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Diversity in Leaf Blade Anatomy Among Philippine *Hoya* R. Br. Species

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ABSTRACT

With over 100 species indigenous to the Philippines, *Hoya* R. Br. is the most species-rich genus of Family Apocynaceae in the archipelago. Most species of this genus are epiphytic, and some species are hemiepiphytic or terrestrial. Epiphytic species must have adaptive features that help them survive water shortages caused by not having their roots anchored to the soil. The anatomical features of the leaf blades of six species native to the Philippines [*H. espaldoniana* Kloppenb., Siar, and Cajano; *H. halconensis* Schltr. ex Kloppenb.; *H. lacunosa* Blume; *H. lucardenasiana* Kloppenb., Siar, and Cajano; *H. madulidii* Kloppenb.; and *H. meliflua* (Blanco) Merr.] were investigated, and emphasis was placed on the comparison between the epiphytic and non-epiphytic species. Diversity was observed among the six species. Two species (*H. lacunosa* and *H. meliflua*) have multiple upper epidermis consisting of two cell layers, contrary to the other species, which have simple epidermis. The three epiphytic species (*H. espaldoniana*, *H. lacunosa*, and *H. lucardenasiana*) have relatively thick cuticle on both upper and lower sides as well as homogeneous mesophyll with few air spaces. This feature helps prevent excessive water loss, thus, partially explaining how these species survive as epiphytes. On the other hand, the non-epiphytic species (*H. halconensis*, *H. madulidii*, and *H. meliflua*) have thinner cuticle layers. It was also observed that the epiphytic species have homogeneous mesophyll while the non-epiphytic species have heterogeneous mesophyll. Anatomical diversity in the Philippine species of *Hoya* must have played a role in the diversification of the genus in the archipelago. Examining the anatomy of their roots and stems will help in further understanding this.

Keywords: Apocynaceae, Asclepiadoideae, epiphyte, mesophyll, multiple epidermis

INTRODUCTION

With over 300 primarily epiphytic species worldwide, wax plants (*Hoya* R. Br., Family Apocynaceae) are widely distributed to eight biodiversity hotspots in the Old World tropics including the Philippine archipelago (Wanntorp et al., 2011; Wanntorp et al., 2014). With several new Philippine indigenous species named in the past ten years (Aurigue et al., 2013; Cabactulan et al., 2017; Kloppenburg & Siar, 2008; Kloppenburg & Siar, 2009; Kloppenburg et al., 2011; Kloppenburg et al., 2012; Kloppenburg et al., 2013), the number of species recorded in the region is more than 100 at present, making *Hoya* the most well-represented genus of Apocynaceae in the archipelago.

Without having their roots anchored to soil, unlike terrestrial plants, epiphytes such as most *Hoya* species are regularly subjected to water shortage (Gurevitch et al., 2006), so they need adaptive features for intercepting and retaining water (Benzing, 1984). Another problem given by not having their roots anchored to soil is mineral procurement. Some characteristics that aid in surviving challenges conferred by epiphytic habit include the presence of adventitious roots for clinging to a substratum, tiny seeds for aerial dispersal, zoophilous pollination, high efficiency of water usage, iteroparity, significant vegetative reduction, and structures for promoting access to unconventional mineral sources and prolonging contact with water. Some anatomical features that can help epiphytic plants conserve water include water-impermeable velamen in orchid roots (Dycus & Knudson, 1957), and thick water-storing leaf hypodermis in *Medinilla* (Rayos & Hadsall, 2016) and *Pleiochiton* (Reginato et al., 2009).

Epiphytism contributed to the successful diversification of *Hoya* in the Indo-Australian archipelago (Wanntorp et al., 2014). Although most species of *Hoya* are epiphytic, there are also terrestrial and hemiepiphytic ones. Epiphytic and hemiepiphytic angiosperms both germinate in parts of other plants (usually tree trunks or branches), but the latter, at a certain point of their life history, establish contact with the ground through aerial roots, thus, gaining access to water from the soil (Zotz, 2013).

The anatomical features of plants can aid in explaining major adaptive shifts (Simpson, 2010). In the case of *Hoya* species, examining their anatomical features can help understand how the genus diversified successfully in the island group.

OBJECTIVES OF THE STUDY

This study aimed to investigate the anatomical features of the leaves of six species of the genus, compare the features of epiphytic and non-epiphytic species, and relate the observed features to their environment.

MATERIALS AND METHODS

Fresh leaves from six species of Philippine *Hoya* [*H. espaldoniana* Kloppenb., Siar, and Cajano (epiphytic); *H. halconensis* Schltr. ex Kloppenb. (hemiepiphytic); *H. lacunosa* Blume (epiphytic); *H. lucardenasiana* Kloppenb., Siar, and Cajano (epiphytic); *H. madulidii* Kloppenb. (terrestrial); and *H. meliflua* (Blanco) Merr. (hemiepiphytic)] varying in habit were collected, and 1 x 3 cm rectangular pieces were cut and then fixed in formalin-alcohol-acetic acid (FAA). The plant specimens used in this study are shown in Fig. 1. They were all taxonomically identified by the authors.

Figure 1. Reproductive shoots of the specimens used in this study (A, *H. espaldoniana*; B, *H. halconensis;* C, *H. lacunosa*; D, *H. lucardenasiana*; E, *H. madulidii;* and F, *H. meliflua*).

The standard paraffin method based on Jensen (1962) was employed in preparing leaf cross-sections. The sections were observed and photographed under a light microscope.

RESULTS AND DISCUSSION

Microscopic observations revealed diversity in leaf anatomy among the six species of indigenous Philippine *Hoya*. All six species have simple lower epidermis, but their upper epidermal layers are either simple or multiple. In all species examined, the stomatal position is hypostomatic, which is the most common condition in the plant kingdom (Evert, 2006). Their mesophyll layers also differ in thickness (in terms of the number of cell layers) and heterogeneity. Size and abundance of air spaces in this tissue were also found to be varying. In all species examined, druse crystals were found in this tissue.

The leaf cross-section of *H. espaldoniana* is shown in Fig. 2. Both the upper and lower epidermal layers are simple, consisting of only one layer of rectangular cells. Both layers are covered with a relatively thick cuticle (almost as thick as the epidermal cells), which aids in minimizing water loss from the leaf surface. Being epiphytic, *H. espaldoniana* needs such an adaptive feature to conserve water. Cuticle, consisting of cutin, which is a polymer of fatty acids, is the primary barrier to excessive loss of water from leaves, and plants adapted to dry environments often have thick cuticle (Riederer & Schreiber, 2001; Simpson, 2010). The stomata are restricted to the lower epidermis (hypostomatic). Unlike most dicotyledonous plants, this species exhibits homogeneous mesophyll, which is 25-30 cell layers thick with few air spaces. Metcalfe & Chalk (1950) mentioned the fleshy leaves of *Hoya* being isobilateral. This allows very efficient storage of water. This feature, also found in *Kalanchoe pinnata*, is associated with plants exhibiting crassulacean acid metabolism (CAM) (Leal-Costa et al., 2010; Moreira et al., 2012; Nelson et al., 2005). CAM is common among epiphytic plants since it helps them survive water shortages (Benzing, 1987). This photosynthetic pathway was reported in *H. carnosa*, which can also undergo CAM-idling, thus, allowing survival during periods of extended drought (Rayder & Ting, 1983). Rayos & Hadsall (2016) observed the scarcity of air spaces in the spongy mesophyll (which was suggested to help prevent water loss) of epiphytic *Medinilla*. Druse crystals were found in the mesophyll tissue. Aside from functioning for defense against herbivores (Franceschi & Horner, 1980), these crystals can also help regulate the calcium levels of cells, with excess calcium being remobilized under certain conditions

(Volk et al., 2002). This answers the mineral procurement problem (in addition to the water stress problem) being faced by these plants.

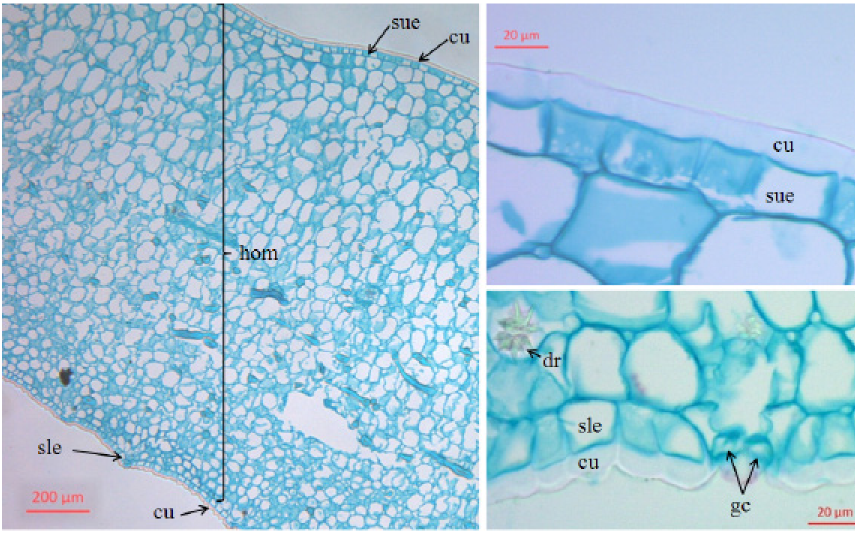

Figure 2. Leaf cross section *H. espaldoniana* showing the whole lamina (A), close-up of upper portion (B), and close-up of lower portion (C) (Legends: cu=cuticle; dr=druse; gc=stomatal guard cells; hom=homogeneous mesophyll; sle=simple lower epidermis; sue=simple upper epidermis).

The leaf cross-section of *H. halconensis* is shown in Fig. 3. Like *H. espaldoniana*, its upper and lower epidermal layers are simple with rectangular cells, and stomata occur only on the lower side. However, the cuticle layers covering both sides are relatively thinner. Unlike *H. espaldoniana*, *H. halconensis* has heterogeneous mesophyll, which is exhibited by most dicots. The palisade mesophyll is made up of two layers of compactly arranged cells, while the spongy mesophyll is made up of 10-11 layers of loosely arranged cells. The air spaces in the spongy layer are noticeably large and abundant. The lacunose structure of the spongy layer allows thorough gas exchange between the environment and the chlorenchyma cells (Esau, 1953). Although not shown in the figure, druse crystals were also observed. Being a hemiepiphytic species, *H. halconensis* gains access to water from the soil in the latter part of its life history. This means that it does not need to have the same adaptive features found in *H. espaldoniana* to survive when its aerial roots reach the ground. However, at early stage, it needs adaptive traits to survive water shortages caused by not having its roots anchored to the soil. Such features can possibly be found in its vegetative organs other than its leaves.

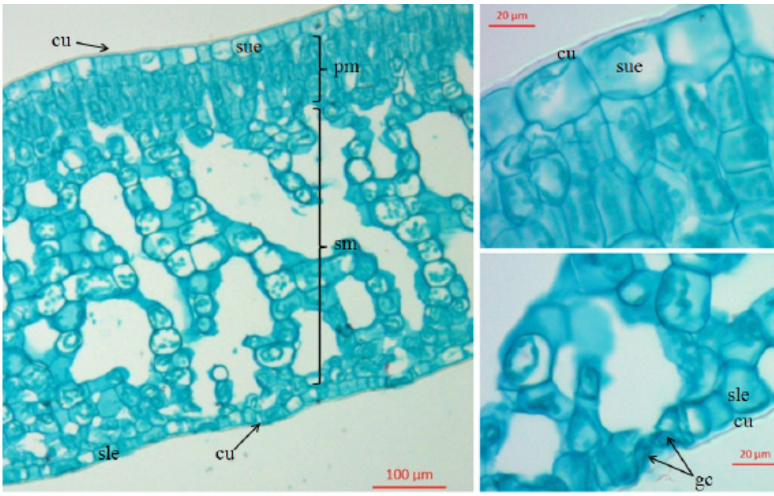

Figure 3. Leaf cross section *H. halconensis* showing the whole lamina (A), close-up of upper portion (B), and close-up of lower portion (C) (Legends: cu=cuticle; gc=stomatal guard cells; pm=palisade mesophyll; sle=simple lower epidermis; sm=spongy mesophyll; sue=simple upper epidermis).

As shown in Fig. 4, *H. lacunosa*, which is an epiphytic species, has multiple upper epidermis with two layers of rectangular cells and simple lower epidermis with papillose cells. Both layers are covered with thick cuticle like in *H. espaldoniana*. Multiple epidermis in leaf is also exhibited by *Nerium oleander* (which also belongs to Family Apocynaceae), with the lower epidermis also being made up of more than one layer of cells (Ladyzhenko, 2014). The velamen of orchid roots mentioned above is an example of multiple epidermis. Multiple epidermis in the leaf can also be found in certain genera of other families such as *Ficus* of Moraceae (Chantarasuwan et al., 2014) and *Peperomia* of Piperaceae (Kaul, 1977). This feature aids in water retention and storage (Beck, 2005). Stomata of this species were found to occur only in the lower epidermis. Like *H. espaldoniana*, this species exhibits homogeneous mesophyll, which is 20-25 cell layers thick with few air spaces. Although not shown in the figure, druse crystals were also observed in this species.

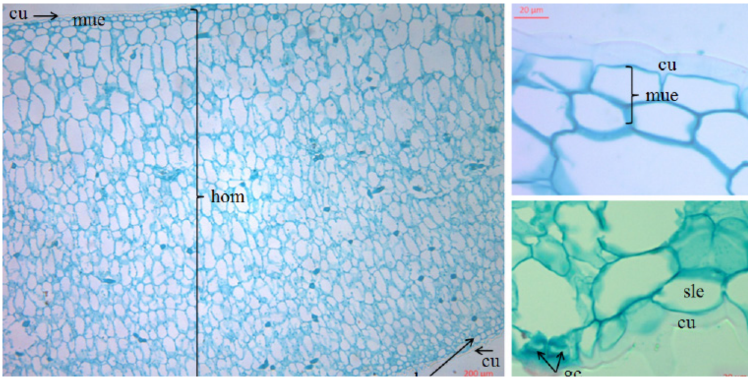

Figure 4. Leaf cross section *H. lacunosa* showing the whole lamina (A), close-up of upper portion (B), and close-up of lower portion (C) (Legends: cu=cuticle; gc=stomatal guard cells; hom=homogeneous mesophyll; mue=multiple upper epidermis; sle=simple lower epidermis).

Fig. 5 shows that *H. lucardenasiana*, an epiphytic species, has a simple upper epidermis with rectangular cells and a simple lower epidermis with papillose cells. Both layers are covered with a thick cuticle, and stomata are found only in the lower epidermis. Like *H. espaldoniana* and *H. lacunosa*, which are also epiphytic, this species has homogeneous mesophyll with minimal air spaces. This tissue layer is 15-20 cell layers thick. Druse crystals were also observed in this tissue.

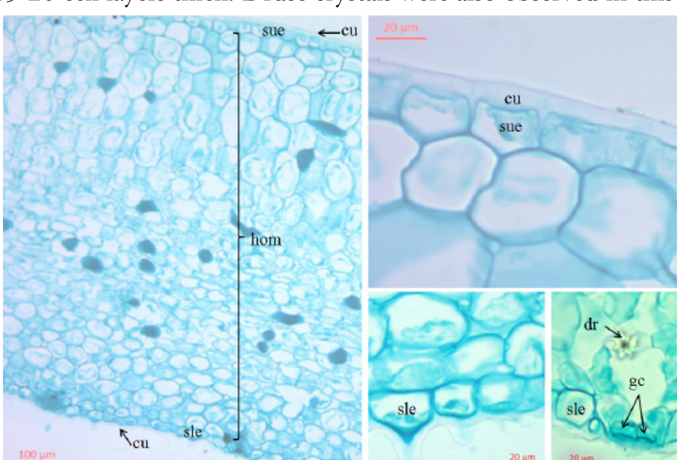

Figure 5. Leaf cross section *H. lucardenasiana* showing the whole lamina (A), close-up of upper portion (B), and close-up of lower portion (C and D) (Legends: cu=cuticle; dr=druse; gc=stomatal guard cells; hom=homogeneous mesophyll; sle=simple lower epidermis; sue=simple upper epidermis).

H. madulidii, a terrestrial species, as shown in Fig. 6, has simple upper and lower epidermal layers with rectangular cells. Both layers are covered by relatively thin cuticle. Stomata are found only in the lower epidermis. Like *H. halconensis*, this species exhibits heterogeneous mesophyll, but its palisade mesophyll is thicker, being four to five cell layers thick. Similar to *H. halconensis*, the spongy layer has 10-11 layers of parenchymatous cells with large and abundant air spaces. Druse crystals were also observed in this species. With its roots having access to water from the soil, this species does not need the same adaptive features that help its epiphytic relatives survive water shortages.

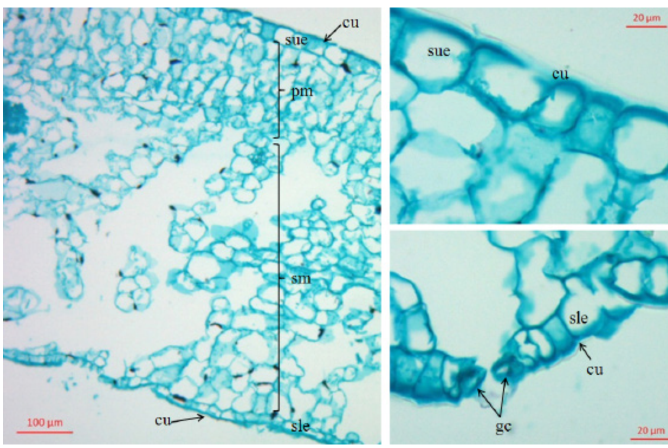

Figure 6. Leaf cross section *H. madulidii* showing the whole lamina (A), close-up of upper portion (B), and close-up of lower portion (C) (Legends: cu=cuticle; gc=stomatal guard cells; pm=palisade mesophyll; sle=simple lower epidermis; sm=spongy mesophyll; sue=simple upper epidermis).

H. meliflua, a hemiepiphytic species, as shown in Fig. 7, has multiple upper epidermis with two layers of rectangular cells similar to *H. lacunosa* and a simple lower epidermis with rectangular cells. Both layers are covered with relatively thin cuticle. Although its roots reach the soil in the latter part of its life history, this species also needs to have means of conserving water at an earlier stage. Multiple upper epidermis most likely contributes to its survival before its roots gain contact with the soil. Stomata occur only in the lower epidermis. Heterogeneous mesophyll is being exhibited by this species with eight to ten cell layers in palisade mesophyll (much thicker than in *H. halconensis* and *H. madulidii*) and 25-30 cell layers in spongy mesophyll. Unlike in *H. halconensis* and *H. madulidii*, the air spaces are small in the spongy layer of this species. This also probably contributes to water conservation. Although not shown in the figure, druse crystals were also seen in this species.

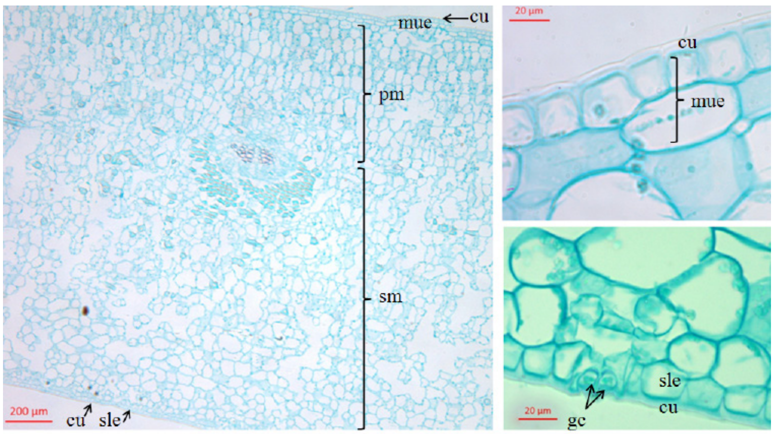

Figure 7. Leaf cross section *H. meliflua* showing the whole lamina (A), close-up of upper portion (B), and close-up of lower portion (C) (Legends: cu=cuticle; gc=stomatal guard cells; mue=multiple upper epidermis; pm=palisade mesophyll; sle=simple lower epidermis; sm=spongy mesophyll).

The comparisons in the epidermis of the six species are summarized in Table 1, while for the mesophyll, the comparisons are presented in Table 2. It is noteworthy that the three epiphytic species investigated have relatively thicker cuticle than the non-epiphytic species. Thick cuticle preventing excessive water loss is a very advantageous feature related to epiphytism as mentioned above. Another significant difference between epiphytic and non-epiphytic species was seen in the structure of their mesophyll. The epiphytic species exhibited homogeneous mesophyll while the non-epiphytic species exhibited heterogeneous mesophyll. As discussed earlier, homogeneous mesophyll gives advantage to plants that are regularly subjected to water shortage. In previous anatomical studies about *Medinilla* (Rayos & Hadsall, 2016; Rayos & Hadsall, 2018), another species-rich genus in the Philippine archipelago, it was noted that the leaves of epiphytic species differ from those of non-epiphytic species in having thicker hypodermis (for water storage) between the upper epidermis and palisade mesophyll. In this study, significant anatomical differences were also seen between the epiphytic and non-epiphytic Philippine species of *Hoya*.

Table 1

Comparisons in the epidermis among six selected indigenous Philippine species of Hoya

Species	Habit	Number of cell layers	Shape of cells	Stomate position	Relative thickness of cuticle
H. espaldoniana Kloppenb., Siar, and Cajano	epiphytic	upper and lower layers simple	rectangular in upper and lower layers	hypostomatic	thick in upper and lower layers
H. halconensis Schltr. ex Kloppenb.	hemiepiphytic	upper and lower layers simple	rectangular in upper and lower layers	hypostomatic	thin in upper and lower layers
H. lacunosa Blume	epiphytic	upper layer multiple (two layers); lower layer simple	rectangular in upper layer; papillose in lower layer	hypostomatic	thick in upper and lower layers
H. lucardenasiana Kloppenb., Siar, and Cajano	epiphytic	upper and lower layers simple	rectangular in upper layer; papillose in lower layer	hypostomatic	thick in upper and lower layers
H. madulidii Kloppenb.	terrestrial	upper and lower layers simple	rectangular in upper and lower layers	hypostomatic	thin in upper and lower layers
H. meliflua (Blanco) Merr.	hemiepiphytic	upper layer multiple (two layers); lower layer simple	rectangular in upper and lower layers	hypostomatic	thin in upper and lower layers

Table 2

Comparisons in the mesophyll among six selected indigenous Philippine species of Hoya

Species	Habit	Type	Thickness	Air spaces
H. espaldoniana Kloppenb., Siar, and Cajano	epiphytic	homogeneous	25-30 layers of cells	scarce
H. halconensis Schltr. ex Kloppenb.	hemiepiphytic	heterogeneous	two layers of cells in palisade layer; 10-11 layers of cell in spongy layer	scarce in palisade layer; large and abundant in spongy layer
H. lacunosa Blume	epiphytic	homogeneous	20-25 layers of cells	scarce
H. lucardenasiana Kloppenb., Siar, and Cajano	epiphytic	homogeneous	15-20 layers of cells	scarce
H. madulidii Kloppenb.	terrestrial	heterogeneous	four to five layers of cells in palisade layer; 10-11 layers cells in spongy layer	scarce in palisade layer; large and abundant in spongy layer
H. meliflua (Blanco) Merr.	hemiepiphytic	heterogeneous	eight to ten layers of cells in palisade layer; 25-30 layers of cells in spongy layer	scarce in palisade layer; small and abundant in spongy layer

CONCLUSIONS

Diversity in leaf blade anatomy was observed among the six species of *Hoya* investigated in this study. In terms of cuticle thickness and mesophyll structure, differences were observed between the epiphytic and non-epiphytic species. Multiple epidermis, thick cuticle, and homogeneous mesophyll with minimal air spaces are among the features with adaptive significance for water shortage. Variation in leaf anatomy favored the adaptive radiation of the genus in the Philippine archipelago. Further investigation of the anatomical features of their roots and stems will provide better understanding of how they successfully diversified in the region.

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