

# Diversity of parasitoids (Hymenoptera) associated with tephritids (Diptera) parasitising cucurbits in two agroecological zones of Cameroon, Central Africa

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Many parasitoid wasps (Hymenoptera) parasitise tephritids (Diptera), but little is known about the influence of host plants on this parasitism in sub-Saharan Africa. From June 2008 to January 2011, a study was conducted at three localities in two agroecological zones of Cameroon (Central Africa): Ngoa-Ekelé and Olembé (Southern Plateau) and Koutaba (Western Highlands), to assess the guild of parasitoids and their parasitism on tephritids attacking cucurbits. Data were collected on 3 249 fruits attacked of nine cucurbit species, from which were identified: 45 575 tephritids belonging to four species (*Dacus bivittatus*, *D. ciliatus*, *D. punctatifrons*, and *D. vertebratus*) and 3 330 parasitoids belonging to four families and 11 species of Hymenoptera. Most of the parasitoids collected were solitary koinobionts (mainly Braconidae - Opiinae (> 50%) and Eulophidae). The parasitism rate varied significantly between the localities ( $p < 0.001$ ), with the lowest value obtained in Koutaba ( $4.98 \pm 0.68\%$ ) and Ngoa-Ekelé ( $9.68 \pm 0.54\%$ ), areas characterised by high agricultural activity and urbanisation respectively, and the highest in Olembé ( $23.93 \pm 1.80\%$ ), a more natural area. *Psytalia perproxima* and *Tetrastichus dacicida* were numerically abundant in all three localities, followed by *Fopius* spp. and *Phaenocarpa* sp. in Olembé. Regardless of the study localities, *D. bivittatus* and *D. ciliatus* were dominant and were parasitised by most of the parasitoids. Species richness and parasitism rates were higher on *Cucurbita moschata* fruits, while no parasitoid emerged from *Sechium edule* fruits. From a biological control perspective, the tephritid-parasitoid association was species-rich and included many potential tephritid biological control agents.

## INTRODUCTION

Cucurbits, such as gourds, pumpkins, or melons, are among the major horticultural crops that have been domesticated for multiple purposes worldwide (Chomicki et al. 2020). Rich in fibre, minerals, and bioactive compounds, fruits and seeds are particularly used as dietary supplements for their proteins, vitamins, and carbohydrates (Ifeoluwapo 2019). Some of the world's most important fruit species are cucurbits cultivated for food and/or pharmacopeia interests because of their high concentration of cucurbitacin (Aeri et al. 2015). Fruits have anti-inflammatory, anti-tumour, hepatoprotective, cardiovascular and immunoregulatory properties when consumed regularly (Mondal et al. 2020). Unfortunately, fruits are attacked by diseases and insect pests at all stages of development (Djiéto-Lordon et al. 2007; Mokam et al. 2018).

The Dacini tribe (Diptera: Tephritidae), is one of the most economically important group of insect pests worldwide (Haran et al. 2019). They cause serious damage to fresh fruits and vegetables (Doorenweerd et al. 2018). In sub-Saharan Africa, tephritids of the genera *Dacus* (e.g. *D. bivittatus* Bigot, *D. ciliatus* Loew, *D. vertebratus* Bezzi, and *D. punctatifrons* Karsch) and *Zeugodacus* (e.g. *Z. cucurbitae* (Coquillett)), cause damage on fruits, thereby reducing the consumption of healthy fruits and their marketability (Dhillon et al. 2005; De Meyer et al. 2012; Mokam et al. 2014; Badii et al. 2015; De Meyer et al. 2015; Mwatawala et al. 2015; Mokam et al. 2018; Haran et al. 2019; Gomina et al. 2020; Layodé et al. 2020). Without effective pest management, tephritid attacks on cucurbits can reach 60–80% in the tropics and are considered a major constraint to their production (Mokam et al. 2018). Meanwhile, natural biological control of these pests by parasitic Hymenoptera remains the first step in reducing their populations to manageable levels (Purcell 1998; Mohamed et al. 2016; Dias et al. 2018; Haran et al. 2019; Nanga Nanga et al. 2019; Garcia et al. 2020).

Cataloguing natural enemies of pests, especially parasitoids, is therefore key to successful biological control programmes to reduce damage and dependence on insecticides (Mahmoud et al. 2019). Nevertheless, the diversity of indigenous parasitoids is poorly documented in Central Africa (Steck et al. 1986), despite numerous studies in West Africa (Vayssières et al. 2002; Vayssières et al. 2011; Kadio et al. 2011; Vayssières et al. 2012; Badii et al. 2016; Gomina et al. 2020; Layodé et al. 2020; Zida et al. 2022), East Africa (Copeland et al. 2006; Muriithi et al. 2020) and, South Africa (Haran et al. 2018, 2019). In the eastern Amazon, Miranda de Sousa et al. (2021), reported many generalists (oligophagous or polyphagous) and widely distributed braconid parasitoids as potential biological control agents of tephritids.

The present study followed previous work on the species diversity of insects associated with cucurbits (Mokam et al. 2014) and documented the host susceptibility of tephritids attacking cucurbits

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## SUPPLEMENTARY MATERIAL

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in Cameroon (Central Africa) (Mokam et al. 2018). Our objectives were to: (i) inventory the parasitoids of cucurbit tephritid species, (ii) assess natural parasitism, and (iii) study the distribution and preference of associated parasitoids through cucurbit-tephritid host relationships. Collecting data on parasitoids associated with tephritids provides baseline data necessary for the design and implementation of integrated management of these economically important pests.

## MATERIALS AND METHODS

### Study locations

Data collection on *Dacus* species attacking cucurbits and their parasitoids was carried out from June 2008 to January 2011 in Yaoundé and Koutaba. Yaoundé, located in the agroecological zone of the Southern Plateau of Cameroon, is characterised by a humid tropical climate with a bimodal rainfall regime (Suchel 1988). Koutaba, located in the agroecological zone of the Western Highlands of Cameroon, is characterised by a humid tropical climate with a unimodal rainfall regime.

In Yaoundé, the experimental plots were established at Ngoa-Ekelé in the research garden of the University of Yaoundé 1 (3°51'28.9" N; 11°29'52.2" E; 729 m a.s.l) and at Olembé (3°57'46.3"; 11°31'51.4"E; 673 m a.s.l), about 18 km from Ngoa-Ekelé. Ngoa-Ekelé is a semi-natural agricultural landscape dominated by university buildings, while Olembé, a suburb of the city of Yaoundé, was a natural area at the time of this study. In Koutaba, the experimental plot was in the domain of the Catholic Cistercian monastery (5°38'47" N; 10°48'20" E; 1180 m a.s.l), about 336 km from Ngoa-Ekelé. Landscape of Koutaba was dominated by crops, with intensive application of pesticides. The geographical and climatic characteristics of the three study localities have been previously described by Mokam et al. (2014, 2018).

### Experimental plot and sampling method

The experimental design was implemented at each study locality. It consisted of 18 ridges of soil of 8 m × 2 m, separated by 50 cm wide furrows, on which seeds of nine cucurbit species were sown (Mokam et al. 2014; 2018). Each plant species occupied two ridges. The cucurbit species studied were: *Citrullus lanatus* (Thünberg) Matsumara and Nakai var. egusi, *Citrullus lanatus* (Thünberg) Matsumara and Nakai var. watermelon, *Cucumeropsis mannii* Naudin, *Cucumis melo* L. var. charantais, *Cucumis melo* L. var. agrestis, *Cucumis sativus* L. var. poinsett, *Cucurbita moschata* (Duchesne ex Lamarck) Duchesne ex Poiret, *Lagenaria siceraria* (Molina) Standley, and *Sechium edule* (Jacquin) Swartz. Wherever possible, two replications of the experimental design were made per year, due to the short development cycle of more than four months of the cucurbits studied, except for *S. edule*, which is a perennial plant. Plots were weeded once a month and watered during the dry season, but not during the wet season.

The majority of tephritids associated with cucurbits lay their eggs in immature fruits (Wang et al. 2021), except for *S. edule*, which is susceptible to tephritid attacks when the fruit begins to ripen. To assess the tri-trophic relationships between cucurbits, tephritid and their parasitoids, all damaged fruits of each cucurbit species were sampled weekly at Ngoa-Ekelé, fortnightly at Olembé and monthly at Koutaba from the onset of tephritid attacks in the experimental garden until the end of the growing cycle of each cucurbit species. Fruit sample size was the total number of fruits damaged for each cucurbit species (Wang et al. 2021). Each damaged fruit was kept at room temperature (24–25 °C) in transparent incubation box filled with sterilised sand at the Laboratory of Zoology of the Faculty of Science, University of Yaoundé 1. The size of the fruit attacked by tephritids determined the volume of the boxes. The sand was sterilised in an oven. Flies that attack *S. edule* pupate inside seeds within the fruit. In contrast, for the other eight cucurbits, pupation occurs in the soil.

Each fruit was monitored until the emergence of tephritids and/or parasitoids.

### Identification

All adult insects were removed from each incubator using a mouth aspirator, fixed in 70% ethanol in a Petri dish, and then sorted by morphospecies under a binocular loupe using a pair of smooth tweezers. The identification method for tephritids was described in a previous study by Mokam et al. (2014). The identification of parasitoids was conducted at CIRAD-CBGP in Montpellier (France), using the key of Wharton and Gilstrap (1983), and the online database of Wharton and Yoder, available at <http://paroffit.org>.

### Assessment of species richness, relative abundance, and occurrence of parasitoids

Species richness of parasitoid is the total number of parasitoid species (Latimer 2014) in an identified unit of study (e.g., locality, cucurbit species or *Dacus* species). Abundance is a fundamental measure in ecology that can be assessed at different trophic levels (cucurbit, *Dacus*, parasitoid species) by comparing relative abundance (Pi), using the following formula:  $P_i = \text{abundance of a parasitoid species} / \text{abundance of all parasitoids in the community}$ . The value of Pi is expressed as a percentage (%) and can be assessed according to the index of Dajoz (Dajoz 1982) as follows: most abundant ( $P_i \geq 50\%$ ); abundant ( $25\% \leq P_i < 50\%$ ); less abundant ( $1\% \leq P_i < 25\%$ ) and scarce ( $P_i < 1\%$ ). Occurrence was calculated as the number of fruits from a given cucurbit species, at a given study locality, that had a species of tephritid from which parasitoids emerged.

### Evaluation of parasitism rate

Up to four *Dacus* species may co-exist in attacked cucurbits (Mokam et al., 2014 and 2018). However, because *Dacus* spp. pupae are morphologically similar, parasitism was confirmed in all cases where a *Dacus* species and a parasitoid wasp emerged together from an attacked cucurbit fruit (Leonel et al. 1995). The parasitism rate was calculated as  $a / (a + b) \times 100$ , where a = abundance of a given parasitoid species and b = abundance of a given *Dacus* species (Vayssières et al. 2012). The parasitism rate was 100% if all *Dacus* pupae were parasitised.

### Data analysis

Data were analysed with a General Linear Model (GLM) using the nested-ANOVA associated to Tukey post-hoc test in STATISCA 12 software. Mean parasitism rates was compared between location, host plant, and tephritid species.

## RESULTS

A total of 48 905 insects, comprising four tephritid species of *Dacus* (*Dacus bivittatus*, *Dacus ciliatus*, *Dacus punctatifrons* and *Dacus vertebratus*) and 11 associated parasitoids emerged on 3 249 fruits attacked of nine cucurbit species (Table 1). This sample of cucurbits comprised 1 949 fruits attacked from which 28 605 tephritids and their associated parasitoids emerged at Ngoa-Ekelé; 537 fruits attacked from which 12 510 insects were reared at Olembé; and 763 fruits (7 790 insects) at Koutaba (Table 1). In addition, the sample of parasitoids constituted 6.26%, 9.26% and 6.81% of the insect community, reared from 20.22%, 35.38% and 21.33% respectively (Table 1).

### Parasitoids composition at each location

The parasitoids associated with the fruit flies consisted of 3 330 insects (Tables 2 and 3), obtained from 694 fruits attacked of eight cucurbit species, distributed as follows in the three study localities: 395, 190, and 109 at Ngoa-Ekelé, Olembé and Koutaba respectively (Table 4). At these locations, no parasitoid emerged

**Table 1.** Abundance of tephritids and their associated parasitoids collected on cucurbit fruits attacked by tephritids in three localities of Cameroon, from June 2008 to January 2011.

Localities	Host-plants	Ab teph + para	Nb fr att teph	Ab para (%)	Emer para (%)
Ngoa-Ekelé	<i>Citrullus lanatus</i> var. egusi	1 612	103	5.52	15.53
	<i>Citrullus lanatus</i> var. watermelon	533	18	5.07	27.78
	<i>Cucumeropsis mannii</i>	1 823	65	4.28	27.69
	<i>Cucumis melo</i> var. agrestis	158	25	0	0
	<i>Cucumis melo</i> var. charentais	2 606	79	2.00	12.66
	<i>Cucumis sativus</i>	5 982	210	5.57	23.81
	<i>Cucurbita moschata</i>	12 544	1251	9.27	22.38
	<i>Lagenaria siceraria</i>	1 986	119	2.47	12.61
	<i>Sechium edule</i>	1 361	79	0	0
	Sub-total	28 605	1949	6.26	20.22
Olembé	<i>Citrullus lanatus</i> var. egusi	1 319	63	14.56	42.86
	<i>Citrullus lanatus</i> var. watermelon	23	2	8.70	50.00
	<i>Cucumeropsis mannii</i>	2 867	90	9.70	48.89
	<i>Cucumis melo</i> var. agrestis	166	10	12.65	20.00
	<i>Cucumis melo</i> var. charentais	811	61	12.33	31.15
	<i>Cucumis sativus</i>	1 254	25	4.31	20.00
	<i>Cucurbita moschata</i>	4 850	234	9.90	35.90
	<i>Lagenaria siceraria</i>	956	39	3.24	20.51
	<i>Sechium edule</i>	264	13	0	0
	Sub-total	12 510	537	9.26	35.38
Koutaba	<i>Citrullus lanatus</i> var. egusi	297	32	10.77	12.50
	<i>Citrullus lanatus</i> var. watermelon	284	19	7.39	21.05
	<i>Cucumeropsis mannii</i>	274	14	1.09	14.29
	<i>Cucumis melo</i> var. agrestis	19	3	5.26	33.33
	<i>Cucumis melo</i> var. charentais	60	1	0	0
	<i>Cucumis sativus</i>	1 055	86	1.71	4.65
	<i>Cucurbita moschata</i>	5 494	580	5.02	15.00
	<i>Lagenaria siceraria</i>	261	23	10.73	30.43
	<i>Sechium edule</i>	46	5	0	0
	Sub-total	7 790	763	4.87	14.29
	Total	48 905	3249	6.81	21.33

Note: Ab teph + para = Abundance of tephritids and their associated parasitoids reared on cucurbit fruit species attacked by tephritids; Nb fr att teph = Number of cucurbit fruit species attacked by tephritids; Ab para (%) = Relative abundance of parasitoids collected; Emer para (%) = Percentage of cucurbit fruits attacked by tephritids from which parasitoids emerged.

from *Sechium edule* attacked by tephritids, like at Ngoa-Ekelé on *Cucumis melo* var. agrestis (Table 1). Three fruits of *Cucumis melo* var. agrestis and one of *Cucumis melo* var. Charentais, both attacked by tephritids at Koutaba and, two of *Citrullus lanatus* var. watermelon at Olembé (Table 1), did not provide sufficient information for statistical analysis of the data.

A total of 1 793 parasitoids of 11 species belonging to four families of Hymenoptera were counted at Ngoa-Ekelé, 1 158 (8 species; four families) at Olembé, and 379 (6 species; three families) at Koutaba (Tables 2 and 3).

The contribution of families to parasitism varied both numerically and in species richness. Within each community, the family Braconidae was significantly the most abundant ( $p < 0.001$ ) with 59.34%, 93.87%, and 71.24% at Ngoa-Ekelé, Olembé and Koutaba respectively; and the most speciose with six, four, and four species respectively (Table 2). Except for *Phaenocarpa* sp. (Alysiinae), all other braconid wasps collected belong to the subfamily Opiinae. The family Eulophidae is the second most abundant. This family was abundant at Ngoa-Ekele (31.57%; two species), and Koutaba (27.97%; one species), but less abundant at

Olembé (5.53%, two species) (Table 2). The family Pteromalidae had a low abundance at both Ngoa-Ekele (8.09%; two species) and Olembé (0.52%, one species), and was absent at Koutaba. The family Diapriidae was rare at all three localities (Table 2).

In general, two to three parasitoid species dominated at each location. *Psytalia perproxima* Silvestri (Braconidae) was the most abundant parasitoid (54.10%, 48.62%, and 67.81% at Ngoa-Ekelé, Olembé and Koutaba respectively) (Tables 2 and 3) and the most frequent parasitoid to emerge from cucurbits (78.23%, 55.79%, and 83.49% respectively) (Table 4). Furthermore, at the host-plant level, *P. perproxima* occurred on all cucurbits attacked by tephritids, except for the plants that were excluded in the analyses. This parasitoid was followed by *Tetrastichus dacicida* Silvestri (Eulophidae), abundant at Ngoa-Ekelé (29.78%), and Koutaba (27.97%), to less abundant at Olembé (Tables 2 and 3), but with low occurrence (< 20%) at the three locations (Table 4). At Olembé, *Fopius* spp. (*Fopius ottomoanus* (Fullaway) and *Fopius desideratus* (Bridwell)) constituted 33.16% of the assemblage, and *Phaenocarpa* sp. (Braconidae) was 11.83% of the assemblage (Tables 2 and 3). *Fopius* spp. were less abundant (< 5%) at Ngoa-

**Table 2.** Species composition of parasitoids attacking tephritids on cucurbits in three localities of Cameroon, from June 2008 to January 2011.

Hymenoptera Family	Scientific name of parasitoids collected	Relative abundance (%) per location		
		Ngoa-Ekelé	Olembé	Koutaba
Braconidae	<i>Asobara</i> sp. <sub>1</sub>	1.23	0	0
	<i>Asobara</i> sp. <sub>2</sub>	1.39	0	2.11
	<i>Diachasmimorpha</i> sp.	0.39	0.26	0.79
	<i>Fopius</i> spp.*	1.34	33.16	0
	<i>Phaenocarpa</i> sp.	0.89	11.83	0.53
	<i>Psytalia perproxima</i> (Silvestri)	54.10	48.62	67.81
	Sub-total (species richness)	59.34 (6 species)	93.87 (4 species)	71.24 (4 species)
Diapriidae	<i>Trichopria</i> spp.	1.00	0.09	0.79
Eulophidae	<i>Tetrastichus dacicida</i> Silvestri	29.78	5.44	27.97
	<i>Tetrastichus giffardianus</i> Silvestri	1.78	0.09	0
	Sub-total (two species)	31.57 (2 species)	5.53 (2 species)	27.97 (1 species)
Pteromalidae	<i>Pachycrepoideus vindemiae</i> (Rondani)	5.41	0	0
	<i>Spalangia</i> sp.	2.68	0.52	0
	Sub-total (two species)	8.09 (2 species)	0.52 (1 species)	0
Total (species richness)		1793 (11 species)	1158 (8 species)	379 (6 species)

Note: *Fopius* spp.\* = *Fopius ottomoanus* (Fullaway) and *Fopius desiderarus* (Bridwell).

Ekelé and absent at Koutaba, while *Phaenocarpa* sp. was scarce (< 1%) at these locations (Table 3). *Diachasmimorpha* sp. and *Trichopria* spp. were at each location less abundant (< 1%) or scarce, and less frequent (Tables 2 and 3). *Tetrastichus giffardianus* Silvestri (Eulophidae) and *Spalangia* sp. (Pteromalidae) were not recorded at Koutaba, like *Asobara* sp.<sub>2</sub> at Olembé and, *Asobara* sp.<sub>1</sub> and *Pachycrepoideus vindemiae* (Rondani) (Pteromalidae) at both Olembé and Koutaba (Tables 2 and 3).

#### Parasitism of hymenopteran on tephritids associated with cucurbits

The parasitism rate of hymenopterans on tephritids associated with cucurbits was significantly different between locations and cucurbit species ( $F(2, 3125) = 24.46; p < 0.001$ ). The mean parasitism rate was higher at Olembé ( $26.26 \pm 1.83\%$ ) than at Ngoa-Ekelé ( $9.90 \pm 0.57\%$ ) and Koutaba ( $5.37 \pm 0.64\%$ ) (Figure 1). Moreover, the mean parasitism rate was significantly higher ( $F(18, 3125) = 2.65; p < 0.001$ ) on *Cucumeropsis mannii* and *Cucurbita moschata* at both Olembé and Ngoa-Ekelé and, on *Lagenaria siceraria* at Koutaba (Figure 2). The lowest parasitism rates were found on *L. siceraria* and *Cucumis melo* var. charentais at Ngoa-Ekelé, on *Cucumis sativus* at Olembé and on *Cucumeropsis mannii* at Koutaba (Figure 2).

#### Host-plant effect on hymenopteran parasitism of *Dacus bivittatus*

Co-emergences of *D. bivittatus* with associated parasitoids were observed on 17.76% of the attacked cucurbit fruits collected at the three locations (Table 5). At Ngoa-Ekelé, of 1 001 fruits of nine cucurbit species from which this fly emerged, 18.48% of the fruits of seven cucurbit species, harboured 11 species of parasitoids (Online supplement, Table S1). At Olembé, 17.85% of six cucurbit species attacked by *D. bivittatus*, harboured five parasitoid species (Online supplement, Table S1), while at Koutaba, 15.87% of six cucurbit species attacked, harboured five parasitoid species (Online supplement, Table S1).

At the three locations, it was noted that *Psytalia perproxima* exhibited a tendency to select fruits that had been attacked by

*Dacus bivittatus*. The parasitism rate of this parasitoid was high on *Cucurbita moschata* at Ngoa-Ekelé ( $F(20, 459) = 3.94; p < 0.001$ ); Olembé ( $F(24, 430) = 2.04; p = 0.003$ ) and Koutaba; and on *Cucumis melo* var. charentais at Olembé (Online supplement, Table S1). *Fopius* spp. individuals were not obtained on *Cucumis melo* var. agrestis at Olembé; where its parasitism rate was high on *Cucumeropsis mannii*. At Ngoa-Ekelé, this parasitoid was reared on four cucurbit species attacked by this fruit fly. *Phaenocarpa* sp. showed the highest value of parasitism rate on *L. siceraria* and on *Cucurbita moschata* at Ngoa-Ekelé. For the eight other parasitoids, which are typically less prevalent or opportunistic, it was observed that their contribution to the parasitism rate was always lower than 3% at the three locations (Figure 3).

#### Host-plant effect on Hymenopteran parasitism of *Dacus ciliatus*

For the three study localities combined, *D. ciliatus* parasitoids were assessed from 16.31% of attacked cucurbit fruits (Table 5). At Ngoa-Ekelé, of 1 022 attacked fruits of eight cucurbit species from which this fly emerged, 17.22% of six cucurbit species, harboured 10 species of parasitoids (Online supplement, Table S2). At Olembé, 12.96% of six cucurbit species attacked by *D. ciliatus*, harboured four parasitoid species on two host-plants, while at Koutaba, 13.50% of seven cucurbit species harboured four parasitoid species on three host-plants (Online supplement, Table S2).

The parasitism rate of *P. perproxima* was significantly higher ( $F(3, 54) = 4.42; p = 0.007$ ) on *Cucurbita moschata* only at Koutaba (Online supplement, Table S2). Moreover, *Diachasmimorpha* sp. was not associated with the fly *D. ciliatus* at the three localities.

#### Host-plant effect on Hymenopteran parasitism of *Dacus punctatifrons*

Parasitoids emerged in association with *D. punctatifrons* on 10.12% of attacked cucurbit fruits (Table 5). At Ngoa-Ekelé, of 163 attacked fruits of nine cucurbit species from which *D. punctatifrons* emerged, 15.95% attacked fruits of six host-plant species, harboured five parasitoid species (Online supplement, Table S3). At Olembé, 3.57% of cucurbit species



**Table 3.** Relative abundance of parasitoids attacking tephritids on cucurbit fruits species in three localities of Cameroon, from June 2008 to January 2011.

Loc	Host plants	Abundance of each parasitoid species from attacked cucurbit fruits (%)											Ab
		1	2	3	4	5	6	7	8	9	10	11	
Ngoa-Ekelé	<i>Citrullus lanatus</i> var. egusi	0	0	0	0	19.10	5.62	42.70	0	32.58	0	0	89
	<i>Citrullus lanatus</i> var. watermelon	0	0	0	0	0	0	82.76	0	17.24	0	0	29
	<i>Cucumeropsis mannii</i>	0	0	0	12.82	0	1.28	84.62	0	0	1.28	0	78
	<i>Cucumis melo</i> var. agrestis	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Cucumis melo</i> var. charentais	0	0	1.92	1.92	0	0	76.92	0	15.38	0	3.85	52
	<i>Cucumis sativus</i>	0.30	0	0.30	2.70	16.52	1.50	67.57	1.50	9.61	0	0	333
	<i>Cucurbita moschata</i>	1.81	2.06	0.09	0.17	2.15	0.09	46.43	3.61	39.55	2.67	1.38	1 163
	<i>Lagenaria siceraria</i>	0	2.04	8.16	4.08	0	8.16	75.51	2.04	0	0	0	49
	Sub total	1.23	1.39	0.39	1.34	5.41	0.89	54.10	2.68	29.78	1.78	1.00	1 793
Olembé	<i>Citrullus lanatus</i> var. egusi	0	0	0	24.48	0	15.63	59.38	0	0.52	0	0	192
	<i>Citrullus lanatus</i> var. watermelon	0	0	0	50.00	0	0	50.00	0	0	0	0	2
	<i>Cucumeropsis mannii</i>	0	0	0	47.48	0	16.91	30.22	0.72	4.32	0	0.36	278
	<i>Cucumis melo</i> var. agrestis	0	0	0	90.48	0	0	9.52	0	0	0	0	21
	<i>Cucumis melo</i> var. charentais	0	0	2	11.00	0	5.00	77.00	0	4	1	0	100
	<i>Cucumis sativus</i>	0	0	0	29.63	0	7.41	62.96	0	0	0	0	54
	<i>Cucurbita moschata</i>	0	0	0.21	30.21	0	10.21	49.38	0.83	9.17	0	0	480
	<i>Lagenaria siceraria</i>	0	0	0	41.94	0	6.45	45.16	0	6.45	0	0	31
	Sub total	0	0	0.26	33.16	0	11.83	48.62	0.52	5.44	0.09	0.09	1 158
Koutaba	<i>Citrullus lanatus</i> var. egusi	0	0	0	0	0	0	31.25	0	68.75	0	0	32
	<i>Citrullus lanatus</i> var. watermelon	0	0	0	0	0	0	100	0	0	0	0	21
	<i>Cucumeropsis mannii</i>	0	0	0	0	0	0	33.33	0	66.67	0	0	3
	<i>Cucumis melo</i> var. agrestis	0	0	0	0	0	0	100	0	0	0	0	1
	<i>Cucumis melo</i> var. charentais	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Cucumis sativus</i>	0	0	0	0	0	0	83.33	0	16.67	0	0	18
	<i>Cucurbita moschata</i>	0	2.17	1.09	0	0	0.72	72.83	0	22.46	0	0.72	276
	<i>Lagenaria siceraria</i>	0	7.14	0	0	0	0	28.57	0	60.71	0	3.57	28
	Sub total	0	2.11	0.79	0	0	0.53	67.81	0	27.97	0	0.79	379
Total		0.66	0.99	0.39	12.25	2.91	4.65	53.75	1.62	21.11	0.99	0.66	3 330

Note: Some fruits may host more than one parasitoid species. Loc = Location; Ab = Abundance of parasitoid per cucurbit fruit species attacked by tephritids between the three localities. 1 = *Asobara* sp.1, 2 = *Asobara* sp. 2, 3 = *Diachasmimorpha* sp., 4 = *Fopius* spp., 5 = *Pachycrepoideus vindemiae*, 6 = *Phaenocarpa* sp., 7 = *Psytalia perproximus*, 8 = *Spalangia* sp., 9 = *Tetrastichus dacicidae*, 10 = *Tetrastichus giffardianus*, 11 = *Trichopria* spp.

from which *D. punctatifrons* emerged, harboured one parasitoid species on two host plants (Online supplement, Table S3); while at Koutaba, 6.54% of 214 fruits of six cucurbit species from which *D. punctatifrons* emerged, harboured four parasitoid species on three host plants (Online supplement, Table S3).

*Psytalia perproxima* was not obtained from *Cucumeropsis mannii* attacked by *D. punctatifrons* at Ngoa-Ekelé; its contribution to the parasitism rate was not significantly different between host plants. At Koutaba, this parasitoid was collected on three host plants. At Olembé, only *Fopius ottomoanus* emerged from the one fruit of *C. moschata* (Online supplement, Table S3). The contribution of each of the rest of parasitoids in parasitism rate was low and not significantly different between host plant.

## DISCUSSION

In agricultural production systems, parasitoids are the main natural enemies used to control tephritids (Haran et al. 2018; Haran et al. 2019; Garcia et al. 2020; Miranda de Sousa et al. 2021). The present study is the first intensive field sampling of parasitoids attacking tephritids associated with cucurbits in Cameroon. It highlighted the diversity of parasitoids of three major cucurbits-associated tephritids: *Dacus bivittatus*,

*Dacus ciliatus*, and *Dacus punctatifrons*, and assessed natural parasitism rates in relation to cucurbit fruit and study localities.

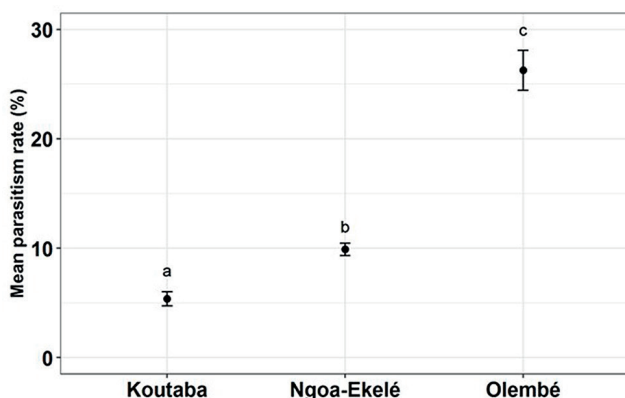
Of the nine cucurbit species studied, fruits of *Sechium edule*, although attacked by tephritids in this system (Mokam et al. 2014; Mokam et al. 2018), was not a suitable host fruit for parasitoids due to the structure of the fruit. In general, tephritids lay their eggs under the pericarp of the fruit, but in the case of *S. edule*, the gravid tephritid females lay their eggs in the large and unique seed, barely visible from the outside until the fruit is ripe (Mokam et al. 2018). In addition, the flesh of this fruit is filled with translucent and viscous juice. Thus, only the seed provides a favourable habitat for tephritids to develop. During oviposition, female parasitoids may face a challenge due to the narrow passage through which they must extend their ovipositor. This constraint potentially hinders the establishment of parasitoids in this fruit.

Species richness of parasitoids are significantly impacted by the composition and characteristics of the agricultural landscape (Zhao et al. 2013). Koutaba and Olembé, two agricultural landscapes dominated by mixed crops, had the lowest richness, with 6 and 8 parasitoid species respectively, belonging to four families each. In contrast, Ngoa-Ekelé, a semi-natural landscape dominated by university infrastructure, had the highest richness, with 11

**Table 4.** Occurrence of parasitoids attacking tephritids on cucurbit fruits species in three localities of Cameroon from June 2008 to January 2011.

Loc	Host-plants	Emergence of each parasitoid species from attacked cucurbit fruits (%)											Tt nb fr
		1	2	3	4	5	6	7	8	9	10	11	
Ngoa-Ekelé	<i>Citrullus lanatus</i> var. egusi	0	0	0	0	6.25	6.25	75.00	0	18.75	0	0	16
	<i>Citrullus lanatus</i> var. watermelon	0	0	0	0	0	0	100	0	16.67	0	0	6
	<i>Cucumeropsis mannii</i>	0	0	0	16.67	0	5.56	83.33	0	0	5.56	0	18
	<i>Cucumis melo</i> var. agrestis	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Cucumis melo</i> var. charentais	0	0	10.00	10.00	0	0	60.00	0	20.00	0	10.00	10
	<i>Cucumis sativus</i>	2.00	0	2.00	6.00	6.00	6.00	84.00	2.00	10.00	0	0	50
	<i>Cucurbita moschata</i>	4.29	3.57	0.36	0.71	1.79	0.36	77.14	3.21	18.93	1.07	2.14	280
	<i>Lagenaria siceraria</i>	0	6.67	13.33	6.67	0	6.67	80.00	6.67	0	0	0	15
	Sub-total	3.29	2.78	1.27	2.53	2.28	1.77	78.23	2.78	16.20	1.01	1.77	395
	Olembé	<i>Citrullus lanatus</i> var. egusi	0	0	0	44.44	0	29.63	70.37	0	3.70	0	0
<i>Citrullus lanatus</i> var. watermelon		0	0	0	100	0	0	100	0	0	0	0	1
<i>Cucumeropsis mannii</i>		0	0	0	45.45	0	27.27	40.91	2.27	18.18	0	2.27	44
<i>Cucumis melo</i> var. agrestis		0	0	0	50.00	0	0	50.00	0	0	0	0	2
<i>Cucumis melo</i> var. charentais		0	0	10.53	21.05	0	10.53	57.89	0	5.26	5.26	0	19
<i>Cucumis sativus</i>		0	0	0	20.00	0	20.00	80.00	0	0	0	0	5
<i>Cucurbita moschata</i>		0	0	1.19	30.95	0	25.00	55.95	2.38	20.24	0	0	84
<i>Lagenaria siceraria</i>		0	0	0	25.00	0	12.50	62.50	0	25.00	0	0	8
Sub-total		0	0	1.58	35.26	0	23.68	55.79	1.58	15.26	0.53	0.53	190
Koutaba		<i>Citrullus lanatus</i> var. egusi	0	0	0	0	0	0	75.00	0	25.00	0	0
	<i>Citrullus lanatus</i> var. watermelon	0	0	0	0	0	0	100	0	0	0	0	4
	<i>Cucumeropsis mannii</i>	0	0	0	0	0	0	50.00	0	50.00	0	0	2
	<i>Cucumis melo</i> var. agrestis	0	0	0	0	0	0	100	0	0	0	0	1
	<i>Cucumis melo</i> var. charentais	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Cucumis sativus</i>	0	0	0	0	0	0	75.00	0	25.00	0	0	4
	<i>Cucurbita moschata</i>	0	3.45	1.15	0	0	1.15	86.21	0	12.64	0	1.15	87
	<i>Lagenaria siceraria</i>	0	14.29	0	0	0	0	57.14	0	14.29	0	14.29	7
	Sub-total	0	3.67	0.92	0	0	0.92	83.49	0	13.76	0	1.83	109
	Total for the three localities		1.87	2.16	1.30	11.10	1.30	7.64	72.91	2.02	15.71	1.44	694

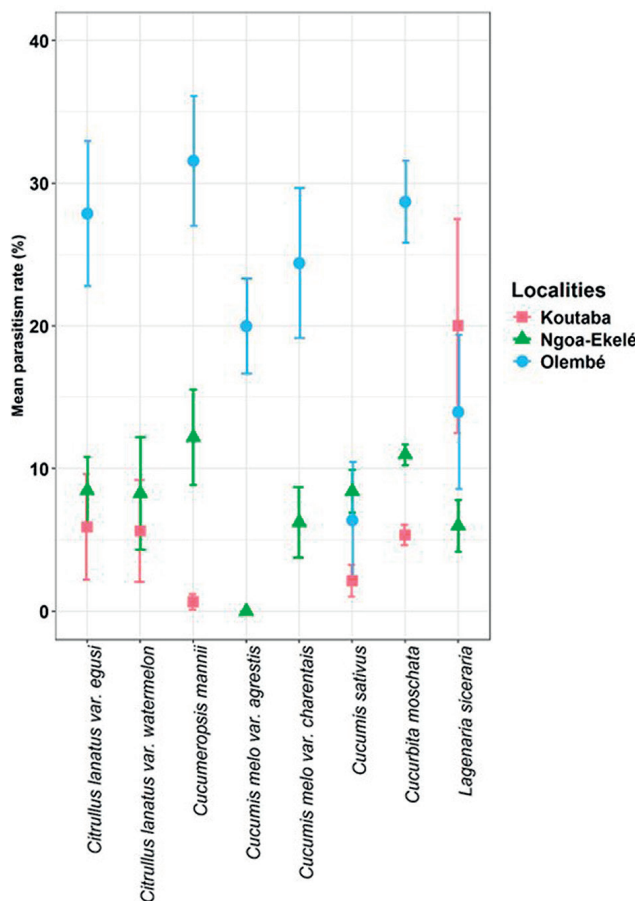
Note: Some fruits may host more than one parasitoid species so the sum per line may be more than 100%. Tt nb fr = Total number of cucurbit fruits species attacked by tephritids from which parasitoids emerged. Loc = Location; Ab = Abundance of parasitoid per cucurbit fruit species attacked by tephritids between the three localities. 1 = *Asobara* sp.1, 2 = *Asobara* sp.2, 3 = *Diachasmimorpha* sp., 4 = *Fopius* spp., 5 = *Pachycrepoideus vindemiae*, 6 = *Phaenocarpa* sp., 7 = *Psytalia perproximus*, 8 = *Spalangia* sp., 9 = *Tetrastichus dacicidae*, 10 = *Tetrastichus giffardianus*, 11 = *Trichopria* spp.



**Figure 1.** Mean parasitism rate of hymenopterans attacking tephritids associated to cucurbit fruit species at three localities in Cameroon, from June 2008 to January 2011.  $F(2, 3125) = 24.46$ ,  $p < 0.001$ ; values with a different alphabetical letter were significantly different at  $p < 0.05$ ; error bars delineate Standard Error (S.E).

parasitoid species belonging to five families of Hymenoptera. Therefore, the richness and abundance of parasitoids can be influenced by abundance and density of host fruits, habitat and

plant diversity, environmental conditions, tephritid composition and density, and agro-ecological factors (Gomina et al. 2020; Mahat 2020). Although *S. edule* is the host plant most susceptible to tephritid attacks (Mokam et al., 2018), *Cucurbita moschata* was found to host more parasitoids than the other cucurbits, leading to higher rates of parasitism and species richness of parasitoids in this system. Therefore, the effectiveness of natural biological control of *Dacus* spp. attacks on *S. edule*, which can be attributed to the fruit's characteristics. The largest sample size of *Cucurbita moschata* fruits in this system may potentially explain why this plant was the most selected by all the parasitoids. In West Africa, nine native hymenopterans species were associated with eight tephritid species in southern Togo (Gomina et al. 2020); eight parasitoid species associated with four tephritid species in Côte d'Ivoire (Kadio et al. 2011); seven parasitoid species associated with six tephritid species in Senegal (Vayssières et al. 2012), and six parasitoid species associated with *Ceratitis* spp. fruit flies on mango in Mali (Vayssières et al. 2002). In South Africa, three parasitoid species were associated with *Ceratitis capitata* in Mpumalanga (Manrakhan et al. 2010). Moreover, it was observed in the subsequent study that *D. bivittatus* was the most susceptible



**Figure 2.** Mean parasitism rate of tephritids by Hymenoptera according to cucurbit host plants, at three locations in Cameroon, from June 2008 to January 2011.  $F(18, 3125) = 2.65$ ,  $p < 0.001$ ; values with a different alphabetical letter were significantly different at  $p < 0.05$ ; error bars delineate standard error.

tephritid out of the four species identified in this system. This observation justifies the high species richness and the parasitism rates on this tephritid.

Not surprisingly, most of the parasitoid species collected are Braconidae, particularly Opiinae (solitary koinobionts), which was the predominant subfamily used in classical biocontrol of tephritids (Wharton and Gilstrap 1983; Quilici and Rouse 2012; Vayssières et al. 2002). *Fopius*, *Psytalia*, and *Diachasmimorpha* are genera that include many introduced parasitoids around the world (Mohamed et al. 2016). The families Eulophidae (gregarious koinobionts) and Pteromalidae (solitary idiobionts) followed in abundance in this study. This pattern was also observed in Benin (Central Africa) on mango, guava, cashew, pepper, and major wild fruit crops (Vayssières et al. 2011). Nevertheless, these two families are rarely used for biological control of tephritids because of their low specialisation on tephritids, e.g. *P. vindemiae* (Pteromalidae) (Owens et al. 2015), and *Tetrastichus* spp. (Eulophidae) (Mohamed et al. 2016) are generalists on various Diptera species and cannot be used as introduced auxiliaries in classical biological control (Vayssières et al. 2002). However, these parasitoids are valuable tools in conservation biological control because they reinforce the local guild of tephritid parasitoids. The family Diapriidae, which was scarce in this study, was dominant in tephritids associated with cultivated and wild fruits in Togo (Gomina et al. 2020). In South America, parasitoids of the families Braconidae (especially Opiinae), Pteromalidae, and Diapriidae, contributed most to the natural reduction of tephritids of the genera *Anastrepha* and *Rhagoletis* (Garcia et al. 2020).

*Psytalia perproxima* (Braconidae), which was the most abundant and most frequent parasitoid recorded during this

study, is widespread in sub-Saharan Africa where it was reared on *Bactrocera*, *Dacus*, *Ceratitis* and *Trirhithrum* (Mohamed et al. 2016; Yu et al. 2016). The association of this parasitoid with tephritid fauna of Cameroon is not new, as it was obtained on *D. bivittatus* attacking *Cucurbita pepo melopepo* Alef. at Nkolbisson (Steck et al. 1986). However, the association of *D. punctatifrons* with *P. perproxima* had not yet been documented. The absence of this parasitoid on *S. edule* may also be due to its short ovipositor length (Vayssières et al. 2011). Numerous *Psytalia* species have been found in other agricultural systems. *Psytalia phaeostigma* (Wilkinson) is a parasitoid of *D. ciliatus*, *D. vertebratus* and *Zeugodacus cucurbitae* attacking watermelons in Benin (Layodé et al. 2020). *Psytalia cosyrae* is a major parasitoid of *C. cosyra* and *Psytalia fletcheri*, a parasitoid of *Z. cucurbitae* throughout India, Sri Lanka, Malaysia and Indonesia, as far as Hawaii, the Solomon Islands and the Northern Mariana Islands (Vargas et al. 2012). All these observations suggest that parasitoids of the genus *Psytalia* are potentially important in the natural regulation of tephritids of economic importance and may be good candidates for future biological control programmes.

*Fopius desideratus* was obtained on wild fruits attacked by *C. cosyra* in Casamance (Ndiaye et al. 2015) and by *D. bivittatus*, *Ceratitis ananæ*, *C. capitata* and *Trirhithrum coffeae* in Cameroon, Congo, Nigeria, Togo and Uganda (Mohamed et al. 2016). *Fopius ottomoanus* has already been mentioned in Cameroon, but only on *Dacus* spp. (Mohamed et al. 2016). However, these two species have not been reported in the Western Highlands of Cameroon. Agroclimate and/or host plants may explain their absence in this agroecological zone, although information on their biology and ecology is not available.

*Phaenocarpa* is a poorly studied genus in the Afro tropics. Like all Alysiniinae, they develop on cyclorrhaphes (Diptera). However, host-plant data are scarce, especially in Tephritidae, which makes this association with *Dacus* spp. attacking cucurbits interesting, even if we could not identify it to species level. Its high representation in Olembé in this study could be related to the border effect of host plants.

Parasitoids of the genera *Tetrastichus*, *Pachycrepoideus*, *Spalangia* and *Trichopria* found in the present study have been reported abundantly on *Dacus* spp. (Mohamed et al. 2016; Mahmoud et al. 2019). *Tetrastichus dacicida* was abundant compared to *T. giffardianus*, which was less abundant in our system (Purcell et al. 1994) but considered as a biocontrol agent of tephritids in western Burkina Faso (West Africa) (Zida et al. 2022). *Tetrastichus giffardianus*, like other larval parasitoids, is abundant when rotting fruit is incubated (Purcell 1998). This parasitoid is not new to the tropics as it has been obtained on fruits attacked by *D. bivittatus*, *D. ciliatus*, *Dacus demmerezi*, *Ceratitis* spp. *Trithromyia cyanescens* and *Trirhithrum queritum* in Benin, Nigeria, Egypt, Kenya, Sierra Leone, Tanzania, South Africa and Réunion (Mohamed et al. 2016). It has been successfully used in Hawaii (USA) to manage *Ceratitis capitata* (Weidemann) (Purcell, 1998), and in Sudan for the natural control of *Bactrocera zonata* (Saunders), which attacks guava (Mahmoud et al., 2019).

Parasitism rates varied among the locations, with Olembé having higher rates than Ngoa-Ekelé and Koutaba. These results suggest that the anthropisation of the location of Ngoa-Ekelé and the intensive pesticide applications in the location of Koutaba (Vayssières et al., 2012) have a detrimental effect on the parasitoid population. The low levels of parasitism in these locations may be explained by this situation (Vayssières et al. 2011), in comparison to the less disturbed ecological services in the location of Olembé, as reported by Zida et al. (2022).

This study has identified four genera of parasitoids: *Psytalia*, *Tetrastichus*, *Fopius* and *Phaenocarpa* of potential interest for biological control. These potential biological agents are of interest for use in conservation biological control practices and possibly

**Table 5.** Abundance of fruits per cucurbit species attacked by three tephritid species and percentage of emergence of their associated parasitoids in three localities of Cameroon from June 2008 to January 2011.

Teph col	Host-plants	Ngoa-Ekelé		Olembé		Koutaba		Nb fr att	Emer para (%)
		Nb fr att	Emer para (%)	Nb fr att	Emer para (%)	Nb fr att	Emer para (%)		
<i>Dacus bivittatus</i>	<i>Citrullus lanatus</i> var. egusi	62	11.29	43	25.58	25	16.00	130	16.92
	<i>Citrullus lanatus</i> var. watermelon	15	33.33	1	0	17	23.53	33	27.27
	<i>Cucumeropsis mannii</i>	47	25.53	66	30.30	14	14.29	127	26.77
	<i>Cucumis melo</i> var. agrestis	21	0	8	0	1	100	30	3.33
	<i>Cucumis melo</i> var. charentais	51	11.76	33	18.18	1	0	85	14.12
	<i>Cucumis sativus</i>	145	22.76	22	18.18	54	7.41	221	18.55
	<i>Cucurbita moschata</i>	511	23.09	138	13.77	263	17.11	912	19.96
	<i>Lagenaria siceraria</i>	70	5.71	29	10.34	17	17.65	116	8.62
	<i>Sechium edule</i>	79	0	13	0	5	0	97	0
	Sub-total	1001	18.48	353	17.85	397	15.87	1751	17.76
<i>Dacus ciliatus</i>	<i>Citrullus lanatus</i> var. egusi	22	13.64	4	25	8	0	34	11.76
	<i>Citrullus lanatus</i> var. watermelon	3	0	0	0	5	20.00	7	14.29
	<i>Cucumeropsis mannii</i>	17	23.53	1	0	0	0	18	22.22
	<i>Cucumis melo</i> var. agrestis	5	0	0	0	3	0	8	12.50
	<i>Cucumis melo</i> var. charentais	27	3.70	2	0	1	0	30	3.33
	<i>Cucumis sativus</i>	49	14.29	1	0	7	0	57	12.28
	<i>Cucurbita moschata</i>	859	17.93	43	13.95	283	14.13	1185	16.88
	<i>Lagenaria siceraria</i>	40	17.50	3	0	4	25.00	47	17.02
	<i>Sechium edule</i>	0	0	0	0	0	0	0	0
	Sub-total	1022	17.22	54	12.96	311	13.50	1386	16.31
<i>Dacus punctatifrons</i>	<i>Citrullus lanatus</i> var. egusi	14	7.14	1	0	12	16.67	27	11.11
	<i>Citrullus lanatus</i> var. watermelon	4	25.00	0	0	3	0	7	14.29
	<i>Cucumeropsis mannii</i>	11	9.09	7	0	3	0	21	4.76
	<i>Cucumis melo</i> var. agrestis	2	0	0	0	0	0	2	0
	<i>Cucumis melo</i> var. charentais	4	0	1	0	0	0	5	0
	<i>Cucumis sativus</i>	43	16.28	6	0	47	4.26	96	9.38
	<i>Cucurbita moschata</i>	78	19.23	13	7.69	148	6.76	239	10.88
	<i>Lagenaria siceraria</i>	4	25.00	0	0	1	0	5	20.00
	<i>Sechium edule</i>	3	0	0	0	0	0	3	0
	Sub-total	163	15.95	28	3.57	214	6.54	405	10.12

Note: Teph col = Tephritid species collected; Nb fr att = Number of cucurbit fruits attacked by tephritids per plant species; Emer para (%) = percentage of cucurbit fruits per plant species attacked by tephritids from which parasitoids emerged.

mass-rearing and releases to augment field populations (Nanga Nanga et al. 2019; Steck et al. 1986). This perspective should be encouraged, as it would ultimately reduce the intensive use of chemical pesticides, and increase the production of fresh and healthy fruit, thus improving the health and welfare of society.

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#### AUTHOR CONTRIBUTIONS

This study was initiated by Dr D.G. Mokam under the supervision of Professors C. Djiéto-Lordon and C.F. Bilong Bilong. D.G. Mokam also collected the field data and followed the rearing in the laboratory. Drs P. Rousse and G. Delvare provided valuable assistance in the identification of the collected parasitoids. Prof. L.S. Ngamo Tinkeu revised the first draft of the manuscript. All co-authors have also revised the manuscript.

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