

Verhuellia revisited—unravelling its intricate taxonomic history and a new subfamilial classification of *Piperaceae*

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The small poorly studied genus *Verhuellia* has usually been included in the genus *Peperomia*. However, a recent molecular study has revealed that *Verhuellia* is sister to all *Piperaceae* and neither part of, nor sister to *Peperomia* as expected. The genus currently includes three species, and with eight taxa described, has had a complex taxonomic history, including wrong synonymizations. Hence a thorough review of all publications mentioning *Verhuellia* and a detailed study of the herbarium specimens involved has been undertaken. In this paper we present a survey of the chaotic taxonomy of *Verhuellia* and clarify all nomenclatural obscurities. Additionally, as a consequence of the novel position of the genus, the traditional division of the family *Piperaceae* into two subfamilies *Peperomioideae* and *Piperoideae* is reconsidered.

KEYWORDS: nomenclature, *Peperomia*, *Piper*, *Piperaceae*, *Piperoideae*, subfamilial classification, typification, *Verhuellia*, *Verhuellioideae*, *Zippelioideae*

INTRODUCTION

The genus *Verhuellia* has generally been treated as closely related to, or even synonymous with the giant genus *Peperomia*. However, plants of the two genera have a different habit: all species of *Verhuellia* are prostrate with three to four leaves in a whorl at one side of the stem whereas the genus *Peperomia* is much more diverse. If species of *Peperomia* are prostrate, the leaves are always alternate. Other important differences between the two genera can be found in flower morphology. For example, *Verhuellia* has three to four stigmas, whereas *Peperomia* has only one stigma (seldom bipartite).

These morphological differences are supported by a recent molecular study (Wanke & al., 2007b) where *Verhuellia* appears as sister to all other *Piperaceae*: (*Verhuellia* + ((*Zippelia* + *Manekia*) + (*Piper* + *Peperomia*))), thereby putting character evolution in this family and in the perianthless *Piperales* in a different light. In other recent studies on *Peperomia* and *Piperales* by Wanke & al. (2006, 2007a), *Verhuellia* could not be included due to lack of material.

The genus *Verhuellia* was first described by Miquel in 1843, in the tribe *Peperomieae* of the family *Piperaceae*, with three species: *Verhuellia elegans* Miq., *Verhuellia brasiliensis* Miq. and *Verhuellia serpens* (Sw.) Miq. (Miquel, 1843–1844). The genus was named after Quirijn “Maurits” Rudolf Ver Huell (1787–1860), who made a

series of illustrations for Miquel’s *Systema Piperacearum* (1843–1844) and *Illustrationes Piperacearum* (1847).

In the description of the first species, Miquel placed a question mark before the included name *Piper reniforme* (“? *Piper reniforme* Willd. Herb. n. 742”), meaning that *V. elegans* might be identical to this specimen (Miquel, 1843–1844). In 1844, this question mark before *Piper reniforme* is no longer present, so it can be concluded that Miquel then considered the two names as synonymous (Miquel, 1844). However, Miquel did not have to change the name of *V. elegans* as “*Piper reniforme* Willd. Herb. n. 742” was not validly published. Unfortunately, later authors seem to have overlooked that the latter name is a nomen nudum, resulting in the use of the names “*Verhuellia reniformis* C. DC.” and “*Verhuellia reniformis* (Willd.) C. DC.” until today. Only Candolle (1902) finally came to a correct solution after making mistakes himself (e.g., Candolle, 1866). In 1902, Candolle apparently realized that *Verhuellia elegans* Miq. and “*Piper reniforme* Willd. Herb. n. 742” were based on the same collection as *Peperomia lunaria* Ham. (Hamilton, 1825), resulting in the new combination *Verhuellia lunaria* (Ham.) C. DC. Unfortunately, the last name has not been adopted by any subsequent author. *Verhuellia elegans* Miq. has only recently been designated as lectotype of the generic name (Saralegui Boza, 2004) and this has been accepted by Samain & al. (2007).

Verhuellia is mentioned in few studies and this might be largely due to its restricted distribution, poorly known

collection localities, limited availability in herbaria and complete absence in living botanical collections. Until recently, no material was available for molecular phylogenetic and morphological studies.

One species from the Dominican Republic has now become available as a living plant in the botanical gardens of Ghent and Dresden. Study of living specimens of all species is desirable for a thorough revision of the genus and additional field work is thus required.

The aims of this study are twofold: (1) to present a survey of the names published in the genus *Verhuellia* and clarify the nomenclatural situation, and (2) to present a new subfamilial classification for the family Piperaceae, consistent with new molecular and morphological data. In contrast with Saralegui Boza (2004) who recognized only two species (one from Cuba and one occurring in both Cuba and Hispaniola), three species are recognized in this paper (two in Cuba and one on Hispaniola).

TAXONOMY AND HISTORY OF VERHUELLIA

The genus and the three currently accepted species are discussed, followed by three combinations in *Verhuellia* that should be treated as synonyms of *Peperomia* species.

Verhuellia Miq., Syst. Piperac.: 45, 47. 1843 – Lectotype (designated by Saralegui Boza, 2004): *Verhuellia elegans* Miq. See under *Verhuellia lunaria* for the history of the name *V. elegans*.

Key and survey of the currently recognized *Verhuellia* species

- 1a Leaves cordate to rounded, diameter 0.4–0.6 cm [Cuba] **1. *V. hydrocotylifolia***
 1b Leaves rounded to reniform, 0.6–1.0 × 0.6–1.5 cm [Cuba or Hispaniola] **2**
 2a Leaf main veins 7 [Hispaniola] **2. *V. lunaria***
 2b Leaf main veins 3–5 [Cuba] **3. *V. pellucida***

1. *Verhuellia hydrocotylifolia* (Griseb.) C. DC. ex Wright in Anales Acad. Ci. Méd. Habana 7: 510. 1871 ≡ *Mildea hydrocotylifolia* Griseb., Cat. Pl. Cub.: 63. 1866 ≡ *Verhuellia cordifolia* C. DC., Prodr. 16: 391. 1869, nom. illeg. – Type: Cuba, Wright 2266 (holotype: GOET; isotypes: BM!, G-DC!, GH!, HAC, K!, MA!, P!, S!).

History. – Grisebach (1866) published the new genus *Mildea* with two species, *M. hydrocotylifolia* and *M. elegans*. He recognized the similarity with *Verhuellia* but referred to the different stigma “nature” and growth form. Candolle (1869) synonymized *Mildea* with *Verhuel-*

lia, but without maintaining the specific epithet *hydrocotylifolia* for the first species, as he renamed this taxon *Verhuellia cordifolia*. Wright (1871) corrected this and made the new combination *V. hydrocotylifolia*, and this was also followed by other authors (e.g., Candolle, 1902; Trelease, 1926).

Distribution. – Endemic to the eastern and western extremities of Cuba.

Specimens studied. – CUBA. Oriente, Guantánamo, Monte Libanon near Monterus, alt. 700–800 m., 28 Nov 1922, Ekman 15846 (S); Pinar del Rio, Viñales, Sierra de la Guasasa, 10 Mar 1924, Ekman 18684 (S); Oriente, Guantánamo, Monte Ojo de Toro, 14 Oct 1861, Wright 2266 (BM, G-DC, GH, K, MA, P, S).

2. *Verhuellia lunaria* (Ham.) C. DC. in Urban, Symb. Antill. 3: 216. 1902 ≡ *Peperomia lunaria* Ham., Prodr. Pl. Ind. Occid.: 2. 1825 ≡ *Verhuellia elegans* Miq., Syst. Piperac.: 48. 1843 ≡ *Piper lunare* D. Dietr., Syn. Pl. 1: 111. 1839 – Type: Hispaniola, Poiteau s.n. (holotype G-DC; isotypes: B-W!, BM!, C, HAL!, L!, P!, S!, U!).

History. – The description of *V. elegans* (Miquel, 1843–1844: 48) was based on a Poiteau specimen “in Herb. De Less.” (Herbarium Delessert now at G). The specimen in B, annotated with the names “*Piper reniforme*” (and a later “*Verhuellia elegans* Miq.”; Willdenow herbarium 742, deposited by Rudolphi), is mentioned with a question mark. In 1844, Miquel probably realized that both specimens were from the same Poiteau collection (see Stafleu & Cowan, 1983: 974), as the name *Piper reniforme* as a synonym is no longer preceded by a question mark (Miquel, 1844). However, *Piper reniforme* is a nomen nudum and has never been validly published, although the name has several times been listed, e.g., by Link (1820; “*Piper reniforme*. Unter diesem Namen ist eine sehr zweifelhafte Pflanze von Rudolphi aus S. Domingo im Herbarium. Es ist nicht *Piper reniforme* Roem. et Sch. l. 316, aber wegen undeutlicher Blüten schwer zu bestimmen”) and Roemer & Schultes (1822; “*Piperis reniformis* nomine in *Herb. Willd.* asservari specimen e *S. Domingo* a *D. Rudolphi* communicatum maxime problematicum ob flores imperfectos, sed omnino diversum ab hoc *reniformi*” [italics in original]). The combination was in any case preoccupied. Poirét (1804) had published another *Piper reniforme* occurring in “*Indii*”, although Dietrich (1831) considered this a species of *Peperomia*, resulting in the new combination *Peperomia reniformis* (Poir.) A. Dietr.

The confusion about the valid publication of *Piper reniforme* and the use of the name *Verhuellia elegans* versus *V. reniformis* continued for more than 20 years in nearly all publications where the genus is mentioned. Candolle (1866: 245) was the first author to “replace” the name *V. elegans* Miq. with “*V. reniformis* Miq.” in the

caption of a drawing of the species concerned, although he later considered this as a typographical error (Candolle, 1902; “*errore typ. sub V. reniformis*”). Even in 1869 he recognized *V. elegans* Miq. and mentioned “*Piper reniforme* Willd. Herb. n. 742” and “*Peperomia reniformis* A. Dietr.” among the synonyms. *Piper reniformis* Poir., the basionym of the latter species name, is not mentioned by Candolle as this name was considered as “species incerta” by Miquel (1843–1844: 50).

Schmitz (1872: 422, in obs.) recognized that *Verhuellia reniformis* Miq. as mentioned by Candolle (1866) was an error (“ein Versehen”). Later authors also mentioned “*Verhuellia reniformis* C. DC.” (e.g., Candolle, 1920, Trelease, 1927, Peguero & al., 2005; the latter two as *Verhuellia reniformis* (Willd.) C. DC.).

In 1902, Candolle apparently realised that *Peperomia lunaria* Ham. (Hamilton, 1825) was based on the same Poiteau collection as *V. elegans*, as he published the new combination *Verhuellia lunaria* (Ham.) C. DC. Among the synonyms cited were “*V. elegans* Miq.”, which he recognized to have been erroneously placed under *V. reniformis* as a consequence of a typographical error, “*Piper reniforme* Willd. Herb. n. 742” and “*Peperomia reniformis* A. Dietr.”. The erroneous inclusion of the latter, which is actually *Peperomia serpens* (Sw.) Loudon, is quite incomprehensible as Candolle excluded its basionym, *Piper reniforme* Poir., from the synonymy list.

In conclusion, *Verhuellia elegans* Miq. must now be considered a synonym of *Peperomia lunaria* Ham. and this species should be named *Verhuellia lunaria* (Ham.) C. DC. Even although the names are based on the same Poiteau collection, the later, *V. elegans*, is not illegitimate as each author specified a particular, and different, specimen, upon which his name was based (i.e., there are no syntypes of either name and Miquel did not include the holotype of *P. lunaria*, cf. Art. 52.2 of the ICBN, McNeill & al., 2006), the evident holotype of *V. elegans* being in Herb. Delessert (now at G) and that of *P. lunaria* in Herb. Desvaux (now at P).

Distribution. – Endemic to Hispaniola (Haiti and Dominican Republic).

Specimens studied. – HAITI. Massif des Cahos, Morne Basile, alt. 1,300–1,450 m., 15 Nov 1924, *Ekman H 2508* (C, K, S); Massif des Cahos, Petite-Rivière de l’Artibonite, Pérodin, alt. 900 m., 5 Mar 1925, *Ekman H 3414* (S); Massif du Nord, Marmelade, Morne Coudré, alt. 750 m, 29 May 1927, *Ekman H 8298* (S); Massif de la Hotte, Jérémie, between Source-Cahouane and La Source Chaude, alt. 150 m, 4 Jul 1928, *Ekman H 10241* (S). DOMINICAN REPUBLIC. Prov. Barahona, La Filipina, Loma Travesía, alt. 700–800 m, 1 Jan 1977, *Liogier 26186* (NY); without locality, 1803, *Poiteau s.n.* (B-W, BM, G-DC, HAL, L, P, S, U), and probably also *Ventenat s.n.* (C); Sierra de Bahoruco, Prov. Baharóno,

Filipinas, alt. 800 m, 24 Dec 2003, *Jiménez & García 3560* (JBSD, GENT).

Notes. – Miquel (1843–1844) mentioned in his protologue of *Verhuellia elegans* two syntypes: *Poiteau s.n.* in Herb. Delessert (G) and *Rudolphi s.n.* in Herb. Willdenow n. 742 (B). We were able to examine several more duplicates and it became obvious that these all belong to the same collection made in the Dominican Republic by the French plant collector Pierre-Antoine Poiteau in 1803. Karl Asmund Rudolphi (1771–1831), who never collected in the Dominican Republic, was responsible for depositing duplicates in the Willdenow (B) and Swartz (S) herbarium. The specimen from Herb. Ventenat (C) probably is also one of the Poiteau duplicates. Unfortunately, the name of the collector is not mentioned on all the duplicates, resulting in different citations of the collection: (1) with the name of the collector (Poiteau), (2) with the name of the person depositing the specimen (Rudolphi), (3) with the name of the author who used one of the specimens to describe a new species (e.g., Hamilton) or (4) with the name of the owner of the herbarium in which the specimen was deposited (Desvaux, Drake, Jussieu, Richard, Ventenat, etc.). Following careful comparison of the specimen labels and tracing the history of each duplicate, it seems that at least 13 duplicates of this collection are available.

Due to the historical confusion about the use of the names *V. elegans*, *V. reniformis* and *V. lunaria* for this particular species, most specimens are currently annotated *V. elegans*.

3. *Verhuellia pellucida* Schmitz, *Flora* 27: 420. 1872 ≡ *Mildea elegans* Griseb., *Cat. Pl. Cub.*: 63. 1866 – Type: *Wright 2264* (holotype: GOET; isotypes: BM!, G-DC!, GH!, HAC, K!, MA!, NY!, P!, S!, W!).

History. – In 1866 Grisebach published *Mildea elegans*, and in 1869 Candolle synonymized this species with *Verhuellia elegans* Miq. However, Schmitz (1872) disagreed with Candolle and stated that *Mildea elegans* and *Verhuellia elegans* were not identical. He noticed the leaves of *V. elegans* consistently have seven main nerves whereas *V. pellucida* (*Mildea elegans*) has three to five main nerves. Together with some minor differences in leaf size and shape, he considered this as sufficient to keep the two taxa distinct. As a consequence, he had to establish a new *Verhuellia* name for the former *Mildea elegans*: *Verhuellia pellucida*. *Verhuellia pellucida* has been synonymized recently with *V. elegans* (Saralegui Boza, 2004), although it is not clear on what basis.

Note. – Saralegui Boza (2004: 57) designated *Mildea elegans* Griseb. as the lectotype of *Mildea* Griseb.

Distribution. – Endemic to Cuba.

Specimens studied. – CUBA. Oriente, Sierra Maestra, alt. 200–400 m., 8 Aug 1922, *Ekman 14761* (NY, S, US); Oriente, Sierra Maestra, alt. 600–900 m., 9 Aug 1922,

Ekman 14812 (NY, S); Cuba, without precise locality or date, *Wright 510* (NY); Cuba Oriente, 1861, *Wright 2264* (BM, G-DC, GH, K, MA, NY, P, S, W).

The following *Verhuellia* combinations are synonyms of *Peperomia* species; the currently accepted names are in bold.

Verhuellia brasiliensis Miq., Syst. Piperac.: 48. 1843 ≡ ***Peperomia brasiliensis*** (Miq.) Miq., Fl. Bras. (Martius) 4(1): 10. 1852 ≡ *Peperomia verhuellia* C. DC., Prodr. 16: 398. 1869, nom. illeg.

Verhuellia knoblechteriana (Schott) C. DC., Prodr. 16: 391. 1869 ≡ *Peperomia knoblechteriana* Schott in Bot. Zeitung (Berlin) 9: 225. 1851 = ***Peperomia pellucida*** (L.) Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 1: 64. 1815.

Verhuellia serpens (Sw.) Miq., Syst. Piperac.: 48. 1843 ≡ *Piper serpens* Sw., Prodr. 16: 1788 ≡ ***Peperomia serpens*** (Sw.) Loudon, Hort. Brit.: 13. 1830.

A NEW SUBFAMILIAL CLASSIFICATION FOR THE FAMILY PIPERACEAE

The family *Piperaceae* is traditionally subdivided into two subfamilies, *Peperomioideae* and *Piperoideae*. However, as the relationships within the family are now recognized as (*Verhuellia* + ((*Zippelia* + *Manekia*) + (*Piper* + *Peperomia*))), this classification needs to be revised. It is proposed to divide the family in three subfamilies, congruent with the clades recovered by Wanke & al. (2007b).

Subfamily 1. *Verhuellioideae* Trel. ex Samain & Wanke, **subfam. nov.** – Type: *Verhuellia* Miq.

Herbae parvae perennes prostratae, caulibus filiformibus, foliis verticillis unilateralibus, laminis rotundatis vel reniformibus, membranaceis, nervatura palmata, inflorescentiae spicis parvis solitariis terminalibus, floribus remotis, antheris 2, stigmatibus 3–4.

Small, perennial, prostrate herbs with thread-like stems and adventitious roots. Monoecious. Leaves in whorls of three to four at each node, membranous; lamina rounded to reniform, with venation palmate. Inflorescence a solitary spike, terminal (“leaf-opposed”). Flowers distantly placed on the rachis, lacking perianth; stamens 2; stigmas 3–4.

Comprising a single genus, *Verhuellia* Miq., with three species in Cuba and Hispaniola.

Note. – The “subfamily *Verhuellieae*” has once been mentioned by Trelease (1930), although with a wrong termination. However, there is no description of the group

in this publication and the name *Verhuellieae* thus has not been validly published according to Art. 41.1 of the ICBN.

Subfamily 2. *Piperoideae* Arn., Encycl. Brit., ed. 7, 5: 130. 1832 – Type: *Piper* L.

Shrubs, lianas and terrestrial or epiphytic herbs, usually perennial, seldom annual. Dioecious or monoecious. Leaves alternate or whorled, occasionally peltate, membranous, coriaceous or succulent; lamina highly variable with venation palmate or pinnate. Inflorescence a solitary spadix, or compound, terminal, axillary or “leaf-opposed”. Flowers distantly to densely placed on the rachis, lacking perianth; stamens 2–6; stigmas 1–4.

About 3,600 pantropically distributed species. Comprising two genera: *Piper* L. (c. 2,000 species according to Quijano-Abril & al., 2006) and *Peperomia* Ruiz & Pav. (c. 1,600 species according to Wanke & al., 2006).

Subfamily 3. *Zippelioideae* Samain & Wanke, **subfam. nov.** – Type: *Zippelia* Blume.

Validating description that of Tribus *Zippelieae* Miq., Comm. Phytogr. 33, 41. 1840.

Perennial herbs (*Zippelia*) or lianas (*Manekia*). Monoecious. Leaves alternate, lamina ovate-cordate in *Zippelia* and variable in *Manekia*, with venation palmate. Inflorescences pedunculate (racemose in *Zippelia*; spicate, axillary, terminal, solitary or in pairs in *Manekia*). Flowers distantly to densely placed on the rachis, lacking perianth; stamens 4 (*Manekia*) to 6 (*Zippelia*); stigmas 3–5 (*Manekia*: 4–5; *Zippelia*: 3–4).

Comprising two genera: one occurring in China, Indonesia, Malaysia and perhaps surrounding countries (*Zippelia* Blume, monotypic), the other in Central and South America (*Manekia* Trel. with perhaps five species according to Arias & al., 2006).

ACKNOWLEDGEMENTS

We thank the curators of the herbaria B, BM, C, G, GH, K, NY, MA, S, U and US for making their *Verhuellia* specimens available for this study. The cooperation with F. Jiménez and Alexandra Stoll (Dresden) to obtain living material is gratefully acknowledged. We are grateful to Rosette Heynderickx (Ghent University) for assistance with tracing of several historical publications. Thanks to Dan H. Nicolson (Smithsonian Institution, Washington) for advice on the valid publication or otherwise of *Verhuellieae*. Many thanks to the editors Tony Orchard (Centre for Plant Biodiversity Research, CSIRO Plant Industry, Canberra, Australia) and John McNeill (Royal Botanic Garden, Edinburgh, Scotland, U.K.), and to an anonymous reviewer for the careful review of the manuscript. Our work is supported by the Research Foundation-Flanders (FWO G.0172.07), the Ger-

man Science Foundation (DFG NE 681/5-1), the German Academic Exchange (DAAD) Postdoc Program, the Department of Biology, Ghent University, and the Friends of the Botanical Garden, Gent.

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