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Research Article

Floral Trichomes Micromorphology of Selected *Hoya* R.Br. Species (Apocynaceae) in Peninsular Malaysia

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ABSTRACT

Trichomes, which are specialised structures found in the epidermis, are essential for the protection of plants and the secretion of secondary metabolites. This study examines the structures and density of trichomes on the flowers of five selected *Hoya* species: *Hoya callistophylla* T.Green., *Hoya caudata* Hook.f., *Hoya elmeri* Merr., *Hoya maingayi* Hook.f. and *Hoya parviflora* Wight. Through the application of light microscopy (LM) and scanning electron microscopy (SEM), we identified the types, morphology and localisation of trichomes in relation to floral glands. The findings indicated the existence of glandular trichomes, simple trichomes and papillae exhibiting various shapes, including conical, filamentous, finger-like, falcate and stalked capitate apical prostrusion located on the adaxial epidermis of corolla petals and pedicels. This investigation deepens the comprehension of *Hoya's* floral structure and adds to the taxonomic and ecological insights regarding the genus in Peninsular Malaysia.

Key words: *Hoya*, micromorphology, trichomes

INTRODUCTION

Hoya R.Br. is gaining popularity globally as a decorative plant due to its unique and attractive flowers, along with its ability to emit a pleasant aroma (Lamb & Rodda, 2016; Kuang *et al*., 2025). *Hoya* is characterised as an epiphytic liana plant, possessing succulent-type leaves (Rahayu *et al*., 2018). The flowers exhibit a fascinating morphology resembling a star shape, showcasing a range of colour variations including white, yellow, orange, pink, green and blackish purple (Rahayu, 2011; Kuang *et al*., 2025). *Hoya,* often referred to as a wax flower due to the waxy texture of its flowers and leaves, also exudes a white, rubbery substance when cut (Lakshmi *et al*., 2010; Rahayu, 2011; Basir *et al*., 2022).

Hoya has been observed to release a distinctive and diverse scent that serves as a means of communication with insects and other plants, while also adapting in response to pathogens (Das *et al*., 2013). The fragrance of flowers serves as a crucial indicator for attracting pollinators, facilitating the process of pollination (Wiemer *et al*., 2009). The emergence of this aroma is a consequence of the production of metabolites in plant tissue and cells (Ramya *et al*., 2013). In plants, specific structures that contribute to the production of aromatic substance particularly in the floral regions, are secretory cells. One of the key floral microstructures contributing to this is the trichome.

Trichomes represent one of the secretory cells that outgrowths from epidermal cells and are characterised by a wide range of morphology, size and structure with varying functions that depend on their specific location within the plants (Demarco, 2017a). Trichomes are extensively present on the surfaces of various organs and tissues across different plant species, displaying diverse morphological characteristics and exhibiting various shapes, including head, stalk, hood and scale (Wang *et al*., 2021).

Trichomes can be classified into two categories: glandular and simple trichomes (non-glandular). The identification of the trichome type is based on its morphology and its ability to store or release metabolite which enhance the plant's functionality in relation to its environment (Kolb & Müller, 2004; Demarco, 2017a, Noraini *et al*., 2019). Previous studies on *Hoya* have shown the presence of protein and lipids in trichomes of *H. cagayanensis*, *H. lacunosa*, *H. coriacea* and *H. pentabhlebia,* suggesting their role as support structures in reward release or interactions with pollinators (Basir *et al*., 2022; 2024). This study focuses on five selected *Hoya* species from Peninsular Malaysia, aiming to investigate and characterise the micromorphology of floral trichomes in selected *Hoya* species using scanning electron microscopy (SEM) and light microscopy (LM), and to assess the taxonomic implications of these characters.

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MATERIALS AND METHODS

Materials

An anatomical and micromorphological study of flower structure was conducted on five species of *Hoya* flowers, namely *H. callistophylla* T. Green., *H. caudata* Hook.f., *H. elmeri* Merr., *H. maingayi* Hook.f. and *H. parviflora* Wight. The specimens used in this study are fresh specimens taken from several localities in Malaysia (Perlis, Kedah & Melaka). Fresh and blooming flower specimens of each species were fixed in a mixed solution of concentrated Acetic acid and 70% ethanol in a ratio of 1:3 (AA) for 72 hr for use in these studies (Basir *et al*., 2024).

Methods

Micromorphological studies were conducted using a scanning electron microscope, following the methodologies established by Wiemer *et al*. (2009) and Kowalkowska *et al*. (2015), to examine the micromorphological characteristics of the trichome type on both the abaxial and adaxial surfaces of each flower part. Flower samples that were preserved in AA fixation solution were rinsed with phosphate buffer solution (PBS) at a concentration of 0.1 M, pH 7.4, three times (10 min each) to ensure pH stability of the biological sample. The dehydration process involved a sequential immersion in ethanol concentrations (30%, 50%, 70%, 80%, 90% & 99%) with each stage for 10 min. The procedure was conducted three times using a 99% ethanol concentration. Flower samples were subjected to drying using the critical point drying (CPD) (Leica ® EM CPD 300) for a duration of one hr. Next, affix the flower sample to a stub with a diameter of 20 mm utilising a double-sided tape. The surface of the flower sample underwent platinum plating utilising a plating machine (GVC-1000 Ion Sputter Coater) for a duration of 10 min. The micromorphological characteristics of flowers were examined using FESEM-Thermoscientific Quattro S, with magnifications ranging from 50 to 1500 times. The acquired image is subsequently saved in tagged image file format.

For the anatomy study using a light microscope following method was used, Anton *et al*. (2012), with modifications according to the suitability of the flower texture. Five flower samples from each species were collected during field work. A cross-section of the entire flower sample was obtained using a sliding microtome (Leica SM 2000R) through the application of the cross-section method. The subsequent phase involves the clarification process aimed at eliminating the sample's colour to enhance the colour absorption procedure. The sample was subjected to immersion in a 25% bleaching agent (Clorox) for 3 min. Next, the cells present in the slices were stained using Safranin (Sigma-Aldrich) and Alcian Blue (Sigma-Aldrich) dyes. The removal of water from the sample slices is achieved via dehydration through a sequence of ethanol immersions at concentrations of 50%, 70%, 90% and 99% (5 min each). Excess dye on the sample slices was removed by dripping concentrated hydrochloric acid (HCl) in 70% ethanol, followed by continued immersion of the sample slices in 90% and 99% ethanol. A fixed slide was prepared with the use of Euparal mount. The anatomical and trichomes were observed on the slice samples using a light microscope (Olympus BX43) linked to a camera (NVScope TC-HDMI-4K) with the aid of ToupView software. Images were captured at magnifications of 4x - 40x and stored in tagged image file format (TIFF). An anatomical feature comparison was conducted among replications of sample slices to examine the characteristics of trichomes found in each part of the study flower.

RESULTS

In this study, glandular trichomes were found at the adaxial epidermis of the corolla surface for all species. Conical-shape glandular trichomes (*cgt*), which are unicellular and have smooth surfaces, have average widths and heights of 10.5 µm and 18.5 µm, respectively, but are not dense in *H. callistophylla* (Figure 1d-f). Filament-shaped glandular trichomes (*fmtg*), which have unicellular, echinate ornamentation and various widths and heights (average 28.04 µm, 51.35 µm), are not dense in *H. caudata* (Figure 2d-f). Finger-like glandular trichomes (*flgt*) are unicellular, possess a smooth surface, have an average width of 12.73 µm and an average height of 67.5 µm and are densely present in *H. elmeri* (Figure 3d-f). Falcate-shaped glandular trichomes (*fgt*) were found in *H. maingayi* with unicellular, smooth surfaces, densely present with various widths and heights (84.04 µm, 214.36 µm) (Figures 4c, e & f). Meanwhile, stalked capitate glandular trichomes (*scgt*) with apical protrusion, multicellular and smooth surface, are densely present with an average size of width and height (22.4 µm, 97.52 µm) in *H. parviflora* (Figure 5d-f) (Table 1).

Unicellular simple trichomes with echinate ornamentation were discovered in the epidermis of the pedicel of *H. callistophylla* with an average size (width 21.83 µm, height 244.1 µm) and not dense (Figure 1g & i). Meanwhile, in *H. caudata,* unicellular simple trichomes were found in the epidermis of the pedicel (with echinate ornamentation, not dense with width and height (8.47µm, 98.9 µm) (Figures 2e & h) and on the edge of the corolla (smooth surface, densely present, with various average widths 27.40 µm and 192.34 heights µm) (Figures 2e & g). The presence of papillae was only observed in *H. callistophylla* on the adaxial part of the corolla and epidermis of the pedicel (Figures 1 h, g & j) (Table 1).

DISCUSSION

This study demonstrates the variability of trichome and density in five *Hoya* species studied. Glandular trichome exhibiting various shapes, including conical, filamentous, finger-like, falcate and stalked capitate apical protrusions located on the adaxial epidermis of corolla petals. Simple trichomes and papillae were found at the pedicels and on the edge of the corolla. In the corolla, glandular trichomes are more common and denser than trichomes in the pedicel area. This study indicates that the corolla has denser glandular and simple trichomes than the pedicel of *H. caudata*, which only has simple trichomes. Wang *et al*. (2021) and McDowell *et al*. (2011) demonstrate that trichome density varies across different organs; notably, the density on the leaf blade is considerably greater than that on the abaxial surface of the blade. Moreover, the densely trichome characteristics are consistently linked to protective mechanisms and adaptations to elevated light intensity (Ridzuan & Kalu, 2023; Ichie *et al*., 2016). According to Seyedi and Salmaki (2015), this characteristic is considered a valuable indicator for distinguishing between the genus.

Previous studies have shown that the identification of conical, cylindrical and falcate glandular trichomes in *Hoya* species has been documented for the first time (Basir *et al*., 2022). In this study, we have discovered a novel form of glandular trichome in *Hoya* species, characterised as filamentous, finger-like and stalked capitate with an apical protrusion. This finding adds valuable

information to the understanding of the *Hoya* genus and the Apocynaceae family. The anatomical study of glandular trichomes was first reported in the Asclepiadoidae family, especially within the genus *Matelea*, focusing on the species *Matelea denticulata* in 1969 (Stevens, 1988; Demarco, 2017b). The study identified multicellular glandular trichomes exhibiting characteristics similar to stinging-type trichomes on the pedicel and abaxial surface of the sepals in the flower (Stevens, 1988; Demarco, 2017b). Additionally, El-Taher *et al*. (2020) examined species within the Apocynaceae family, revealing 15 distinct types of trichome variations that are used in species classification.

Glandular trichomes in flowering plants are specialised epidermal outgrowths that serve as natural cell factories, synthesising, storing and secreting substantial amounts of speciality secondary metabolites, including terpenoids, flavonoids, acyl sugars and phenylpropanoids. Metabolites are essential in plants' defence, deterring herbivores and inhibiting pathogens, thereby enhancing resistance to various pests, including arthropods. This concept is exemplified in wild tomato species, where specific types of glandular trichomes effectively serve as protection against natural pesticides (Glas *et al*., 2012; Schuurink & Tissier, 2020). The secretion may exhibit volatility, stickiness or toxicity, thereby establishing both chemical and physical defences against herbivory. In addition to their defensive role, glandular trichomes protect against abiotic stresses, including UV-B radiation and drought, by synthesising compounds that absorb harmful radiation and mitigate water loss (Huchelmann *et al*., 2017). Glandular trichomes attract pollinators through the secretion of aromatic substances and nectar, facilitating reproduction. Histochemical studies indicate that glandular trichomes contain protein and lipids, suggesting their role as support structures in reward release or interactions with pollinators (Kuang *et al*., 2025). In certain medicinal plants, such as *Artemisia annua*, glandular trichomes serve as the location for the biosynthesis and accumulation of significant pharmacologically active compounds, including artemisinin. In this study, all glandular trichomes were found at the corolla region, specifically in proximity to the nectar pool, which serves as the reward area. The existence of glandular trichomes, potentially housing metabolite could be significant in directing insects towards the reward area, thereby facilitating the pollination process (Basir *et al*., 2024).

In contrast, simple (non-glandular) trichomes were found at the epidermis of the pedicel of *H. callistophylla* and *H. caudata* and on the edge of the corolla of *H. caudata.* Previous studies show that the trichomes found in *H. coronaria* are present as single entities, characterised as unicellular, elongated and sharply pointed apical cells on both surfaces of the leaf epidermis (Ridzuan & Kalu, 2023). Simple trichomes are hair-like epidermal projections that do not secrete metabolites; their primary function is to provide mechanical and physical defence. These structures create a protective barrier that discourages herbivores by rendering the plant's surface less palatable or more difficult to access, while also trapping or obstructing small insects and fungal spores (Huchelmann *et al*., 2017). Simple trichomes diminish water loss by establishing a boundary layer of stagnant air on the leaf surface, thereby reducing transpiration. They also reflect surplus sunlight, safeguarding tissues from damage induced by intense light and ultraviolet radiation. Additionally, they aid in temperature regulation by decreasing heat absorption. Simple trichomes possess UV-absorbing compounds, including flavonoids, which augment their protective function against radiation (Wang *et al*., 2021).

In this study, papillae were discovered only on the corolla's abaxial surface and the pedicel's surface of *H. callistophylla.* A previous study indicated that papillae were reported absent in high density on the abaxial surfaces of the leaves of *H. caudata* and *H. verticillata* (Ridzuan & Kalu, 2023). Papillae, which are tiny projections on the external surface of epidermis cells and in several species, have been recognised as significant systematic features (Judd *et al*., 1999; Moraes *et al*., 2011). Although several theories have been put out, papillae may help regulate temperature and light, which could provide adaptive benefits in xerophytic environments (Patterson, 1964; Proctor, 1990). However, their functional purpose is still unclear despite a lot of interest. Their diverse forms and location of trichomes play a significant role in the ongoing revision, identification and classification of this complex genus within Apocynaceae. The discovery of glandular trichomes, simple trichomes and papillae in this study represents a novel finding in the genus *Hoya*. These valuable characteristics may serve as a useful reference for classifying species within the genus *Hoya* and provide additional information in the taxonomic classification of this genus.

Table 1. Species, type, location, micromorphological characteristics and size of trichomes in *Hoya* species

Species	Type of trichomes	Location of trichomes	Trichomes characteristic	Trichomes size (widths, heights) (mean)
H. callistophylla	Unicellular conical-shape glandular trichomes (*cgt*).	Adaxial epidermis of the corolla surface	Smooth surfaces	10.5µm, 18.5µm
	Unicellular simple trichomes.	Epidermis of the pedicel	Echinate ornamentation	21.83µm, 244.1µm
	Papillae.	Adaxial of the corolla and epidermis of the pedicel	-	-
H. caudata	Unicellular filament-shaped glandular trichomes (*fmtg*).	Adaxial epidermis of the corolla surface	Echinate ornamentation	28.04µm, 51.35µm
	Unicellular simple trichomes.	Epidermis of the pedicel and the edge of the corolla	Echinate ornamentation and smooth surface	8.47µm, 98.9µm, 27.40µm, 192.34 µm
H. elmeri	Unicellular finger-like glandular trichomes (*flgt)*.	Adaxial epidermis of the corolla surface	Smooth surface	12.73µm, 67.5µm
H. maingayi	Unicellular falcate-shape glandular trichomes (*fgt*).	Adaxial epidermis of the corolla surface	Smooth surfaces	84.04µm, 214.36µm
H. parviflora	Multicellular stalked capitate glandular trichomes (*scgt*).	Adaxial epidermis of the corolla surface	Apical protrusion and smooth surface	22.4µm, 97.52µm

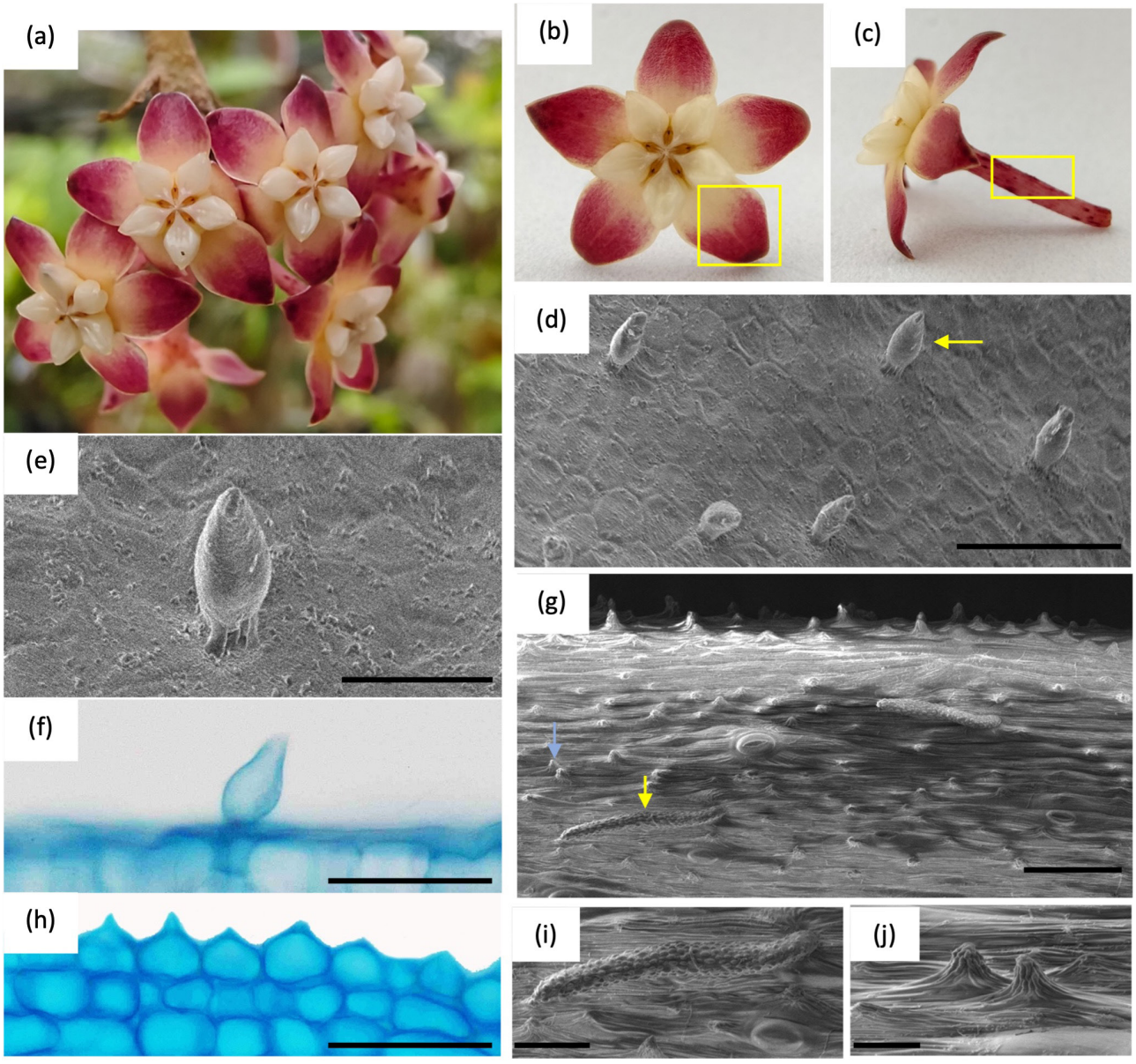

Fig. 1. Micromorphological and anatomical structure of *H. callistophylla*. (**a-c**) Flower of *H. callistophylla* with five corolla (*cl*), five corona lobes (*co*) and five guide rails (*gr*) in between each *co*. (**d & e**) SEM images of corolla (*cl*) at (**b**) (yellow box); (**e**) Enlargement in (**d**) (yellow arrow) indicates the presence of con-shaped glandular trichomes (*cgt*). (**f & h**) LM images of corolla (*cl*). (**f**) Conical-shaped glandular trichomes (*cgt*) at the adaxial surface of *cl* and (**h**) indicate the presence of papillae on the surface of abaxial of *cl*. (**g, i** & **h**) SEM images of the pedicel at (**c**) (yellow box). (**i & j**) Enlargement in (**g**) (yellow and blue arrow) indicates the presence of simple trichomes (*st*) (**I**) and papillae (**j**) at the epidermis of the pedicel. *cl* = corolla; *co* = corona; *gr* = guide rail. Scale: (**f** & **h**) = 100 m; (**d** & **g**) = 50 μm; (**i**) = 30 μm; (**e**) = 20 μm and (**j**) = 10 μm.

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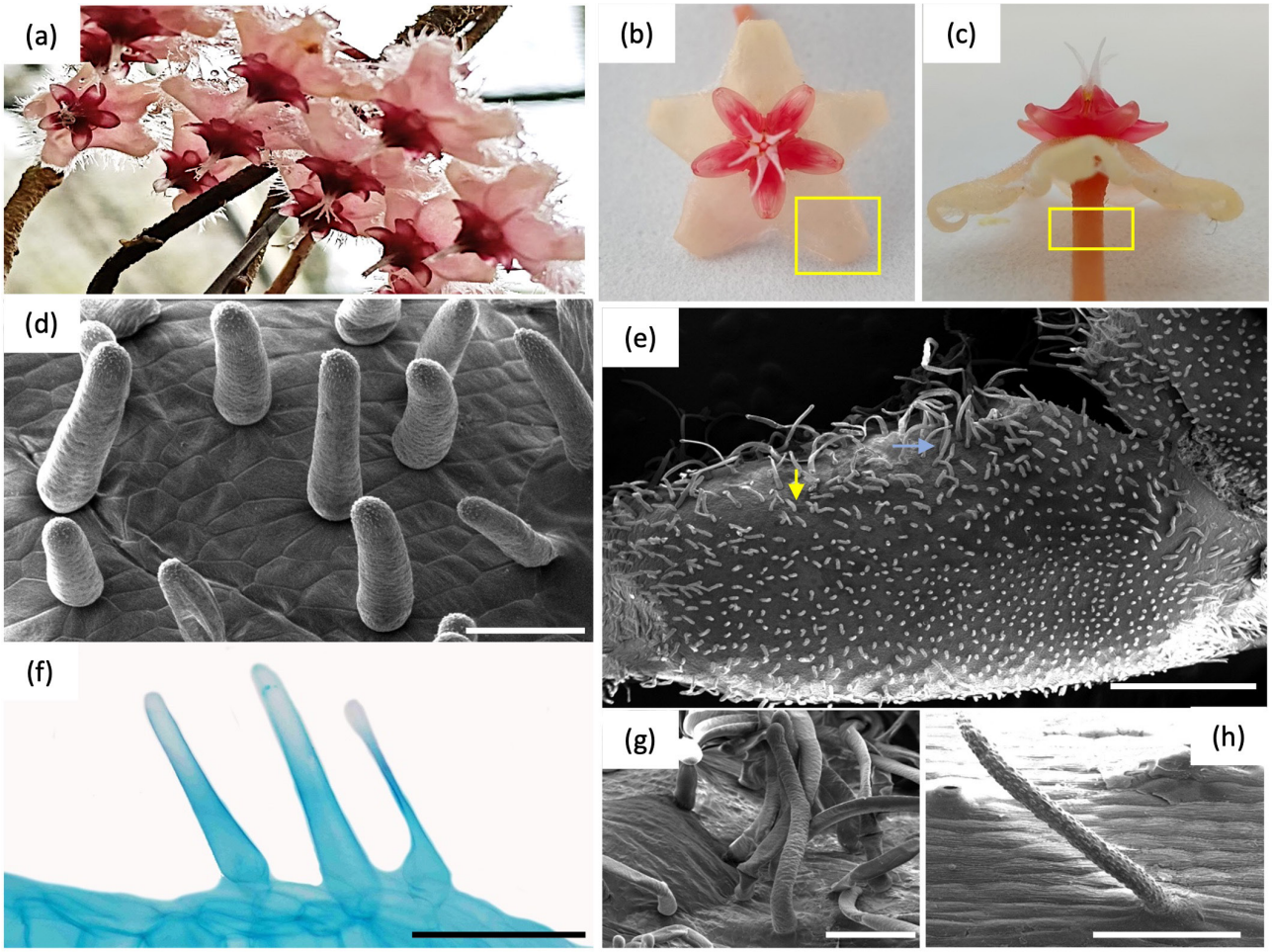

Fig. 2. Micromorphological and anatomical structure of *H. caudata* (**a**-**c**) Flower of *H. caudata* with five corolla (*cl*), five corona lobes (*co*) and five guide rails (*gr*) in between each *co*. (**d**, **e** & **g**) SEM images of corolla (*cl*) at (**b**) (yellow box); (**d & g**) Enlargement in (**e**) (yellow and blue arrow) indicates the presence of filament-shaped glandular trichomes (*fmtg*) (**d**) and simple trichomes (*st*) (**g**). (**f**) LM images of filament shape glandular trichomes (*fmtg*) at the adaxial surface of the *cl*. (**h**) SEM images of the pedicel at (**c**) (yellow box). (**h**) indicate the presence of simple trichomes (*st*) at the epidermis of the pedicel. *cl* = corolla; *co* = corona; *gr* = guide rail. Scale: (**e**) = 1 mm; (**f-h**) = 100 m and (**d**) = 50 μm.

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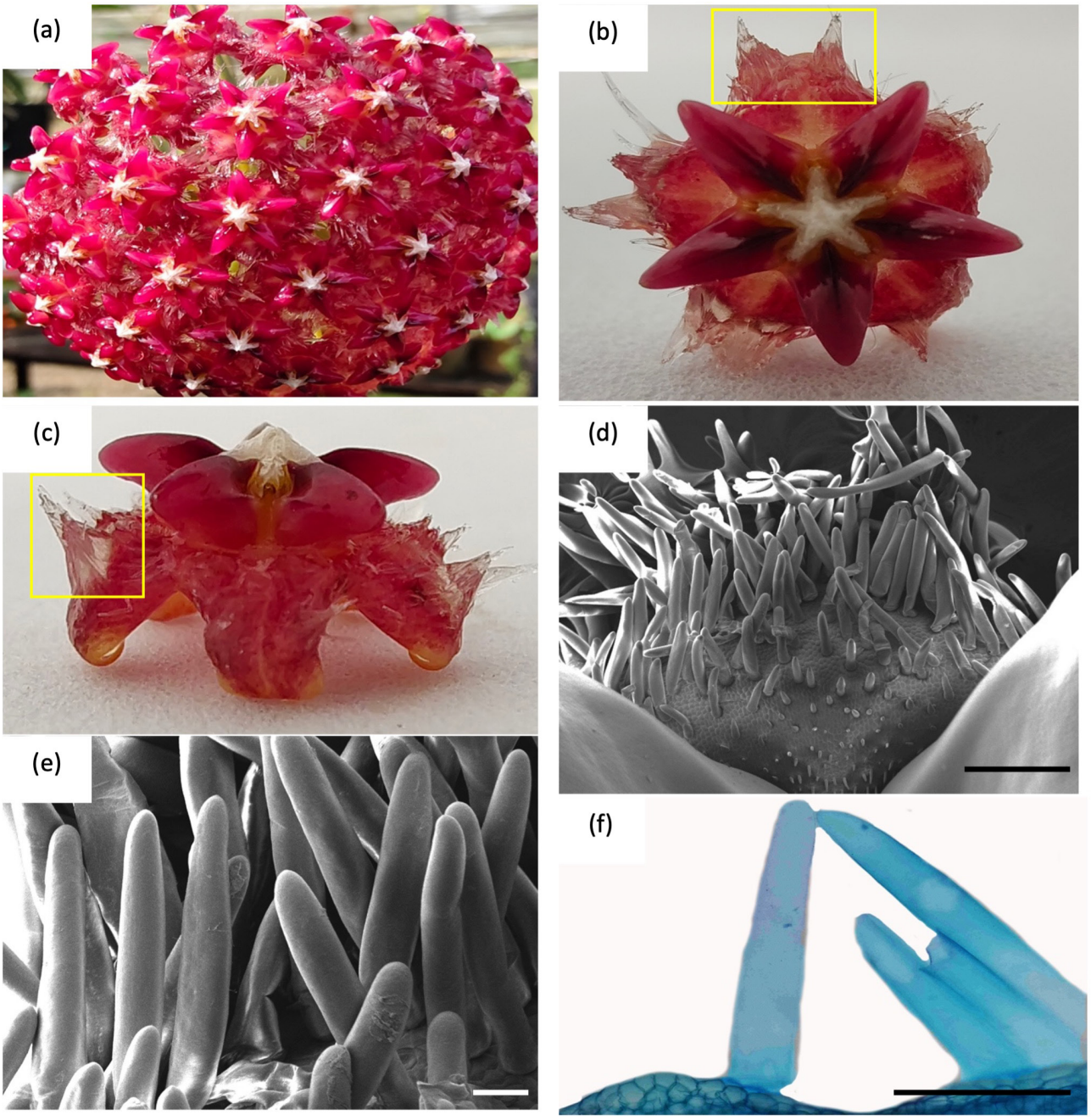

Fig.3. Micromorphological and anatomical structure of *H. elmeri* (**a**-**c**) Flower of *H. elmeri* with five corolla (*cl*), five corona lobes (*co*) and five guide rails (*gr*) in between each *co*. (**d** & **e**) SEM images of corolla (*cl*) at (**b**) and (**c**) (yellow box); (**e**) Enlargement in (**d**) (yellow arrow) indicates the presence of finger-like glandular trichomes *(flgt*). (**f**) LM images of finger-like glandular trichomes (*flgt*) at the adaxial surface of *cl*. *cl* = corolla; *co* = corona; *gr* = guide rail. Scale: (**d**) = 500 μm, (**f**) = 200 m and (**e**) = 100 μm.

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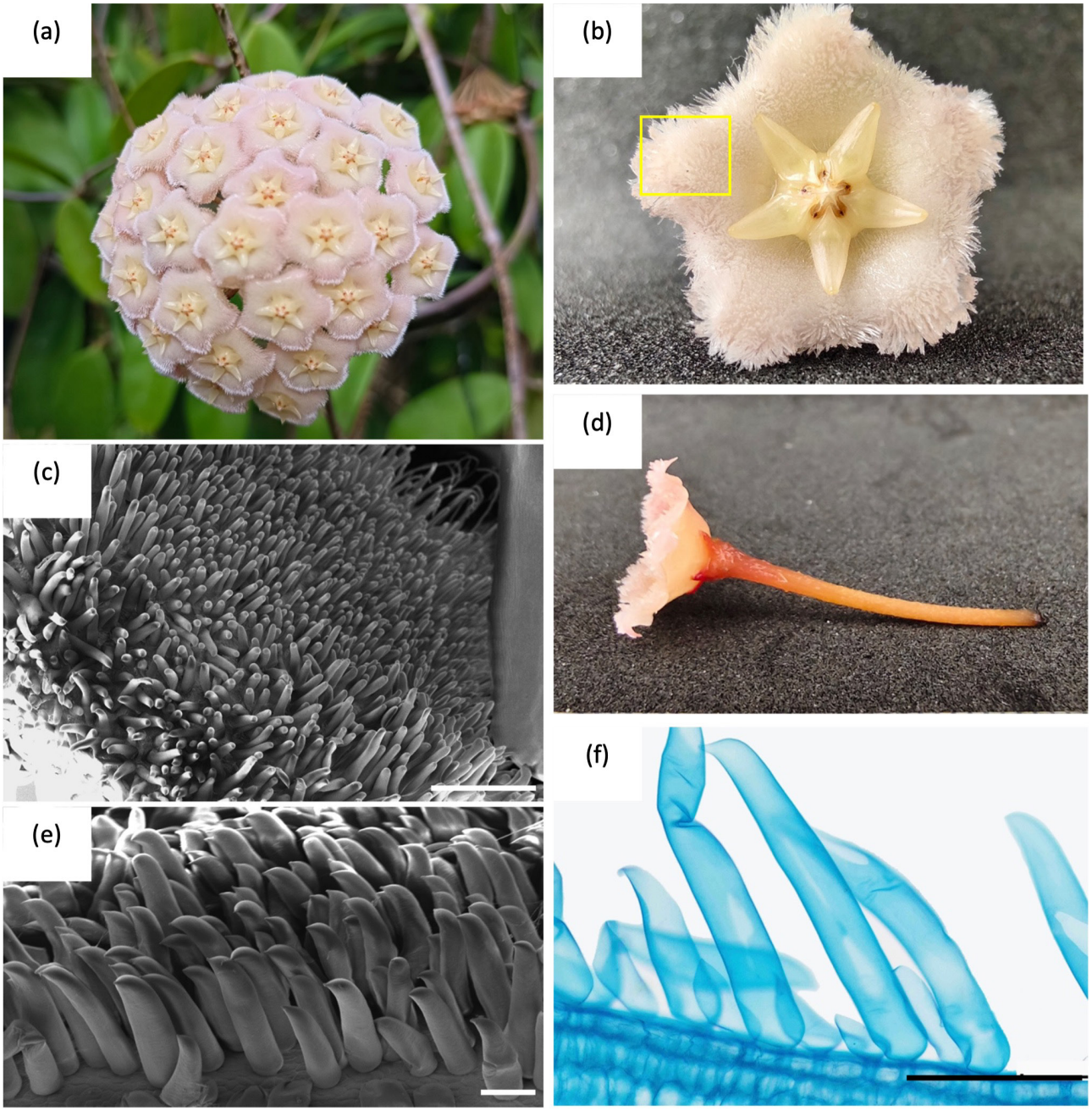

Fig. 4. Micromorphological and anatomical structure of *H. maingayi*. (**a**, **b** &**d**) Flower of *H. maingayi* with five corolla (*cl*), five corona lobes (*co*) and five guide rails (*gr*) between each *co*. (**c** & **e**) SEM images of corolla (*cl*) at (**b**) (yellow box); (**e**) Enlargement in (**c**) indicates the presence of falcate-shaped glandular trichomes *(fgt*). (**f**) LM images of falcate shape glandular trichomes (*fgt*) at the adaxial surface of *cl*. *cl* = corolla; *co* = corona; *gr* = guide rail. Scale: (**c**) = 500 μm, (**f**) = 200 μm and (**e**) = 100 μm.

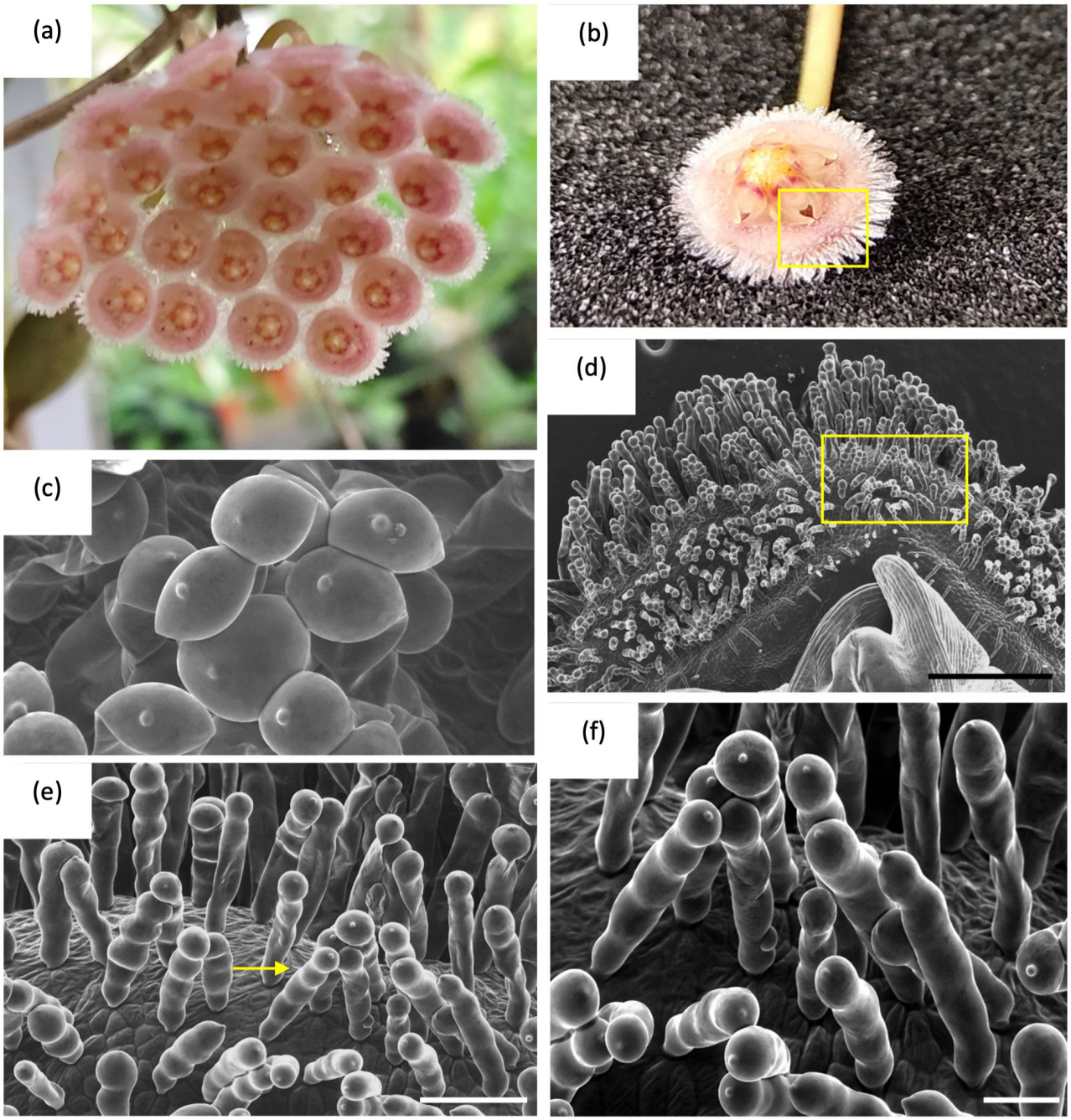

Fig. 5. Micromorphological structure of *H. parviflora*. (**a** & **b**) Flower of *H. parviflora* with five corolla (*cl*), five corona lobes (*co*) and five guide rails (*gr*) in between each *co*. (**c-f**) SEM images of corolla (*cl*) at (**b**) (yellow box); (**c, e & f**) Enlargement in (**d**) (yellow arrow) indicates the presence of stalked capitate glandular trichomes with apical protrusion *(scgt*). *cl* = corolla; *co* = corona; *gr* = guide rail. Scale: (**d**) = 500 μm, (**e**) = 100 μm and (**f**) = 50 μm.

CONCLUSION

This study successfully characterised the structure and density of floral trichomes across five *Hoya* species. The variation in trichome structure and placement indicates important functional and taxonomic implications. The results enhance the understanding of micromorphological taxonomy within the genus *Hoya*, proposing novel characteristics for classification and the preservation of biodiversity by documenting microscopic structures that could respond to environmental changes. Additional investigations that combine chemical profiling of trichome secretions with ecological studies would enhance the comprehension of *Hoya* pollination biology and its adaptations.

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ETHICAL STATEMENT

Not applicable.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

REFERENCES

Anton, S., Kaminska, M. & Stpiczynska, M. 2012. Comparative structure of the osmophores in the flower of *Stanhopea graveolens* Lindley and *Cycnoches chlorochilon* Klotzsch (Orchidaceae). Acta Agrobotanica, 65(2). https://doi.org/10.5586/aa.2012.054

Basir, S., Saad, M.F.M., Rahman, M.R.A., Talip, N., Baharum, S.N. & Bunawan, H. 2022. Floral nectary and trichome structure of *Hoya cagayanensis*, *Hoya lacunosa*, and *Hoya coriacea* (Apocynaceae, Marsdenieae). Horticulturae, 8(5): 420. https://doi.org/10.3390/horticulturae8050420

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. https://doi.org/10.55230/mabjournal.v53i6.14

Das, A., Lee, S.H., Hyun, T.K., Kim, S.W. & Kim, J.Y. 2013. Plant volatiles as method of communication. Plant Biotechnology Reports, 7(1): 9-26. https://doi.org/10.1007/s11816-012-0236-1

Demarco, D. 2017a. Histochemical analysis of plant secretory structures. In: Histochemistry of Single Molecules: Methods and Protocols. Springer New York, New York. pp. 313-330. https://doi.org/10.1007/978-1-4939-6788-9_24

Demarco, D. 2017b. Staminal wing and a novel secretory structure of asclepiads. Botany, 95(7): 763-772. https://doi.org/10.1139/cjb-2016-0239

El-Taher, A.M., Gendy, A.E.N.G.E., Alkahtani, J., Elshamy, A.I. & Abd-ElGawad, A.M. 2020. Taxonomic implication of integrated chemical, morphological and anatomical attributes of leaves of eight Apocynaceae taxa. Diversity, 12(9): 334. https://doi.org/10.3390/d12090334

Glas, J.J., Schimmel, B.C., Alba, J.M., Escobar-Bravo, R., Schuurink, R.C. & Kant, M.R. 2012. Plant glandular trichomes as targets for breeding or engineering of resistance to herbivores. International Journal of Molecular Sciences, 13(12): 17077-17103. https://doi.org/10.3390/ijms131217077

Huchelmann, A., Boutry, M. & Hachez, C. 2017. Plant glandular trichomes: Natural cell factories of high biotechnological interest. Plant Physiology, 175(1): 6-22. https://doi.org/10.1104/pp.17.00727

Ichie, T., Inoue, Y., Takahashi, N., Kamiya, K. & Kenzo, T. 2016. Ecological distribution of leaf stomata and trichomes among tree species in a Malaysian lowland tropical rain forest. Journal of Plant Research, 129(4): 625-635. https://doi.org/10.1007/s10265-016-0795-2

Judd, W.S., Campbell, C.S., Kellogg, E.A., Stevens, P.F. & Donoghue, M.J. 1999. Plant Systematics: A Phylogenetic Approach. Sinauer Associates, Sunderland. 464 pp.

Kolb, D. & Müller, M. 2004. Light, conventional and environmental scanning electron microscopy of the trichomes of *Cucurbita pepo* subsp. pepo var. styriaca and histochemistry of glandular secretory products. Annals of Botany, 94(4): 515-526. https://doi.org/10.1093/aob/mch180

Kowalkowska, A.K., Kozieradzka-Kiszkurno, M. & Turzyński, S. 2015. Morphological, histological and ultrastructural features of osmophores and nectary of *Bulbophyllum wendlandianum* (Kraenzl.) Dammer (B. section Cirrhopetalum Lindl., Bulbophyllinae Schltr., Orchidaceae). Plant Systematics and Evolution, 301(2): 609-622. https://doi.org/10.1007/s00606-014-1100-2

Kuang, Y., Ouyang, K., Xia, M., Feng, C. & Kang, M. 2025. Near-complete reference genome assembly of *Hoya carnosa*. Scientific Data, 12(1): 1210. https://doi.org/10.1038/s41597-025-05587-4

Lakshmi, S.R., Benjamin, J.F., Kumar, T.S., Murthy, G.V.S. & Rao, M.V. 2010. In vitro propagation of Hoya wightii ssp. palniensis K.T. Mathew, a highly vulnerable and endemic species of Western Ghats of Tamil Nadu, India. African Journal of Biotechnology, 9(5). https://doi.org/10.5897/AJB09.846

Lamb, A. & Rodda, M. 2016. A Guide to Hoyas of Borneo. Natural History Publications (Borneo), Kota Kinabalu.

McDowell, E.T., Kapteyn, J., Schmidt, A., Li, C., Kang, J.H., Descour, A. & Gang, D.R. 2011. Comparative functional genomic analysis of Solanum glandular trichome types. Plant Physiology, 155(1): 524-539. https://doi.org/10.1104/pp.110.167114

Moraes, T.M.D.S., Rabelo, G.R., Alexandrino, C.R., Silva Neto, S.J.D. & Da Cunha, M. 2011. Comparative leaf anatomy and micromorphology of *Psychotria* species (Rubiaceae) from the Atlantic Rainforest. Acta Botanica Brasilica, 25: 178-190. https://doi.org/10.1590/S0102-33062011000100021

Noraini, T., Ruzi, A.R. & Amirul-Aiman, A.J. 2019. Anatomi dan Mikroskopik Tumbuhan. Universiti Kebangsaan Malaysia, Bangi. (Malay).

Patterson, P.M. 1964. Problems presented by bryophytic xerophytism. The Bryologist, 67(4): 390-396. https://doi.org/10.1639/0007-2745(1964)67[390:PPBBX]2.0.CO;2

Proctor, M.C.F. 1990. The physiological basis of bryophyte production. Botanical Journal of the Linnean Society, 104(1-3): 61-77. https://doi.org/10.1111/j.1095-8339.1990.tb02211.x

Rahayu, S. 2011. Hoya sebagai tumbuhan obat. Warta Kebun Raya, 11(1): 15-21. (Indonesian).

Rahayu, S., Fakhrurrozi, Y. & Putra, H.F. 2018. Hoya species of Belitung Island, Indonesia, utilization and conservation. Biodiversitas Journal of Biological Diversity, 19(2): 369-376. https://doi.org/10.13057/biodiv/d190203

Ramya, H.G., Palanimuthu, V. & Rachna, S. 2013. An introduction to patchouli (Pogostemon cablin Benth.): a medicinal and aromatic plant: It's importance to mankind. Agricultural Engineering International: CIGR Journal, 15(2): 243-250.

Ridzuan, K. & Kalu, M. 2023. Comparative micromorphology leaf surface of selected *Hoya* spp. (Apocynaceae) from Sarawak. Reinwardtia, 22(2): 69-77. https://doi.org/10.55981/reinwardtia.2023.4504

Schuurink, R. & Tissier, A. 2020. Glandular trichomes: micro-organs with model status? New Phytologist, 225(6): 2251-2266. https://doi.org/10.1111/nph.16283

Seyedi, Z. & Salmaki, Y. 2015. Trichome morphology and its significance in the systematics of *Phlomoides* (Lamiaceae; Lamioideae; Phlomideae). Flora - Morphology, Distribution, Functional Ecology of Plants, 213: 40-48. https://doi.org/10.1016/j.flora.2015.04.003

Stevens, W.D. 1988. A synopsis of Matelea subg. *Dictyanthus* (Apocynaceae: Asclepiadoideae). Annals of the Missouri Botanical Garden, 75: 1533-1564. https://doi.org/10.2307/2399300

Wang, X., Shen, C., Meng, P., Tan, G. & Lv, L. 2021. Analysis and review of trichomes in plants. BMC Plant Biology, 21(1): 70. https://doi.org/10.1186/s12870-021-02840-x

Wiemer, A.P., More, M., Benitez-Vieyra, S., Cocucci, A.A., Raguso, R.A. & Sersic, A.N. 2009. A simple floral fragrance and unusual osmophore structure in *Cyclopogon elatus* (Orchidaceae). Plant Biology, 11(4): 506-514. https://doi.org/10.1111/j.1438-8677.2008.00140.x