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Comparative leaf anatomy between two sister species: *Artocarpus odoratissimus* (Lumok) and *A. mutabilis* (Pingan) in Sarawak

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Abstract

The indigenous Iban of Sarawak recognize *Artocarpus odoratissimus* Blanco as two distinct species, lumok and pingan, leading to the recent recognition of the latter as *A. mutabilis* Becc. While the morphology of these two species is similar, they differ in fruit, stipule, and twig characters. This study aims to identify distinguishing leaf anatomical characters in these taxa and aid in species delimitation. Lumok and pingan samples from primary and secondary forests in central and Southern Sarawak were preserved, sectioned, and mounted. Samples were observed using light and scanning electron microscopy. Findings have shown that these species differ in the type of epidermal walls, the number of cells in the glandular trichomes, the length of non-glandular trichomes, the number of vascular bundles in the midrib and petiole, and the number of collenchyma layers, which distinguish these two species. These anatomical differences support the distinction between *A. odoratissimus* and *A. mutabilis*, providing a practical tool for future anatomical and ecological studies of *Artocarpus*.

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Introduction

Moraceae, or the mulberry family, comprises c. 48 genera (POWO, 2025) and 1,200 species worldwide (Gardner *et al.* 2021). The family comprises several ecologically and economically important genera, including *Artocarpus* J.R.Forst. & G.Forst., which has c. 70 species native to Southeast Asia and Oceania (William *et al.* 2017). Many species of *Artocarpus* produce large, edible syncarps, and several are widely cultivated in the tropics, including *A. heterophyllus* Lam., *A. integer* (Thunb.). Merr (Cempedak), and *A. altilis* (Parkinson) Fosberg. Many other species also serve as local food sources for humans and forest animals (Abu Bakar *et al.* 2015). The wood of many *Artocarpus* species has economic importance and is utilized as a timber source for furniture, construction materials, and musical instruments (Raihandhany *et al.* 2018).

Artocarpus odoratissimus and *A. mutabilis* are two sister species. Previously considered conspecific and both known as tarap by Malays, the Iban people have long recognized these species as distinct. Pingan is a wild tree characterized by smaller leaves, less-sweet fruits with thinner pulp, and often, but not always, features long hair on its vegetative parts. In contrast, lumok is a cultivated tree with large leaves, thick twigs, large, sweet fruits with thick pulp, and short hairs on its twigs. These distinctions, also recognized by the Dusun people of Sabah, have led to the recent recognition of *A. odoratissimus* (lumok) and *A. mutabilis* (pingan) as separate scientific species (Gardner *et al.* 2022).

While *A. odoratissimus* is commonly cultivated in Borneo and the Philippines and found occasionally in secondary forests, *A. mutabilis* is rarely cultivated and is restricted to Borneo, where it is common in primary and secondary lowland and hill forests.

Among the local communities in Sarawak, the fruits of pingan and lumok are eaten fresh, fried with flour, or made into soups. The seeds of *Artocarpus odoratissimus* (lumok) can also be eaten roasted and fried, similar to potato chips, and the rough leaves are sometimes used to scrub an oily pot or wok (Tang *et al.* 2013). *Artocarpus odoratissimus* (lumok) is categorized as an underutilized fruit in Borneo (Salma *et al.* 2006); therefore, it is important to study it and its nearest wild relative, *A. mutabilis* (pingan), for conservation purposes. Therefore, this study aims to investigate and compare the leaf anatomical characters of *A. odoratissimus* (lumok) and *A. mutabilis* (pingan) to identify diagnostic features that can reliably distinguish the two taxa. By documenting and evaluating these anatomical differences, this study seeks to provide additional evidence supporting their taxonomic delimitation and to contribute practical anatomical characters for future identification, ecological, and systematic studies of *Artocarpus*.

Materials and methods

Taxon sampling

Five replicates of lumok leaves were collected from Kuching, Kampung Tanjung Bundong, Kota Samarahan and around Kapit district. Five replicates of pingan leaves were collected from Mount Matang, Kuching and Bukit Raya, Kapit. Herbarium specimens were prepared and deposited at Sarawak Herbarium (SAR). Table 1 shows the specimens used in this study.

Table 1. Specimens of *Artocarpus mutabilis* (pingan) and *A. odoratissimus* (lumok) used in this study.

Species	District	Locality	Collector's name	Collection number
Artocarpus mutabilis (pingan)	Kuching	On the way to the summit of Mt. Matang	Elliot, Raihan and Norazira	EG 893
	Kuching	On the way to the summit of Mt. Matang	Elliot, Raihan and Norazira	EG 896
	Kapit	Bukit Raya, next to the logging road	Elliot and Salang	EG 520
	Kapit	Sut River, old logging area	Elliot and Salang	EG 538
	Kapit	Sut River, old logging area	Elliot and Salang	EG 540
Artocarpus odoratissimus (lumok)	Kota Samarahan	Near the roadside of Tanjung Bundong Village	Raihan and Norazira	RR 01
	Kota Samarahan	Near the roadside of Tanjung Bundong Village	Raihan and Norazira	RR 02
	Kuching	Near the roadside of Viva City Mall	Raihan and Norazira	RR 03
	Kapit	In the backyard of Mr. Salang's house	Raihan, Elliot, Norazira and Aida	RR 12
	Kuching	Bung Jagoi	Elliot, Jugah Tagi and Wan Nur Fatiha	EG 625

Anatomical analysis

The leaves were preserved in a fixed AA solution (70% ethanol and glacial acetic acid in a 3:1 ratio) following Cutler *et al.* (2008). The midrib and petiole were transversely sectioned using a sliding microtome (Leica SM2000R) of 14–20 µm. All samples were decolorized using a 70% sodium hypochlorite solution and double-stained with safranin O and Alcian blue solution. Dehydration took place in ascending ethanol concentration, and permanent histological slides were prepared. The images were taken using a video camera DP72 Olympus, coupled with an Olympus microscope, and processed using Cell-DX 15 software.

For epidermal cell observation, the lamina was cut into a 1 × 1 cm square and boiled until the layers separated. The layers were then bleached with 70% sodium hypochlorite solution and washed with distilled water. The layers were stained with safranin O and dehydrated in ascending ethanol concentration and the images were analyzed using the same method as preparing histological slides for cross-sections. For an analysis of the Field Emission Scanning Electron Microscope (FESEM), the samples were prepared following the method by Nikara *et al.* (2020), with a slight modification to the timing for bleaching the samples. The timing for bleaching the leaf epidermis using sodium hypochlorite was reduced to one to three minutes per replicate until a clear result was achieved.

Results

The leaves of *Artocarpus odoratissimus* and *A. mutabilis* exhibit distinct gross morphological differences. Generally, *A. odoratissimus* has larger leaves with a relatively shorter and sparser indumentum. In contrast, *A. mutabilis* tends to have smaller leaves that are more densely covered in longer indumentum, particularly in specimens collected from Kapit, which show significantly thicker and more persistent hair coverage compared to other localities. Furthermore, the leaves of *A. mutabilis* appear somewhat golden due to its thicker indumentum compared to *A. odoratissimus*. Comparative analysis of the leaf anatomy between the two species reveals both shared traits and distinct structural differences that may support species delimitation and ecological adaptation.

Micromorphological study of leaf epidermal characters of both species indicated some similarities where the anomocytic stomata were only found on the abaxial surface (hypostomatic) (Fig. 1a, b). Druses were present in both species and scattered around the midrib in the parenchyma, collenchyma cells, and vascular bundles (Fig. 2a, b).

Notable differences were observed in the leaf epidermis and cross sections of the midrib and petiole. Glandular and non-glandular trichomes on the abaxial side were present in all pingan and lumok samples. The peltate glandular trichomes were six-celled in pingan (Fig. 1a) and eight-celled in lumok (Fig. 1b). Pingan samples had two types of non-glandular trichomes: a) simple multicellular trichomes in two lengths, the short hairs with a mean length of 556 μm, and the long hairs with a mean length of 1375 μm with acute apex and echinate ornamentation and b) simple multicellular trichomes with a smooth surface and uncinate ornamentation (Fig. 1c). By contrast, only one type of non-glandular trichome was present in lumok: simple multicellular trichomes in two lengths, the short hairs with a mean length of 116 μm, and the long ones with a mean length of 545 μm with acute apex and echinate ornamentation (Fig. 1d). The leaf epidermis showed a straight to curved anticlinal walls in pingan (Fig. 2c) and sinuous anticlinal walls in lumok (Fig. 2d). The leaf venation in pingan and lumok species also have no veinlet endings (Fig. 2e, f). Comparison of the transverse plane of the leaf epidermis was summarized in Table 2.

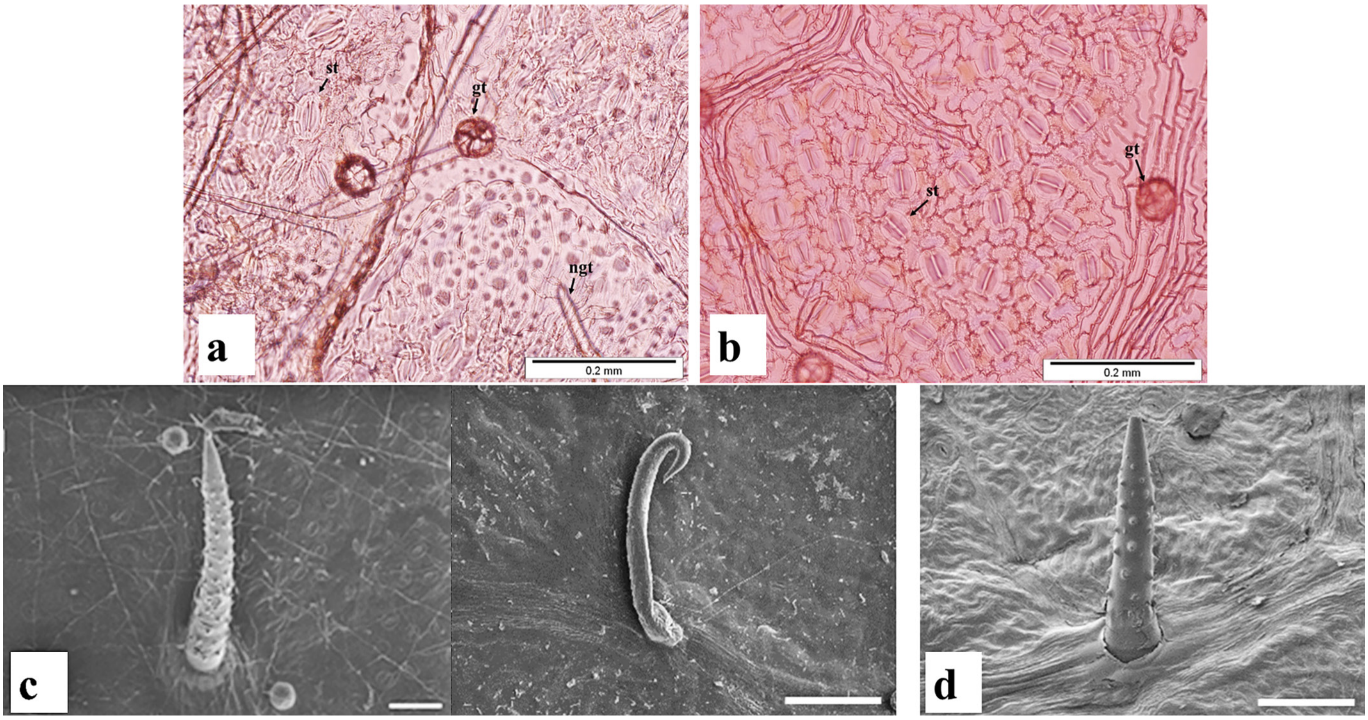

Figure 1. Leaf anatomy of *Artocarpus mutabilis* (pingan) and *A. odoratissimus* (lumok). a) Abaxial surface showing anomocytic stomata, glandular trichome and non-glandular trichome in pingan; b) Abaxial surface showing anomocytic stomata, and glandular trichome in lumok; c) Scanning electron micrograph showing two types of simple non-glandular multicellular trichome in pingan; d) Scanning electron micrograph showing a type of simple non-glandular multicellular trichome in lumok. Abbreviations: ngt = non-glandular trichome, gt = glandular trichome, st = stomata. Scale bars: a, b = 0.1 mm; c–d = 10 μm.

Table 2. Summary of leaf epidermal peel in *Artocarpus mutabilis* (pingan) and *A. odoratissimus* (lumok).

Characters	Pingan	Lumok
Adaxial surface	Epidermis with straight to curved anticlinal walls, no stomata.	Epidermis with sinuous anticlinal walls, no stomata.
Abaxial surface	Epidermis with straight to curved anticlinal walls, anomocytic stomata present.	Epidermis with sinuous anticlinal walls, anomocytic stomata present.
Glandular trichomes	Peltate, 6 cells.	Peltate, 8 cells.
Non-glandular trichomes	Simple multicellular trichomes; long hairs acute, ornamentation echinate. Short hairs av. length 556 μm; long hairs av. length 1375 μm.	Simple multicellular trichomes; long hairs acute, ornamentation echinate. Short hairs av. length 116 μm; long hairs av. length 545 μm.
	Simple multicellular trichome; long, smooth surface and uncinate ornamentation.	Absent.
Leaf venation	Closed areolar venation with no veinlets ending.	Closed areolar venation with no veinlets ending.

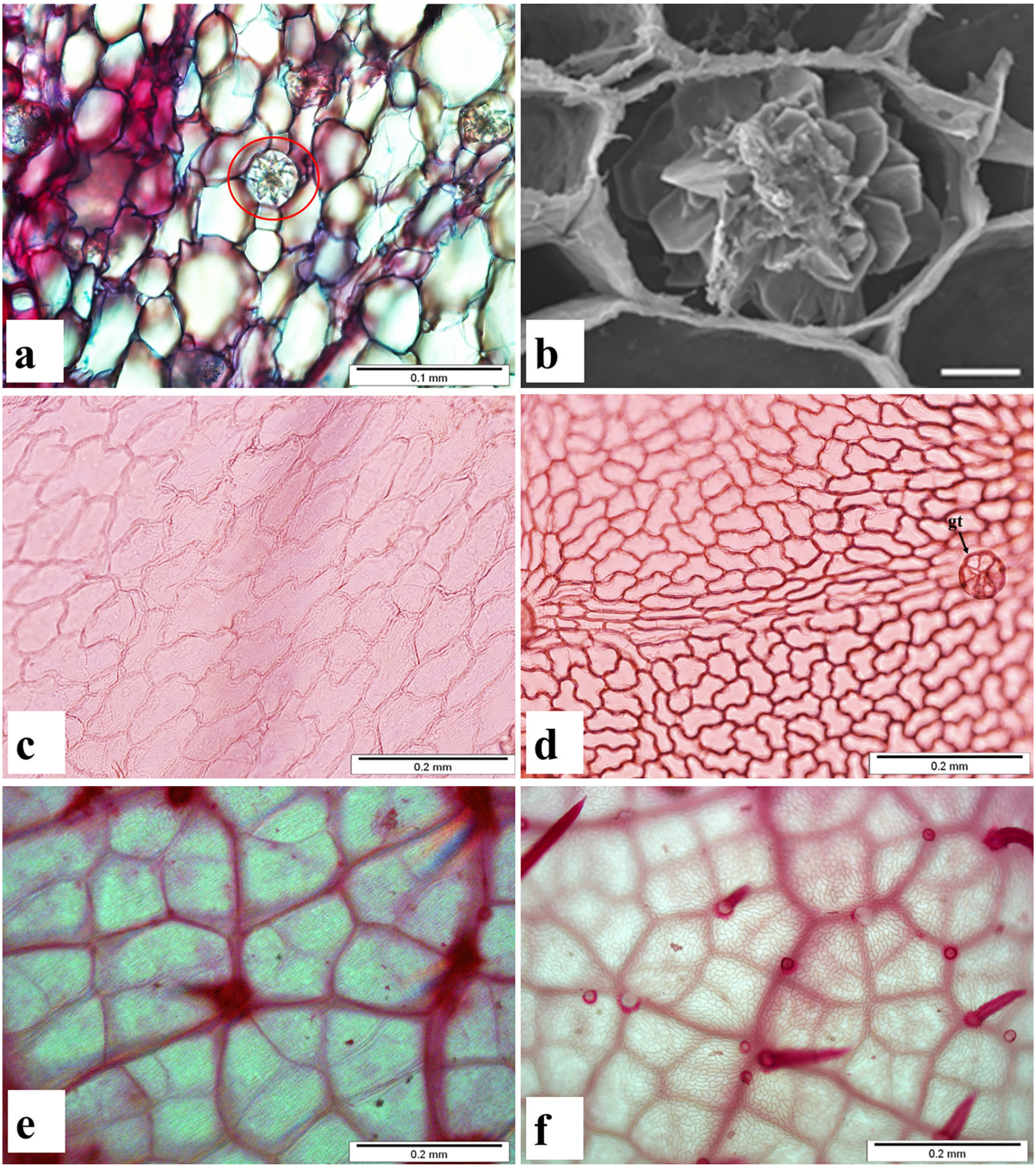

Figure 2. Leaf anatomy of *Artocarpus mutabilis* (pingan) and *A. odoratissimus* (lumok). a) Presence of druses (red circle) in midrib cross-section of pingan; b) Close-up image of druse in scanning electron micrograph of the midrib; c) Adaxial surface showing the straight to curve anticlinal walls in pingan; d) Abaxial surface showing sinuous anticlinal walls and glandular trichome in lumok; e) Leaf clearing showing no veinlet venation in pingan; f) Leaf clearing showing no veinlet venation in lumok. Abbreviations: gt: glandular trichome. Scale bars: a = 0.1 mm; b = 10 µm; c–f = 0.2 mm.

Observation of the midrib showed that the adaxial outline of both species was convex with an inverted U shape. In contrast, the abaxial outline was convex, broadly U-shaped to semicircular (Figs 3a, b; 5a, b). The outer vascular bundles were co-lateral (Fig. 3c, d), arranged in a closed system consisting of an 'O' ring shape for pingan (c. 49 vascular bundles) and lumok (c. 33 vascular bundles). Medullary vascular bundles of pingan (c. 22 vascular bundles) and lumok (c. 20 vascular bundles) were scattered randomly in the parenchyma cortex area. Pingan had an additional vascular bundle located on the right of the outer vascular bundles (≥ 1 vascular bundle), while additional vascular bundles in lumok were located on the right and left above the outer vascular bundles (c. 3 vascular bundles). The lower part of the vascular bundle of pingan was closer to the abaxial part of the midrib than lumok (Fig. 5a, b). Three or four layers of collenchyma cells are located below the adaxial epidermis in pingan (Fig. 3e), but in lumok, there are eight to ten layers (Fig. 3f). Several layers of sclerenchyma cells are present under the epidermal cells of the midrib and ensheathing the outer vascular bundles of both types (Fig. 5a, b). The characteristics of the transverse section of the midrib are summarized in Table 3.

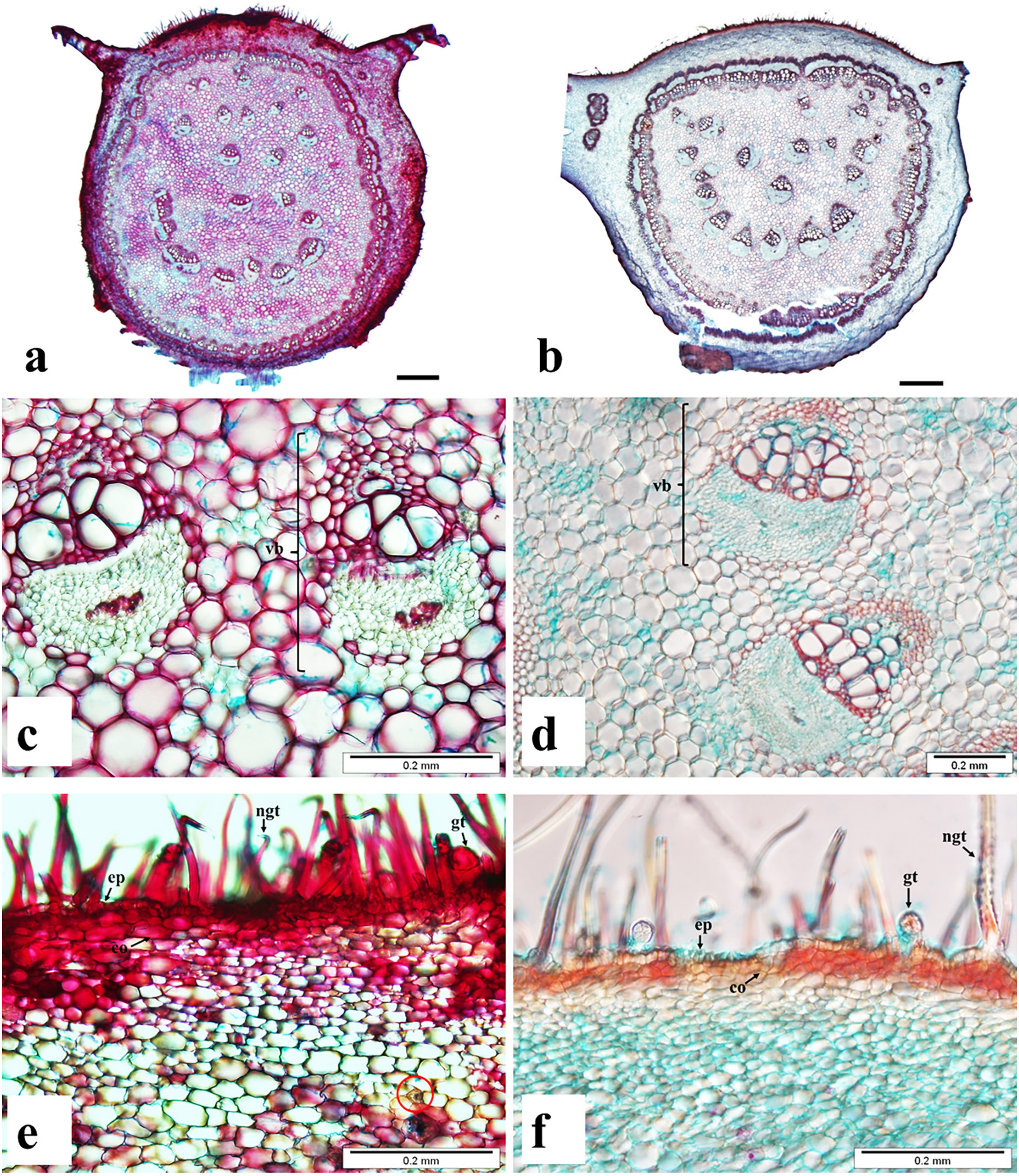

Figure 3. Leaf anatomy of *Artocarpus mutabilis* (pingan) and *A. odoratissimus* (lumok). a) Cross-section of the midrib of pingan; b) Cross-section of the midrib of lumok; c) Vascular bundle system showing vascular bundle arranged in collateral type in pingan; d) Vascular bundle system showing vascular bundle arranged in collateral type in lumok; e) Cross-section showing the layer of epidermis, collenchyma layers, trichomes and druses in red circle in pingan; f) Cross-section showing the layer of epidermis, collenchyma layers and trichomes in lumok. Abbreviations: vb = vascular bundle, ep = epidermis, co = collenchyma, ngt = non-glandular trichome, gt = glandular trichome. Scale bars: a, b = 0.1 mm; c–f = 0.2 mm.

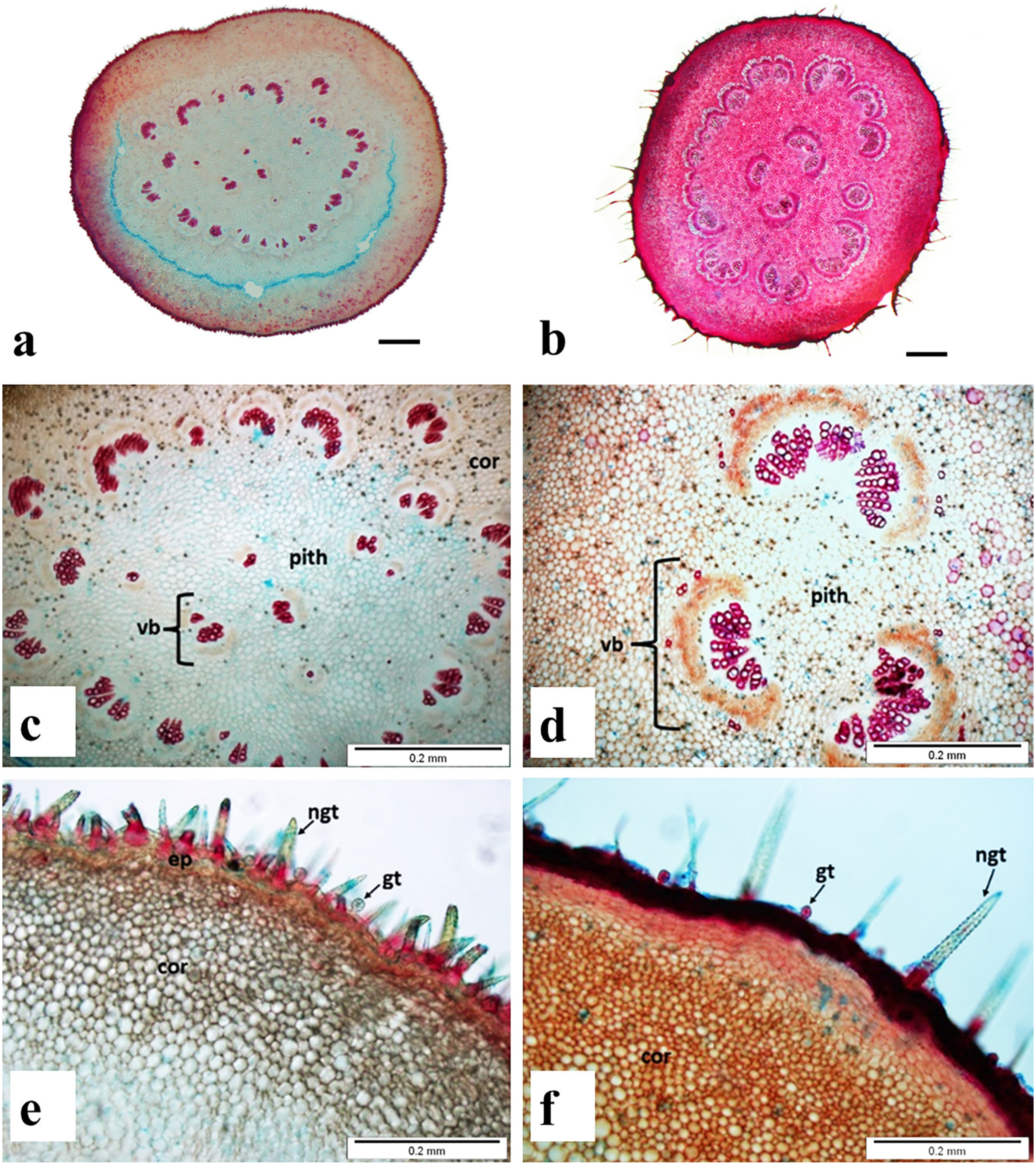

Figure 4. Leaf anatomy of *Artocarpus mutabilis* (pingan) and *A. odoratissimus* (lumok). a) Cross-section of the petiole of pingan; b) Cross-section of the petiole of lumok; c) Vascular bundles system arranged in collateral type in pingan; d) Vascular bundles system arranged in collateral type in lumok; e) Cross-section showing the layer of the epidermis, collenchyma layers, cortex, and trichomes in pingan; f) Cross-section showing the layer of the epidermis, collenchyma layers, cortex, and trichomes in lumok. Abbreviations: vb = vascular bundles, cor = cortex, ep = epidermis, ngt = non-glandular trichome, gt = glandular trichome. Scale bars: a, b = 0.1 mm; c–f = 0.2 mm.

The transverse section of the petiole showed that the outline of the petiole in pingan and lumok is rounded (Figs 4a, b; 5c, d). The vascular bundles arrangement for pingan and lumok is collateral and arranged in an interrupted ring shape (Fig. 4c, d). Besides that, several layers of sclerenchyma are present under the epidermal cells and ensheathing the outer and medullary vascular bundles (Fig. 4e, f). Pingan has c. 18 outer vascular bundles while lumok has c. 14 vascular bundles. Pingan has c. 6 medullary vascular bundles, while lumok has c. 3 vascular bundles. The trichomes in lumok are shorter, the shorter hairs c. 452 µm average length and the longer hairs c. 1014 µm average length compared to pingan which has short hairs c. 933 µm average length and longer hairs c. 2221 µm average length (Fig. 4e, f). The non-glandular and glandular trichomes are also notable characteristics in the petiole of pingan and lumok (Fig. 4e, f). A comparison of the cross-section for both types of the petiole is summarized in Table 4.

Table 3. Summary of the transverse section of the leaf midrib of *Artocarpus mutabilis* (pingan) and *A. odoratissimus* (lumok).

Characters	Pingan	Lumok
Adaxial outline	Convex, an inverted U shape.	Convex, a broadly inverted U shape.
Abaxial outline	Convex, broadly U-shaped to semicircular.	Convex, broadly U-shaped to semicircular.
Vascular bundles	c. 49 primary vascular bundles arranged continuously in one closed ring. c. 22 medullary vascular bundles scattered in the parenchyma cortex area. Additional vascular bundles arranged on the right above the primary vascular bundle (≥ 1 vascular bundle).	c. 33 primary vascular bundles arranged continuously in one closed ring. c. 20 medullary vascular bundles scattered in the parenchyma cortex area. Additional vascular bundles arranged on the right and left side above the primary vascular bundles (≥ 3 vascular bundles).
Collenchyma layers	3 or 4 layers.	8–10 layers.
Sclerenchyma layers	Present continuously under epidermal cells and ensheathing the primary vascular bundles.	Present continuously under epidermal cells and ensheathing the primary vascular bundles.
Crystals	Druses present, scattered in the midrib.	Druses present, scattered in the midrib.

Discussion

The comparative leaf anatomical study between *Artocarpus odoratissimus* and *A. mutabilis* revealed significant micromorphological and anatomical differences that support their recognition as distinct species. These findings align with previous taxonomic distinctions made by local communities (Gardner *et al.* 2022) and contribute to a better understanding of their morphological adaptations, ecological preferences, and potential conservation strategies. Although both species are hypostomatic with anomocytic stomata, a common trait among Moraceae, including *Ficus* L. and *Morus* L. species, notable differences emerge in epidermal and internal leaf structures (Erarslan *et al.* 2022; Ogunkale and Oladele 2008; Sonibare *et al.* 2005).

The sinuous adaxial epidermal walls observed in lumok contrast sharply with the straighter walls in pingan indicating species-specific cell wall patterning and aiding in taxonomic differentiation (Zakaria *et al.* 2022).

The number of outer vascular bundles in the midrib of pingan is higher than in lumok (49 in pingan vs 33 in lumok), and the number of medullary vascular bundles in the petiole is also greater in pingan. Both species possess additional vascular bundles, but their positions differ. In pingan, these additional bundles are located directly above the outer vascular bundles, while in lumok, they are positioned at the upper left and right of the outer vascular bundles.

According to Cutler (2008), vascular arrangement is typically consistent and holds great systematic value. These results are further supported by a study by Ishak *et al.* (2021) on Euphorbiaceae taxa, which demonstrated variability in anticlinal wall patterns, the number and arrangement of midrib vascular bundles, and stomatal types of traits which are useful in species classification and differentiation. These anatomical differences also corroborate the findings of Gardner *et al.* (2022), who provided phylogenetic evidence that *Artocarpus odoratissimus* and *A. mutabilis* are two distinct species.

Sclerenchyma or collenchyma layers are commonly associated with the vascular bundles in the *Ficus* family and can be found close to the epidermis, where it usually forms adaxial and abaxial plates in the midrib or subepidermal rings in the petiole (Chantarasuwan *et al.* 2014). In this study, sclerenchyma layers are present ensheathing both outer and medullary vascular bundles of pingan and lumok. In contrast, the differences in the number of collenchyma layers between lumok and pingan (Table 3) suggest that these two species are distinct. This result is supported by Akinloye *et al.* (2015), who stated that the distribution of the sclerenchyma and collenchyma layers can give valuable data for taxonomic delimitation of the *Artocarpus* species.

Both species exhibit hypostomatic leaves with anomocytic stomata. This trait is also observed in other *Artocarpus* species such as *A. altilis* and *A. heterophyllus* (Gangadhara and Inamdar, 1977). However, Gangadhara and Inamdar (1977) reported that two stomatal types—anomocytic and actinocytic can occur in *Artocarpus*, indicating a broader variation within the genus. The presence of anomocytic stomata on the abaxial surface of lumok and pingan supports this pattern. Gangadhara and Inamdar (1977) further noted that anomocytic, anisocytic, and, rarely, paracytic stomata are observed in members of the Urticaceae, *Dorstenia* L. and *Artocarpus*. Similarly, Sá *et al.* (2019) confirmed the presence of anomocytic and anisocytic stomata in *A. altilis* and *A. heterophyllus*. These findings suggest that stomatal type may be a useful character for discriminating species within the genus *Artocarpus*.

This study identified two trichome types: (1) glandular and (2) non-glandular. In Moraceae, glandular trichomes typically exhibit a multicellular head and a unicellular peduncle, although the number of head cells varies among species (Schnetzler *et al.* 2017). While Jarrett (1959) reported that *Artocarpus odoratissimus* (encompassing both lumok and pingan) possesses glandular trichomes with 8–16-celled heads, our results demonstrate a distinction between the two taxa: lumok has eight-celled peltate glandular trichomes, whereas pingan has six-celled heads (Table 2). In a study by Schnetzler *et al.* (2017) also noted that peltate trichomes are found exclusively in species of *Artocarpus*, suggesting that this feature may have diagnostic value for the genus.

Table 4. Summary of the transverse section of the leaf petiole of *Artocarpus mutabilis* (pingan) and *A. odoratissimus* (lumok).

Characters	Pingan	Lumok
Petiole shape	Rounded.	Rounded.
Vascular bundles	c. 18 primary vascular bundles arranged in one interrupted ring located near the cortex. c. 6 medullary vascular bundles arranged randomly between the primary vascular bundles and pith area.	c. 14 primary vascular bundles arranged in one interrupted ring located near the cortex. c. 3 medullary vascular bundles scattered randomly near the pith.
Glandular trichome	Peltate, eight cells.	Peltate, four cells.
Non-glandular trichome	Present. Av. length of short hairs 933 μm; av. length of long hairs 2221 μm.	Present. Av. length of short hairs 452 μm; av. length of long hairs 1014 μm.
Crystals	Druses present, scattered in the petiole.	Druses present, scattered in the petiole.

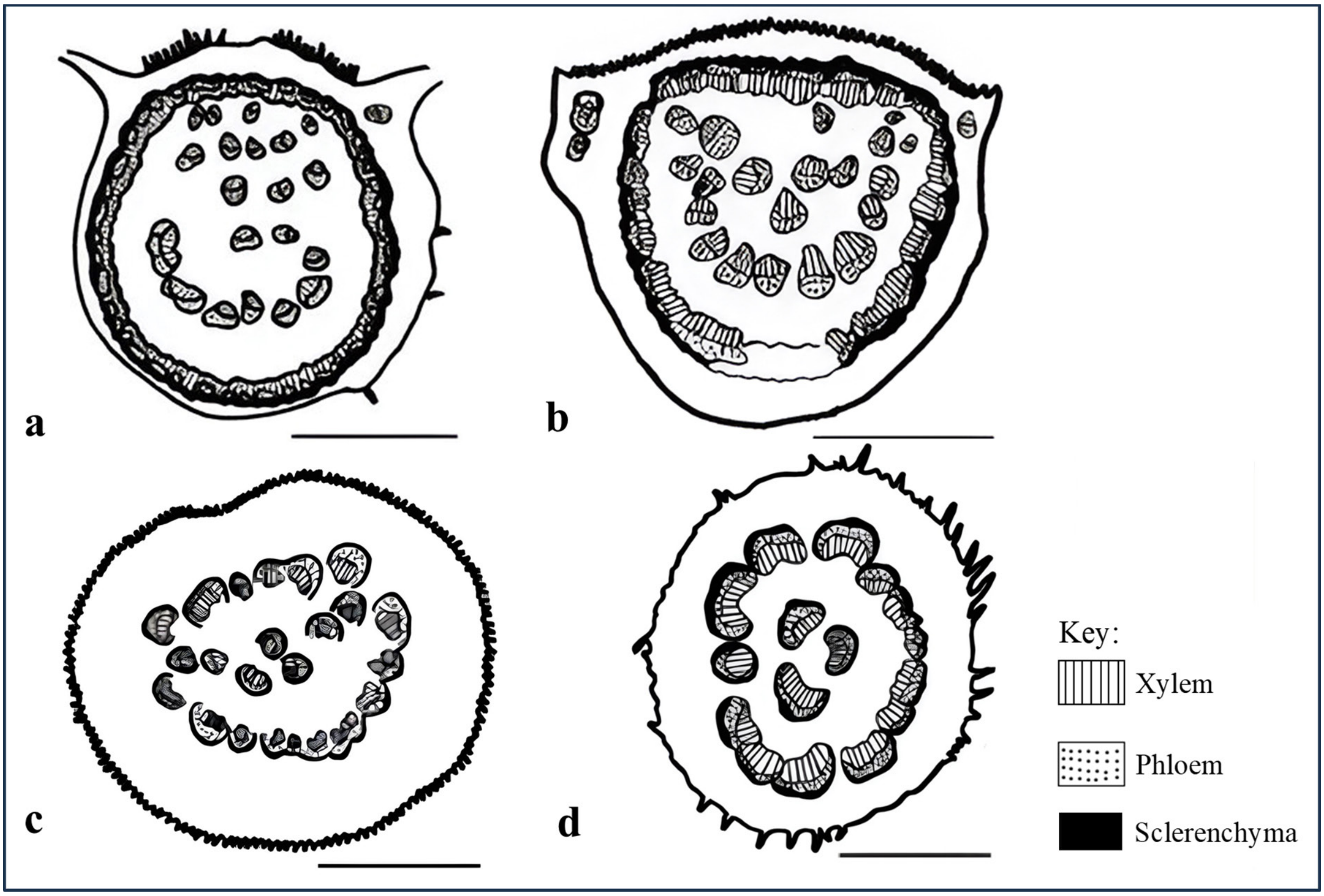

Figure 5. Leaf anatomy of *Artocarpus mutabilis* (pingan) and *A. odoratissimus* (lumok). a) Line drawing of pingan and lumok: a) Midrib of pingan; b) Midrib of lumok; c) Petiole of pingan; d) Petiole of lumok. Scale bars: = 0.2 mm.

The non-glandular trichomes described as simple, hooked, and conical are commonly found in *Artocarpus* species as reported by Gangadhara and Inamdar (1977). Between the two taxa, pingan showed two types of non-glandular trichomes while lumok species only has one type, as summarized in Table 2. Additionally, the results showed the average length of non-glandular trichomes in pingan is longer than in lumok (Table 2 and Table 4), contributing to a rougher leaf texture in pingan when touched. Valkama *et al.* (2013) highlighted that leaf trichome structure is significant in distinguishing between Finnish *Betula* L. species, supporting the idea that trichome characteristics are valuable for species identification.

In the present study, FESEM analysis revealed that the elements with the highest absorbance peaks were carbon, oxygen, and calcium—confirming the presence of druses have been found abundantly in the midrib and petiole of lumok and pingan. Other than that, druses were also found and reported in other *Artocarpus* species, such as *A. altilis* (Parkinson) Fosberg (Akinloye *et al.* 2015). This finding is also supported by Periyanayagam and Karthikeyan (2013) and Sá *et al.* (2019), who reported that druses were also found abundantly in the leaf of *A. heterophyllus* indicating that druses can be commonly found in the leaf of *Artocarpus*. The presence of these druses in both lumok and pingan, particularly surrounding the midrib and abundantly in the cortex of the petiole, supports their placement within the genus *Artocarpus*.

While leaf anatomical characters provide useful diagnostic features for distinguishing *Artocarpus odoratissimus* and *A. mutabilis*, several limitations should be acknowledged. Leaf anatomical traits may exhibit a degree of phenotypic plasticity influenced by environmental factors such as habitat type, light intensity, and moisture availability, which may contribute to intraspecific variation. In addition, this study focuses exclusively on leaf anatomy and sampling from selected localities in Sarawak; therefore, it does not discuss calcium oxalate druses in the leaves of *Artocarpus*. These do not capture the full geographic or morphological variation of both taxa across their entire distribution.

Some anatomical characters observed here, including stomatal type and the presence of calcium oxalate druses, are shared widely within the genus *Artocarpus* and thus have limited taxonomic resolution when used in isolation. Anatomical evidence should therefore be regarded as complementary to other data sources. To date, no studies have yet directly linked specific genes or molecular pathways to these anatomical traits observed in *Artocarpus*. Nevertheless, molecular phylogenetic studies have demonstrated clear genetic differentiation between *A. odoratissimus* and *A. mutabilis*. Using genome-scale nuclear data generated through targeted capture sequencing (Hyb-Seq) and complementary microsatellite analyses, Gardner *et al.* (2022) provided strong molecular evidence supporting the recognition of these taxa as distinct species.

Future studies integrating molecular markers, which are generally more stable and less influenced by environmental conditions, with anatomical and ethnobotanical data would provide a more robust framework for species delimitation and evolutionary studies within *Artocarpus*.

In conclusion, this anatomical study revealed significant differences between lumok (*Artocarpus odoratissimus*) and pingan (*A. mutabilis*), reinforcing the phylogenetic findings of Gardner *et al.* (2022) and supporting the Iban communities' recognition of lumok and pingan as distinct species. By integrating anatomical evidence with ethnobotanical context such as traditional knowledge and domestic use, this finding contributes to a more comprehensive approach to species delimitation, conservation, and the potential domestication of under-utilized fruits like lumok in Borneo.

Acknowledgements

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