



## Distant populations of a *Xanthosoma* (Araceae) species have different floral scents but the same cyclocephaline beetle pollinators

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### ABSTRACT

We report on the reproductive biology, pollinators, and thermogenesis of the widely distributed Araceae species, *Xanthosoma striatipes*. We analyzed the floral scent in one population and compared it to a previous study. *Xanthosoma striatipes* was studied at three sites in Brazil, São Paulo, Minas Gerais and Maranhão. The results showed constancy of the reproductive biology and main pollinator species across sites. The pollinators at all three sites were two species of cyclocephaline scarabs, *Cyclocephala atricapilla* and *C. ohausiana*. The scent composition of the strongly scented inflorescences of plants of a site in São Paulo differed from plants recently studied in Central Brazil. Of the 39 and 23 compounds detected, in the present and the previous study, respectively, only seven compounds, were in common. We discuss that the two main constituents identified in samples at both sites, the aromatic compound methyl salicylate and the terpenoid (*E*)-4,8-dimethyl-1,3,7-nonatriene, alone seem to be sufficient for the attraction of the beetles. However, it is also possible that different compounds are involved in attracting the same beetle species to plants of the different populations.

**Keywords:** beetle behavior, cyclocephaline scarabs, floral scent, GCMS-analyses, thermogenesis

## Introduction

The actual numbers of Araceae comprise 125 genera and 3525 species (Boyce & Croat 2016). The Neotropical genus *Xanthosoma* Schott is part of the tribe Caladieae Schott (Mayo *et al.* 1997), and its 140 described species (Boyce & Croat 2016) are distributed from Mexico and the West Indies to northern Argentina.

The spadix of the inflorescence of *Xanthosoma* carries unisexual flowers distributed in zones, with basal pistillate and distal staminate flowers, separated by several rows of sterile staminate flowers. The whole spadix is covered

by a large leafy bract, the spathe, which is constricted at the middle, forming an inflated chamber called tube or kettle, and a more expanded and boat-shaped apical portion called lamina. Pistillate and sterile staminate flowers are distributed within the tube. Among several genera of the Caladieae, including *Xanthosoma*, either nitidulids (Nitidulidae) or cyclocephaline scarab (Melolonthidae, Cyclocephalini) beetles act as key pollinators (Maia & Schindwein 2006; Chartier *et al.* 2014; Gibernau 2016; Milet-Pinheiro *et al.* 2017).

In spite of the existence of several studies on pollination and scent emission in tropical Araceae (Maia & Schindwein 2006; Maia *et al.* 2012; Dötterl *et al.* 2012; Maia *et al.* 2013a; b;

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Gottsberger *et al.* 2013; Pereira *et al.* 2014; Gibernau 2016; Milet-Pinheiro *et al.* 2017), we know little about the constancy of pollinating beetle species in different regions and whether floral scent emissions are similar among distant populations or not. To this end, the present paper presents data on pollinators and floral biology of the widely distributed species *Xanthosoma striatipes* from sites in the Brazilian states of São Paulo, Minas Gerais, and Maranhão. The distance between the southernmost study site in São Paulo and the northernmost in Maranhão is approximately 2,050 km. We also analyzed the floral scents of a population in São Paulo and compared it to a previous study performed in Central Brazil, in the Distrito Federal, about 750 km north, far away from the São Paulo site. Thus, the widely distributed South American species *X. striatipes*, with apparent native occurrences in Bolivia, North Brazil, Southeast Brazil, West-Central Brazil, Colombia, French Guiana, Guyana, Paraguay and Venezuela (Brummit 2001) is a suitable study species.

## Materials and methods

We studied *Xanthosoma striatipes* (Kunth & C.D. Bouché) Madison at different sites (Fig. 1). The first site was in the surroundings of the city of Botucatu in the state of São Paulo (city coordinates 22°53'9" S, 48°26'42" W, alt. 756-920 m, approximately 230 km northwest of the city of São Paulo). In the years 1978, 1980, 1981 and 2007, we always observed six individuals in a population of about 25 individuals. The plants were growing in a marshy field between a gallery forest (called Mata de Pinheirinho, because of the presence of the gymnosperm *Podocarpus sellowii*) and a Campo Cerrado. The scent samples presented in this publication are from this site.

The second site was a private property called "Fazenda Bela Tanda" (coordinates 19°3' S, 47°57" W) in the municipality of Indianópolis, approximately 40 km southeast of the city of Uberlândia, and approximately 370 km south of the federal capital Brasília, in the state of Minas Gerais (Fig. 1). The population there consisted of about 30 individuals, which grew in marshy places along a river. We also observed six individuals, from December 4 to 13, 1986.

Our third study site was in the state of Maranhão, Northeastern Brazil, in the surroundings of Codó, approximately 220 km southeast of São Luís, the capital city of this state, also in a private property, "Fazenda Canto da Roça" (4°30' S, 43°54' W) (Fig. 1). The population was growing in a swamp extended in an area of approximately 10 x 30 m (Fig. 2). On February 20-21, 1982, we registered 147 fertile individuals in various stages, from flowering to fruiting, and studied 6 inflorescences.

Further information about visiting beetles and scent analyses of *X. striatipes* is from the publication of Milet-

Pinheiro *et al.* (2017). Their collection sites were in Guará, close to Brasília in the Distrito Federal (city coordinates 15°49'53" S, 47°58'48" W), and another one in Arraias in the state of Tocantins (city coordinates 12°55'51" S, 46°56'16" W), approximately 340 km northeast of Brasília (Fig. 1). We compare the data of Milet-Pinheiro *et al.* (2017) with our data in the discussion section.

Plant voucher specimens are deposited in the herbaria of Botucatu (BOTU), Brasília (UB) and Ulm (ULM).

### *Characteristics of inflorescences, flowering, anthesis and beetle visitation*

Although the population sizes of *Xanthosoma* varied, at each site we observed six inflorescences, their flowering, and their opening and closing in the pistillate and staminate stages. We assessed the functionality of pistils (pistillate = female stage) by the production of stigmatic exudates, and the effective function of stamens (staminate = male stage) by the release of pollen and its accessibility to insect visitors. We also observed the behavior of the visiting beetles, distinguishing their sex, and collected a total of 15 individuals for identification.

### *Warming rhythm of inflorescences*

To study the increase in temperature (thermogenesis) we used temperature loggers and recorded the temperature of the inflorescences in relation to ambient temperature. We inserted the thermocouples into the upper staminate part of the inflorescences, which is the region of the spadices with the highest temperatures (based on previous tests). As a control, a second probe hung freely at approximately the same height and pointed away from the spadix, to record ambient temperatures. We protected the inflorescences and equipment from rain and direct sunlight. Inflorescence and ambient sensors were fully cross-calibrated to ensure data consistency. We used a Bioblock Scientific 16200 equipment (Portugal) for measurements. In addition, temperature of the inflorescences and the ambient air were measured continuously or discontinuously during the night and day with a NiCr-Ni temperature sensor (Therm 2256-1, Ahlborn Meß- und Regeltechnik, Germany).

### *Scent sampling and GC-MS analyses*

In Botucatu, we collected the scent of one inflorescence per plant of two different individuals. As the inflorescences of *X. striatipes*, like in other species, heat up more during the receptive pistillate (female) stage, we conducted the sampling at this stage through dynamic headspace extraction, for which we used freshly cut inflorescences kept in water. This cutting does not seem to influence the scents emitted from aroid inflorescences (Milet-Pinheiro *et al.* 2017, and references therein). We enclosed the two inflorescences separately in PET film oven bags (Bratschlauch, Melitta GmbH, Germany) for nearly one hour (19:00 to 19:55 h) to



enrich the scents. Afterwards the scented air inside the bags with the inflorescences was drawn for 60 min (from 20:00 to 21:00 h, sample one) and 120 min (from 20:00 to 22:00 h, sample two) by a membrane pump (Rietschle Thomas, Puchheim, Germany) at a constant flow rate of 200 mL min<sup>-1</sup>. The air enriched with scent compounds was trapped in glass tubes containing adsorbent polymer (500 mg), consisting of a 1:1 mixture of Tenax™ TA (80/100 mesh, Supelco, USA) and Carboxpack™ X (20/40 mesh, Supelco, USA).

Samples were stored in a freezer until analysis. The tubes were eluted with 1 ml of high-grade acetone (Merck, Germany), and obtained samples were stored in a freezer until analysis (-20 °C).

### Chemical analysis

The inflorescence scent samples were analyzed on a Varian Saturn 2000 mass spectrometer coupled to a Varian 3800 gas chromatograph equipped with a 1079 injector



**Figure 1.** Location of the study sites of *Xanthosoma striatipes* in Brazil in the States São Paulo (Botucatu), Minas Gerais (Indianópolis) and Maranhão (Codó) used in the present study as well as in the Distrito Federal (Guará) and Tocantins (Arraias) used in the study by Milet-Pinheiro *et al.* (2017). The distance between the southernmost site, Botucatu, and the northernmost site, Codó, is approximately 2,050 km. The dotted lines on the map indicate major rivers.

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(Varian Inc.), which had been fitted with the ChromatoProbe kit, following Dötterl *et al.* (2006). 1 µl of each sample was placed in a quartz vial, which was then injected in the GC by means of the ChromatoProbe (Dötterl *et al.* 2005). The injector split vent was opened and the injector was heated to 40 °C to flush any air from the system. The split vent was closed after 2 min. The injector was heated at 200 °C min<sup>-1</sup>, then held at 200 °C for 4.2 min, after which the split vent was opened and the injector cooled down. Separations were achieved with a fused silica column ZB-5 (5% phenylpolysiloxane; 60 m long, inner diameter 0.25 mm, film thickness 0.25 µm; Phenomenex, Torrance, CA, USA). Electronic flow control was used to maintain a constant helium carrier gas flow of 1.0 ml min<sup>-1</sup>. The GC oven temperature was held for 7 min at 40 °C, and then increased by 6 °C min<sup>-1</sup> to 250 °C and held for 1 min. The MS interface worked at 260 °C and the ion trap at 175 °C. Mass spectra were taken at 70 eV (in EI mode) with a scanning speed of 1 scan s<sup>-1</sup> from m/z 30 to 350. GC/MS data were processed using the Saturn Software package 5.2.1.

Identification of the components was carried out using the mass spectral libraries Wiley 9, Nist 2011, FFNSC 2, and Adams (2007), as well as the database available in MassFinder 3. Some of the compounds were confirmed by comparing their mass spectra and retention times with those of standard components available in the reference collection of the Plant Ecology Laboratory of the University of Salzburg. Samples from ambient air were used to discriminate between contaminants and inflorescence scents.



**Figure 2.** The large *X. striatipes* population in Codó, State of Maranhão, growing in a swamp.

## Results

### *Population sites, characteristics of inflorescences, flowering, and anthesis*

The populations in Botucatu and Indianópolis had 25-30 individuals, while the population in Codó consisted of 147 individuals. At all sites, *X. striatipes* flowered during

the rainy season. The inflorescence had a long peduncle, longer than the fertile part of the inflorescences. The spathe and the spadix had the same length of 13 to 17 cm each. The external basal part of the spathe was greenish and changed to light yellowish at the top. The internal part of the spathe and the spadix were also greenish at the base and became whitish, sometimes with a yellowish tinge in the upper part. The stigmata of the pistillate flowers were yellow. *Xanthosoma striatipes* had a two-night protogynous reproductive rhythm.

### *Warming rhythm of inflorescences*

We measured the increase in temperature of inflorescences of *X. striatipes* in Botucatu (São Paulo state) and Bela Tanda (Minas Gerais state; Fig. 3A-B). At both sites, the temperature of the spadix was somewhat higher in the pistillate than the staminate stage. The peak temperature of a pistillate stage inflorescence in Botucatu was at 20:15 h, the staminate stage peak was already at 19:30 h. Measurements of inflorescences at Bela Tanda revealed that the temperature peak of the pistillate stage coincided with the temperature peak of the staminate stage. In Botucatu, in the measured inflorescence, the maximum temperature reached 33.6 °C (7.9 °C above ambient air temperature) in the pistillate stage and 27.8 °C (6.7 °C above ambient air temperature) in the staminate stage. The four measured inflorescences in Bela Tanda, reached at maximum 36.8 °C in the pistillate stage (20.5 and 19.5 °C above ambient air temperature, respectively), and 31.8 °C (14.5 °C above ambient air temperature) in the staminate stage. The peak heating temperatures of inflorescences and the timing at the two sites were thus slightly different, whereas the differences in temperatures between the spadix and the ambient air were twice as high in Bela Tanda than in Botucatu.

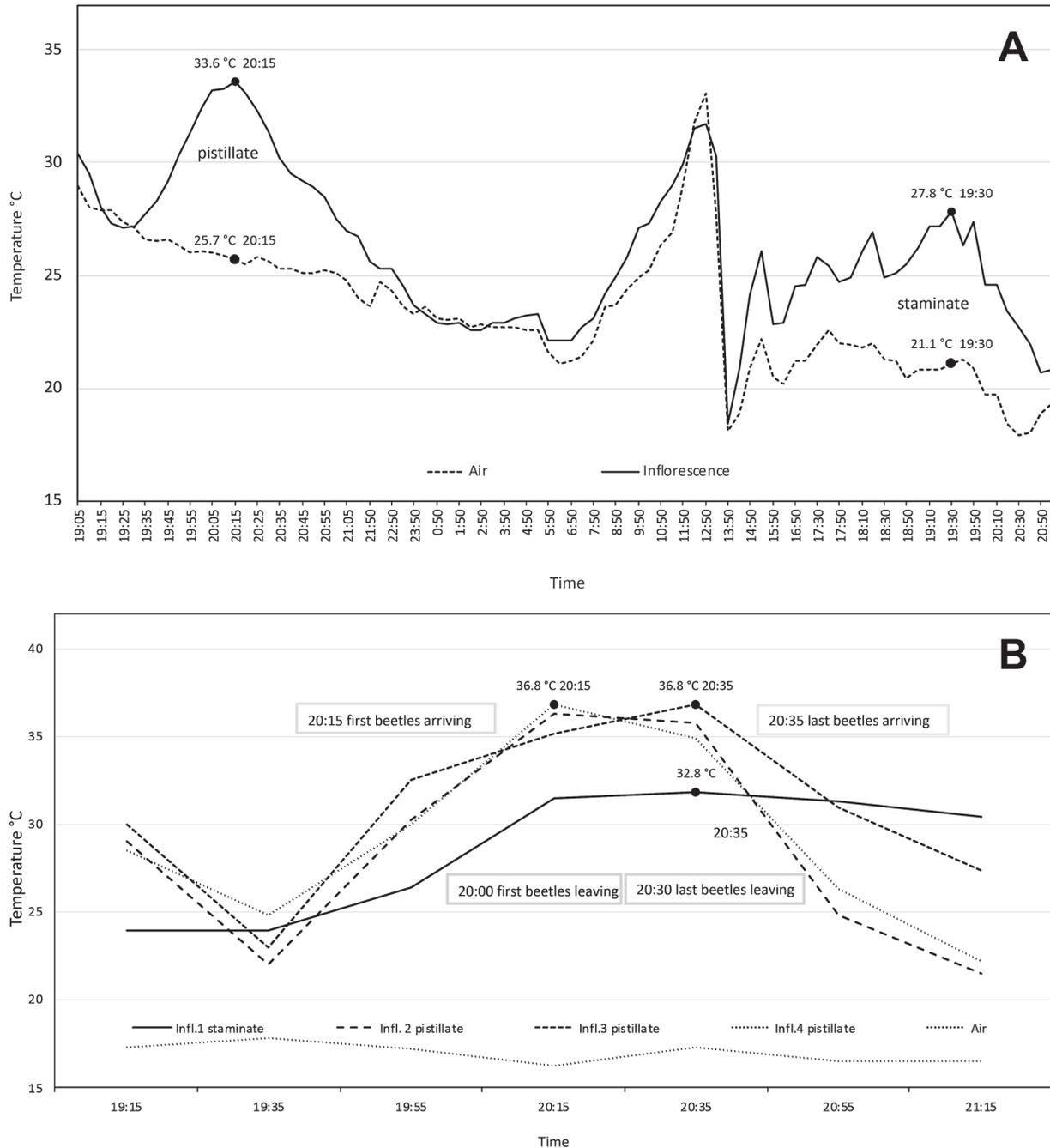
### *Behavior of pollinating beetles*

During the scent emitting pistillate stage of *X. striatipes* at all sites, the beetles of the two species *Cyclocephala atricapilla* (Mannerheim) and *C. ohausiana* Höhne visited the inflorescences (Figs. 4, 5). They approached the inflorescences between 20:15 and 20:45 h (Fig. 3B). After arriving and settling on the spathe or spadix (Fig. 4A), they crawled down into the tube to the receptive, sticky pistillate flowers (Fig. 4B). In the next morning, the beetles were still actively eating from the sterile staminate flowers and some of them were mating. Between 18:45 and 19:00 h of the second evening, the beetles started to feed on pollen, while crawling up the spadix (Fig. 5A-B). At 20:00 h, the first beetles flew away, while others were still feeding on pollen, leaving the inflorescences as late as 20:30 h (Fig. 3B). When leaving, the pollen-covered beetles crawled up to the top of the spadix, from where they flew away.



As visitors of *X. striatipes* at the Botucatu site, we registered 56 individuals of *C. ohausiana* and four individuals of *C. atricapilla*, during three observation days. At the Indianópolis site, during four observation days, 19 individuals of *C. atricapilla*, and 12 individuals of *C. ohausiana* were registered. In Codó, in one observation day, only two *C. atricapilla* and one *C. ohausiana* were verified. The numerical proportion of the two beetle species varied among observation days. For example, in the Botucatu population,

on December 1, 1978, we counted four *C. atricapilla* and 11 *C. ohausiana*, and on January 20, 1980, only 20 *C. ohausiana* were registered. The representation of the two sexes also differed between the two beetle species. For example, in Botucatu, out of 56 *C. ohausiana* individuals, 42 were males and 14 females, while out of four registered *C. atricapilla* individuals, two were males and two females. At all three sites, a common number of beetles on one inflorescence was two-six individuals.

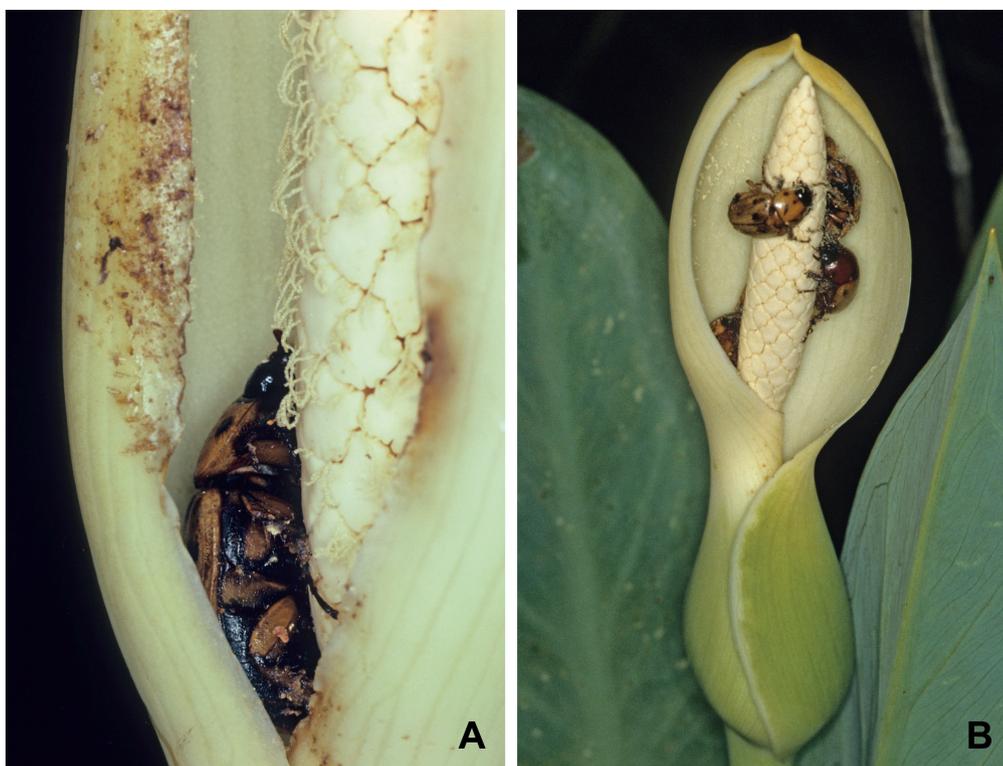


**Figure 3. A.** Warming of one inflorescence of *X. striatipes* in Botucatu, State of São Paulo, during the pistillate and the staminate stage in two subsequent days (November 18 and 19, 2007). **B.** Warming of four inflorescences of different individuals of *X. striatipes*, one in the staminate and the other three in the pistillate stage during one day (Indianópolis, State of Minas Gerais (December 12, 1986)).

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**Figure 4.** *Xanthosoma striatipes* at Indianópolis, State of Minas Gerais. **A.** One individual of *Cyclocephala ohausiana* (left) and an individual of *C. atricapilla* (right) have approached a warm and smelling spadix in the pistillate stage. **B.** An opened inflorescence in the pistillate stage. Several individuals of *C. ohausiana* and probably also of *C. atricapilla* in the basal tube are contacting the receptive stigmas and gnawing on sterile staminate flowers. The length of the beetles is ca. 1.8 cm.



**Figure 5.** An inflorescence in the second night in the staminate stage, with male flowers producing pollen grains in form of chains, which are eaten by beetles coming out of the tube and crawling upwards. **A.** Probably, a *C. ohausiana* beetle eating pollen. **B.** Several *C. ohausiana* individuals in search of remnants of pollen shortly before flying away. The length of the beetles is ca. 1.8 cm.



In the large Codó population in Maranhão, we could see that the visiting beetles were essential for fruit production. Inflorescences without signs of previous beetle visitation, such as gnawing marks or remnants of their feces, did not produce fruits (46 individuals), while those inflorescences, which apparently had been visited by beetles (26 individuals), set fruits.

### Floral scents

At the time when beetles were attracted, the inflorescences released a strong fruity odor. Scent was much weaker, and somewhat stinking at the staminate stage. The analyses of the two scent samples collected during the pistillate stage from plants of the Botucatu site revealed in total 39 compounds, including 11 unknown compounds, and overall a very similar scent composition (Tab. 1). Most of the compounds occurred only in low amounts, with only seven compounds contributing at least 2 % to the total scent

in any of the two samples. The most prominent compounds in both samples were the aromatics methyl salicylate, methyl *o*-anisate and 1,3,5-trimethoxybenzene, the cyclic compound methyl jasmonate, the terpenoids (*E*)- and (*Z*)-4,8-dimethyl-1,3,7-nonatriene, and the S-containing 4-methyl-5-vinylthiazole.

### Discussion

As in other Araceae species, for instance in *Philodendron selloum* (Gottsberger & Silberbauer-Gottsberger 1991), the beetles in *Xanthosoma striatipes*, are also attracted by the whitish-yellowish spathe together with the strong scent of the inflorescences. *Xanthosoma striatipes* also presents thermogenesis, which is certainly important and decisive for the successful attraction of the cyclocephaline scarab beetles. As known from previous studies of other cyclocephaline

**Table 1.** Relative amount of scent compounds (%) detected in the two scent samples of *Xanthosoma striatipes* analysed in the present study and in the two samples of this species analysed by Milet-Pinheiro *et al.* (2017). The samples of the present study were collected in Botucatu, São Paulo, those of Milet-Pinheiro *et al.* (2017) in Guará, Distrito Federal und Arraias, Tocantins. tr: < 0.05 %. Compounds are ordered according to chemical classes and within classes according to retention time. The identification of the compounds marked with an asterisk is based on synthetic reference compounds. Compounds printed in italics were only detected in the study of Milet-Pinheiro *et al.* (2017), and underlined compounds were found both in the present and the previous study.

	Sample 1	Sample 2	Data of Milet-Pinheiro <i>et al.</i> 2017		Sample 1	Sample 2	Data of Milet-Pinheiro <i>et al.</i> 2017
<b>Aliphatics</b>				<b>Terpenoids</b>			
<i>Butan-2-yl acetate</i>			4.1 <sup>c</sup>	<i>Sabinene</i> *	tr	0.1	
<i>Pent-1-en-3-yl acetate</i>			0.1 <sup>c</sup>	<u><i>β-Myrcene</i></u> *	tr	0.1	0.2 <sup>c</sup>
<b>Aromatics</b>				<i>Limonene</i>			tr <sup>c</sup>
<i>Methyl benzoate</i>			tr <sup>c</sup>	<u><i>Eucalyptol</i></u> *	0.1	0.8	tr <sup>c</sup>
<u>1,2-Dimethoxybenzene</u> *	tr	tr	tr <sup>c</sup>	<i>(Z)-β-Ocimene</i>			tr <sup>c</sup>
<u>1,4-Dimethoxybenzene</u> *	tr	tr		<u><i>(E)-β-Ocimene</i></u> *	0.1	0.4	0.2-0.9
<u>Methyl salicylate</u> *	32.7	23.8	4.9-6.5	<i>γ-Terpinene</i> *	tr	tr	
<i>Isobutyl benzoate</i>	0.1	0.2		<i>(E)-Linalool oxide furanoid</i> * + <i>Terpinolene</i> *	tr	0.1	
<i>Methyl o-anisate</i> *	19.0	16.3		<i>(Z)-4,8-Dimethyl-1,3,7-nonatriene</i> *	0.4	2.1	
<i>1,2,4-Trimethoxybenzene</i> *	0.1	0.1		<i>Linalool</i> *	0.3	0.2	
<i>1,3,5-Trimethoxybenzene</i> *	17.2	17.7		<u><i>(E)-4,8-Dimethyl-1,3,7-nonatriene</i></u> *	9.9	14.6	0.5-82.4
<i>a Tetramethoxybenzene</i>	0.1	0.2		<i>α-Terpineol</i> *	0.3	1	
<b>C5-branched chain compounds</b>				<i>(E)-4,8-Dimethylnona-1,3,7-trien-5-yl acetate</i> *	tr	tr	
<i>Methyl 2-methylbutyrate</i> *	tr	1.1					
<b>Miscellaneous cyclic compounds</b>				<i>Theaspirane isomer 1</i>			0.1 <sup>c</sup>
<i>Isojasmol</i> <sup>a</sup>			21.6 <sup>c</sup>	<i>Theaspirane isomer 2</i>			tr <sup>c</sup>
<i>Dehydrojasmon</i> <sup>b</sup>			16.9 <sup>c</sup>	<u><i>β-Caryophyllene</i></u> *	0.1	0.2	tr <sup>c</sup>
<i>(E)-Jasmone</i>			tr <sup>c</sup>	<i>(E)-β-Farnesene</i> *	tr	tr	
<i>(Z)-Jasmone</i>			0.1-51.2	<i>(E)-8(9)-dehydro4(5)-dihydrotheaspirone</i>	tr	tr	
<i>Dihydro-β-ionone</i>			8.0 <sup>c</sup>	<i>α-Caryophyllene</i> *	tr	0.0	
<i>7,8-Dihydro-β-ionol</i>			0.1 <sup>c</sup>	<b>Unknowns</b>			
<i>Methyl jasmonate</i> *	17.2	18.1		Sum unknowns <sup>11</sup> pooled	0.5	0.6	
<b>S-containing compounds</b>				<i>unknown mw 91, 119, 105, 40, 77</i>			0.9 <sup>c</sup>
<u>4-Methyl-5-vinylthiazole</u> *	1.7	2.2		<i>unknown mw 79, 69, 41, 81, 93</i>			0.1 <sup>c</sup>
<u>4-Methyl-5-formylthiazole</u>	tr	tr		<i>unknown mw 117, 91, 94, 95, 79</i>			1.1 <sup>c</sup>

<sup>a</sup> and <sup>b</sup> these compounds were listed by Milet-Pinheiro *et al.* (2017) as unknown with retention indices 1301 and 1305, respectively. See text for more details about the identity of these compounds. tr = trace

<sup>c</sup> compound occurred only in one of the two samples analysed by Milet-Pinheiro *et al.* (2017).

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pollination systems in regions with a well-defined rainy and dry season, such as the Brazilian uplands and/or Cerrado, flowering of *Xanthosoma* also occurred in the rainy season (Dötterl *et al.* 2012; Gottsberger *et al.* 2012; 2013).

Contrary to most other pollinators, beetles are often stationary flower visitors, remaining in flowers or inflorescences for many hours (Gottsberger 2016). The protogynous flowering rhythm is adequate for efficient pollen transfer in beetle pollination. In inflorescences, such as that of *Xanthosoma*, beetles find mating partners, feed on the sterile nutritious staminate flowers, and, just before leaving the inflorescence, they eat enormous amounts of pollen grains. Additionally, the increased temperature warms them up and facilitates their eventual flight to a pistillate stage inflorescence (Gottsberger 2016).

In the states of São Paulo, Minas Gerais and Maranhão, along a south-north distribution, the beetle species *Cyclocephala atricapilla* and *C. ohausiana* are the constant pollinators of *X. striatipes*. Milet-Pinheiro *et al.* (2017) also mention those two beetle species visiting *X. striatipes* at their study sites, and additionally *C. celata* Dechambre, 1980 and *Erioscelis emarginata* Endrödi, 1966.

In contrast to the two scent samples analyzed in the present study, which were quite similar (Tab. 1), the two samples of *X. striatipes* analyzed by Milet-Pinheiro *et al.* (2017) strongly differed between each other. Further, there were marked differences in the scent samples in the present study compared to the previous one. Our analyses revealed 39 compounds, while Milet-Pinheiro *et al.* (2017) detected 23 compounds in their samples, with only seven components common to both studies. Of the seven compounds that contributed at least 2% to the total scent in any of the two samples analyzed in the present study, only two, (methyl salicylate and (*E*)-4,8-dimethyl-1,3,7-nonatriene) occurred also in the samples of Milet-Pinheiro *et al.* (2017). Beside these two compounds, Milet-Pinheiro *et al.* (2017) found another four compounds that contributed in one of their samples at least 2% to the total scent discharge: butan-2-yl acetate, (*Z*)-jasmone, dihydro- $\beta$ -ionone, and two unknown compounds (Milet-Pinheiro *et al.* 2017). Based on retention index and mass spectral information given by these authors, and recently published papers on novel scents in cyclocephaline pollinated plants (Maia *et al.* 2019a; b) and in floral chemistry of Cyclanthaceae (Teichert *et al.* 2018), these unknown compounds are isojoasmol and dehydrojasmone. None of these compounds were detected in our samples (Tab. 1). This high overall intraspecific variation in scent was unexpected given that within-species variation in scent is limited in other species pollinated by cyclocephaline beetles (e.g., Gottsberger *et al.* 2012; 2013; Maia *et al.* 2013b; 2019a).

In their comparative study of floral scent chemistry of 13 *Xanthosoma* species (including *X. striatipes*), Milet-Pinheiro *et al.* (2017) mentioned that some of the species had only

a small number of compounds. This phenomenon occurs not only in Araceae, but also in other plants pollinated by cyclocephalini beetles, among them Annonaceae and Magnoliaceae (Dötterl *et al.* 2012; Gottsberger *et al.* 2012; Maia *et al.* 2012; 2013a; Pereira *et al.* 2014). Apparently, a few prominent compounds suffice to attract the beetles, as demonstrated in some previous studies (Pereira *et al.* 2014, and references therein). Given that *C. atricapilla* and *C. ohausiana* visit *X. striatipes* over its large distribution range, we expected that dominant compounds commonly present at different sites are responsible for attraction of these two beetle species, *i.e.* methyl salicylate and (*E*)-4,8-dimethyl-1,3,7-nonatriene. However, it also seems possible that different scent compounds are involved in attracting these insects at different sites. One of these compounds might be (*Z*)-jasmone, which was the most common (12 of the 13 species), and in some of the species (including one sample of *X. striatipes*) also the most abundant compound in the *Xanthosoma* species studied by Milet-Pinheiro *et al.* (2017). Indeed, this compound increases the attractiveness of another compound in another cyclocephaline, *Erioscelis emarginata* (Dötterl *et al.* 2012). Another compound responsible for attracting *C. atricapilla* and *C. ohausiana* to inflorescences of *X. striatipes* might be 4-methyl-5-vinylthiazole, which was only detected in the present study. This compound was highly attractive to a few cyclocephaline species, among them *C. atricapilla* (Maia *et al.* 2012). 4-Methyl-5-vinylthiazole also attracts *Cyclocephala celata* (Maia *et al.* 2012). Its absence at our sites might be associated with the natural distribution of *Cyclocephala celata*, or the seasonality of local populations of the insects.

Overall, despite the availability of just a few scent samples of *Xanthosoma striatipes*, the variation among them was higher than the intraspecific variation recorded in other cyclocephaline pollinated plant species. Further, our study shows that *C. atricapilla* and *C. ohausiana* are constant visitors of this species despite these variations in scents. This finding can be explained by either a rather specific olfactory search image of the beetles that relies on the few compounds commonly present, or by a less specialized olfactory search image, in case beetles would be attracted to plants at different sites by different compounds.

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