

# Antennal sensilla of specialist and generalist *Anastrepha* species

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## Abstract

The antennal sensilla of generalist and specialist species of fruit flies *Anastrepha* (Diptera Tephritidae) were analysed by scanning electron microscopy. The antennae of species in this genus have three segments, scape, pedicel and flagellum (or funiculus) and a long filamentous arista protruding from the flagellum. The antennal flagellum is covered by microtrichia, and four types of olfactory sensilla, basiconica, clavate, coeloconica and trichoidea. Although the total number (weighted by the flagellar area) of sensilla is similar in the generalist and specialist species, differences do exist. Basiconica and trichoidea sensilla are the most abundant in both, generalist and specialist species. Trichoidea occur in similar number in both group of species while basiconica is more numerous in the specialist one differing from the general claim that this sensilla are more abundant in generalist species. There are no significant differences in the number of the clavate and coeloconica sensilla in both group of species. The sensilla are not evenly distributed along the antennal flagella, and positive correlations were found between the number of each type of sensilla and the size of the flagella.

**Key words:** olfactory sensilla, true fruit flies, Tephritidae.

## Introduction

The Tephritidae family encompasses about 4,500 species belonging to 471 genera, with 675 species and 82 genera being registered around the tropical and subtropical regions of the world (Norrbon *et al.*, 2013). Characteristically, adult females deposit their eggs in live plant tissues, in which larval development does occur. Therefore, species that attack fruits of commercial value are considered pests of the world fruticulture. Although less than 6% of species are of economic importance, the damage is devastating for fruticulture worldwide, amounting to billions of US dollars every year (White and Elson-Harris, 1992; Rendón and Enkerlin, 2021). In Brazil, attacks of commercial varieties of fruits cause losses of around 120 million dollars a year (Oliveira *et al.*, 2012; Taira *et al.*, 2013). The species of frugivorous fruit flies considered as pests of fruticulture belong to the genera *Anastrepha*, *Bactrocera*, *Ceratitidis*, *Dacus*, *Rhagoletis* and *Toxotrypana* (White and Elson-Harris, 1992). The genus *Anastrepha* Schiner, endemic to the Neotropical Region, has around 250 described species (Norrbon *et al.*, 2013), being 112 registered in Brazil (Zucchi and Moraes, 2022). The *Anastrepha* species are arranged into 22 infrageneric taxonomic groups, based on morphological characters (Norrbon *et al.*, 2013). From an economic point of view, only seven species of *Anastrepha* are considered relevant in Brazil: *Anastrepha fraterculus* (Wiedemann), *Anastrepha grandis* (Macquart), *Anastrepha obliqua* (Macquart) known as the Antillean fruit fly, *Anastrepha pseudoparallela* (Loew), *Anastrepha sororcula* Zucchi, *Anastrepha striata* Schiner and *Anastrepha zenildae* Zucchi (Zucchi and Moraes, 2022). Among these, *A. fraterculus* (*sensu lato*) (Wiedemann), also known as the South American fruit fly, is distributed from the south of the USA to the north of Argentina and Chile and comprises a complex of cryptic species, the *Anastrepha fraterculus* complex, that has been recently characterized (Hernández-Ortiz *et al.*, 2004; 2012; 2015; Selivon *et al.*, 2004; 2005; 2022; Hendrichs *et al.*, 2015;

Prezotto *et al.*, 2019).

In Brazil, the occurrence of the nominal species *Anastrepha fraterculus* is registered for an extensive number of host plants, but for about 56% of the *Anastrepha* species, their hosts are unknown (Zucchi, 2007; Zucchi and Moraes, 2022). Some *Anastrepha* species are capable to live on many species of host fruits while others exhibit specificity in the use of fruits for larval development. It is noteworthy that specificity in the use of certain food resources, e.g. plants that have toxic secondary compounds, requires that the explorer insect possess an enzymatic arsenal capable of dealing with the toxicity of these compounds, as *Anastrepha pickeli* Lima and *Anastrepha montei* Lima that live on *Manihot esculenta* Crantz fruits, and of *Anastrepha dissimilis* Stone and *A. pseudoparallela* that live on *Passiflora*, host plant species in which Hydrogen Cyanide (HCN) compounds are present (Morgante *et al.*, 1993). On the other hand, there are species capable of using a wide range of hosts, although they can display preference for fruits of a given family. This is the case, for example, of *A. fraterculus* and *A. obliqua*, belonging to the *fraterculus* infrageneric taxonomic group, both with an extensive list of host fruits, but attacking preferentially fruits of Myrtaceae and Anacardiaceae families, respectively. They are among the most polyphagous in the genus (Zucchi, 2007). However, intermediate categories are also recognized between the extremes of monophagy and polyphagy. Monophagous species are also named “specialists” and the polyphagous species are also named as “generalists” (Rauscher, 1993; Aluja, 1994) and these terms will be adopted in the present study.

Generalist *Anastrepha* species usually present an elaborate sexual signalling system in which are involved emission of chemical compounds, as well as visual and acoustic signalization. On the other hand, specialist species often exhibit a simpler system: The males establish territories in fruits available for oviposition, attract the females and when they arrive, they jump over them “forcing” the copula (Aluja, 1994).

In detection of host plants, the phytophagous insects are oriented by chemical compounds emanated from the host plants and in the reproductive processes the insects detect pheromones and cuticle hydrocarbons (Crnjar *et al.*, 1988; Dickens *et al.*, 1988; Malo *et al.*, 2005; Liscia *et al.*, 2013). Perception of these chemical compounds is mediated by sensory inputs through several types of gustatory and olfactory sensilla usually present in the palps and the antennae, respectively. Indeed, the distinct morphological antennae found among the insects indicates that it may be shaped by the optimization of odours perception that are perceived as signals or as cues (Schneider, 1964; Chapman, 1982; Zacharuk, 1985). The distinct olfactory sensilla would respond differentially to these stimuli and are usually categorized accordingly to their function as chemoreceptors, mechano-receptors and thermo-hygroreceptors (Schneider, 1964; Altner and Prillinger, 1980; Chapman, 1982; Altner and Loftus, 1985; Zacharuk, 1985; Dickens *et al.*, 1988; Liscia *et al.*, 2013).

Among the tephritid fruit flies, olfactory sensilla have been described in: *Bactrocera carambolae* Drew et Hancock (Manoj *et al.*, 2005; Hu *et al.*, 2010), *Bactrocera cucurbitae* Coquillet (Dickens *et al.*, 1988; Hu *et al.*, 2010), *Bactrocera dorsalis* Hendel (Dickens *et al.*, 1988; Hu *et al.*, 2010; Liu *et al.*, 2021), *Bactrocera oleae* (Rossi) (Hallberg *et al.*, 1984; Liscia *et al.*, 2013), *Bactrocera tryoni* (Froggatt) (Gianakakis and Fletcher 1985; Hull and Cribb, 1997), *Bactrocera zonata* (Saunders) (Awad *et al.*, 2014; 2015), *Ceratitidis capitata* (Wiedemann) (Levinson *et al.*, 1987; Mayo *et al.*, 1987; Dickens *et al.*, 1988; Bigiani *et al.*, 1989), *Toxotrypana curvicauda* Gerstaecker (Arzuf *et al.*, 2008), *Anastrepha ludens* (Loew) (Dickens *et al.*, 1988), *Anastrepha serpentina* (Wiedemann) (Castrejón-Gómez and Rojas, 2009), *A. fraterculus* (Bisotto-de-Oliveira *et al.*, 2011) and *A. sp.1 affinis fraterculus* (Perre, 2017).

Four basic types of olfactory sensilla are usually described by scanning electron microscopy analyses of the flagellar surface: basiconica, clavate, coeloconica and trichoidea. Subtypes of sensilla has also been described, basiconica (types I and II), clavate (types I and II), coeloconica (multiporous grooved sensilla, also named styloconica) and trichoidea types I and II (thick-walled pitted sensilla and thin-walled pitted sensilla). Besides the olfactory sensilla in the antennae of tephritid fly species two non-porous structures, the microtrichia setae and the

sensilla chaetica, a mechanoreceptor sensilla are also observed.

It has also been shown that divergence in chemical signals and cues may lead to differences in the number, size and type of the olfactory sensilla (Chapman, 1982; Chapman and Lee, 1991; Rogers and Simpson, 1997; Elgar *et al.*, 2018).

In relation to perception of cues Chapman (1982) suggested that species of insects that uses large number of hosts (generalists) would have a greater number of sensilla than the specialist ones. However, as pointed out by Elgar *et al.* (2018), there is evidence in favour as well as contrary to Chapman's suggestion: there are generalist species exhibiting a larger number of basiconica sensilla but do exists specialist ones also bearing a greater number of these sensilla. Thus, regarding the spectrum of host that tephritid fruit flies live on would generalist and specialist *Anastrepha* species exhibit differences in the number of olfactory sensilla?

The present report describes the organization of olfactory sensilla in the antennae of samples of specialist and generalist species of *Anastrepha* that occur in Southeastern Brazil. These analyses are expected to add a basic knowledge on the *Anastrepha* antennal morphology, and to verify if the sensilla of generalist and specialist *Anastrepha* species would be in accordance with Chapman's suggestion.

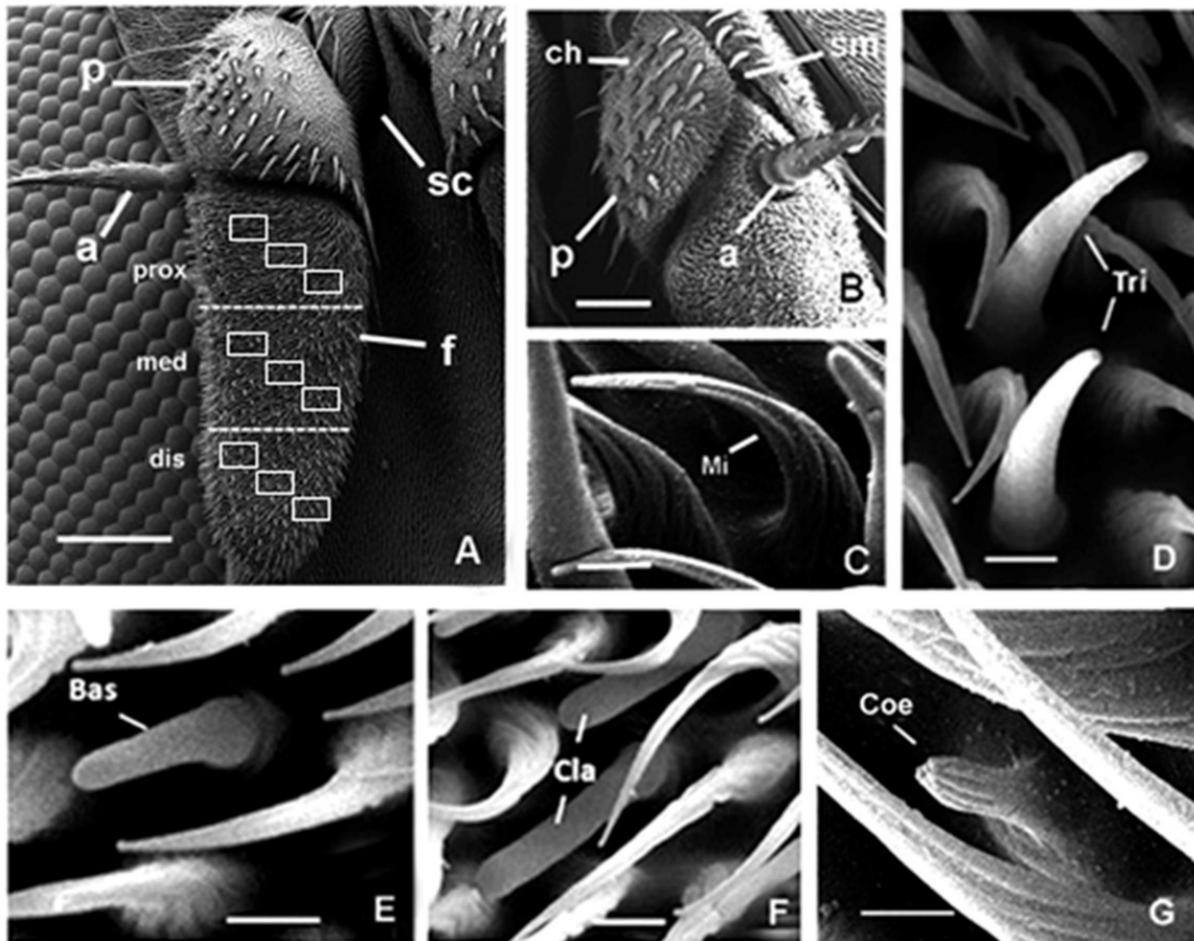
## Materials and methods

### Sample collection

The *Anastrepha* species employed in the present study derived from infested fruit collected in five locations in Eastern Brazil (table 1). The infested fruits were transported to the laboratory and maintained according to standard conditions until collection of pupae and emergency of the adults (Selivon *et al.*, 2005). Adult females were employed for species identification based on established criteria (Zucchi and Moraes, 2022) except for *A. sp.2 affinis fraterculus* that was identified according to Selivon *et al.* (2005; 2022). The specialist species of *Anastrepha* are considered those that live on a single host as well as those that explore host species of a given family of plants (Aluja, 1994), e.g. *A. grandis* that explore Cucurbitaceae. The specialist species herein analysed were *Anastrepha bistrigata* Bezzi, *A. grandis*, *A. montei* and

**Table 1.** *Anastrepha* species, host fruits and localities of collection.

<i>Anastrepha</i> spp.	Host fruits	Localities
<i>A. obliqua</i> (Macquart)	<i>Averroa carambolae</i> L.	Indaiatuba, SP 47.2118W 23.0900S
<i>A. bistrigata</i> Bezzi	<i>Psidium guineense</i> Swartz	Itatiba, SP
<i>A. grandis</i> (Macquart)	<i>Cucurbita pepo</i> L.	46.9071W 23.4343S
<i>A. serpentina</i> (Wiedemann)	<i>Manilkara zapote</i> L.	São Sebastião, SP
<i>A. sp.2 affinis fraterculus</i> (s. Selivon)	<i>Terminalia catappa</i> L.	45.4241W 23.8268S
<i>A. sororcula</i> Zucchi	<i>Terminalia catappa</i> L.	Ubatuba, SP 45.0204W 23.4408S
<i>A. montei</i> (Lima)	<i>Manihot sculenta</i> Crantz	São Carlos, SP
<i>A. pickeli</i> (Lima)		47.9122W 21.9356S



**Figure 1.** Scanning electronic images of the antennae of *A. fraterculus*. (A) General view of the antenna showing the scape (sc), pedicel (p), flagellum (f), the arista (a), the three arbitrary regions of the flagellum and the three rectangles per region where the sensilla were counted. (B) Show images of the pedicel (p) with the seam (sm), chaetica sensilla (ch) and the insertion of the arista (a) in the flagellum. (C) Microtrichia setae (Mi); (D-G) Images of the different type of the flagellar sensilla: Tri, trichoidea (D); Bas, basiconica (E); Cla, clavate (F) and Coe, coeloconica (G). Bars in A = 100  $\mu\text{m}$ , in B = 60  $\mu\text{m}$ , C-G = 2.5  $\mu\text{m}$ .

*A. pickeli*, while the generalist species were *A. obliqua*, *A. serpentina*, *A. sororcula*, *A. sp.2 affinis fraterculus*. In the present analysis only female specimens were employed, since identification of the species is based mainly on the morphology of the aculeus tip of the ovipositor which is the most important taxonomic character at the species level (Norrbon *et al.*, 1999).

#### Scanning electron microscopy

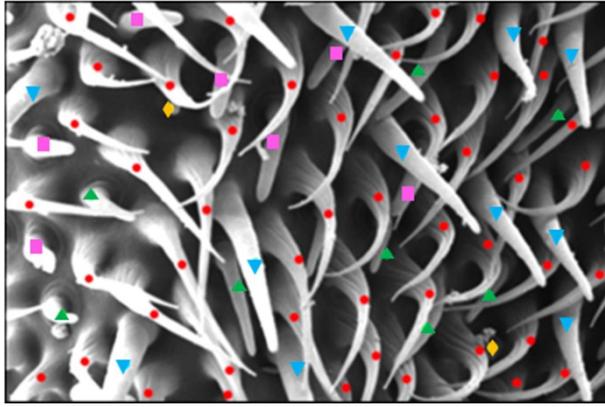
The antennae were prepared according to Bisotto-de-Oliveira *et al.* (2011) with slight modifications. Briefly, adult females anesthetized by cold have their heads removed and fixed in acidified 2,2-dimethoxypropano (DMP) (Bjerker *et al.*, 1979). After washed in ethanol, critical point dried (Balzers CPD030), glued to stubs, covered by gold in a sputtering device (Balzers SCD050), the heads were examined in a Zeiss 940 DSM scanning electron microscope.

The heads of six specimens from each species were mounted in single stubs. In the scanning electron microscopic analysis, the length of the antennae flagellum (or funiculus) from each sample was measured and comp-

ared among samples. Nine photos of 1,823  $\mu\text{m}^2$  each (at magnification of 2,000 $\times$ ) were taken, three at each the proximal, median and distal regions of the flagellum, as shown in figure 1. The sensilla types and number existing in each photo from the samples of each species were registered (figure 2). The density of sensilla was estimated by the sum of the number of sensilla in the counted nine areas, comprising a total area of 16,407  $\mu\text{m}^2$ . Estimates of the total number of sensilla in the flagellum surface was made by extrapolating the density to the whole area of the flagellum (Bisotto-de-Oliveira *et al.*, 2011).

#### Statistical analysis

The flagellar length of the two groups of species was compared by one-way ANOVA followed by Tukey HSD test. The total number of each sensilla type weighted by the area of the flagellum, as explained above, was compared between the two groups of species by a Student's-t test. The data, after standardization, were analysed employing the Statistica10 (STATSOFT 2010®) package.



**Figure 2.** Example of a scanning electronic image identifying the flagellar sensilla: microtrichia setae (red ●); sensilla trichoidea (blue ▼), basiconica (green ▲), coeloconica (yellow ◆), clavate (pink ■). Scale bar = 4  $\mu$ m.

**Table 2.** Comparison of length and width ( $\mu$ m) of flagella in specialist and generalist *Anastrepha* species. Distinct letter indicates significant difference (Tukey,  $p < 0.05$ ).

Group	Species	Length	Width
Specialist	<i>A. bistrigata</i>	360.6 $\pm$ 42 a	146 $\pm$ 17 a
Specialist	<i>A. grandis</i>	487.2 $\pm$ 82 b	169 $\pm$ 28 a
Specialist	<i>A. montei</i>	401.4 $\pm$ 40 ab	180 $\pm$ 18 a
Specialist	<i>A. pickeli</i>	416.0 $\pm$ 23 ab	178 $\pm$ 10 a
Generalist	<i>A. fraterculus</i> sp.2	384.5 $\pm$ 33 a	176 $\pm$ 15 a
Generalist	<i>A. obliqua</i>	391.7 $\pm$ 36 a	181 $\pm$ 17 a
Generalist	<i>A. serpentina</i>	487.7 $\pm$ 13 b	160 $\pm$ 5 a
Generalist	<i>A. sororcula</i>	383.6 $\pm$ 30 a	177 $\pm$ 14 a

## Results

The antennae of the examined *Anastrepha* species have three segments, scape, pedicel and flagellum (or funiculus). In the proximal dorso-lateral region of the flagellum arises the long arista (figure 1A). The scape is a semicircular structure attached to the frontal head plate and is connected to the pedicel. The pedicel has a conical configuration with a seam at the dorsal side and is connected to the scape and to the third segment, the flagellum (figure 1B). The mean length of the flagellum varied significantly between the studied species the shortest found in specimens of *A. bistrigata* (360.6  $\mu$ m) and the longest in *A. serpentina* and *A. grandis* (487  $\mu$ m), but the width differences are not significant, as shown in table 2. None-

theless, significant difference was found between the flagella length of specialist (mean 416.3  $\pm$  20  $\mu$ m) and generalist (mean 411.9  $\pm$  25  $\mu$ m) group of species (ANOVA;  $F = 6.353$ , d.f. = 38,  $p = 0.002$ ).

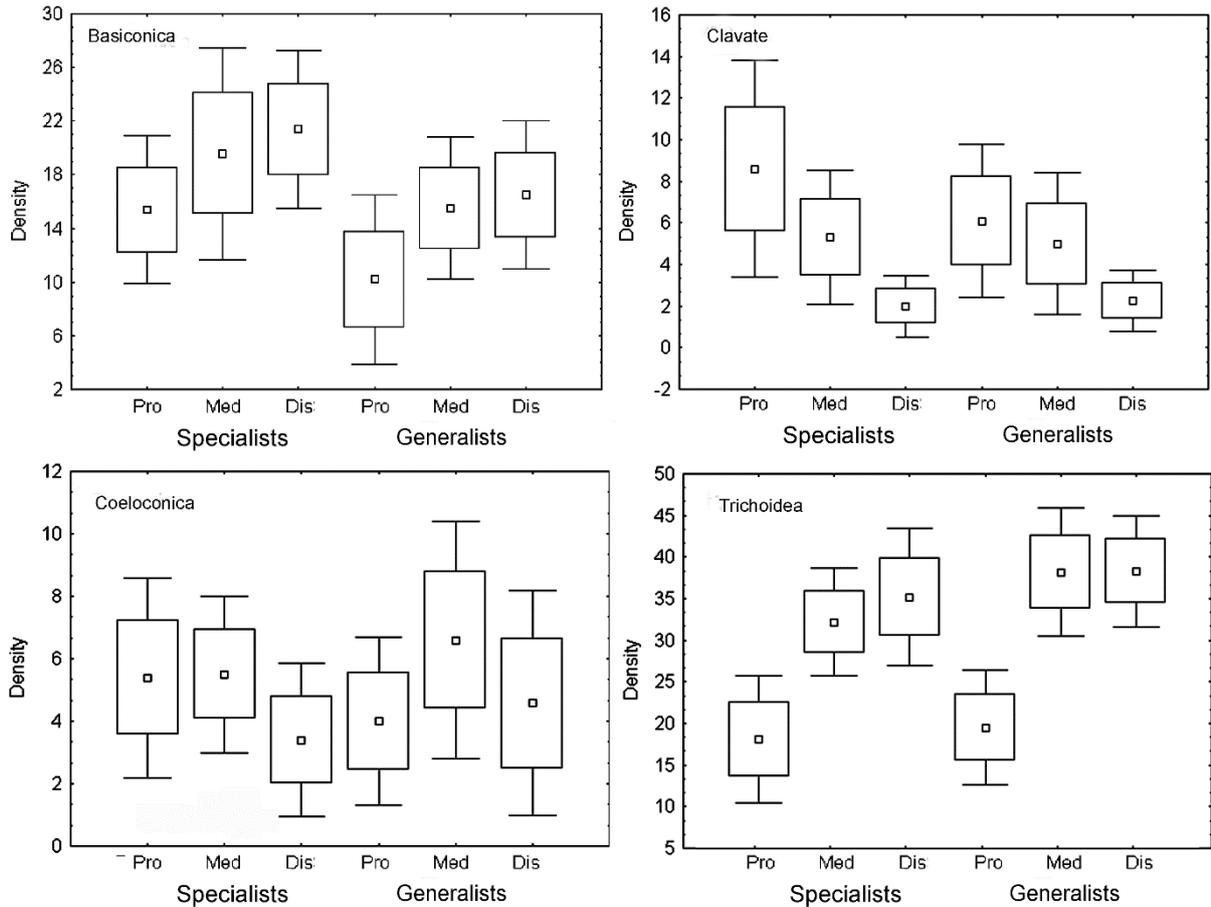
In the *Anastrepha* species herein analysed, the scape and pedicel, are paved with a small, curved setae, the microtrichia, and the pedicel contains also a mechano-sensory sensilla, the chaetica (figure 1B-C). The flagella are covered by microtrichia and by the olfactory sensilla (figure 1D-G, figure 2). The four basic types of sensory sensilla in the flagella were found in all analysed: basiconica, clavate, coeloconica and trichoidea. Significant differences in the density and in the number of distinct sensilla in estimated total area of the flagella: The most numerous sensilla observed was the trichoidea followed by the basiconica while the lowest abundant were the clavate and coeloconica sensilla in the two groups of species. Comparison of the estimated density and/or the number of the four types of sensilla taken together in the flagellum showed no significant differences between the specialist and generalist group of species (table 3). However, significant differences in the patterns was found, the basiconica sensilla being more numerous in the specialist species and although the trichoidea was slightly more numerous in the generalist ones the difference was not significant (table 3); no significant differences were found between the density and total number of the clavate and coeloconica sensilla between the two group of species (table 3). However, significant differences were found in the distribution of the distinct sensilla along the flagella. The basiconica and trichoidea sensilla exhibit lower density in the proximal region of the flagella, increasing in the median toward the distal region. On the contrary the clavate sensilla decreases, being rare at distal region while the coeloconica shows a higher density in the median region. These patterns are similar between the specialist and generalist group of species (figure 3). Despite of the differences in the distribution of the sensilla along the flagella, it was observed significant positive correlations between the mean number of each sensilla type and the whole area of the flagella of the specialist and generalist species, as shown in figure 4.

## Discussion

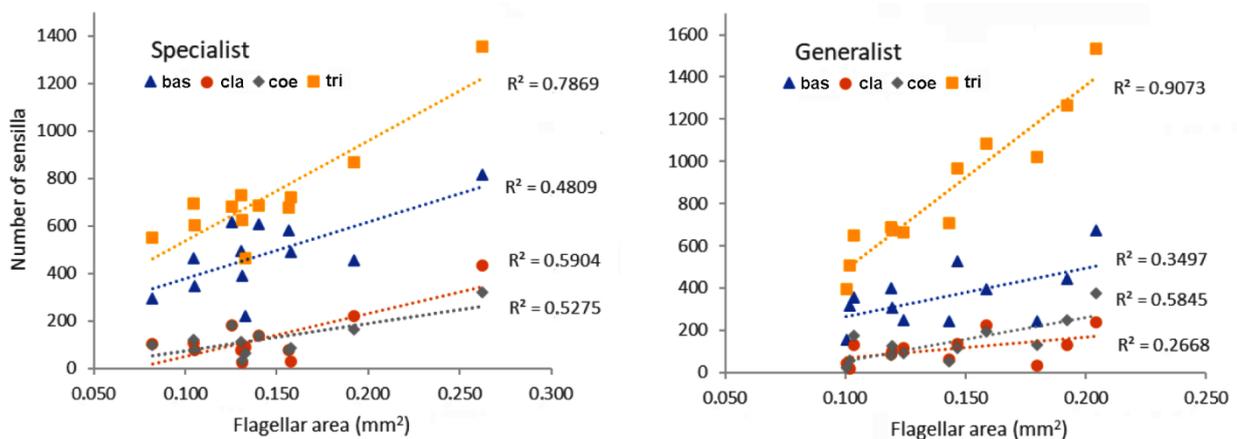
The antenna of the eight studied *Anastrepha* species are of *aristate sensu lato* type as defined by McAlpine (1989), having three segments, scape, pedicel and flagellum, and a long arista, similar in their structure and length to those

**Table 3.** Mean number ( $\pm$  SD) of sensilla in the counted area (Density) and estimated for the whole mean area (Total) of the flagella in specialist and generalist *Anastrepha* species; Student's t-test (\*\*  $p < 0.01$ ).

Sensilla\Group	Specialist		Generalist		t-test, p	
	Density (1)	Total (2)	Density (3)	Total (4)	(1) x (3)	(2) x (4)
Basiconic	56.6 $\pm$ 15.3	507.2 $\pm$ 194.1	42.1 $\pm$ 13.6	360.5 $\pm$ 134.7	<0.001**	0.008**
Clavate	14.2 $\pm$ 8.3	134.6 $\pm$ 104.3	12.9 $\pm$ 7.3	111.7 $\pm$ 69.7	0.658	0.274
Coeloconica	14.1 $\pm$ 6.4	133.1 $\pm$ 81.2	15.1 $\pm$ 8.6	135.4 $\pm$ 89.3	0.819	0.468
Trichoidea	85.2 $\pm$ 16.3	741.0 $\pm$ 195.4	96 $\pm$ 17.1	812.6 $\pm$ 168.8	0.058	0.223
Totals	169.7 $\pm$ 37	1515.9 $\pm$ 458.2	165.5 $\pm$ 38	1420.1 $\pm$ 308.8	0.673	0.445



**Figure 3.** Mean density of the sensilla in the proximal (pro), median (med) and distal (dis) regions of the flagella in the specialist and generalist species of *Anastrepha*.



**Figure 4.** Correlation between number of sensilla and flagella size for specialist and generalist species of *Anastrepha*. Values in the graphs are Pearson's correlation coefficients.

of other *Anastrepha* species, *A. ludens* (Dickens *et al.*, 1988), *A. serpentina* (Castrejón and Rojas, 2009), *A. fraterculus* (Bisotto-de-Oliveira *et al.*, 2011), *A. sp.1* affinis *fraterculus* (Perre, 2017) and other genera of tephritid flies, *Bactrocera*, *Ceratitis* and *Toxotriplana* (Hallberg *et al.*, 1984; Levinson *et al.*, 1987; Bigiani *et al.*, 1989; Dickens *et al.*, 1988; Hull and Crib, 1997; Arzuf *et al.*, 2008; Liscia *et al.*, 2013; Liu *et al.*, 2021).

The present analysis of the antennal surface by scanning electron microscopy revealed two non-olfactory structures, microtrichia setae and chaetica sensilla and numerous olfactory sensilla (i.e. basiconica, clavate, coeloconica, trichoidea). The general pattern of non-olfactory sensilla in *Anastrepha* species, is that the microtrichia, a curved, longitudinally ridge setae, was the most abundant being found covering the three segments

of the antennae while the chaetica, a long, straight and longitudinally ridged sensillum, was found in the pedicel. They occur in similar numbers in the generalist and specialist species of *Anastrepha*. This pattern is similar to that found in the *Anastrepha* species previously studied, *A. ludens*, *A. serpentina*, *A. fraterculus* and *A. sp.1 affinis fraterculus* (Dickens *et al.*, 1987; Castrejón and Rojas, 2009; Bisotto-de-Oliveira *et al.*, 2011; Perre, 2017). It was also observed in other genera of fruit flies, *Bactrocera*, *Ceratitidis*, and *Toxotripiana* (Hallberg *et al.*, 1984; Giannakakis and Fletcher, 1985; Dickens *et al.*, 1987; Levinson *et al.*, 1987; Hull and Cribb, 1997; Arzuf *et al.*, 2008; Hu *et al.*, 2010) although differences were observed. In *B. zonata* for example, besides the chaetica, trichoidea and basiconica sensilla were also found in different numbers in the scape and pedicel (Awad *et al.*, 2015). The microtrichia and the chaetica sensilla found in both generalist and specialist species of *Anastrepha* may have the function of mechanoreceptors as described for other fruit fly species and other insects (Altner and Prellinger 1980; Zacharuk 1980; Dickens *et al.*, 1988; Arzuf *et al.*, 2008).

Four types of olfactory sensilla were herein found in the flagella of the *Anastrepha* species, either generalist or specialists, i.e. basiconica, clavate, coeloconica and trichoidea without sub-types being observed. Sensilla sub-types usually are described when the internal structure of the sensilla is included in the analysis, for example, the trichoidea sensilla of *B. oleae* with two sub-types, thick- and thin-walled multiporous (Hallberg *et al.*, 1984; Dickens *et al.*, 1988) or different number of internal sensory cells (Liu *et al.*, 2021). In some instance, flagellar surface analyses distinguish sub-types of sensilla morphology, for example, the clavate I and II of *A. fraterculus* (Bisotto-de-Oliveira *et al.*, 2011), the long and short basiconica of *B. dorsalis* (Liu *et al.*, 2021).

The most conspicuous of the olfactory sensilla was the trichoidea which occur as a single type in both groups of *Anastrepha* species (present analysis), including *A. serpentina*, for which two types of trichoidea has been described (Castrejón and Rojas, 2009). However, in our samples, the distinction between the trichoidea subtypes (thick- and thin-walled multiporous) was not consistent. Differences between samples and or condition in the laboratory colonies could be invoked to explain this discrepancy. A single type of trichoidea was also observed in *A. fraterculus* (Bisotto-de-Oliveira *et al.*, 2011) and in *A. sp.1 affinis fraterculus* (Perre, 2017). In other species of fruit flies this sensilla received distinct names, for example, as single type trichoidea in *B. oleae* (Liscia *et al.*, 2013), in *C. capitata* (Levinson *et al.*, 1987; Bigiani *et al.*, 1989), long single-walled multiporous sensilla in *B. oleae* (Hallberg *et al.*, 1984), single-walled multiporous in *B. dorsalis* (Liu *et al.*, 2021).

The number of trichoidea sensilla was slightly higher in the generalist species but the difference was not significant. This sensilla was the most abundant in many species of the tephritid fruit flies, as *A. fraterculus* (Bisotto-de-Oliveira *et al.*, 2011), *A. ludens* (Dickens *et al.*, 1988), *B. tryoni* (Giannakakis and Fletcher, 1985; Hull and Cribb, 1987), *T. curvicauda* (Arzuf *et al.*, 2008), *C. capitata* (Levinson *et al.*, 1987), *B. dorsalis* (Dickens *et al.*, 1988;

Liu *et al.*, 2021), *B. cucurbitae* (Dickens *et al.*, 1988). The number of trichoidea sensilla is higher at the distal region of the flagella in the *Anastrepha* species herein described as well as in other species of tephritid (Bisotto-de-Oliveira *et al.*, 2011; Levinson *et al.*, 1987; Dickens *et al.*, 1988). However, in some species they are uniformly distributed in the flagella, like in *B. tryoni* (Giannakakis and Fletcher, 1985) and *B. dorsalis* (Liu *et al.*, 2021).

The sensilla basiconica are finger-like with a round tip and are the second more abundant sensilla in several species of tephritid flies but on the contrary, they are the most numerous in *C. capitata* (Mayo *et al.*, 1987; Bigiani *et al.*, 1989). In the present study it was shown that their number are significantly higher in the specialist species of *Anastrepha* and a single type was found similarly as in *A. serpentina* previously studied (Castrejón and Rojas, 2009), *A. ludens* (Dickens *et al.*, 1988) and in other species of fruit flies (Giannakakis and Fletcher, 1985; Hull and Cribb, 1987; Mayo *et al.*, 1987; Arzuf *et al.*, 2008). In other species, two types have been described mainly related to length of the sensilla as in *B. dorsalis* (Liu *et al.*, 2021). The basiconica sensilla are more abundant at the proximal region of the flagella in the species of *Anastrepha* as well as in *A. fraterculus* (Bisotto-de-Oliveira *et al.*, 2011), in *A. sp.1 affinis fraterculus* (Perre, 2017) and other species of fruit flies (Dickens *et al.*, 1988). In *C. capitata* they are scattered over the entire flagella (Mayo *et al.*, 1987; Bigiani *et al.*, 1989).

The clavate sensilla are one of the less numerous in the flagella of tephritid species (Mayo *et al.*, 1987; Bigiani *et al.*, 1989), occurring in approximate similar numbers in the generalist and specialist species of *Anastrepha*, in *A. serpentina* (Castrejón and Rojas, 2009) and *A. sp.1 affinis fraterculus* (Perre, 2017). In the nominal species *A. fraterculus* two types of clavate sensilla were described (Bisotto-de-Oliveira *et al.*, 2011) while a single type was found in the other species of fruit flies. This sensilla was not described (or found) in *B. dorsalis* (Liu *et al.*, 2021) nor in other species in the study by Dickens *et al.*, (1988). Clavate sensilla are distributed preferentially at the proximal region of the flagella in the *Anastrepha* species as well as in *B. tryoni* (Giannakakis and Fletcher, 1985) and was not found at the flagellar distal region in *T. curvicauda* (Arzuf *et al.*, 2008).

Coeloconica sensilla, also known as multiporous grooved sensilla or styloconica, are characterized by having finger-like processes and longitudinal grooves and are the smallest in size and one of the least numerous in species of fruit flies (Giannakakis and Fletcher, 1985; Levinson *et al.*, 1987; Dickens *et al.*, 1988; Hull and Cribb, 1997; Arzuf *et al.*, 2008; Castrejón and Rojas, 2009; Bisotto-de-Oliveira *et al.*, 2011; Awad *et al.*, 2015; Perre, 2017; Liu *et al.*, 2021). They are more abundant in the middle region of the flagella in the *Anastrepha* species (present results; Bisotto-de-Oliveira *et al.*, 2011; Perre *et al.*, 2017).

The variable number of sensilla is in line with the observation that in large number of insect species there is a positive correlation between the length/size of the antennae and the number of olfactory sensilla but according to Elgar *et al.*, (2018) it is still not clearly ascertained

if efficiency of perception is enhanced by the size of the antennae. Another aspect that was revealed in the present analysis is the distribution of the sensilla along the flagella, the clavate and coeloconica being more numerous in the proximal and medial regions of the flagella while the basiconica and trichoidea increases in number toward the distal extremity of the segment. Likewise, in several insect species it is possible that the antennae morphology in *Anastrepha* be shaped to optimize the perception of odorants and the differential concentration of sensilla along the flagella suggests that other factors seem to be involved in the efficiency of the sensorial perception of odorants as was discussed by Elgar *et al.* (2018). Since the present data are the results of a morphological analysis, the function of the *Anastrepha* sensilla herein studied will be assumed to be those of sensilla with similar structure whose function was described as olfactory receptors in other insect species (Zacharuk, 1980; Chapman, 1982; 2013; Levinson *et al.*, 1987; Dickens *et al.*, 1988; Elgar *et al.*, 2018). The basiconica sensilla, for example, seems to respond to plant volatiles (cues) while the trichoidea sensilla seems to be insensitive to plant emission perceiving pheromones and other species-specific infochemicals (Chapman, 1982; Zacharuk, 1985; Mayo *et al.*, 1987; Elgar *et al.*, 2018; Lopes *et al.*, 2002).

The species that composed the specialist and of generalist groups had, in both, representatives of distinct taxonomic infrageneric groups: groups *fraterculus* and *serpentina* within the generalists, and groups *grandis*, *striata* and *spatulata* in the specialists one (*sensu* Norrbom *et al.*, 2013). Thus, it seems reasonable to suppose that the differences between the two groups of species may be the result, of different selective pressures related not only to generalist and specialist resource exploitation habits but also to differences in the complex reproductive behaviour of the two group of species (Aluja, 1994). Either process, resource exploitation and mating behaviour, involve pheromones and other cues that would be related to the more numerous trichoidea and basiconica sensilla differently in the two groups of species. The data herein described seems to indicate that the number of the antennae sensilla of *Anastrepha* would not follow Chapman's suggestion since the basiconica sensilla occurred in larger numbers among the specialist species. However, the results seem to be in line with the description in other insects regarding to the perception of minute amounts of plant odorants (cues) that may arrive to the vicinity of the receptors (specialist species), and/or to the distinct species-specific pheromones or chemical signals emitted in the reproductive process of generalist species (Elgar *et al.*, 2018).

## Conclusions

The study revealed differences in number of the basiconica and trichoidea antennal sensilla in specialist and generalist species of *Anastrepha* that could be related to the distinct resource exploitation and the complex

reproductive behaviour between them. The expansion of this type of study to a larger number of fruit fly species, allied to functional analyses will be able to improve the knowledge of these sensitive structures. A deeper understanding of the sensorial system in fruit flies may contribute to development of control strategies of pest species, especially those involving odorants perception, or the development of compounds that block the function of the sensorial structures.

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