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Updated information on qualitative leaf anatomical characters of *Eusideroxylon zwageri* from East Kalimantan, Indonesia

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Abstract. *Dewi AP, Wulansari TYI, Senjaya SK, Arifiani D, Wanda IF, Lisnawati Y, Sunardi, Prawestri AD, Martiansyah I, Evana, Satrio RD, Hartono AMNK, Suyoko, Yuswandi AY, Syukur M, Sari DK, Rasyl CA. 2025. Updated information on qualitative leaf anatomical characters of* Eusideroxylon zwageri *from East Kalimantan, Indonesia. Nusantara Bioscience 17: 322-336.* *Eusideroxylon zwageri*, the sole species of its genus (*Eusideroxylon)* and one of the most economically and culturally significant timbers of Borneo known as Bornean ironwood or "kayu ulin", has been extensively studied for its ecology, genetics, and conservation, yet its foliar anatomy remains poorly documented. This study provides an updated qualitative assessment of leaf anatomical characters of *E. zwageri* based on 66 accessions representing five subpopulations in East Kalimantan, Indonesia. Transverse and paradermal sections of the lamina, midrib, and petiole were prepared following standard microtechnique procedures, and 37 anatomical traits were recorded. The results showed that most foliar anatomical features of *E. zwageri* are consistent with the Lauraceae family. A single character appears diagnostic for *E. zwageri*—osteosclereids present in the mesophyll of the lamina. Several anatomical features of *E. zwageri* indicate functional adaptation, including superficial stomata (related to efficient CO_2 intake), sclereids (contributing to the hardness and durability of the wood), oil cell distribution (which helps prevent pest attacks), suggesting functional adaptations related to gas exchange efficiency, mechanical reinforcement, and defense against herbivory. Nevertheless, understanding pronounced lignification of sclerenchyma and sclereids may constrain regeneration, posing challenges for conservation. These updated anatomical data provide a foundation for future taxonomic, ecological, and conservation research, particularly in developing propagation strategies to support large-scale restoration of this Vulnerable species.

Keywords: Anatomical markers, conservation, Lauraceae, sclereids, taxonomy

INTRODUCTION

Eusideroxylon zwageri Teijsm. and Binn. was first described in 1863 in the publication Natuurkundig Tijdschrift voor Nederlandsch-Indië. Vol. 25 (Koninklijke Natuurkundige Vereeniging in Nederlandsch Indië., and Natuurkundige Vereeniging in Nederlandsch Indië 1850). *E. zwageri* became the sole species of the genus *Eusideroxylon* after the other species, *E. melagangai,* was recognized under a different genus, *Potoxylon melagangai* (Symington) Kosterm. (Kostermans 1978). In Indonesia, *E. zwageri* is considered one of the most economically valuable timber commodities due to its exceptional durability. Its wood is widely used in marine constructions, including pilings, wharfs, docks, sluices, dams, and ships (keels, ribs, and decking) (Slik 2009). It is also widely utilized in heavy constructions for bridges, power line poles, masts, piles, and house posts (Slik 2009). Culturally, *E. zwageri* plays a significant role among the Dayak people, whose iconic long houses are constructed using ironwood as the main structural frame and pillars (Slik 2009; Suciyati et al. 2021). Local tribes considered the tree sacred and believed to possessed mystical powers (Slik 2009; Zahorka 2020). Ecologically, *E. zwageri* is favored as a nesting tree by orangutans in its natural habitat (Sayektiningsih and Rayadin 2011).

The species is classified under the family Lauraceae, and phylogenetic study indicates that it is closely related to *Cryptocarya*, *Beilschmiedia,* and *Potameia* (Chanderbali et al. 2001). The species has been categorized as Vulnerable (VU) according to the IUCN Red List Assessment (Asian Regional Workshop (Conservation and Sustainable Management of Trees, Viet Nam, August 1996) 1998). Consequently, research efforts on *E. zwageri* have primarily focused on several key areas, including habitat distribution, plant association, and carbon dating (Kurokawa et al. 2003; Arbain 2015; Prayoga et al. 2019; Saputro et al. 2022; Sunardi et al. 2022), plant development and propagation (Hakim 2008; Purba et al. 2019), and population genetics (Rimbawanto et al. 2006; Md-Isa et al. 2021; Ridzqya et al. 2024). Despite this extensive body of work, comparatively few studies have focused on the morphology (Sidiyasa et al. 2013; Irawan et al. 2016; Aiso-Sanada et al. 2020; Dewi et al. 2023) and anatomical characters of *E. zwageri* (Gusmalawati et al. 2014; Dewi et al. 2023). The pioneering anatomy reference, "Anatomy of the Dicotyledons" by Metcalfe and Chalk (1957), describes the anatomy of many families, including Lauraceae. However, it does not provide information on the anatomy of *Eusideroxylon*.

Despite the ecological and cultural importance of *E. zwageri*, its foliar anatomy remains poorly documented. Existing studies have focused primarily on stem structure or reported only scattered quantitative leaf traits, and no research has provided an integrated description of the lamina, midrib, and petiole across multiple subpopulations. Moreover, potential intraspecific variation in leaf anatomy has never been examined, and diagnostic characters for species-level delimitation within Lauraceae remain unresolved. This knowledge gap limits our understanding of the species' adaptive biology, taxonomic placement, and regeneration constraints, hindering efforts to improve propagation and conservation of this Vulnerable tree species.

While numerous studies have focused on the genetic diversity and conservation strategies of *E. zwageri* (Widyatmoko et al. 2011; Md-Isa et al. 2021; Sukartiningsih et al. 2025), anatomical aspects, particularly leaf anatomy, remain underexplored. Leaf anatomy plays a critical role in understanding the ecological adaptability and physiological resilience of long-lived tropical tree species. The anatomical structure of leaves, including cuticle thickness, stomatal density, mesophyll organization, and vascular tissue arrangement, reflects the plant's adaptation to environmental stressors such as water availability, light intensity, and temperature fluctuations (Yang et al. 2018).

Gusmalawati et al. (2014) described the anatomical traits of *E. zwageri,* but limited their description to stem anatomy. Meanwhile, Dewi et al. (2023) only mentioned several quantitative characters derived from leaf anatomy. However, a comprehensive profile integrating the morphological and anatomical characters of *E. zwageri* is still lacking. It could serve as a crucial taxonomic tool and provide insights into its adaptive biology, and needs to be produced.

This study aims to provide updated information on the anatomical structure of *E. zwageri* by conducting a thorough examination of the essential vegetative organ, the leaf. Specimens were collected from East Kalimantan, Indonesia, a region reported to harbor higher genetic richness and broader distribution of the *E. zwageri* (Sukartiningsih et al. 2025). The findings are expected to reveal potential anatomical variations within the species, which may serve as a key character for identification and future taxonomic work.

MATERIALS AND METHODS

Study area

We collected 66 leaf samples during field exploration from 2021 to 2024. The exploration sites are located in East Kalimantan Province, Indonesia (Figure 1) and include five subpopulations: Kongbeng Sub-district, Modang Village, Paser Sub-district (Taman Hutan Rakyat Lati Petangis and Tanjungpinang Village), and Kutai National Park (Table 1). We collected anatomical samples following Sass (1951), with several leaves collected from each plant, ranging from two to three. We stored the sample in 70% alcohol as the fixative solution. Herbarium specimens and anatomical slide preparations were deposited as collections under the management of the Herbarium Bogoriense, Directorate of Scientific Collection Management, Indonesian National Research and Innovation Agency (BRIN).

Procedures

Anatomy slide preparation

We prepared the anatomical slides in the Plant Anatomy Laboratory in Pilot Plant 4 Building, Science and Techno Park of Dr. (H.C.) Ir. Soekarno, located in Cibinong, Bogor, West Java, Indonesia. We followed Sass (1951) to prepare transverse sections and applied the Cutler (1978) method to make semi-permanent paradermal slides. Transverse sections were made by cutting the leaves at the center (midrib included), about 1 × 0.5 cm. The leaf samples were treated with a dehydration solution of tert-butanol, ethanol, and water and with Neo-Clear as a clearing agent. The slides were stained using double staining, 1% safranin and 2% fast green, then sections were covered with entellan. Paradermal sections were prepared by cutting leaves measuring 1 × 1 cm and boiling them in nitric acid until the epidermis separated. The section was then placed on a glass slide and stained with 2% safranin to create a colour contrast. The sections were treated with glycerin and covered with a cover glass; nail polish was used to seal the edges.

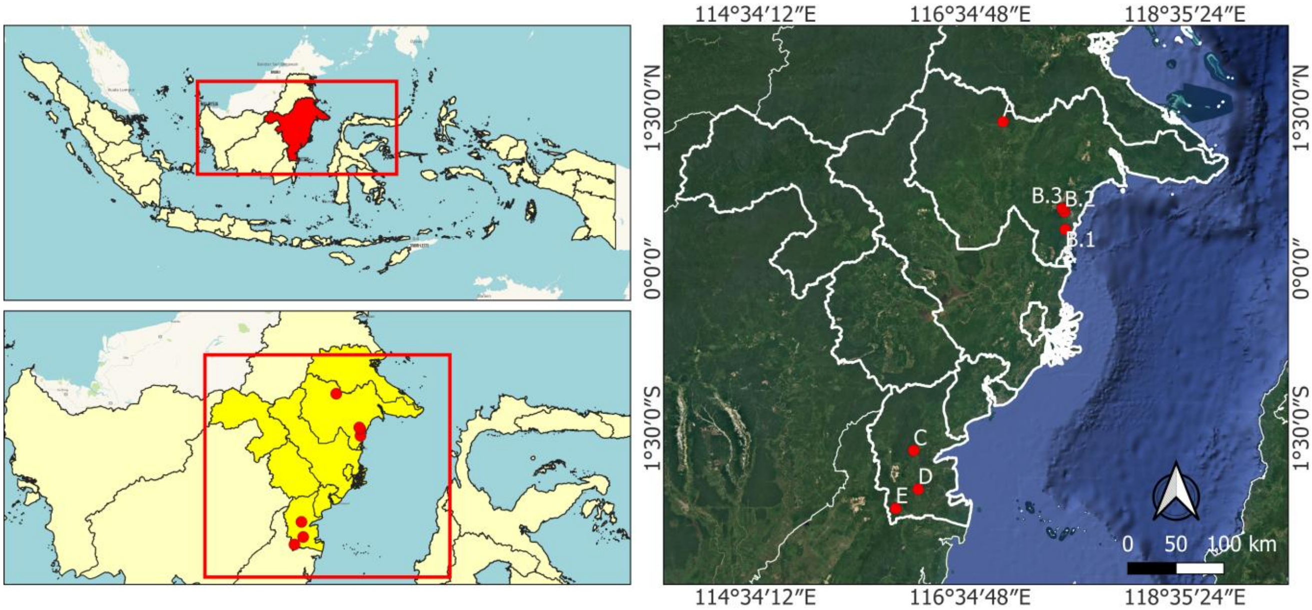

Figure 1. Map of East Kalimantan, Indonesia, showing five subpopulations of *Eusideroxylon zwageri*: A. Subpopulation 1: Kongbeng Sub-district - Sungai Seleq; B. Subpopulation 2: Kutai National Park, including Mentoko, Prevab, and Sangkima research area; C. Subpopulation 3: Kuaro Sub-district - Modang Village; D. Subpopulation 4: Paser Sub-district - Taman Hutan Rakyat Lati Petangis; E. Subpopulation 5: Paser Sub-district - Tanjung Pinang Village

Table 1. Leaf samples of *Eusideroxylon zwageri* were collected from East Kalimantan, Indonesia

Subpopulation	Accession code*	Total samples
Kongbeng Sub-district	GGA 21 (1-21)	21
	GGA 21-N (1-4)	4
	GGA MER (1-3)	3
	GGA KUN (1-4)	4
	GGA HP (1-5)	5
	GGA HA (2-11)	10
Kutai National Park (Mentoko, Prevab, Sangkima)	DA (2405, 2408, 2413, 2463, 2487, 2494)	6
Kuaro Sub-district (Modang Village)	MOD (1-5)	5
	DA (2369-2371)	3
Paser Sub-district (Taman Hutan Rakyat Lati Petangis)	THR (1-3)	3
Paser Sub-district (Tanjung Pinang Village)	TNJ (1-2)	2
Total		**66**

Note: *: Accession code followed by sample number

Data analysis

Observation and characterization of anatomical characters

Observations were carried out using a Nikon Eclipse 80i light microscope and XCAM Indomicro HDMI camera (1080 PHB; 2.4 × 2.4 megapixels) using Betaview software. Measurements were taken from at least 10 photos of each sample. The observation was taken from three leaf parts (lamina, midrib, and petiole) with 37 characters (Table 3). The characters were chosen from previous studies on Lauraceae anatomy (Metcalfe and Chalk 1957; Metcalfe 1987; Nishida and Christophel 1999). The characters then scored with a multivariate score. Each character that presents only a single character state was scored with "1"; meanwhile, characters with multiple variations of character state were scored with various numbers. The list of scoring characters is shown in Table 2.

Principal Component Analysis (PCA) of leaf anatomical characters

Principal Component Analysis (PCA) was conducted using PAST version 5.2.2 (Hammer et al. 2001) to explore patterns of variation and clustering among samples based on 18 scored anatomical leaf characters with multiple character states. All data were standardized before analysis to eliminate scale bias among variables. PCA was used to reduce dimensionality while retaining the maximum variance in the dataset. The resulting principal components were visualized using 2D and 3D scatter plots to observe sample distribution and grouping. To identify which characters contributed most to the clustering, loading plots were examined, highlighting the variables with the strongest influence on the principal components.

Table 2. Anatomical leaf characters with discrete states used in principal component analysis

No.	Character description	Character states and scores
1	Stomatal type	(1) Dominant tetracytic; (2) Tetracytic with anomocytic variation
2	Adaxial epidermis trichome	(1) Present; (2) Absent
3	Spongy mesophyll density	(1) Dense; (2) Less dense
4	Crystal in the lamina	(1) Present; (2) Absent
5	Sclereid in the lamina	(1) Present; (2) Absent
6	Adaxial midrib shape (micromorphology section)	(1) Slightly convex with entire margin; (2) Flat with entire margin
7	Abaxial midrib shape (micromorphology section)	(1) Convex and rounded, with undulate to wavy margin; (2) Convex and rounded, with entire margin; (3) Convex and triangular, with undulate to wavy margin
8	Adaxial epidermis cell shape (in the midrib)	(1) Square; (2) Square and oval
9	Abaxial epidermis cell shape (in the midrib)	(1) Oval; (2) Square and oval
10	Trichome type (in the midrib)	(1) Unicellular, scattered; (2) Absent
11	Vascular bundle shape in the midrib (adaxial-abaxial)	(1) Flat/convex adaxial and U-shaped to ¾ rounded abaxial; (2) Flat/convex adaxial and V-shaped to triangular abaxial; (3) Flat/convex adaxial and rounded abaxial
12	Sclereid in the midrib	(1) Present; (2) Absent
13	Crystal in the midrib	(1) Present; (2) Absent
14	Petiole morphological shape	(1) Rounded with flat canal; (2) Oval with flat canal; (3) Rounded and oval with flat canal
15	Vascular bundle type in the petiole	(1) Single, closed system with oval shape; (2) Double, closed system with oval shape
16	Unicellular trichome density in the petiole	(1) Present (dense or scattered); (2) Absent
17	Crystal in petiole	(1) Present; (2) Absent
18	Number of oil cell layers below the epidermis	(1) 1-2 layers; (2) More than 2 layers

RESULTS AND DISCUSSION

Results

The leaf is the most noticeable vegetative organ in almost all Spermatophyta; it is the primary organ responsible for photosynthesis. The morphological and anatomical characters of leaves often reflect a species' life cycle and functional responses to environmental conditions. Consequently, detailed examination of leaf traits provides key insights into how a species interacts with its habitat and adapts to ecological pressures. In this study, we observed 37 characters from three leaf parts: lamina, midrib, and petiole (Table 3). All samples were collected from lowland tropical rain forests, with the highest elevation where *E. zwageri* was found is Modang village (c. 400-500 m asl). Generally, the qualitative characteristics of different organ parts from different accession numbers are similar due to the conservative character commonly found in the woody plant species. Our findings show that the lamina has 13 consistent characters and 5 variable characters; the midrib has 2 consistent characters and 8 variable characters; and the petiole has 4 consistent characters and 5 variable characters.

The study examined 37 anatomical characters of the lamina, midrib, and petiole to capture the full range of foliar structural diversity in *E. zwageri*. The selection of these characters reflects the traits most consistently used in Lauraceae systematics, as shown in the comparative data in Table 3, including stomatal configuration, mesophyll arrangement, vascular bundle morphology, sclereid types, and the presence of crystals and oil cells. These characters represent both conservative and variable components of leaf architecture, as illustrated in Figure 7, where the lamina shows the highest number of stable traits. At the same time, the midrib and petiole display greater variation across accessions. By incorporating characters that are taxonomically informative and anatomically diverse, the dataset enables a comprehensive qualitative assessment and provides a robust framework for detecting potential intraspecific variation among subpopulations.

General anatomy description of Eusideroxylon zwageri

Leaf. Stomata are superficial, hypostomatic, mostly tetracytic (paratetracytic, anomotetracytic) and anomocytic, with some paracytic (hemiparacytic, brachyparacytic, paratetracytic) variation present (Figure 2). The abaxial epidermis shows straight to rounded anticlinal cell walls; the shape of cells is irregular (in paradermal) and square and rectangular (in transverse section). The adaxial epidermis shows a straight anticlinal cell wall; the shape of cells is square to polygonal (in paradermal section) and square (in transverse section) (Figure 3).

Table 3. Observation of thirty-seven anatomical characters of the lamina, midrib, and petiole of *Eusideroxylon zwageri* compared with other genera of Lauraceae

No	Anatomical characters	*Eusideroxylon zwageri*	*Cinnamomum*	*Beilschmiedia*	*Cryptocarya*
Leaf					
1	Stomatal position through the epidermis	Superficial	Sunken[5,6,17]	Sunken[14], raised and superficial[3]	Superficial (Based on picture)[8]
2	Stomatal type	Mostly tetracytic, and anomocytic, sometimes paracytic	Anomocytic[2], laterocytic, brachyparacytic[9]	Paracytic[14]	Paracytic and anomocytic[8,15]
3	Presence of stomata	Hypostomatic	Hypostomatic[2]	Hypostomatic[14]	Hypostomatic[15]
4	Type of abaxial epidermis anticlinal cell wall	Straight to rounded	Straight to undulate[2]	Angular, rounded, undulate, branched, and sinuous[14]	Usually straight to moderately curved, but sometimes undulate[15]
5	Abaxial epidermis shape (in paradermal section)	Irregular shape	Rectangle, isodiametric, tetragonal to polygonal or tabloid with different sizes or sinuous[2]	Angular, roundish to irregular shape[13]	Angular, roundish to irregular shape[15]
6	Abaxial epidermis shape (in transverse section)	Square and rectangle	Square and rectangle[18], some possess papillae, varying from dome-shaped to club-shaped[4]	Square[13]	Rectangle, some species have a papillate structure[8]
7	Type of adaxial epidermis anticlinal cell wall	Straight	Straight to curved[2], sinuous[18]	Angular, sinuous, branched[13]	Usually straight to moderately curved, but sometimes undulate[15]
8	Adaxial epidermis shape (in paradermal section)	Square to polygonal	Polygonal, angular, roundish[2] to irregular shape[18]	Polygonal, angular, roundish to irregular shape[13]	Polygonal, angular, roundish to irregular shape[15]
9	Adaxial epidermis shape (in transverse section)	Square	Square and rectangle[4,18]	Square[13]	Square and rectangle[8]
10	Abaxial epidermis trichome	Unicellular trichome, with peg-like attachment and radial basal cell	Some species have unicellular [4], unbranched, non-glandular, solitary, and have an acute apex[2]	Simple with a poral base[14]	Some species have unicellular trichome[8]
11	Adaxial epidermis trichome	Unicellular trichome with peg-like attachment and a radial basal cell is rarely present	Some species have unicellular trichomes[2,4,18]	Simple with a poral base[13]	Present in some species[8]
12	Cuticle	Slightly thick cuticle present	Present both surface[2]	Present both surface[14]	Present both surfaces
13	Palisade mesophyll	Dorsiventral	Dorsiventral[2]	Dorsiventral[14]	Dorsiventral[16]
14	Number of palisade mesophyll layers	Mostly 2-3 layers, rarely 1 or 4 layers	Mostly 1 layer[2,4], rarely 2-3 layers[4]	Mostly 1-2 layers of palisade tissue, but some species have 3 layers[14]	2-3 layers of palisade tissue[16]
15	Spongy mesophyll	Dense or slightly dense rarely lose	Dense or slightly dense (based on pictures[7,12])	Dense or slightly dense (based on picture[13])	Dense, less dense, in some cases, contains large lacunae[16]
16	Crystal	Mostly absent; raphide or prismatic crystal is rarely present in the spongy mesophyll or around the vascular bundles	Present in the mesophyll and around the vascular bundle. The form of crystals is variable[2]	Acicular to rhomboid crystal found in *B. tawa*[10]	Crystal found in parenchyma cells of *Cryptocarya* aff. *aschersoniana* Mez[8]

17	Sclerenchyma	Osteosclereids are present among the mesophyll, sometimes elongated through the palisade and spongy, or only between the palisade or spongy mesophyll area. Rarely absent	The periclinal walls of palisade and the cell of spongy parenchyma show sclerification. Sclerenchymatous bundle sheath[4]	The sclerenchyma is 2-3-layered in bundle sheath[14]	-
18	Idioblast and oil cells	Idioblasts are present between the palisade or spongy mesophyll	Idioblasts and oil cells are present in mesophyll cells [4]	Oil cells are often observed in the palisade tissue[14]	Oil cells are found in the mesophyll of some *Cryptocarya* species[16]
Midrib					
1	Adaxial midrib morphology	Entire margin, flat to slightly convex	Convex, flat[18] and concave[2,6]	Flat to concave[14]	Concave in *Cryptocarya* aff. *Aschersoniana*[8]
2	Abaxial midrib morphology	Convex with a rounded shape (rarely triangle) with an undulate, wavy, or entire margin	Flat to convex[2,6,18]	Convex to wavy margin[14]	Convex in *Cryptocarya* aff. *aschersoniana*[8]
3	Adaxial epidermis shape	Square or square to oval	Square[2,6,18]	Square to rectangular[14]	Square in *Cryptocarya* aff. *aschersoniana*[8]
4	Abaxial epidermis shape	Oval or square to oval	Oval or square to oval[2,6,18]	Square to oval (based on picture [13])	-
5	Trichome	Unicellular hair and scattered (rarely absent)	Unicellular hair[2]	Trichome present in some species (based on picture [13])	Trichome present in some species[8]
6	Cuticle	Slightly thick cuticle present	Present[1]	Present[13]	Present[8]
7	Shape of vascular bundle	Closed system with a single vascular bundle, flat to convex adaxial side, but varies in abaxial (dominant U-shape to ¾ rounded, V-shape to triangular, and rarely full rounded)	One open arch central vascular bundle that was different in shape (oval, elongated, irregular, V-shaped, partially dissected into 2 or 3 segments)[2,6,18]	Dominant flattened arc and closed system rings with variation [14]	Open system, rounded in *Cryptocarya* aff. *Aschersoniana*[8]
8	Oil cells	Scattered among the peripheral and central cortex, around the vascular bundle, and sometimes between the vascular bundles, are cell complexes	Present in the cortex and a complex vascular bundle[2]	Present[13]	Present in *Cryptocarya* aff. *Aschersoniana*[8]
9	Sclereid	Brachysclereids and astrosclereids are present in the cortex, rarely absent	Present[2]. Brachysclereid in the cortex of *C. pauciflorum*[6]	-	Sclerified cells are also observed as supporting tissues in the midrib and at the leaf margins[8]
10	Crystal	Absent (prismoid or raphida crystal rarely present in cortex)	Present in the vascular bundle[2]	-	-
Petiole					
1	Morphological shape	Oval, rounded, or oval and rounded, with a flat canal side	Rounded (with flat canal), reniform, and oval[1]	Rounded[13]	-
2	Epidermis cells shape	Square or square to oval	Square or square to oval[1]	-	-

3	Vascular bundles shape	Closed system, mostly single (double vascular bundles are rarely found), with a wavy oval shape	Simple open arc, partially or clearly separated into 3 segments[1,12]	Three bundles at the base of the petiole, they may branch halfway along the length of the petiole to give five or seven bundles, which commonly reunite or perform ring-form at the petiole's distal end[11,14]	-
4	Trichome	Unicellular hair is present with dense or scattered, rarely absent	Some species have trichomes (unicellular or multicellular)[1]	Some species have trichomes[13]	-
5	Cuticle	Slightly thick cuticle present	Present[1]	Present[13]	-
6	Crystal	Absent or present (if present, raphide crystals found in cortex)	Present (sand, elongated, acicular, rectangular, and box-shaped crystal)[1]	-	-
7	Sclereid	Brachysclereids and astrosclereids are present in the cortex or between the vascular bundle complex	Brachysclereid[1]	-	-
8	Oil cells	Oil cells are present in the peripheral and central cortex, around the vascular bundles, and between the vascular bundles complex	Present in *C. sulphuratum* and *C. verum*[12]	Present in cortex[13]	-
9	Number of oil cell layers	1, 2, or 3 layers	2-3 layers[12]	-	-

Note: References: [1]Abeysinghe and Scharaschkin (2019), [2]Abeysinghe (2024), [3]Babalola et al (2021), [4]Bakker et al. (1992), [5]Baruah and Nath (1997), [6]Baruah and Nath (2006), [7]Bottoni et al (2021), [8]de Moraes (2006), [9]Fadhila et al. (2023), [10]Knowles and Beveridge (1982), [11]Metcalfe (1987), [12]Narayana et al. (2019), [13]Nishida (1998), [14]Nishida and Christophel (1999), [15]Nishida et al. (2016), [16]Petzold (1907), [17]Santose (1930), [18]Wulansari et al. (2020)

Trichomes are hair-shaped, unicellular, with peg-like attachments and radial basal cells; mostly present in the abaxial epidermis and rarely in the adaxial epidermis. Slightly thick cuticle present. The palisade mesophylls are dorsiventral, mostly 1-3 layers, and sometimes up to four layers. Spongy mesophylls are mostly dense, occasionally loose. Crystal is absent primarily, seldom present in raphide or prismatic form, found in spongy mesophyll or around vascular bundles. Osteosclereids mostly perform in the mesophyll, elongated through palisade and spongy, or are only present in the palisade and spongy area. Idioblasts and oil cells are present between the palisade and the spongy mesophyll.

Midrib. The adaxial midrib is slightly convex or sometimes flat, with an entire margin and a square to rectangular epidermis. The abaxial midrib is convex with a rounded shape and rarely triangular, with an undulate, wavy, or entire margin, epidermis dominant oval, or sometimes square. Slightly thick cuticle present. Trichome is occasionally absent, or unicellular hair is rarely present in the abaxial region. Vascular bundles are present in a closed system with a single vascular bundle, flat to convex in adaxial, but vary in abaxial, with dominant U-shape to ¾ rounded and V-shape to triangular, rarely fully rounded (Figure 4). Oil cells are mostly scattered throughout the peripheral and central cortex, around vascular bundles, and sometimes between the vascular bundles' cell complexes. Brachysclereids and astrosclereids are present in the cortex and rarely absent (Figure 5). Crystal prismoid or raphide is sometimes present in the cortex, but mostly absent.

Petiole. Oval, rounded, or oval and rounded with flat canal side, epidermal cells square or square to oval (Figure 6). Vascular bundles are arranged in a closed system, with single vascular bundles mostly present and wavy-oval in shape. Slightly thick cuticle present, with unicellular hair dense, scattered, or rarely absent. Brachysclereids and astrosclereids are present in the cortex or between the vascular bundle complex, while raphide crystals are present (in the cortex) or absent. Oil cells are sparsely distributed in the peripheral and central cortex, around the vascular bundles, and between the vascular bundles; in the peripheral cortex, they are present in one to three layers.

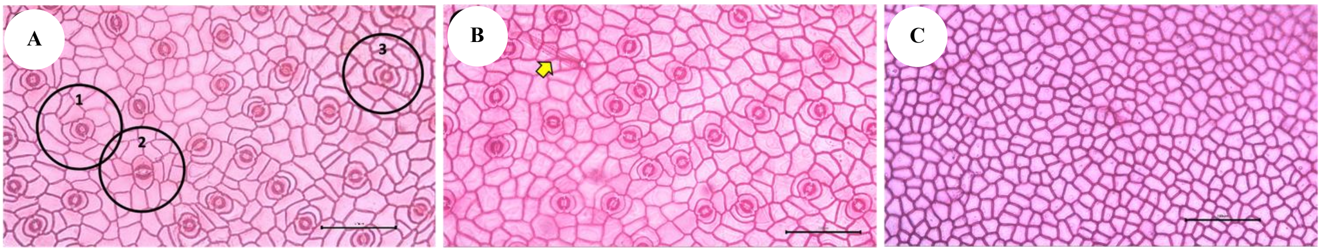

Figure 2. Anatomical appearance of leaf epidermis tissue of *Eusideroxylon zwageri*. A. Several types of stomata were found in abaxial epidermis: 1. Hemiparacytic; 2. Anomocytic; 3. Brachyparacytic, B. A unicellular hair trichome (yellow arrow) was also found in abaxial epidermis, C. No stomata were found in adaxial epidermis. Scale: A-C: 100 µm, magnification level 20x

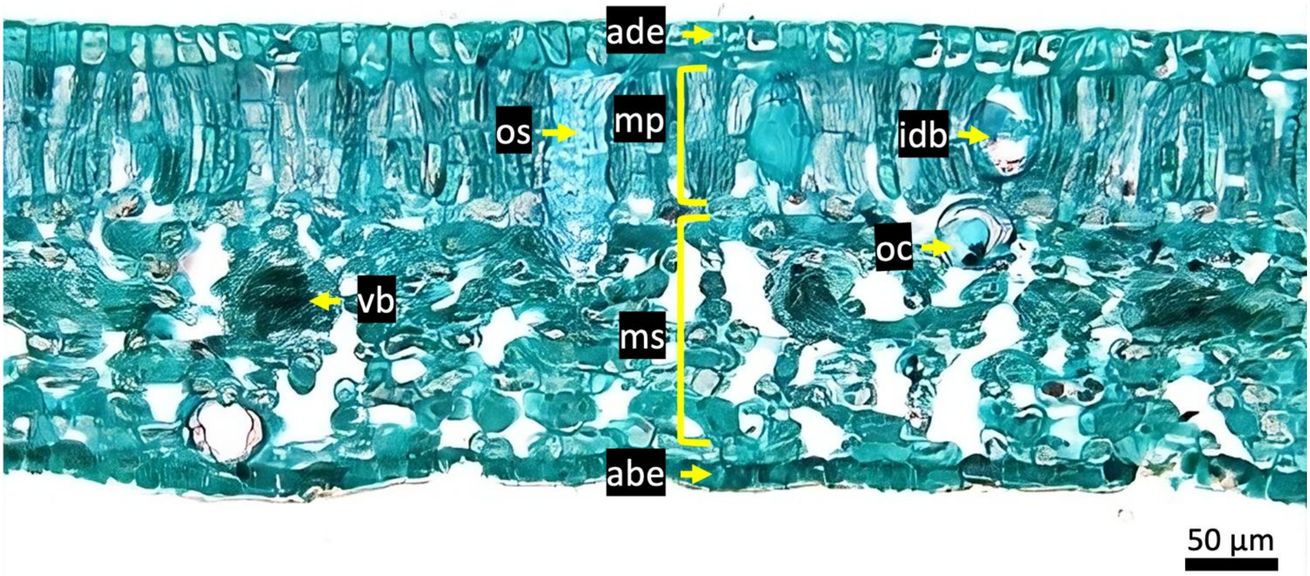

Figure 3. Transverse section of lamina *Eusideroxylon zwageri*
Note: abe: Abaxial epidermis; ade: Adaxial epidermis; idb: Idioblast; mp: Mesophyll palisade; ms: Mesophyll sponge; oc: Oil cells; os: Osteosclereid; vb: Vascular bundle. Magnification level: 20x

Figure 4. Variation of morphology and vascular bundles shape in the midrib of *Eusideroxylon zwageri*. A-B. Half-rounded midrib with an entire margin and ¾ to half-rounded vascular bundles arrangement, C. Rounded midrib with entire margin and almost fully rounded vascular bundle arrangement, D. Triangular midrib with slightly undulate margin and triangular vascular bundles arrangement, E. Triangular midrib with wavy margin and triangular vascular bundles arrangement. Scale: A,C,E: 100 µm; B,D: 200 µm; magnification level: 4x

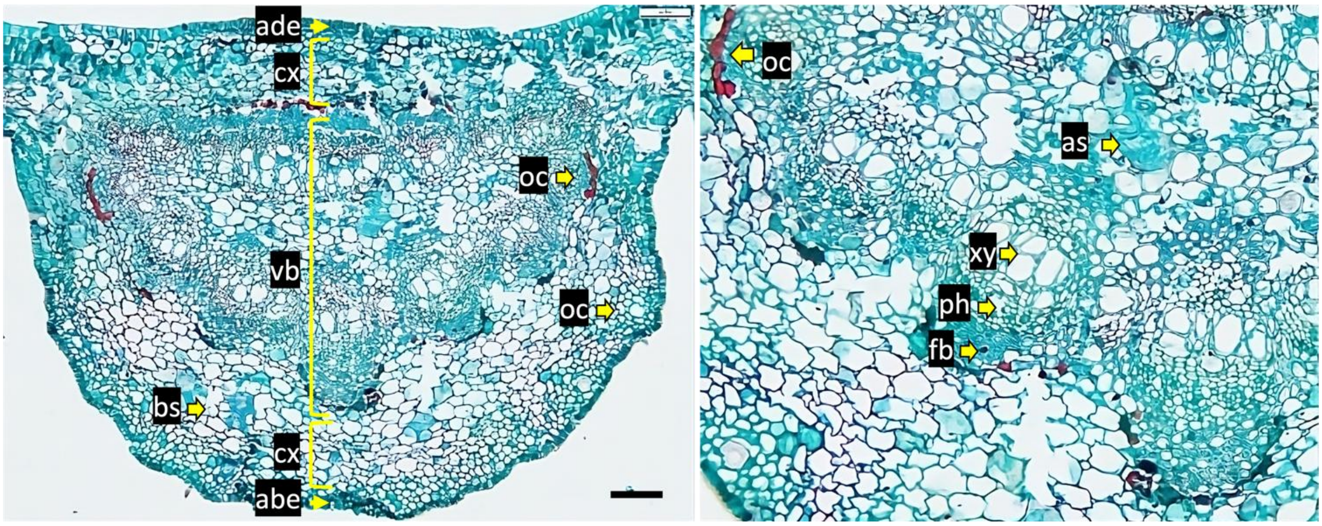

Figure 5. Anatomy structure of the midrib of *Eusideroxylon zwageri.* as: Astrosclereid; bs: Brachysclereid; cx: Cortex; fb: Fibers; oc: Oil cell; ph: Phloem; vb: Vascular bundle complex; xy: Xylem. Scale: 200 µm, magnification level 4x (left) and 10x (right)

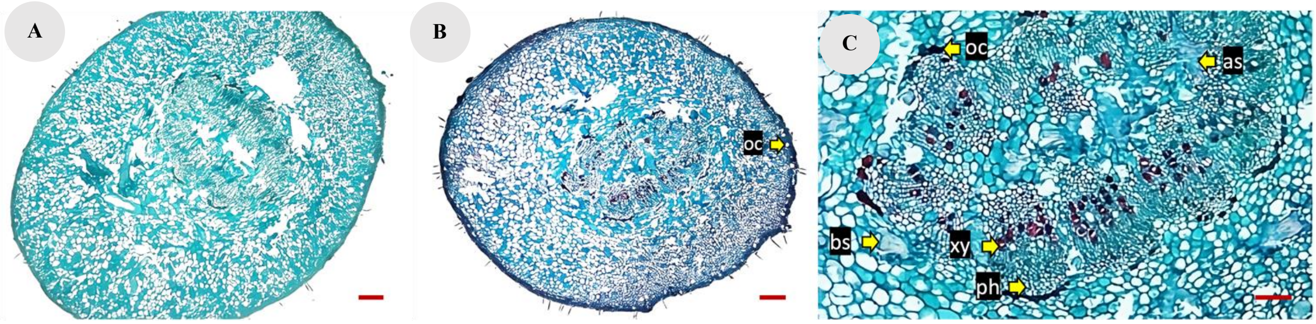

Figure 6. Transverse section of the petiole of *Eusideroxylon zwageri.* A. Petiole with an oval shape, B. Petiole with a rounded shape, C. Vascular bundle complex. as: Astrosclereid; fb: Fibers sheath; oc: Oil cells; ph: Phloem; xy: Xylem. Scale: A-B: 200 µm; C-D: 100 µm, magnification level 4x (A,B) and 10x (C)

Variation among sub-populations of E. zwageri

Based on the characters determined for each accession and subpopulation, the lamina showed the highest number of consistently present characters across all accessions and subpopulations, with 13 characters observed. In contrast, most characters in the midrib and petiole were more varied than those in the lamina (Figure 7). No anatomical character was found to be uniquely associated with any specific subpopulation. Kongbeng Sub-district, as the largest subpopulation, had the highest number of character states (56) across all 47 accessions, but this difference was not significant compared with the Modang subpopulation, which had only 8 accessions and displayed 53 character states. Subpopulations with smaller sample sizes showed lower character state variation, namely Kutai National Park (6 accessions, 46 character-states), Tanjung Pinang Village (2 accessions, 41 character-states), and Taman Hutan Rakyat Lati Petangis (3 accessions, 39 character-states) (Figure 8). Overall, these patterns indicate that the number of accessions collected from a subpopulation did not substantially influence the amount of variation observed.

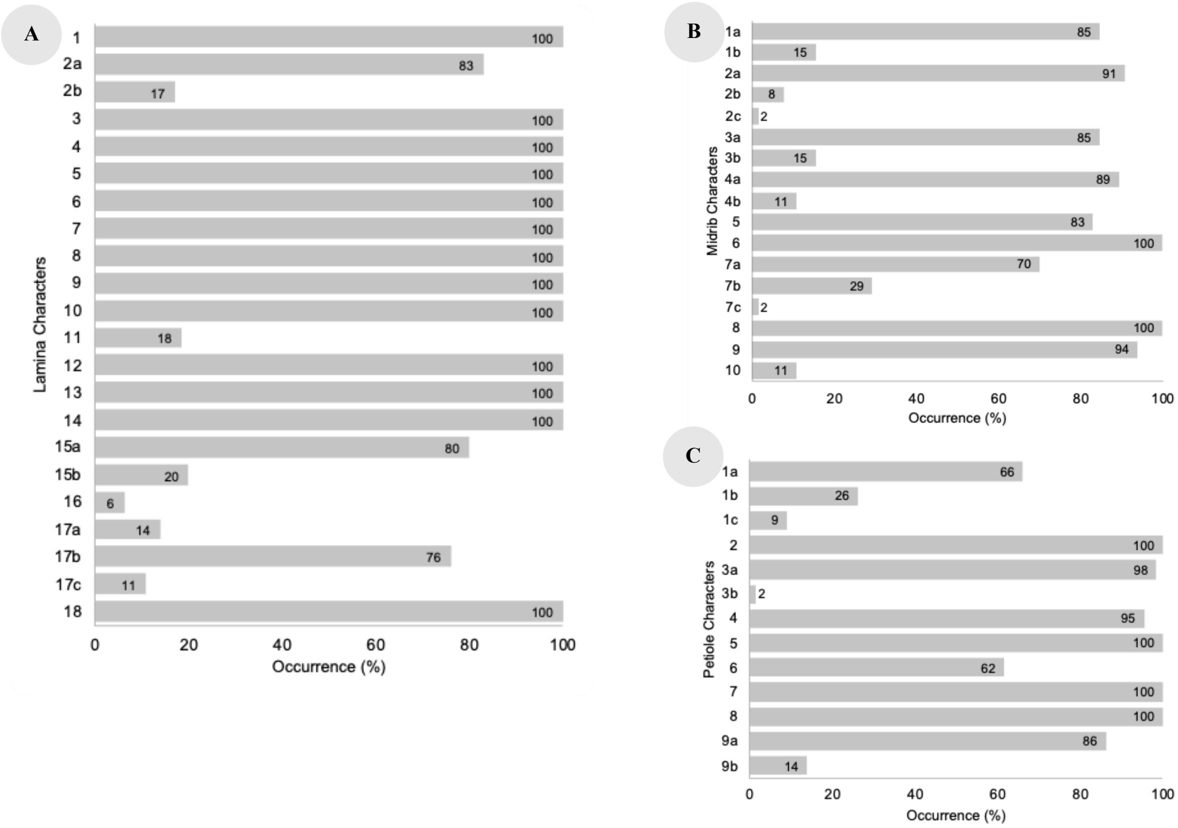

Figure 7. Presentation of characters presented in the accession of *Eusideroxylon zwageri*. A. Lamina characters: 1. Stomatal position through the epidermis (phanerophore); 2a. Stomatal type (tetracytic, anomocytic); 2b. Stomatal type (paracytic, tetracytic and anomocytic); 3. Presence of stomata (hypostomatic); 4. Type of abaxial epidermis anticlinal cell wall (straight to rounded); 5. Abaxial epidermis shape in paradermal section (irregular); 6. Abaxial epidermis shape in transverse section (square and rectangle); 7. Type of adaxial epidermis anticlinal cell wall (straight); 8. Adaxial epidermis shape in paradermal section (square to polygonal); 9. Adaxial epidermis shape in transverse section (square); 10. Abaxial epidermis with unicellular trichome, base peg-like, and basal sel radial; 11. Adaxial epidermis with unicellular trichome; 12. Cuticle; 13. Palisade mesophyll (dorsiventral); 14. Number of palisade mesophyll layers (1-3 layers, sometimes up to 4 layers); 15a. Spongy mesophyll (dense); 15b. Spongy mesophyll (loose); 16. Crystal; 17a. Sclereid (abundant); 17b. Sclereid (rare); 17c. Sclereid absent; 18. Idioblast and oil cells (between mesophyll and sponge palisade). B. Midrib characters: 1a. Adaxial midrib (slightly convex with entire margin); 1b. Adaxial midrib (flat with entire margin); 2a. Abaxial midrib (convex and rounded, with undulate to wavy margin); 2b. Abaxial midrib (convex and rounded with entire margin); 2c. Abaxial midrib (convex and triangle with undulate to wavy margin); 3a. Adaxial epidermis shape (square); 3b. Adaxial epidermis shape (square and oval); 4a. Abaxial epidermis shape (oval); 4b. Abaxial epidermis shape (square and oval); 5. Trichome (unicellular, scattered); 6. Cuticle; 7a. Vascular bundle closed system with flat to convex adaxial and U-shape,1/2, or 3/4 rounded abaxial; 7b. Vascular bundle closed system with flat to convex adaxial and V-shape to triangular abaxial; 7c. Vascular bundle closed system with flat to convex adaxial and rounded abaxial; 8. Oil cells; 9. Sclereid; 10. Crystal. C. Petiole characters: 1a. Morphological shape (rounded with flat canal); 1b. Morphological shape (oval with flat canal); 1c. Morphological shape (rounded and oval with flat canal); 2. Epidermis cells shape (square or square to oval); 3a. Vascular bundles shape (single, closed system with oval shape); 3b. Vascular bundles shape (double, closed system with oval shape); 4. Unicellular trichome present (dense or scattered); 5. Cuticle; 6. Crystal; 7. Sclereid presents between cortex and vascular bundle complex; 8. Oil cells presents below epidermis, around vascular bundle complex, and among vascular bundle cells; 9a. Number of oil cell layers below epidermis 1-2 layers; 9b. Number of oil cell layers below epidermis, more than 2 layers

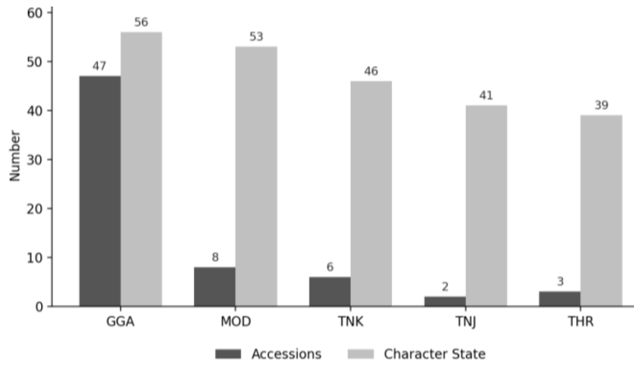

Figure 8. Comparison of the number of accessions from each population with the number of character states observed. GGA: Kongbeng Sub-district, East Kalimantan, Indonesia, subpopulation; MOD: Modang Village; TNK: Kutai National Park; TNJ: Tanjung Pinang Village; THR: Taman Hutan Rakyat Lati Petangis

PCA analysis

The scatter plot from PCA showed that all accession numbers cluster close to the center of the axis, indicating that nearly all of the accession numbers share a similar data pattern. The only accession numbers separated from other accessions are GGA HP1 from Kongbeng Sub-district and DA 2413 from Kutai National Park (Figure 9). Kongbeng Sub-district and Kutai National Park had a similar, highly wet climate, according to climate data based on the Schmidt-Ferguson classification. Therefore, the outlier status of these two accession numbers was unlikely to be caused by climate factors. Those two accession numbers have two characters which offered as the strongest character separating them from one another, i.e., (i) shape of the midrib vascular bundle is a closed system with flat to convex adaxial and V-shape to triangular abaxial (dominantly closed system with flat to convex adaxial and U-shape,1/2, or 3/4 rounded abaxial), and (ii) the petiole morphological shape is rounded and oval with a flat canal (dominantly rounded with flat canal).

Furthermore, another variation found in GGA HP1 is that the midrib adaxial epidermis is square and oval. In contrast, DA 2413 has trichomes on the lamina adaxial epidermis, and the midrib abaxial epidermis is convex and rounded with an entire margin. However, compared with the 3D scatter plot, the two accession numbers were not included among the highlighted results shown in this figure.

Based on the 3D scatter plot, two subpopulations, namely Taman Hutan Rakyat Lati Petangis (grouped in PC3, accession numbers THR1, THR2, THR3), and Tanjung Pinang (placed in PC1, accession numbers TNJ1, TNJ2), are potentially different and placed quite far from the center axis (Figure 10). The Taman Hutan Rakyat Lati Petangis subpopulation lacks crystals in all leaf organs observed, whereas another subpopulation has crystals present in at least one part (petiole or midrib only). The Tanjung Pinang subpopulation shows high variation in its character states, even though it consists of only two accession numbers; it has at least four characters bearing eight character states, indicating that this subpopulation could exhibit greater variation as the sample size increases. However, these results were relatively small and weak and still warrant further investigation using complementary approaches (e.g., molecular studies) to determine whether they represent significant infraspecific variation.

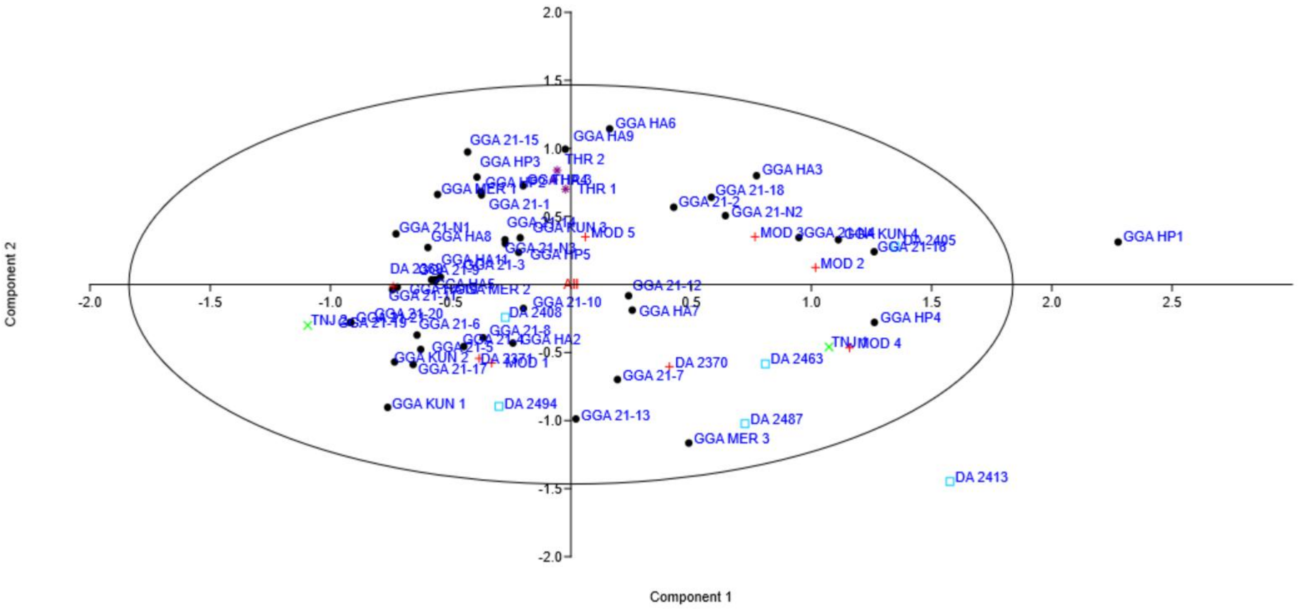

Figure 9. Scattered plot of the *E. zwageri* samples collected from five subpopulations shows only two accession numbers placed outside of the main cluster

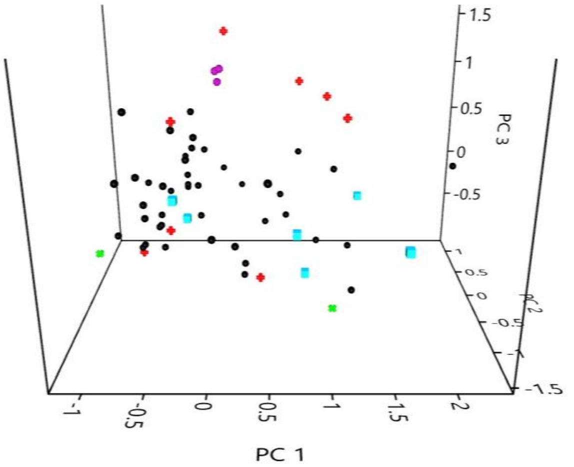

Figure 10. Scatter chart of *E. zwageri* subpopulation in East Kalimantan, Indonesia. Black dot: Kongbeng Sub-district; Plus red: Modang Village; Square blue: Kutai National Park; Star purple: Taman Hutan Rakyat Lati Petangis; Cross green: Tanjung Pinang Village. Variance percentage: PC1: 19.06; PC2: 12.544; PC3: 11.363

Discussions

Comparison of anatomical traits of Eusideroxylon zwageri *with the sister taxa and determining the diagnostic characters*

A previous study by Dewi et al. (2024) analyzed morphological traits in combination with five quantitative anatomical variables: leaf thickness, adaxial and abaxial epidermal thickness, mesophyll thickness, and stomatal density. The samples were collected from two subpopulations: the Kongbeng and Kayan Mentarang (North Kalimantan). The results indicated no statistically significant differences due to overlapping ranges across traits. Building on these findings, the present study focused on qualitative anatomical traits to determine whether diagnostically informative characters exist for *E. zwageri.*

Comparative analyses of the lamina, midrib, and petiole with approximately 360 species from three closely related Lauraceae genera (Petzold 1907; Santose 1930; Knowles and Beveridge 1982; Metcalfe 1987; Bakker et al. 1992; Baruah and Nath 1997; Nishida 1998; Nishida and Christophel 1999; Baruah and Nath 2006; de Moraes 2006; Nishida et al. 2016; Abeysinghe and Scharaschkin 2019; Narayana et al. 2019; Wulansari et al. 2020; Babalola et al. 2021; Bottoni et al. 2021; Fadhila et al. 2023; Abeysinghe 2024)*,* reveal that most anatomical characters of *E. zwageri* overlap with those found elsewhere in Lauraceae (Table 3). For example, the paracytic stomata type was widely seen in sister genera of *Eusideroxylon,* such as *Cryptocarya* (*Cryptocarya densiflora* and *C. ferrea* (Fadhila et al. 2023)), and other species of Lauraceae, such as *Ocotea indecora*, *Nectandra barbellata,* and *Endlicheria paniculata* (Gonçalves et al. 2018). The 2-3 palisade layers of *E. zwageri* are comparable to other genera of Lauraceae, which have 1-3 palisade layers (Metcalfe and Chalk 1950).

Sclereids—particularly osteosclereids and astrosclereids—occur extensively throughout the vegetative organs of *E. zwageri*, indicating a strong lignification strategy. Although sclereids are known from other Lauraceae taxa (e.g., Ravensara), the distribution pattern observed here differs in its consistency and abundance. Idioblasts and oil cells, found in the lamina, midrib, and petiole, also correspond to traits widely documented in Lauraceae (Metcalfe and Chalk 1950; Nishida and Christophel 1999; Serebrynaya et al. 2017; Gonçalves et al. 2018; Aini and Wisanti 2023).

In the midrib, the fiber rings around the outer vascular bundles of *E. zwageri* resemble those in *Persea* (Metcalfe and Chalk 1950), *Cinnamomum* (Abeysinghe 2024), *Nectandra*, *Endlicheria,* and *Ocotea* (Gonçalves et al. 2018). The midrib exhibits various shapes of vascular bundle complexes, i.e., U-shape, ¾ rounded, V-shape, triangular, and rounded forms. All of these constitute a single closed system vascular bundle similar to an unbroken circle. Comparable traits are found in *Beilschmiedia,* a genus in the same tribe (Cryptocaryeae) (Table 2) (van der Werff and Richter 1996). This structure may extend into the petiole, consistent with previous studies that *Beilschimiedia* has vascular bundles that branch halfway along the petiole into five or seven bundles and commonly curve or reunite into a ring-like form at the distal end of the petiole (Table 2) (Metcalfe 1987; Nishida and Christophel 1999).

One distinctive trait does, however, appear exclusive to the genus: the presence of osteosclereids within the lamina mesophyll, sometimes extending from the palisade zone into the spongy mesophyll. This character, absent from closely related genera, constitutes the only robust qualitative diagnostic marker identified. Although PCA highlighted several characters—such as petiole morphology (19.9%), presence of crystals in the petiole (12.67%), and midrib vascular-bundle shape (11.36%)—these traits overlap with those of other Lauraceae and therefore lack diagnostic utility.

Functional anatomical traits related to adaptation

The presence of stomata in a plant was often related to the environmental conditions. In *E. zwageri*, several characters, such as stomatal types, sclereids, and oil cells, indicate appropriate adaptations. The presence of superficial stomata (parallel to the leaf surface), which reflected the rainfall intensity in Kalimantan forests ranging from 1600-4100 mm/year, was quite efficient for the process of CO_2 intake during photosynthesis. In plants exposed to drier conditions, stomata were typically more submerged to prevent water loss (Šantrůček 2022).

Eusideroxylon zwageri contains many sclereids and oil cells, especially in the stems. Sclereids are thick, lignin-rich cells that contribute to the hardness and durability of the ironwood (Evert 2006). Oil cells, usually associated with axial parenchyma (Richter and Dallwitz 2000), were also found in its leaves. Leaf sclereids, such as osteosclereids, provide additional protection against pests (Mauseth 1988), including leafhoppers, ladybugs, shoot-eating caterpillars, and green grasshoppers (Susilawati and Rahmi 2020), by rendering the tissue coarse and unpalatable (Mauseth 1988). As mechanical tissue, sclerenchyma also contributes to leaf resilience, reduces wilting damage, and protects them from direct light irradiation (Terashima 1992), which serves as an adaptation to the dry season. Meanwhile, leaf oil cells are generally rich in lipophilic plant secondary metabolites, likely functioning in chemical defense, enabling early detection and response to herbivore attacks (Divekar et al. 2022). Together, these anatomical features underscore the importance of sclereids and oil cells in reinforcing the structural and chemical adaptations of ironwood.

Future perspective for conservation efforts informed by anatomical features of E. zwageri

The strong lignification indicated by extensive sclerenchyma and sclereids contributes to the exceptional hardness of *E. zwageri* but also likely underlies its slow growth and regeneration. The species exhibits a low annual diameter increment (0.25 cm/year) and an extremely low volume increment (0.00024 cm^3/year) (Suharja and Jumani 2017). Combined with long-term overexploitation, these traits have contributed to its Vulnerable status under the IUCN Red List (Asian Regional Workshop (Conservation and Sustainable Management of Trees, Viet Nam, August 1996) 1998).

Low seedling production success rates further challenge conservation efforts. Natural regeneration remains limited, while vegetative propagation—through cuttings, air layering, and tissue culture—typically yields 30–40% rooting success (Utami et al. 2005; Maharani et al. 2021). Tissue culture approaches also remain constrained by low induction rates (Wahyuni et al. 2019). Expanding anatomical knowledge could inform improved propagation protocols, helping identify tissue types or developmental stages more responsive to vegetative techniques.

Ironwood's tolerance of nutrient-poor soils and diverse textures—from sandy to clay (Irawan 2015)—supports its potential for restoration programs. However, successful establishment requires appropriate silvicultural treatments, including the use of seedlings at least 40–60 cm in height (Maharani et al. 2021), nutrient supplementation, and integrated pest management. Pest attack intensity in ironwood seedlings is relatively low (30%) compared with other species, such as Shorea balangeran (42.14%) (Priatna et al. 2023), a resilience likely linked to the presence of leaf sclereids (Susilawati and Rahmi 2020).

In conclusion, this study provides updated qualitative anatomical data for *E. zwageri*, demonstrating that most foliar traits align with the broader Lauraceae family while confirming osteosclereids in the lamina as the only clear diagnostic marker. The pronounced lignification and abundance of sclereids and oil cells highlight key adaptive features but may also contribute to the species' slow regeneration and restricted recovery. Future research integrating quantitative anatomical measurements, molecular analyses of intraspecific variation, and the application of anatomical insights to vegetative propagation techniques may significantly enhance large-scale restoration and long-term conservation efforts for this ecologically and culturally important species.

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