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Floral Structures and Volatile Metabolites of *Hoya mcgregorii* Schltr.: Revealing Structural Complexity and Metabolite Distribution

(Struktur Bunga dan Metabolit Meruap *Hoya mcgregorii* Schltr.: Mendedahkan Kerumitan Struktur dan Taburan Metabolit)

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ABSTRACT

Hoya R.Br. is a well-known ornamental genus valued for its distinctive floral morphology and the emission of a wide range of floral scents. However, the structural basis underlying scents production in *Hoya* flowers remain insufficiently explored. This study focuses on *Hoya mcgregorii* Schltr and aims to identify and characterise the types and spatial distribution of secretory structures and their associated metabolites through an integrative anatomical, histochemical and phytochemical approach. Using light microscopy, electron microscopy and histochemical staining, two distinct secretory structures were identified: secretory nectaries (*sn*) located on the corona lobes and unicellular conical shaped glandular trichomes (*cgt*) distributed along the adaxial epidermis of corolla. Histochemical stanning showed that the *sn* actively secreted lipids, proteins, starch grains and polysaccharides, while the *cgt* produced lipid and proteins. Further analysis of the floral scent composition using gas chromatography-mass spectrometry (GC-MS) identified 33 volatile organic compounds (VOCs), with β-ocimene constituting the dominant component (26.23%). These findings show the presence of morphologically and functionally distinct floral glands in *H. mcgregorii* and provide new insights into the structural and chemical adaptations involved in scent emission of genus *Hoya*.

Keywords: β-ocimene; *Hoya*; nectary; trichome

ABSTRAK

Hoya R.Br. merupakan salah satu tumbuhan hiasan terkenal kerana morfologi bunganya yang unik dan keupayaanya menghasilkan pelbagai bauan bunga. Walau bagaimanapun, struktur asas dan mekanisme biokimia yang terlibat dalam penghasilan bauan bunga *Hoya* masih kurang diterokai. Kajian ini memberikan tumpuan kepada *Hoya mcgregorii* Schltr. bertujuan untuk mengenal pasti dan mencirikan jenis serta taburan reruang struktur rembes dan metabolit berkaitannya melalui pendekatan translasi merangkumi anatomi, histokimia dan fitokimia. Dengan menggunakan mikroskop cahaya, mikroskop elektron dan pewarnaan histokimia, dua struktur rembes yang berbeza telah dikenal pasti: sekretori nektari (*sn*) yang terletak pada bahagian lobus korona dan trikom kelenjar berbentuk kon sel tunggal (*cgt*) yang dijumpai sepanjang permukaan adaksial epidermis korola. Analisis histokimia menunjukkan bahawa *sn* secara aktif merembeskan lipid, protein, butiran kanji dan polisakarida, manakala *cgt* menghasilkan lipid dan protein. Analisis lanjut terhadap komposisi bauan bunga menggunakan kromatografi gas-spektrometri jisim (GC-MS) mengenal pasti 33 sebatian organik meruap (VOCs) dengan kehadiran β-ocimena dominan (26.23%). Penemuan ini menunjukkan kehadiran struktur rembes yang berbeza dari segi morfologi dan fungsi pada *Hoya mcgregorii* dan memberi pandangan baharu tentang penyesuaian struktur dan kimia yang terlibat dalam pelepasan bauan bunga genus *Hoya*.

Kata kunci: β-ocimena; *Hoya*; nektar; trikom

INTRODUCTION

Hoya R.Br., belong to the Apocynaceae family, represents a rich lineage of tropical epiphytes renowned for their ornamental appeal, floral diversity and emission of distinctive fragrances (Rodda & Simonsson 2022). With over 500 species distributed across Southeast Asia and the Pacific Islands, *Hoya* has become a focal genus for botanists, ecologists and horticulturists alike (Jayagoudar et al. 2024). The flowers of *Hoya* species are distinguished by their unique structure, usually consisting of cluster of waxy, five-lobed corollas surrounding a central corona (Rodda, Juhonewe & Ercole 2013; Rodda et al. 2020). This unique structure in genus *Hoya* serves not only as a visual signature but also supports the plant's specialized pollination strategies and its capacity to attract a variety of pollinators, including month, bees and butterflies (Basir et al. 2024). In addition to their visual allure, *Hoya* flowers are renowned for emitting a diverse array of volatile organic compounds (VOCs), which not only contribute to their olfactory signature but also essential for facilitating ecological interactions and reproductive success (Basir et al. 2022b; Lo et al. 2024).

Floral scent is a key trait involved in plant-pollinator interactions and reproductive success. In many angiosperms, including *Hoya* species, the production and emission of VOCs are mediated by specialized secretory structures such as nectaries and glandular trichomes (Basir et al. 2024, 2022a). These structures have often intricately evolved and strategically positioned within floral organs to maximize pollinator specificity and effectiveness. In *Hoya*, previous studies have indicated the presence of secondary metabolites with aromatic properties, yet the anatomical basis and histochemical pathways that contribute to scents production and release are still poorly understood.

Hoya mcgregorii Schltr. was selected in this study due to its delicate morphology, unique floral structure and scent release. The ability of *H. mcgregorii* to emit complex floral scents suggests the presence of specialized anatomical adaptations. However, to date, there has been no comprehensive study that shows the localization, structure and chemical activity of its floral secretory structure. This represents a critical gap in our understanding of not only the floral biology of *H. mcgregorii* but also the broader evolutionary strategies of the *Hoya* genus.

To address this, the present study aims to conduct a comprehensive anatomical, micromorphological and histochemical analysis of the floral structure of *H. mcgregorii* using a multi-angled investigative approach. The research focuses on identifying and characterizing the types and spatial distribution of secretory structures and determining the chemical composition of floral volatiles associated with scent emission. Techniques employed include light microscopy and scanning electron microscopy for structural elucidation, histochemical staining to localize compound class (lipid, proteins, polysaccharides) and gas chromatography-mass spectrometry (GC-MS) for volatile profiling thereby linking structural specialization to chemical output and ecological function.

MATERIALS AND METHODS

PLANTS MATERIALS

Fresh floral specimens of *H. mcgregorii* were collected from Kedah. For structural and histological analyses, the flowers were fixed in a solution of glacial acetic acid and 70% ethanol (v/v) (1:3 ratio) (Noraini et al. 2025). For volatile compound analysis, the samples were collected in the morning (8-10 am); approximately 40 g of fresh flowers were placed into 20 mL headspace vials, which were sealed with parafilm to prevent air. The vials were immediately transferred into an icebox containing dry ice to maintain optimal temperature and humidity, thus preserving the freshness and chemical integrity of the floral samples. Upon arrival at the laboratory, all samples were stored at 80 °C until further analysis.

STRUCTURAL ANALYSIS

LIGHT MICROSCOPY (LM)

The anatomical features of secretory structures were examined using light microscopy. Floral tissues were hand-sectioned using a sliding microtome (Leica SM2000R) equipped with Leica 818 microtome blades. Sections of 25 μm thickness were stained with Safranin and Alcian Blue (Sigma-Aldrich) for 15-20 min to differentiate cell structures. Samples were dehydrated through an ethanol series from 50% (v/v) to 99% (v/v) and mounted in Euparal (Noraini et al. 2024). Observation was made using an Olympus BX43 light microscope fixed with Olympus DP72 and Canon EOS 700D cameras. Images were saved in TIFF format using Analysis Docu and EOS Utility 2 software (Basir et al. 2022a).

SCANNING ELECTRON MICROSCOPY (SEM)

Floral tissues were cut into 1 cm × 1 cm and rinsed three times in 0.1M phosphate buffer solution for 10 min to maintain physiological pH. Dehydration was carried out through a graded ethanol series (35% to 100%) (v/v) for 10 min per stage, repeated three times at 99% (v/v). The dehydrated samples were then dried using critical point drying with liquid CO_2 and spitter-coated with gold using an SC500 electroplating machine for 10 min. Secretory structures were examined using Philips XL30 and FESEM-Zeiss SUPRA 55VP scanning electron microscopes at magnifications ranging from 50x to 1500x. Images were saved in TIFF format for documentation and analysis (Basir et al. 2024).

HISTOCHEMICAL ANALYSIS

Histochemical staining was performed to identify the presence and localization of metabolite in the secretory cells. Sudan Black B (SBB) was used to detect lipids, Coomassie Blue (CB) for proteins, Lugol's iodine for starch and the Periodic Acid-Schiff (PAS) reaction for polysaccharides (Basir et al. 2024; Spence 2001). Each test was performed in triplicate to ensure reproducibility. Microscopic observations were conducted using a microscope (Olympus BX43) equipped with a camera (Olympus DP72 and Canon EOS 700D). Images were captured for all stained sections.

PHYTOCHEMICAL ANALYSIS

SOLID PHASE MICROEXTRACTION AND GAS CHROMATOGRAPHY-MASS SPECTROMETRY (SPME-GC-MS)

Volatile compounds were extracted using a solid phase microextraction (SPME) fiber coated with DVB/CAR/PDMS (80 μm, grey needle). The fiber was preconditioned at 250 °C for 30 min in the injections port of the GC-MS system. It was the inserted in the vial with the fiber exposed to the headspace for 30 min at 35 °C to adsorb volatile. Volatile compounds were examined via an Agilent 7890A gas chromatograph conjunction with a 5975C mass selective detector (MSD) and equipped with a DB-5MS UI capillary column (30 × 0.25 mm × 0.25 μm, 5% phenyl methyl polysiloxane w/v). The temperature was set to rise from 50 °C to 250 °C at a rate of 3 °C/min, followed by a final ramp to 150 °C at 5 °C/min. Peaks were identified with National Institute of Standards and Technology (NIST) mass spectral library (version 2.0). Compounds not originating from plants were excluded from the final analysis (Basir et al. 2022b).

RESULTS AND DISCUSSION

ANATOMICAL CHARACTERIZATION OF SECRETORY STRUCTURES AND HISTOCHEMICAL LOCALIZATION OF METABOLITES

Microscopic examination of *H. mcgregorii* flowers showed two distinct types of secretory structures: secondary nectaries (*sn*), localized at the inner regions of the corona lobes (Figure 1(A) &1(B)), and unicellular conical-shaped glandular trichomes (*cgt*), prominently along the adaxial epidermis of the corolla (Figure 1(C) & 1(D)). The *cgt* is a single structure with non-uniform size (mean width 15 μm, height 35 μm). Meanwhile, SEM showed the *cgt* exhibited a smooth outer surface and lacked echinate exine ornamentation (Figure 1(G) - 1(H)). Additionally, multicellular simple trichomes (*mst*) were identified beneath the outer region of the ovary (Figure 1(E)). The *mst* appeared as single structures composed of five distinct cells, positioned within the epidermal layer with varied size (mean width 5 μm, height 78 μm).

Recent anatomical investigation on related species, such as *Hoya pentaphlebia*, *Hoya cagayanensis, Hoya lacunosa,* and *Hoya coriaceae* have begun to shed light on diversity and function of floral secretory structure (Basir et al. 2024, 2022a). In these species, two primary secretory structures were identified: secondary nectaries located on the corona lobes and various glandular trichomes; conical shaped trichomes in *H. caganensis* and *H. pentaphlebia*, cylindrical trichomes (*H. lacunosa*) and falcate trichomes (*H. coriacea*), which distributed along the adaxial epidermis of the corolla. The findings of this study also indicate that diverse trichome morphologies can be used for species classification and possess distinct functions.

Histochemical staining showed distinct localization patterns of primary metabolites within the secretory glands. The secondary nectaries and conical shaped trichomes were found to secrete a various of metabolites, with the *sn* showed active staining for lipids, proteins, starch grains and polysaccharides (Figure 2(A)-2(D)), and the *cgt* exhibited staining primarily for lipids and proteins (Figure 2(E) & 2(F)) (Table 1). Previous studies on histochemical shown in other *Hoya* species, such as *H. pentaphlebia*, *H. lacunosa*, *H. cagayanensis,* and *H. coriacea*, also showed the presence of various of metabolites, including proteins, lipids, polysaccharides and starch grains in *sn* and *ctg* (Basir et al. 2024, 2022b). Light microscopy (LM) and scanning electron microscopy (SEM) demonstrated the structural integrity and specialized morphology of these glands, with the *sn* exhibiting a centralized basal opening suggesting active secretion, while the *cgt* displayed a pointed apex that may indicate a direct volatilization pathway.

The primary metabolites in the secretory glands of *H. mcgregorii* act as important carbon and energy sources for the biosynthesis of secondary metabolites, including some volatile organic compounds (VOCs) that provide floral odors. In addition to their metabolic function, carbohydrate and mineral salts function as osmolytes in glandular tissue, producing the turgor pressure required for the mechanical release of floral secretions (Borghi & Fernie 2017). These metabolites, mainly sugars and amino acids, are excreted as direct nutritional rewards that provide metabolic energy to visiting insects, thereby facilitating efficient pollination (Borghi & Fernie 2017). Comparative studies show that although *H. mcgregorii* uses these metabolites to generate its unique odor profile, variations in the abundance of certain primary precursors compared to species such as *H. lacunosa* and *H. coriacea* result in distinct olfactory signatures and diverse ecological interactions (Basir et al. 2022b).

The *sn* located at the corona, functions as the primary site for nectar production and resource presentation. This central positioning is characteristics of a reward-based hub, where nectar composition including sugars and biogenic amines serves to sustain and behaviorally modulate pollinators during contact with reproductive organs (Barberis et al. 2023; Nepi & Stpiczyńska 2008). In contrast, the diffuse distribution of *cgt* across the corolla acts as a signals-dispersion networks. These capitate glandular trichomes are specialized for the biosynthesis and emission of VOCs, facilitating long-distance chemical signaling rather than direct nutritional reward (Ghissing & Mitra 2022; Thosteman 2024). This structural compartmentalization aligns with established models of floral signaling recruitment while localized nectaries finalize the mutualistic interaction.

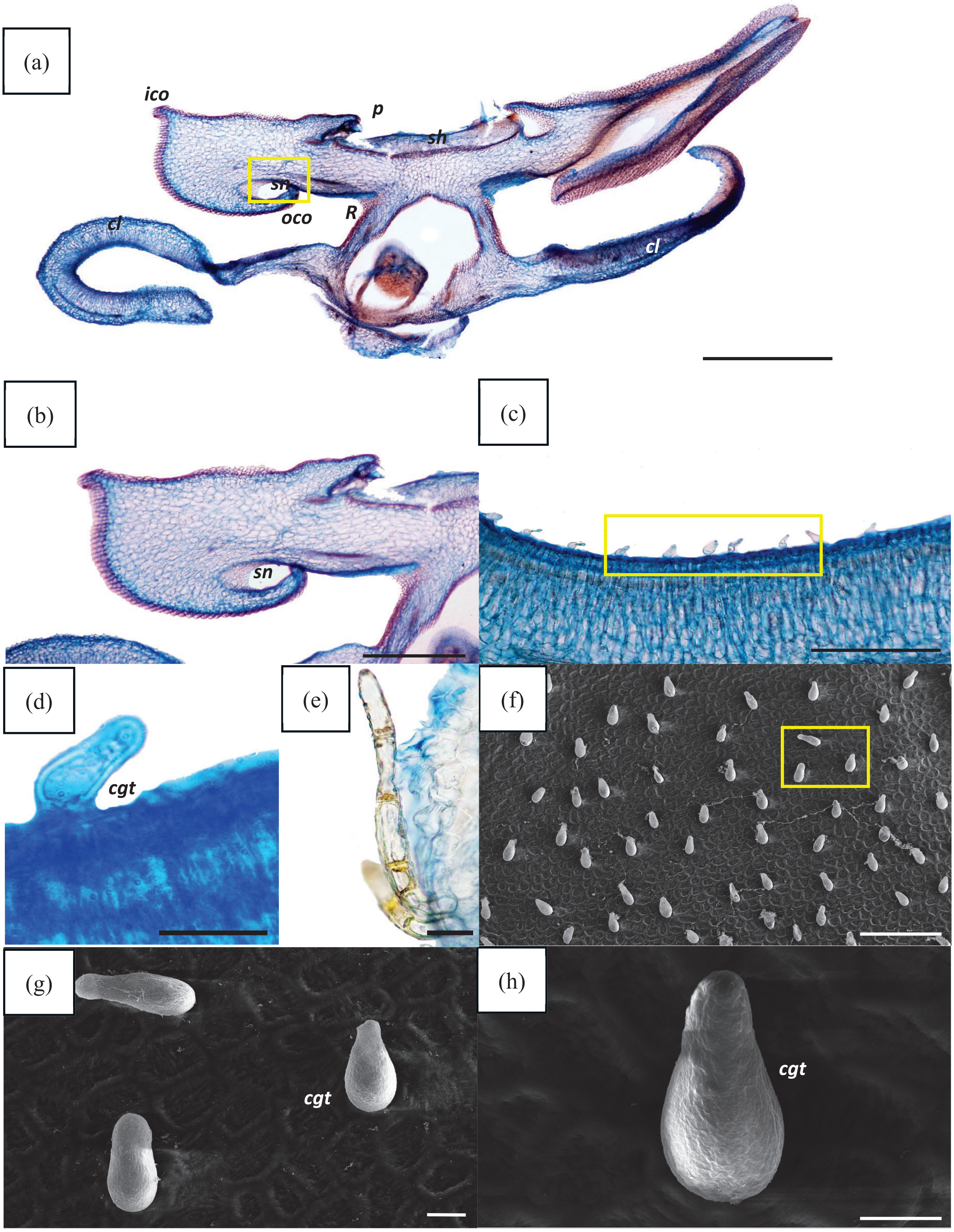

FIGURE 1. Anatomical and micromorphological structure of *H. mcgregorii.* (a-e) Anatomy features under light microscope (LM); (a) The overview cross-section of the flower. (b) Secondary nectaries (*sn*) were observed in the corona lobe (*co*); (c) Cross-sections of corolla petals (*cl*) showed the presence of unicellular conical-shaped glandular trichomes (*cgt*) (yellow square); (d) enlargement of *cgt* in (c); (e) the presence of multicellular simple trichome. (f-h) SEM features of the corolla petals (*cl*);. (g & h) enlargement of (f) (yellow square), showed the presence of numerous *cgt*. *cl* =corolla petals; *co* =corona; *ico* =inner corona; *oco* =outer corona; *sn* =secondary nectaries; *p* =pollinia; *R* =nectar pool; Scale: (a) = 1000 µm; (b) = 500 µm; (c & f) = 100 µm; (e) = 50 µm; (d) = 20 µm; (g & h) = 10 µm

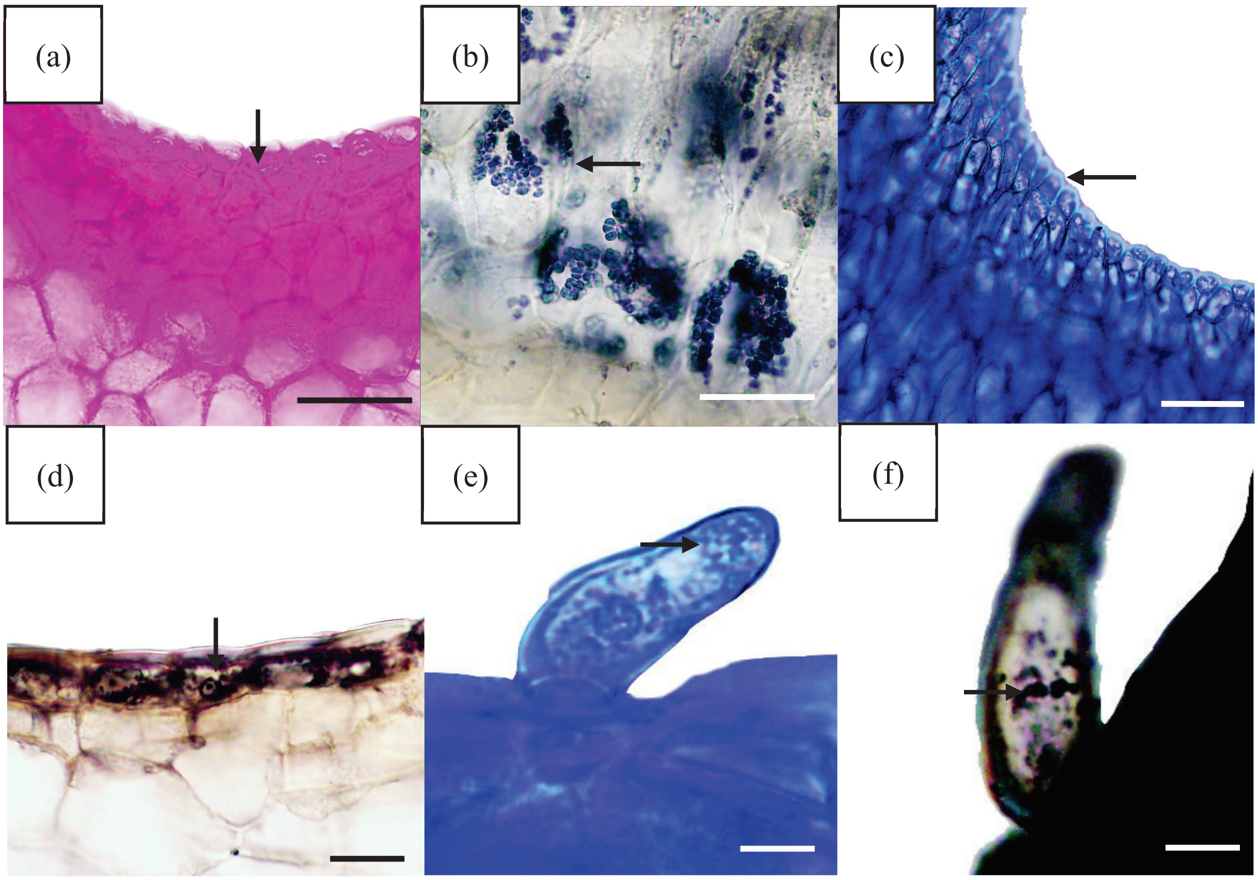

FIGURE 2. Histochemical stanning for nectaries and glandular trichomes of *H. mcgregorii*, with (a-d) Secondary nectaries (*sn*), while (e & f) Unicellular conical glandular trichomes (*cgt*). (a) Polysaccharides in *sn* exhibited a pink hue following PAS reagent stanning, (b) Starch grains were detected in *sn* using IKI reagent; (c & e) *sn* and *cgt* had a blue stanning with protein using CB; (d & f) Lipid droplets were observed in *sn* and *cgt* subsequent to SBB stanning. Scale: (c) = 100µm; (a &b) = 50 µm; (d,e,f) = 20 µm. PAS= periodic acid-Schiff reagent; IKI= Lugol's reagent; CB = Commassie blue; SBB= Sudan black B

TABLE 1. Histochemical analysis of secondary nectaries (*sn*) and unicellular conical shaped trichomes (*cgt)* in flower of *H. mcgregorii*

Stanning	Targeted compounds	Observation	*sn*	*cgt*
PAS reagent	Polysaccharides	Pink/ magenta	+	-
Lugol's solution	Starch grain	Blue to black	+	-
Coomassie Blue	Protein	Blue	+	+
Sudan black	Lipid	Dark blue to black	+	+

The functional specialisation of floral features in *H. mcgregorii* certainly indicates a concerted evolutionary strategy for attracting and sustaining pollinators. The disparity between incentive (nectaries) and attractants (trichomes) is well documented characteristic of the Marsdenieae tribe, where diverse metabolic outputs are allocated to enhance reproductive efficiency, despite the lack of direct field observations.

PHYTOCHEMICAL PROFILING OF FLORAL VOLATILES

A total of 33 distinct VOCs with varying percentages were emitted by *H. mcgregorii* flowers. Analysis of the floral volatile profile showed the presence of four major classes of chemical compounds: terpenoids, alcohols, benzenoids and aldehydes (Table 2). While most of these compounds were detected in relatively low concentrations, only one compound exhibited a relatively abundance

TABLE 2. Identification of volatile organic compounds in *H. mcgregorii* flowers based on their relative percentages

Formula	CAS. No	Compound	Relative percentage (%)
$C_6H_{12}O$	000066-25-1	Hexanal	0.35
$C_{10}H_{16}$	028634-89-1	β-Thujene	0.83
$C_{10}H_{16}$	007785-70-8	(R)-α-Pinene	0.59
$C_{10}H_{14}$	000104-51-8	n-Butylbenzene	0.47
$C_{10}H_{16}$	003387-41-5	β-Sabinene	5.59
$C_{10}H_{16}$	028634-89-1	β-Thujene	8.57
$C_8H_{24}O_4Si_4$	000556-67-2	Octamethylcyclotetrasiloxane	0.58
$C_8H_{16}O$	003391-86-4	1-Octen-3-ol	3.78
$C_{10}H_{16}$	000127-91-3	β-Pinene	2.33
$C_{10}H_{16}$	000099-84-3	β-Terpinen	1.88
$C_{10}H_{16}$	002867-05-2	α-Thujene	0.53
$C_{10}H_{14}$	000535-77-3	m-Cymene	0.52
$C_{10}H_{16}$	005989-27-5	D-Limonene	1.66
$C_{10}H_{16}$	003779-61-1	trans-β-Ocimene	0.61
$C_{10}H_{16}$	013877-91-3	β-Ocimene	26.23
$C_{10}H_{16}$	000099-85-4	γ-Terpinene	0.73
$C_{10}H_{18}O$	000078-70-6	Linalool	2.53
$C_5H_{10}Br_2$	000111-24-0	Pentamethylene bromide	0.60
$C_{10}H_{30}O_5Si_5$	000541-02-6	Decamethylcyclopentasiloxane	2.84
$C_{10}H_{16}$	007216-56-0	allo-Ocimene	0.47
$C_{10}H_{16}O$	000547-61-5	L-Pinocarveol	1.37
$C_{10}H_{16}O$	000473-67-6	Verbenol	0.88
$C_{10}H_{18}O$	000507-70-0	Borneol	0.85
$C_8H_8O_3$	000119-36-8	Methyl salicylate	6.20
C_9H_{12}	003105-29-1	Triasterane	1.54
$C_{10}H_{16}O$	000515-00-4	Myrtenol	1.44
$C_{10}H_{14}O$	001196-01-6	Levoverbenone	7.99
$C_{10}H_{16}O$	005392-40-5	Citral	0.42
$C_{12}H_{36}O_6Si_6$	000540-97-6	Dodecamethylcyclohexasiloxane	0.83
$C_{15}H_{24}$	018794-84-8	(E)-β-Farnesene	8.69
$C_{15}H_{24}$	000502-61-4	α-Farnesene	0.30
$C_{20}H_{34}O$	001113-21-9	Geranyl linallol	0.50
$C_{15}H_{26}O$	000142-50-7	Nerolidol	6.48

exceeding 10%, which is β-ocimene (26.23%) (Table 2), a monoterpenoid known for its role in attracting specific pollinators such as bees and butterflies (Granero et al. 2005; Pecetti et al. 2002). The terpenoid group was the most prominent of the total VOCs composition.

A comprehensive analysis of VOCs composition in *H. incrassate*, *H. heuschkeliana,* and *H. cagayanensis* showed that these species also emitted high concentration of ocimene metabolites, with (Z)-ocimene (26.4%) in *H. incrassate,* (E)-ocimene (37.5%) in *H. heuschkeliana* and β-ocimene (25.78%) in *H. cagayanensis*. Morphologically, all these species exhibit relatively less vibrant floral coloration, a trait they share with *H. mcgregorii.* Based on the high emission of β-ocimene, a monoterpene found to dominate the scent profile of *H. cagayanensis* (Basir et al. 2022b), we infer that this compound may serve as a compensatory olfactory signal. In related taxa, such as *H. pottsii*, nocturnal scent emission is known to facilitate pollination by erebid months (*Hypopyra vespertilio*) (Landrein, Zhou & Song 2021). Furthermore, β-ocimene is established as a key generalist attractant for both hymenopterans and lepidopterans (Farré-Armengol et al. 2017). While behavioral trials for *H. mcgregorii* are currently lacking, its chemical profile suggests a similar reliance on scents-mediated attraction to overcome visual inconspicuousness, potentially targeting crepuscular or nocturnal generalist pollinators (Jürgens et al. 2004).

According to the comprehensive review by Kundan et al. (2026), trans-ocimene is present in the floral scent profiles of 71% of 90 plants families. Similarly study by Farré-Armengol et al. (2017) reported the presence of this compound counted 75% of 63 plant families examined, underscoring its widespread occurrence and potential functional role in angiosperms. Beyond its abundance, β-ocimene has been implicated in ecological interactions, particularly as a semi-chemical involved in pollinator attraction (Dötterl & Vereecken 2010; Farré-Armengol et al. 2017; Gurr et al. 2023). Several studies have demonstrated its role as a volatile cue or pheromone that appeals to a variety of pollinators, including moths, bees and butterflies (Granero et al. 2005; Pecetti et al. 2002; Zviely & Li 2013).

The dominance of β-ocimene likely reflects a generalized strategy for pollinator attraction, which may benefit *H. mcgregorii* in forest habitats where pollinator populations may be less diverse or seasonally variable (Thosteman 2024). While the VOC profiles of sympatric species were not assessed due to the focus on the baseline chemical characterisation of *H. mcgregorii*, the presence of diverse terpenoids and aromatic aldehydes is also consistent with established frameworks in floral chemical ecology. These studies demonstrate that floral scents often serve a dual function, acting as attractive signals for mutualistic pollinators while simultaneously serving as defensive barriers to repel florivores or inhibit the growth of microbial pathogens (Junker & Blüthgen 2010). Specifically, β-ocimene is recognized as a ubiquitous generalist attractant that also plays a documented role in priming plant defences (Farré-Armengol et al. 2017; Pandey et al. 2023).

The findings highlight a complex interplay between floral structure and secondary metabolites production in *H. mcgregorii*, suggesting a high degree of evolutionary refinement. The anatomical differentiation between *sn* and *cgt*, coupled with the specialized chemical scent release in each, underscores the plant's adaptation to its ecological niche. From an evolutionary perspective, the integration of scent emission and visual floral traits in *H. mcgregorii* likely reflects selective pressure favoring reproductive efficiency through optimized pollinator interactions. The localization of VOCs in epidermal structures such as *cgt* is consistent with trends seen in other species and highly specialized angiosperm, indicating convergent evolution in floral chemical ecology.

By integrating anatomical, histochemical, and phytochemical analysis, this study provides a holistic view of the mechanism driving scent production in *H. mcgregorii*. The results have broader implications for the study of plant secondary metabolism, floral evolution, ecological, and interaction. Moreover, the findings contribute to broader understanding of the structural-functional evolution of secretory systems in the Apocynaceae family. Future research should seek to broaden these findings to encompass other *Hoya* species, exploring the evolutionary pathway of pathways of secretory structure and scent composition within the genus.

CONCLUSION

This study presents an integrative anatomical, histochemical and phytochemical investigation into the floral secretory system of *H. mcgregorii.* By characterizing the types, distribution and biochemical activity of its secretory glands, the research provides new insights into the structural complexity and adaptive function of floral organs. The dual presence of secondary nectaries and glandular trichomes was discovered for the first time in *H. mcgregorii* and each of which exhibits locality differences and may have functional differentiation. Furthermore, the identification of a diverse array of floral VOCs, particularly the dominance of β-ocimene, suggests an evolving strategy to attract specific pollinators. In conclusion, this research advances our understanding of the interplay between floral form and chemical function and reinforces the value of integrative botanical studies in uncovering the fundamental principles underlying plant-environment interactions.

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REFERENCES

Kundan et al. 2026.

Barberis, M., Calabrese, D., Galloni, M. & Nepi, M. 2023. Secondary metabolites in nectar-mediated plant-pollinator relationships. *Plants* 12(3): 550.

Basir, S., Talip, N., Bunawan, H. & Rahman, R.A. 2024. Anatomical and histochemical analysis of *Hoya pentaphlebia* Merr. flower: Insights into structure and chemical composition. *Malaysian Applied Biology* 53(6): 105-114.

Basir, S., Saad, M.F.M., Rahman, M.R.A., Talip, N., Baharum, S.N. & Bunawan, H. 2022a. Floral nectary and trichome structure of *Hoya cagayanensis*, *Hoya lacunosa*, and *Hoya coriacea* (Apocynaceae, Marsdenieae). *Horticulturae* 8(5): 420.

Basir, S., Akbar, M.A., Talip, N., Baharum, S.N. & Bunawan, H. 2022b. An integrative volatile terpenoid profiling and transcriptomics analysis in *Hoya cagayanensis, Hoya lacunosa* and *Hoya coriacea* (Apocynaceae, Marsdenieae). *Horticulturae* 8(3): 224.

Borghi, M. & Fernie, A.R. 2017. Floral metabolism of sugars and amino acids: Implications for pollinators' preferences and seed and fruit set. *Plant Physiology* 175(4): 1510-1524.

Dötterl, S. & Vereecken, N.J. 2010. The chemical ecology and evolution of bee–flower interactions: A review and perspectives. *Canadian Journal of Zoology* 88(7): 668-697.

Farré-Armengol, G., Filella, I., Llusià, J. & Peñuelas, J. 2017. β-Ocimene, a key floral and foliar volatile involved in multiple interactions between plants and other organisms. *Molecules* 22(7): 1148.

Ghissing, U. & Mitra, A. 2022. Biology of floral scent volatiles in ornamental plants. In *Floriculture and Ornamental Plants. Handbooks of Crop Diversity: Conservation and Use of Plant Genetic Resources*, edited by Datta, S.K. & Gupta, Y.C. Singapore: Springer. pp. 777-817.

Granero, A.M., Sanz, J.M.G., Gonzalez, F.J.E., Vidal, J.L.M., Dornhaus, A., Ghani, J. & Chittka, L. 2005. Chemical compounds of the foraging recruitment pheromone in bumblebees. *Naturwissenschaften* 92: 371-374.

Gurr, G.M., Liu, J., Pickett, J.A. & Stevenson, P.C. 2023. Review of the chemical ecology of homoterpenes in arthropod–plant interactions. *Austral Entomology* 62(1): 3-14.

Jayagoudar, S., Bhat, P., Hegde, S., Ghane, S.G. & Hegde, H.V. 2024. A systematic review of phytoconstituents and tissue culture studies of the genus *Hoya* R.Br. *Micropropagation of Medicinal Plants* 2(1): 275-281.

Jürgens, A., Dötterl, S., Liede-Schumann, S. & Meve, U. 2010. Floral scent composition in early diverging taxa of Asclepiadoideae, and Secamonoideae (Apocynaceae). *South African Journal of Botany* 76(4): 749-761.

Junker, R.R. & Blüthgen, N. 2010. Floral scents repel facultative flower visitors, but attract obligate ones. *Annals of Botany* 105(5): 777-782.

Landrein, S., Zhou, Z.Y. & Song, S.J. 2021. Pollinators of *Hoya pottsii*: Are the strongest the most effective? *Flora* 274: 151734.

Lo, M.M., Benfodda, Z., Molinié, R. & Meffre, P. 2024. Volatile organic compounds emitted by flowers: Ecological roles, production by plants, extraction, and identification. *Plants* 13(3): 417.

Nepi, M. & Stpiczyńska, M. 2008. The complexity of nectar: Secretion and resorption dynamically regulate nectar features. *Naturwissenschaften* 95: 177-184.

Noraini Talip, Syazwani Basir, Che Nurul Aini Che Amri, Mohd. Norfaizal Ghazalli, Ahmad Fitri Zohari, Muhammad Amirul Aiman Ahmad Juhari, Mohamad Ruzi Abdul Rahman & Hamidun Bunawan. 2025. Taxonomic significant of leaf anatomical characteristics of selected *Globba* L. (Zingiberaceae) species in Peninsular Malaysia. *Tropical Life Sciences Research* 36(2): 59-82.

Noraini Talip, Raj Kumar, Hamidun Bunawan, Mohamad Ruzi Abdul Rahman, Nordahlia Abdullah Siam & Syazwani Basir. 2024. Kesan jangkitan virus Sauropus yellowing (SaYV) kepada anatomi daun *Sauropus androgynus* (L.) Merr. *Sains Malaysiana* 53(9): 2045-2055.

Pandey, P., Tripathi, A., Dwivedi, S., Lal, K. & Jhang, T. 2023. Deciphering the mechanisms, hormonal signaling, and potential applications of endophytic microbes to mediate stress tolerance in medicinal plants. *Frontiers in Plant Science* 14: 1250020.

Pecetti, L., Tava, A., Felicioli, A., Pinzauti, M. & Piano, E. 2002. Effect of three volatile compounds from lucerne flowers on their attractiveness towards pollinators. *Bulletin of Insectology* 55: 21-28.

Rodda, M. & Simonsson, N. 2022. Contribution to a revision of Hoya (Apocynaceae: Asclepiadoideae) of Papuasia. Part II: eight new species, one new subspecies. *Blumea-Biodiversity, Evolution and Biogeography of Plants* 67(2): 139-155.

Rodda, M., Juhonewe, N.S. & Ercole, E. 2013. *Hoya corymbosa* (Apocynaceae, Asclepiadoideae), a new unusual species from Sabah, Borneo, and its systematic position based on phylogenetic analysis. *Systematic Botany* 38(4): 1125-1131.

Rodda, M., Simonsson, N., Ercole, E., Khew, G., Niissalo, M., Rahayu, S. & Livshultz, T. 2020. Phylogenetic studies in the *Hoya* group (Apocynaceae, Marsdenieae): The position of *Anatropanthus* and *Oreosparte*. *Willdenowia* 50(1): 119-138.

Spence, J. 2001. Plant histology. In *Plant Cell Biology*, edited by Hawes, C. & Satiat-Jeunemaitre, B. Oxford: Oxford University Press. pp. 189-206.

Thosteman, H. 2024. Floral scent in a generalized pollination system: Ecological dynamics and evolutionary implications. Doctoral Thesis. Scania: Lund University (Unpublished).

Zviely, M. & Li, M. 2013. Ocimene a versatile floral ingredient. *Perfumer & Flavorist* 38(1): 42-45.

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