



Taxonomy of *Peperomia* (Piperaceae) in Taiwan

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ABSTRACT: The taxonomy of *Peperomia* (Piperaceae) in Taiwan is reconsidered. In the present study, six taxa are recognized, based on detailed morphological observations and ITS sequences derived from fresh material obtained from living plants. Details of the characters are discussed, including the morphology of the leaf epidermis and pollen grains. Synonyms are treated. Descriptions of the species, phenology and a key to *Peperomia* in Taiwan is also provided.

KEY WORDS: *Peperomia*, Piperaceae, Taxonomy, Morphology, Molecular phylogeny, Palynology, Phenology, Taiwan.

INTRODUCTION

Piperaceae include 5 genera and approximately 3,600 species (Horner *et al.*, 2015), with most of the species in the genera *Piper* and *Peperomia* (Smith *et al.*, 2008). The widely pantropical *Peperomia*, one of the largest and most diverse genera of basal angiosperms, includes 1,487 accepted species as to July 2020 (Mathieu 2001–2020), but more than 3,000 names have been proposed. Because of these large numbers and the highly reduced reproductive organs of *Peperomia*, the genus has been quite difficult to study (Wanke *et al.*, 2006). *Peperomia* was published by Ruiz and Pavón in 1794. They described all species as erect or decumbent succulent herbs with entire leaves and terminal or axillary spadices. Kunth (1815) reported the spadices to be cylindrical, stamens 2 and stigma undivided. Since those characters are not sufficient to clearly distinguish *Peperomia* from other taxa, other taxonomists have tried to find more distinguishing characteristics.

The earliest record of *Peperomia* in Taiwan was of *Peperomia dindygulensis* Miq. in *A List of Plants from Formosa* (Henry, 1896). Matsumura and Hayata (1906), Hayata (1908, 1917), C. de Candolle (1920), Yamamoto (1926), Sasaki (1928), Masamune (1936, 1954), F.-L. Wang (1973), Liu and Wang (1976), Kuo (1978), Chen and Zhu (1982), Lin and Lu (1995, 1996), Tseng *et al.* (1999) also recorded and published species of *Peperomia* in Taiwan (Table 1). Past studies have used many characteristics to distinguish the species. The flowers of *Peperomia* are highly reduced, without perianth (Alejandra Jaramillo *et al.*, 2004) and 2 stamens in each flower (Tucker, 1980). The fruit has been used as a basis for infrageneric classification (Dahlstedt, 1900). The few species that have been studied reported the pollen grains of *Peperomia* to be inaperturate and verrucate (Lei and Liang, 1998; Samain *et al.*, 2010).

A revised subgeneric classification of *Peperomia* was presented by Frenzke *et al.*, (2015), who used

molecular phylogeny combined with morphological characteristics. Parallel evolution in *Peperomia* makes the species difficult to separate by using traditional or single characters, hence it is necessary to find new characteristics. (Wanke *et al.*, 2006; Horner *et al.*, 2009; Samain *et al.*, 2009).

Five species and one uncertain species have been recognized in *Flora of Taiwan* (FOT), 2nd ed. (Lin and Lu, 1996). Tseng *et al.* (1999) treated several species from Taiwan, including *P. formosana*, *P. japonica*, *P. laticaulis* and *P. sui* as synonyms of *P. blanda* in their treatment of the genus in the *Flora of China* (FOC). They considered the taxa to be difficult to separate, but they examined only dried specimens of the Taiwanese species without seeing living plants (Michael Gilbert, personal communication). Since *Peperomia* is succulent, there are many differences between living plants and dried specimens. Some characteristics of living plants easily disappear in dried materials. Moreover, *P. blanda* is an exclusively South America species. The correct name to be used for this widely distributed paleotropical species that occurs in Taiwan, is *P. leptostachya* (Mathieu, 2020). Therefore, we believe there are still taxonomic problems between similar species of *Peperomia* and further work is necessary to resolve them.

In this report, we recognize 6 taxa of *Peperomia* in Taiwan. Conclusions are based on morphological features and a phylogeny derived from ITS sequences obtained from living plants (fresh material). Descriptions, with detailed information on the morphology of each organ, the leaf epidermis and pollen grains, are provided. Phenology is discussed and a key to the species of *Peperomia* in Taiwan is presented.

MATERIALS AND METHODS

Morphology

Living plants of all species discussed in this study were examined except *Peperomia formosana* and *P. laticaulis*.



Table 1. Nomenclatural history of *Peperomia* in Taiwan.

Literature	A list of plants from Formosana	Enumeratio Plantarum Formosanarum	Flora Montana Formosae	Supplement to Icons Plantarum Formosanarum VI	Annuaire du Conservatoire et Jardin Botaniques de Genève
Year	1896	1906	1908	1917	1920
Authors	A. Henry	J. Matsumura & B. Hayata	B. Hayata	B. Hayata	C. de Candolle
<i>P. dindygulensis</i> Miq. 1843	<i>P. dindygulensis</i> →	<i>P. dindygulensis</i> →	<i>P. dindygulensis</i> →	<i>P. dindygulensis</i> →	
<i>P. japonica</i> Makino 1901					
<i>P. laticaulis</i> C. DC. 1920					* <i>P. laticaulis</i> →
<i>P. blanda</i> (Jacq.) Kunth 1816					
<i>P. sui</i> T. T. Lin & S. Y. Lu 1995					
<i>P. formosana</i> C. DC. 1920					* <i>P. formosana</i> →
<i>P. rubrivenosa</i> C. DC. 1901					
<i>P. kotoensis</i> Yamamoto 1926					
<i>P. nakaharai</i> Hayata 1908				* <i>P. nakaharai</i> →	<i>P. nakaharai</i> →
<i>P. reflexa</i> (L. f.) A. Dietr. 1831		<i>P. reflexa</i> →	<i>P. reflexa</i> →	<i>P. reflexa</i> →	
<i>P. tetraphylla</i> (G. Forst.) Hook. & Arn. 1832					
<i>P. pellucida</i> (L.) Kunth 1816					

Supplementa Iconum Plantarum Formosanarum Vol. 2	List of Plants of Formosa	Short Flora of Formosa	A list of vascular Plants of Taiwan	Revision of Piperales in Taiwan	Flora of Taiwan, 1 st ed. Vol. 2	Quarterly journal of Chinese forestry, 11(3)
1926	1928	1936	1954	1973	1976	1978
Y. Yamamoto	S. Sasaki	G. Masamune	G. Masamune	F. L. Wang	T. S. Liu & F. L. Wang	C. M. Kuo
	→ <i>P. dindygulensis</i> →	→ <i>P. dindygulensis</i> →	→ <i>P. dindygulensis</i> →	→ <i>P. dindygulensis</i> →	→ <i>P. japonica</i> →	
	→ <i>P. formosana</i> →	→ <i>P. formosana</i> →	→ <i>P. formosana</i> →	→ <i>P. formosana</i> →	→ <i>P. formosana</i> →	
				→ <i>P. rubrivenosa</i> →	→ <i>P. rubrivenosa</i> →	
* <i>P. kotoensis</i> →	→ <i>P. kotoensis</i> →	→ <i>P. kotoensis</i> →	→ <i>P. kotoensis</i> →			
	→ <i>P. nakaharai</i> →	→ <i>P. nakaharai</i> →	→ <i>P. nakaharai</i> →	→ <i>P. nakaharai</i> →	→ <i>P. nakaharai</i> →	
	→ <i>P. reflexa</i> →	→ <i>P. reflexa</i> →	→ <i>P. reflexa</i> →	→ <i>P. reflexa</i> →	→ <i>P. reflexa</i> →	
						<i>P. pellucida</i> →

Flora Reipublicae Popularis Sinicae, Vol.20(1)	Taiwania, 40(4)	Flora of Taiwan, 2 nd ed. Vol. 2	Flora of China, Vol. 4	Taxonomic Studies of Piperaceae in Taiwan
1982	1995	1996	1999	2011
P. S. Chen & P. Z. Zhu	T. T. Lin & S. Y. Lu	T. T. Lin & S. Y. Lu	Y. C. Tseng, N. H. Xia & M. G. Gilbert	K. N. Kung
<i>P. dindygulensis</i> →				
	→ <i>P. japonica</i> →			
<i>P. laticaulis</i> →				
	* <i>P. sui</i> →	→ <i>P. sui</i> →		
<i>P. formosana</i> →		→ <i>P. formosana</i> →		
<i>P. rubrivenosa</i> →		→ <i>P. rubrivenosa</i> →	→ <i>P. rubrivenosa</i> →	→ <i>P. rubrivenosa</i> →
				→ <i>P. japonica</i> var. <i>japonica</i> →
				→ <i>P. sui</i> →
				→ <i>P. japonica</i> var. <i>formosana</i> →
				→ <i>P. rubrivenosa</i> →
<i>P. nakaharai</i> →	→ <i>P. nakaharai</i> →	→ <i>P. nakaharai</i> →	→ <i>P. nakaharai</i> →	→ <i>P. nakaharai</i> →
	→ <i>P. reflexa</i> →			
<i>P. tetraphylla</i> →		→ <i>P. tetraphylla</i> →	→ <i>P. tetraphylla</i> →	→ <i>P. tetraphylla</i> →
				→ <i>P. pellucida</i> →

**Table 2.** DNA sequences (ITS) of *Peperomia* in this study

Taxon	Geographic origin of the sequenced material	Voucher no.	GenBank no.	Remark
<i>Peperomia bicolor</i>	Berlin Botanical Garden	Wanke 052	FJ424465	
<i>P. blanda</i>	Berlin Botanical Garden	Wanke 055	FJ424455	
<i>P. pellucida</i>	Gent Botanical Garden	S. & V. 2005-009	FJ424437	
<i>P. pellucida</i>	–	–	EF450291	
<i>P. rhombea</i>	Berlin Botanical Garden	Wanke 053	FJ424429	
<i>P. rhomboidea</i>	–	–	DQ868700	
<i>P. tetraphylla</i>	–	–	AF203631	
<i>P. tetraphylla</i>	Gent Botanical Garden, Bocono-Mosquey, Venezuela	S. & V. 2005-006	FJ424428	
<i>P. urvilleana</i>	Lord Howe Island	–	JF950798	
<i>Peperomia</i> sp.	Solomon Island	SITW3557	MW114862	(TNM)
<i>Peperomia</i> sp.	St. Vincent	Y.C.Lu 146	MW114872	(TNM)
<i>P. boninsimensis</i>	Makino Botanical Garden, Japan	Y.C.Lu 148	MW114861	Imported from Makino Botanical Garden, Japan (TNM)
<i>P. japonica</i>	Pingtung, Taiwan	Y.C.Lu 104	MW114868	Plant green; puberulous uniform on adaxial surface (TNM)
<i>P. japonica</i>	Nantou, Taiwan	P.H.Lin 104	MW114863	Plant green; puberulous around veins and edge on adaxial surface (TNM)
<i>P. japonica</i>	Hualien, Taiwan	Y.C.Lu 145	MW114865	Plant green; puberulous uniform on adaxial surface (TNM)
<i>P. japonica</i>	Nantou, Taiwan	Y.C.Lu 151	MW114866	Sometimes reddish at petiole and midrib (abaxial surface); puberulous around veins and edge on adaxial surface (TNM)
<i>P. japonica</i>	Makino Botanical Garden, Japan	Y.C.Lu 106	MW114864	Imported from Makino Botanical Garden, Japan (TNM)
<i>P. japonica</i>	Fujian, China	S.T.Geng 161	MW114867	Collected in Fujian, China (TAI).
<i>P. leptostachya</i>	Yunnan, China	T.Y.A. Yang 23898	MW114859	(TNM)
<i>P. leptostachya</i>	Taichung, Taiwan	Y.C.Lu 58	MW114860	(TNM)
<i>P. nakaharae</i>	Taichung, Taiwan	Y.C.Lu 109	MW114869	(TNM)
<i>P. pellucida</i>	Taichung, Taiwan	Y.C.Lu 147	MW114873	(TNM)
<i>P. rubrivenosa</i>	Lanyu, Taiwan	Y.C.Lu 94	MW114870	(TNM)
<i>P. tetraphylla</i>	Taichung, Taiwan	Y.C.Lu 108	MW114871	(TNM)
<i>Piper betle</i>	Taichung, Taiwan	Y.C.Lu 152	MW114858	(TNM)

Source materials were collected in the field, imported from the Makino Botanical Garden (Japan) or cultivated in the greenhouse of the National Museum of Natural Science (NMNS), Taichung, Taiwan. Voucher specimens have been deposited in the herbarium TNM.

Epidermal micromorphology was directly observed and photographed using a Hitachi TM3000 tabletop scanning electron microscope (SEM) without extra processing.

Pollen grains were treated in two ways to study their surface. Samples for light microscopy (LM) were prepared in acetic acid with an added drop of safranin, subsequently and gradually transferred to 50% ethanol (ethanol series: 95, 80, 70, 60, 50%) and then to 50% glycerin. They were then placed in an oven (40°C) to evaporate the ethanol. After 1 hour, the pollen was placed in glycerin on a microscope slide, covered with a glass cover slip, then sealed and examined under a Zeiss Axioplan (LM) microscope. We also used a FEI Inspect S scanning electron microscope (SEM) to observe and photograph the pollen without any treatment.

We used herbarium specimens from B, K, P, PPI, LINN, MAK, TAI, TAIF, TI and TNM to compare the morphological characteristics and to record phenological phase information.

Molecular phylogeny

The species selected for sampling were based on previous studies of *Peperomia* (Lin and Lu, 1996; Tseng *et al.*, 1999). Specimens were mainly from areas near Taiwan (China, Japan). The morphology of nearly all sampled specimens was studied in detail. Nine sequences were downloaded from GenBank. Voucher specimens of the sequences downloaded from GenBank were not examined; we accept the identity of the specimens as given in the database. Among the Taiwanese species, *Peperomia japonica* is the most variable, hence, we collected material from populations with varied habit. A list of the samples is provided in tables 2.

DNA isolation, amplification and alignment

DNA sequences were obtained from the nrITS gene. Amplifications were carried out with a pair of newly designed primers from Samain *et al.* (2009) as follows: ITS-F (5'-AATGGTCCGGTGAAGTGTTCCGG-3') and ITS-90R (5'-GCTTCTACAGACTACAATTTCG-3'). Initial denaturation at 94°C for 5 min, followed by 35 cycles at 94°C for 30 s, annealing at 52°C for 30 s, elongation at 72°C for 45 s, and final extension at 72°C for 5 min, then keep at 4°C. The Polymerase Chain Reaction (PCR) master mix contains 5 µl 10X Taq buffer, 1.5 µl dNTPs

**Table 3.** Morphological characteristics of *Peperomia* in Taiwan.

species	<i>P. japonica</i>	<i>P. leptostachya</i>	<i>P. nakaharae</i>	<i>P. pellucida</i>	<i>P. rubrivenosa</i>	<i>P. tetraphylla</i>	
Phyllotaxis	3-9-verticillate	opposite, 3- or 4-verticillate distally	opposite or 3-5-verticillate	opposite, verticillate or alternate	opposite or 3-verticillate	4-verticillate, rarely 3	
Leaf shape	rhomboid to obovate, elliptic to oblong, apex obtuse to rounded	rhomboid to obovate, nearly orbicular, apex acute to obtuse	obovate, apex emarginate	cordate to reniform, orbicular	obovate to orbicular, or elliptic	obovate to orbicular, elliptic	
Adaxial surface	puberulous uniform or around veins and edge	puberulous uniform	glabrous on both surfaces, only minutely pubescent at apex	glabrous	sparsely pilose	nearly glabrous	
Abaxial surface	puberulous uniform	puberulous uniform		glabrous	sparsely pilose	glabrous	
Petiole	puberulous	puberulous	glabrous	glabrous	sparsely pilose	puberulous	
micromorphology							
Adaxial surface	polygonal with anticlinal walls straight to arched	papillose	polygonal with anticlinal walls straight to arched	polygonal with anticlinal walls straight to arched	polygonal with anticlinal walls straight to arched	polygonal with anticlinal walls straight to arched, granular and linear ridges	
Abaxial surface	irregular with anticlinal walls straight to arched	polygonal with anticlinal walls straight to arched		irregular with anticlinal walls sinuous			
Stomatal complexes	anisocytic	anisocytic	anisocytic	anisocytic	anisocytic	anisocytic	
reproductive organs							
Spike	tufted; terminal or axillary	tufted; terminal or axillary	solitary; terminal	solitary or tufted; terminal or axillary	tufted; terminal or axillary	solitary; terminal	
Rachis	glabrous	glabrous	glabrous	glabrous	glabrous	puberulous	
Ovary	obovoid	obovoid	obovoid	ovoid	obovoid	ovoid	
Bract	green	reddish on upper edge	reddish on upper edge	green	green	green	
Bract stalk	pyramidal	pyramidal	pyramidal	nearly sessile	pyramidal	cylindrical	
pollen grains							
		Chinese material	Taiwanese material				
Size (µm)	10–13	13–15	11–15	10–12	15	10–13	12–15
Verrucae surface	granulose	granulose	granulose	granulose	without granules	granulose	granulose
Verrucae margin	sharp corner	smooth	sharp corner	smooth	smooth	sharp corner	smooth

(2 mM each), 1 µl ITS-F primer (10 µM each), 1 µl ITS-90R primer (10 µM each), 0.2 µl Taq DNA polymerase (5U/µl), 40.3 µl ddH₂O and 1 µl DNA template.

Double stranded sequences were edited and aligned using Geneious 8.1.5 (Kearse *et al.*, 2012) and ClustalW (Thompson *et al.*, 1994), after examining complimentary strands. Phylogenetic analyses were conducted using Maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) analysis. Maximum parsimony analysis was performed with MEGA 6.0.6 (Tamura *et al.*, 2013). Evaluation of the MP tree was performed using the Bootstrap approach (1000 replicates).

A maximum likelihood analysis was conducted using Phyml 3.0 (Guindon *et al.*, 2010) applying the GTR model and sampling 1000 rapid bootstrap replicates. The best-fitting model was tested using jModelTest v. 2.1.7 (Darriba *et al.*, 2012). Bayesian inference was performed using MrBayes 3.2.5 (Ronquist *et al.*, 2012), running for 1 million generations. The first 25% trees were discarded as burn-in.

RESULTS

Scientific names used hereafter, follow current internationally accepted names. They are *Peperomia japonica*, *P. leptostachya*, *P. nakaharae*, *P. pellucida*, *P. rubrivenosa* and *P. tetraphylla*.

Morphology

The species of *Peperomia* in Taiwan are erect, tufted or procumbent at the base. Some species produce new shoots from the base each year. Stems are terete or angular-sulcate, green or red and pubescent or glabrous. The leaves are opposite, whorled or rarely alternate, petiolate, entire or with an emarginate apex. The blade is rhombic, obovate, oblong-obovate, orbicular, elliptic, cordate or reniform and pubescent or glabrous (Table 3). Inflorescences are spadices, (fleshy spikes), terminal or axillary, solitary or clustered with a glabrous or pubescent rachis. The flowers are densely arranged. Each flower bears 2 stamens and 1 pistil, both subtended



by a peltate bract. The upper edge of the bracts are green or red. The stalk of the bracts is inverted triangular pyramidal or cylindrical. Sepals and petals are lacking. Each stamen is composed of an anther and a filament. The anthers are ellipsoid of nearly globose, bisporangiate (Fig. 1) and dehisce by longitudinal slits at maturity. The pistil is obovoid or ovoid with a penicillate stigma (Table 3). The surface of the bract and anther in most of species usually has linear ridges as seen under SEM. Stomata also occur on the bracts and rachis. The green or brown fruits are ovoid to oblong-ovoid drupes with or without a papillose sticky pericarp. The fruit is pedicellate or sessile and may be embedded in the rachis.

Leaf epidermal micromorphology

The micromorphology of the leaf epidermal cells in *Peperomia* may differ between species and between the adaxial and abaxial surface in the same species. The adaxial epidermis can be classified into three types: papillose in *P. leptostachya* (Fig. 2A, B), polygonal with anticlinal walls straight to arched in *P. japonica*, *P. nakaharae*, *P. pellucida* and *P. rubrivenosa* (Fig. 2C, D, E, F) and polygonal with anticlinal walls straight to arched and with granular and linear ridges on the surface in *P. tetraphylla* (Fig. 2G). Four types of abaxial epidermis are distinguishable: polygonal with anticlinal walls straight to arched in *P. leptostachya* (Fig. 3A, B); irregular with anticlinal walls straight to arched in *P. japonica*, *P. nakaharae* and *P. rubrivenosa* (Fig. 3C, D, F); irregular with anticlinal walls sinuous in *P. pellucida* (Fig. 3E); polygonal with anticlinal walls straight to arched and with granular and linear ridges on the surface in *P. tetraphylla* (Fig. 3G). Both the adaxial and abaxial epidermis may have ball-like glands.

Stomatal complexes

All species of *Peperomia* examined in this study are hypostomatic with anisocytic stomatal complexes on the abaxial surface. Most species produce lip-shaped guard cells. *Peperomia tetraphylla* has circular depressions along the stoma (Fig. 4G). The guard cells of *P. pellucida* protrude upward (Fig. 4E).

Palynology

The pollen grains of *Peperomia* in this study were about 10–15 μm in diameter, approximately spherical, inaperturate. Irregularly shaped verrucae of uneven size were closely spaced on the exine surface (Table 3). The pollen of *P. leptostachya* (Chinese material) was 13–15 μm in diameter. The verrucae had a granulose surface and smooth margin (Fig. 5A-C). The pollen grains of *P. leptostachya* (Taiwanese material) were 11–15 μm in diameter and the verrucae had a granulose surface with sharp corner margins (Fig. 5D-F). The pollen of *P. japonica* was 10–13 μm in diameter, the verrucae had a granulose surface with sharp corner margins (Fig. 5G-I).

The pollen grains of *P. nakaharae* were 10–12 μm in diameter. The verrucae had a granulose surface and smooth margin (Fig. 5J-L). The pollen grains of *P. pellucida* were about 15 μm in diameter. The surface of the verrucae was without granules and had a smooth margin (Fig. 5M-O). The pollen grains of *P. rubrivenosa* were 10–13 μm in diameter. The verrucae had a granulose surface with sharp corner margins (Fig. 5P-R). The pollen grains of *P. tetraphylla* were 12–15 μm in diameter. The verrucae had a granulose surface and smooth margin (Fig. 5S-U).

Molecular phylogeny

Twenty-five sequences were amplified and aligned (Table 2). Each sequence comprised 670 base pairs of the nrITS. The phylogenetic tree was reconstructed from Bayesian inference analysis with support from maximum parsimony analysis and maximum likelihood analysis.

In all of our analyses, the species of *Peperomia* showed nearly clear monophyly (Fig. 6). Clade A was mainly formed by *P. tetraphylla* (BI/MLBS/MPBS = 1.0/97/100). Material of *P. leptostachya* from China and Taiwan was monophyletic with high support (BI/MLBS/MPBS = 1.0/100/100) in clade B. All populations of *P. japonica* were clearly resolved as a single species (BI/MLBS/MPBS = 1.0/99/99). *Peperomia pellucida* also had high independent support (BI/MLBS/MPBS = 1.0/100/100). The remaining species, including *P. nakaharae*, and *P. rubrivenosa*, appeared in several clades within our tree without high support. We are therefore unable to determine their location on the tree.

Phenology

The time of flowering, pollination and distribution affect gene exchange between individuals. Without gene exchange between individuals and populations, speciation may occur over time. Hence, understanding the reproductive period can help identify species. We combined the data from field observations, reference specimens records and follow up of living plants in the greenhouse to determine the reproductive period. Some species produce flowers two or three times each year, and *P. pellucida* flowers throughout the year. Although *P. japonica* and *P. leptostachya* are morphologically similar and are sympatric, their reproductive periods are staggered. Therefore, reproductive period can be used as an aid to distinguish species when examining dried specimens. The phenology of *P. leptostachya* in China is the same as it is for *P. leptostachya* in Taiwan and that of *P. japonica* in Japan is the same as is for *P. japonica* in Taiwan.

DISCUSSION

Several species of *Peperomia* look similar and are sometimes difficult to distinguish. Taiwanese species, identified as *P. formosana*, *P. laticaulis* and *P. sui*, were

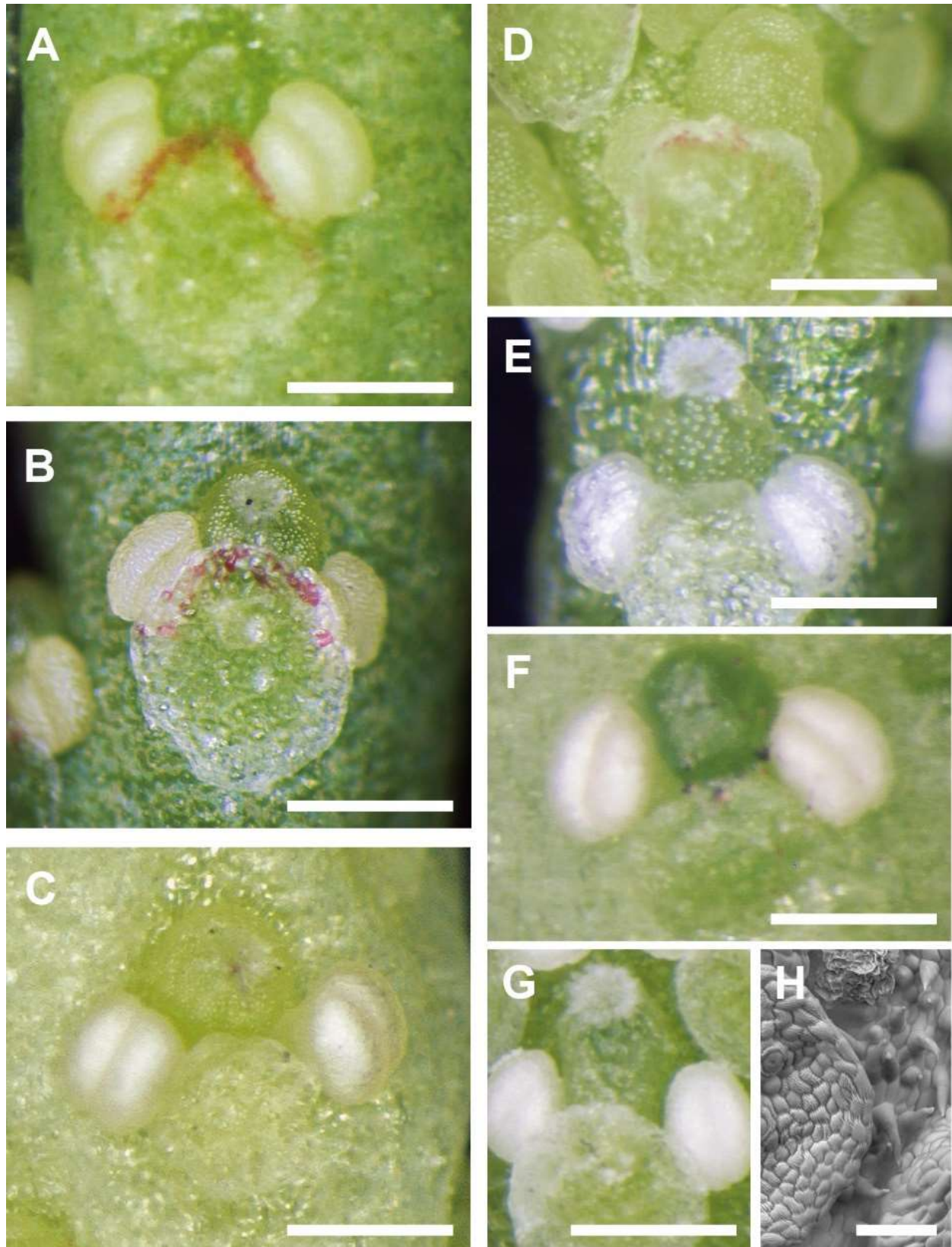


Fig. 1. Morphological characteristics of flowers of *Peperomia*. **A.** *P. leptostachya* (Chinese material); **B.** *P. leptostachya* (Taiwanese material); **C.** *P. japonica*; **D.** *P. nakaharai*; **E.** *P. pellucida*; **F.** *P. rubrivinosa*; **G.** *P. tetraphylla*; **H.** rachis of *P. tetraphylla*. Scale bars: A, B, C, D, E, F, G = 500 μ m; H = 90 μ m.

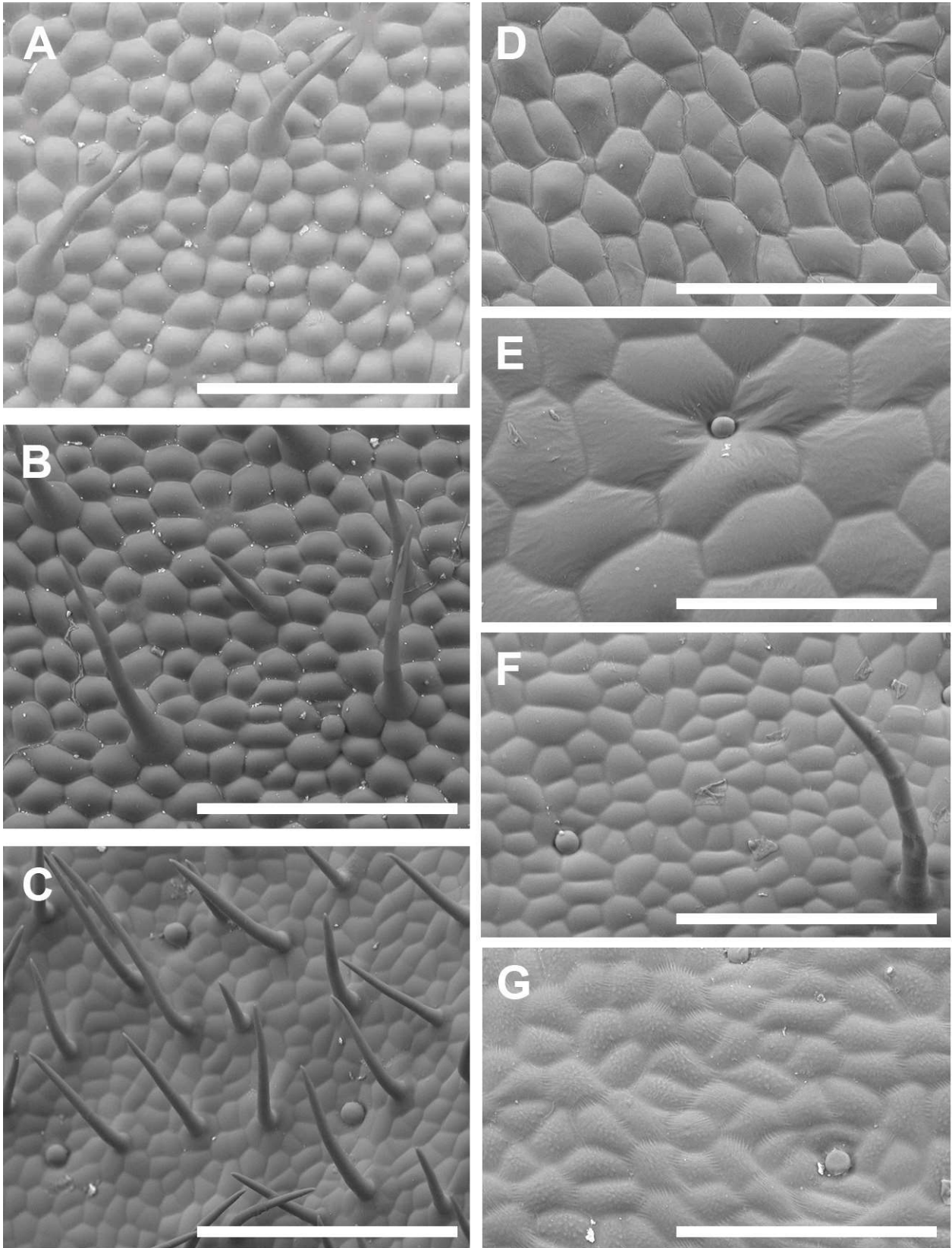


Fig. 2. Micromorphological characteristics of leaf adaxial surface of *Peperomia*. A. *P. leptostachya* (Chinese material); B. *P. leptostachya* (Taiwanese material); C. *P. japonica*; D. *P. nakaharai*; E. *P. pellucida*; F. *P. rubrivenosa*; G. *P. tetraphylla*. Scale bars = 300 μ m.

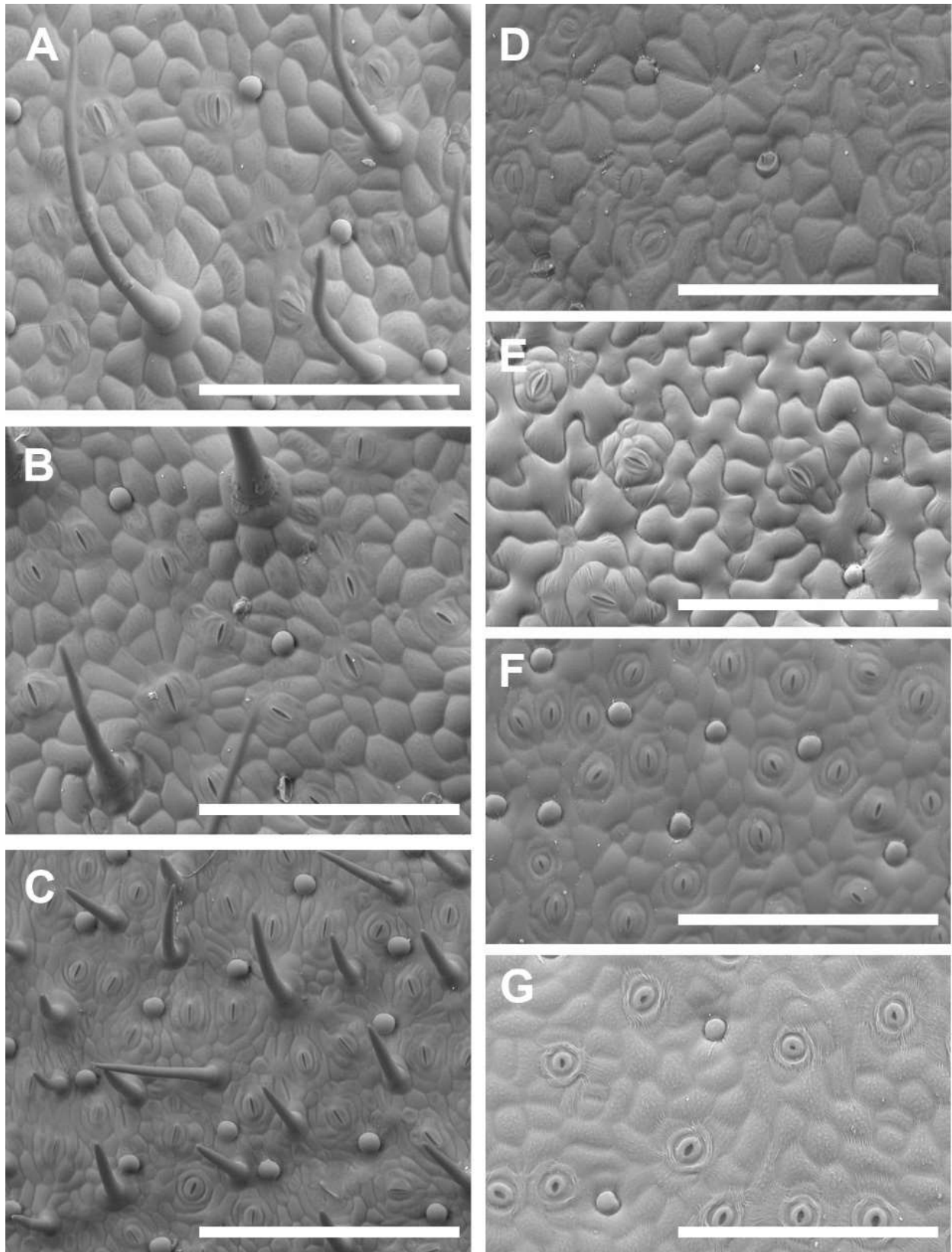


Fig. 3. Micromorphological characteristics of leaf abaxial surface of *Peperomia*. **A.** *P. leptostachya* (Chinese material); **B.** *P. leptostachya* (Taiwanese material); **C.** *P. japonica*; **D.** *P. nakaharai*; **E.** *P. pellucida*; **F.** *P. rubrivenosa*; **G.** *P. tetraphylla*. Scale bars = 300 μ m.

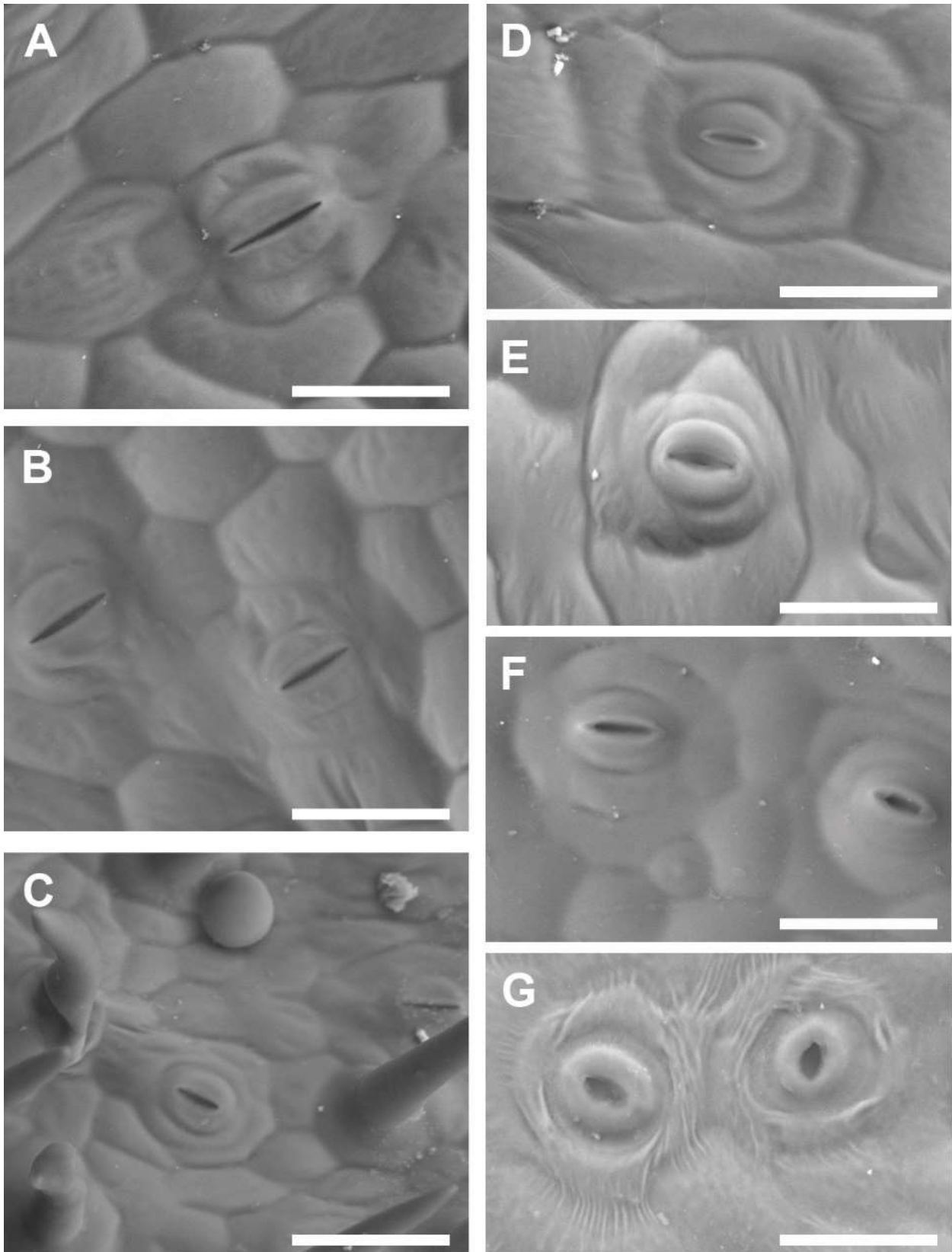


Fig. 4. Micromorphological characteristics of stomatal complexes of *Peperomia*. A. *P. leptostachya* (Chinese material); B. *P. leptostachya* (Taiwanese material); C. *P. japonica*; D. *P. nakaharai*; E. *P. pellucida*; F. *P. rubrivenosa*; G. *P. tetraphylla*. Scale bars = 50 μ m.

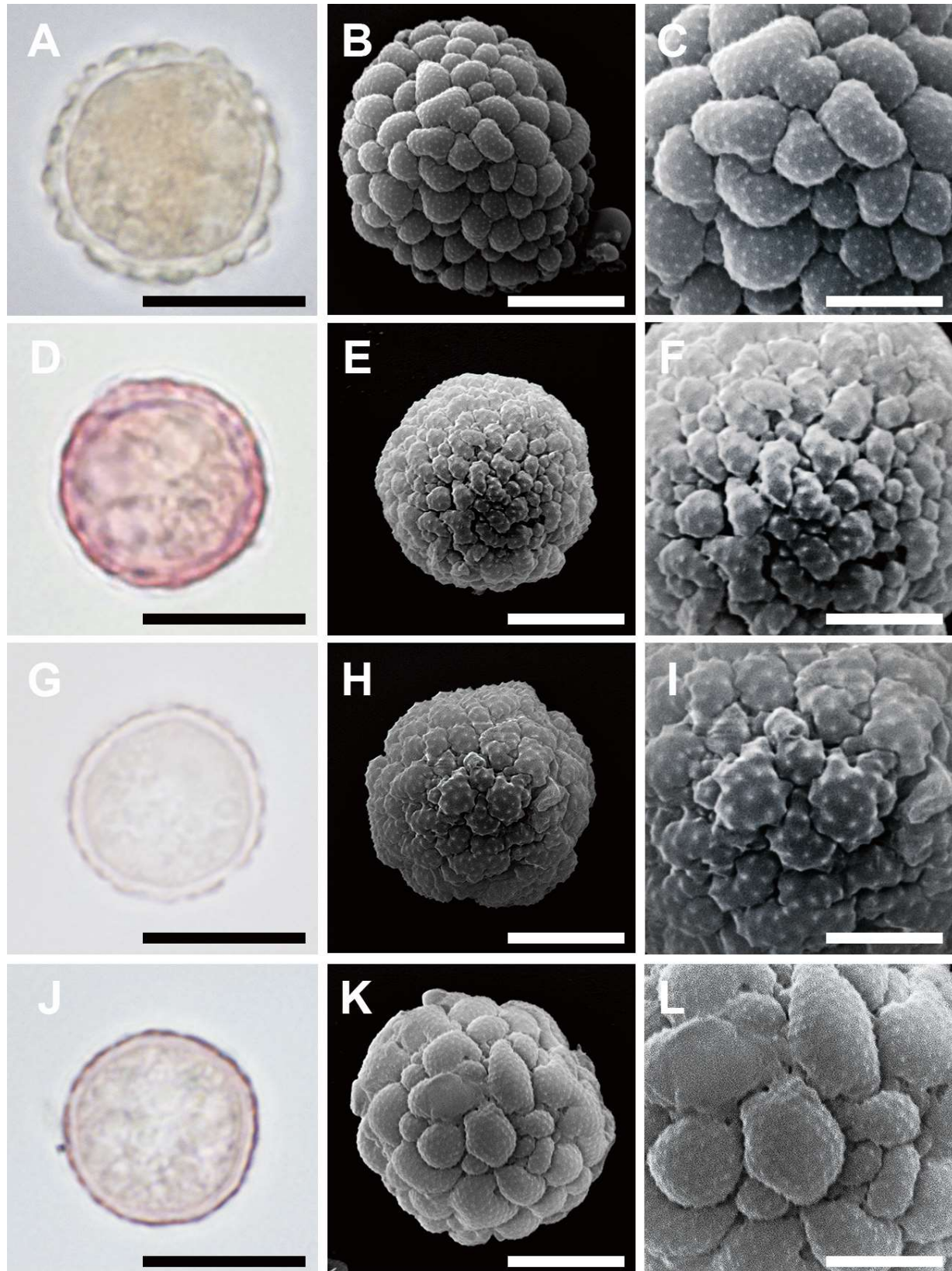


Fig. 5. Morphological characteristics of pollen grains of *Peperomia*. **A-C.** *P. leptostachya* (Chinese material); **D-F.** *P. leptostachya* (Taiwanese material); **G-I.** *P. japonica*; **J-L.** *P. nakaharai*. **A, D, G, J** (LM images); **B, C, E, F, H, I, K, L** (SEM images). Scale bars: **A, D, G, J** = 10 μm ; **B, E, H, K** = 4 μm ; **C, F, I, L** = 2 μm .

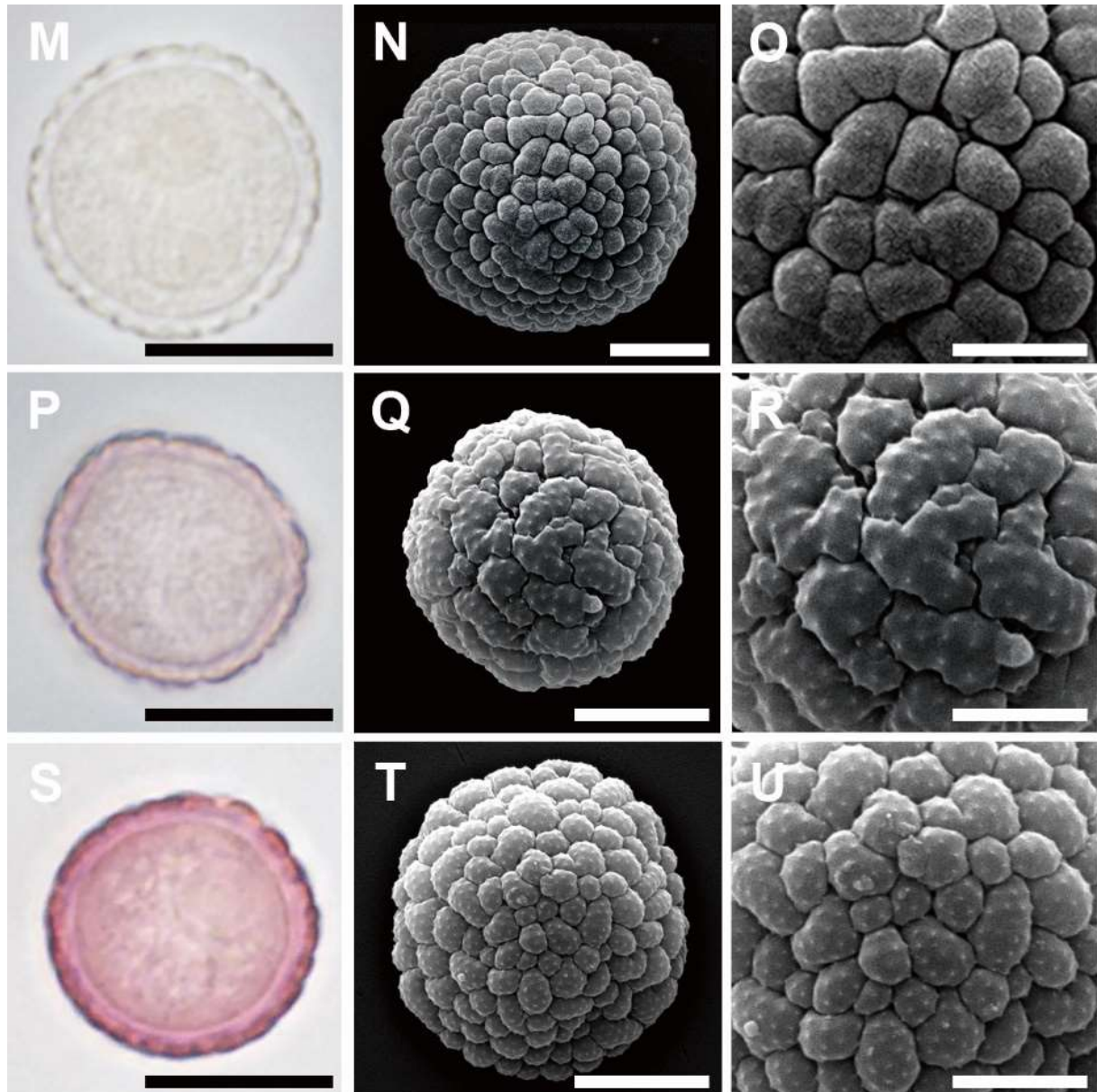


Fig. 5. Continued: M-O. *P. pellucida*; P-R. *P. rubrivenosa*; S-U. *P. tetraphylla*. M, P, S (LM images); N, O, Q, R, T, U (SEM images). Scale bars: M, P, S = 10 μ m; N, Q, T = 4 μ m; O, R, U = 2 μ m.

treated as synonyms of the *P. blanda* complex in FOC (Tseng *et al.*, 1999). However, researchers (Kung, 2011; Suwanphakdee *et al.*, 2017; Mathieu, 2020) showed that several characters do not match the original description and type of *P. blanda*. Moreover, Mathieu (2020) suggested that *P. leptostachya*, a widely distributed paleotropical species, is the correct name for this taxon.

In our phylogenetic tree, *Peperomia leptostachya* from China and *P. sui* show up on the same branch. After observation of living plants of *P. sui* and comparison of its type and protologue, we consider *P. sui* to be the same as *P. leptostachya* and treat it as its synonym.

Peperomia japonica is on a separate branch in the phylogenetic tree. *Peperomia japonica* exhibits

considerable morphological variation, but we found that it can be distinguished from *P. leptostachya* by the number and position of the leaves, by micromorphological leaf epidermal features, by the size of the bracts and by phenology, also by the leaf pubescence and the leaf apex. Thus, considerable evidence shows *P. japonica* to be different from *P. leptostachya*.

Peperomia formosana and *P. laticaulis* were published by C. de Candolle in 1920. Since then, there have been few additional collections. Lin and Lu (1996) considered *P. formosana* to be close to *P. japonica*, but differing in its glabrous peduncle. They treated it as an uncertain species. In the original description, the stems of *P. laticaulis* were described as stout. Suwanphakdee *et al.*

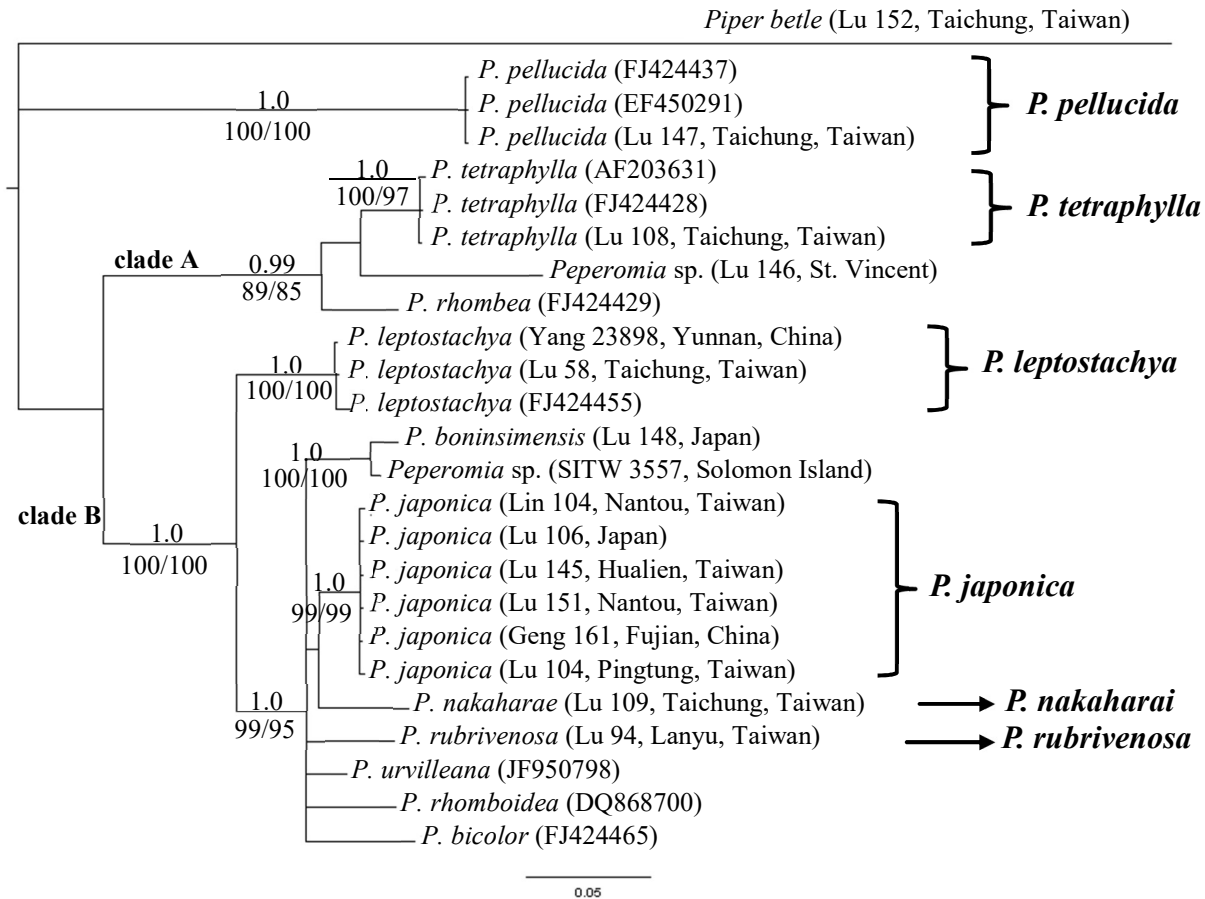


Fig. 6. A Bayesian inference (BI) tree of the *Peperomia* species and outgroups used in this study, based on nrITS sequences. Support values = $\frac{BI}{MPBS/MLBS}$

(2017) treated *P. formosana* and *P. laticaulis* as synonyms of *P. dindygulensis* (a synonym of *P. leptostachya*). After comparing the type specimens and original references, these two taxa are different from *P. leptostachya* but closer to *P. japonica*. Except for its larger size, *P. laticaulis* does not differ from *P. japonica*. *P. formosana* was described to differ from *P. japonica* only by its glabrous peduncles. However, we found the pubescence of the peduncles of *P. japonica* very variable, from clearly pubescent to almost glabrous. Therefore, we consider these two taxa to be morphological variants of *P. japonica* and treat them as synonyms of *P. japonica*.

Pollen grains of *Peperomia* show only small differences in their surface features, but *P. leptostachya* from China and Taiwan differs in the margins of the verrucae, even though they are in the same clade on the phylogenetic tree. Geographic isolation may have led to gradual variation.

Based on morphology and the results from molecular phylogeny, we recognize six species of *Peperomia* in Taiwan; *P. japonica*, *P. leptostachya*, *P. nakaharai*, *P. pellucida*, *P. rubrivenosa* and *P. tetraphylla*.

TAXONOMIC TREATMENT

- 1a. Stems glabrous 2
- 1b. Stems pubescent 3
- 2a. Apex of leaves emarginate *P. nakaharai*
- 2b. Apex of leaves acute or rounded to obtuse *P. pellucida*
- 3a. Stems angular-sulcate; spadix solitary, terminal; rachis pubescent. *P. tetraphylla*
- 3b. Stems cylindrical; spadices numerous, terminal or axillary; rachis glabrous 4
- 4a. Stems and petiole sparsely pilose or glabrescent *P. rubrivenosa*
- 4b. Stems and petiole densely puberulent 5
- 5a. Leaves opposite, 3- or 4-verticillate distally; stems and petiole red; leaf apex acute to obtuse; flowering May to August *P. leptostachya*
- 5b. Leaves 3-9-verticillate; stems and petiole green or reddish; leaf apex obtuse to rounded; flowering November to March *P. japonica*

1. *Peperomia japonica* Makino, Bot. Mag. Tokyo **15**: 145. 1901; Liu & Wang, Fl. Taiwan **2**: 557. 1976; Lin & Lu, Fl. Taiwan **2** (2nd ed.): 624. 1996. **Type specimen**: Japan: Heshima Island, *T. Makino s.n.*, 17 Jun. 1887 (lectotype designated here: MAK-151125!); Tosa, *K. Naganuma s.n.*, 1886 (paralectotype: MAK!); Tosima, *T.*



Yoshinaga s.n., 17 Jun. 1887 (paralectotype: MAK!); Ryukyu, *S. Kuroiwa s.n.*, s.d. (paralectotype: MAK!); Amami-oshima Island, *T. Makino s.n.*, Nov. 1901 (paralectotype: MAK!); Heshima Island, *Y. Yoshinaga s.n.* (paralectotype: TI!).

Peperomia formosana C. DC. Ann. Conserv. Jard. Bot. Genève 21: 223. 1920; Sasaki, List Pl. Form. 141. 1928; Liu & Wang, Fl. Taiwan 2: 559. 1976; Lin & Lu, Fl. Taiwan 2 (2nd ed.): 624. 1996. **Type specimen:** Taiwan: Keelung Samtianneapass, *O. Warburg 9338*, Jan. 1888 (holotype: B!).

Peperomia laticaulis C. DC., Ann. Conserv. Jard. Bot. Genève 21: 223-224. 1920. **Type specimen:** Taiwan, in *rupibus montium* Kushaka, *U. Faurie 481*, 8 Jun. 1903 (lectotype: G, designated by Gilbert & Xia, 1999; isolectotypes: B!, BM-image!, P!, W-image!).

Herb, perennial, succulent, 10–40 cm tall. Stems erect, tufted, rooting at base, nodes, internodes and young branchlets often reddish, densely soft puberulous. Leaves 3-9-verticillate, usually 5; petiole 0.3–1.5 cm long, puberulous, sometimes reddish; blade 1–6.5 cm long, 0.6–5 cm wide, rhombic to obovate, elliptic to oblong, apex rounded to obtuse, base obtuse to attenuate, margins entire, adaxial surface uniformly puberulous or puberulous around veins and margin, abaxial surface puberulous, adaxially green, paler green or midrib reddish abaxially, 3- or 5-nerved. Spadices erect, terminal or axillary, 3–11 cm long, rachis glabrous; peduncle pubescent, sometimes glabrous; bracts peltate, 0.48–0.5 mm in diameter, green, with pyramidal stalk; filaments *ca.* 0.3–0.38 mm long, anthers ellipsoid, *ca.* 0.4–0.42 mm long, 0.3–0.35 mm wide; ovary obovoid, *ca.* 0.4 mm long, 0.35 mm wide; stigmas penicillate. Fruit drupes, globose-ovoid, pericarp sticky, minutely papillose, on pedicels perpendicular to rachis of infructescence.

Distribution: Japan, mainland China (Yunnan and Fujian) and Taiwan. In Taiwan, widely distributed in wet places in forests below 1000 m.

Phenology: In Taiwan, flowering (November-) December to March (-April); fruiting (January-) February to June (-July).

Notes: Syntype specimens of *Peperomia japonica* are deposited in the herbarium of University of Tokyo (TI) and Makino Herbarium (MAK), Japan. We choose the specimen from Japan, Heshima, T. Makino *s.n.*, 17 Jun. 1887 (MAK-151125) as the lectotype. It bears a complete inflorescence and was collected by T. Makino himself.

Material from Fujian (China, Fujian, *S.T. Geng 161*, Nov. 29, 2014 [TAI]) was also used in the molecular analysis and ended in the clade of *P. japonica* in the phylogenetic tree. The FOC does not treat *P. japonica* as being on the mainland. *Peperomia japonica* is therefore a new record for China.

Specimens examined: Taiwan: New Taipei City, Sanzhi Dist., Palaka Road, *H.L. Chiang 1828*, Feb. 25, 2001 (TAIF). Taipei City, Beitou Dist., Mt. Chungchengshan, *C.M. Wang & Y.H. Tsai 2971*, Apr. 3, 1998 (TNM). Keelung City, Keelung, *S. Sasaki s.n.*, Mar. 1, 1913 (TAIF). Taoyuan City, Fuxing Dist., Paleng, *S.Y. Lu 19135*, May 6, 1986 (TAIF). Hsinchu County, Jianshi Township, Ssumakussu

Bridge, *H.Y. Chen 1213*, Jun. 12, 1999 (TNM). Taichung City, Heping Dist., Prov. #8 Hwy, *Y.C. Lu 59*, Jul. 19, 2013 (TNM). Nantou County, Lugu Township, Mt. Fenghuangshan, *S.Z. Yang 10521*, Jul. 14, 1987 (PPI). Chiayi County, Alishan Township, Laichi, *H.F. Yen 26834*, Jun. 17, 2003 (TNM). Kaohsiung City, Jiashian Dist., Mt. Paiyunshan, *H.F. Yen 2666*, Jun. 28, 1988 (TNM). Pingtung County, Fangliao Township, Chinsuiyin, *S.Z. Yang 22888*, Apr. 27, 1990 (PPI). Yilan County, Datong Township, Sunchitsun, *S. Suzuki s.n.*, Oct. 23, 1928 (TAI). Hualien County, Fuli Township, Mt. Hsinkangshan, *H.Y. Shen et al. 653*, Apr. 15, 1995 (TNM). Taitung County, Beinan Township, Chihpen-Chuifen, *S. Suzuki 10627*, Aug. 28, 1932 (TAI).

Japan: The Kochi Prefectural Makino Botanical Garden, *Y.C. Lu 106*, Aug. 12, 2013 (TNM).

China: Fukien, *S.T. Geng 161*, Nov. 29, 2014 (TAI). (All examined specimen list in supplementary)

2. *Peperomia leptostachya* Hook. & Arn., Bot. Beechey Voy. 2: 96. 1832.

Peperomia blanda var. *leptostachya* (Hook. & Arn.) Düll. in Bot. Jahrb. Syst. 93: 110. 1973. **Type specimen:** Hawaii: Oahu, s.d., *Beechey s.n.* [*Lau & Collie s.n.*] (holotype: K; isotype: G).

Peperomia dindygulensis Miq., Syst. Piperac. 1: 122. 1843. **Type specimen:** India: in *rupibus* Prov. Dindygul, *R. Wight* in *N. Wallich 6663B* (lectotype: K-image!, designated by Gilbert & Xia, 1999; isolectotypes: BM, BR, E, G, G-DC, P!, PRC, U).

Peperomia sui T.T. Lin & S.Y. Lu, Taiwania 40: 353. 1995; Lin & Lu, Fl. Taiwan 2 (2nd ed.): 626. 1996. **Type specimen:** Taiwan: Taitung Co., Taitung Hongye Village Taitung Cycas Nature Reserve, *T.T. Lin 1399*, 9 Jun. 1994 (holotype: TAI!); Taichung City, Kukuian, *S.Y. Lu 24730*, 19 May 1995; Taichung City, Chichi, *S.Y. Lu 24731*, 20 May 1995 (paratypes: TAI!).

Herb, perennial, succulent, 10–50 cm tall. Stems erect, tufted, rooting at base, red, densely soft puberulous. Leaves opposite, 3- or 4-verticillate distally; petiole 0.5–2 cm long, puberulous, red; blade 0.8–5.5 cm long, 0.9–3.5 cm wide, rhomboid to obovate, nearly orbicular at base of stem, apex acute to obtuse, base obtuse to attenuate, entire, both surfaces puberulous, green adaxially, red or with red patches abaxially, 3-nerved. Spadices erect, terminal or axillary, 4–12 cm long, rachis glabrous, peduncle sparsely puberulous; bracts peltate, 0.66–0.7 mm in diameter, upper edge often reddish, with pyramidal stalk; filaments *ca.* 0.3 mm long, anthers ellipsoid, *ca.* 0.38–0.4 mm long, 0.25 mm wide; ovary obovoid, *ca.* 0.45 mm long, 0.35 mm wide; stigmas penicillate. Fruit drupes, globose-ovoid, pericarp sticky, minutely papillose, pedicellate, on pedicels perpendicular to rachis.

Distribution: wide paleotropical distribution (Africa, Asia, Pacific Islands, Oceania). In Taiwan, widely distributed in wet places in forests below 1000 m.

Phenology: In Taiwan, flowering May to August (-September); fruiting June to October (-November).

Notes: *Peperomia leptostachya* is somewhat similar to *P. japonica* from which it can be distinguished by leaves opposite, 3- or 4-whorled vs. 3-9-whorled (Fig. 7), with coarser trichomes (Fig. 2 & 3), adaxial epidermis of leaves papillose vs. cells polygonal with anticlinal walls straight to arched and flowering season May-Sep. vs. Dec.-Feb.



Specimens examined: Taiwan: New Taipei City, Wulai Dist., *T. Ito s.n.*, Apr. 1, 1915 (TAIF). Taichung City, Heping Dist., Prov. #8 Hwy, *Y.C. Lu 58*, Jul. 19, 2013 (TNM). Nantou County, Renai Township, Wenfeng Village, *C.M. Wang & P.F. Lu 10404*, Jul. 8, 2007 (TNM). Yunlin County, Gukeng Township, Tsaoling, *T.Y.A. Yang & S.J. Huang 22977*, May 6, 2011 (TNM). Kaohsiung City, Maolin Dist, Shanping, *S.Y. Lu 16124*, Sep. 5, 1985 (TAIF). Pingtung County, Manzhou Township, Nanjenshan Working Station, *T.Y.A. Yang et al. 23104*, Jun. 27, 2011 (TNM). Hualien County, Fuli Township, Luoshan waterfall, *C.M. Wang & K.C. Chang 14097*, Nov. 13, 2010 (TNM). Taitung County, Haiduan Township, *Z.W. Lee 184*, Wulu, Aug. 11, 2002 (TNM).

China: Yunnan Province, Kai-Hua Town, Xi-Hua Park, *T.Y.A. Yang et al. 23898*, Dec. 10, 2013 (TNM).

(All examined specimen list in supplementary)

3. *Peperomia nakaharae* Hayata, J. Coll. Sci. Univ. Tokyo **25**: 188. 1908; Liu & Wang, Fl. Taiwan **2**: 557. 1976; Lin & Lu, Fl. Taiwan **2** (2nd ed.): 625. 1996; Tseng *et al.*, Fl. China **4**: 130. 1999. **Type specimen:** Taiwan: Chiayi Co., Yushan, *T. Kawakami & U. Mori 1997*, 18 Oct. 1906 (lectotype: TI, designated here, image!; isolectotype: TAIF!), *G. Nakahara s.n.*, Nov. 1906 (syntypes: TI!).

Herb, perennial, succulent, 5–10 cm tall. Stems erect, decumbent, tufted, rooting at base, nodes and internodes always reddish striped, glabrous, with slender longitudinal grooves. Leaves opposite or 3-verticillate, rarely 5-verticillate; petiole 0.2–0.3 cm long, glabrous, reddish at base; blade 0.3–1.5 cm long, 0.2–0.5 cm wide, obovate, apex emarginate, base acute, margins entire, both surfaces glabrous, only minutely pubescent at apex, green adaxially, paler green abaxially, 1-nerved. Spadices erect, solitary, terminal, 0.5–4 cm long, both rachis and peduncle glabrous; bracts peltate, 0.43–0.5 mm in diameter, apical margin usually reddish, with pyramidal stalk; filaments *ca.* 0.3 mm long, anthers globose-oval, *ca.* 0.25 mm long, 0.23 mm wide; ovary obovoid, 0.38–0.4 mm long, 0.35 mm wide; stigmas penicillate. Fruit drupes, globose-ovoid, pericarp sticky, minutely papillose, pedicellate, on pedicels perpendicular to rachis.

Distribution: Endemic to Taiwan; in wet places above 2000 m in the central part of the island.

Phenology: In Taiwan, flowering April to June and October to January; fruiting May to July and (November-) December to February.

Specimens examined: Taiwan: Miaoli County, Taian Township, Chiuchiu Shelter-Matalahsi, *W.L. Chiou & T.T. Lin 11798*, Aug. 4, 1984 (TAIF). Taichung City, Heping Dist., Mt. Anmashan, *J.C. Wang et al. 5004*, Aug. 7, 1987 (TAI). Chiayi County, Alishan Township, Mt. Alishan, *S. Sasaki s.n.*, Dec. 3, 1933 (TAD). Kaohsiung City, Maolin Dist., Takueihu, Oct. 6, 1986, *S.Y. Lu 20293* (TAIF). Pingtung County, Taiwu Township, Kuaikushanchuang, *S.Z. Yang & C.G. Lin 11991*, Feb. 7, 1990 (PPI). Yilan County, Datong Township, Mt. Taipingshan, *S. Suzuki 944*, Jul. 16, 1929 (TAI). Hualien County, Xiulin Township, Mt. Chingshuishan, *W.L. Chiow & M.C. Ho s.n.*, Apr. 27, 1983 (TAIF). Taitung County, Haiduan Township, Liyuan-Hsiangyang, *S.W. Chung & T.Y. Hsieh 7349*, Oct. 7, 2004 (TAIF).

(All examined specimen list in supplementary)

4. *Peperomia pellucida* (L.) Kunth, Nov. Gen. Sp. 1: 64. 1816; Tseng *et al.* Fl. China **4**: 130. 1999. **Type specimen (iconotype):** Linnaeus, Hort. Cliff t.4.1739 (designated as lectotype by Stearn, 1957).

Piper pellucidum L. Sp. Pl. 1: 30. 1753.

Herb, annual, succulent, 4–40 cm tall. Stems erect, branched, sometimes reddish striped, glabrous. Leaves opposite, verticillate or alternate; petiole 0.3–2 cm long, glabrous, sometimes reddish striped, blade 0.5–4 cm long, 0.5–3 cm wide, cordate to reniform, orbicular, apex acute to obtuse, base cordate to rounded, margins entire, both surfaces glabrous, adaxially green, abaxially paler, translucent, 5- or 7-nerved. Spadices erect, terminal or opposite leaves, 0.8–6 cm long, both rachis and peduncle glabrous; bracts peltate, 0.3–0.35 mm in diameter, green, nearly sessile; filaments *ca.* 0.15–0.2 mm long, anthers ellipsoid, 0.18–0.2 mm long, 0.1 mm wide; ovary ovoid, *ca.* 0.4 mm long, 0.2–0.25 mm wide; stigmas penicillate. Fruit drupes, globose-ovoid, sticky but not papillose, subsessile.

Distribution: Widely distributed in the tropics and subtropics. In Taiwan, in open places, naturalized at low elevations.

Phenology: Throughout the year.

Specimens examined: Taiwan: Taipei City, Daan Dist., Herbarium of National Taiwan University, *C.C. Hsu 5670*, Aug. 9, 1969 (TAI). Taichung City, North Dist., National Museum of Natural Science, *Y.C. Lu 147*, May 27, 2015 (TNM). Nantou County, Lugu Township, Lugu Village, *C.W. He s.n.*, Sep. 21, 2002 (TAIF). Chiayi City, East Dist., Chiayi Branch, Taiwan Agricultural Research Institute, 1993, *H.F. Yen 8130*, Aug. 17 (TNM). Chiayi County, Zhuqi Township, Kuanyin waterfall, *C.M. Wang & Y.M. Hsu 7704*, Sep. 9, 2004 (TNM). Pingtung County, National Pingtung Teachers College, *M.C. Chen s.n.*, Aug. 2, 2001 (TAIF). Pingtung County, Gaoshu Township, Beside the Yenshan Road, *S.Z. Yang 28616*, Dec. 22, 1999 (TNM). Hualien County, Jian Township, *Y.Y. Chang s.n.*, Aug. 12, 1991 (TAIF). Hualien County, Hualien City, Meilun Industrial Park, *S.T. Hung s.n.*, Nov. 18, 2000 (TAIF).

(All examined specimen list in supplementary)

5. *Peperomia rubrivenosa* C. DC., Philip. J. Sci. Bot. **5**: 409. 1910; Liu & Wang, Fl. Taiwan **2**: 559. 1976; Lin & Lu, Fl. Taiwan **2** (2nd ed.): 625. 1996; Tseng *et al.*, Fl. China **4**: 130. 1999. **Type specimen:** Philippines: Luzon, Province of Benguet, Baguio, *R.S. Williams 1083*, May (holotype: PNH (missing); G! (drawing); isotype: NY).

Peperomia kotoensis Yamamoto, Suppl. Ic. Pl. Formosan. **2**: 9. f. 4. 1926. **Type specimen:** Taiwan: Taitung, Lanyu, *S. Sasaki s.n.*, May 1924 (holotype: TI!).

Herb, perennial, succulent, 8–25 cm tall. Stems erect, procumbent at base, internodes sometimes with scattered petiole 0.3–1 cm long, sparsely pilose, green; blade 1.5–4 cm long, 1–3 cm wide, obovate to orbicular or elliptic, apex rounded to obtuse, base acute to rounded, margins entire, both surfaces sparsely pilose, adaxially green, abaxially paler green, 3-nerved. Spadices erect, terminal or axillary, 1.5–5 cm long, both rachis and peduncle glabrous; bracts peltate, 0.35–0.4 mm in diameter, green,

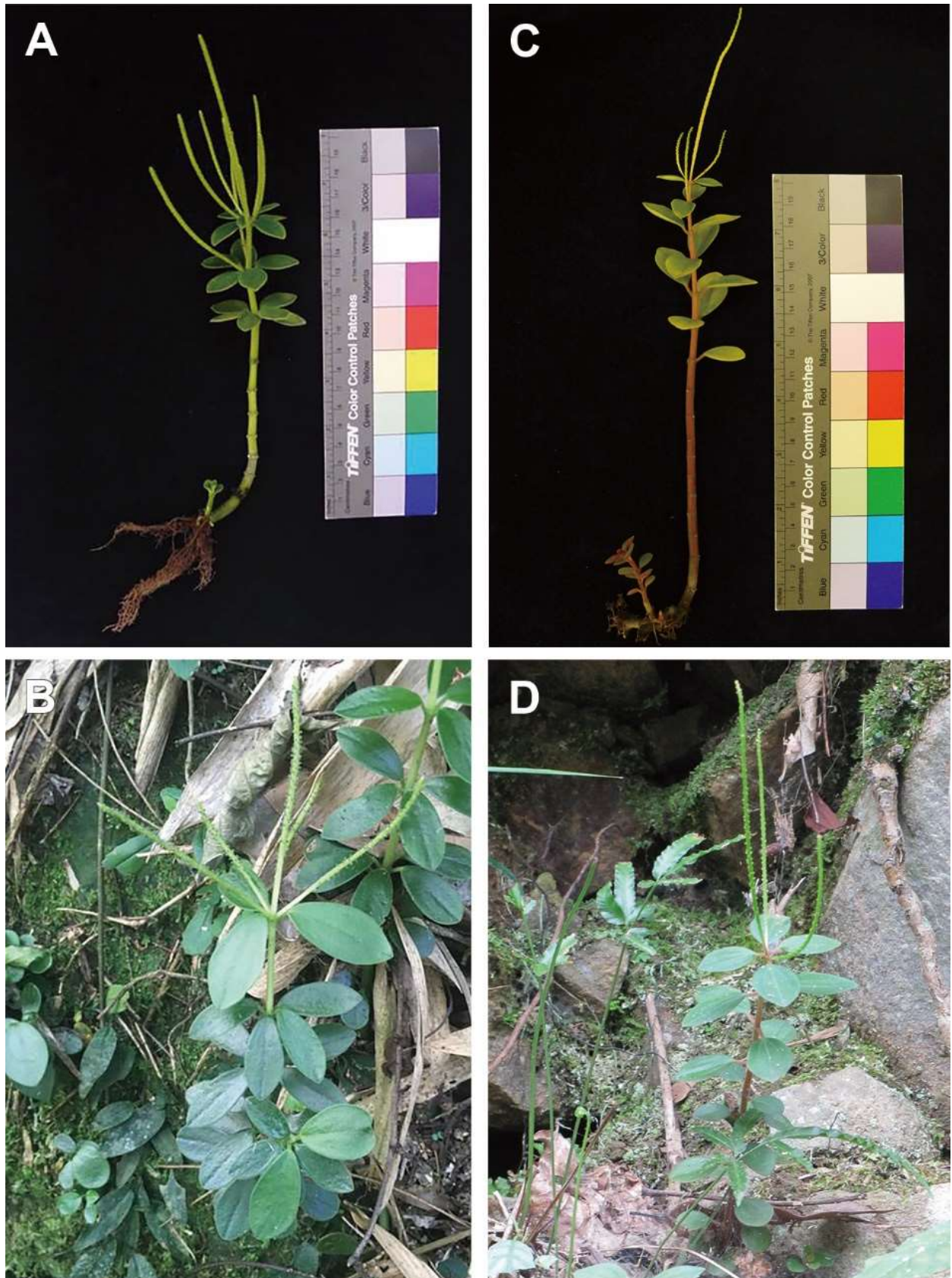


Fig. 7. Living materials of *Peperomia japonica* and *P. leptostachya*. A, B. *P. japonica*; C, D. *P. leptostachya*.



with pyramidal stalk; filaments 0.2–0.25 mm long, anthers ellipsoid *ca.* 0.4 mm long, 0.3 mm wide; ovary obovoid, *ca.* 0.35 mm long, 0.25–0.3 mm wide; stigmas penicillate. Fruit drupes, globose-ovoid, pericarp sticky, minutely papillose, on pedicels perpendicular to rachis. reddish spots, sparsely pilose or glabrescent, with slender longitudinal grooves. Leaves opposite or 3-verticillate.

Distribution: Philippines and Taiwan. In Taiwan, in forests on Lanyu Island and in northern Taiwan.

Phenology: In Taiwan, flowering December to March (-April); fruiting season February to August.

Specimens examined: Taiwan: New Taipei City, Shuangxi Dist., Mt. Wangxingshan, *C.F. Chen 6127*, Jul. 15, 2014 (TAIF). **Taitung County**, Lanyu Township, *G. Masamune 4179*, May 10, 1943 (TAD).

(All examined specimen list in supplementary)

6. *Peperomia tetraphylla* Hook. & Arn., Bot. Beechey Voy. 2: 97, 1832; Tseng *et al.*, Fl. China 4: 129. 1999.

Type specimen: Hawaiian Islands, Oahu, *F.W. Beechey s.n.* (holotype: K!).

Piper tetraphyllum G. Forst., Fl. Ins. Austr. 5: 5. 1786. **Type specimen:** Society Island, *J.G.A. Forster s.n.* (lectotype: K!, designated by Florence, 1997).

Peperomia reflexa (L. f.) A. Dietr., Sp. Pl. 180. 1831; Hayata, Fl. Mont. Form. 188. 1908; Sasaki, List Pl. Form. 141. 1928; Masamune, Short Fl. Form. 38. 1936, List Vasc. Pl. Taiwan. 38. 1954; Wang, Taxon. Rev. Ord. Pip. Taiwan 13. 1973; Liu & Wang, Fl. Taiwan 2: 557. 1976; Lin & Lu, Fl. Taiwan 2 (2nd ed.): 625. 1996. *non P. reflexa* Kunth, 1815.

Piper reflexum L. f., Suppl. Pl. 91. 1781. **Type specimen:** South Africa: Cap. bonae fpei, *Thunberg s.n.* (holotype: UPS) [GUID: UPS:BOT:V-000752].

Herb, perennial, succulent, 10–25 cm tall. Stems erect, tufted, rooting at base, always reddish near the nodes, puberulous, angular-sulcate. Leaves 4-verticillate, rarely 3; petiole 0.2–0.3 cm long, puberulous, sometimes reddish at base; blade 0.6–1.5 cm long, 0.5–1 cm wide, obovate to orbicular, elliptic, apex rounded to obtuse, base acute to rounded, margins entire, green and nearly glabrous on adaxially, paler green and glabrous on abaxially, only midrib conspicuous. Spadices erect, solitary, terminal, fleshy, 1–4 cm long, both rachis and peduncle puberulous; bracts peltate, about 0.35 mm in diameter, green, stalk cylindrical; filaments *ca.* 0.2 mm long, anthers ellipsoid, 0.2–0.25 mm long, *ca.* 0.15 mm wide; ovary ovoid, *ca.* 0.45 mm long, 0.28–0.3 mm wide, deeply immersed in pit; stigmas penicillate. Fruit drupes, ovoid to narrowly ovoid, pericarp not papillose, with sticky basal pseudocupula, partially embedded in pit of rachis.

Distribution: Widely distributed in tropical and subtropical America, Africa, Asia and Oceania. In Taiwan, in wet places above 1,800 m in the central part of the island.

Phenology: In Taiwan, flowering (January-) February to April and (June-) July to August (-October); fruiting season (March-) April to June and (July-) August to October.

Specimens examined: Taiwan: New Taipei City, Sanxia Dist., Mt. Peichatienshan, *H.L. Chiang, 256*, Jan. 23, 2000 (TAIF). **Hsinchu County**, Jianshi Township, Chenghsipao, *Y.C. Lu 96*, Jun. 22,

2013 (TNM). **Miaoli County**, Nanchuang Township, Mt. Chialishan, *C.M. Wang et al. 8626*, Feb. 25, 2006 (TNM). **Taichung City**, Heping Dist., *C.I. Huang et al. 175*, Nov. 7, 1998 (TAIF). **Nantou County**, Lugu Township, Chitou, *T.Y.A. Yang & T.S. Wang 3153*, Sep. 14, 1986 (TNM). **Chiayi County**, Alishan Township, Mt. Alishan, *B. Hayata & S. Sasaki s.n.*, Jan. 23, 1912. (TAIF). **Kaohsiung City**, Liugui Dist., Liukuei, *M.T. Kao 79*, Dec. 18, 1961 (TAI). **Pingtung County**, Chunri Township, Mt. Shihkechienshan, *P.H. Chen 91*, Oct. 10, 2012 (PPI). **Yilan County**, Chienching, *S. Suzuki 10804*, Aug. 29, 1932 (TAD). **Hualien County**, Jian Township, Mt. Chungyangchienshan, *T. Suzuki 16176*, Jul. 27, 1936 (TAI). **Taitung County**, Beinan Township, Lichia Logging Trail, *S.W. Chung 9329*, Jan. 13, 2009 (TAIF).

(All examined specimen list in supplementary)

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