; (36) Wharton 2009; (37) Yoder and Wharton 2002; (38) Fischer and Madl 2008; (39) Vayssières et al. 2012; (40) van Noort et al. 2015; et al. 2011; (16) Kimani-Njogu and Wharton 2002; (17) Kimani-Njogu et al. 2000; (18) Monaco 1978; (19) Narayanan and Chawla 1962; (20) Neuenschwander 1982; 1914b; (28) Silvestri 1915; (29) Steck et al. 1986; (30) Stibick 2004; (31) Thompson 1943; (32) Wharton 1999a; (33) Wharton 1999b; (34) Wharton et al. 2000; (35) 41) Gilstrap and Hart 1987; (42) Waterhouse 1993; (43) Copeland et al. 2006; (44) Wharton 2006; (45) Vayssières et al. 2002 The rich diversity of the African tephritid parasitoid fauna continues to be unravelled as more new species are described and careful studies on their biology and host specificity are made. For example, *Fopius ceratitivorus* Wharton was first described by Wharton in 1999 and recognized as an important egg-larval parasitoid of *C. capitata* (Wharton 1999a); *Fopius okekai* and *Rhynchosteres mandibularis* were described in 2002 (Kimani-Njogu and Wharton 2002). More recently, two new Kenyan species have been described: *Psyttalia halidayi* Wharton (from the Natal fruit fly, *Ceratitis rosa* Karsch) and *Psyttalia masneri* Wharton (from an uncommon tephritid, *Taomyia marshalli* Bezzi, in cornstalk dracaena, *Dracaena fragrans* [L.] Ker Gawl) (Wharton 2009). In general, coffee, *Coffea arabica* L. and wild olive, *Olea europaea* ssp. *cuspidate* (Wall. ex G. Don) Cif, the closest relative to cultivated olives, supported the greatest diversity of parasitoid fauna (Clausen et al. 1965; Greathead 1972; Steck et al. 1986; Wharton et al. 2000; Copeland et al. 2004; Hoelmer et al. 2004, 2011).

It is important to note that some taxa reported in these early records have undergone several taxonomic revisions and changes in nomenclature (Fischer 1972, 1977, 1987; Wharton 1983, 1987; Wharton and Gilstrap 1983). Lists of synonyms and previously used combinations have been produced for the Braconidae and Opiinae (Wharton 1989) and for the superfamily Chalcidoidea (Noyes 2012).

3 Contribution of Indigenous Parasitoids to Fruit Fly Management

The level of parasitism achieved by indigenous parasitoid species in various fruit fly species on cultivated fruits is variable but generally quite low (<5%) (Steck et al. 1986; Lux et al. 2003; Vayssières et al. 2012). For example, Vayssières et al. (2012) reported combined parasitism by seven parasitoid species of various wild and cultivated crops to be just 2.4%. These observations may not entirely reflect the field situation as some parasitized larvae might have already left the sampled fruits to pupate in the soil, thus escaping observation (Lux et al. 2003). Also, unripe fruits collected during the surveys are likely to yield fewer larval parasitoids than ripe fruits, especially of *Psyttalia* species which have short ovipositors and prefer mature larvae close to the surface of ripe and fallen fruits. Wong and Ramadan (1987) working in Maui Island, Hawaii reported 19% parasitism of *C. capitata* and *B. dorsalis* larvae in green fruit samples compared with 43% in ripe and fallen fruits. Similar relationships between fruit ripeness and rates of parasitism have been reported for *Psyttalia fletcheri* (Silvestri) (Purcell and Messing 1996).

Of all the cultivated crops, coffee not only supported the highest diversity of parasitoids attacking fruit flies, but also high levels of parasitism. Steck et al. (1986) recorded a combined percent parasitism by *Psyttalia perproximus* (Silvestri), *Fopius caudatus* (Szépligeti) and *Fopius caudatus* auc C, *Diachasmimorpha fullawayi* (Silvestri), *Fopius desideratus* (Bridwell) and an undescribed species of *Opius* that

ranged between 10 and 56%; the average was 35% parasitism in a research plantation and 17% parasitism in a commercial plantation. This could be because coffee has a relatively small fruits compared with mango, *Mangifera indica* L., guava, *Psidium guajava* L., and papaya, *Carica papaya* L.. Opiine larval parasitoids do not enter the infested fruits to locate fruit fly larvae and their success is, therefore, limited by the length of their ovipositor and the size of the fruit. Moreover, in coffee ripe fruits remain on the tree allowing for full larval exposure to parasitoids.

Other tephritid host plants that support high levels of parasitism are members of the family Oleaceae, e.g. Olea europaea ssp. cuspidata (Wall. ex G. Don). During the 1999-2003 survey for insects associated with fruits of indigenous species of Oleaceae in Kenya, the rates of parasitization of B. oleae by Psyttalia lounsburyi (Silvestri) alone exceeded 30 % in some of the collections (Copeland et al. 2004). In a recent study by Mkize et al. (2008) on wild olives in the Eastern Cape Province, South Africa, the combined percent parasitism of B. oleae and Bactrocera biguttula (Bezzi) by Psyttalia concolor (Szépligeti), P. lounsburyi, Utetes africanus (Szépligeti) and Bracon celer Szépligeti, was in some instances as high as 83 %, leading to very low infestation levels (1–8%). The authors indicated that these parasitoids were more closely associated with B. oleae as the number of B. oleae recovered was far smaller than the number of B. biguttula recovered. They also argued that fruit flies might not have become economic pests of commercial olives in the Eastern Cape due to the activity of these natural enemies. In Egypt, El-Heneidy et al. (2001) reported parasitism rates for *P. concolor* and *Pnigalio agraules* (Walker) (= Pnigalio mediterraneus (F.)), attacking B. oleae of 39% and 11%, repectively.

The performance of native parasitoids on different fruit fly species has been evaluated under laboratory conditions; high to moderate rates of parasitism were achieved in some host species. For example, Mohamed et al. (2003) reported parasitism rates of 37 and 46% by *Psyttalia cosyrae* (Wilkinson) in *C. capitata* and the mango fruit fly, *Ceratitis cosyra* (Walker), respectively. In a different study the same authors, reported parasitism rates by *P. concolor* of 46 and 28% in *C. capitata* and *C. cosyra*, respectively (Mohamed et al. 2007). Both parasitoid species were unable to develop on the *C. rosa, Ceratitis fasciventris* (Bezzi), *Ceratitis anonae* (Graham) and *Z. cucurbitae* (Mohamed et al. 2003, 2007) (Fig. 16.1). In contrast, the Eulophid *Tetrastichus giffardii* Silvestri achieved parasitism rates of 44.3 and 41.8% on *C. capitata* and the lesser pumpkin fly, *Dacus ciliatus* Loew, respectively. Although members of the genus *Tetrastichus* are known to be rather generalist parasitoids, *T. giffardii* achieved zero parasitism on all members of the *Ceratitis* FAR group (*C. fasciventris*, *C. annonae* and *C. rosa*) as well as on the exotic *Bactrocera* species (*Z. cucurbitae* and *B. dorsalis*) (Fig. 16.1).

Although the role of pupal parasitoids in biological control of fruit flies cannot be denied, no systematic studies to evaluate their impact on fruit fly populations have been made, and hence no accurate statistics are available on their role as biological control agents. They are not host specific and may also attack nontarget Diptera in the suborder Cyclorhapha (e.g. Agromyzidae, Drosophilidae, Muscidae). Also they are difficult to evaluate in the field as they need to be collected by sifting

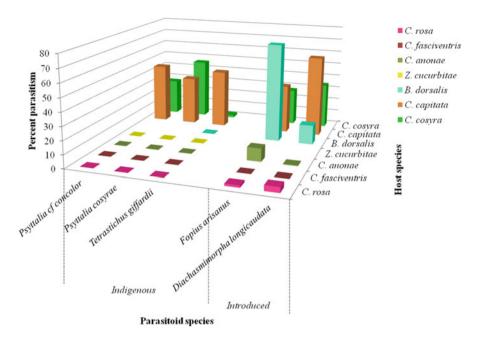


Fig. 16.1 Performance of indigenous and introduced parasitoid species on key native and invasive fruit flies in Africa

the soil to retrieve fruit fly pupae, compared with collecting and incubating fruits to evaluate parasitoid species attacking the egg and larval stages of their hosts (M.M. Ramadan unpublished data; Wang and Messing 2004a, b).

4 Exploration for Fruit Fly Parasitoid Species in Africa for Introduction Elsewhere

Numerous species of hymenopteran fruit fly parasitoids have been recorded from native African tephritids since Silvestri's famous survey in 1912 (Table 16.1). The table includes parasitoid species reared from fruit-infesting Tephritidae but excludes parasitoids specialized on tephritids infesting flowerheads (e.g. the African *Psyttalia vittator* group), stem and gall forming tephritids, various African opiines from agromyzid leafminers (e.g. *Opius importatus* Fischer and *Opius phaseoli* Fischer imported from Africa into Hawaii in 1969), and seed feeders (e.g. *Psyttalia sanctamariana* [Fischer] reared from the seed tephritid and *Spathulina acroleuca* [Schiner]). Parasitoids without confirmed host records, doubtful hosts, or doubtful identifications (e.g. *Psyttalia insignipennis* [Granger] from Madagascar and Singapore), are not reported here.

The African fruit fly species, C. capitata, has invaded and become established in many parts of the world including Western Australia and the Hawaiian Islands from as early as 1897 and 1910, respectively (Froggatt 1909; Compere 1912; both cited in Headrick and Goeden 1996). Being an alien pest, and lacking resident parasitoids in these countries, it continued to cause massive yield losses on various types of fruit. This prompted searches for efficient natural enemies of this devastating pest. The first classical biological control attempt was directed against C. capitata by George Compere when he was hired by the government of Western Australia between 1902 and 1907 to search for natural enemies of C. capitata (Wharton 1989). However, Compere was unable to determine the native range of *C. capitata*, and hence the parasitoids that he introduced to Australia from Brazil and India never established in C. capitata populations. A decade later, following the accidental introduction and establishment of C. capitata in Hawaii (then the Territory of Hawaii), Filippo Silvestri travelled to Africa and Australia, on behalf of the Hawaiian Board of Agriculture and Forestry, to search for efficient natural enemies of C. capitata (Silvestri 1914a, b). He identified 21 species of African hymenopteran parasitoids as having potential as biological control agents of C. capitata; he made collections from fruit infested with ten Ceratitis species and seven Dacus species. However, few parasitoids survived his long steamship trip and he returned to Hawaii with only Dirhinus giffardii Silvestri, Coptera silvestrii (Kieffer), Psyttalia humilis (Silvestri) and Psyttalia perproximus (Silvestri) from Africa, and Diachasmimorpha tryoni (Cameron) from Australia.

Silvestri returned from Hawaii to Italy in 1913 with some *D. giffardii* and *C. silvestrii* for biological control of *B. oleae*. A year later, he travelled back to East Africa (Eritrea), this time in search of more parasitoids for classical biological control of *B. oleae* in his homeland of Italy. He found 14 species attacking *B. oleae*, ten of which were reared and released in Italy although none became established. Fullaway, travelled to Nigeria in 1914 to re-collect parasitoid species that had not survived Silvestri's expedition and he returned with *Tetrastichus giffardianus* Silvestri and *Diachasmimorpha fullawayi* (Silvestri), which were then released and established in Hawaii (Fullaway 1914).

Although Silvestri and Fullaway collected many parasitoid species belonging to different genera and families, only a few survived the long voyage to Hawaii. Amongst those that survived, four species were released and established of which three were from Africa. These were, *P. humilis* from South Africa and, *D. fullawayi* and *D. giffardii* both from West Africa. The two former species are koinobiont larval parasitoids while the latter is an idiobiont pupal parasitoid. Two decades after introduction in to Hawaii the combined parasitism rates achieved by *P. humilis* and another introduced Australian parasitoid, *D. tryoni* in *C. capitata* populations ranged from 46 to 94% (Willard and Mason 1937). The two parasitoid species achieved approximately equal levels of parasitism in *C. capitata* populations. As a result, *C. capitata* infestations were significantly reduced on coffee and, to a lesser extent, on other fruits; success was not so good against *C. capitata* in large sized fruits such as mangoes (http://paroffit.org/public/site/paroffit/home). Subsequently, *P. humilis* was mass reared and redistributed from Hawaii to several other countries with teph-

ritid fruit fly problems (Table 16.1). However, this parasitoid has not been recorded in Hawaii since 1933, even in recent surveys (M.M. Ramadan unpublished data) and is thought to be extinct there (http://paroffit.org/public/site/paroffit/home). Similarly, although it did establish after introduction, *D. fullawayi* has only rarely been recorded in Hawaii since 1949 (Bess 1953; Bess et al. 1961). From Hawaii, *D. fullawayi* and *P. humilis* were also introduced into Spain, Puerto Rico and Australia, without success (Table 16.1). Following its introduction into Hawaii, *D. giffardii* became established in *C. capitata* populations; it was later introduced from Hawaii into Australia in 1956, Mexico in 1955, Puerto Rico in 1935 and Bolivia in 1971 (Bennett and Squire 1972), and Israel in 1956 for biological control of *C. capitata* and other resident tephritids (Table 16.1).

During a separate expedition at around the same time, the gregarious parasitoid, *T. giffardianus* was also introduced into Hawaii from West Africa by D.T. Fullaway and J.C. Bridwell in 1914, where it became established (Clausen et al. 1965). Subsequently, this species was mass-reared and redistributed from Hawaii to the Pacific Islands and Latin American countries. For example, it was imported into Brazil in 1937 where it established (Ovruski and Schliserman 2012), and from there it was also imported into Argentina in 1947 (Flávio et al. 2013) (Table 16.1).

Africa was also targeted in world-wide surveys for parasitoids made during the Hawaiian biological control campaign against *B. dorsalis*, in the 1950s. Import of African fruit flies into Hawaii (from South Africa in 1949, from Kenya in 1949–1950, from Congo in 1950–1951, and from Cameroon in 1951) with the purpose of collecting any parasitoids that emerged, was comprised of 571,995 pupae from 26 different tephritid species (Clausen et al. 1965). At least 22 different parasitoid species were recovered from these shipments, propagated and evaluated for their ability to develop on, *B. dorsalis*, *Z. cucurbitae* and *C. capitata*. Only six parasitoid species were released (*D. giffardii*, *T. giffardii*, *T. giffardianus*, *Fopius bevisi* (Brues), *Psyttalia phaeostigma* (Wilkinson) and an *Opius* sp. (Clausen et al. 1965).

Within the framework of a USDA grant (2001-2004) through the Texas A&M University entitled 'Facilitating Identification and Suppression of African Fruitinfesting Tephritidae (Diptera): Invasive Species That Threaten U.S. Fruit and Vegetable Production' the recently described parasitoid species, Fopius ceratitivorus Wharton and a related species, Fopius caudatus (Szépligeti) were imported from Kenya into the USDA-APHIS/MOSCAMED quarantine facility in Guatemala (Lopez et al. 2003), and from Guatemala into Hawaii. They where both evaluated for potential effects on non-target hosts and found not to parasitize eggs or larvae of the non-target tephritids, Procecidochares alani Steyskal, a biological control agent of the invasive weed, Ageratina riparia (Regel), and the native Hawaiian tephritid Trupanea dubautia (Bryan) found in the flowerheads of the endemic shrub, Dubautia raillardioides Hillebr. (Bokonon-Ganta et al. 2007; Wang et al. 2004). Under the same initiative P. phaeostigma and P. halidayi were, respectively, sent to St. Helena for control of D. ciliatus (2000-2001) and La Réunion (2000-2001) for control of C. rosa (S.A. Mohamed unpublished data). However, no follow up on their release and establishment has been made.

Psyttalia concolor a parasitoid of North African origin that is similar to the South African *P. humilis*, was initially imported from Tunisia (Monastero 1931; Silvestri 1939), and then released in Italy in 1913 for control of *B. oleae*, where it only became established at low densities. Since then, biological control of *B. oleae* in southern European countries has been almost exclusively based on importation and repeated releases of *P. concolor* (Raspi 1995; Raspi and Loni 1994). This parasitoid also parasitizes *C. capitata* in the Mediterranean basin.

In Israel, classical biological control targeting *C. capitata* and *B. oleae* has a relatively long history (Argov and Gazit 2008 and references therein). Between 2002 and 2004 four parasitoid species were imported from Hawaii and released against *C. capitata*. Two of these parasitoid species, the egg-larval parasitoid, *F. ceratitivorus* and the larval parasitoid, *P. concolor* were originally from Kenya. Of the African parasitoid species, *F. ceratitivorus* has shown signs of long-term establishment in Israel (Argov and Gazit 2008). A few years later (2009–2010), two other African parasitoid species were imported in to Israel, this time targeting *B. oleae*. These were *P. lounsburyi* (from Kenya and South Africa), and *Psyttalia* sp. nr. *concolor* (also called *P. humilis*) (from Namibia). A total of 37,000 and 97,000 wasps of the former and the later species, respectively were released in Israeli olive groves.

In 1998 B. oleae was detected in Californian olive groves (Rice et al. 2003). On the recommendation of earlier explorers highlighting the high diversity of B. oleaeassociated parasitioids in Africa (e.g. Silvestri 1914a, b; Neuenschwander 1982), more expeditions across Africa were made to study these parasitoid species further. The parasitoid, *P. concolor*, was obtained from tephritid fruit flies infesting coffee in Kenya, reared on C. capitata in Guatemala by USDA-APHIS, PPQ, and then imported and released in Californian olive groves for biological control of *B. oleae*. Following this further exploration was attempted, this time for parasitoids that were more specific to B. oleae on wild African olives. Robert Copeland, an American entomologist based at icipe, Nairobi, Kenya, was contracted by USDA-APHIS to search for parasitoids attacking B. oleae in Kenya. He collected P. concolor, P. lounsburyi and Utetes africanus for importation into California via the USDA-ARS European Biological Control Laboratory (EBCL) in Montferrier, Montpellier, France (Copeland et al. 2004). This was followed by more expeditions to Kenya, South Africa, Namibia, La Réunion and Morocco. During these expeditions, P. lounsburyi, P. humilis, P. concolor, Bracon spp. and U. africanus were reared from wild olives and shipped to California for release via France (Hoelmer et al. 2011).

In Central America, African parasitoids were also the main focus for classical biological control of *C. capitata*. For example, in Costa Rica two African parasitoids, *D. giffardii* and *P. concolor* were introduced following the invasion by *C. capitata* in 1955 (Purcell 1998). A further six African parasitoid species were obtained by Gary Steck during his exploration for natural enemies of *C. capitata* in Togo and Cameroon between 1980 and 1982 (Steck et al. 1986). Following mass-rearing in Guatemala, *F. ceratitivorus* from Kenya was released on a large scale against *C. capitata* in the coffee-growing highlands along the Mexican borders (Sivinski and Aluja 2012). Detailed information regarding African parasitoid introductions for classical biological control of tephritid fruit flies in other countries is given in Table 16.1.

5 Introduction of Exotic Parasitoid Species into Africa for Biological Control of Invasive Fruit Flies

The first, though unsuccessful, attempt at classical biological control of exotic, invasive fruit flies in Africa was done in 1905. During this period, Charles Lounsbury and Claude Fuller, entomologists from South Africa, travelled to South America (Sao Paulo and Bahia, Brazil) to collect natural enemies for control of C. capitata in South Africa because, at the time, the native range of C. capitata was unknown (Lounsbury 1905 as cited in Ovruski et al. 2000). They collected the braconid, Opius trimaculatus Spinola and another unidentified parasitoid, from fruits infested by Anastrepha fraterculus (Wiedemann) and Anastrepha serpentina (Wiedemann) (Table 16.2). According to Wharton and Gilstrap (1983) this braconid could have been a misidentification of Opius bellus Gahan, Utetes anastrephae (Viereck), or a Doryctobracon sp. Opius trimaculatus was an important species to collect as field parasitism rates ranged from 7% in large guava fruits to 38% in the smaller fruits of Surinam cherry, Eugenia uniflora L. Because of the length of the trip from Brazil to South Africa via England, none of the imported braconid parasitoids survived the journey. Three years later, from a laboratory-reared colony in Australia, G. Compere sent to South Africa 20,000 Aceratoneuromyia indica (Silvestri) parasitoids, which he had initially collected from India during his expedition for natural enemies of C. capitata in Western Australia (Table 16.2). However, this parasitoid never became established in South Africa (Clausen 1956). Other failed attempts included the introduction of Diachasmimorpha longicaudata (Ashmead), Opius sp., Psyttalia incisi (Silvestri) and P. phaeostigma into Mauritius; and D. tryoni into both Mauritius and La Réunion (Fischer and Madl 2008).

Apart from the initiatives already mentioned, and despite the fact that Africa has been invaded by four Asian *Bactrocera* species (see De Meyer and Ekesi 2016), for which the first records date back to the 1930s (White and Elson-Harris 1992), classical biological control programmes for invasive fruit flies in Africa have not been taken up in the same way as in other continents that have been invaded by exotic species. For example, in Hawaii where *C. capitata* and three species in the genus *Bactrocera* have become established as key pests of fruits and vegetables, several expeditions were undertaken to various parts of the world in search of co-evolved natural enemies of these pests for introduction in to Hawaii. This resulted in the most successful classical biological control programme ever undertaken against tephrtids fruit flies (Wharton 1989; Purcell 1998).

In Africa, the earliest record of successful classical biological control of an exotic fruit fly species was in 1995, when *P. fletcheri* was introduced from Hawaii for biological control of *Z. cucurbitae* on the island of La Réunion (Quilici et al. 2004) (Table 16.2). The parasitoid is currently well established on the island though rates of parasitism of *Z. cucurbitae* are quite variable ranging from 1 to 75% on bitter gourd, *Momordica charantia* L (Cucurbitaceae) (Quilici et al. 2008). This was followed by introduction of another parasitoid species, the egg-larval parasitoid *Fopius arisanus* (Sonan) for biological control of another alien invasive pest,

Table 16.2 Hymenopteran larval and egg-larval parasitoids introduced into Africa for classical biological control against invasive fruit flies

Parasitoid species	Family and subfamily	Country/region of origin (where reared and where exported to)	Country and year of introduction	Target hosts	Status	References
Aceratoneuromyia indica (Silvestri)	Eulophidae, Tetrastichinae	India, Malaysia, Sri Lanka (mass reared, redistribution via Australia 1908). Southeast Asia (mass reared on <i>C.</i> <i>capitata</i> , redistribution via Hawaii 1957).	Egypt, Mauritius (1957–1959), Reunion (1972), South Africa (1908), Tunisia	Ceratitis capitata Ceratitis rosa	Established on Mauritius, La Réunion South Africa, Tunisia	2, 5, 6, 8
Aganaspis daci (Weld)	Figitidae, Bucoilinae	Southeast Asia (mass reared in Hawaii on Bactrocera dorsalis and B. latifrons. Strain ex. C. capitata from Greece, redistribution via Hawaii).	Egypt 2009 via Hawaii Reunion 1975 via Malaysia	Bactrocera zonata Ceratitis capitata	Egypt, established in <i>C.</i> capitata and <i>B.</i> zonata populations 2010, ongoing evaluations.	9, M.M. Ramadan unpublished data
Fopius arisanus (Sonan)	Braconidae Opiinae	Indo Malayan, Asia (mass reared on <i>Bactrocera dorsalis</i> , redistribution via Hawaii).	Benin (2009). Botswana (2015?). Cameroon (2009?). Comoros (2015). Egypt (2009). Kenya (2006, 2010). Madagascar (1993). Mauritius (1957–1959). Morocco. Mozambique (2009, 2012). Namibia (2015). Reunion (1965, 1972, 1995, 2003, 2009). Senegal (2012). Tanzania (2010). Togo (2009). Uganda. Zambia (2015).	Bactrocera dorsalis Bactrocera zonata Ceratitis capitata Ceratitis rosa Dacus ciliatus, Dacus demmerezi, Neoceratitis cyanescens	Established in all except Egypt	2, 3, 7, 11

Malaya d on Ba	Indo Malayan, Asia (mass Egypt (2009) reared on <i>Bactrocera</i>		Ceratitis capitata Pending release Bactrocera zonata in Egypt	Pending release in Egypt	M.M. Ramadan unpublished data
dorsalis, redistribution via Hawaii).			,		
Southeast Asia (mass	Kenya (2	Kenya (2006, 2010).	Bactrocera	Established in all	6, 2, 5, 8, 11,
n via	gypt (20	de.	Bactrocera zonata	cycept imaminus	VIIATI
Hawaii).	[adagas		Ceratitis capitata	Pending release	
<u> </u>	rozamo eunion 2010). Z	Mozambique (2009). Reunion (1971). Tanzania (2010). Zambia	Ceratitis rosa	in Egypt	
Queensland, Australia to Hawaii (mass reared on Is	57? Al lands, C	ry Egypt	Bactrocera zonata Egypt not establishe	Egypt not established.	2, 5, 11
(2) (2) (2) (2) (2) (2) (3) (4) (5) (6) (7) (7) (7) (7) (7) (7) (7) (7) (7) (7	009). N auritius outh Afi	(2009). Madagascar. Mauritius. Reunion (1995). South Africa, Zambia	Ceratitis capitata	Established in Mauritius on Ceratitis sp.	
Queensland Australia to Eg Hawaii (mass reared on Bactrocera latifrons, redistribution via Hawaii).	Egypt (2009)		Bactrocera zonata Pending release in Egypt	Pending release in Egypt	M.M. Ramadan unpublished data
S	Egypt (2009).		Ceratitis capitata	Established	9, 10
_ ·	Réuni	La Réunion (1995)	Bactrocera cucurbitae	Pending release in Egypt	
redistributed 1995–1997,		I	Dacus ciliatus		
via fiawaii.		1	Dacus demmerezi		
			Neoceratitis		
			cvanescens		

Table 16.2 (continued)

Parasitoid species	Family and subfamily	Country/region of origin (where reared and where exported to)	Country and year of introduction	Target hosts	Status	References
Psyttalia incisi (Silvestri)	3	Indo Malayan region, mass Egypt (2009). reared in Hawaii on Mauritius Bactroeera dorsalis, redistributed via Hawaii.	Egypt (2009). Mauritius	Bactrocera zonata Not established Ceratitis rosa? Pending release in Egypt	Not established Pending release in Egypt	M.M. Ramadan unpublished data
Phaedrotoma trimaculata (Spinola)	3	Brazil reared on Anastrepha spp., Chile and Argentina ex. Drosophila flavopilosa (Drosophilidae).	South Africa (1905)	Ceratitis capitata Not established	Not established	1, 2, 4
Opius sp.	3	Southeast Asia to Hawaii for Bactrocera dorsalis, redistribution via Hawaii.	Mauritius. Morocco (1954)	Ceratitis capitata Not established Bactrocera oleae	Not established	7

(?) Indicates uncertain interpretation, or host information not based on rearing or experiments, e.g. when parasitoids emerged from fruit infested by more than References cited in table: (1) van Achterberg and Salvo 1997; (2) Clausen 1978; (3) Ekesi and Billah 2006; (4) Fischer 1971; (5) Greathead and Greathead one tephritid species

1992; (6) Noyes 2012; (7) Mohamed et al. 2008; (8) Orian and Moutia 1960; (9) Quilici et al. 2004; (10) Quilici et al. 2000; (11) CABI 2016

B. zonata, on the same island (Rousse et al. 2006). A survey conducted on Indian almond, *Terminalia catappa* L., on which *B. zonata* is the dominant species, found that the level of parasitism on this host-fruit could reach 70–80% (Quilici et al. 2008).

The most prominent fruit fly classical biological control programme in Africa to date was directed against B. dorsalis after it proved to be lacking resident parasitoid species capable of regulating its populations; all indigenous parasitoid species evaluated failed to form new associations with this pest due to its strong immune system, resulting in encapsulation and melanization of parasitoid eggs (Mohamed et al. 2006; S.A. Mohamed unpublished data). For example, two solitary larval parasitoids, P. cosyrae and P. phaeostigma and one gregarious parasitoid, T. giffardii were evaluated. Bactrocera dorsalis was readily accepted as a potential host by adult female T. giffardii and to a lesser extent by females of the two Psyttalia species. However, all eggs of the two *Psyttalia* species and nearly all the eggs of *T. giffardii* were encapsulated within larvae of B. dorsalis (Mohamed et al. 2006; S.A. Mohamed unpublished data). None of the T. giffardii progeny that escaped encapsulation were able to complete development to the adult stage. Furthermore, 34,430 kg of various host fruits of B. dorsalis were sampled in East Africa (Rwomushana et al. 2008) and West Africa (Vayssières et al. 2012; R. Hanna unpublished data), but not a single parasitoid species was recovered, confirming the fact that the indigenous African parasitoids were unable to parasitize B. dorsalis. These findings paved the way for identification and introduction of efficient parasitoids that had a shared history and origin with B. dorsalis. In this regard, the subsequent and logical approach was exploration for co-evolved parasitoid species in the pest's presumed native range of Sri Lanka. Three expeditions were made between 2005 and 2008 by scientists from the International Centre of Insect Physiology and Ecology (icipe), Nairobi, Kenya, the International Institute of Tropical Agriculture (IITA) and the University of Bremen, Germany, in collaboration with staff from the Horticultural Crop Research and Development Institute (HORDI), Peradeniya, Sri Lanka within the framework of the Mango IPM BMZ-funded project. Eight parasitoid species from different guilds (one egg-larval, five larval and two pupal) including F. arisanus, D. longicaudata and P. fletcheri were recovered from the sampled fruits and evaluated in the laboratory against target hosts (Billah et al. 2008; S.A. Mohamed unpublished data). Despite this, none were introduced into Africa due to issues relating to the Convention on Biological Diversity (CBD) to which Sri Lanka is a signatory. Thereafter, contacts were made between scientists on the *icipe*-led African Fruit Fly Programme and scientists at the USDA-ARS Pacific Basin Agricultural Research Center at Hilo, Hawaii and the University of Hawaii at Manoa. This led to introduction of the egg-larval parasitoid F. arisanus and the larval parasitoid, D. longicaudata into Africa (Table 16.2). These parasitoid species had been credited with outstanding success in the biological control of B. dorsalis following its invasion and establishment in Hawaii in 1944/1945 (Fullaway 1949). The two parasitoid species were imported into the icipe quarantine facility in 2006, following the FAO code of conduct for the importation and release of exotic biological control agents (IPPC 2005), and were later released in Kenya in 2008, in Tanzania in 2010, and in Mozambique in 2012. *Fopius arisanus* was also released in the Comoros Islands in 2015. In Western Africa and under the umbrella of the same collaborative project, IITA released *F. arisanus* in Benin, Cameroon and Togo from a colony initially obtained from *icipe* in 2006 and subsequently maintained by IITA at Yaoundé, Cameroon and Cotonou, Benin. A detailed account of the release, establishment and spread of this parasitoid in Benin is given in Gnanvossou et al. (2016).

The post release assessment of colonization of these parasitoid species so far indicates that F. arisanus has established in all the countries where it was released but to varying degrees; the rates of B. dorsalis parasitism achieved on cultivated fruits was 33–40 % in Kenya at the Northern Coast region of Kilifi (elevation>400 masl) (Ekesi et al. 2010, 2016; S. Ndlela, unpublished data). On wild host fruit rates of B. dorsalis parasitism reached 46.5% on bush mango, Irvingia gabonensis (Aubry-Lecomte), in Benin (Gnanyossou et al. 2016). While establishment of D. longicaudata has been reported only in Kenya, at Embu in the Eastern Province (elevation range of 694M–1509 masl) and the Coast region (elevation < 400 masl) with parasitism rates of up to 17% and 15.4%, respectively. Under a separate initiative, yet still targeting B. dorsalis, USDA-APHIS in collaboration with the Senegalese Plant Protection Department introduced F. arisanus into Senegal from Hawaii (Vargas et al. 2016). Between 2013 and 2014 14 shipments of 66,000 parasitoids were received in Senegal and released in the Casamance region (Vargas et al. 2016). This resulted in 20–30 % parasitism of B. dorsalis. The authors indicated that additional parasitoid shipments were sent from Hawaii and released in other regions of Senegal to improve control during the mango fruiting season (Vargas et al. 2016).

In southern Africa, within the framework of the BONAZAZI FAO-funded project for suppression of *B. dorsalis*, both *F. arisanus* and *D. longicaudata* have recently been introduced into Botswana, Namibia, Zambia and Zimbabwe. However, a post evaluation survey to evaluate their establishment will only be undertaken during the 2016/2017 mango fruiting season.

In North Africa there has been a control programme targeted at another exotic invasive species, *B. zonata*. This species was first detected in 1997 and has since become widespread over most of the Egyptian governorates causing serious damage to many fruit crops. The Agricultural Research Centre (ARC), Giza, Egypt in collaboration with the State of Hawaii Department of Agriculture, have imported five parasitoid species from Hawaii for evaluation and release in Egypt (El-Heneidy and Ramadan 2010). These are *Aganaspis daci* (Weld), *F. arisanus*, *D. kraussii*, *D. tryoni* and *D. longicaudata* (Table 16.2). The five species were evaluated in the laboratory against *B. zonata*. Surprisingly, *F. arisanus*, which achieved high rates of parasitism on *B. zonata* in La Réunion, performed poorly on the same host in Egypt (El-Heneidy personal communication).

Following the promising performance in the laboratory evaluation of *A. daci* against *B. zonata*, this parasitoid has been released in the El-Arish district, North Sinai Governorate, during the guava season of 2010, and was recovered 1 month after release. Post-release assessment in the El-Arish district indicated 9.7% parasitism. Further studies on its natural dispersal and effectiveness in suppressing *B. zonata* and other tephritid fruit fly populations in Egypt, are still in progress

(El-Heneidy unpublished data). This parasitoid is an important candidate for *B. zonata* control, especially in large sized fruits (mango, peach, and guava), as it uses an ingress and sting strategy (i.e it enters the fruits to parasitize the larvae). All opines use only drill and sting strategies; therefore, their accessibility to the host inside the fruit can be limited by the length of their ovipositors.

Currently, efforts are underway to introduce *F. arisanus* and *D. longicaudata* from *icipe* into Sudan for control of *B. zonata* and Ethiopia and South Africa for control of *B. dorsalis*.

6 Prospects and Potential Use of Parasitoids for Fruit Fly Management in Africa

Since the turn of last century, considerable advances have been made in both classical and augmentative biological control of fruit flies. However, this has not progressed at the same pace in Africa.

In general, parasitoids are unlikely to provide complete control of tephrid fruit flies because they act in a density dependant manner. Furthermore, the majority of susceptible produce is high-value fruit, making the damage threshold extremely low to ensure that the consumers' zero tolerance to blemished fruits is achieved. Nevertheless, parasitoids can significantly reduce fruit fly populations when used within the framework of an area-wide IPM approach. This is evidenced by the outstanding success of biological control programmes using parasitoids against the same and/or related tephritid fruit fly species in other parts of the world. Undeniably, the outcome of B. dorsalis and C. capitata control in Hawaii, and B. dorsalis, B. kirki and B. tryoni control in French Polynesia using F. arisanus and D. longicaudata (Vargas et al. 2007) are good examples of success that can be achieved and could be replicated in Africa. Indeed, the earlier explorers such as Silvestri (1914a, b) and van Zwaluwenburg (1937) indicated that C. capitata was rare in West Africa; the former author attributed the paucity of C. capitata in West Africa to the role of parasitoids. Also Steck et al. (1986) stated that C. capitata was of no economic importance in Central and West Africa due to the action of natural enemies. Similar observations of low infestation levels on olives in the Eastern Cape, South Africa have also been attributed to the action of parasitoids (Hancock 1989; Mkize et al. 2008).

Although *Bactrocera invadens* (as *B. dorsalis* was initially called in Africa) was recently synonymized with *Bactrocera dorsalis sensu stricto* (Schutze et al. 2015) populations in the native range could still be phenotypically different to populations in Africa with respect to their susceptibility to parasitoids; for example, African populations of *B. dorsalis* performed differently compared with the Hawaiian population where there are no reports of host immunity to *D. longicaudata* and *F. arisanus* (Mohamed et al. 2006, 2008). Therefore, more expeditions to the pest's area of origin are needed in Southeast Asia to evaluate the parasitoid species that did not

establish in Hawaii during the *B. dorsalis* biological control programme in 1950s. Although Z. cucurbitae was presumed to have invaded Africa in the 1930s, no parasitoid species were introduced for its control. Considering that Z. cucurbitae mounts a strong immune response against almost all African parasitoid species and only P. fletcheri from its native range is capable of overcoming its immune system, it would be worthwhile to source this parastoid species from its native range and release it in Africa. Indeed, this parastoid species has been imported and released for classical biological control in several countries with promising results. For example, the release of *P. fletcheri* in Hawaii resulted in up to 29.8 and 96.9 % rates of parasitism of Z. cucurbitae on cucumber and wild bitter gourd, respectively (Willard 1920). Other parasitoids that are promising candidates for classical biological control of Z. cucurbitae need to be considered for importation into Africa and include four opiine parasitoids: Diachasmimorpha albobalteata (Cameron) from North Borneo, Diachasmimorpha dacusii (Cameron) from North India, Diachasmimorpha hageni (Fullaway) from Fiji and Fopius skinneri (Fullaway) from Thailand. Fopius skinneri should be considered due to its tendency to parasitize tephritid larvae in cucurbits rather than other fruits (Waterhouse 1993). The larval-pupal parasitoid, A. daci, introduced into Hawaii from Queensland, Australia and Malaysia in 1949, has been reported as a primary parasitoid of Z. cucurbitae as has an Aceratoneuromyia sp. from northern Thailand (Ramadan and Messing 2003). However, a strain of A. daci from Greece was unable to develop in Z. cucurbitae (M.M. Ramadan unpublished data).

Although *B. latifrons* is of less economic importance than some species it can be a serious pest on solanaceous crops in the absence of natural enemies. Its management in Africa would greatly benefit from introduction of a co-evolved and efficient exotic parasitoid species from its native range. Laboratory experiments showed that most of the parasitoid species that attack *B. dorsalis* and *C. capitata* can survive in *B. latifrons*. *Diachasmimorpha kraussii* was released in Hawaii after it was successfully reared on *B. latifrons*, but subsequently it was rarely recovered from *B. latifrons* in wild fruits in the field. Exploration for parasitoids attracted to infested solanaceous fruits in the Indo-Malaysian region is required.

The introduction of *F. arisanus* for biological control of *B. zonata* resulted in mixed outcomes. This also calls for exploration and evaluation of more efficient parasitoid species from its native range. Such expeditions should aim at finding parasitoid species attacking both egg and larval stages of *B. zonata* to maximize the chances of pest suppression. Moreover, *A. daci* which has been promising for *B. zonata* control in Egypt should be evaluated further as a potential candidate for classical biological control of *B. zonta* in other African countries that are affected.

The native fruit fly, *C. rosa*, and its close relatives in the FAR complex, were immune to all the indigenous solitary and gregarious parasitoid species evaluated (Mohamed et al. 2003, 2006, 2007); furthermore, the two introduced parasitoids, *F. arisanus* and *D. longicaudata*, performed very poorly on *Ceratitis* species in the FAR complex (Mohamed et al. 2008, 2010). For these reasons a search for efficient parasitoids against these pests is urgently needed. Fortunately, the recently described *P. halidayi* was reared from field-collected *C. rosa* developing in fruits of

Lettowianthus stellatus Diels in coastal Kenya (Wharton 1996b) and its efficiency against *C. rosa* was further confirmed in laboratory studies (S.A. Mohamed unpublished data). Therefore, this parasitoid is a promising candidate that could be developed for biological control of *C. rosa* in mainland Africa; it could also be introduced for classical biological control in La Réunion and Mauritius where *C. rosa* has invaded. There is also a need for further research to identify parasitoid species that can overcome the immune response and develop successfully in *C. fasciventris* and *C. anonae* which cause significant yield losses in many tropical fruits (White and Elson-Harris 1992; Copeland et al. 2006).

Augmentation of parasitoid populations should also be considered to boost the efficiency of introduced parasitoids. In the same way, the role of native parasitoids in controlling native fruit flies could be enhanced by augmentative releases. This calls for involvement of the private sector in mass rearing of these parasitoids.

Parasitoid conservation, whether introduced or indigenous, is a fundamental pillar in ensuring the success of biological control programmes. It is, therefore, essential to make fruit and vegetable growers in Africa more aware of how to conserve parasitoids by using more eco-friendly management approaches rather than expensive blanket cover sprays of insecticide. Additionally, growers should be encouraged to practice habitat management that provides refuges and food sources for parasitoids in the areas surrounding orchards and gardens. Finally, the role of pupal parasitoids, particularly for biological control of native species should not be overlooked.

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