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Research

Anatomical Characteristics of Selected Dennstaedtiaceae Species From Peninsular Malaysia

Haja Maideen[1], Norlaila Najwa Rahman[2], Nur Aliah[1], Nurul Nadhirah[1], Noraini Talip[1], Nik Norhazrina[1], Nur Aqilah Bakray[1], Ahmad Fitri Zohari[1], Nur Farah Ain Zainee[1], Mohd Nizam Mohd Said[1], Shamsul Khamis[1], Nur Syazwani Mohamad Basir[1]

1. Department of Biological Sciences and Biotechnology, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, 43600 UKM Bangi, Selangor, Malaysia
2. MAHSA University, Jalan SP2, Bandar Saujana Putra, 42610 Jenjarom, Selangor, Malaysia
*Corresponding author: deen@ukm.edu.my

ABSTRACT

Dennstaedtiaceae is a monophyletic fern family widespread in tropical and temperate regions. Data on the anatomy of its species in Peninsular Malaysia are still scarce. Here, we examined anatomical characteristics (leaf venations & shape of steles) among ten species of seven Dennstaedtiaceae genera recorded in Peninsular Malaysia. Two types of vein patterns were observed, most of them having open-leaf venation whereas closed venation was observed only in *Histiopteris* species. Four types of steles which were 'U'-shaped, 'I'-shaped, scattered, and a combination of 'S' and 'W'-shaped and a combination of inverted 'C' and 'W'-shaped' were observed among all the Dennstaedtiaceae species studied.

Key words: Anatomy, Dennstaedtiaceae, ferns, morphology, taxonomy

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INTRODUCTION

Dennstaedtiaceae is a medium-sized family ca. 10–15 genera with about 270 species (Tryon & Tryon, 1982; Kramer, 1990; Smith *et al*., 2008; PPG I, 2016) having sub-cosmopolitan distribution mainly due to the widely-distributed bracken ferns, *Pteridium* Gled ex Scop. (Tryon, 1941; Der *et al*., 2009). Members in this family mostly have long-creeping rhizomes, with multicellular hairs, large leaves, lamina bipinnate to pentapinnate, and absence of true scales (Schwartsburd, 2017). The sori of the species in this family can be found at the abaxial side of the fronds and are located at the margin and the terminal of the veins, usually arranged in elongated or round and are often protected by indusia that are usually in a cup or linear-shaped. The vein of the leaves is usually free and rarely anastomose (Smith *et al*., 2008).

The classification of Dennstaedtiaceae was first introduced by Christensen (1938), where he grouped all Dennstaedtiaceae species in the subfamily Dennstaedtioideae under the family Polypodiaceae which includes two tribes namely Dennstaedtieae and Hypolepideae. The family Dennstaedtiaceae was established by Ching (1940) with two subfamilies, Dennstaedtieae and Saccolomeae. However, Copeland (1947) placed all seven genera in Dennstaedtiaceae (*Dennstaedtia, Microlepia, Monachosorum*, *Paesia*, *Hypolepis, Pteridium,* and *Histiopteris)* under the family Pteridaceae based on characters such as their spore morphology.

Dennstaedtiaceae *sensu* Holttum lumped all 48 genera of Malaysian Dennstaedtiaceae into 11 subfamilies (Holttum, 1954; Soepadmo & Khoo, 1977). In the 1970s and 1980s, a more natural system of classification on Dennstaedtiaceae members was attempted by pteridologists in their studies such as Atkinson (1973) and Mickel (1973) by including modern and advanced techniques such as anatomical, cytological, phytochemical, and biochemical. Erdtman and Sorsa (1971) included palynological aspects in the classification of Dennstaedtiaceae where they studied spore morphology of those 48 genera of Dennstaedtiaceae *sensu* Holttum. Tryon and Tryon (1982) placed the tribe Dennstaedtieae, Lindsaeae, and Monachosoreae under one family Dennstaedtiaceae based on their spore characteristics using Scanning Electron Microscope (SEM) images. Nine genera (*Dennstaedtia, Hypolepis, Pteridium, Paesia, Histiopteris, Blotiella, Lonchitis, Saccoloma, Microlepia)* were included in the tribe Dennstaedtieae. A year later, Brownsey (1983) proposed a new phyletic scheme for Dennstaedtiaceae with three major lineages.

With the advent of DNA sequences and phylogenetic analysis used in fern systematics and evolution, the first phylogenetic work on Dennstaedtiaceae species was conducted by Wolf *et al*. (1994) and Wolf (1995). Besides, the classification systems based on molecular phylogeny by Smith *et al*. (2006) have led to many changes occurring in the nomenclature of ferns (Delos Angeles & Buot, 2012). According to Smith *et al*. (2006), families Davalliaceae, Oleandraceae, Tectariaceae, Lomariopsidaceae, Dryopteridaceae, Blechnaceae, Aspleniaceae, Pteridaceae and Lindsaeaceae that were once placed in a big family Dennstaedtiaceae as sub-families should be separated from family Dennstaediaceae and formed a family of their own in the order Polypodiales and class Polypodiopsida.

Smith *et al*. (2006) grouped 11 genera in Dennstaedtiaceae which are *Blotiella, Coptodipteris, Dennstaedtia, Histiopteris, Hypolepis, Leptolepia, Microlepia, Monachosorum, Oenotrichia, Paesia* and *Pteridium.* As currently described, Dennstaedtiaceae is a medium-sized family consisting of approximately 310 taxa, with the largest genera being *Hypolepis* and *Microlepia* (Yan *et al*., 2013; Schwartsburd & Prado, 2015; Schwartsburd, 2018). In Malaysia, Parris and Latiff (1997) recorded 11 genera (*Dennstaedtia*, *Histiopteris*, *Hypolepis*, *Lindsaea*, *Microlepia*, *Odontosoria*, *Paesia*, *Pteridium*, *Saccoloma*, *Tapeinidium* and *Xyropteris* with ca. 70 species in this family. To date, no comprehensive study on the anatomy of Dennstaedtiaceae species has been done in Malaysia, except only for the genus *Histiopteris* by Faridah-Hanum *et al*. (2008). According to Metcalfe and Chalk (1979), identification of species using anatomical features is very significant as it can be used to determine the botanical identity of a species. Although characters of fronds such as sporangia and sori are used extensively in the identification and classification of ferns, anatomical features of the rhizome and frond also have proved to be diagnostic for many families and genera (Keating, 1968; Bidin & Walker, 1985; Schneider 1996; Noraini *et al*., 2014; Maideen *et al*., 2018, 2019, 2023). Hence, we present here anatomical studies on ten species of seven Dennstaedtiaceae genera recorded in Peninsular Malaysia to examine anatomical characteristics that can be used for species identification and classification.

MATERIALS AND METHODS

Fresh specimens of ten selected Dennstaedtiaceae species from seven genera (*Dennstaedtia*, *Pteridium*, *Histiopteris*, *Paesia*, *Hypolepis*, *Microlepia & Monachosorum*) were collected from various localities in Peninsular Malaysia (Table 1). The stipe samples were fixed in bottles containing AA solution (70% Alcohol: 30% Acetic Acid) for 48 hours before being sectioned using Reichert sliding microtome (Johansen, 1940). Sections of stipe were stained in Safranin and Alcian green, followed by dehydration through a series of alcohol concentrations: 50%, 70%, 95%, and 100%. Subsequently, all sections were mounted on slides, following usual procedures in plant anatomy (Johansen, 1940; Saas, 1958). For leaf venation, the clearing and staining procedures were done following Johansen (1940) and Vasco *et al*., (2014). Both the sections of stipe and leaf venation were photographed using a video camera (JVC) attached to a Leica Diaplan Microscope and images were processed using Docu Analysis Software (Sass, 1958).

RESULTS AND DISCUSSIONS

Leaf venation

The principal characteristics of the leaf venation pattern of a species are genetically fixed which thus provides the basis for using the leaf venation as a taxonomic tool. Leaf venation in plants is considered a two-dimensional ramifying structure and due to its importance for systematic classification, attention is paid mainly to the architectural properties of leaf venation. The pattern of veins has been used for fern classification at levels of species, genus, and family (Wagner, 1979). Besides, it has been useful in fern fossil species identification for example *Barthelopteris germarii* (Roth-Nebelsick *et al*., 2001).

Variation in vein topology is the result of the arrangement of network elements resulting in a visually striking diversity of vein leaf systems (Sack & Scoffoni, 2013). Hickey (1973) and Ellis *et al*., (2009) classified vein systems with 'types' for each order for example first-order veins and second-order veins.

According to Niklas (1992), leaf venation served two main functions: for the transport of substances and mechanical stabilization. In this study, we identified two types of leaf venation in the selected Dennstaedtiaceae species.

Table 1. List of Dennstaedtiaceae species studied

Species	Specimen Number	Locality	Collectors
Dennstaedtia ampla (Bak.) Bedd.	L21	Pahang, Fraser Hills, Pine Tree Trail	Nurlaila, Haja Maideen, Iwani Amir Asyraf
Pteridium aquilinum (L.) Kuhn	L13	Pahang, Cameron Highlands, Parit Fall	Nurlaila, Haja Maideen, Iwani, Amir Asyraf
Pteridium esculentum (Forst.) Nakai	HM-2015-11-16	Pahang, Fraser Hills, UKM Research Centre	Nurlaila, Haja Maideen, Iwani, Amir Asyraf
Histiopteris incisa (Thbg.) J. Sm.	L9	Pahang, Cameron Highlands, Mt. Berinchang	Nurlaila, Haja Maideen, Iwani, Amir Asyraf
Histiopteris stipulacea (Hk.) Copel.	L22	Pahang, Fraser Hills, Pine Tree Trail	Nurlaila, Haja Maideen, Iwani, Amir Asyraf
Paesia elmeri Copel.	L3	Pahang, Cameron Highlands, Mt. Berinchang	Nurlaila, Haja Maideen, Iwani, Amir Asyraf
Hypolepis brooksiae Alderw.	L11	Pahang, Cameron Highlands, Mt. Berinchang	Nurlaila, Haja Maideen, Iwani, Amir Asyraf
Microlepia ridleyi Copel.	L5	Pahang, Lata Jarum, Sematau River	Nurlaila, Haja Maideen, Iwani, Amir Asyraf
Microlepia speluncae (L.) Moore	L4	Pahang, Lata Jarum, Sematau River	Nurlaila, Haja Maideen, Iwani, Amir Asyraf
Monachosorum subdigitatum (Bl.) Kuhn	RJ 5307	Sabah, Kinabalu Park, Mesilau Nature Trail to Nepenthes Rajah Trail	Nurlaila, Haja Maideen, Iwani, Amir Asyraf

Open leaf venation

Open leaf venation was observed in *D. ampla*, *Mic. speluncae*, *Mic. ridleyi*, *H. brooksiae*, *Pte. aquilinum,* and *Pte. esculentum*. The leaf branched one time in *D. ampla* and *Mic. speluncae* whereas two times branching was observed in *Pte. aquilinum*, *Pte. esculentum*, *Mic. ridleyi,* and *H. brooksiae* (Figure 1). The type of simple open venation can be seen in *Pae. elmeri* and *Mon. subdigitatum* (Figure 2*)*. The branching of the veins occurs only at the lobe of the basal pinnae. Wagner (1979) defined the terms 'open' or 'free' vein structure in the botanical literature as a leaf venation without anastomoses.

The evolution of the leaf venation architecture begins with plants having open venation. In the early Devonian and Carboniferous period, the majority of plants having fern-like leaves such as ferns and gymnosperms appear to have had an open venation. The open venation, formed by the bifurcation of veins represents primitive architecture and served as an origin for later modern network patterns (Roth-Nebelsick *et al*., 2001).

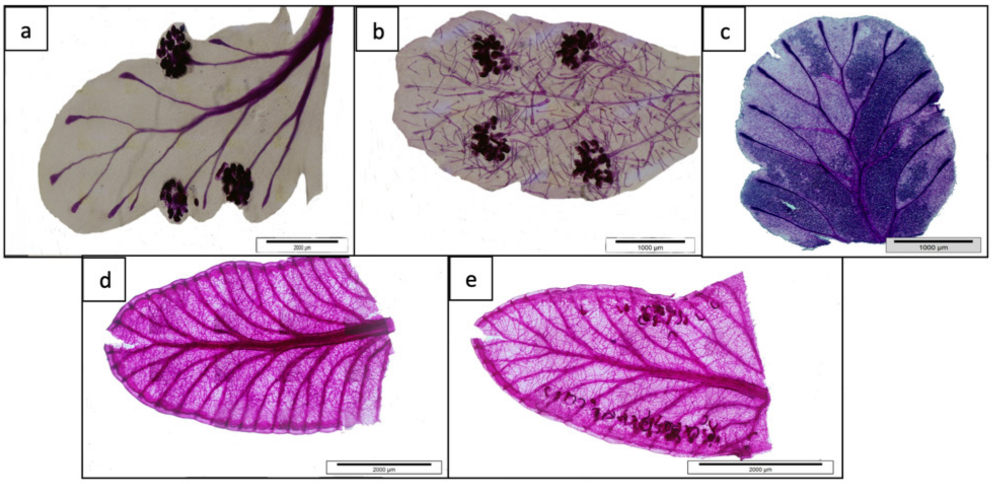

Fig. 1. Open leaf venation. (a) *Dennstaedtia ampla*, (b) *Microlepia speluncae*, (c) *Hypolepis brooksiae*, (d) *Pteridium esculentum*, (e) *Pteridium aquilinum*.

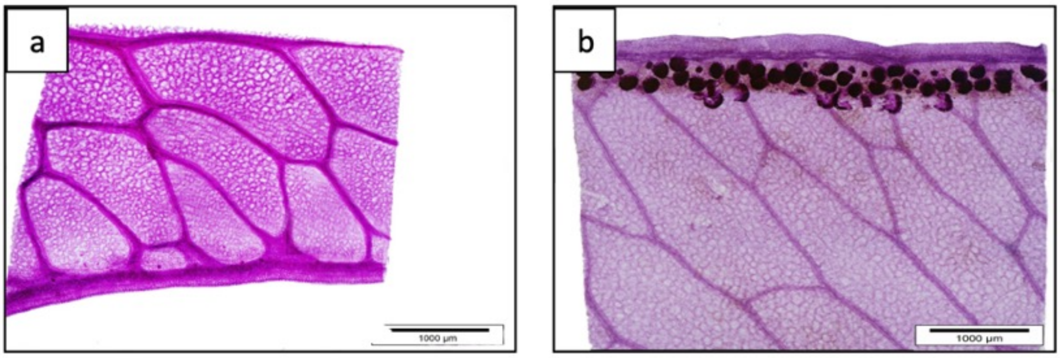

Fig. 2. Simple open leaf venation. (a) *Paesia elmeri*, (b) *Monachosorum subdigitatum*.

Close leaf venation

Close leaf venation also defined as reticulate venation can be seen in two Dennstaedtiaceae species studied, *Histiopteris incisa* and *H. stipulacea* (Figure 3). The reticulate venation of *H. incisa* is similar to Faridah-Hanum *et al*., 2008, but differs in the margin of the veins. Our study showed that the reticulate venation observed in *H. insica* was a closed reticulate venation, compared to the incomplete reticulate venation in Faridah-Hanum *et al*., (2008). From our observations, the reticulate venations in *H. incisa* formed a dense, interconnected network without significant gaps or interruptions, creating a closed pattern at the margin. Characterizing leaf venation patterns using topological aspects termed graph theory was first introduced by McDonald (1983). He indicates that a continuous series of edges is termed a path and a cycle is a path that repasses a node, thus introducing anastomosis. Roth-Nebelsick *et al*., (2001) defined the term 'cycle' as the topological term for a mesh or an anastomosis in which if the ramification pattern shows anastomoses, it is considered as a 'network' or 'close' system. Hence the term 'closed' is established in the botanical literature as denoting an anastomosing leaf venation. Simple reticulate patterns showing a network arrangement of their leaf conduit system can be seen in two Dennstaedtiaceae studied, *H. incisa* and *H. stipulacea* also seen in fossil fern species such as *Barthelopteris germarii*.

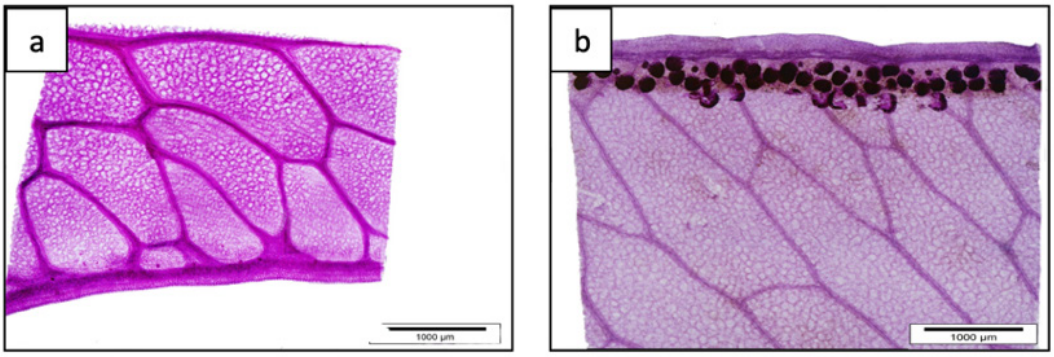

Fig. 3. Close leaf venation. (a) *Histiopteris incisa*, (b) *Histiopteris stipulacea.*

According to Korn (1998), vein formation in ferns seems to be more amenable to analysis compared to angiosperms due to various reasons including the nature of fern leaves that arise apogamously indicating no other organ initiates or dictates pattern in such a way that the mechanism of vein formation comes entirely from within the leaf (Whittier, 1962; Korn, 1993). Our study supported the recent findings on the combination data based on molecular phylogeny and morphological analysis of Dennstaedtiaceae by Schwartsburd *et al*. (2020). Based on their results, only species included in the clade containing *Blotiella* + *Histiopteris* which in our study only *Histiopteris* species having close or netted veins. According to Schwartsburd *et al*. (2020), based on their phylogeny construction, free veins are one of the characteristics of the ancestor of Dennstaedtiaceae species.

Stele shape

The cross-section of the stipe is as significant to the rhizome structure. It possesses a layer of longitudinally elongated epidermal cells, a cortex, endodermis, and stele (Noraini *et al.*, 2012). According to Ogura (1972), stipe anatomy is suitable for systematic study as it possesses some variations for example in the shape, and type of stele as well as the presence of sclerenchyma cells under the epidermal layer. Noraini *et al.*, (2012) stated that variations in stipe anatomical characteristics can be seen especially in its shape and outline. In the stipe cross-section, five types of stele shapes observed in Dennstaedtiaceae species studied which were 'U'-shaped, 'I'-shaped, a combination of 'S' and 'W'-shaped, a combination of inverted 'C' and 'W'-shaped and scattered stele (Figure 4–6).

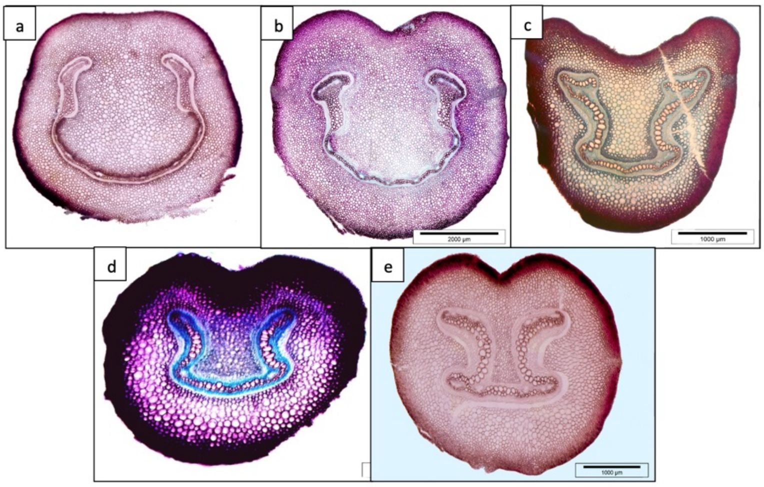

Fig. 4. ‘U’-shape stele. (a) *Microlepia ridleyi*, (b) *Microlepia speluncae*, (c) *Dennstaedtia ampla*, (d) *Paesia elmeri*, (e) *Hypolepis brooksiae*.

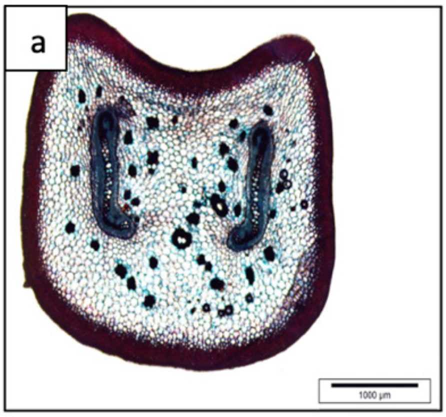

Fig. 5. ‘I’-shaped stele. *Monachosorum subdigitatum*.

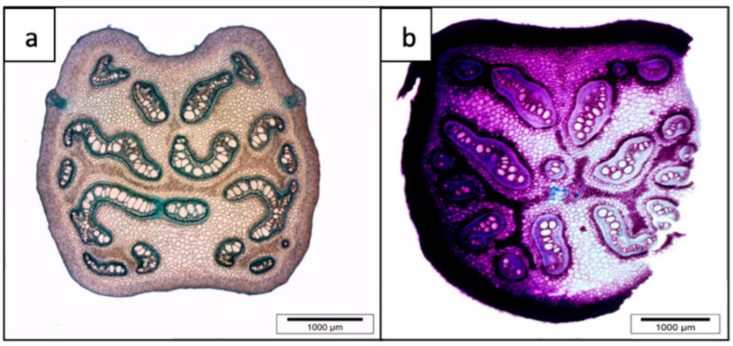

Fig. 6. Scattered stele. (a) *Pteridium aquilinum*, (b) *Pteridium esculentum.*

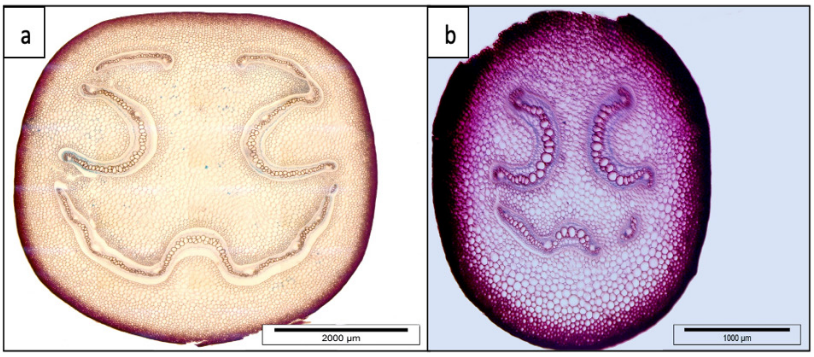

Fig. 7. (a) Combination of 'S' and 'W' form: *Histiopteris incisa*; (b) Combination of a set of inverted 'C' and 'W' forms: *Histiopteris stipulacea.*

Five out of ten species studied have a 'U'-shaped stele which are *Mic. ridleyi, Mic. speluncae, D. ampla, H. brooksiae,* and *Pae. elmeri*. Both *Microlepia* species have 'U'-shaped stele but *Mic. ridleyi* has a thicker adaxial xylem with a little curve at the end compared to its abaxial xylem which has a curved line xylem forming a semi-circle whereas the abaxial xylem in *Mic. speluncae* formed a curved semicircle (Figure 4). *Paesia elmeri* also has a 'U'-shaped stele in which the two lines of its adaxial xylem diverge and join at the abaxial xylem forming a slightly curved horizontal line. Similarly, the adaxial xylem of *H. brooksiae* diverged out and connected with a horizontal line abaxial xylem that has vertices at both of its sides forming a stele with a 'U' shape. Meanwhile, the 'U'-shaped stele observed in *D. ampla* has a diverged adaxial xylem and is connected with an abaxial xylem that forms a horizontal line (Figure 4). Our results support a previous study that identified a 'U'-shaped stele in the genus *Microlepia* (Nayar & Molly, 1980). Other fern species having 'U'-shaped stele include *Taenitis blechnoides* and *T. interrupta* (Maideen *et al*., 2023).

Only one species, *Monachosorum subdigitatum* has the shape of a stele which is 'I'-shaped (Figure 5). Meanwhile, both *Pteridium* species have many scattered steles (Figure 6). This result supported the findings of Lin and DeVol (1978), whereby the genus *Pteridium* showed a diversified pattern of vascular arrangement with more than 20 bundles in the cross-section of the stipe. For the *Histiopteris* genus, both species generally have a similar shape of stele (Figure 7). *Histiopteris incisa* (Figure 7a) has a stele that has a combination of 'S'-shaped facing each other in the adaxial xylem and 'W'-shaped in the abaxial xylem. There is a difference in the shape of the adaxial xylem of *Histiopteris stipulacea* (Figure 7b) as it has a combination of two inverted 'C' and 'W'-shaped in the abaxial xylem. Our findings supported the stele observations of the lowest part of the stipe in the *Histiopteris* genus by Faridah-Hanum *et al*., 2008. According to Faridah-Hanum *et al*., (2008) the stele shape for *Histiopteris* varies along the stipe, from rigid structure to less enhance in shape at the end of the stipe. This is in agreement with Ogura (1972) and Noraini *et al*., (2012) who stated that the length of the stipe displays different patterns of the steles at the lower, middle, and upper parts in some species and shows similar patterns in others. Other families that have similar stipe characters as Dennstaedtiaceae are the Adiantaceae and Pteridaceae in which the cross sections of the stipes are mostly terete and their stipes usually have a single bundle. In conclusion, the shape of the stele is one of the significant characteristics that can be used in the classification of a fern as stele has specific forms that are only owned by specific families and genus (Lin & DeVol, 1978).

CONCLUSION

In this study, anatomical features such as leaf vein patterns and stele shapes were identified as useful in differentiating the selected Dennstaedtiaceae species. Further thorough collections including more genera and species of Dennstaedtiaceae throughout Malaysia should be conducted to enhance the robustness of classification data for the Dennstaedtiaceae family. Future research integrating morphological, molecular, and anatomical data will be crucial for a comprehensive understanding of Dennstaedtiaceae species, encompassing aspects of taxonomy, evolutionary history, and ecological significance.

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ETHICAL STATEMENT

Not applicable.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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