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Uncovering the grape-like aroma of *Atlides polybe* (Linnaeus, 1763) (Lepidoptera: Lycaenidae, Theclinae)

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Abstract

In our study, we examined the volatile androconial scent chemistry of *Atlides polybe* (Linnaeus, 1763), a Lycaenidae species known for its distinctive "grape-like" aroma. This is the first Theclinae species to have its androconial secretions chemically investigated. Analysis of solvent sample using gas chromatography-mass spectrometry revealed 13 ion peaks corresponding to distinct volatile compounds. Among these, methyl anthranilate emerged as the dominant compound, primarily associated with the aldehydes heptanal, octanal, and (*E*)-2-decenal. This study marks the first report of methyl anthranilate as a volatile compound in Papilionoidea. Interestingly, methyl anthranilate is widely used as the primary grape flavoring agent in the flavor and fragrance industry, matching the scent emitted by *A. polybe*. The presence of methyl anthranilate as an androconial constituent, along with aldehydes imparting fruity odors, delineates a unique chemical bouquet among Papilionoidea. This composition likely serves as a sex pheromone and may also fulfill complementary functions, such as predator deterrence.
Keywords: Lepidoptera, Lycaenidae, Theclinae, androconia, CG-MS, male pheromones, secondary sexual organs, semiochemicals, VOCs.

Descubriendo el aroma de uva de *Atlides polybe* (Linnaeus, 1763) (Lepidoptera: Lycaenidae, Theclinae)

Resumen

En nuestro estudio, analizamos los compuestos químicos volátiles de los aromas de las androconias de *Atlides polybe* (Linnaeus, 1763), una especie de Lycaenidae que es conocida por su aroma que se asemeja al de las uvas. Esta es la primera especie de Theclinae que posee secreciones androcónicas analizadas bajo una óptica química. Los análisis de muestras de solventes utilizando cromatografía de gases-espectrometría de masas permitió observar 13 picos de iones correspondientes a diferentes compuestos volátiles. Entre ellos, el antranilato de metilo se destacó como el compuesto dominante y estuvo primariamente asociado con los aldehídos heptanal, octanal y (*E*)-2-decenal. Este estudio representa el primer registro de antranilato de metilo como un compuesto volátil en Papilionoidea. Curiosamente, el antranilato de metilo es ampliamente utilizado como el agente saborizante primario de uvas dentro de la industria de los sabores y olores, combinado con el aroma emitido por *A. polybe*. La presencia del antranilato de metilo como un compuesto androcónico, juntamente con aldehídos que están relacionados a los olores frutales, representan un ramo químico único entre los Papilionoidea. Esta composición probablemente sirve como una feromona sexual y puede también poseer funciones complementaras, para evitar a los depredadores.
Palabras clave: Lepidoptera, Lycaenidae, Theclinae, androconia, CG-MS, feromonas masculinas, órganos sexuales secundarios, semioquímicos, COV.

Desvendando o aroma de uva da *Atlides polybe* (Linnaeus, 1763)
(Lepidoptera: Lycaenidae, Theclinae)

Resumo

Em nosso estudo, analisamos os compostos químicos voláteis das androcônias de *Atlides polybe* (Linnaeus, 1763), um Lycaenidae conhecido por seu aroma que se assemelha ao de uva. Esta é a primeira espécie de Theclinae a ter suas secreções androconiais examinadas do ponto de vista químico. A análise por cromatografía de gases/espectrometria de massas do extrato androconial de *A. polybe* permitiu a observação de 13 picos de íons, correspondentes a diferentes compostos voláteis. Entre eles, antranilato de metila se destacou como composto dominante, associado principalmente aos aldeídos heptanal, octanal e (*E*)-2-decenal. Este estudo representa o primeiro registro de antranilato de metila como composto volátil em Papilionoidea. Curiosamente, antranilato de metila é amplamente usado como o principal agente flavorizante de uva pela indústria de aromas e combina com o odor de *A. polybe* percebido pelo olfato humano. A presença de antranilato de metila como principal constituinte androconial, juntamente a aldeídos que emitem odores frutados, delineia um buquê químico único entre os Papilionoidea. Tal composição provavelmente atua como feromônio sexual e pode desempenhar funções complementares, como deterrência de predadores.

Palavras-chave: Lepidoptera, Lycaenidae, Theclinae, androconia, CG-MS, feromonas masculinas, órgãos sexuais secundários, semioquímicos, COVs.

Introduction

The term “pheromone” was coined in 1959 by Peter Karlson and Mark Lürscher in close association with the chemical characterization of bombykol, a volatile unsaturated fatty alcohol secreted by female silk moths (*Bombyx mori* Linnaeus, 1758; Bombycidae) that stimulates the sex-oriented behavior of conspecific males (Butenandt et al. 1959). Since then, many species of Lepidoptera have been found to use a variety of volatile organic compounds in their chemical communication, with a particular focus on agronomical pests (El-Sayed, 2024).

While not all volatile organic compounds (VOCs) emitted by lepidopterans are perceivable to humans as scents, lepidopterologists have long described the perfumes of collected specimens (see Ando et al. 2004; Ehlers & Schulz, 2023). Among the Papilionoidea, for example, unpleasant and noxious smells are emitted by the larvae of *Parnassius* spp. (Papilionidae) and *Danaus* spp. (Nymphalidae), which are derived - at least partially - from glycosides and alkaloids sequestered from toxic plants they feed on (Bjarnholt et al. 2012; Schulz, 1998). Conversely, adult males of *Pieris napi* (Linnaeus, 1758) (Pieridae) give off a citric aroma during flight, attributed to the emission of geranial and neral (Bergström & Lundgren, 1973). Among the Lycaenidae, male theclines (Eumaeini) are known for the pleasant perfumes in their androconia, described as intensely floral, chocolaty, or fruity (Longstaff, 1912; Müller, 1878). However, very little is known about the chemistry of androconial volatile organic compounds (VOCs) in this group (Ehlers & Schulz, 2023).

Atlides polybe (Linnaeus, 1763) (Figure 1), is a Neotropical species widely distributed from Mexico through Central America to northern Argentina (Warren et al. 2023). Despite its widespread distribution, it seems to be a naturally rare species in nature (Brown, 1992; Godman & Salvin, 1887). Like other species in the *Atlides* Section of Eumaeini, it is recognizable and praised for its exuberant colors. Furthermore, collectors have also reported a distinctive “grape-like” aroma from male specimens (Nobre & Schlindwein, 2016; Robbins et al. 2012), presumably originating from their forewing androconial organs (Müller, 1878). These secondary sexual structures are composed of a proximal scent pad that contains secretory cells inside a cavity between the wing membranes, and a distal scent patch of clustered black scales (Martins et al. 2019; Robbins et al. 2012). Our objective was to investigate the volatile scent chemistry of the wing androconia of *A. polybe* and identify the likely compound(s) responsible for the characteristic aroma of this species.

Material and methods

We collected an adult male of *A. polybe* in the municipality of Areia Branca (10º45'35"S, 37º20'36"W; 170 m.a.s.l.), state of Sergipe, northeastern Brazil, for the characterization of androconial VOCs. Following capture, the specimen was sacrificed by thorax pinching, sealed into a clean PTFE plastic envelope (5 x 5 cm), and kept under -24º C refrigeration for ~ 120 h until processing.

Sample collection and preparation were performed following standard protocols for solvent extraction (refer to Nobre et al. (2021) for details). The hind and forewings of the collected specimen were excised using micro scissors and placed in a clear 2 mL silanized glass vial containing 1.5 mL hexane (≥ 99.7% purity, Sigma-Aldrich, USA). The crude solvent extract was filtered through a silanized glass Pasteur pipette plugged with silanized glass wool (Sigma-Aldrich, USA) to remove floating scales and other debris. The sample was then concentrated to 0.25 mL under a laminar N_2 flow and stored at -24ºC until analysis (see below). A solvent negative control was obtained under the same conditions.

Samples were analyzed on a gas chromatograph coupled to a mass spectrometer (GC-MS; Agilent 7890A™ gas chromatograph, Agilent 5975C Series MSD™ mass spectrometer) and equipped with a non-polar HP-5ms column (Agilent J&W; 30 m x 0.25 mm i. d., 0.25 µm film thickness. A split/splitless inlet was fitted with an Agilent Thermal Separation Probe (TSP). For the analysis of samples, 1 µL was injected into a quartz micro vial which was then inserted in the TSP vial holder. The GC inlet operated on split mode (1:5) and the injector temperature was set to 250º C. The GC oven temperature started at 40º C for 1 minute and then increased at a rate of 6º C/min up to 270º C. Helium (He) carrier gas flow was maintained at 1.5 mL/min. MS source and quadrupole temperatures were set at 230º C and 150º C, respectively. Mass spectra were taken at 70 eV (in EI mode) with a scanning speed of 1.0 scan/s from m/z 35-450.

Compounds were tentatively identified by comparison of linear retention indices (RIs) based on a series of n-alkanes (C7-C30; Van den Dool & Kratz, 1963) and mass spectral data available in reference libraries (FFNSC 2, MACE r04, NIST20). Confirmation of the identity of targeted compounds was further obtained by comparison with authentic synthetic standards (Sigma-Aldrich Co./Supelco, USA). For analysis, only ion chromatogram peaks which contributed to at least 0.5 % of the total ion signal were contemplated, and contaminants were ignored. Since our objective was focused on volatile compounds, we only considered those that eluted earlier than pentacosane (RI = 2500), following Mann et al. (2017).

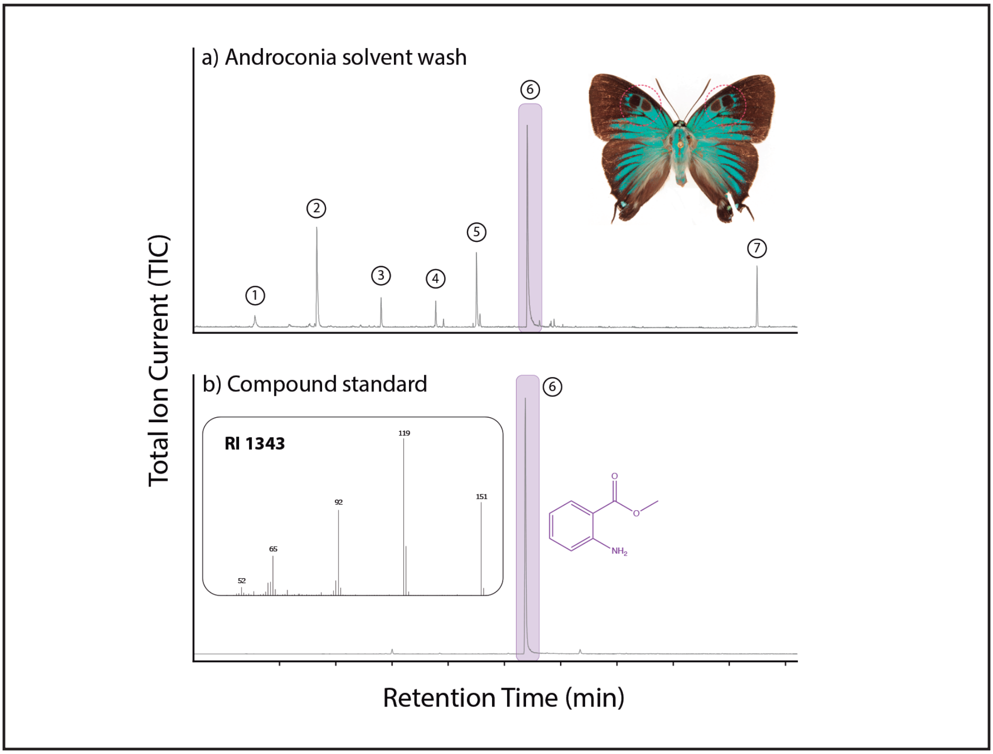
Results

Table 1. Total relative amounts of representative compounds isolated from solvent extract of androconia of *Atlides polybe*.

Kovats Index (RI)	Compound	Relative Amount (%)
902	Heptanal	9.89
999	Decane	1.89
1002	Octanal	21.60
1103	Nonanal	5.21
1192	2-decanone	3.89
1261	(E)-2-decenal	10.13
1341	Methyl anthranilate	26.68
1398	Tetradecane	1.15
1498	Pentadecane	1.25
1586	*m/z*: 135, 150, 43, 79, 151	1.14
1815	Hexadecanal	6.87
2093	Heneicosane	1.53
2296	Tricosane	1.07
-	Other compounds	7.71

The collected male specimen of *A. polybe* emitted a strong fruity fragrance, which, after excision of the wings, was much more intensely perceived in the androconial areas. The ion chromatogram of the androconial extract sample showed a dominant peak at 16.47 min (corresponding to *RI* 1343) (Figure 1A, Table 1). The *RI* and mass fragmentation spectrum of this peak was identical to those of methyl anthranilate (methyl 2-aminobenzoate) (Figure 1B). Additionally, we tentatively identified 12 other volatile compounds from the androconial extract sample. Among these, octanal, (*E*)-2-decenal, heptanal, hexadecanal, and nonanal were found to have the highest relative amounts, comprising 21.6%, 10.13%, 9.89%, 6.87%, and 5.21% of the total sample, respectively (see Figure 1A; Table 1).

Figure 1. Chromatograms of **(a)**, solvent extract from androconia of *Atlides polybe*, and **(b)**, methyl anthranilate standard sample, along with its mass spectrum and molecular structure. Numbered peaks: **1**, Heptanal; **2**, Octanal; **3**, Nonanal; **4**, 2-decanone; **5**, (*E*)-2-decenal; **6**, Methyl anthranilate; **7**, Hexadecanal. The purple-highlighted peaks indicate methyl anthranilate.



Discussion

The idiosyncratic "grape aroma" of the male *A. polybe* specimen was found to persist even after 120 hours of refrigeration prior to processing. Through our analysis we have identified the main compound responsible for this odor as methyl anthranilate, which corresponds to the dominant VOC peak in the androconial extract chromatogram (Figure 1). This nitrogen-containing benzoate ester is a natural compound and serves as the primary flavoring agent for artificial grape aromas in the flavor and fragrance industry (Furia & Bellanca, 1975). The biosynthesis of methyl anthranilate involves the condensation of anthranilic acid with methanol, catalyzed by a methyltransferase enzyme (Wang & Luca, 2005). Anthranilic acid, an intermediate in the tryptophan metabolic pathway, is produced through the decarboxylation of indole-3-acetic acid or tryptophan. In plants, methyl anthranilate is mostly found in flowers (Knudsen et al. 2006), where it serves as a deterrent to herbivores (Bernklau et al. 2016) and an attractant to pollinators (Murai et al. 2000), being reported as semiochemical in multitrophic plant-herbivore-predator interactions (Landolt et al. 2000). The fact that methyl anthranilate is also a powerful and widely used avian repellent (see references in Aronov & Clark, 1996) suggests multiple functions in the chemical signaling repertoire of papilionoids, which require further investigation.

Among other less representative compounds, the following linear-chained aldehydes: octanal, (*E*)-2 decenal, heptanal and nonanal also appeared in substantial amounts in our samples, together with hexadecanal. These compounds are extensively used as pheromones, allomones and kairomones among various insect taxa (see El-Sayed, 2024). In the likeness of methyl anthranilate, all abovementioned aldehydes have strong fruity odors (Kim et al. 2023) and seem to be complementary compounds in composing the characteristic fragrant blend of *A. polybe*.

Among insects, methyl anthranilate has been most notably documented as a constituent of the alarm pheromones of ants (Duffield & Wheeler, 1980; Oldham et al. 1994). Lavogez et al. (2017) identified methyl anthranilate along with other volatile aromatic benzenoids, in the hair pencil androconia of *Prophantis smaragdina* (Butler, 1875) (Lepidoptera: Crambidae) and speculated on its role in mating behavior. To our knowledge, this is the first report of methyl anthranilate in Papilionoidea. Similarly, (*E*)-2-decenal and octanal, though the latter was previously identified in the hairpencils of *Amauris* spp. (Nymphalidae: Danainae) (Schulz et al. 1993), but not documented in the wings of papilionoids until now. Likewise, hexadecanal has been sparsely reported in Papilionoidea, with previous mentions limited to the androconial blends of *Byciclus anyana* (Butler, 1879) (Nymphalidae: Satyrinae) (Nieberding et al. 2008) and *Phoebis argante* (Fabricius, 1775) (Pieridae: Coliadinae) (Nobre et al. 2021). Conversely, heptanal and nonanal appear to have been widely identified in Papilionoidea. Heptanal is present in the wings of both sexes of *Erynnis montanus* (Bremer, 1861) (Hesperiidae: Pyrginae) (Ômura & Honda, 2011) and, along with nonanal, as minor compounds in the wings several species of Papilionidae (Honda, 1980; Ômura et al. 2001; Ômura & Honda, 2005; Yoshimori et al. 2017). Nonanal has also been found in low relative concentration on the wings of *Anthocharis scolymus* (Butler, 1866) (Pieridae: Pierinae) (Okumura et al. 2016), as well as a constituent of the androconial secretions of many species of *Heliconius* (Nymphalidae: Heliconiinae) (Darragh et al. 2020), and of *Plebejus argyrognomon* (Virgstrassir, 1779) (Lycaenidae: Polyommatinae) (Lundgren & Bergström, 1975).

Although not the primary focus of our investigation, we speculate that the putative fixative properties of the lowly volatile fatty acyls found in the analyzed sample may explain why dry-mounted individuals of *A. polybe* retain their fragrance even after months of storage in collection drawers (Nobre & Schlindwein, 2016).

This study marks only the third investigation into the chemistry of androconial secretions in Lycaenidae and the first to address a species within the large, mainly Neotropical subfamily Theclinae. By focusing on one of the least studied Papilionoidea families in this regard, there are limited comparisons to be drawn regarding compound composition. Apart from nonanal, which is the only compound shared with *A. polybe*'s bouquet, hexadecyl acetate, δ-cadinol (Lundgren & Bergström, 1975), lavender lactone, and δ-decalactone (Ômura et al. 2013) are the only reported androconial compounds for lycaenids.

To date, the scent chemistry of *A. polybe* appears to be as divergent as the androconial morphology between the two subfamilies of Lycaenidae. The secreting structures of the referred polyommatines are "battledore" scales, scattered between ordinary scales throughout their wings (Lundgren & Bergström, 1975; Ômura et al. 2013), whereas in *A. polybe*, typical for theclines, the androconial scales are densely arranged in patches, pads, or pouches on the wings (Martins et al. 2019; Robbins et al. 2012). Nonetheless, the androconial blend of *A. polybe* appears unique compared to what is known among Papilionoidea, prompting speculation about the relationship between androconial form and secretion composition in the Theclinae, potentially related to divergent biosynthetic pathways adopted by the group. However, this is highly conjectural, and significant effort is required to draw any firm conclusions.

It would be desirable to investigate an array of phylogenetically related taxa to *A. polybe* to determine if the identified compounds (or classes of) are recurrent. The scent-producing/secreting organs of the Eumaeini are unique and diverse (Martins et al. 2019; Robbins, 1991), and it would be fascinating to ascertain if the androconial chemistry of its VOCs follows suit.

The dominant presence of methyl anthranilate, associated with complementary fragrant compounds in the androconia of *A. polybe*, aligns with empirical observations that fruity, strong odors are a distinct feature of males bearing androconial brands in Eumaeini (Müller, 1878; Robbins et al. 2012). Combined with the fact that wing androconia in the *Atlides* Section primarily function for intraspecific recognition (Martins et al. 2019), our findings provide strong evidence that methyl anthranilate and associated aldehydes outline a distinct chemical bouquet acting as a sex pheromone.

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Conflict of interests

The authors declare that there is no known financial interests or personal relationships that could have influenced the work presented in this article.

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