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 of 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 infragenic 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), 2\textsuperscript{nd} 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* (Matsumiu, 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.

<table>
<thead>
<tr>
<th>Literature</th>
<th>A list of plants from Formosana</th>
<th>Enumeratio Plantarum Formosanarum</th>
<th>Flora Montana Formosae</th>
<th>Supplement to Icons Plantarum Formosanarum VI</th>
<th>Annuaire du Conservatoire et Jardin Botaniques de Genève</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>1896</td>
<td>1906</td>
<td>1908</td>
<td>1917</td>
<td>1920</td>
</tr>
<tr>
<td>Authors</td>
<td>A. Henry</td>
<td>J. Matsumura &amp; B. Hayata</td>
<td>B. Hayata</td>
<td>B. Hayata</td>
<td>C. de Candolle</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Authors</th>
<th>Voucher Specimen Details</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. dindygulensis</em></td>
<td>1843</td>
<td>Miq.</td>
<td></td>
</tr>
<tr>
<td><em>P. japonica</em></td>
<td>1901</td>
<td>Hayata</td>
<td></td>
</tr>
<tr>
<td><em>P. laticaulis</em></td>
<td>1920</td>
<td>C. DC.</td>
<td></td>
</tr>
<tr>
<td><em>P. blanda</em> (Jacq.) Kunth</td>
<td>1816</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. sui</em> T. T. Lin &amp; S. Y. Lu</td>
<td>1995</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. formosana</em></td>
<td>1920</td>
<td>C. DC.</td>
<td></td>
</tr>
<tr>
<td><em>P. rubrivenosa</em></td>
<td>1901</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. kotoensis</em> Yamamoto</td>
<td>1926</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. nakaharai</em> Hayata</td>
<td>1908</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. reflexa</em> (L. f.) A. Dietr.</td>
<td>1831</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. tetraphylla</em> (G. Forst.) Hook. &amp; Am.</td>
<td>1832</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. pellucida</em> (L.) Kunth</td>
<td>1916</td>
<td></td>
<td></td>
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</tbody>
</table>

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<tr>
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<tbody>
<tr>
<td>Literature</td>
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</thead>
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<td>Literature</td>
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<td></td>
<td></td>
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</tr>
</tbody>
</table>

- *P. dindygulensis* Miq. 1843
- *P. japonica* Makino 1901
- *P. laticaulis* C. DC. 1920
- *P. blanda* (Jacq.) Kunth 1816
- *P. formosana* C. DC. 1920
- *P. rubrivenosa* C. DC. 1901
- *P. kotoensis* Yamamoto 1926
- *P. nakaharai* Hayata 1908
- *P. reflexa* (L. f.) A. Dietr. 1831
- *P. tetraphylla* (G. Forst.) Hook. & Am. 1832
- *P. pellucida* (L.) Kunth 1916

- *P. formosana* C. DC. 1920
- *P. rubrivenosa* C. DC. 1901
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- *P. nakaharai* Hayata 1908
- *P. reflexa* (L. f.) A. Dietr. 1831
- *P. tetraphylla* (G. Forst.) Hook. & Am. 1832
- *P. pellucida* (L.) Kunth 1916

501
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'-AATGGTCCGTTAAGGTTTCGG-3') and ITS-90R (5'-GCTTCTACAGACTACATTCCG-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>
<thead>
<tr>
<th>Taxon</th>
<th>Geographic origin of the sequenced material</th>
<th>Voucher no.</th>
<th>GenBank no.</th>
<th>Remark</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peperomia bicolor</td>
<td>Berlin Botanical Garden</td>
<td>Wanke 052</td>
<td>FJ424465</td>
<td></td>
</tr>
<tr>
<td>P. blanda</td>
<td>Berlin Botanical Garden</td>
<td>Wanke 055</td>
<td>FJ424455</td>
<td></td>
</tr>
<tr>
<td>P. pellucida</td>
<td>Gent Botanical Garden</td>
<td>S. &amp; V. 2005-009</td>
<td>FJ424437</td>
<td></td>
</tr>
<tr>
<td>P. pellucida</td>
<td>–</td>
<td>–</td>
<td>EF450291</td>
<td></td>
</tr>
<tr>
<td>P. rhomboidea</td>
<td>Berlin Botanical Garden</td>
<td>Wanke 053</td>
<td>FJ424429</td>
<td></td>
</tr>
<tr>
<td>P. rhomboidea</td>
<td>–</td>
<td>–</td>
<td>DQ868700</td>
<td></td>
</tr>
<tr>
<td>P. tetraphylla</td>
<td>–</td>
<td>–</td>
<td>AF203631</td>
<td></td>
</tr>
<tr>
<td>P. tetraphylla</td>
<td>Gent Botanical Garden, Bocono-Mosquey, Venezuela</td>
<td>S. &amp; V. 2005-006</td>
<td>FJ424428</td>
<td></td>
</tr>
<tr>
<td>P. urvilleana</td>
<td>Lord Howe Island</td>
<td>–</td>
<td>JF950798</td>
<td></td>
</tr>
<tr>
<td>Peperomia sp.</td>
<td>Solomon Island</td>
<td>STW3557</td>
<td>MW114862 (TNM)</td>
<td></td>
</tr>
<tr>
<td>Peperomia sp.</td>
<td>St. Vincent</td>
<td>Y.C.Lu 146</td>
<td>MW114872 (TNM)</td>
<td></td>
</tr>
<tr>
<td>P. boninsimensis</td>
<td>Makino Botanical Garden, Japan</td>
<td>Y.C.Lu 148</td>
<td>MW114861</td>
<td>Imported from Makino Botanical Garden, Japan (TNM)</td>
</tr>
<tr>
<td>P. japonica</td>
<td>Pingtung, Taiwan</td>
<td>Y.C.Lu 104</td>
<td>MW114868</td>
<td>Plant green; puberulous uniform on adaxial surface (TNM)</td>
</tr>
<tr>
<td>P. japonica</td>
<td>Nantou, Taiwan</td>
<td>P.H.Lin 104</td>
<td>MW114863</td>
<td>Plant green; puberulous around veins and edge on adaxial surface (TNM)</td>
</tr>
<tr>
<td>P. japonica</td>
<td>Hualien, Taiwan</td>
<td>Y.C.Lu 145</td>
<td>MW114865</td>
<td>Puberulous uniform on adaxial surface (TNM)</td>
</tr>
<tr>
<td>P. japonica</td>
<td>Nantou, Taiwan</td>
<td>Y.C.Lu 151</td>
<td>MW114866</td>
<td>Sometimes reddish at petiole and midrib (abaxial surface), puberulous around veins and edge on adaxial surface (TNM)</td>
</tr>
<tr>
<td>P. japonica</td>
<td>Makino Botanical Garden, Japan</td>
<td>Y.C.Lu 106</td>
<td>MW114864</td>
<td>Imported from Makino Botanical Garden, Japan (TNM)</td>
</tr>
<tr>
<td>P. japonica</td>
<td>Fujian, China</td>
<td>S.T.Geng 161</td>
<td>MW114867</td>
<td>Collected from Fujian, China (TAI).</td>
</tr>
<tr>
<td>P. leptostachya</td>
<td>Yunnan, China</td>
<td>T.Y.A.Yang 23898</td>
<td>MW114859</td>
<td>(TNM)</td>
</tr>
<tr>
<td>P. leptostachya</td>
<td>Taichung, Taiwan</td>
<td>Y.C.Lu 58</td>
<td>MW114860</td>
<td>(TNM)</td>
</tr>
<tr>
<td>P. nakaharae</td>
<td>Taichung, Taiwan</td>
<td>Y.C.Lu 109</td>
<td>MW114869</td>
<td>(TNM)</td>
</tr>
<tr>
<td>P. pellucida</td>
<td>Taichung, Taiwan</td>
<td>Y.C.Lu 147</td>
<td>MW114873</td>
<td></td>
</tr>
<tr>
<td>P. rubrivenosa</td>
<td>Lanyu, Taiwan</td>
<td>Y.C.Lu 94</td>
<td>MW114870</td>
<td></td>
</tr>
<tr>
<td>P. tetraphylla</td>
<td>Taichung, Taiwan</td>
<td>Y.C.Lu 108</td>
<td>MW114871</td>
<td></td>
</tr>
<tr>
<td>Piper betle</td>
<td>Taichung, Taiwan</td>
<td>Y.C.Lu 152</td>
<td>MW114858</td>
<td></td>
</tr>
</tbody>
</table>

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

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.

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

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

(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. japonica*, *P. nakaharae* and *P. rubrivenosa* (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).

### Polynology

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 = 1.00/99/99). *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. suti*, 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. rubrivenosa*; G. *P. tetraphylla*; H. rachis of *P. tetraphylla*. Scale bars: A, B, C, D, E, F, G = 500 µm; H = 90 µm.
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 µm.
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 µm.
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 µm.
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.
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*. 510
Fig. 6. A Bayesian inference (BI) tree of the Peperomia species and outgroups used in this study, based on nrITS sequences. Support values = BI/MP/ML/BS.

(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 form 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. nakaharae, P. pellucida, P. rubrivenosa and P. tetraphylla.

TAXONOMIC TREATMENT


2. Peperomia leptostachya Yang 23898, Yunnan, China

3. Peperomia nakaharae (Lu 109, Taichung, Taiwan)

4. Peperomia pellucida (EF450291)

5. Peperomia rubrivenosa (Lu 106, Japan)

6. Peperomia tetraphylla (AF203631)

7. Peperomia sp. (Lu 146, St. Vincent)

8. Peperomia sp. (Lu 147, Taichung, Taiwan)

9. Peperomia sp. (Lu 148, Japan)

10. Peperomia sp. (Lu 149, Hualien, Taiwan)

11. Peperomia sp. (Lu 150, Pingtung, Taiwan)

12. Peperomia sp. (Lu 151, Nantou, Taiwan)

13. Peperomia sp. (Lu 152, Taichung, Taiwan)

14. Peperomia sp. (Lu 153, Nantou, Taiwan)

15. Peperomia sp. (Lu 154, Pingtung, Taiwan)

16. Peperomia sp. (Lu 155, Taichung, Taiwan)

17. Peperomia sp. (Lu 156, Nantou, Taiwan)

18. Peperomia sp. (Lu 157, Pingtung, Taiwan)

19. Peperomia sp. (Lu 158, Taichung, Taiwan)

20. Peperomia sp. (Lu 159, Nantou, Taiwan)

21. Peperomia sp. (Lu 160, Pingtung, Taiwan)

22. Peperomia sp. (Lu 161, Taichung, Taiwan)

23. Peperomia sp. (Lu 162, Nantou, Taiwan)

24. Peperomia sp. (Lu 163, Pingtung, Taiwan)

25. Peperomia sp. (Lu 164, Taichung, Taiwan)

26. Peperomia sp. (Lu 165, Nantou, Taiwan)

27. Peperomia sp. (Lu 166, Pingtung, Taiwan)

28. Peperomia sp. (Lu 167, Taichung, Taiwan)

29. Peperomia sp. (Lu 168, Nantou, Taiwan)

30. Peperomia sp. (Lu 169, Pingtung, Taiwan)

31. Peperomia sp. (Lu 170, Taichung, Taiwan)

32. Peperomia sp. (Lu 171, Nantou, Taiwan)

33. Peperomia sp. (Lu 172, Pingtung, Taiwan)

34. Peperomia sp. (Lu 173, Taichung, Taiwan)

35. Peperomia sp. (Lu 174, Nantou, Taiwan)

36. Peperomia sp. (Lu 175, Pingtung, Taiwan)

37. Peperomia sp. (Lu 176, Taichung, Taiwan)

38. Peperomia sp. (Lu 177, Nantou, Taiwan)

39. Peperomia sp. (Lu 178, Pingtung, Taiwan)

40. Peperomia sp. (Lu 179, Taichung, Taiwan)

41. Peperomia sp. (Lu 180, Nantou, Taiwan)

42. Peperomia sp. (Lu 181, Pingtung, Taiwan)

43. Peperomia sp. (Lu 182, Taichung, Taiwan)

44. Peperomia sp. (Lu 183, Nantou, Taiwan)

45. Peperomia sp. (Lu 184, Pingtung, Taiwan)

46. Peperomia sp. (Lu 185, Taichung, Taiwan)

47. Peperomia sp. (Lu 186, Nantou, Taiwan)

48. Peperomia sp. (Lu 187, Pingtung, Taiwan)

49. Peperomia sp. (Lu 188, Taichung, Taiwan)

50. Peperomia sp. (Lu 189, Nantou, Taiwan)

51. Peperomia sp. (Lu 190, Pingtung, Taiwan)
**Yoshinaga s.n.,** 17 Jun. 1887 (paratype: MAK!); Ryukyu, S. Kuroiwa s.n., s.d. (paratype: MAK!); Amami-oshima Island, T. Makino s.n., Nov. 1901 (paratype: MAK!); Heshima Island, Y. Yoshinaga s.n. (paratype: TII).


**Type specimen:** Taiwan: Keelung Santianneapcasus, O. Warburg 9358, Jan. 1888 (holotype: BI).


Herb, perennial, succulent, 10–40 cm tall. Stems erect, tufted, rooting at base, nodes, internodes and young branches 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 obolate, 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 petaloid, 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 pedicles 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 [TAIF]) 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.


(All examined specimen list in supplementary)


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 ovate, 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 pubescent; bracts petaloid, 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, on pedicles perpendicular to rachis of infructescence.

**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 (September)–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-nerved vs. 3-9-nerved (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.

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

Herb, annual, succulent, 4–40 cm tall. Stems erect, branched, sometimes reddish stripped, glabrous. Leaves opposite, verticillate or alternate; petiole 0.3–2 cm long, glabrous, sometimes reddish stripped, blade 0.5–4 cm long, 0.5–3 cm wide, ciliate 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: Taitung Co., Fuli Township, Beside the Yenshan Road, S.Z. Yang s.n. (TNM). **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 Co., Shuili Township, Chichuan Shelter-Matalahi, W.L. Chiu & T.T. Lin 11798, Aug. 4. 1984 (TAIF). **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 Co., Shuili Township, Chichuan Shelter-Matalahi, W.L. Chiu & T.T. Lin 11798, Aug. 4. 1984 (TAIF). **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.
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 pedicle perpendicular to rachis. reddish spots, sparsely piloose 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, March (-April); fruiting season February to August.


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

**Piper reflexum** G. Forst., Fl. Ins. Austr. 5: 1786.


**Piper reflexum** L., Suppl. Pl. 91. 1781.

**Type specimen:** South Africa: Cape, bonae paei, 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, ovate 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.


(All examined specimen list in supplementary)

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**LITERATURE CITED**


Supplementary materials are available from Journal Website.