BIODIVERSITAS
Volume 22, Number 10, October 2021
Pages: 4379-4390

ISSN: 1412-033X
E-ISSN: 2085-4722
DOI: 10.13057/biodiv/d221031

Leaf geometric morphometric analyses of *Callicarpa* and *Geunsia* (Lamiaceae) in the Malesian region

JENNIFER S. DANILA[1,♥], GRECEBIO JONATHAN D. ALEJANDRO[1,2]
[1]The Graduate School, University of Santo Tomas. España Blvd., 1015 Manila, Philippines. ♥email: jennifer.danila.gs@ust.edu.ph
[2]College of Science and Research Centre for the Natural and Applied Sciences, University of Santo Tomas. España Blvd., 1015 Manila, Philippines

Manuscript received: 8 August 2021. Revision accepted: 24 September 2021.

Abstract. *Danila JS, Alejandro GJD. 2021. Leaf geometric morphometric analyses of* Callicarpa *and* Geunsia *(Lamiaceae) in the Malesian region. Biodiversitas 22: 4379-4390.* Leaves are one of the most substantial organs of plants for it serves as a basis of species identification. Leaf morphology provides distinguishing features that help in the discrimination of plant species as well as investigation of leaf features among populations. This study aimed to investigate leaf shape variations between the two genera *Geunsia* Blume group and its closely related taxon, *Callicarpa* L. (Lamiaceae) using a landmark-based geometric morphometric method. The differences in the leaf shape among former members of *Geunsia*, namely *C. apoensis, C. basilanensis, C. flavida, C. paloensis, C. pentandra, C. ramiflora,* and *C. surigaensis* are also evaluated. Two primary landmarks and 14 semilandmarks were assigned in all samples to represent changes around the leaf margin. The Procrustes fit was generated using MorphoJ software which displays the mean and landmark position for individual configurations. Canonical Variate Analysis (CVA) and Mahalanobis Distance (MD) were able to discriminate all samples of *Geunsia* species using a scatter plot. Furthermore, Procrustes ANOVA showed a significant difference (P = 0.0082) among the seven species of the *Geunsia* group. Based on the results obtained, geometric morphometrics of leaf shape is effective in interspecific discrimination within members of *Geunsia*. However, the result of Discriminant Analysis (DA) showed that *Geunsia* and *Callicarpa* groups made leaf shape differences inefficient in discriminating the two genera. Therefore, further morphological studies on landmark-based geometric morphometrics of leaf shape involving a larger number of samples especially in the study of intergeneric classification are suggested.

Keywords: *Callicarpa***,** Canonical Variate Analysis, *Geunsia*, landmark, leaf shapes, mahalanobis distance, procrustes analysis

INTRODUCTION

The taxonomy between *Callicarpa* L. and *Geunsia* Blume was among the most controversial genera in the family Lamiaceae (Bramley 2009). Since *Geunsia* was described by Blume (1823), members of the group have been known as synonyms of several *Callicarpa* species. Currently, *Geunsia* is regarded as a synonym of the genus *Callicarpa* (Cantino 1992; Harley et al. 2004; Bramley 2009; IPNI 2021; POWO 2021) based on the examination of morphological characters (Lam and Bakhuizen van den Brink 1921; van Steenis 1967; Govaerts et al. 2007) and molecular data (Bramley 2009). However, several rejections of previous characters (Lam 1919; Lam and Bakhuizen van den Brink 1921; Ridley 1923; Moldenke 1982) continue to challenge the relationship of the two genera.

The most widespread, *C. pentandra* Roxb. together with other former members of the *Geunsia* group, namely *C. basilanensis* Merr., *C. flavida* Elmer, *C. ramiflora* Merr., *C. surigaensis* Merr., and *C. apoensis* Elmer led to a complicated taxonomic relationship between *Geunsia* and *Callicarpa* (Bramley 2011). The inclusion of several species like *C. pentandra* and its affinities in the genus *Callicarpa* led to a complex species classification whether to separate conspecific species or retain its infraspecific classification. According to Lam (1919), species of *Geunsia* can be distinguished through leaf arrangement, conspicuous ridge in the petioles, anthers opened by widening of the upper part of the parallel fissures, and the ovary (three-)five-celled, the cells are two seeded. However, the circumscription of the genus *Geunsia* remains uncertain due to overlapping characters (Lam 1919; Bramley 2009; Danila and Alejandro 2020). The members of *Geunsia* in the Philippines as having similar features to the three varieties of *C. pentandra* based on indumentum but classification seems inappropriate due to various overlapping of species (Lam and Bakhuizen van den Brink 1921). Based on the taxonomic revision of Philippine *Callicarpa* reported by Bramley (2013), members of *Geunsia* have been classified and showed shared characters, e.g., alternate leaves, 4-merous flowers, and shape of corolla and anthers but appeared distinct based on leaf morphology and inflorescence. To avoid confusion, he also conducted a further leaf morphological study to classify species but characters like leaf shapes appeared insufficient to successfully separate species using identification key because leaf shape is very variable across its distribution.

The taxonomy of *Geunsia* is extremely complex due to wide geographical distribution, species overlap, high levels of variability, and phenotypic plasticity (Kawakubo 1986; Palmer 2012). These variables were often observed through their effects on the leaf structures (Vieira et al. 2014; Li et al. 2018; Morais et al. 2019). Therefore, leaf morphology is considered the most valuable answer in identifying taxa particularly for species belonging to the family Lamiaceae (Balant et al. 2019). Thus, leaf description has great relevance for its species discrimination along with effective diagnostic techniques and procedures. However, leaves vary in shape features depending on their leaf tips, leaf bases, and leaf margin. Currently, no studies have identified the leaf variation among *Callicarpa* and *Geunsia* groups to further separate or combine species based on leaf shapes.

This study described for the first-time accessions of members of *Geunsia* and *Callicarpa* within the Malesian region through leaf geometric morphometrics, contributing to a better understanding of the species variation through leaf shapes. Furthermore, this study aimed to discriminate *Geunsia* and *Callicarpa* species and determine taxonomic characters to differentiate *Geunsia* and *Callicarpa* species. Thus, a promising approach to species characterization like geometric morphometrics, which allows identification of shape components (Viscosi and Cardini 2011) to assess complicated genera like *Geunsia* and *Callicarpa* is hereby introduced.

MATERIALS AND METHODS

Study area

Leaf morphology and morphometric study were carried out from selected digital herbarium samples of A, HBG, K, L, MW, NY, P, SNSB, USTH, and US (abbreviations following Index Herbariorum, Thiers) and field collections in various localities of the Philippines (Table 1). This study focuses on specimens of *Geunsia* and *Callicarpa* collected in the selected localities in the Malesian region (Figure 1). A total of 96 leaflets were sampled from 63 online accessions and 33 individual specimens from the field. Online accessions were obtained in Global Biodiversity Information Facility (GBIF) database via the web interface, while field collections were obtained from the open lowland to hill forests of the provinces of Isabela, Sorsogon, and Samar in the Philippines. Online images and descriptions were downloaded using 'Darwin Core Archive' format, which contains the URLs of the images and information in GBIF (Table S1). On the other hand, samples from the field have undergone herbarium sample collection protocol of preparation, pressing, mounting, identification, and deliberation of voucher specimen to the University of Santo Tomas Herbarium (USTH), the Philippines.

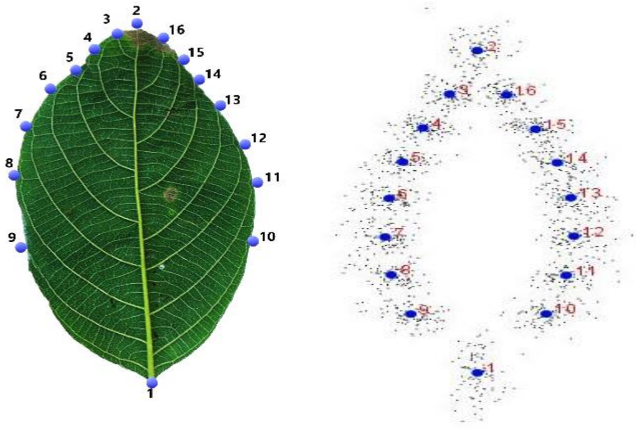
Procedures: Sampling preparation and data gathering

An initial of 96 leaflets were used to create a file for data manipulation and digitization. Based on the digital images, TPS files were created using tpsUtil32 software (Rohlf 2015). This TPS file contains the landmarks and image IDs to be used in digitizing images. In digitization, tpsDig232 software (Rohlf 2010) was used to assign landmarks on each image. Coordinates of 16 key landmarks of leaves were obtained to perform morphometric analysis (Figure 2.A). The abaxial surface of leaves was preferable because of the prominent secondary veins. Landmarks 1 and 2 were assigned, which corresponds to the junction of the petiole to the leaf tip of the primary vein (Gunz and Mitteroecker 2013).

Figure 1. Localities of selected *Geunsia* and *Callicarpa* species used in this study in the Malesian region. Philippines (A-H): A. Bangsamoro (Basilan, Cotabato, Lanao, Sulu), B. Bicol (Catanduanes, Sorsogon), C. Caraga (Agusan, Dinagat, Surigao), D. Eastern Visayas (Samar, Leyte), E. Central Visayas (Cebu), F. Davao G. Isabela, H. Zamboanga Peninsula, I. China, (J-K): Indonesia J. Kalimantan K. Sulawesi, L. Malaysia, M. Myanmar, N. Papua New Guinea, O. Vietnam, P. Singapore. (Map: www.scribblemaps.com).

Table 1. Populations and samples of *Geunsia* and *Callicarpa* groups were used in this study

Species	Localities	Acc. no.	Herbaria
Geunsia			
C. apoensis Elmer	Indonesia	L.4316447	Naturalis Biodiversity Center (AMD)
	Indonesia	L.4316456	Naturalis Biodiversity Center (AMD)
	Davao, Philippines	HBG513403	Herbarium Hamburgense (HBG)
	Davao, Philippines	103976	The New York Botanical Garden (NY)
	Davao, Philippines	93867	Harvard University Herbaria (HUH)
	Indonesia	L332108	Naturalis Biodiversity Center (AMD)
	Davao, Philippines	K000194933	Royal Botanic Gardens, Kew (K)
C. basilanensis Merr.	Basilan, Philippines	L2762581	Naturalis Biodiversity Center (AMD)
	Zamboanga, Mindanao	714485	National Museum of Natural History, Smithsonian Institution (US)
	Basilan, Philippines	119043	National Museum of Natural History, Smithsonian Institution (US)
	Zamboanga, Philippines	P03392618	MNHN - Museum National d'Histoire Naturelle (P)
	Zamboanga, Philippines	P03597180	MNHN - Museum National d'Histoire Naturelle (P)
	Basilan, Philippines	P03392619	MNHN - Museum National d'Histoire Naturelle (P)
C. flavida Elmer	Agusan, Philippines	119053	National Museum of Natural History, Smithsonian Institution (US)
	Dinagat Island, Philippines	L2753770	Naturalis Biodiversity Center (AMD)
	Agusan, Philippines	2270734	Missouri Botanical Garden (MO)
	Agusan, Philippines	2787903	National Museum of Natural History, Smithsonian Institution (US)
	Agusan, Philippines	93872	Harvard University Herbaria (HUH)
	Agusan, Philippines	93873	Harvard University Herbaria (HUH)
	Agusan, Philippines	U0007022	Naturalis Biodiversity Center (AMD)
	Davao, Philippines	119056	National Museum of Natural History, Smithsonian Institution (US)
	Davao, Philippines	93875	Harvard University Herbaria (HUH)
	Davao, Philippines	L2753771	Naturalis Biodiversity Center (AMD)
	Davao, Philippines	K000194994	Royal Botanic Gardens, Kew (K)
C. paloensis Elmer	Sorsogon, Philippines	2787975	National Museum of Natural History, Smithsonian Institution (US)
	Sorsogon, Philippines	2787974	National Museum of Natural History, Smithsonian Institution (US)
	Palo, Leyte	103990	The New York Botanical Garden (NY)
	Palo, Leyte	93883	Harvard University Herbaria (HUH)
	Sulawesi, Indonesia	L2757220	Naturalis Biodiversity Center (AMD)
	Sulu, Philippines	P03598409	MNHN - Museum National d'Histoire Naturelle (P)
	Agusan, Mindanao	K000194946	Royal Botanic Gardens, Kew (K)
	Agusan, Mindanao	K000194949	Royal Botanic Gardens, Kew (K)
C. pentandra Roxb.	Cebu, Philippines	K000248661	Royal Botanic Gardens, Kew (K)
	Kalimantan, Indonesia	K00094945	Royal Botanic Gardens, Kew (K)
	Davao, Philippines	K000194931	Royal Botanic Gardens, Kew (K)
	Papua New Guinea	K000194977	Royal Botanic Gardens, Kew (K)
	Kalimantan, Indonesia	K000249402	Royal Botanic Gardens, Kew (K)
	Surigao, Philippines	K000194992	Royal Botanic Gardens, Kew (K)
	Davao, Philippines	K000194930	Royal Botanic Gardens, Kew (K)
	Cebu, Philippines	K000248662	Royal Botanic Gardens, Kew (K)
	Singapore	K001114363	Royal Botanic Gardens, Kew (K)
	Samar, Philippines	JDS008	University of Santo Tomas, Philippines (USTH)
	Samar, Philippines	K000674786	Royal Botanic Gardens, Kew (K)
C. ramiflora Merr.	Catanduanes, Philippines	U0040805	Naturalis Biodiversity Center (AMD)
	Leyte, Philippines	2788026	National Museum of Natural History, Smithsonian Institution (US)
	Leyte, Philippines	L2762376	Naturalis Biodiversity Center (AMD)
	Catanduanes, Philippines	2788025	Naturalis Biodiversity Center (AMD)
	Leyte, Philippines	L2754623	Naturalis Biodiversity Center (AMD)
	Zamboanga, Philippines	119049	National Museum of Natural History, Smithsonian Institution (US)
	Lanao del Sur, Philippines	119084	National Museum of Natural History, Smithsonian Institution (US)
	Lanao Lake, Mindanao	M0111549	Staatliche Naturwissenschaftliche Sammlungen Bayerns (SNSB)
	Catanduanes, Philippines	P03598371	MNHN - Museum national d'Histoire Naturelle (P)
C. surigaensis Merr.	Surigao, Philippines	2788017	Smithsonian Institution, NMNH, Botany (US)
	Surigao, Philippines	2788016	National Museum of Natural History, Smithsonian Institution (US)
	Surigao, Philippines	1269210	Smithsonian Institution, NMNH, Botany (US)
	Surigao, Philippines	1269211	Smithsonian Institution, NMNH, Botany (US)
	Surigao, Philippines	1107985	Smithsonian Institution, NMNH, Botany (US)
	Surigao, Philippines	P03598359	MNHN - Museum national d'Histoire Naturelle (P)
Callicarpa			
C. arborea Roxb.	Samar, Philippines	JES008	University of Santo Tomas, Philippines (USTH)
C. erioclona Schauer	Sorsogon, Philippines	SOR006	University of Santo Tomas, Philippines (USTH)
C. pedunculata R.Br.	Isabela, Philippines	JDS001	University of Santo Tomas, Philippines (USTH)
C. rubella Lindl.	Vietnam	MW0757612	Lomonosov Moscow State University (MW)
	Vietnam	2808046	The New York Botanical Garden (NY)
	Vietnam	P00991455	MNHN - Museum National d'Histoire Naturelle (P)
	Myanmar	2648823	The New York Botanical Garden (NY)
	China	2787428	National Museum of Natural History, Smithsonian Institution (US)
	Myanmar	3231815	The New York Botanical Garden (NY)
	Malaysia	L0534846	Smithsonian Institution, NMNH, Botany (US)



A **B**

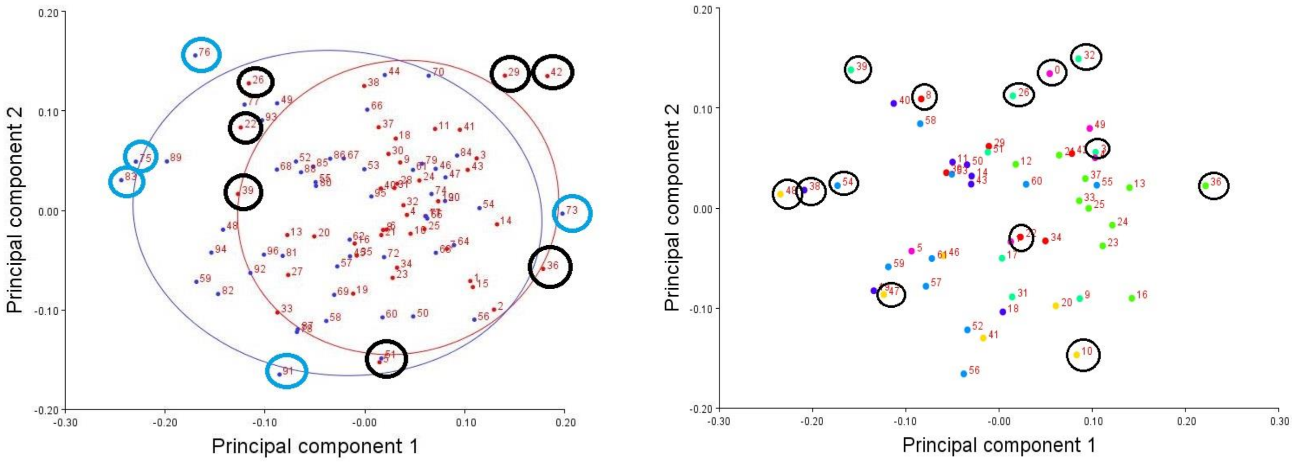
Figure 2. Leaf morphometrics. A. Abaxial surface with primary landmarks (1-2) and semilandmarks (3-16) of *C. pentandra* (Photo: University of Minnesota Bell Museum (2021). Bell Museum plants. Occurrence dataset https://doi.org/10.15468/bihrxd accessed via GBIF.org on 2021-08-02. https://www.gbif.org/occurrence/2265568305), B. Mean landmarks (large dots) and individual landmarks in all samples of *Geunsia* and *Callicarpa* (small dots) before elimination of outliers

Fourteen semi landmarks of secondary veins were assigned to represent changes around the leaf margin. The number of semi landmarks determined in a study depends on the complexity of curves and the position of the veins (Gunz and Mitteroecker 2013). After assigning landmarks, consensus files were generated from landmark images used in the populations of *Geunsia* and *Callicarpa* species. To create a data set, the TPS file was imported into the software package MorphoJ (Klingenberg 2011). The Procrustes fit was generated, showing the mean and landmark position for individual configurations in all samples (Figure 2.B). A preliminary transformation was conducted by eliminating outliers within the scatter plot generated during Principal Component Analysis (PCA) (Hotelling 1933). In this study, PC1 and PC2 were used to identify outliers. Potential outliers were detected by identifying data points separated from the main scatter plot ellipses (Viscosi and Cardini 2011) and cross-checked for further leaf shape deviation using MorphoJ. Outliers were deleted from the data before the computation of the mean leaf configurations of the final dataset. Outliers may contain noise that was obtained from the digital images and may affect the accuracy of the study (Du et al. 2007).

Data analysis

Multivariate analysis of outliers

In the study between *Geunsia* and *Callicarpa* groups, the analysis led to the identification of 12 outliers out of 96 data points of leaves (12.50%) observed in PC1 and PC2. *Geunsia* and *Callicarpa* have percentage values of outliers, 9.43%, and 16.28%, respectively. The new set of samples consisted of 84 leaflets from 36 and 48 leaflets of *Callicarpa* and *Geunsia*, respectively. Likewise, a separate analysis of outliers was done exclusively for the species of *Geunsia*, which led to the identification of 13 outliers out of 53 leaves (25%) thereby creating a new dataset of 40 leaflets. All the outliers identified through this procedure were eliminated from the data matrices of landmarks for each sample. All samples were separately extracted to create new datasets for subsequent multivariate analysis of intergeneric and interspecific classification (Figure 3.A-B).



A **B**

Figure 3. Selection of outliers (encircled) among samples of: A. *Geunsia* and *Callicarpa* (black: *Callicarpa*; blue: *Geunsia*; B. combined seven species of *Geunsia* (black: randomly selected species of *Geunsia*)

Multivariate analysis of leaf shape variability

The new dataset was subjected to various statistical analyses like PCA, Canonical Variate Analysis (CVA), and Discriminant Function Analysis (DFA). PCA was used to check the total leaf shape variation of 84 individuals of combined *Geunsia* and *Callicarpa* samples and 40 individuals of the *Geunsia* species. PCA treats all configurations for each sample regardless of species or any form of group classification into one population. Principal component axes or shape trends were visualized through thin-plate spline reconstructions of the shapes which correspond to the leaf changes of the significant PCs. Likewise, Eigenvalues were included to measure the amount of variation explained on each PCs. In this study, data were assessed between *Geunsia* and *Callicarpa* groups and within the treatment group. CVA was used to classify samples into known groups by measuring the strength of the relationship based on the highest correlated calculation (Klingenberg 2011). The canonical variates (CVs) show which axes best discriminate between the group and within-group variation (Zelditch et al. 2004). The discrimination was best observed when using a scatterplot which allows separation of species based on treatment groups assigned. In this study, CVA was performed to discriminate samples of *Geunsia* based on species. Procrustes and Mahalanobis distances were also used to show patterns of morphological similarity between groups of *Callicarpa* and *Geunsia* species and among members of *Geunsia* through pairwise comparison. Mahalanobis Distance (MD) measures the distance between a distinct point of the specimen relative to the mean position of all points of an object. In this case, one can estimate the degree of a specimen to belong to a group whose mean is the closest (Viscosi and Cardini 2011). In comparison, Procrustes Distance (PD) refers to the measure of the absolute magnitude of shape deviation based on mean landmark changes of two samples to quantify the similarity and differences (Bookstein 1996). Likewise, a cross-validation test (permutation test with 10,000 rounds) was performed to evaluate the classification accuracy of *Geunsia* and *Callicarpa* and among members of *Geunsia* based on MD. The Procrustes ANOVA (Analysis of Variance) was also used for testing the shape differences among the samples of the *Geunsia* group if statistically significant ($p \leq 0.05$). All analyses were performed using the software MorphoJ (Klingenberg 2011).

RESULTS AND DISCUSSION

Leaf geometric morphometrics between *Geunsia* and *Callicarpa* species

Significant variations from all 84 samples mostly occurenced in the first four principal components (PC1, PC2, PC3, and PC4) with a cumulative variance of 77.24% (Table 2). The proportion of variance method to retain a considerable number of PCs which accounts from the highest percentage to 5-10% of the total variance was considered, whereby the proportion of variance is obtained by dividing eigenvalue for the component of interest by total eigenvalues of the correlation matrix (Jackson 1993). All *Geunsia* and *Callicarpa* species were united inside their respective ellipses (Figure 4.A-B). However, the two ellipses in both diagrams showed an overlap which suggests that leaf shapes similarities exist between groups. The PC1 score (31.49%) represents changes in the width of the leaf resulting in ovate to narrowly ovate leaves (Figure 4.C). The PC2 score (23.31%) represents a change in the leaf shape showing a minimal extension of the apical and distal region of the leaf. While PC3 and PC4 both constitute a low score, 14.19%, and 8.26%, respectively, but the changes became conspicuous due to asymmetric variation on the leaf shape mostly found either on one side of bases or tips of the leaves.

Comparisons between the groups were performed using the Canonical Variate Analysis (CVA), wherein the first canonical variate (CV1) was accounted for 100% of the total variance (Table 3). MD and PD were also obtained by pairwise comparison between the *Geunsia* and *Callicarpa* and showed highly significant differences (permutation 10,000 rounds in MorphoJ: P<.0001) of 1.7965 and 0.0569, respectively. A significant difference in the *P*-values from the permutation test for MD and PD among groups were <.0001 and 0.0024, respectively. Most of the shape changes between the groups generally accounted for the width of the leaf. Despite this, the result of Discriminant Analysis (DA) (Figure 4.D, Hotelling's $T^2 = 66.39$, *P*-value = 0.0708) in comparing the two taxa showed that leaf shape does not differentiate them sufficiently to allow distinction. Likewise, the cross-validation of correctly classified *Callicarpa* (61.11%) and *Geunsia* (60.42%) showed low percentage and overlap made leaf shape difference ineffective for separating genus *Geunsia* from *Callicarpa*.

Table 2. The first ten of a Principal Component Analysis (PCA) of leaf shape in 84 individuals of *Callicarpa* and *Geunsia* species

PC	Eigenvalues	% Variance	Cumulative %
1	0.00585	31.488	31.488*
2	0.00433	23.306	54.795*
3	0.00264	14.185	68.98*
4	0.00154	8.263	77.243*
5	0.00088	4.748	81.991
6	0.00076	4.097	86.088
7	0.00057	3.073	89.16
8	0.00043	2.337	91.497
9	0.00029	1.544	93.042
10	0.00026	1.379	94.421

*Note: Only the first four are significant according to the proportion of variance with 5-10% of the total variance. Eigenvalues are derived from a matrix of 84 Procrustes-aligned configurations of 16 landmarks.

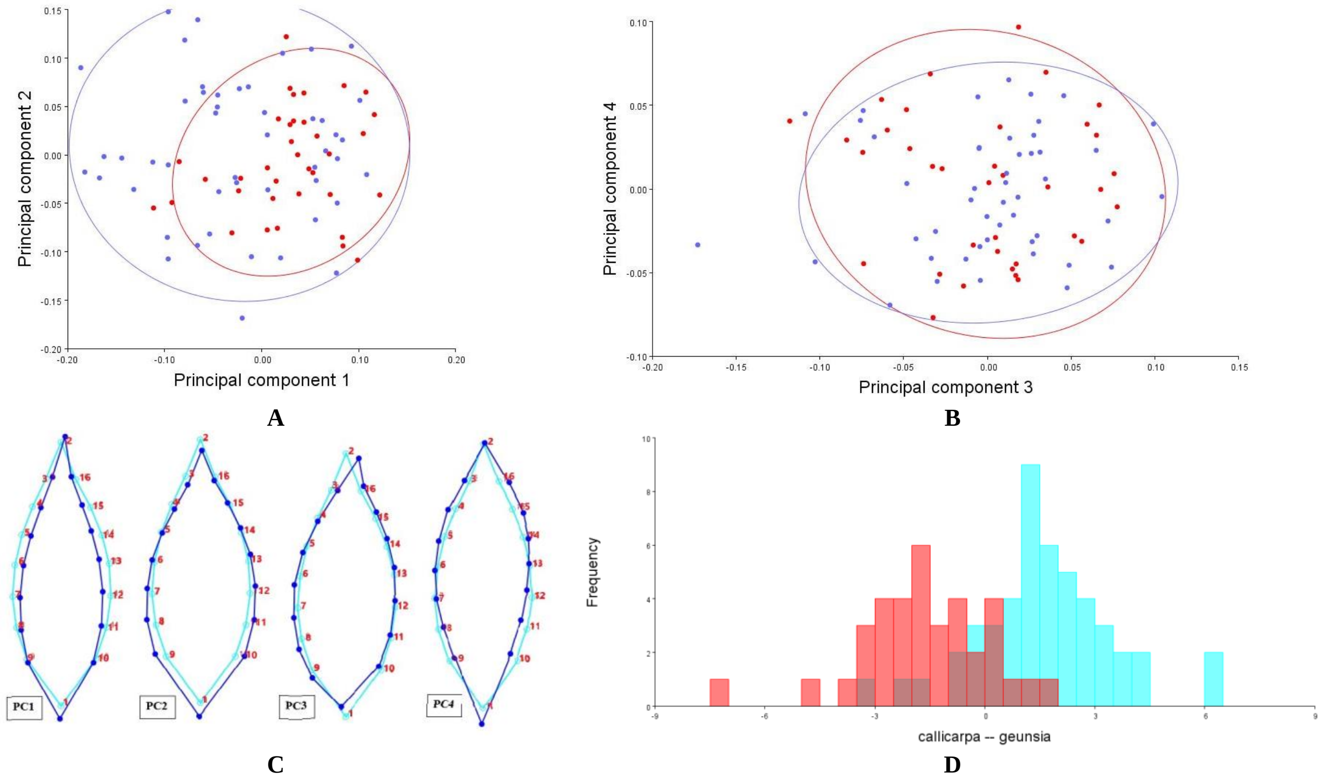


Figure 4. The Principal Component Analysis (PCA). A-B. Scatter plot of 4 PCs in the leaf of all 84 individuals of *Geunsia* (blue) and *Callicarpa* (red) group of *Callicarpa*, C. Axis components of PC1, PC2, PC3, and PC4 showing the variation in leaf shape, D. Discriminant analysis (DA) between *Geunsia* and *Callicarpa* (red bars: *Callicarpa*; blue bars: *Geunsia*) Hotelling's T^2 = 66.39, P = 0.0708. Computed in Morpho J (Klingenberg 2011).

Table 3. Differences in leaf shape of *Callicarpa* species between groups of *Geunsia* and *Callicarpa* species analyzed with Canonical Variate Analysis (CVA), percentage of correctly classified specimens, and variation among groups, scaled by the inverse of the within-group variation

	Geunsia	***Callicarpa***	**% of correctly classified**	***P* values Mahalanobis Distance**	***P* values Proscrustes Distance**	**Eigenvalues**	**Variance %**	**Cumulative %**
Geunsia		0.0569	60% (29/48)	<.0001	0.0024	PC1 0.80962244	100	100
Callicarpa	**1.7965**		61% (22/36)					

Note: Mahalanobis Distances (bold, underlined) and Procrustes Distances (narrow, underlined). *P*-values based on permutation 10,000 rounds in MorphoJ: $P < 0.0001$)

The morphometric approach confirmed leaf shape variations between *Geunsia* and *Callicarpa* (Figure 4.C). In addition, the extremely reconstructed outlines along the axes and the scatter plot (Figure 4.A-B) showed that *Geunsia* and *Callicarpa* correspond to the ovate to narrowly ovate shape pattern. This pattern is supported by collections of the field and herbarium (Bramley 2009, 2013). However, species discrimination based on CVA and DA analyses does not show a reliable pattern that distinguishes the two genera (Figure 4.D). Thus, a weak indication of leaf shape differentiation between the two taxa suggests a tendency for some samples to be less distant from the other, resulting in an overlap in the intergeneric comparison. According to Adebowale et al. (2012), an overlap in morphological characters like leaf shape in the application of geometric morphometrics could have environmental and genetic explanations. Moreover, an overlap manifested in the intergeneric assessment is possibly due to the presence of hybrid in the individual samples in species occupying similar habitat; thus similarity in leaf shape could reflect evolutionary adaptation to environmental conditions (Adebowale et al. 2012; Mirouze et al. 2012). *Callicarpa* has been reported to show the incidence of hybridization in several plant species (Tsukaya et al. 2003). Hence, this may affect the result of geometric morphometrics to discriminate *Geunsia* and *Callicarpa* and may underline the limitation of a single approach in solving taxonomic problems.

Leaf geometric morphometrics among members of *Geunsia* species

After eliminating the outliers, the Principal Component Analysis (PCA) from all 40 samples of the *Geunsia* group is presented in Table 4. The PCA indicated that the first five components (PC1, PC2, PC3, PC4, and PC5) were responsible for 82.610% of the significant leaf shape variation obtained from the selected samples of *Geunsia*. PC1 of 33.022% showed the highest variation representing leaf tip changes from acute to attenuate and a minimal expansion of the leaf bases. PC2 (25.871%) was responsible for width changes of leaves from narrowly ovate to ovate shape. While PC3, PC4, and PC5 of 9.417%, 8.175%, and 6.124%, respectively refer to the non-symmetric shape patterns of the leaf (Table 4, Figure 5.A). PC3 is responsible for unequal extension of the apical region with a slight curvature on its tip and a minimal contraction in the proximal part of the leaf, while PC4 and PC5 showed inconspicuous expansion in the width, distal and proximal part of the leaf.

Table 4. The Principal Component Analysis (PCA) of leaf shape in 40 individuals of *Geunsia* species

PC	Eigenvalues	% Variance	Cumulative %
1	0.0048015	33.022	33.022*
2	0.0037616	25.871	58.893*
3	0.0013693	9.417	68.310*
4	0.0011886	8.175	76.485*
5	0.0008905	6.125	82.610*
6	0.0006784	4.665	87.275
7	0.0003981	2.738	90.013
8	0.0003150	2.166	92.180
9	0.0002201	1.513	93.693
10	0.0001875	1.290	94.983

*Note: Only the first five are significant according to the proportion of variance with 5-10% of the total variance. Eigenvalues are derived from a matrix of 40 Procrustes-aligned configurations of 16 landmarks

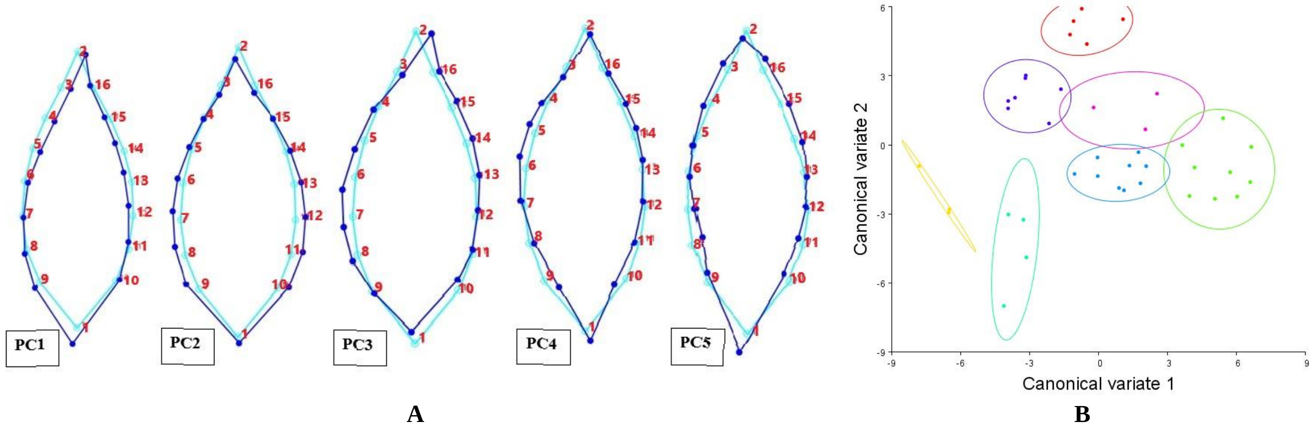


Figure 5. Analysis in all leaf samples of 40 individuals of *Geunsia* group. A. Axis components of PC1 (33.02%), PC2 (25.87%), PC3 (9.42%), PC4 (8.18%), and PC5 (6.13%) showing the variation in leaf shape of *Geunsia* group; B. The canonical variate analysis (CVA) [*C. apoensis* (🟥 red), *C. basilanensis* (🟨 yellow), *C.flavida* (🟩 green), *C. paloensis* (⬜ light blue), *C. pentandra* (🟦 blue), *C. ramiflora* (🟦 dark blue), *and C. surigaensis* (🟪 purple)].

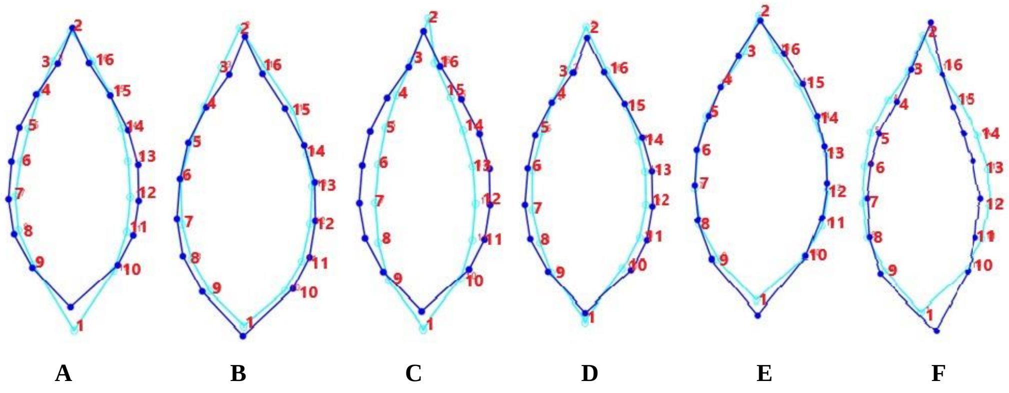


Figure 6. Transformation grids illustrate the shape changes from the overall mean shape of *C. pentandra* among other members of *Geunsia.* A. *C. apoensis,* B. *C. basilanensis,* C. *C. flavida,* D. *C. paloensis,* E. *C. ramiflora,* F. *C. surigaensis*. Dots indicate the mean shape of *C. pentandra* and the line represents the change in leaf shape relative to the position of other members of *Geunsia*

Canonical Variate Analysis (CVA) was able to generate six variables among samples of the *Geunsia* species (Table 5). The scatter plot of CV1 and CV2 were accounted for 68.888% of the variation and shows that all samples (*C. basilanensis, C. pentandra, C. flavida, C. ramiflora, C. paloensis, C. apoensis,* and *C. surigaensis*) were clearly identified and successfully placed into its distinct groups (Figure 5.B). Likewise, the MD scores were obtained, which range from 6.3015 (*C. ramiflora* and *C. apoensis*) to 12.6607 (*C. flavida* and *C. basilanensis*) by pairwise comparisons (Table 6). Using multivariate normal distribution, one can estimate the degree of a specimen to belong to a group whose mean is the closest (Viscosi and Cardini 2011). In this study, *C. ramiflora* and *C. apoensis* showed the nearest distance to the central point or the overall mean of data points in all samples. Furthermore, all samples used in the pairwise comparison was statistically significant in their distance relative to the centroid (Table 7). Thus, MD provided an effective and convenient way to quantitatively compare the magnitude of cluster separation in an ambiguous taxon like the *Geunsia* species. While PD scores ranged from 0.0684 (*C. ramiflora* and *C. pentandra*) to 0.1607 (*C. ramiflora* and *C. flavida*) also showed highly significant differences on a few samples of the *Geunsia* group (Table 8). Procrustes distance showed significant difference among *C. ramiflora* and *C. flavida* (<.0001), *C. pentandra* and *C. flavida* (0.0003), *C. basilanensis* and *C. flavida* (0.0048), *C. flavida* and *C. apoensis* (0.0099) and *C. paloensis* and *C. flavida* (0.0103) (Table 9). In this regard, the difference among these species could be explained by their leaf shape difference. Likewise, Procrustes ANOVA results showed significant differences among populations of *Geunsia* species (Table 10). Leaf shape differences among taxa were statistically significant (P = 0.0082), and strong clustering made overall leaf shape difference effective in separating members of *Geunsia*.

Table 5. Canonical variate analysis (CVA) of 40 samples of *Geunsia* species

CV	Eigenvalues	% Variance	Cumulative %
1	15.920517	44.200	44.200
2	8.8924508	24.688	68.887
3	4.7232715	13.113	82.000
4	2.9410219	8.165	90.166
5	2.0241605	5.620	95.785
6	1.5181756	4.215	100.000

Table 6. Mahalanobis distances among groups showed differences in leaf shape of *Geunsia* species among groups based on species analyzed with Canonical Variate Analysis (CVA)

	APO	BAS	FLA	PAL	PEN	RAM
BAS	10.5466					
FLA	8.8952	12.6607				
PAL	10.5837	6.9693	10.025			
PEN	7.9616	9.9683	6.4654	7.2779		
RAM	6.3015	8.2473	9.4752	7.7460	6.3831	
SUR	8.3237	11.801	8.3311	10.0538	6.7831	8.0964

Note: *C. apoensis* (APO), *C. basilanensis* (BAS), *C. flavida* (FLA), *C. paloensis* (PAL), *C. pentandra* (PEN), *C. ramiflora* (RAM), and *C. surigaensis* (SUR).

Table 7. *P*-values from permutation tests (10000 permutation rounds) for Mahalanobis Distances among groups

	APO	BAS	FLA	PAL	PEN	RAM
BAS	0.0128					
FLA	0.0002	0.0036				
PAL	0.0044	0.0342	0.0004			
PEN	0.0001	0.0014	0.0001	0.0006		
RAM	<.0001	0.0083	<.0001	0.0029	<.0001	
SUR	0.0071	<.0001	0.0048	0.0188	0.0039	0.0044

Note: All values were statistically significant. (permutation 10,000 rounds in MorphoJ: $P < 0.0001$)
Note: see the previous table (abbreviations)

Table 8. Procrustes Distances among groups showed differences in leaf shape of *Geunsia* species among groups based on species analyzed with canonical variate analysis (CVA)

	APO	BAS	FLA	PAL	PEN	RAM
BAS	0.1223					
FLA	0.1006	0.1447				
PAL	0.0805	0.067	0.0998			
PEN	0.095	0.0764	0.1424	0.0766		
RAM	0.0831	0.1202	0.1607	0.0995	0.0684	
SUR	0.0842	0.1463	0.0929	0.0999	0.1176	0.1149

Note: see the previous table (abbreviations)

Table 9. *P*-values from permutation tests (10000 permutation rounds) for Procrustes Distances among groups

	APO	BAS	FLA	PAL	PEN	RAM
BAS	0.0547					
FLA	0.0099	0.0048				
PAL	0.3414	0.6587	0.0103			
PEN	0.1140	0.5676	0.0003	0.4064		
RAM	0.1689	0.0802	<.0001	0.1056	0.2913	
SUR	0.7019	0.308	0.2708	0.5625	0.2192	0.1526

Note: Statistically significant (bold) and not significant (narrow) (permutation 10,000 rounds in MorphoJ: $P < 0.0001$)
Note: see the previous table (abbreviations)

Table 10. Shape, procrustes ANOVA among *Geunsia* species

Source	SS	MS	Df	F	P
Between Treatments	636.970461	106.161744	6	3.53	0.0082
Within Treatments	991.703317	30.051616	33		

Note: SS = the sum of squares; MS = mean of the square; Df = degrees of freedom; F = F-value; *P* = *P*-value

According to Lam and Bakhuizen van den Brink (1921 and Bramley (2013), *C. pentandra* shares morphological characters within the species of the *Geunsia* group. For example, a closely related species, *C. flavida* shares morphological characters like alternate leaves, 4-5-merous flowers, and the shape of corolla and anthers with *C. pentandra*. In a pairwise comparison of *C. pentandra* with other members of *Geunsia*, *C. flavida* showed the nearest distance to the centroid (MD=6.4654) relative to *C. pentandra*. All specimens of the two taxa were clustered and showed distinct groups. Similarly, PD (0.1424) (Figure 6.C) reveals a significant difference ($P = 0.0003$) (Table 9) between *C. pentandra* and *C. flavida*. The two taxa show conspicuous leaf shape variations represented by width expansion from ovate to narrowly ovate. Thus, this study showed that leaf morphometrics has great relevance in the discrimination of species belonging to *Geunsia* group.

The study of seven *Geunsia* species using geometric morphometric analyses uncovered important leaf shape characters to discriminate species. The transformation grids' shape changes from the overall mean shape confirmed that leaf tips, leaf bases, and width expansion are the main diagnostic characters (Figure 5.A). This also proved that symmetric variations play a major role in determining leaf shape among *Geunsia* species. As symmetric variations dominate overall changes in the leaf shape, asymmetrical variations were also observed among the *Geunsia* species showing a left-right pattern at the basal and apical ends of the leaves (Figure 5.A). Fluctuating Asymmetry (FA) (van Valen 1962) may exist in *Geunsia* samples, whereas they normally exist as bilaterally symmetrical on leaf shapes. FA usually occurs when species from the same population show abnormal growth resulting in unequal development, leading to asymmetrical morphological characters (Leary and Allendorf 1989). Several studies linked FA with environmental and genomic factors that may affect an organism's overall development (Cowart and Graham 1999; Mal 2002). Likewise, the result of the CVA analysis in comparing the species of *Geunsia* showed that leaf shape discriminated them sufficiently to allow identification. At the same time, MD and PD among groups of *Geunsia* species analyzed with CVA identify species that are closely related to each other based on leaf shape. It reveals that leaf shape showed to be a stable character and informative on the phylogenetic and evolutionary relationship of the *Geunsia* species.

In conclusion, geometric morphometric analysis of leaf shapes was highly reliable and could be used as an additional method to discriminate members of the genus *Geunsia*. The existence of morphological distinction in leaf variations, such as acute to attenuate leaf tips and ovate to narrowly ovate leaf shapes can be useful in grouping members of *Geunsia*. Leaf characters like leaf shapes and leaf tips were recognized as important diagnostic characters in the study of *Geunsia* species. This method also allows complicated species like *C. pentandra* to distinguish and identify their relationship with other members of the *Geunsia* group. This study can be a precursor for any future morphological, environmental and genomic analysis to investigate the relationship of the members of *Geunsia* with its closely related species like members of the genus *Callicarpa*. Future morphological studies on landmark-based geometric morphometric analysis of leaf shape involving a larger number of samples are encouraged in the study of interspecific and intergeneric classification.

ACKNOWLEDGEMENTS

The authors would like to thank the curators of A, HBG, K, L, MW, NY, P, SNSB, US, and USTH and the Global Biodiversity Information Facility (GBIF) for allowing us to access their digital collections for study. We thank the curator of the University of Santo Tomas (USTH) for giving us accessions to our specimens. Likewise, we would like to thank the Department of Environment and Natural Resources (DENR) for granting us the gratuitous permit to collect specimens in Isabela, Samar, and

Sorsogon province. Lastly, the first author also would like to thank the Commission on Higher Education (CHEd) for the Scholarship and Dissertation grant.

REFERENCES

Adebowale A, Nicholas A, Lamb J, Naidoo Y. 2012. Elliptic fourier analysis of leaf shape in southern African *Strychnos* section *Densiflorae* (Loganiaceae). Bot J Linn Soc 170 (4): 542-553. DOI: 10.1111/j.1095-8339.2012.01308.x

Balant M, Glasnović P, Fišer Pečnikar Ž, Clementi M, Surina B. 2019. In search of an identity for *Salvia bertolonii* (Lamiaceae). Phytotaxa 413 (2): 117-136. doi: 10.11646/phytotaxa.413.2.2

Blume CL. 1823. Catalogus van Eenige der Merkwaardigste Zoo in- Als Uit-Heemsche Gewassen, te Vinden in's Lands Plantentuin te Buitenzorg, Batavia.

Bookstein FL. 1996. Combining the tools of geo- metric morphometrics. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE (eds) Advances in Morphometrics. Plenum, New York. DOI: 10.1007/978-1-4757-9083-2_12

Bramley G. 2009. The genus *Callicarpa* (Lamiaceae) on Borneo. Bot J Linn Soc 159 (3): 416-455. DOI: 10.1111/j.1095-8339.2009.00907.x

Bramley G. 2011. Distribution patterns in Malesian *Callicarpa* (Lamiaceae). Gard Bull Singapore 63 (1 & 2): 287-298.

Bramley G. 2013. The genus *Callicarpa* (Lamiaceae) in the Philippines. Kew Bull 68 (3): 369-418. DOI: 10.1007/s12225-013-9456-y

Cantino PD. 1992. Evidence for a polyphyletic origin of the Labiatae. Ann Missouri Bot Gard 79 (2): 361-379. DOI: 10.2307/2399774

Cowart NM, Graham JH. 1999. Within- and among individual variation in fluctuating asymmetry of leaves in the fig (*Ficus carica* L.). Int J Plant Sci 160 (1): 116-121. DOI: 10.1086/314104

Danila J, Alejandro GJD. 2020. Pollen morphology and infrageneric classification of selected *Callicarpa* species (Lamiaceae) from the Philippines and Borneo. Biodiversitas 21 (12): 5736-5746. DOI: 10.13057/biodiv/d211234.

Du JX, Wang XF, Zhang GJ. 2007. Leaf shape-based plant species recognition. Appl Math Comput 185 (2): 883-893. DOI: 10.1016/j.amc.2006.07.072

Govaerts R, Paton AJ, Harvey Y, Navarro T. 2007. World Checklist of Lamiaceae. The Board of Trustees of the Royal Botanic Gardens, Kew. http://www.kew.org/wcsp

Gunz P, Mitteroecker P. 2013. Semilandmarks: a method for quantifying curves and surfaces. Hystrix Ital J Mammal 24 (1): 103-109

Harley RM, Atkins S, Budantsev AL, Cantino PD, Conn BJ, Grayer R, Harley MM, de Kok RPJ, Krestovskaja T, Morales R, Paton AJ, Ryding O, Upson T. 2004. Labiatae. In: Kubitzki K (ed) The Families and Genera of Vascular Plants, Vol. 4. SpringerVerlag, Berlin.

Hotelling H. 1933. Analysis of a complex of statistical variables into principal components. J Educ Psychol 24 (6): 417. DOI: 10.1037/h0071325

IPNI. 2021. International Plant Names Index. Published on the Internet http://www.ipni.org, The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Botanic Gardens.

Jackson DA. 1993. Stopping rules in principal components analysis: A comparison of heuristical and statistical approaches. Ecology 74 (8): 2204-2214. DOI: 10.2307/1939574

Kawakubo N. 1986. Morphological variation of three endemic species of *Callicarpa* (Verbenaceae) in the Bonin (Ogasawara) Islands. Plant Species Biol 1 (1): 59-68. DOI: 10.1111/j.1442-1984.1986.tb00015.x

Klingenberg CP. 2011. MORPHOJ: An integrated software package for geometric morphometrics. Mol Ecol Resour 11 (2): 353-357. DOI: 10.1111/j.1755-0998.2010.02924.x

Lam HJ. 1919. The Verbenaceae of the Malayan Archipelago. de Waal, Groningen.

Lam HJ, Bakhuizen van den Brink RC. 1921. Revision of the Verbenaceae of the Dutch East-Indies and surrounding countries. Bull Jard Bot Série III 3: 1-116 & I-III.

Leary RF, Allendorf FW. 1989. Fluctuating asymmetry as an indicator of stress: implications for conservation biology. Trends Ecol Evol 4 (7): 214-217. DOI: 10.1016/0169-5347(89)90077-3

Li Y, Liu Y, Song J, Zhang R, Yan Y, Wang Y, Du FK. 2018. Geometric morphometric analyses of leaf shapes in two sympatric Chinese oaks: *Quercus dentata* Thunberg and *Quercus aliena* Blume (Fagaceae). Ann For Sci 75 (4): 1-12. DOI: 10.1007/s13595-018-0770-2

Mal TK, Uveges JL, Turk KW. 2002. Fluctuating asymmetry as an ecological indicator of heavy metal stress in *Lythrum salicaria*. Ecol Indic 1 (3): 189-195. DOI: 10.1016/S1470-160X(02)00004-3

Mirouze E, Staquet A, Vezy R. 2012. Morphometric and morphological analysis of leaves in two species of Araceae: *Montrichardia linifera* and *Montrichardia arborescens* among different French Guiana populations. J Ecofog 3: 1-15.

Moldenke HN. 1982. Additional notes on the genus *Geunsia*. Phytologia 50: 143-151.

Morais DV de, Nunes LA, Mata VP da, Costa MAP de C, Sodré G da S, Carvalho CAL de. 2019. Leaf geometric morphometrics among populations of *Dalbergia ecastaphyllum* (L.) Taub. Biosci J 35 (6): 1789-1798. DOI: 10.14393/BJ-v35n6a2019-39814

Palmer CM, Bush SM, Maloof JN. 2012. Phenotypic and developmental plasticity in plants. eLS. DOI: 10.1002/9780470015902.a0002092.pub2

POWO 2021. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; http://www.plantsoftheworldonline.org/

Ridley HN. 1923. The Flora of the Malay Peninsula Vol. 2. Reeves, London. DOI: 10.2307/4115416

Rohlf FJ. 2010. tpsDig, digitize landmarks and outlines, ver. 2.16. State University of New York, Stony Brook.

Rohlf FJ. 2015. tpsUtil, file utility program. version 1.61. Department of Ecology and Evolution, State University of New York, aStony Brook.

Tsukaya H, Fukuda T, Yokoyama J. 2003. Hybridization and introgression between *Callicarpa japonica* and *C. mollis* (Verbenaceae) in central Japan, as inferred from nuclear and chloroplast DNA sequences. Mol Ecol 12 (11): 3003-3011. DOI: 10.1046/j.1365-294x.2003.01961.x

van Steenis CGGJ. 1967. Miscellaneous Botanical Notes XVII: A remarkable myrmecophyte, *Callicarpa saccata* n. sp., from Sarawak and some allied species. Blumea 15 (1): 145-155.

van Valen L. 1962. A study of fluctuating asymmetry. Evolution 16: 125-142. DOI: 10.1111/j.1558-5646.1962.tb03206.x

Vieira M, Mayo SJ, de Andrade IM. 2014. Geometric morphometrics of leaves of *Anacardium microcarpum* Ducke and *A. occidentale* L. (Anacardiaceae) from the coastal region of Piauí, Brazil. Rev Bras Bot 37 (3): 315-327. DOI: 10.1007/s40415-014-0072-3

Viscosi V, Cardini A. 2011. Leaf morphology, taxonomy and geometric morphometrics: a simplified protocol for beginners. PLoS ONE 6: e25630. DOI: 10.1371/annotation/bc347abe-8d03-4553- 8754-83f41a9d51ae.t0023.cn

Zelditch, ML, Swinderski DL, Sheets HD, Fink WL. 2004. Geometric Morphometric Analysis for Biologists: A Primer. Elsevier Press, San Diego.

Table S1. Authors and URLs of the digital images obtained from online herbarium used in this study

AUTHOR	**HTTP URL**
Bijmoer R, Scherrenberg M, Creuwels J (2021). Naturalis Biodiversity Center (NL) - Botany. Naturalis Biodiversity Center. Occurrence dataset https://doi.org/10.15468/ib5ypt accessed via GBIF.org on 2021-07-16.	https://www.gbif.org/occurrence/2517003371 https://www.gbif.org/occurrence/2517278400, https://www.gbif.org/occurrence/2515569033 https://www.gbif.org/occurrence/2516411626 https://www.gbif.org/occurrence/2516540585 https://www.gbif.org/occurrence/2517036420 https://www.gbif.org/occurrence/2516540443 https://www.gbif.org/occurrence/2516542437 https://www.gbif.org/occurrence/2517572837 https://www.gbif.org/occurrence/2514466640
GBIF.org (02 August 2021) GBIF Occurrence Download	https://doi.org/10.15468/dl.9bfpye https://doi.org/10.15468/dl.kmzyh8 https://doi.org/10.15468/dl.hm7vp6 https://doi.org/10.15468/dl.be359z https://doi.org/10.15468/dl.82s3d4 https://doi.org/10.15468/dl.bnvgt7 https://doi.org/10.15468/dl.bg7525 https://doi.org/10.15468/dl.tjzn5p
Herbarium Hamburgense. Herbarium Hamburgense. Occurrence dataset https://doi.org/10.15468/31iaih accessed via GBIF.org on 2021-07-16.	https://www.gbif.org/occurrence/1699806604
Kennedy J (2021). Harvard University Herbaria: All Records. Harvard University Herbaria. Occurrence dataset https://doi.org/10.15468/o3pvnh accessed via GBIF.org on 2021-07-16.	https://www.gbif.org/occurrence/1999138342 https://www.gbif.org/occurrence/1999202121 https://www.gbif.org/occurrence/1999385187 https://www.gbif.org/occurrence/1998787852 https://www.gbif.org/occurrence/1999414059
MNHN, Chagnoux S (2021). The vascular plants collection (P) at the Herbarium of the Muséum national d'Histoire Naturelle (MNHN - Paris). Version 69.218. MNHN - Museum national d'Histoire naturelle. Occurrence dataset https://doi.org/10.15468/nc6rxy accessed via GBIF.org on 2021-07-16.	https://www.gbif.org/occurrence/2270292394 https://www.gbif.org/occurrence/474634504 https://www.gbif.org/occurrence/1317659317 https://www.gbif.org/occurrence/474961514 https://www.gbif.org/occurrence/474798295 https://www.gbif.org/occurrence/474782917
Orrell T, Informatics Office (2021). NMNH Extant Specimen Records. Version 1.45. National Museum of Natural History, Smithsonian Institution. Occurrence dataset https://doi.org/10.15468/hnhrg3 accessed via GBIF.org on 2021-07-16.	https://www.gbif.org/occurrence/1852124824 https://www.gbif.org/occurrence/1852108544 https://www.gbif.org/occurrence/1322874688 https://www.gbif.org/occurrence/1843559302 https://www.gbif.org/occurrence/1843543073 https://www.gbif.org/occurrence/1318901945 https://www.gbif.org/occurrence/1317659317 https://www.gbif.org/occurrence/1318649487 https://www.gbif.org/occurrence/1852159253 https://www.gbif.org/occurrence/1317268996 https://www.gbif.org/occurrence/1322680890 https://www.gbif.org/occurrence/1322649092 https://www.gbif.org/occurrence/1852124565 https://www.gbif.org/occurrence/1852129539 https://www.gbif.org/occurrence/1852095165
Ramirez J, Tulig M, Watson K, Thiers B (2021). The New York Botanical Garden Herbarium (NY). Version 1.35. The New York Botanical Garden. Occurrence dataset https://doi.org/10.15468/6e8nje accessed via GBIF.org on 2021-07-16.	https://www.gbif.org/occurrence/1929940867 https://www.gbif.org/occurrence/1929638283 https://www.gbif.org/occurrence/1929689660 https://www.gbif.org/occurrence/1928558617 https://www.gbif.org/occurrence/1928284058
Royal Botanic Gardens, Kew (2021). Royal Botanic Gardens, Kew - Herbarium Specimens. Occurrence dataset https://doi.org/10.15468/ly60bx accessed via GBIF.org on 2021-07-16.	https://www.gbif.org/occurrence/912176866 https://www.gbif.org/occurrence/912176860 https://www.gbif.org/occurrence/912176851 https://www.gbif.org/occurrence/912176867

Seregin A (2021). Moscow University Herbarium (MW). Version 1.189. Lomonosov Moscow State University. Occurrence dataset https://doi.org/10.15468/cpnhcc accessed via GBIF.org on 2021-07-16.	https://www.gbif.org/occurrence/3004116377
Solomon J, Stimmel H (2021). Tropicos Specimen Data. Missouri Botanical Garden. Occurrence dataset https://doi.org/10.15468/hja69f accessed via GBIF.org on 2021-07-16.	https://www.gbif.org/occurrence/1259567810
Staatliche Naturwissenschaftliche Sammlungen Bayerns. The Vascular Plant Collection at the Botanische Staatssammlung München. Occurrence dataset https://doi.org/10.15468/vgr4kl accessed via GBIF.org on 2021-07-16.	https://www.gbif.org/occurrence/2981260539
The Herbarium Catalogue, Royal Botanic Gardens, Kew. Published on the Internet http://www.kew.org/herbcat [accessed on 10 July 2021]	http://specimens.kew.org/herbarium/K000194933 http://specimens.kew.org/herbarium/ K000194994 http://specimens.kew.org/herbarium/ K000194946 http://specimens.kew.org/herbarium/ K000194949 http://specimens.kew.org/herbarium/K000248661 http://specimens.kew.org/herbarium/K00094945 http://specimens.kew.org/herbarium/K000194931 http://specimens.kew.org/herbarium/K000194977 http://specimens.kew.org/herbarium/K000249402 http://specimens.kew.org/herbarium/K000194992 http://specimens.kew.org/herbarium/K000194930 http://specimens.kew.org/herbarium/K000248662 http://specimens.kew.org/herbarium/K001114363 http://specimens.kew.org/herbarium/ K000674786
University of Minnesota Bell Museum (2021). Bell Museum plants. Occurrence dataset https://doi.org/10.15468/bihrxd accessed via GBIF.org on 2021-08-02.	https://www.gbif.org/occurrence/2265568305