

# Integrative Redescription of *Peperomia heyneana* Miq. (Piperaceae) Based on Morphological and Molecular Evidence

ARJUN THOMAS

[arjunthomas@alberts.edu.in](mailto:arjunthomas@alberts.edu.in)

St. Albert's College (Autonomous) Ernakulam

J. JAMESON

St. Albert's College (Autonomous) Ernakulam

---

## Research Article

**Keywords:** *Peperomia heyneana*, Integrative taxonomy, Fruit morphology, rbcL phylogeny, Micropiper, Piperaceae, Species circumscription

**Posted Date:** October 15th, 2026

**DOI:** <https://doi.org/10.21203/rs.3.rs-10705634/v1>

**License:** © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

**Additional Declarations:** No competing interests reported.

---

# Abstract

*Peperomia heyneana* Miq. (Piperaceae) was originally described by Miquel in *Systema Piperacearum* (1843) from the Chandragiri Hills of Nepal. The original protologue is extremely brief and lacks several diagnostic morphological characters, making accurate identification of the species difficult. Furthermore, subsequent taxonomic treatments have provided inconsistent descriptions, particularly with respect to fruit morphology, resulting in persistent taxonomic ambiguity. This study presents an integrative redescription of *P. heyneana* based on detailed morphological observations and *rbcL* phylogenetic evidence. A comprehensive taxonomic account, including macro- and micromorphological descriptions, colour photographs, line illustrations, phenology, ecology, and distribution, is provided. The study documents for the first time the fruit surface morphology of *P. heyneana*. The species conforms to the diagnostic fruit characters of subgenus *Micropiper*, including a beaked fruit apex with a subapical stigma and a rounded to conical pseudopedicel, but differs from all currently recognized members by possessing a smooth basal region with sticky papillae restricted to the apical region rather than papillae uniformly covering the entire fruit surface. Molecular phylogenetic analysis based on the *rbcL* gene recovered *P. heyneana* as sister to *P. urvilleana* A. Rich., supporting its placement within subgenus *Micropiper*. The revised species circumscription provides a reliable basis for accurate identification and improves the taxonomic understanding of *P. heyneana*.

## INTRODUCTION

The genus *Peperomia* Ruiz & Pav. (Piperaceae) is one of the species-rich genera of angiosperms comprising 1500–1700 species distributed pantropically (Wanke *et al.*, 2006). Twelve species of *Peperomia* have been reported from India, including the recently described *P. albertiae* Arjun & J. Jameson, *P. ekakesara* Syam & S. Nampy, *P. emarginatifolia* J. Mathew, *P. mangalbaria* P. Rai & G. Mathieu, and *P. vellarimalica* J. Mathew & P.M. Salim. The genus can be epiphytic, epilithic or terrestrial in moist or wet forests and cloud forests (Guimarães *et al.*, 1984; Tebbs 1993). Miquel (1843a-c) led the infrageneric investigation on the genus *Peperomia* and later Dahlstedt (1900) based it on the fruit morphology as fruit characteristics are an important distinguishing feature in this genus. Based on the morphological and molecular data Frenzke *et al.*, (2015) updated the infrageneric classification and this classification is most commonly used at present. *Peperomia heyneana* was first described by Miquel, Friedrich Anton Wilhelm in *Systema piperacearum* (1843) from Chandragiri Hills (Kathmandu) Nepal. The original protologue of *Peperomia heyneana* by Miquel (1843) is extremely brief and lacks several key diagnostic characters, making the species difficult to identify accurately. Furthermore, subsequent descriptions differ in important morphological features, particularly fruit morphology, resulting in persistent taxonomic confusion regarding the species.

A major contribution of this study is the documentation of a previously unreported diagnostic fruit character in *Peperomia heyneana*. The fruits possess a smooth basal region and a sticky papillate apical region, whereas all other examined species of subgenus *Micropiper* exhibit papillae distributed uniformly

over the entire fruit surface (Frenzke et al., 2015). This distinctive character provides a reliable diagnostic feature for recognizing *P. heyneana* and supports its taxonomic circumscription.

During multiple botanical expeditions as part of the study on vascular epiphytes of Tropical montane cloud forests of southern Western Ghats, Kerala, India We encountered *heyneana* from different parts of the cloud forest of Kerala, based on detailed studies in morphology, type specimen, herbarium and recent literature (Frenzke et al., 2015), this species shows lot of morphological variations in vegetative parts. In India Hooker (1890) reported this species in the Flora of British India and South India Gamble (1921) reported it in the Flora of Presidency of Madras, while in the Kerala region, Sasidharan (2013) in Flowering plants of Kerala enlisted *P. heyneana*. The original description is incomplete and all available descriptions have inconsistencies with the essential character of this species like fruit morphology being too narrowly defined. This species has eight synonyms making this species difficult to identify. In the present study, an amended and extended modern description of *P. heyneana* is provided. It is based on data obtained from recently collected material in both living and herbarium species from Indian and other Asian localities.

## MATERIALS AND METHODS

### Taxon sampling

Specimens were collected from different cloud forests localities of Western Ghats of Kerala, India during different seasons from 2019 to 2022. Habit and habitat photographs were taken with Fujifilm FinePix HS20EXR. Fresh specimens were preserved in FAA (formalin–acetic acid–alcohol), herbarium preparations were done according to Jain and Rao (1977) and floral photographs, illustrations, and detailed studies were done using a Leica EZ4W stereo microscope. We examined 50 living plants and 40 herbarium specimens from different localities across India including type including type specimens and specimens housed at CAL, MH, KFRI, and SAC.

**Additional Specimens examined. INDIA.** West Bengal, Darjeeling, June 1880, *J. S. Gamble 380689* (CAL!); same locality, 28 May 1884, *C. B. Clarke 380690* (CAL!); Manipur, Kopra, 1882 *G. Watt 381046* (CAL!); Manipur, Kassome, 10 January 1882 *G. Watt 380679* (CAL!); Sikkim, 1881 *J. S. Gamble 380697* (CAL!); Manipur, Kassome, 10 January 1882, *G. Watt 380679* (CAL!); Sikkim, 1862, *T. Anderson 380688* (CAL!); Sikkim, Suriel, 30 May 1947, *K. Biswas* (CAL!); Meghalaya, Nolgo, 29 June 1961, *D. B. Del 55510* (CAL!); Arunachal Pradesh, Kameng, Bompou hill, 28 March 1957, *G Panigrabi 555511* (CAL!); Nagaland, Naga hills, 1886, *D. Prain 380676* (CAL!); Palakkad, Parathode, Silent Valley National Park, s.dt, *Stephen & Joy 007260* (KFRI!); Palakkad, Victoria, Nelliampathy, s.dt, *M. Kumar & Stephen 006751* (KFRI!);

### DNA isolation, Sequencing and Phylogenetics

Total DNA was extracted using CTAB, followed by electrophoresing the DNA in 1% Agarose and visualized under UV. The *rbcl* region was PCR amplified with primers (Table. 1) and amplicon was

checked for appropriate size by agarose gel visualization. Amplicon was gel purified using a commercial column-based purification kit (Invitrogen, USA) and sequencing was performed with forward and reverse primers in ABI 3730 XL cycle sequencer. Forward and reverse sequences were assembled and contig was generated after trimming the low-quality bases. Amplification and sequence analysis are the same as described in Wattoo et al., (2016). The sequences produced were edited and used for BLAST search. The phylogenetic tree (Maximum likelihood (ML) was constructed from the sequence of this study in MEGA version 11 (Tamura et al., 2021) with 1000 bootstrap.

| Gene name | Primer Sequence       | Product length |
|-----------|-----------------------|----------------|
| rbcl BF   | 5ATGTCACAC∇ACAG∇AC3   | 743bps         |
| rbcl 724R | 5TCGCATGTCCTGCAGTAGC3 |                |

Details of molecular markers and primers used for PCR amplification and sequencing.

## RESULTS AND DISCUSSION

### Taxonomic Treatment

**Peperomia heyneana** Miq., Syst. Piperac. 1: 123. 1843; *Peperomia wightiana* Miq. in Hook.'s London J. Bot. 5: 548. 1846; Hook.f., Fl. Brit. Ind. 5: 98. 1886; C. DC. in A.DC., Prodr. 16(1): 453. 1869; Gamble, Fl. Pres. Madras 1210(847).1925; Long in Grierson and Long, Fl. of Bhutan 1(2): 345. 1984; Ramach. & V.J. Nair, Fl. Cannanore Dist. 385. 1988; Gilbert & Nianhe, Novon 9 (2): 191. 1999; Yongqian *et al.* in Wu & Raven, Fl. China 4: 22. 1999; Manilal, Fl. Silent Valley 230. 1988; *Peperomia wightiana* Miq.in Muktesh, Epiphytic Fl. Western Ghats 69l; Sasidh., Fl. Periyar Tiger Reserve 337. 1998. Sasidh., Fl. Parambikulam WLS 261. 2002; Mohanan & Sivad., Fl. Agasthyamala 551. 2002; Ratheesh Narayanan, Fl. Stud. Wayanad Dist. 685. 2009.

Types: Chandragiri Hills (Kathmandu) Nepal, *Wallich* 6663C (holo- type **K-W!** isotypes **G-DC! GZU, H-T, U**).

Synonymous: *P.duclouxii* C.DC., *P.haycockii* C.DC., *P.kurzii* C.DC., *P.portulacoides* var. *hirtella* Wawra., *P. wightiana* Miq., *P. zeylanica* Walp., *Piper oblongum* Wall.

Perennial herbs, 5–15 cm or higher, creeping, ascending. Stems green or red, diffusely branched creeping and rooting, Stolons present; internode 3–6 cm long, Leaves succulent, opposite and whorled on terminal branchlets, 3–4- verticillate, lamina coriaceous when dry, obovate-oblong with pubescent or glabrous; lower surface puberulous or glabrous with or without red spots, upper surface glabrous or puberulous, asymmetric 0.5–3 by 0.5–1.5 cm, base cuneate, apex obtuse or emarginate with ciliate, venation: very prominent usually single (rarely up to 3); petiole 0.5–1.5 cm long, puberulous or glabrous cylindrical, green or red; Inflorescence (1 –) 2–4 spadix per shoot, terminal or in the axils of the upper

leaves, 1.5–5.5 × 0.1–0.2 cm, erect, cylindrical green; rachis glabrous with sparingly flowered; peduncle 0.5–1.5 cm long, puberulent or glabrous. Flowers with an orbicular flower bract, 0.5 mm diam with a short stalk, covering the basal part of the ovary. Stamens: filaments short; anthers 0.16–0.19 × 0.18–0.2 mm ditheous, dehiscent transversely, pollen white. Ovary ovoid, oblique, immersed within the rachial pit, stigma glabrous. Fruit (nutlet) with pseudo pedicel, ovoid, 0.4 × 0.8 mm diam, apex; rostrated – rostrum shorter than body slightly curved, subapical stigma, surface; smooth fruit base, rounded sticky papillae at upper part. Figure 1 and 2 (Plant species from India, Kerala, Idukki district, Devikulam, Eravikulam National Park, Anamudi, 2158 m, 10° 9' 56" N, 77° 4' 15" E, 02 October 2020, SAC 499).

**Notes:** The present study is the first to provide a detailed account of the fruit surface morphology of *Peperomia heyneana*. According to the infrageneric classification of Frenzke et al. (2015), fruits of subgenus *Micropiper* are characterized by (1) a scutellate or beaked apical protuberance with a subapical stigma, (2) a fruit surface uniformly covered with sticky papillae, and (3) a rounded to conical pseudopedicel. *Peperomia heyneana* conforms to the first and third characters but differs markedly in the second. Unlike all other examined members of subgenus *Micropiper*, the fruit surface of *P. heyneana* is smooth in the basal region, with sticky papillae restricted to the apical portion. This previously undocumented feature represents a novel diagnostic character for the species and refines its taxonomic circumscription. This previously undocumented character constitutes a reliable diagnostic feature for distinguishing *P. heyneana* from other members of the subgenus and further supports its taxonomic circumscription. *P. heyneana* exhibits morphological variations in vegetative parts like red pigmentation in stems and on the lower surface of leaves whereas half of the studied species have stem green without red pigmentation on the abaxial surface. Another morphological variation observed during studies was the presence or absence of hair in the stems and leaves. These variations were most probably due to ecological factors. According to Gould et al., (2010) anthocyanin pigments were induced in green stems exposed to full and Johnson (1975) explains that pubescence is positively associated with a harsh moisture regime. Floral parts of all the specimens studied were the same.

## Distribution

☐ Bhutan, China, India, Myanmar, Nepal, Sri Lanka, Thailand. Elevation from 800–2330 m. Map 1.

## Phenology

☐ Flowering and fruiting between August to November.

**Ecology.** ☐ Epiphytic on the lower trunk of phorophyte inside the cloud forests and ravines, wet, moss-covered rocks. Associated with moss and lichen.

## Conservation status

☐ *Peperomia heyneana* was assessed with the provisional rating of Least Concern (LC) according to the IUCN (2014) criteria.

## Vernacular name

☐ Without vernacular name

H. Stamen; I. Gynoecium; J. Bract; K. Fruits: see rachis showing fruits and pits of fallen fruits; L. Young fruit; M. Mature fruit attached to rachis; N. Detached mature fruits. PHOTOS: A.THOMAS.

## Phylogenetics

The *rbcl* sequence generated for *Peperomia heyneana* was deposited in GenBank under accession number OP179289. BLAST analysis of the *rbcl* sequence of *Peperomia heyneana* showed 99.43% sequence identity with *P. urvilleana* A. Rich., with 98% query coverage and an E-value of 0, indicating a high degree of molecular similarity between the two species. Phylogenetic analysis recovered *P. heyneana* and *P. urvilleana* as sister taxa with strong bootstrap support (98%), forming a well-supported clade (Fig. 3). This result confirms the close evolutionary relationship between the two species while supporting the taxonomic placement of *P. heyneana* within subgenus *Micropiper*. *Peperomia urvilleana* is an epiphytic perennial succulent native to several Pacific islands, including Norfolk Island, Solomon Islands, Vanuatu, New Caledonia, New Zealand, the Kermadec Islands, Fiji, and Samoa. The close molecular affinity between the Asian species *P. heyneana* and the Pacific island species *P. urvilleana* is noteworthy and suggests a historical biogeographic connection between Asian and Pacific lineages of *Peperomia*. However, the present phylogenetic analysis is based on a limited number of taxa and a single molecular marker; therefore, it is insufficient to distinguish between alternative historical scenarios such as Gondwanan vicariance and long-distance dispersal. Broader taxon sampling, additional nuclear and plastid markers, and formal biogeographic analyses would be required to evaluate these hypotheses rigorously.

Previous studies have proposed that floristic exchanges between Southeast Asia, Australia, and the Indian subcontinent have contributed to the present distribution of several tropical plant lineages (Mani, 1974). The sister relationship observed between *P. heyneana* and *P. urvilleana* is consistent with the possibility of historical connections among these regions, although the present dataset does not allow definitive conclusions regarding their evolutionary origin.

The Southwest Pacific harbours relatively few species of *Peperomia*, represented mainly by the subgenera *Micropiper* and *Pseudocupula*, including *P. urvilleana*, *P. leptostachya*, and *P. tetraphylla*. Notably, *P. leptostachya* and *P. tetraphylla* also occur in tropical Asia, indicating floristic links between the two regions. The pantropical distribution of these subgenera, including their occurrence on remote oceanic islands, has been attributed to effective long-distance dispersal mechanisms (Frenzke et al., 2015).

**Map 1.** Distribution of *Peperomia heyneana* (red stars) and *P. urvilleana* (red circles).

A characteristic feature of many *Peperomia* species is the production of sticky fruits, which facilitate epizoochorous dispersal by adhering to birds or other animals. Such dispersal mechanisms are considered important in the colonization of remote islands and have been proposed as a major factor underlying the pantropical distribution of the genus (Frenzke et al., 2015). Earlier studies also documented remarkable cases of interoceanic long-distance dispersal in *Peperomia*, representing some of the longest dispersal events reported among angiosperms (Valdebenito et al., 1990, 1992). The unique fruit morphology of *P. heyneana*, characterized by a smooth basal region and a sticky papillate apex, may represent an adaptation for epizoochorous dispersal and is consistent with the dispersal mechanisms proposed for the genus. Nevertheless, additional phylogenomic and biogeographic studies are required to clarify the evolutionary history and dispersal pathways of *P. heyneana*.

## Declarations

## CONFLICT OF INTEREST

All authors declare that they have no conflicts of interest.

## Author Contribution

A. Thomas and Dr. J. Jameson designed the study and Arjun Thomas performed the Field collections, and laboratory work, edited and aligned the sequences. The first and second authors performed all the analyses and prepared a draft manuscript. A. Thomas prepared figures. All authors A. Thomas Dr. J. Jameson worked on the first draft and provided valuable comments to improve the manuscript.

## Acknowledgement

The authors are thankful to St. Albert's College (Autonomous), Kerala, India for providing research facilities. We would like to express our sincere gratitude to Dr Marie-Stéphanie Samain, Senior Researcher (Instituto de Ecología, A.C.) Michoacán, Mexico for comments, information and discussion on affirming the novelty of the specimen. The authors would like to thank Dr. Siju M.Varghese (Assistant Professor & HoD Botany, St. Albert's College (Autonomous) for valuable pieces of advice during molecular studies and Dr Stephen Sequeira (Assistant Professor, Maharaja's College, Ernakulam) for his comments on during the preparation of this manuscript. We extend our most sincere thanks to the Divisional forest officer and range officer (Munnar Wildlife Division / Eravikulam National Park) for permitting the park for research. We would also like to thank the Directors and staff of Herbaria. SAC, CAL, MH.

## Data Availability

The sequence data were deposited in the GenBank database under accession number OP179289 and are available at the following URL: <https://www.ncbi.nlm.nih.gov/nuccore/OP179289>.

## References

1. Beentje H (2010) The Kew Plant Glossary: an illustrated dictionary of plant terms. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.
2. De Lange PJ, Sawyer JWD, Rolfe JR (2006) New Zealand indigenous vascular plant checklist. New Zealand Plant Conservation Network, Wellington.
3. Frenzke L, Scheiris E, Pino G, Symmank L, Goetghebeur P, Neinhuis C, Wanke S, Samain MS (2015) A revised infrageneric classification of the genus *Peperomia* (Piperaceae). *Taxon* 64:424–444.
4. Gamble JS (1921) Piperaceae. In: The Flora of Presidency of Madras, Vol. 2. Adlard and Son Ltd., London, 1202 pp.
5. Gould KS, Dudle DA, Neufeld HS (2010) Why some stems are red: cauline anthocyanins shield photosystem II against high light stress. *Journal of Experimental Botany* 61:2707–2717.
6. Guimarães EF, Ichaso CLF, Costa CG (1984) Piperáceas. 4. *Peperomia*. In: Reitz R (ed.), *Flora Ilustrada Catarinense*. CNPq, IBDF, HBR, Itajaí, pp. 33–136.
7. Hooker JD (1890) Piperaceae. In: Hooker JD (ed.), *Flora of British India*, Vol. 5. L. Reeve & Co., London, 96 pp.
8. Howell CJ, Sawyer JWD (2006) New Zealand naturalised vascular plant checklist. New Zealand Plant Conservation Network, Wellington.
9. IUCN Standards and Petitions Committee (2019) Guidelines for using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee.
10. Johnson HB (1975) Plant pubescence: an ecological perspective. *The Botanical Review* 41:233–258.
11. Kumar MSM (1998) Studies on the epiphytic flora in the tropical forest ecosystem of Western Ghats with special reference to Nilgiri Biosphere Reserve. KFR I Research 139. Kerala Forest Research Institute, Peechi, Kerala, India.
12. Mai P, Rossado A, Bonifacino JM, Waechter JL (2016) Taxonomic revision of *Peperomia* (Piperaceae) from Uruguay. *Phytotaxa* 244:125–144.
13. Mathew J, Radhamany PM, Picham MS, Kadakasseril VG (2018) Two new species of *Peperomia* Ruiz & Pav. (Piperaceae) from South Western Ghats, India. *Species* 19:162–166.
14. Mathieu G (2020) Taxonomic repertory of the genus *Peperomia*. Available at: <http://www.peperomia.net/repertory.asp> (accessed 17 April 2022).
15. Radh SS, Nampy S (2018) *Peperomia ekakesara*: a new species of Piperaceae from Mathikettan Shola National Park, Kerala, India. *Phytotaxa* 364:283–288.
16. Rai P, Mathieu G (2023) *Peperomia mangalbaria* (Piperaceae), a new species from Sikkim Himalaya, India. *Phytotaxa* 609:138–144.

17. Ray R, Chattopadhyay B, Garg KM, Ramachandra TV, Ray A (2020) Western Ghats Myrtaceae are not Gondwana elements but likely dispersed from south-east Asia. *bioRxiv*, 2020–04.
18. Sasidharan N (2013) Flowering plants of Kerala: CD-ROM, version 2.0. Kerala Forest Research Institute, Peechi, Kerala, India.
19. Scotese CR (2001) Atlas of Earth History, Volume 1: Paleogeography. PALEOMAP Project, Arlington, Texas, USA, 52 pp.
20. Suwanphakdee C, Hodkinson TR, Chantaranothai P (2014) New records of *Peperomia* (Piperaceae) in Thailand. *Thai Forest Bulletin (Botany)* 42:61–67.
21. Suwanphakdee C, Hodkinson TR, Chantaranothai P (2017) New species and a reinstatement in *Peperomia* (Piperaceae) from Thailand. *Kew Bulletin* 72:1–15.
22. Tamura K, Stecher G, Kumar S (2021) MEGA11: molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution* 38:3022–3027.
23. Tebbs MC (1993) Piperaceae. In: Kubitzki K, Rohwer JG, Bittrich V (eds), *Flowering Plants · Dicotyledons: The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin, Heidelberg, pp. 516–520.
24. Thiers B (2015) Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available at: <http://www.sweetgum.nybg.org> (accessed 9 March 2023).
25. Thomas A, Jameson J (2022) *Peperomia albertiae* (Piperaceae), a new species from India. *Kew Bulletin* 77:341–346. <https://doi.org/10.1007/s12225-022-10006-7>
26. Wattoo JI, Saleem MZ, Shahzad MS, Arif A, Hameed A, Saleem MA (2016) DNA barcoding: amplification and sequence analysis of *rbcL* and *matK* genome regions in three divergent plant species. *Advancements in Life Sciences* 4:03–07.
27. Wight R (1840) Piperaceae. In: *Icones Plantarum Indiae Orientalis*, Vol. 6. JB Pharoah, Madras, pp. 1–5, pls 1–24.
28. Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organisms Diversity & Evolution* 5:237–247.
29. Yongqian C, Nianhe X, Gilbert MG (1999) Piperaceae. In: Wu ZY, Raven PH (eds), *Flora of China*, Vol. 4. Science Press, Beijing & Missouri Botanical Garden Press, St Louis, Missouri, USA, pp. 110–141.

## Map

Map 1 is available in the Supplementary Files section.

## Figures

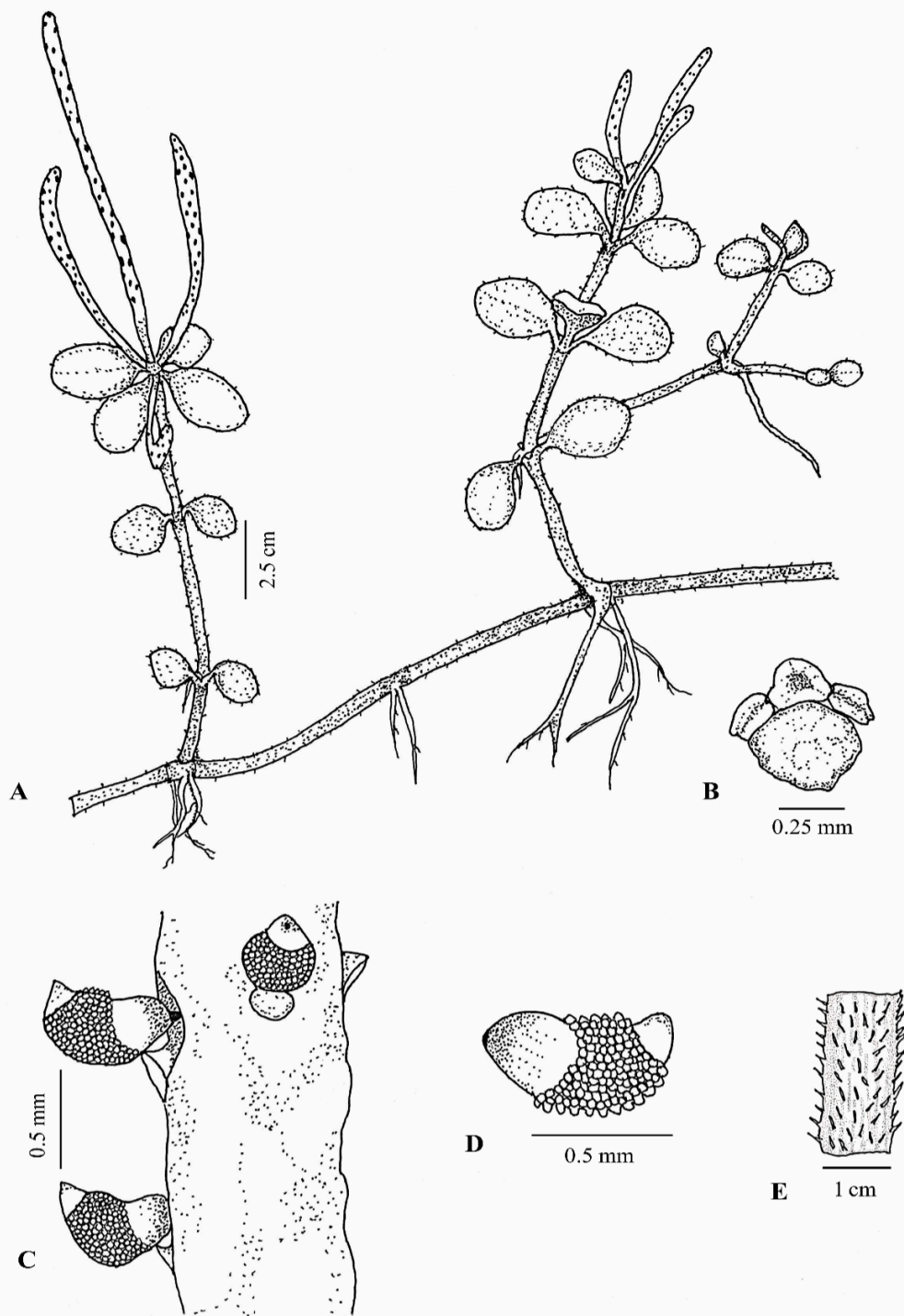


**Figure 1**

*Peperomia heyneana* : A. Habit; B. Flower; C. A portion of Infructescences; D. Fruit; E. Puberulous stem.  
DRAWN BY A. THOMAS.

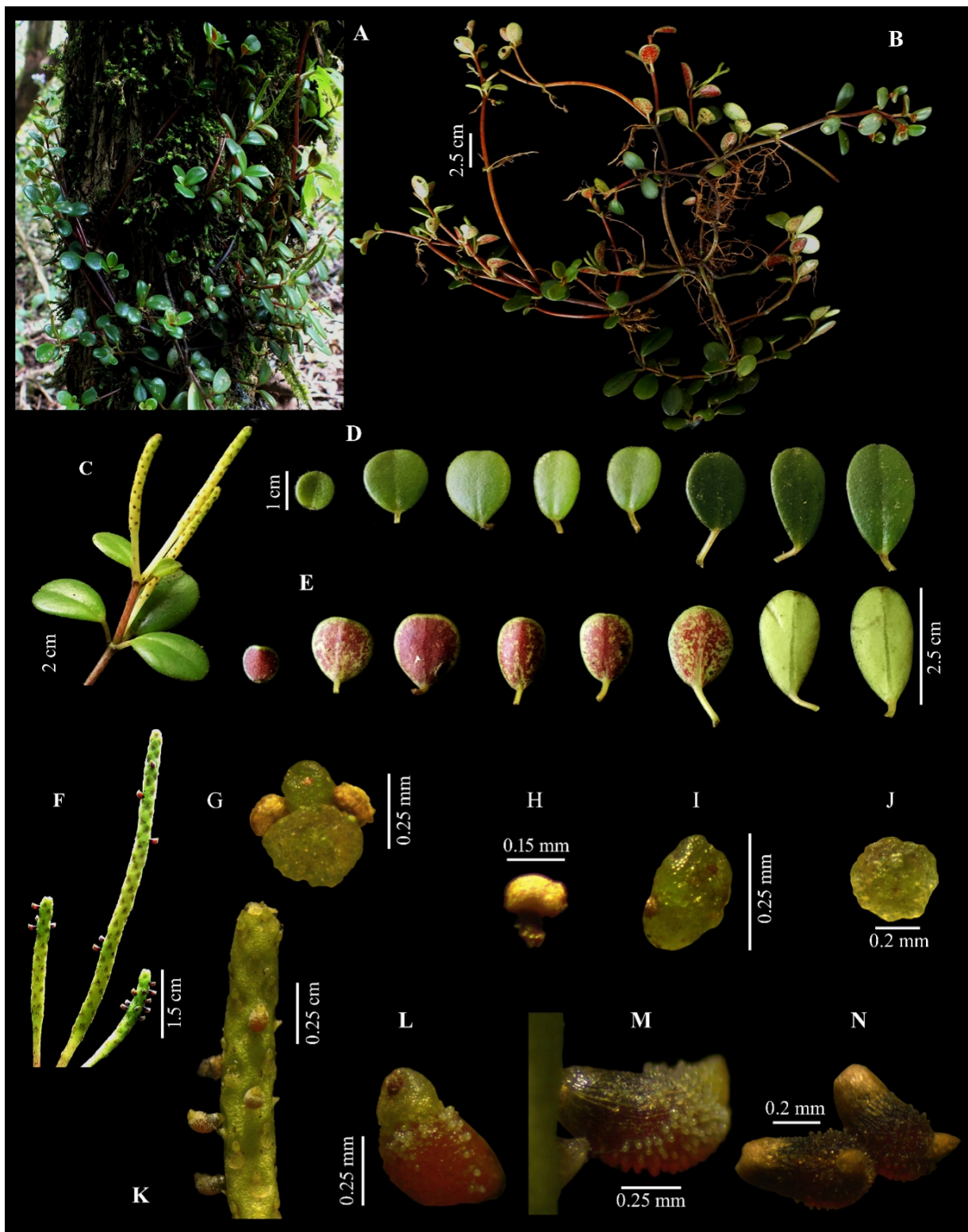


**Figure 2**

*Peperomia heyneana* : A, B. Plant habit; C. Branch with inflorescence; D. Leaves adaxial surface; E. Leaves abaxial surface; F. Infructescences; G. Flower;

H. Stamen; I. Gynoecium; J. Bract; K. Fruits: see rachis showing fruits and pits of fallen fruits; L. Young fruit; M. Mature fruit attached to rachis; N. Detached mature fruits. PHOTOS: A.THOMAS.

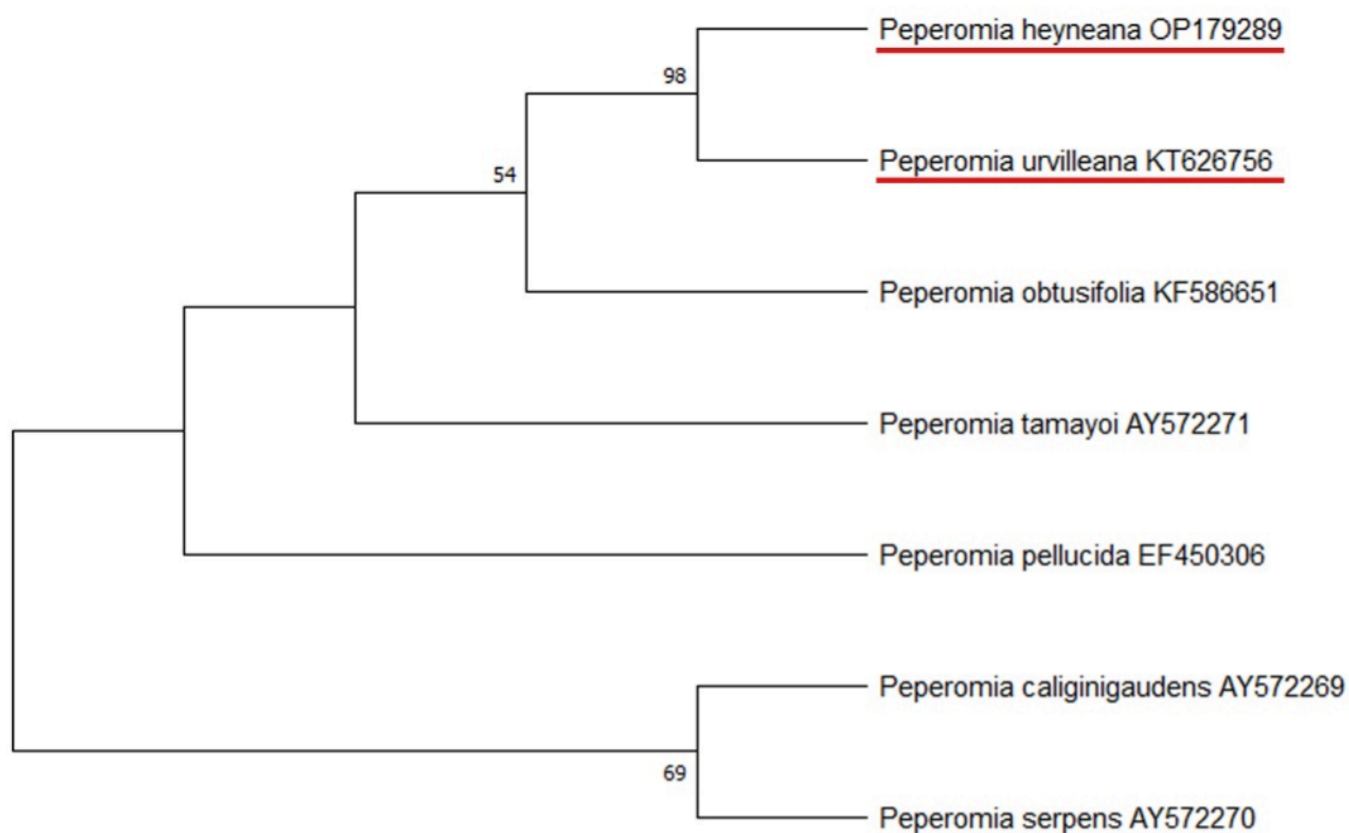


**Figure 3**

Phylogram generated from MEGA11 of *rbcl* sequence data. Bootstrap support values greater than 50% are given above the branches. Taxon with GenBank accession number for *rbcl* gene.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [floatimage4.jpeg](#)