

RESEARCH ARTICLE



Morpho-anatomy of cape gooseberry flowers (*Physalis peruviana* L.) at various stages of development

Utaminingsih¹, Laurentius Hartanto Nugroho², Tri Rini Nuringtyas² & Maryani^{2*}

¹Biology Doctoral Study Program, Faculty of Biology, Universitas Gadjah Mada, Yogyakarta 55281, Indonesia ²Tropical Biology Department, Faculty of Biology, Universitas Gadjah Mada, Yogyakarta 55281, Indonesia

*Email: mmyani@ugm.ac.id

ARTICLE HISTORY

Received: 24 March 2024 Accepted: 30 November 2024 Available online Version 1.0 : 30 January 2025 Version 2.0 : 30 January 2025

Check for updates

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/ journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc See https://horizonepublishing.com/journals/ index.php/PST/indexing_abstracting

Copyright: © The Author(s). This is an openaccess article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution and reproduction in any medium, provided the original author and source are credited (https://creativecommons.org/licenses/ by/4.0/)

CITE THIS ARTICLE

Utaminingsih, Nugroho LH, Nuringtyas TR, Maryani. Morpho-anatomy of cape gooseberry flowers (*Physalis peruviana* L.) at various stages of development. Plant Science Today. 2025; 12(1): 1-9. https:// doi.org/10.14719/pst.3597

Abstract

As an indigenous remedy for a variety of ailments, cape gooseberry (Physalis peruviana L.), a member of the Solanaceae family, has historically contributed significantly to health promotion. The metabolites contained in Physalis fruit have been used traditionally by some Chinese communities to treat and prevent various diseases, such as cancer and hepatitis. Research related to the analysis of secondary metabolites in cape gooseberry fruit has been widely conducted, but studies on the morphology and anatomy of flower development, especially in P. peruviana have not been carried out. This study aimed to examine the morphological and anatomical structure of P. peruviana flowers at various stages of development. The procedures included: collection of flower morphology data, preparation of anatomical slides of flowers using the paraffin embedding method and gualitative analysis. The observation results demonstrate that P. peruviana has a complete and perfect flower, which grows as a single axillary type with 5 sepals. attached to each other and is conventionally green with a purple tinge. The corolla is sticky and yellow, with a purple tinge on the neck. The stamen comprises 5 pale yellow anthers and a purple filament. From the bud initiation to anthesis, the development takes 13 days. The anther has 2 lobes or 2 thecae (dithecous) with four microsporangia (tetrasporangiate). The anther wall consists of 4 layers in stages I-V and 2 layers in stages VI and VII. Isobilateral microspores are of the tetrad type. The ovary comprises 2 carpels, while the ovule is anatropus type and has bitegmic structure. This study detailed the reproductive characteristics of P. peruviana and provided a reference framework for subsequent studies by aligning the floral reproductive development perspective to a phenological scope.

Keywords

anatomical development; flowers; morphology; Physalis peruviana L.

Introduction

The Solanaceae family is a plant family with several species that possess noteworthy economic value. The *Physalis* genus comprises approximately 100 species worldwide, including *Physalis peruviana* L. In Indonesia, *Physalis*, known locally as ciplukan and commonly as cape gooseberry, is a group of annual herbaceous shrubs that typically grow in tropical to subtropical habitats (1). This plant originates from the American continent but has since expanded its habitat to the Asian and African continents (2). From an agricultural perspective, *P. peruviana* is a profitable cash crop for dry areas, as it grows easily in wild and arid regions with minimal effort and investment required for cultivation (3).

The fruit of *Physalis* is widely used as a source of nutrition and vitamins (vitamin C, B3 and B6). The secondary metabolites in *Physalis* fruit have been

traditionally utilized by many communities in China to treat and prevent various diseases (4). *P. peruviana* is considered both a therapeutic herb (antispasmodic, diuretic, antiseptic, sedative and analgesic) and a nutraceutical. Additionally, this plant contains many active components such as essential minerals, α linolenic acid, iron, vitamins and phytosterols. Its multifunctional potential in the beverage, food and nutraceutical industries underscores its importance as a crop for cultivation (2).

Several species of Solanaceae share similar characteristics, especially in their flower morphology. For instance, species Solanum melongena and Capsicum frutescence have sepals and petals fused to form a tube. Furthermore, these flowers are bisexual, possessing both male and female reproductive organs, with floral accessories typically attached to the flower stalk (5). The unique structure of fruit development in Physalis is interesting (1). After fertilization, while parts like the corolla generally fall off in most species, in P. peruviana, the sepals continue to enlarge alongside the developing ovary, eventually enclosing the fruit until it is fully ripened. This characteristic, known as the Chinese lantern or inflated calyx syndrome, occurs after fertilization (6).

Research on the flower morphology of *Physalis* has previously been conducted on *P. ixocarpa* (7). The study revealed that perigenous with a superior ovary and its synsepalous calyx was composed of 5 green sepals. Corolla is sympetalous, consisting of 5 yellow petals with a dark blue or brownish pattern at the basal part. The androecium comprises 5 stamens of varying heights, with the basal portion attached to the petals. The stamens are positioned lower than the stigma. However, these studies did not examine the morphology and anatomy of flowers at various stages of development. Anatomical analysis of flower development, especially sporogenesis and gametogenesis, is an important study because these processes determine the success of fertilization, which impacts the success of fruit and seed formation.

Previous research on fruit development in Solanaceae has been conducted in Solanum sect. Acanthopora (8) and Solanum sect. Torva (9), highlighting the interconnected processes of sporogenesis and gametogenesis that occur in the stamen and pistillum. The correlation between anther in stamen and ovule in pistillum structure on flower development can be utilized to predict phases of and characterize the microsporogenesis. megasporogenesis and megagametogenesis by observing flower morphology (10). Anatomical analysis of flower development, especially microsporogenesis, megasporogenesis and megagametogenesis, is a pivotal study because these processes determine the success of fertilization and impact the success of fruit and seed formation. In addition, studying the anatomical development of flower parts such as sepals and petals is also crucial, considering the function of sepals, which play a role in fruit development and the function of petals in attracting pollinators. Thus, this study aims to examine the morphology and anatomy of P. peruviana flowers at various developmental stages.

Materials and Methods

Study site

This research was conducted from August 2022 to March 2023. The planting and maintenance of *P. peruviana* were carried out

in Cangkringan, Sleman, Yogyakarta, Indonesia (7°40'10"S 110° 26'37"E). The plants were maintained in polybags with 35 x 40 cm size filled with soils and were watered daily. Morphological and anatomical analyses were performed at the Faculty of Biology, Universitas Gadjah Mada Yogyakarta, Indonesia (7° 45'55"S 110°22'35"E). Flower sample collection was followed by the methodology described in a previous report (24). Flower samples were collected at seven stages of development: stage I (12-13 (Days Before Anthesis (DBA)), stage II (11-10 DBA), stage III (9-8 DBA), stage IV (7-6 DBA), stage V (5-4 DBA), stage VI (3-2 DBA) and stage VII (anthesis/ 0 DBA). The cape gooseberry plant was identified in the Plant Systematic laboratory of the Faculty of Biology, Universitas Gadjah Mada, with the identification number 099/S.Tb./VI/2022.

Analysis of the flower morphology

Morphometric analysis was initially performed on flower samples from each developmental stage for morphological analysis. Bud length and diameter, anther length and ovule diameter were measured and observed using a stereo microscope (Olympus SZ61). Photographs were taken using an Optilab Advance Plus (Miconos, Indonesia) camera and were edited using the Photoroom platform. Apart from morphometry, morphological analysis was carried out descriptively on flowers and flower accessories at each stage of development.

Analysis of the flower anatomy

Anatomical slides comprising cross-sections of flower parts at various developmental stages were prepared using the paraffin embedding method with double staining (11). Samples from stages I to III were performed from the whole individual flowers, whereas for those from stages IV to VII, anatomical slides were prepared from separated flower parts. The samples were fixed with a formalin-aceto-alcohol solution for 24 hr. The fixative was discarded and the samples were successively washed with graded alcohol using a mixture of alcohol and xylol in a ratio of 1:3, 1:1 and 3:1 for 30 min each. Subsequently, the samples were transferred to a mixture of xylol and paraffin (1:9) at 57 °C for 24 hr. Infiltration was then performed by replacing the xylol-paraffin mixture (1:9) with pure paraffin at 57 °C for 24 hr. Afterward, paraffin blocks were made. Paraffin blocks were cut into 8-10 µm thick sections (35) with a rotary microtome (Leica 01963). Slides were double stained with 1% safranin in 70% alcohol, followed by 1% fast green in 95% alcohol. The sections were mounted with Canada balsam, then were observed using a light microscope (Boeco BM-180) and photographed using an optilab (advance V2, Miconos Indonesia) equipped with viewer software (for taking images) and image raster (for providing scale and image pointing). Anatomical data were analyzed descriptively.

Results and Discussion

Flower morphology

Flowers are among the most complex plant structures and serve as a key distinguishing feature between species (12). The flower shoots of *P. peruviana* take approximately 2 weeks to develop from the appearance of buds to the full display of flower accessories. Flower development begins with the emergence of small buds due to the swelling or growth of the fertile parts of the flower. Flowers in this group typically exhibit 4 concentric whorls of organs, i.e., sepals, petals, stamens and carpels, arranged from the outside of the flower to the centre. Adult buds will experience anthesis and the fertilization process will then occur.

Flower buds in members of the Solanaceae family generally emerge from the leaf axils or side buds and solitary, such as in *C. frustescence*, *Whitania somnifera* and the *Physalis* genus, whereas several other species, such as *S. melongena* and *Solanum xanthocarpum*, are cymose types (5). The flower buds of *P. peruviana* appear in the leaf axils (Fig. 1) and are categorized as complete and perfect flowers composed of the calyx, corolla, stamens and pistillum. *Physalis peruviana* flower buds are shaped like hanging lanterns and are green when they first appear (Fig. 2).

The calyx dominates the buds from stage I to stage V (Fig. 2), displaying green and purple tints. It consists of 5 sepals, which are attached to each other (connate). The sepals protect other parts of the flower while still in the buds and are generally green. The corolla, made up of 5 connate type petals, begins to appear in stage VI and continues to develop. Initially, the corolla is green from stage I to stage IV, then changes to yellow with a purple tinge in stage V and finally blooms at stage VII. The stamens comprise anthers and filaments. The anther is green from stage I to stage III, then changes to purplish yellow in stage IV and is fully yellow in stage V until the flower anthesis, while the filament changes color from green (stage I to stage III) to purple (stage IV to stage VII). The anther is attached (adnate) to the corolla and consists of two thecae that open at stage VII. The stigma and style are green in stages I - III and purple in stage IV - VII. The ovaries are green in stages I to III and then turn yellow until the flower opens. Trichomes were found on both sepals at stages I-VII.

Table 1. Flower morphometry of Physalis peruviana L. at various stages of development

The striking difference in each genus or species of Solanaceae members is the color of the corolla. *S. melongena* is purple, *C. frutescence* is white, *W. somnifera* is green and *P. peruviana* is yellow with a purple tint. *P. peruviana* and *W. somnifera* are closely related and have the same characteristic: flower sepals enclosing the fruit (5). This variation is not observed in the flower symmetry. The flower symmetry of *P. peruviana* is actinomorphic or radial with five flower ornaments each, similar to the flowers of other members of the Solanaceae family (34).

Bud length increases along with bud diameter, anther length and ovary diameter expansion (Fig. 3, Table 1). There is a gradual increase in the blossom's length and diameter from stages I to VII. From stages I to V, both the length of the anther and the diameter of the ovary increases; however, the length of the anther remained constant until the occurrence of flower anthesis. The enlargement of the anther is a consequence of the proliferation and augmentation of cells. The anther cells differentiate to produce specific structures and functions that serve as indicators of anther development, including microsporogenesis and microgametogenesis (35).

Flowers anthesis occurs at stage VII, with a bud length of 1.4 cm and diameter of 1.33 cm. During bud development, there is an increase in the number and size of cells as well as the differentiation of cells and tissues to form organs with specific functions. This is supported by a previous report (13), which states that the development process in plants involves growth, differentiation and morphogenesis. When the floral bud was at its maximum length, the filament also reached its longest length, resulting in a peak length ratio of the pistil to the stamen. The anther wall had already collapsed into partially opening flowers



Fig. 1. Plant morphology denotes the flower or inflorescence characters in *Physalis peruviana* L. The red circle indicates the flower inflorescences. (stag

				· · ·		
Stage	Length of bud (cm)	Bud diameters (cm)	Length of anther (cm)	Ovary diameters (cm)	characteristics in morphology	
I	3.70 ± 0.26	1.00 ± 0.11	1.01 ± 0.10	1.11 ± 0.11	Young greenish bud with purple tinge in calyx; corolla less than calyx length; stamens longer than pistil	
Ш	5.70 ± 0.26	2.01 ± 0.20	1.01 ± 0.10	1.11 ± 0.11	Young greenish bud; corolla still shorter than calyx; stamens longer than pistil	
Ш	6.67 ± 0.35	3.02 ± 0.12	2.00 ± 0.11	2.12 ± 0.12	Bud becomes longer and wider, anther elongates rapidly and much longer than pistil	
IV	8.57 ± 0.38	4.01 ± 0.21	3.02 ± 0.12	2.12 ± 0.12	Bud elongates rapidly, corolla growth rapidly; stamen become purple; corolla become yellow color with dark purple-brownish spot	
V	9.33 ± 0.38	5.97 ± 0.16	4.02 ± 0.09	2.12 ± 0.12	Bud increases rapidly; Stamens, especially anther elongate rapidly	
VI	11.60±0.36	7.99±0.17	4.02±0.09	3.11±0.12	Outer whorl of petals opens; corolla increases rapidly	
VII	13.53 ± 0.50	11.93 ± 0.25	4.02 ± 0.09	3.11 ± 0.12	Both whorls of petals are fully open; anthers dehisce and pollen disperses	

Plant Science Today, ISSN 2348-1900 (online)

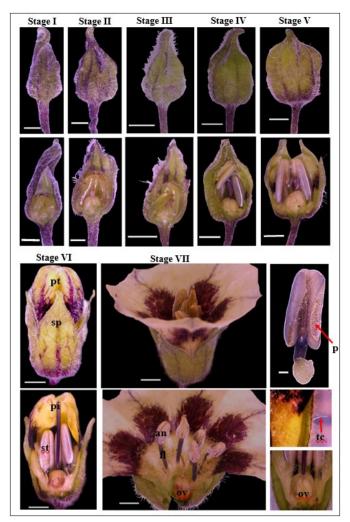


Fig. 2. Morphology of *Physalis peruviana* L. flowers at distinct stages of development: stage I (12-13 DBA); stage II (11-10 DBA); stage III (9-8 DBA); stage IV (7-6 DBA); stage V (5-4 DBA); stage VI (3-2 DBA); stage VII (anthesis/0 DBA); sp. sepal, pt. petal, pi. pistillum, st. stamen, an. anther, fl. Filament, p. polen, tc. trichome. Bar: 1 mm.

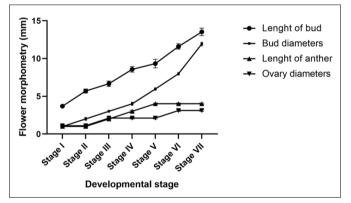


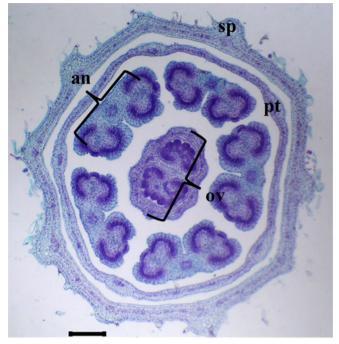
Fig. 3. Flower morphometry of *Physalis peruviana* L. at various stages of development, stage I (12-13 DBA), stage II (11-10 DBA), stage III (9-8 DBA), stage IV (7-6 DBA), stage V (5-4 DBA), stage VI (3-2 DBA) and stage VII (anthesis/0 DBA).

In fully bloomed flowers, the anther walls cracked and pollen grains were released.

Flower anatomy

Sepal Anatomy

Based on observations of the complete cross-section of the flower (Fig. 4), the *P. peruviana* flower comprises 4 main fundamental parts: calyx, corolla, stamen and pistils. There are 5



4

Fig. 4. Cross-section of the complete flower on Physalis peruviana L. in stage I. sp. sepals, pt. petal, an. anther and ov. ovary. Bar: 200 $\mu m.$

sepals composed of calyx, located on the fragment of the flower, attached to the basal part. Likewise, the 5 petals of the corolla are arranged in a circle and are interconnected (adnate). There are 5 stamens and the ovary of the pistil is located in the flower centre.

In general, sepals in flowers have a shape and anatomical structure similar to leaves. The anatomical structure of the sepals in P. peruviana consists of the epidermis (abaxial and adaxial), mesophyll tissue and vascular bundle. The anatomical structure of the sepals in stages 1-IV did not show any significant differences (Fig. 5). At this stage, the adaxial and abaxial epidermis comprises one layer of isodiametrical cells. Among the abaxial epidermal cells, 2 types of glandular trichomes are found, namely capitate glandular trichomes long stalked with terminal unicellular and simple conical trichomes, which are composed of 1-3 cells (Fig. 5C and 5F). This type of trichome is similar to that found in Justicia (14) and P. ixocarpa (6). Glandular trichomes function to biosynthesize specialized metabolites (15). The flower petals of P. solanaceous contain the compound 4, 7didehydrophysalin B (16). In addition to glandular trichomes, panerophore type of stomata are also found on abaxial side of sepals (Fig. 5I) of P. peruviana. This finding is in accordance with a previous study (6), which examined the sepal anatomy in P. ixocarpa.

The sepal mesophyll is composed of homogeneous parenchymatous tissue without intercellular spaces, especially in stages I-III and these spaces begin to form between the mesophyll parenchyma cells in stage IV (Fig. 5E). Intercellular space increases over time with the flower growth. Drusenshaped calcium oxalate crystals were observed in the mesophyll parenchyma (Fig. 5H). In stage VII (anthesis), the abaxial and adaxial epidermis differentiates to form conical papillae, mesophyll cells with many intercellular spaces (17). According to an earlier study (18), papillae are generally found in floral organs and have a secretory function.

The vascular bundles in *Physalis* are open collateral. These open collateral vascular bundles in the sepals consist of

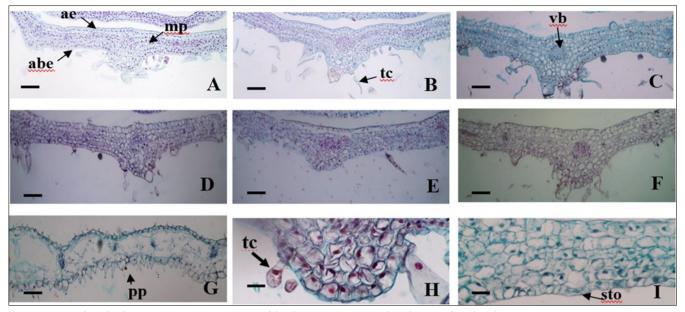


Fig. 5. Anatomy of sepals of *P. peruviana* L. at various stages of development. A. Stage I with trichome in abaxial epidermis, B. Stage II, C. Stage III, D. Stage IV, E. Stage V, F. Stage V, G. Stage VII with papilla in the abaxial, H. glandular trichome in abaxial epidermis of stage III, I. stomata in the abaxial sepal. ae. adaxial epidermis, abe. abaxial epidermis, mp. mesophyll parenchyma, tc. trichome, vb. vascular bundle, pp. papilla, sto. stoma. Bar A-G: 100 µm, bar H, I: 20 µm.

the xylem and phloem, which is consistent with the previous finding that cambium is not formed in flowers (16). This structure of the vascular bundles supports the statement that the vascular bundles in sepals are similar to those in leaves but simpler (19).

Petal Anatomy

Petals are located on the inner circle side of sepals. These structures have various colours and shapes (20) to attract insect pollinators for nectars (21).

The anatomy of petals is generally similar to that of sepals. Petal anatomy in *P. peruviana* comprises adaxial and abaxial epidermis, mesophyll and vascular bundles (Fig. 6). Similar to leaf, stomata and trichomes are found on the epidermis. The panerophore type of stoma is found on the abaxial epidermis of the petal (Fig. 6H). There were no differences in the petal anatomy of stages I-IV, which comprise one layer of isodiametric shaped epidermal cells and homogeneous parenchymatous tissue of mesophyll without intercellular space. The structure of the epidermis undergoes changes in stage V, including epidermal cell elongation in a tangential direction and intercellular space formation between mesophyll parenchyma cells. Elongation of the epidermal cells continues as the growth stage increases and then forms a papilla structure in stage VII (anthesis).

The structure of the petal vascular bundle is very simple

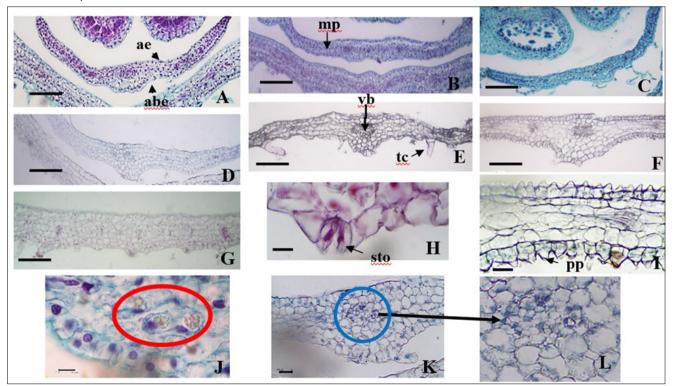


Fig. 6. Anatomy of *Physalis peruviana* L. flower petals at various stages of development. A. Stage I, B. Stage II, C. Stage III, D. Stage IV, E. Stage V, F. Stage V, G. Stage VII, H. Stomata in abaxial petal stage VII, I. Papilla in epidermis stage VI, J. the red circle indicates the calcium oxalate crystal in stage III, K, the blue circle indicates the vascular bundle in stage IV, L. Enlarged image of vascular bundle. ae. adaxial epidermis, abe. abaxial epidermis, mp. mesophyll parenchyma, vb. vascular bundle, pp. papilla, sto. stoma. Bar A-G: 100 µm, H-I: 10 µm, I-L: 20 µm.

and protected by the bundle sheath cells. The vascular bundles in petals are similar to those in leaves but simpler, composed of xylem in the adaxial and phloem in the abaxial sides. No cambium was found in the petals (22). According to a previous study (6), the type of vascular bundle in *P. ixocarpa*, a species closely related phylogenetically to *P. peruviana*, is open collateral. Similar to sepals, drusen calcium oxalate crystals are also observed in mesophyll parenchyma cells, as they are also found in the mesophyll of Gardeniae flowers (23). In the Solanaceae family, calcium oxalate crystals are also located in the layers of the anther walls as well as connective tissue (24).

Anther Anatomy

Plant male reproductive organs consist of a collection of stamens (filament and anther) that form the androecium. The anther is the fertile part of the androecium. Important processes that occur in the anther are microsporogenesis and some microsporangia end is protected by several layers of walls, consisting of epidermis (epithecium), endothecium, middle layer and tapetum (25).

The anther of *P. peruviana* is dithecous, having two lobes (thecae) with four microsporangia (tetrasporangiate) (Fig. 7). The anther lobes are separated by connective tissue composed of parenchyma and vascular bundles. In stage I, the anther wall layers and sporogenic tissue are already formed (Fig. 7A). The wall layers consist of 4 tissues, from outside to inside, are epidermis, endothecium, middle layer and tapetum. Anther wall formation in *Physalis* is of the dicotyledonous type (26).

Sporogenous cells contain dense cytoplasm and undergo mitosis. A structure that forms the stomium has also been formed in stage I. The structure of the anther wall in stage II is identical to stage I (Fig. 7A, 7B).

In stage III, the sporogenic tissue, which functions as a microspore mother cell, undergoes meiotic division, forming tetrads of microspores. The microspore tetrad in *P. peruviana* L. is isobilateral in type (Fig. 8C) (27). In stage IV, the microspore tetrads separate into solitary microspores, while in stage V, the middle layer and tapetum begin to degenerate (Fig. 7E). The degeneration of the tapetum provides nutrients for the microspores development. The tapetum is of glandular type, as observed in W. somnifera, a species closely related to Physalis (28). In addition to the degeneration of the middle layer and tapetum, the secondary cell walls of the endothecium layer thicken, the stomium cells enlarge and the cell arrangement becomes irregular. The right and left lobes combine to form the theca structure in stages V, VI and VII. Solitary microspores develop into mature microspores and stomium is formed in stage VII. The stomium is formed by the endothecium and epidermal cells that experience dehiscence or tissue damage (29).

Ovary Anatomy

The female reproductive organ (gynoecium) consists of 3 fundamental compartments: the stigma, style and ovary. Inside the ovary is an ovule that plays a role in forming megaspores and megagametes (25). Based on observations, the structure of the ovary of *P. peruviana* comprises the ovary wall, septum and ovule chamber. The ovarian wall consists of the epidermis,

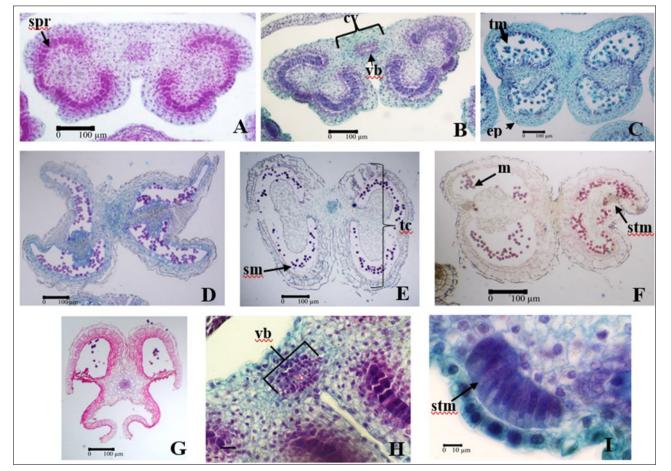


Fig. 7. Cross-section of *Physalis peruviana* L. flower anthers at distinct stages of development. A. stage I with sporogen tissue, B. stage II sporogen tissue undergoes to meiosis, C. stage III show the tetrad microspore, D. stage IV, E. stage V, F. stage VI, G. stage VII., H. vascular bundle in connectivum, I. formation of stomium. spr. sporogen tissue, vb. vascular bundle, cv. connectivum, tm. tetrad microspore, ep. epidermis, en. endothecium, md. middle layer, tp. tapetum, sm. solitare microspore, mm. mature microspore, stm. stomium, tc. theca. Bar A-G: 100 µm, H-I: 10 µm.

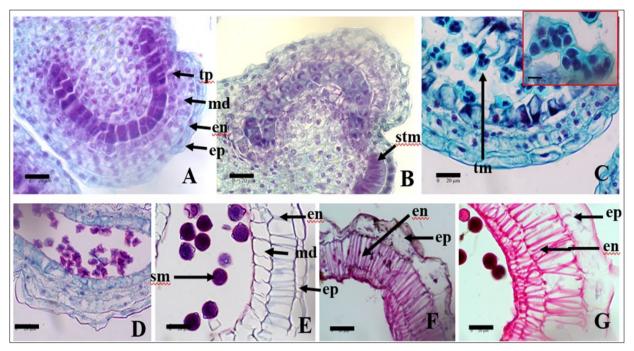


Fig. 8. Anatomy of the anther wall of *Physalis peruviana* L. at various stages of development. A. stage I there are four layers of anther wall, B. stage II the stomium begins to appear, C. stage III with isobilateral microspore, D. stage IV with solitary microspores, E. stage V there is thickening of endothecium wall, F. stage VI, G. stage VII with mature microspore. ep. epidermis, en. endothecium, md. middle layer, tp. tapetum, stm. stomium, tm. tetrad microspore. Bar: 20 µm.

parenchyma and vascular bundles. The septum, which separates the 2 seed chambers, is made up of septal epidermis tissue, parenchyma and vascular bundles. This structure is similar to the ovary in *C. annuum* (30). The ovary of *P. peruviana* comprises 2 carpels (Fig. 9A) and this is different from that of ovary of *P. ixocarpa*, where the gynoecium comprises 3 carpels (6). The ovule occupies the entire space of the ovary chamber.

In stage I, the prospective ovule begins to form as a bulge

bulge originates from the proliferation of septal cells in the periclinal direction. In stage II (Fig. 9B), the prospective ovule continues to develop and in stage III (Fig. 9C), the structure of the ovule is fully formed. The ovule is anatropous and composed of 2 layers of integument (bitegmic) (Fig. 9I). The cell layers compose the ovule wall are the outer integument, inner integument and nucellus. The nucellus has a nutritive function in megaspore formation (31). In the embryo sac, a prospective

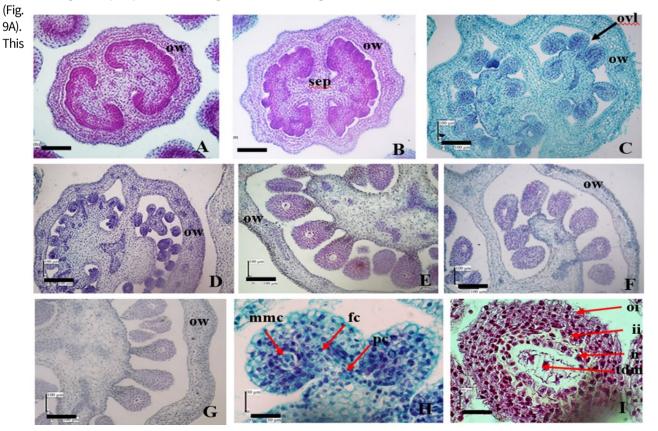


Fig. 9. Cross-section of the ovary/longitudinal section of the ovule of *Physalis peruviana* L. flowers at various stages of development. A. Stage I show the prospective ovule forms a bulge ,B. Stage II show the prospective ovule develops, C. Stage III show the formation of ovule, D. Stage IV, E. Stage V, F. Stage VI, G. Stage VII., H. ovule in megaspore mother cell stage, I. ovule in tetrad megaspore stage. ow. ovary wall, sep. septum, ovl. ovule, fc. foeniculus, pc. placenta, mmc. megaspore mother cell, oi. outer integument, ii. inner integument, n. nuselus, tdm. tetrad megaspore. Bar A-G: 100 µm; H-I: 30 µm.

megaspore will divide by mitosis and meiosis to form a megaspore and a megagamete. The development of ovaries and ovules cannot be separated from megasporogenesis and megagametogenesis (32).

In previous research on ovule formation (25), 2 types of ovule formation were identified: the di-zonate and tri-zonate types. The di-zonate type of ovule primordia is formed by a periclinal division in the subdermal layer or second zone in the placental meristem. This type is found in several families, including Balsaminaceae. Begoniaceae, Droseraceae. Hypericaeae, Gesneriaceae, Lobeliaceae, Monotropaceae and Orobanchaceae. Meanwhile, the tri-zonate type can be formed by a periclinal division in the third zone of the placental meristem. At the beginning of the division, the two outermost walls divide anticlinally. This type is found in several families, including Berberidaceae. Betulaceae, Caricaceae, Casuarinaceae. Cistaceae. Cruciferae, Cucurbitaceae, Euphorbiaceae, Magnoliaceae and Rosaceae, including the family of the cape gooseberry plant studied, Solanaceae (33).

Conclusion

The analysis of the morpho-anatomy of P. peruviana flowers during the development is a valuable tool that provides embryological data of great importance to complement phylogenetic studies in the Solanaceae family. Physalis peruviana L. has a complete and perfect flower, which grows as a single axillary type with the calvx consists of 5 sepals, attached to each other and is conventionally green with a purple tinge. The corolla with 5 petals is sticky and yellow, with a purple tinge on the neck. The stamen comprises 5 pale yellow anthers and a purple filament. From the flower bud initiation to anthesis takes 13 days. The adaxial and abaxial regions of the sepal and petal epidermis are isodiametric in flower buds; later, the epidermis differentiates into papillae. Glandular trichomes were found on the adaxial epidermis of sepals. The anther has 2 lobes or 2 thecae (dithecous) with four microsporangia (tetrasporangiate). The anther wall consists of 4 layers in stage I-V and 2 layers in stage VI and VII. Isobilateral microspores are tetrad type. The ovary comprises 2 carpels-ovule with an anatropus type and bitegmic. Embryologic studies are needed in the remaining species of Solanaceae achieve better progress in phylogenetic studies and improve our understanding of their specialization.

Acknowledgements

The authors deeply acknowledged the Indonesian Endowment Funds for Education (LPDP) and Centre for Higher Education Funding (BPPT) for this research grant with the contract number: 1764/J5.2.3./BPI.06/10/2021.

Authors' contributions

U carried out the experiment, anatomical slides preparation, gathered and analyzed data and drafted the manuscript. LHN and TRN guided the first author for data analysis and manuscript preparation as well as reviewed the manuscript. M guided the data collection and analysis, manuscript preparation and also

reviewed the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

References

- Rengifo E, Vargas-Arana G. *Physalis angulata* L. (Bolsa Mullaca): A review of its traditional uses, chemistry and pharmacology. Buletin Latinoamericano y del Caribe de Plantas Medicinales y Aromaticas. 2013;12(5):431-45. https://www.redalyc.org/pdf/856/85628390001.pdf
- Singh N, Singh S, Maurya P, Arya M, Khan F, Dwivedi DH. An updated review on *Physalis peruviana* fruit: Cultivational, nutraceutical and pharmaceutical aspects. Indian J of Nat Prod and Resour. 2019;10(2):97-110. https://www.researchgate.net/ publication/338449232
- Dwi YWS, Aini N, Waluyo B. *Physalis peruviana* L.: Growth, yield and phytochemical content- A review. Agric Rev. 2019;40(04):328-28.
- Wu J, Zhao J, Zhang T, Gu Y, Khan IA, Zou Z. Naturally occurring physalins from the genus *Physalis*: A review. Phytochem. 2021;191:1-25. https://doi.org/10.1016/j.phytochem.2021.112925
- 5. Jagatheeswari D. Morphological studies on flowering plants (Solanaceae). 2014;15:36-43.
- 6. Wang L, He L, Li J, Zhao J, Li Z, He C. Regulatory change at *Physalis* organ size 1 correlates to natural variation in tomatillo reproductive organ size. Nat Commun. 2014;4271.
- Dyki B, Jankiewicz LS, Staniaszek M. Anatomy and surface micromorphology of tomatillo fruit (*Physalis ixocarpa* Brot.). Acta Soc Bot Pol. 1997;66(1):21-27.
- Chiarini FE, Gloria EB. Fruit anatomy of species of *Solanum* sect. Acanthophora (Solanaceae). Flora. 2009;204:146-56. https:// doi.org/10.1016/j.flora.2008.01.010
- Chiarini FE, Natalia RM, Gloria EB. Fruit anatomy of species of Solanum sect. Torva (Solanaceae). Bol Soc Argent Bot. 2010;245:235-44.
- Yang J, Kang X. Microsporogenesis and flower development in Eucalyptus urophylla × E. tereticornis. Breed Sci. 2015;65(2):138-44.
- 11. Ruzin S. Plant microtechnique and microscopy. New York: Oxford University Press; 1999.
- Alvarez-Buylla ER, Benítez M, Corvera-Poiré A, Chaos Cador Á, de Folter S, Gamboa de Buen A. Flower development. Arab B. 2010;8:0127. https://doi.org/10.1199/tab.0127
- Srivastava LM. Plant growth and development: Hormones and environment. USA: Academic Press Inc.; 2002.
- Amirul-Aiman AJ, Noraini T, Nurul-Aini CAC, Ruzi AR. Petal anatomy of four *Justicia* (Acanthaceae) species. AIP Conf Proc. 2013;1571:368-71.
- Muravnik LE, Kostina OV, Zaporozhets NL. Structure and functions of the glandular trichomes in three *Arnica* species (Asteraceae), depending on their location on leaves and flowers. Flora Morphol Distrib Funct Ecol Plants. 2022;290(152047).
- Pérez-Castorena AL, Hernández IZ, Martínez M, Maldonado E. Chemical study of calyxes and roots of *Physalis solanaceus*. Rec Nat Prod. 2013;7(3):230-33. https://www.researchgate.net/ publication/286386489_Chemical_Study_of_Calyxes_and_Roots _of_Physalis_solanaceus#fullTextFileContent
- Guo J. Comparative micromorphology and anatomy of crested sepals in *Iris* (Iridaceae) The University of Chicago Press. 2015;176

(7):627-42.

- 18. Fahn A. Plant anatomy. New York: Pergamon Press; 1982.
- Mishra SR. Understanding plant anatomy. New Delhi: Discovery Publishing House Pvt. Ltd.; 2009.
- 20. Irish VF. Evolution of petal identity. J Exp Bot. 2009;60(9):2517-27. https://doi.org/10.1093/jxb/erp159
- 21. Costa VBS, Pimentel RMM, Chagas MGS, Alves GD, Castro CC. Petal micromorphology and its relationship to pollination. Plant Biol. 2017;19:115-22. https://doi.org/10.1111/plb.12523
- Ronse L, Wanntorp L, Annals S, October N, Craene LR De, Wanntorp L. Floral development and anatomy of Salvadoraceae. Annal of Bot. 2022;104(5):913-23. https://doi.org/10.1093/aob/ mcp170
- Judkevich MD, Salas RM, Gonzalez AM. Embryology of some flowers of the *Gardenieae complex* (Rubiaceae). Protoplasma. 2022;259(5):1233-54. https://doi.org/10.1007/s00709-022-01734-5
- 24. Rodriguez I. Flower anatomy and morphology of *Exodeconus* maritimus (Solanaceae, Solaneae) and Nicandra physalodes (Solanaceae, Nicandreae). 2000;22(2):187-99. https:// sciencepress.mnhn.fr/sites/default/files/articles/pdf/ a2000n2a3.pdf
- 25. Bhojwani SS, SPB. The embryology of angiosperms. New Delhi: Vikas Publishing House; 1979.
- Suryani T, Susanti S, Utaminingsih. Microsporogenensis of ciplukan (*Physalis angulata* L.). AIP Conf Proceed. 2020;2260:030017-1– 030017-10. https://doi.org/10.1063/5.0016268
- 27. Furness CA, Rudall PJ, Sampson FB. Evolution of microsporogenesis in angiosperms. Int J Plant Sci. 2002;163(2):235-60.
- 28. Ghimire B, Heo K. Embryology of *Withania somnifera* (L.) Dunal (Solanaceae). Acta Biol Cracoviensia Ser Bot. 2012;54(2):69-78.

- 29. Kotia A. Biosystematics of angiospermae, plant development and reproduction. Jaipur: Rajasthan State Cooperative Press; 2017. http://assets.vmou.ac.in/MBO06.pdf
- Dias GB, Gomes VM, Moraes TMS, Zottich UP, Rabelo GR, Carvalho AO. Characterization of *Capsicum* species using anatomical and molecular data. Genet Mol Res. 2013;12(4):6488-501. https:// doi.org/10.4238/2013.february.28.29
- Sato HA, Maria Gonzalez A. Floral development and anatomy of pistillate flowers of *Lophophytum* (Balanophoraceae), with special reference to the embryo sac inversion. Flora Morphol Distrib Funct Ecol Plants. 2016;219:35-47. https://doi.org/10.1016/ j.flora.2016.01.002
- Wang H, Rana S, Li Z, Geng X, Wang Y, Cai Q. Morphological and anatomical changes during floral bud development of the trioecious *Idesia polycarpa* Maxim. Rev Bras Bot. 2022;45(2):679-88. https://link.springer.com/article/10.1007/s40415-022-00792-6#citeas
- Johri BM. Embryology of angiosperms. New York: Springer-Verlag; 1984. https://doi.org/10.1007/978-3-642-69302-1
- Hilgenhof R, Edeline G, Sandra K, Xavier A, Eric JT, Lynn B, et al. Morphological trait evolution in *Solanum* (Solanaceae): Evolutionary lability of key taxonomic characters. Taxon. 2023;72 (4):811-47. https://doi.org/10.1002/tax.12990
- Yanming D, Xinping J, Lijian L, Chunsun G, Xiaobo S. Morphological anatomy, sporogenesis and gametogenesis in flowering process of jasmine (*Jasminum sambac* Aiton). Scientia Horti. 2016;198:257-66.