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Research Article

Flower Structures of *Averrhoa dolichocarpa* Rugayah & Sunarti

Tri Yuni Indah Wulansari[1]*, Seni Kurnia Senjaya[1]*, Inggit Puji Astuti[2]

1) Research Center for Biosystematics and Evolution, National Research and Innovation Agency (BRIN), Jl. Jakarta-Bogor KM 46, Cibinong 16911, West Java, Indoneisa
2) Research Center for Plant Conservation, Botanical Gardens and Forestry, National Research and Innovation Agency (BRIN), Jl. Ir. H. Djuanda No.13, Bogor 16122, West Java, Indonesia
* Corresponding author, email: tyindahw@gmail.com, seni001@brin.go.id

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ABSTRACT

Hermaphrodites are believed to be the ancestral characters of flowering plants. However, plants have developed spatially and functionally in arrangements to reduce the chances of self-fertilization. One well-known spatial arrangement is heterostyly. This arrangement is found in almost all Oxalidaceae species, including *Averrhoa* spp. The question that arises with the discovery of two new species of *Averrhoa* is how the spatial flower arrangement of the new species is. This study observed flowers of *A. dolichocarpa* to prove heterostyly of the species. We also compared morphological and anatomical characteristics among flower morphs of *A. dolichocarpa*. Three flower morphs, S-morph, M-morph, and L-morph, were observed, proving that *A. dolichocarpa* is tristyly. Morphologically and anatomically, there was no significant difference between the three flower morphs. Differences in morphometry were found in three flower morphs. In addition to the notable differences in style length in heterostyly, differences in ovary height between flower morphs were observed. The flower morphology and anatomy of *A. dolichocarpa* are similar to that of *A. carambola* and *A. bilimbi* and follow the general pattern of Oxalidaceae.

INTRODUCTION

The reproductive structures of flowering plants are spectacularly diverse. This diversification results from co-evolution and adaptation to available pollinators in most flowering plants. Pollinators have played an essential role in flower form and function diversification, attributed to unique mating strategies and sexual systems variations. The seed-plant reproductive organs shape mating outcomes through their influence in the pollination and progamic phase (Barrett & Harder 2017).

Hermaphrodite flowers are believed to be the ancestral characters of Angiospermae (Sauquet et al. 2017) and are found in most flowering plants (Barrett 2002). Hermaphroditism increases the chances of successful fertilization in the self-compatible plant through self-pollination. However, self-fertilization increases the risk of inbreeding depression (Charlesworth & Willis 2009). Plants have developed several mechanisms to avoid that risk. The structure of the hermaphrodite flower can be separated spatially within the

flower (herkogamy) or function at different times (dichogamy). Those phenomena thereby reduce the chances of self-pollination. Heterostyly, enantiostyly, and flexistyly are forms of sexual polymorphism in male and female reproductive organ spatial arrangement (Barrett 2002).

Heterostyly is a phenomenon that Darwin first described in his book "Different Forms of Flowers on Plants of the Same Species". In heterostylous species, populations are composed of two (distyly) or three (tristyly) floral morphs, which are distinguished by a reciprocal arrangement of stigma and anther heights (Darwin 1877; Barrett 1992; Lloyd & Webb 1992). Heterostyly was found in 28 families (Barrett 2002), with tristyly only reported in six families (Barrett 1993; Thompson et al. 1996). Oxalidaceae is one of 28 flowering plant families that undergoes heterostyly. Oxalidaceae consists of six genera and homostyly was reported in *Biophytum* and certain species *Oxalis* (Cocucci 2004; Veldkamp 1971). Distyly was found in *Sarcotheca, Dapania pentandra, Averrhoa carambola*, several species of *Oxalis*, and several species of *Biophytum* (Veldkamp 1967, 1971; Cocucci 2004). Meanwhile, tristyly was found in *Oxalis*, *Biophytum*, and *A. bilimbi* (Veldkamp 1967, 1971; Cocucci 2004).

The distribution of style polymorphism in Oxalidaceae can be used to study the evolution of heterostyly. It is also essential to obtain detailed information on flower structure to understand the underlying evolutionary pathways of heterostyly in Oxalidaceae. In this study, we will observe the heterostyly in *Averrhoa dolichocarpa*. *Averrhoa* is a genus of the Oxalidaceae family previously known to consist of two species, one tristylous species and one distylous species (Cocucci 2004; Veldkamp 1971). Later, two wild species of *Averrhoa* were described, *A. dolichocarpa* and *A. leucopetala* (Rugayah & Sunarti 2008). Distyly was reported on *A. dolicocarpha* based on observations of two flower morphologies called short-styled morph (S-morph) and long-styled morph (L-morph) (Kapsah et al. 2016). However, the images on Kapsah et al. (2016) showed L-morph and mid-styled morph (M-morph) flowers. We suspected the species is tristyly. Therefore, we further studied the flowers to gather information on the heterostyly of the species. We also performed a comparative study of floral morphology and anatomy to obtain detailed information on the flower structure of *A. dolichocarpa.*

MATERIALS AND METHODS

Materials

Flowers were collected from four *A. dolichocarpa* individuals in Bogor Botanical Gardens and the Cibinong Science Center (Table 1). Flowers were collected at the anthesis stage and stored in 70% alcohol. *A. dolichocarpa,* as other *Averrhoa,* has two whorls of anthers. The plant is distinguished by the reciprocal arrangement of stigma and anther heights on its flowers. The flower with two anther whorls higher than the flower style is identified as S-morph. Meanwhile, flowers with a style whose height is between two anthers whorls categorized as M-morph. L-morph is determined by a style higher than two anther whorls (Figure 1).

Table 1. Locality and flower morphology of plant materials.

Taxon	Locality	Flower Morphology
A. dolichocarpa	Vak VII.D.96, Bogor Botanical Garden	L-morph
A. dolichocarpa	Kandang Badak Nursery, Bogor Botanical Garden	S-morph
A. dolichocarpa	Gedung IX Nursery, Bogor Botanical Garden	M-morph
A. dolichocarpa	Botany Building Park, Cibinong Science Center	M-morph

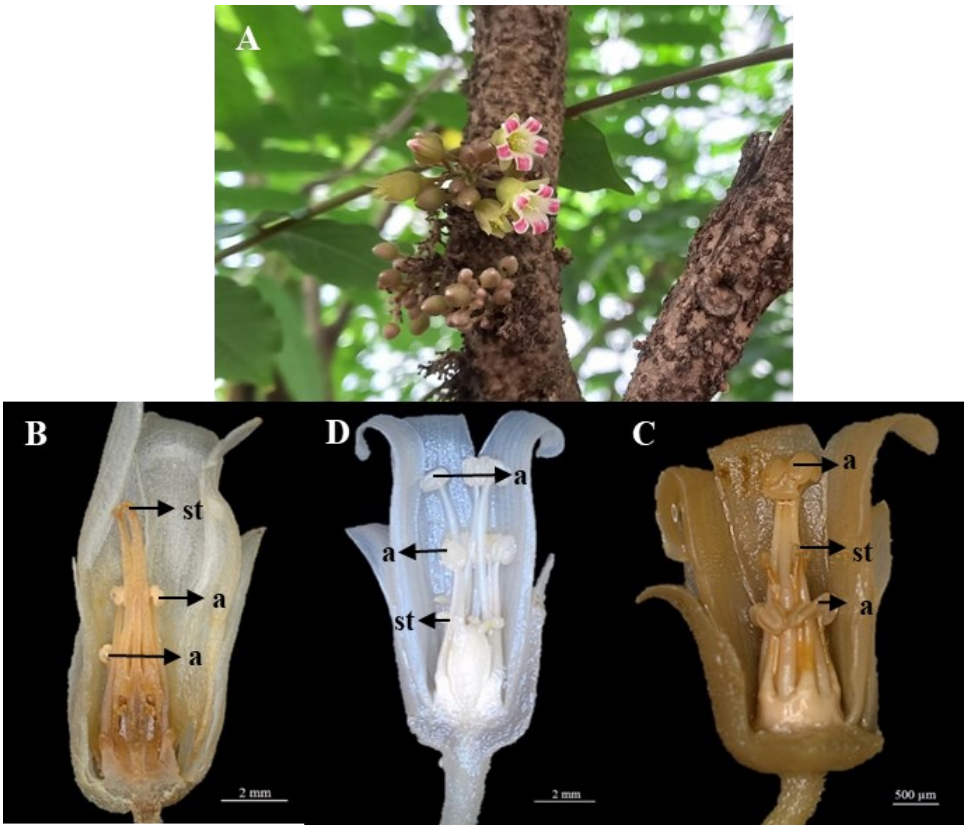


Figure 1. Flower morphology of *A. dolichocarpa*. (A) inflorescence, (B) L-morph flower, (C) M-morph flower, (D) S-morph flower. a: anther, st: stigma.

Methods

Forty flowers per morph were measured. Two sepals and petals are stripped for measurement, and the ovary base is the basis for all sizes except style-stigma (Figure 2). The measurement was conducted under a stereomicroscope (Olympus) with an LC-micro program for the image analyzer. Measured characters are (1) stamen height, (2) anther length, (3) style-stigma height, (4) ovary height, (5) petal length, and (6) sepal length. The ovary height was compared between morphs using one-way ANOVA (α=0.005).

Flower anatomy was observed by making anatomical slides following Sass (1951) method. The examined flowers were in the same stage which was fully developed. Flowers were dehydrated with a multi-grade solution of a combination of aquadest:tert-butanol:ethanol, then infiltrated using paraffin. The samples were sectioned longitudinally and transversally with a rotary microtome (15 - 18 µm). Staining was carried out using safranine and fast-green solution. Slides observation was conducted using Nikon Eclipse 80i and measurements using the Beta View program. For the full pictures, the slides were scanned using a slide scanner.

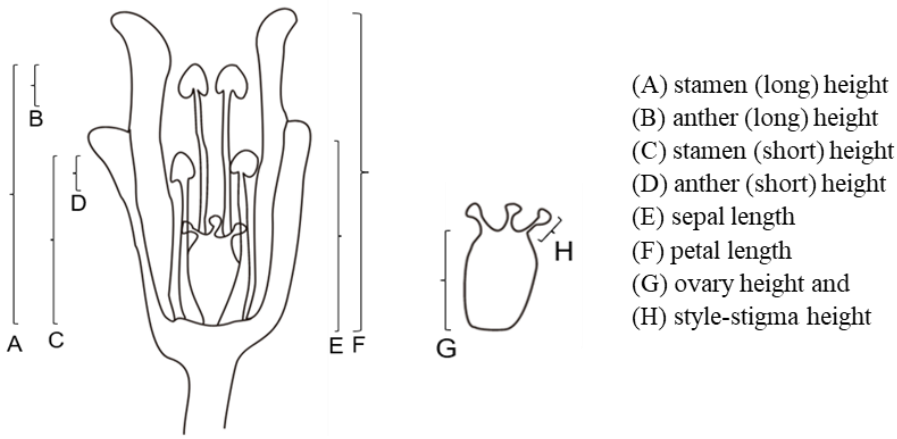


Figure 2. Flower measurement (S-morph flower).

RESULTS AND DISCUSSION

Averrhoa dolichocarpa has cluster-type inflorescence (Figure 1A) with actinomorphic, bisexual, 5-merous (isomerous), and obdiplostemonous flowers. Tristyly can be confirmed in *A. dolichocarpa* with three flower morphs, S-morph, M-morph, and L-morph, observed (Figure 1B-1D). The morphology and anatomy of the three flower morphs of *A. dolichocarpa* have the relatively same structure. However, there are differences in the morphometry of the flower parts as follows.

Calyx: *A. dolichocarpa* calyx has five separate sepals (aposepalous and pentasepalous). Our observation obtained that sepal has the same shape as the previous report by Rugayah & Sunarti (2008), namely lanceolate with a slightly recurved apex. The sepal lengths range of L-morph, M-morph, and S-morph are 6.53-8.72 mm, 5.08-8.05 mm, and 5.25-9.09 mm, respectively (Table 2).

Anatomically, the sepal consists of an epidermis layer with an irregular shape (Figure 3A). Irregular and undifferentiated parenchyma cells are located below the epidermis. There are 2-3 layers of parenchyma cells with small and dense sizes (Figure 3A). The inner part consists of larger parenchyma cells and several simple vascular bundles (Figure 3A). Simple filiform non-glandular trichomes with thick walls were observed in the outer epidermis of all samples (Figure 3A). The result agreed with Rugayah & Sunarti (2008), who stated that the sepal surface of *A. dolichocarpa* is glabrous inside and hairy outside. The presence of trichomes in the L-morph flowers of *A. dolichocarpa* was less in number than the other flower morphs. The presence of trichomes on the sepals with a simple, unicellular, lignified, frequent tanniferous form is a characteristic and representative of all the Oxalidales families (Matthews & Endress 2002).

Corolla: Corolla consists of five petals (pentapetalous) in all observed flowers. As previously described, the petal shape of *A. dolichocarpa* is oblong-ovate (Rugayah & Sunarti 2008). Pentapetalous is also common in other *Averrhoa* species, even though modifications to 4-6 petals in *A. carambola* and *A. bilimbi* were reported (Soumya & Nair 2013). The petals of *A. dolichocarpa* follow the petal-type of Oxalidaceae that are postgenitally united into a basal

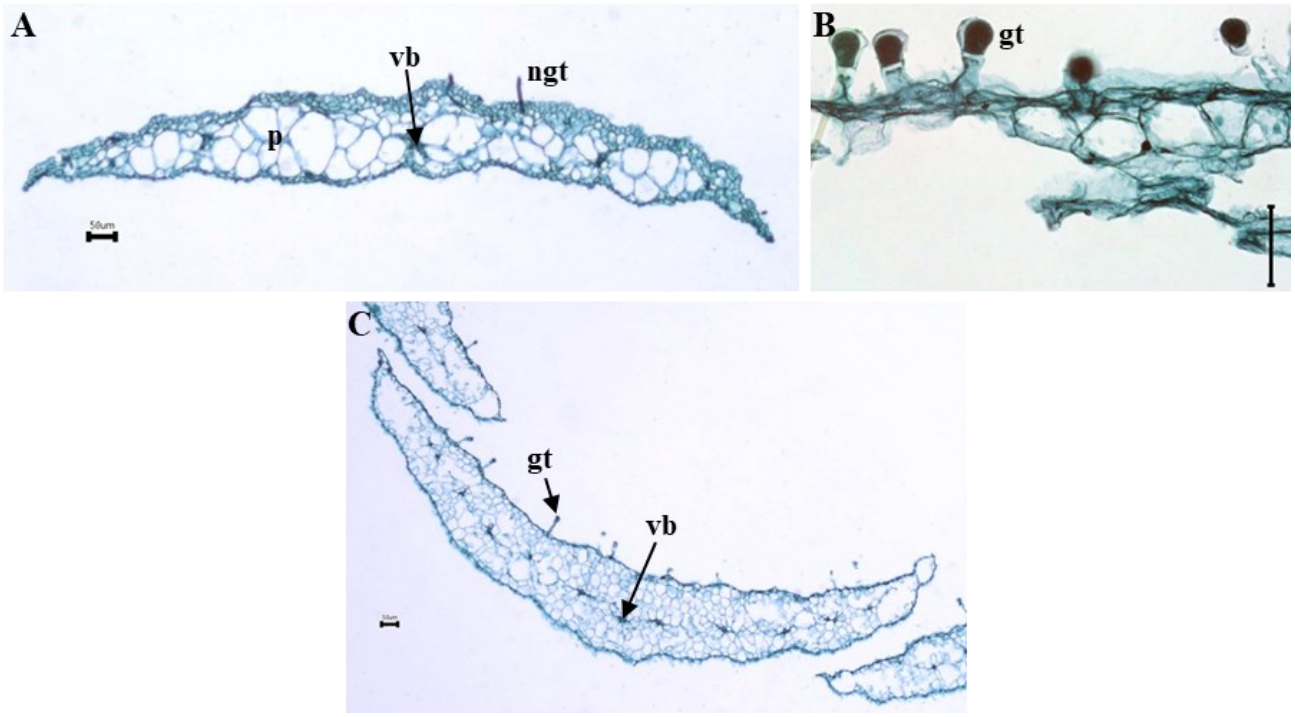


Figure 3. (A) Cross-section of sepal with simple filiform trichome (S-morph), (B) Glandular trichome of M-morph, (C) Cross-section of the petal (S-morph). gt: glandular trichome, ngt: non-glandular trichome, p: parenchyma, vb: vascular bundle. Scale bar: 50 mm.

tube but free at the insertion zone (Matthews & Endress 2002). The petal lengths of L-morph, M-morph, and S-morph are 10.22-13.41 mm, 8.52-12.35 mm, and 9.58-12.44 mm, respectively (Table 2).

The anatomical structure of the corolla consists of a layer of epidermis with a more orderly arrangement than the epidermis of the calyx (Figure 3C). Parenchyma cells of fairly uniform size and several simple vascular bundles are located inside the epidermic cells. Glandular trichomes are capitate forms with rounded heads (Figure 3B). Similar trichomes were also reported in abundance on the petals of *A. carambola* and in small numbers to absent on *A. bilimbi* (Soumya & Nair 2013). These glandular hairs are also common characters on the petal of Oxalidaceae and were found with uni- or multicellular head (Matthews & Endress 2002).

Androecium: Androecium consists of two whorls of stamen, with the outer whorl opposite the petals and the inner whorl opposite the sepals (obdiplostemonous). An alternating arrangement of stamens between five short stamens and five long stamens was found in all observed flowers of *A. dolichocarpa*. The pattern in *A. dolichocarpa* contrasts with *A. bilimbi,* which has an inconsistent pattern and varies 10-12 stamens. The arrangement of the stamens in *A. bilimbi* was modified to 6+6, 6+4, 7+3, 6+5, or 4+6 in different flowers (Soumya & Nair 2013).

The stamens are excurved, curving outward from the axis (Figure 1B-D). The androecium as a whole is not attached to the floral envelope. Based on its attachment, the anther type is dorsifixed with an elongated anther shape. The same anther type was observed in *A. carambola* (Matthews & Endress 2002).

In obdiplostemonous flowers, the epipetalous stamens are generally shorter than the episepalous ones (Matthews & Endress 2002). This size reduction can vary in the filament's length, width, and thickness. An extreme example of the reduction was observed in the absence of anthers in the epipetalous stamen of *A. carambola* (Matthews & Endress 2002; Soumya & Nair 2013). All stamens of *A. dolichocarpa* are fertile. There is a difference in long and short stamen length among flower morphs. The long stamens length for L-morph, M-morph, and S-morph range from 5.49-6.35 mm, 6.13-8.83 mm, and 7.46-8.90 mm, respectively (Table 2). Meanwhile, the short stamen length ranges from 3.38-4.85 mm, 3.30-4.30 mm, and 5.3-6.27 mm for L-morph, M-morph, and S-morph (Table 2). The shortest average of short stamen was observed in M-morph and the longest in S-morph (Table 2).

The longitudinal section showed that the filaments consist of a single layer of the epidermis and rectangular parenchyma cells with a length of 2-3 times the epidermal cells (Figure 4A). The cells are smaller and denser at the ends of the filaments that contact the anthers (Figure 4A). The tip of the filament is connected to the center of the anther. Based on cross-section, the filaments are spherical, with the outermost part being a single-layer epidermis with a square cell shape (Figure 4B, left). Parenchyma cells are composed of polyhedral to rounded cell shapes. The parenchyma cells get smaller towards the middle, and a simple vascular bundle was found in the center (Figure 4B, left).

The cross-section of the anther showed that the anther type is tetrasporangiate (Figure 4C). Observations were made on mature flowers, so the anthers had matured and released their spores. The remaining cells in the anther wall of the mature anther are the epidermis and the endothecium. The epidermis is rounded, while the endothecium is rectangular-trapezoidal with a uniform size (Figure 4C). However, smaller endothecium cells are found in the stomium and facilitate the release of spores as they mature (Figure 4C). Connectivum consists of parenchyma cells, some of which are tanniferous. In the center of the connectivum, vascular bundles originating from the ends of the filaments were found (Figure 4C).

Gynoecium: Gynoecium consists of five attached carpels (syncarp). Variations in the number of carpels with 4-7 carpels were reported in *A. carambola* and *A. bilimbi* (Soumya & Nair, 2013). Meanwhile, there was no varia-

Table 2. Floral dimension of L-morph, M-morph, and S-morph flowers (mm).

Character length (mm)	L-morph			M-morph			S-morph		
	Average	Max	Min	Average	Max	Min	Average	Max	Min
Short stamen	4.11	4.85	3.38	3.69	4.30	3.30	5.86	6.27	5.3
Long stamen	5.89	6.35	5.49	7.64	8.83	6.13	8.33	8.90	7.46
Short anther	0.71	0.82	0.43	0.64	0.88	0.35	0.80	0.96	0.65
Long anther	0.74	0.86	0.56	0.71	0.87	0.54	0.80	0.96	0.69
Style-stigma	5.11	5.82	4.30	2.51	3.17	1.94	0.95	1.14	0.57
Petal	11.72	13.41	10.22	10.29	12.35	8.52	11.31	12.44	9.58
Sepal	7.69	8.72	6.53	6.37	8.05	5.08	7.15	9.09	5.25
Ovary	3.40	4.06	2.72	2.88	3.55	2.27	2.48	3.12	1.84

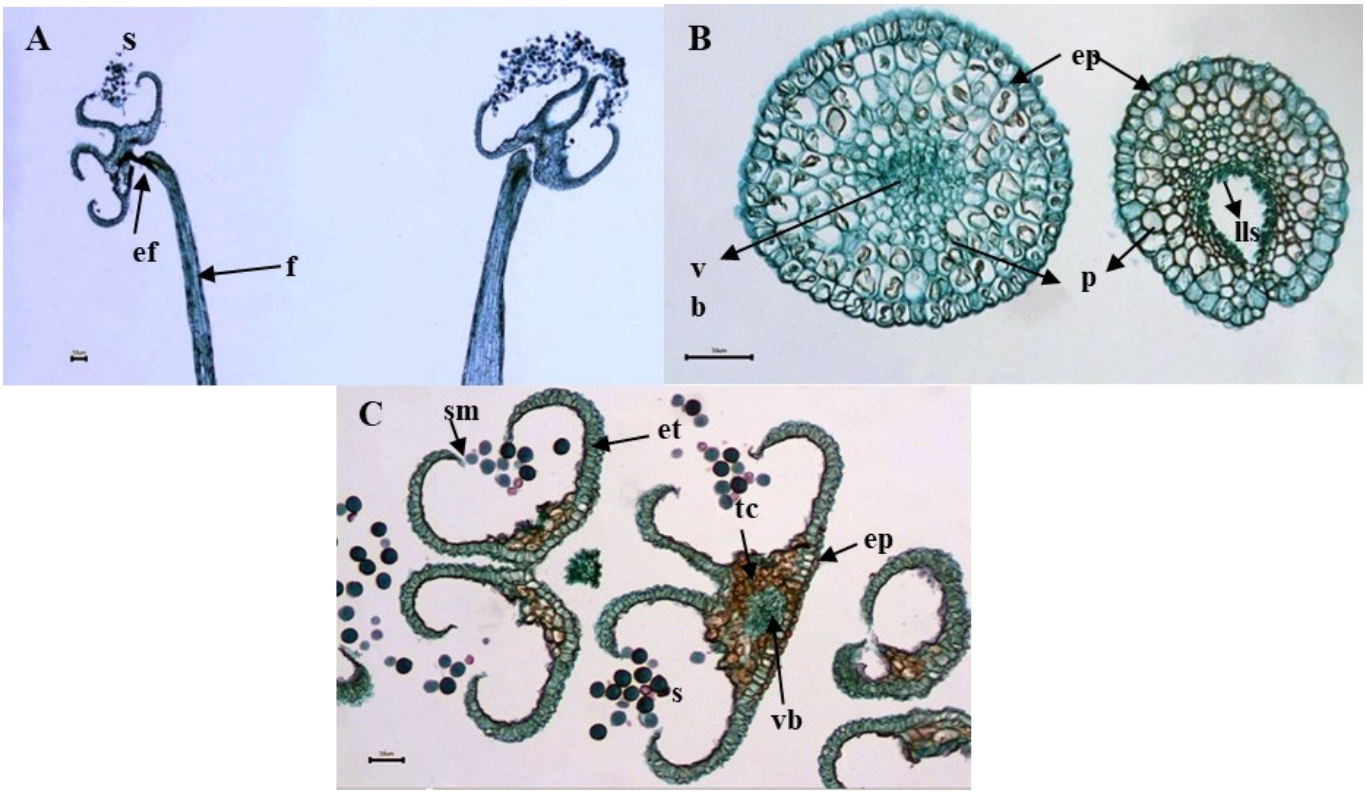


Figure 4. (A) Stamen of L-morph, (B) Filament (left) and stylus (right) of M-morph, (C) Tanniferous cells at connectivum area (M-morph). ep: epidermis, ef: end of filaments, et: endothecium, f: filament, lls: lobe-like structures, p: parenchyma, s: spores, sm: stomium, tc: tanniferous cells, vb: vascular bundle. Scale bar: 50 μm.

tion in the number of carpels of *A. dolichocarpa*. The ovary position is superior, and simple trichomes were found on the ovary, similar to the calyx trichomes (Figure 6A). Trichomes were observed in small numbers in all flower morphs. The difference in style length has long been known as a characteristic of heterostyly plants. It turns out that the height of the ovary in the three *A. dolichocarpa* morphs is also different. The ovary length range from 1.84-3.12 mm in S-morph, 2.27-3.55 mm in M-morph, and 2.72- 4.06 mm in L-morph flowers. One-way ANOVA showed that the ovary height differed significantly (Figure 5).

The type of *A. dolichocarpa* ovule is inverted and straight, with the microphyle situated next to the funiculus (anatropous) (Figure 6A-C). Two ovules in each loculus were found in S-morph flowers (Figure 6A), while four to six ovules per loculus were observed in L-morph and M-morph flowers (Figure 6B-C). The number of ovules in *A. dolichocarpa* corresponds to the number of ovules in each carpel in Oxalidales, which are generally two or slightly more (Matthew & Endress 2002). Three to six ovules per loculus were also reported in *A. bilimbi* (Soumya & Nair 2013). The wall of the ovary consists of a layer of rectangular epidermal cells and several layers of polyhedral to round parenchyma cells and the cell size towards the center increases (Figure 6E). Many tannin cells were found near the epidermis. The vascular bundle is scattered in parenchyma cells. Mature ovules with square outer and rectangular inner integuments can be observed at the loculus. There are three layers of parenchyma cells between the integuments.

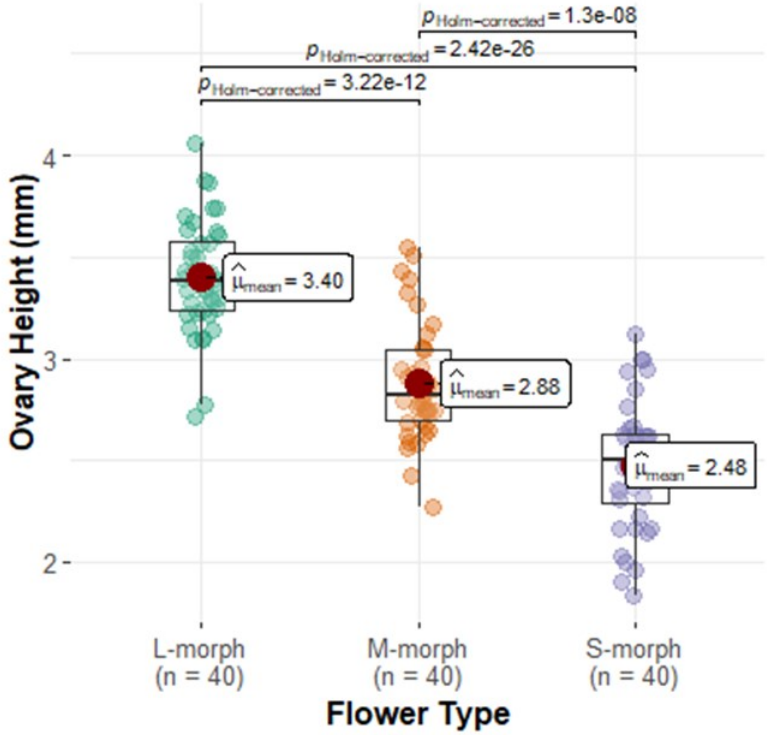


Figure 5. One way ANOVA boxplot comparing ovary height of *A. dolichocarpa*.

Averrhoa dolichocarpa has five branches of stylus ending with five capitate stigmas as reported in most Oxalidales (Matthew & Endress 2002; Rosenfeldt & Galati 2009). The number of stigma in all flower morphs equals the number of carpels. The style area close to the stigma has a hollow texture with a lobe-like structure (Figure 4B, right) that allows entry of the stamens during fertilization. The stylus base (near the ovary) has a solid structure. The center of the stylus develops into the transmission tissue (Figure 6F). The transverse section shows five styli with the same structure (Figure 6G). The epidermis consists of a layer of square-shaped cells. Inside the epidermis, rounded parenchyma cells with a size that is getting smaller towards the center were observed. There are two lateral vascular bundles observed (Figure 6G). The median vascular bundle was discovered on the stylus close to the ovary (Figure 6G).

Floral Vascularization: The vascularization observed in all flower morphs of *A. dolichocarpa* was similar to that in *A. carambola* (Estelita-Teixeira 1980; Matthews & Endress 2002). There is a slight difference with *A. carambola* in the anther tissue unification at the base of the flower. There are 5-6 simple vascular bundles and some small ones in sepal (Figure A1, B1, C1). This result supports Matthews & Endress (2002), who found sepals have at least three main vascular bundles and traces in some species of Oxalidaceae (Matthews & Endress). The vascular bundle in the sepals maintains its shape and presence until several parts of the sepals unite at the base of the flower. The number of vascular bundles in sepals is higher than in petals. Closer to the base of the flower, the bundles that are close together will form more elongated vascular (Figure 7B3-B5) and eventually become a single bundle (Figure 7A4-A5).

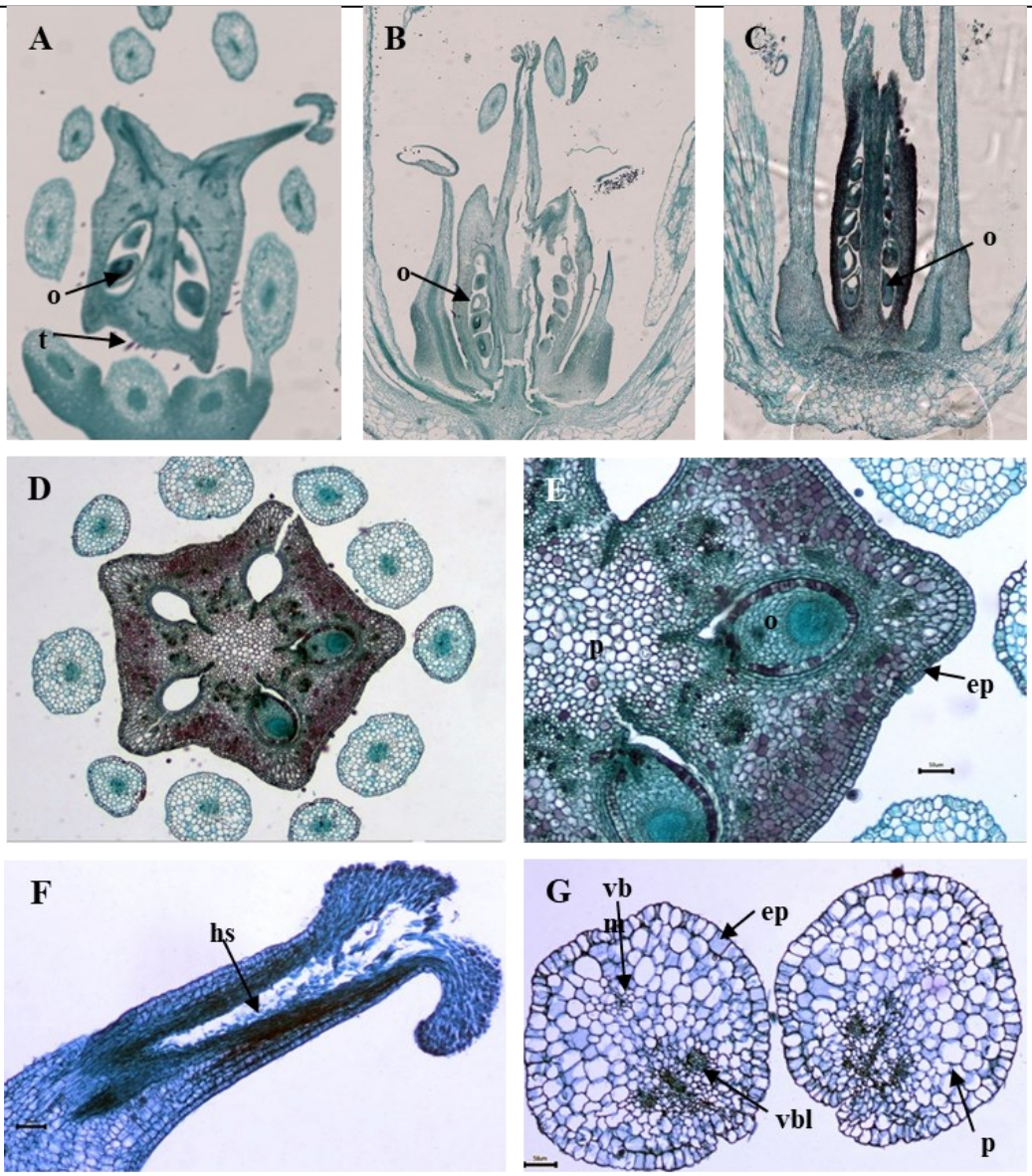
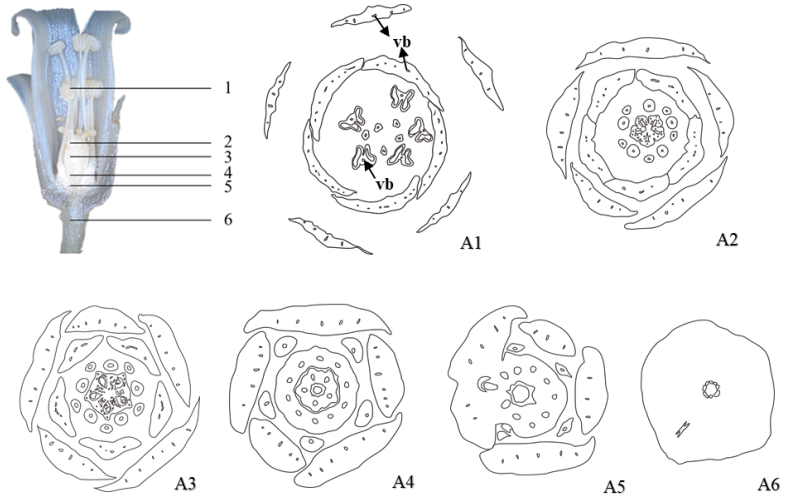


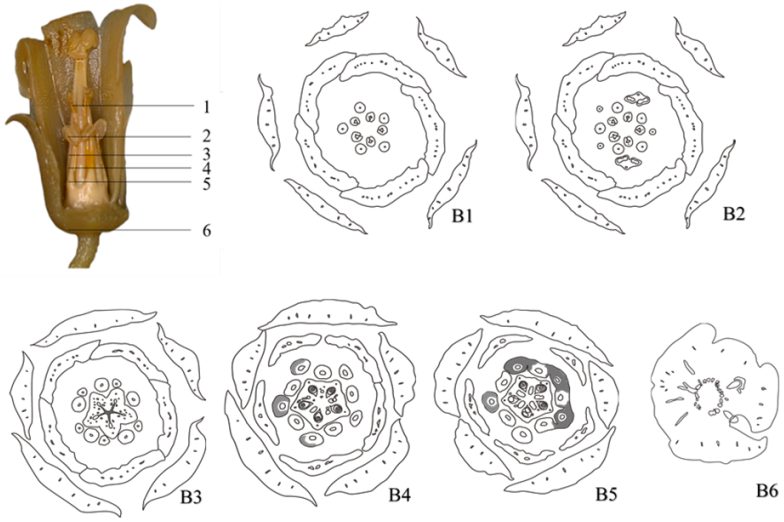
Figure 6. Gynoecium longitudinal section of (A) S-morph, (B) M-morph, and (C) L-morph, (D&E) Cross-section of ovary M-morph, (F) Longitudinal section of stigma S-morph, (G) The stylus of L-morph with two lateral vascular bundles and median vascular bundle (weak). ep: epidermis, hs: hollow structure, o: ovule, p: parenchyma, vbl: lateral vascular bundle, vbm: median vascular bundle. Scale bar: 50 mm.

There is one vascular bundle in the anther. All the anthers will fuse and form ten traces at the base of the flower. Two collateral vascular bundles in the right and left lobes of the stylus were observed. The median vascular bundle is visible on the stylus with a solid center close to the ovary (Figure 7B2). Additional vascular bundles will be formed between the lateral and median bundles and then unite into a larger lateral bundle (Figure 7B5, 7C4). After a larger lateral bundle is formed, the median vascular bundle could still be found at the corner of the ovary and some small bundles could also be observed. Toward the basal of the flower, the sizeable lateral vascular bundles unite in the center of the ovary and form a star-shaped central vascular bundle (Figure 7C5). The median bundle will also merge with the central bundle. Toward the base of the flower, the star-shaped bundle will turn into a circular shape (Figure 7A4-A6) and the transport bundle in the pedicellus will end in a siphonostele form (Figure 7C6).

A. S-morph



B. M-morph



C. L-morp

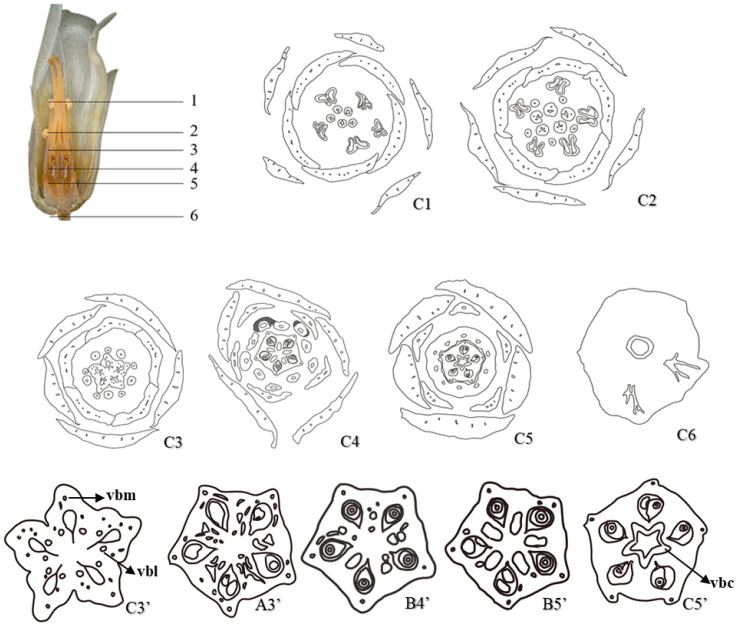


Figure 7. Floral vascularization of *A. dolichocarpa*. (A) S-morph, (B) M-morph, and (C) L-morph. (A1) Slide on short anther dan filament level, (B2, C2) Slides on short anther, filament, and stylus level, (A2, B3, C3) slides on the top of the ovary level, (A3, B4, C4) slides on the middle ovary level, (A4, B5, C5) slides on the low part of the ovary level, (A5) slide on flower receptacle level, (A6, B6, C6) slides on flower pedicel level. (C3'- C5': vascularization in ovary). vb: vascular bundle, vbm: median vascular bundle, vbl: lateral vascular bundle, vbc: central vascular bundle.

CONCLUSION

Averrhoa dolichocarpa was proven tristyly by finding three types of flowers with different arrangements between stigma and anther heights. The flower structure of the three different flower morphs is generally similar. The flower structure of *A. dolichocarpa* follows the general structure of *Averrhoa* and Oxalidaceae. The results of this study provide new information on the anatomy of *A. dolichocarpa* that has not been studied before.

AUTHORS CONTRIBUTION

The description of the author's contributions is listed: T.Y.I.W contributes to the research design, morphometry and anatomical study, and manuscript writing. S.K.S contributes to research concepts, morphometry study, data analysis, and manuscript writing. I.P.A contributes to sample collections and review of the manuscript. All of the authors are responsible for the content writing in this manuscript.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

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