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Short communication:
Leaf architecture of 35 species of Dipterocarpaceae cultivated in Forest Area with Special Purposes in Carita, Banten, Indonesia

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Tel.: +62-274-550541, Fax.: +62-274-550541, ♥email: dtadrianti@ugm.ac.id, meinataa@gmail.com

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Abstract. *MeinataA, Na'iem M, Adriyanti DT, Syahbudin A. 2021. Short communication: Leaf architecture of 35 species of Dipterocarpaceae cultivated in Forest Area with Special Purposes in Carita, Banten, Indonesia. Biodiversitas 22: 2952-2960.* Dipterocarpaceae is a major commercial timber characterized by high unbranched bole, paired stipules, and winged fruit. The identification process in the family becomes problematic, in cases where the generative organ is absent. Therefore, a new approach needs to be established to address any misidentification leading to improper utilization. This study aims to determine the leaf architecture in 35 species of Dipterocarpaceae cultivated in Forest Area with Special Purposes (KHDTK) Carita, Banten, Indonesia. The ten leaf samples collected were the third and fourth leaves from terminal shoots of a single tree of each species. Subsequently, the data were observed and measured based on the 17 morphological characters. Each character was then scored and analyzed using multivariate analyses cluster to determine the relationship between species. Dipterocarpaceae generally has pinnate leaf category, geniculate petiole, and entire margin. Furthermore, the phenon line in the dendrogram is cut at 0.695 similarity level to establish meaningful interpretation. The 35 species observed were grouped into 4 major clusters. Small leaf group, inconsistent tertiary vein pattern group, symmetrical leaves with cordate base leaf group, and other groups that do not resemble mentioned characters. The key determination comprised 34 couplets with three characters repeated due to limited descriptors.

Keywords: Banten, cluster analysis, Dipterocarpaceae, leaf architecture, venation.

INTRODUCTION

Dipterocarpaceae is a tropical rainforest timber species group widely found in Peninsular Malaysia, Sumatra, Java, Lesser Sunda Islands, Lombok, Borneo, the Philippines, Celebes, Moluccas, Papua New Guinea, and Bismarcks (Ashton 1982). According to Dayanandan et al. (1999), Dipterocarpaceae is one of the largest families comprising 523 species belonging to 17 genera worldwide. Meanwhile, most of these genera (76%) occupy the Malesian region, especially Indonesia in a large variety of habitats, from inland to coastal as well as swampy to dryland areas (Purwaningsih 2004), and generally grow in wet tropical regions with rainfall above 1000 mm year^{-1} or dry season lasting below 6 months (Appanah and Turnbull 1998)). Species of Dipterocarpaceae mostly exist in lowland rainforests at altitude 0-1000 m asl. (Ashton 1982; Purwaningsih 2004), and usually grow as emergent trees in hills and slopes above 50 m tall (Appanah and Turnbull 1998).

The Dipterocarpaceae has irregular flowering and uncertain fruiting. Therefore, studies related to species within the family have encountered difficulty in identification, due to the absence of flowers and fruit (Ashton 1982; Newman et al. 1998). Members of the *Cotylelobium, Dipterocarpus, Dryobalanops, Parashorea*, and *Vatica* are largely only identifiable based on flowers and fruit. Therefore, recognizing members of this family based on the use of vegetative organs is unlikely (Whitmore 1962). Furthermore, misidentification is bound to result in improper utilization of timbers, for instance, mersawa wood (*Anisoptera* spp.) and this is unsuitable for heavy construction (Pulan and Buot Jr. 2014).

Leaves are as important as the reproductive organs for species identification, particularly for dicotyledonous species (Hickey 1973). Leaf architecture is a term used to represent elements on leaves, including the pattern, margin, shapes, and gland position (Barral et al. 2013). A study by Huiet et al. (2018) showed pattern in leaves also reveal evolution traits. Meanwhile, Hickey (1999) mentioned the use of architecture referring to formations and constructions generating the leaf venation. The taxonomist's attention to the leaves' size comparison begins with the theory stating the shapes are not affected by the environment (Balduzzi et al. 2017) and the venation is derived genetically (Dickinson et al. 1987; Mishra et al. 2010). Due to the availability and variations, the leaf is organ-rich information and the source of taxonomy data (Kareem et al. 2018; Masungsong et al. 2019). Leaf venation is also used to delineate between two confusing Dipterocarpaceae species in the same genera (Mazo and Aribal 2020). Therefore, the study on leaf architecture is a new approach providing information on disconcerting species and an important aspect of identification (Swaminathan et al. 2012), as leaves are genetically fixed (Roth-Nebelsick et al. 2001).

Leaf architecture is a breakthrough to confirm a species based on venation pattern (Buot Jr. 2020). A leaf's venation pattern is a significant character in the taxonomy's determination (Inamdar and Murthy 1978; Celadiña et al. 2012; Pulan and Buot Jr. 2014; Buot Jr. 2020; Hernandez et al. 2020). Therefore, investigations are required to understand the leaf architecture of Dipterocarpaceae species, for taxonomy and forestry. This study aims to determine the leaf architecture in 35 species of Dipterocarpaceae cultivated in Forest Area with Special Purposes (KHDTK) Carita, Banten, Indonesia.

MATERIALS AND METHODS

Study area

Leaf specimens were collected on February 3-10, 2019, in Forest Area with Special Purposes (KHDTK) Carita plot 70 and 71 with the red dots, Labuan Sub-district, Pandeglang District, Banten, Indonesia (Figure 1). The forest originated from the Forest and Nature Conservation Research and Development (FNCRDC) pseudo-in-situ planting trial project in 1956, where pseudo-in-situ refers to a conservation method adapting ex-situ conservation combined with the suited plot environment condition similar to the site of origin (Thielges et al. 2001). According to Schmidt and Ferguson (1951), the area has climate type A, a temperature of 23-32°C, an average annual rainfall reaching 3900 mm, a humidity level between 77% and 85%, and an altitude of 50 asl. with the total area ± 5 ha (https://www.forda-mof.org/files/Puskonser_Carita.pdf). Carita Forest has greyish alluvial soil type, with low organic layer and high alkali maturity, as well as low permeability and varying soil acidity (Rimbawanto 2006). Subsequently, morphological observations of leaf architecture were conducted in the Tree Improvement Laboratory, Faculty of Forestry, Gadjah Mada University from March to April 2019.

Leaf collection

Leaf sampling was carried out using the exploration method described by Rugayah et al. (2004). The method used involved conducting an exploration of the existing area to determine the targeted species and selecting a mature leaf, the third or fourth leaf from the terminal buds of 10 leaf blades, from each species (Jessica and Buot Jr. 2014). Specimens were collected from the complete leaf organs and branches of the Dipterocarpaceae family for identification purposes.

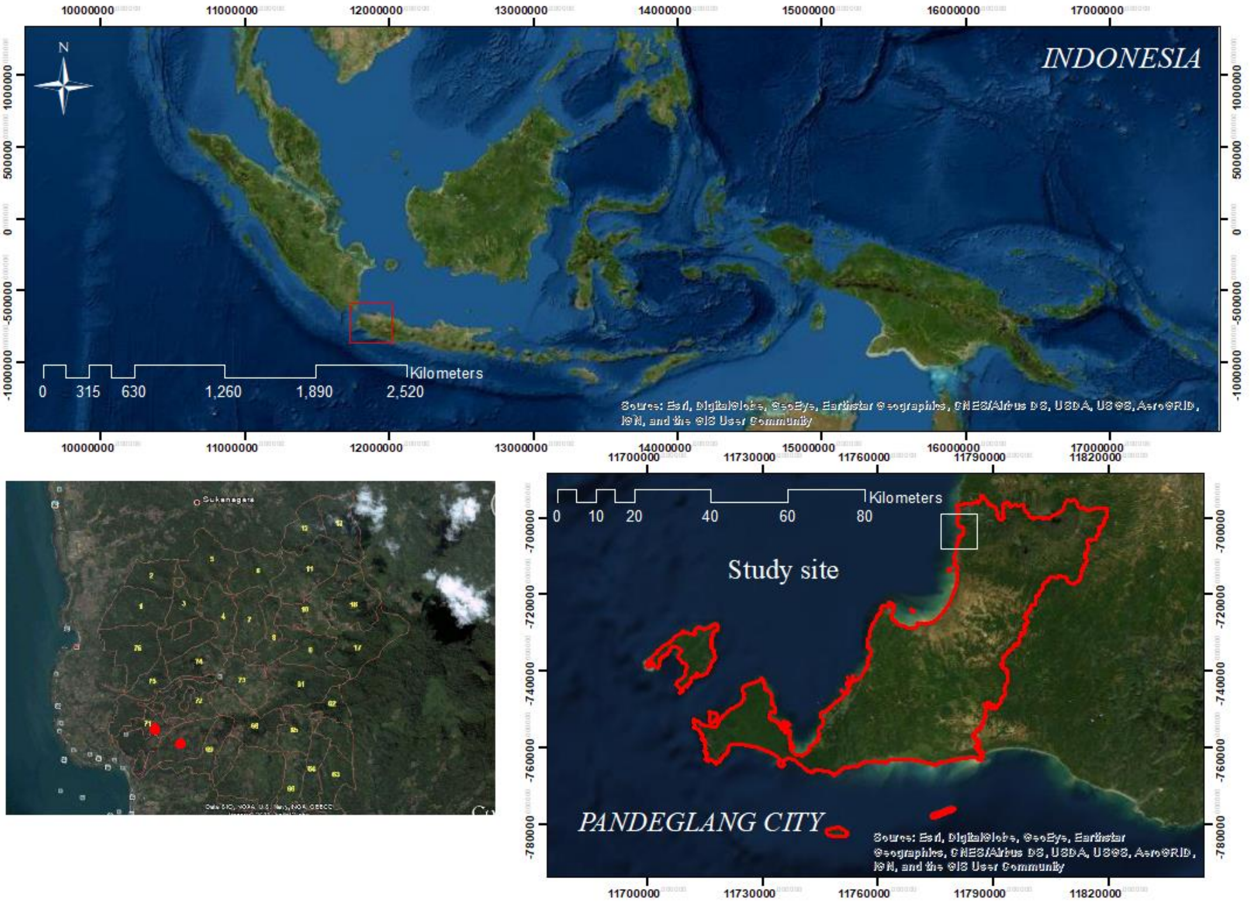

Figure 1. Study area in Forest Area with Special Purposes (KHDTK) Carita, Banten, Indonesia

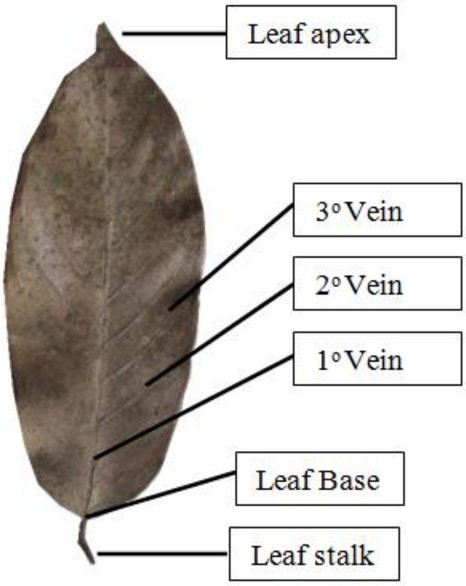

Figure 2. Venation order in single Dipterocarpaceae leaf (Shorea almon) blade, including the leaf stalk, leaf base, 1o, 2o, 3o vein order, and leaf apex

Sample identification

Identification of species names was conducted to provide information on the leaves, after oven-drying for approximately 3 days or until the leaves were completely dry. The documentation was completed using bark picture and complete vegetative sample obtained from the field. Furthermore, the method used involved asking experts, Dr. Dwi Tyaningsih Adriyanti, and peer-to-peer review between researcher and local field expert, Mr. Dulhadi, as well as some references, including Ashton (1982) and Newman et al. (1996a, 1996b).

Leaf characterization

Each leaf sample was characterized following Leaf Architecture Working Group (1999). Leaf characters comprise 17 features extracted from single blade. An example of each part of the venation order is shown in Figure 2.

Data analysis

Data analysis protocol following Maulia (2020) where the leaves' morphological characters, including patterns, margin, length, and width were observed and measured. Subsequently, each species' leaf architecture species were characterized according to the written character. Each feature was then assigned a score according to the existing character. This score consists of various categories, depending on the existent character, meaning laminar category 0-4. The score was then converted into binary numbers (0 and 1) by standardizing the process. This was followed by analyzing the value using MVSP (Multivariate Statistical Package) application 2.1. Subsequently, the similarity of each was determined by SMC (Simple Matching Coefficient), using UPGMA algorithm (Unweighted Pair Group Method with Arithmetic Means) as a clustering algorithm with dendrogram output. In addition, the determination key was formulated based on leaf architecture character. This analysis commonly used in clustering especially using morphological data (Hernandez et al. 2020).

RESULTS AND DISCUSSION

Leaf character variation

This study examined 17 leaf characters and identified the macroscopic leaf architecture variable in 35 species of Dipterocarpaceae comprising five genera, i.e. *Dipterocarpus, Shorea, Parashorea, Hopea,* and *Dryobanalops* (Table 1). The data shows that Dipterocarpaceae species share some similar characters, but also bring great variabilities among the leaf architectural character. All the species resemble two diagnostic characters of Ditperocarpacae: geniculated petiole and pinnate primary venation (Ashton 1982). The other 15 leaf architecture character represent the variability of leaf morphology on each species. The species laminar category varies. There is five-leaf category which spread among species studies, i.e. microphyll (225-2.025 mm^2), notophyll (2.025-4.500 mm^2), mesophyll (4.500-18.225 mm^2), macrophyll (18.225-164.025 mm^2), and megaphyll (>16.025 mm^2). There are three-leaf shapes observed in the measurement process, i.e., elliptic, oblong, and ovate. In the observation of venation character, there are two groups based on their order, i.e. secondary and tertiary vein. Secondary vein comprises of three types, i.e. brochidodromous, craspedodromous, and weakly brochidodromous. Brochidodromous characterize the secondaries joined together in a series of prominent arches, the weakly brochidodromous share the same definition but the venation at the end of secondaries showing the weakened joint between the adjacent secondaries. Meanwhile, the craspedodromous describe the secondaries terminating the margin (Hickey 1975). The other characters describe the variability between the species.

Leaf architecture has been an important topic in taxonomy (Bucksch 2014), especially encountering flowering periodization (Jones 1986; Sack et al. 2008), and leaves as identification tools in the flowering plants are bound to be very useful in the future. The predicted leaf architecture is then reconstructed using computational modelling (Hussein et al. 2021) to identify severely degraded herbarium specimens (Little et al. 2014). The petiole anatomy has proven to be useful as an identification tool in *Shorea* spp. (Hernandez et al. 2020). Several *Shorea* species and *Dipterocarpus gracilis* have slightly geniculate petiole. The petiole has various anatomy and morphological shape between species, and is, therefore, is an important feature in identification. Paudel and Heo (2017) reported that the additional petiole feature in Ebenaceae possibly helps identify the species level, while Niinemets and Fleck (2002) showed that the petiole morphology is strongly connected with the physiological process in *Liriodendron tilupifera*. Dipterocarpaceae leaf varies in laminar size, and the size is reported to be plastic caused by environmental factors (Parkhurst and Loucks 1972). However, the manual minimized the environmental issue by providing a size range in each category.

In this study, the *Dipterocarpus* spp. showed mostly categorized as macrophyll-megaphyll sized leaves. The largest category is megaphyll, owned by *Dipterocarpus elongatus*, while the smallest leaf category is microphyll, owned by *Shorea laevis*. Further studies regarding leaf size are bound to help in distinguishing the process of cell division and expansion (Gallagher 1979). This study found that laminar shape varied between three laminar shapes, i.e., ovate, elliptic, and oblong. This study supports Ashton (1982) that species of Dipterocarpaceae is varied in laminar shape. *Hopea* spp. tend to have ovate laminar shape, while *Shorea* spp. has oblongous shape except in *Shorea fallax*, *S. johorensis*, *S. multiflora*, *S. excelliptica*, *S. laevis*, *S. ovalis*, *S. platyclados*, and *S. pinanga*. In addition, *Dipterocarpus* spp. and *Dryobalanops* spp. are mostly have ellipsoid laminar shapes.

Species of Dipterocarpaceae mostly have symmetrical leaves, but some species of *Hopea* spp. have asymmetric bases. According to Dengler and Tsukaya (2001), leaf symmetry helps to understand the link between leaf development and cell-specific traits. Most species have acute base angle, except *S. compressa*, *S. kunstleri*, and *Hopea mangarawan* with obtuse angle. The leaf apex varied between acute and acuminate, while the base shape varied between cordate, convex, rounded, and complex base. A leaf's shape is related to genetic traits and is hereditary also has a strong influence in determining species in the plant (Gailing et al. 2012). In this study, the species found mostly have entire margin, but some have bumpy margin, such as *Dipterocarpus elongatus*, *D. grandiflorus*, and *D. hasseltii*. Therefore, leaf margin is useful in distinguishing species (Badron et al. 2014) and possibly explains past paleotemperate conditions (Peppe et al. 2018).

Secondary venation is categorized into three kinds, i.e. craspedodromous, brochidodromous, and weakly brochidodromous. Craspedodromous describe where the leaves have secondaries terminating at the margin, while brochidodromous implies the secondaries joined together in a series of prominent arches. Weak brochidodromous resemble brochidodromous type, but with weaker vein joint.

Cluster analysis

All characters presented in Table 1 were used in cluster analysis to determine the similarity between objects of observation. The distance was created to facilitate research in identifying and grouping the species. Furthermore, the cluster analysis used UPGMA and Simple Matching Coefficient logarithms. After the cluster construction, the phenon was created at 0.695 similarity level to classify 35 species of Dipterocarpaceae into four major clusters (Figure 3); the Phenon was created to delineate groups in dendrogram, and create meaningful interpretation in the study.

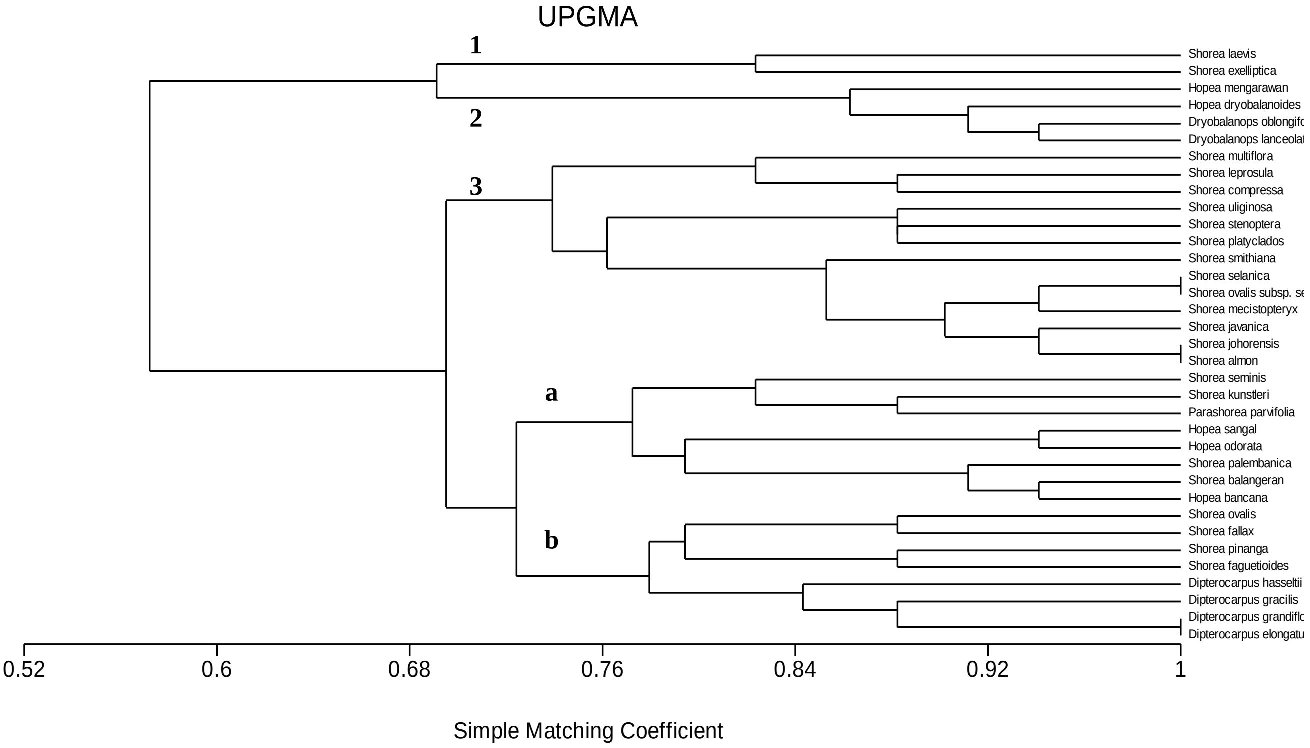

Figure 3. Cluster analysis based on leaf architecture character of 35 species of Dipterocarpaceae using UPGMA

Table 1. Leaf architecture characters of 35 species of Dipterocarpaceae cultivated in Forest Area with Special Purposes (KHDTK) Carita, Banten, Indonesia

Species	**(1) PET**	**(2) LAM**	**(3) LSH**	**(4) LSY**	**(5) BNG**	**(6) BSH**	**(7) ASH**	**(8) LFM**	**(9) PVN**	**(10) SVN**	**(11) SVS**	**(12) SVA**	**(13) ISV**	**(14) TVN**	**(15) TVC**	**(16) TVA**	**(17) TVV**
Dipterocarpus elongatus Korth.	gon	meg	el	sym	ac	cor	acm	bum	pin	bro	uni	uni	abs	mix	sin	obt	uni
Dipterocarpus gracilis Blume	sli	mac	el	sym	ac	cun	acm	ser	pin	cras	uni	uni	abs	mix	sin	obt	uni
Dipterocarpus grandiflorus (Blanco) Blanco	gon	mac	el	sym	ac	cor	acm	bum	pin	bro	uni	uni	abs	mix	sin	obt	uni
Dipterocarpus hasseltii Blume	gon	mes	obg	sym	ac	cvx	acm	bum	pin	bro	uni	uni	abs	mix	sin	obt	uni
Dryobalanops lanceolata Burck	gon	not	el	sym	ac	cvx	acm	ent	pin	bro	uni	uni	str	alt	abs	ire	inc
Dryobalanops oblongifolia Dyer	gon	not	obg	sym	ac	cvx	acm	ent	pin	bro	uni	uni	str	alt	abs	ire	inc
Hopea mengarawan Miq.	gon	mic	ovt	sym	obt	cvx	acm	ent	pin	cras	uni	uni	str	alt	abs	obt	inc
Hopea odorata Roxb.	gon	not	el	basy	ac	cvx	ac	ent	pin	webr	uni	uni	abs	mix	sin	obt	uni
Hopea bancana (Boerl.) Slooten	gon	mes	ovt	basy	ac	cvx	acm	ent	pin	cras	uni	uni	abs	mix	sin	obt	uni
Hopea dryobalanoides Miq.	gon	not	el	sym	ac	cvx	acm	ent	pin	cras	uni	uni	str	alt	abs	obt	inc
Hopea sangal Korth.	gon	not	ovt	basy	ac	cpl	ac	ent	pin	webr	uni	uni	abs	mix	stra	obt	uni
Parashorea parvifolia Wyatt-Sm. ex P.S.Ashton	gon	not	obg	sym	ac	cvx	acm	ent	pin	webr	uni	uni	str	mix	sin	obt	uni
Shorea exelliptica Meijer	sli	mic	el	sym	ac	cvx	ac	ent	pin	webr	uni	uni	abs	mix	sin	obt	inc
Shorea faguetioides P.S.Ashton	sli	mes	el	basy	ac	cvx	acm	ent	pin	webr	uni	uni	abs	mix	sin	obt	uni
Shorea fallax Meijer	gon	mes	el	sym	ac	cvx	ac	ent	pin	bro	uni	uni	abs	mix	sin	obt	uni
Shorea johorensis Foxw.	gon	mac	obg	sym	ac	rou	acm	ent	pin	bro	uni	uni	abs	mix	sin	obt	uni
Shorea kunstleri King	gon	not	ovt	sym	obt	cvx	acm	ent	pin	webr	uni	uni	abs	mix	sin	obt	uni
Shorea laevis Ridl.	sli	not	el	sym	ac	cvx	acm	ent	pin	webr	uni	uni	abs	alt	abs	ire	inc
Shorea leprosula Miq.	sli	mes	obg	sym	ac	rou	acm	ent	pin	webr	uni	uni	abs	mix	sin	obt	uni
Shorea mecistopteryx Ridl.	sli	mac	obg	sym	ac	cor	acm	ent	pin	bro	uni	abr	abs	mix	sin	obt	uni
Shorea multiflora (Burck) Symington	sli	mes	ovt	sym	ac	rou	acm	ent	pin	webr	uni	abr	abs	opp	conv	per	uni
Shorea ovalis Blume	sli	mes	el	sym	ac	cvx	acm	ent	pin	bro	uni	uni	abs	mix	sin	obt	uni
Shorea ovalis subsp. sericea (Dyer) Ashton	gon	mes	obg	sym	ac	rou	acm	ent	pin	bro	uni	abr	abs	mix	stra	obt	uni
Shorea palembanica Miq.	gon	mes	obg	basy	ac	cvx	acm	ent	pin	bro	uni	uni	abs	mix	sin	obt	uni
Shorea platyclados Slooten ex Endert	gon	not	el	sym	ac	cor	acm	ent	pin	webr	abr	abr	wea	mix	sin	obt	uni
Shorea selanica (Lam.) Blume	gon	mes	obg	sym	ac	rou	acm	ent	pin	bro	uni	abr	abs	mix	sin	obt	uni
Shorea seminis Slooten	gon	mes	obg	sym	ac	cpl	acm	ent	pin	webr	uni	uni	abs	mix	conv	obt	uni
Shorea smithiana Symington	gon	mac	obg	sym	ac	rou	acm	ent	pin	webr	uni	uni	wea	mix	sin	obt	uni
Shorea stenoptera Burck	gon	mac	obg	sym	ac	cor	acm	ent	pin	webr	abr	abr	abs	mix	sin	obt	uni
Shorea uliginosa Foxw.	gon	mac	obg	sym	ac	rou	acm	ent	pin	webr	abr	abr	wea	mix	sin	obt	uni
Shorea almon Foxw.	gon	mes	obg	sym	ac	rou	acm	ent	pin	bro	uni	uni	abs	mix	sin	obt	uni
Shorea balangeran Burck	gon	not	ovt	basy	ac	CVX	ACM	ent	pin	cras	uni	uni	abs	mix	sin	obt	uni
Shorea compressa Burck	sli	mes	obg	sym	obt	or	ac	ent	pin	webr	uni	uni	abs	mix	sin	obt	uni
Shorea javanica Koord. & Valeton	gon	mac	obg	sym	ac	cor	ACM	ent	pin	webr	uni	uni	abs	mix	sin	obt	uni
Shorea pinanga Scheff.	gon	mes	el	sym	ac	CVX	ACM	ent	pin	webr	uni	uni	abs	mix	sin	obt	uni

Note : (1) Petiole (PET): a) geniculated (gon), b) slightly geniculated (sli); (2) Laminar size (LAM): a) microphyll (mic), b) notophyll (not), c) mesophyll (mes), d) pinnate macrophyll (mac), e) megaphyll (meg); (3) Laminar shape (LSH): a) elliptic (el), b) oblong (obg), c) Ovate (ovt); (4) Laminar symmetry (LSY): a) symmetrical (sym), b) assymetrical at base (basy); (5) Base angle (BNG): a) acute (ac), b) obtuse (obt); 6) Base shape (BSH): a) cordate (cor), b) cuneate (cun), c) convex (cvx), d) complex (cpl), e) rounded (rou); (7) Apex shape (ASH): a) acute (ac), b) acuminate (acm); (8) Leaf margin (LFM): a) bumpy (bum), b) serrate (ser), c) entire (ent); (9) Primary vein (PVN): pinnate (pin); (10) Secondary vein (SVN): a) brochidodromous (bro), b) craspedodromous (cras), c) weakly brochidodromous (webr); (11) Secondary vein spacing (SVS): a) abruptly decreased toward base (abr), b) uniform (uni); (12) Secondary vein angle (SVA): a) abruptly increased torward base (abr), b) uniform (uni); (13) Intersecondary vein (ISV): a) strong (str), b) absent (abs), c) weak (wea); (14) Tertiary vein (TVN): a) mixed (mix), b) alternate (alt), c) opposite (opp); (15) Tertiary veni course (TVC): a) sinous (sin), b) admedially ramified (abs), c) convex (conv), d) straight (stra); (16) Tertiary vein angle (TVA): a) obtuse (obt), b) irregular (ire), c) perpendicular (per); (17) Tertiary vein variability (TVV): a) uniform (uni), b) inconsistent (inc)

In general, all species studied have pinnate primary leaves and geniculate petiole. Most of the observations had mixed tertiary vein and the phenon line from the 35 different species into four clusters. These are small leaf (microphyll) category, inconsistent tertiary angle pattern toward the primary vein, symmetrical leaves with a round or cordate base, and do not resemble a combination of symmetrical leaf and rounded base. The first cluster consists of two species, i.e., *Shorea laevis,* which belongs to the notophyll category and *S. excelliptica* which has microphyll category. These two laminar size categories belonging to the small leaves group (Shougang et al. 2003) and the two species were easily differentiated from other species by unified the venation order 1º, 2º, and 3º. Both *S. laevis* and *S. excelliptica* have pinnate on the 1º venation, weakly brochidodromous on the 2º venation, and mixed category for 3º venation. Venation provides mechanical, defensive, and hydraulic functions (Blonder et al. 2018) in addition to the main function as a photosynthetic distributor and therefore plays a crucial role (Chung 2012). According to Sack and Scoffoni (2013), venation density contributes to the significance of gas and K exchange inside and out of the leaves, and this shows the significance of identifying the venation structure (Sack and Scoffoni 2013).

The second cluster had an inconsistent tertiary angle pattern toward the primary vein in *Hopea mangarawan, H. dryobalanoides*, *Dryobalanops lanceolata, and D. oblongifolia* with the characteristic of a secondary ladder-like venation (dryobalanoids). These secondary ladder-like venation are very significant in determining species of Dipterocarpaceae, because these characters only resemble certain species, including *Hopea* spp. and *Dryobalanops* spp. (Fernando et al. 2009; Poopath et al. 2017; Talip et al. 2017).

The third cluster had symmetrical leaves with a round or cordate base, and comprised thirteen species, i.e. *Shorea multiflora*, *S. leprosula*, *S. compressa*, *S. uliginosa*, *S. stenoptera*, *S. platyclados*, *S. smithiana*, *S. selanica*, *S. ovalis* subsp. *sericea*, *S. mecistopteryx*, S. *javanica*, *S. johorensis*,*S. almon*. The cordate base is found in other *Shorea* spp. such as *Shorea palosapis* and *Shorea induplicata* (Pulan and Buot Jr. 2014; Ashton 1982). Leaf symmetry could be diagnostic identification tool (Nelson and Dengler 1997; Villareal and Buot Jr. 2015). Dipterocarpaceae genus member, *Vatica* spp. represent strong asymmetrical laminar shape (Ashton 1982). The combination of some morphological characters are able to provide more specific analysis in plant identification (Viscosi and Cardini 2011). *S. selanica,* and *S. ovalis* subsp. *sericea* had the exact similarity index as *S. ovalis* subsp. *sericea*, implying the two species probably have a high resemblance. This is due to the character standardization process in the analysis. The similarity is affected by a binary number change, therefore, some objects are considered equal. However, these two species are distinguishable in the determination *S. selanica* has slightly curved venation, while *S. ovalis* subsp. *sericea* had a straight tertiary vein category. *S. johorensis* and *S. almon* also have a similarity index of about 1. However, the two are distinguishable from the category of leaf size. In addition, *S. johorensis* has macrophyll leaf size, while *S. almon* has the nanophyll.

The fourth cluster's members do not resemble a combination of symmetrical leaf and rounded base, and include *S. fallax*, *S. ovalis*, *S. pinanga*, *S. faguetioides*, *Dipterocarpus hasselti*, *D. gracilis*, *D. grandiflorus*, and *D. elongatus*. In this study, all Dipterocarpus species generally have large leaf sizes, and were therefore covered by the fourth cluster (Maruyama et al. 1997). However, the result conforms with the prior description in Ashton (1982) where *Shorea fallax* indeed has symmetrical leaves, but the leaf base shape is wide obtuse. Meanwhile, *Shorea ovalis* has an oblong shape and obtuse base, which omits the species from the other three clusters. *Shorea pinanga* has a broadly cuneate and subcordate base, alike *Shorea faguetioides* which resemble the leaf base category. Rosdayanti et al. (2019) reported that the base shape category is a valuable character in the morphological delineation of *Shorea* species. In cluster four-node b, there are *Dipterocarpus hasseltii*, *D. grandiflorus*, and *D. elongatus* that share a similar leaf size range macrophyll and megaphylly (Figure 3). Leaf architecture in Dipterocarpaeae is a valuable descriptor in leaf fossil characterization (Lakhanpal and Guleria 1987). The report describes some main features in leaf fossils, there are leaf shape, apex, base shape, texture thickness, and secondary venation. The node a comprises *Shorea seminis*, *S. kunstleri*, *S palembanica*, *S. balangeran*, *Parashorea parvifolia*, *Hopea sangal*, *H. odorata*, and *H. banana* also share similar characters that omits them from the three major clusters. Base asymmetry and ovate-oblong leaf shape are the unifying characters in the nodes (Figure 3).

Qualitative and quantitative anatomical data could support the reliability of morphological data in leaf architecture, especially in classify species in conjunction with relevant molecular and ecological evidence (Talip et al. 2017). Leaf architecture remains a significant character to distinguish plants in species level. This approach could be the solution toward species where the generative part is uncertain to fulfill identification requirements. However, the leaf clearing procedure was not conducted in this study, due to the absence of tools with the capacity to clear big-sized leaves. Therefore, the leaf architecture variable requires further exploration, especially with regard to the microscopy variable of leaf venation. The 4th and 5th vein orders also need to be unveiled to ensure the data is more comprehensive. Further are also required to capture the image of whole leaf architecture character to provide imagery pattern data in all species to enhance preservation. Further studies are bound to be useful to paleobotanists while determining leave fossils based on the leaf architecture features.

Determination key

The determination key of 35 species of Dipterocarpaceae from the collected specimens based on the architectural characterization of leaves using the parallel key is shown as follows:

1. a. Inconsistent tertiary vein angle..2
b. Consistent tertiary leaf vein angle 7
2. a. Geniculated petiole. 3
b. Slightly geniculate petiole. 6
3. a. Notophyll leaf category 4
b. Microphyll leaf category .... *Hopea mengarawan*
4. a. Brochidodromous secondary vein 5
b. Craspedodromous secondary vein.....*Hopea dryobalanoides*
5. a. Elliptic leaf shape..........................*Dryobalanops lanceolata*
b. Oblong leaf shape.......................*Dryobalanops oblongifolia*
6. a. Blunt tertiary leaf vein angle......................*Shorea exelliptica*
b. Irregular tertiary vein angle ....*Shorea laevis*
7. a. Symmetrical leaf with rounded or cordate leaf base............8
b. Other 20
8. a. Mesophyll leaf category and primary vein hairy..................9
b. Other 11
9. a. Secondary vein angle uniform 10
b. Secondary vein angle abruptly increases toward base …….……………………………………… *Shorea multiflora*
10. a. Acute leaf base angle ....*Shorea leprosula*
b. Obtuse leaf base angle ....*Shorea compressa*
11. a. Secondary vein spacing abruptly decrease toward base 12
b. Secondary vein spacing uniform 14
12. a. Primary vein yellow-haired ....*Shorea uliginosa*
b. Primary vein glabrous 13
13. a. Intersecondary vein exist .... *Shorea platyclados*
b. Intersecondary vein absent ....*Shorea stenoptera*
14. a. Weak intersecondary vein ....*Shorea smithiana*
b. String Intersecondary 15
15. a. Secondary vein angle pattern abruptly increase toward base ………………………………………………………….. 16
b. Secondary vein angle pattern uniform 18
16. a. Cordate leaf shape ....*Shorea mecistopteryx*
b. Rounded leaf shape 17
17. a. Straight tertiary vein category...*Shorea ovalis* subsp. *sericea*
b. Curvy tertiary vein category ....*Shorea selanica*
18. a. Primary vein brown-haired..........................*Shorea javanica*
b. Primary vein yellow-haired 19
19. a. Macrophyll leaf category ....*Shorea johorensis*
b. Mesophyll leaf category ....*Shorea almon*
20. a. Entire margin with geniculated petiole 21
b. Not Entire margin with geniculated petiole 28
21. a. Symmetrical leaf 22
b. Leaf asymmetrical at base 24
22. a. Concave leaf base 23
b. Complex leaf base ....*Shorea seminis*
23. a. Strong intersecondary vein ....*Parashorea parvifolia*
b. Intersecondary vein absent ....*Shorea kunstleri*
24. a. Weakly brochidodromous secondary vein 25
b. Other 26
25. a. Elliptic leaf shape ....*Hopea sangal*
b. Ovate leaf shape ....*Hopea odorata*
26. a. Primary vein hair smooth 27
b. Primary vein hair rough ....*Shorea palembanica*
27. a. Notophyll leaf category ....*Shorea balangeran*
b. Mesophyll leaf category ....*Hopea banana*
28. a. Leaf margin entire 29
b. Leaf margin not entire 32
29. a. Brochidodromous secondary vein 30
b. Weakly brochidodromous secondary vein 31
30. a. Leaf apex acute ....*Shorea fallax*
b. Leaf apex acuminate ....*Shorea ovalis*
31. a. Symmetrical leaf ....*Shorea pinanga*
b. Leaf asymmetrical at base ....*Shorea faguetioides*
32. a. Elliptic leaf shape 33
b. Oblong leaf shape ....*Dipterocarpus hasseltii*
33. a. Geniculated petiole 34
b. Slightly geniculate petiole ....*Dipterocarpus gracilis*
34. a. Macrophyll leaf category ....*Dipterocarpus grandiflorus*
b. Megaphyll leaf category ....*Dipterocarpus elongatus*

In conclusion, the general characters of Dipterocarapaceae leaves are pinnate, geniculate petiole, and entire margin. Based on the 35 species of Dipterocarpaceae studied, they have grouped into four major clusters: the first group is the tiny (microphyll) leaf group category, the second group comprised species with inconsistent tertiary vein pattern, the third was characterized by leaves combining two features, symmetrical leaves with cordate base, while the last cluster was characterized by species resembling neither of the mentioned characters. The Phenon was cut at 0.695 similarity level, to establish a meaningful interpretation of the research. Furthermore, the key determination comprised 34 couplets. Therefore, further analysis on the leaf clearing method is required to provide a magnified view of the areolation and more variables in leaf architecture.

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