

# The geophytic *Peperomia* subgenus *Tildenia* (Piperaceae) in the Andes with the description of new species in a phylogenetic framework

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**Background and aims** – The pantropical genus *Peperomia* consists of approximately 1,600 species with an extremely diverse vegetative morphology, especially in the Neotropics. One of the most startling yet overlooked growth forms is the geophytic one, as in subgenus *Tildenia*. This group occurs in seasonal Neotropical habitats with its highest diversity in Mexico-Guatemala and Peru-Bolivia with few species known from in between these hot spots.

**Methods** – Recent fieldwork in Peru and Bolivia combined with herbarium study and a Bayesian analysis of an aligned sequence matrix of the chloroplast *trnK-matK-psbA* gene cluster of one accession of each species resulted in new findings within this subgenus.

**Key results** – Fourteen new species are described, discussed in a phylogenetic framework and illustrated. Two species have a wide distribution and occur from central W. Peru to S. Bolivia: the common *P. cerrateae* and the rare *P. parvisagittata*. Three endemic species are described from the Amotape-Huancabamba Zone which is particularly rich in tuberous *Peperomia* species: *P. gigantea*, *P. jalcaensis* and *P. klopfensteinii*. Two species are only known from their type locality in central W. Peru: *P. ocrosensis* and *P. pugnicaudex*. Five other Peruvian species are *P. ayacuchoana* from Ayacucho, *P. querocochana* from Ancash, *P. wernerrauhii* from Huánuco, *Peperomia umbrosa* from three distant localities, and *P. pseudoverruculosa* which is relatively common in SE Peru. Two species are Bolivian endemics: the rare *P. purpureonervosa* from La Paz and the more common *P. radiatinervosa* from Cochabamba and Chuquisaca. Two former varieties, both endemics of the extreme northern Central Andes, are raised to species rank: *P. lilliputiana* and *P. pseudoperuviana*. Finally, basionym rejection and lectotypification are proposed for the widespread and commonly collected tuberous *Peperomia* in the southern Central Andes: *P. peruviana*. An emended description of *Peperomia* subgenus *Tildenia* is also provided.

**Key words** – *Peperomia*, Peru, Bolivia, Argentina, Ecuador, Colombia, Venezuela, Central Andes, Amotape-Huancabamba Zone, chloroplast *trnK-matK-psbA* gene cluster.

## INTRODUCTION

With approximately 1,600 species, the pantropical genus *Peperomia* described by Ruiz & Pavón in 1794 from Peru belongs to the ten most species-rich genera of angiosperms (Frodin 2004, Samain et al. 2009). Among the 24 *Peperomia* species Ruiz & Pavón described in 1798 are two peculiar tuberous species, *P. umbilicata* and *P. scutellifolia*, both occurring in ‘loma’ vegetation on very few localities along the Peruvian coast. They belong to what is now to be consid-

ered as *Peperomia* subgenus *Tildenia* (Miq.) Miq. (hereafter shortened as *Tildenia*), one of the most easily recognizable infrageneric *Peperomia* clades. This clade consists of approximately thirty currently accepted geophytic species with two easily observable synapomorphies: an entirely or partially underground tuber, and with petioles and peduncles originating directly from the tuber (Wanke et al. 2006, Samain et al. 2009). All these species occur in seasonal habitats of Neotropical mountain areas from Mexico to Argentina, with an

almost equally high diversity in Mexico and Guatemala in the northern hemisphere and in Peru and Bolivia in the southern hemisphere. In between these two hotspots, there are only a few species known from a limited number of localities.

*Tildenia* was originally described by Miquel (1843a) as a separate genus – then consisting of one species, *Tildenia mexicana* Miq. (accepted name = *Peperomia mexicana* (Miq.) Miq.) nom. cons. prop. (Mathieu 2009: 1374) – within the family Piperaceae. Shortly afterwards, Miquel (1843b) transferred *Peperomia umbilicata* Ruiz & Pav. to the genus but named it *Tildenia peruviana* Miq. (see also below). In his Systema Piperacearum, he recognized *Tildenia* as a subgenus ['sectio'] of genus *Peperomia* within the tribe Peperomieae (Miquel 1843c–1844). Dahlstedt (1900) recognized a much more widely circumscribed subgenus *Tildenia*, whereas Hill (1907) placed the tuberous geophytic species within the subsection *Geophila* of the subgenus *Tildenia* sensu Dahlstedt (Samain et al. 2007). However, recent phylogenetic analyses of the genus *Peperomia* based on coding and noncoding plastid DNA show that *Geophila* is clearly separated from the remaining species of *Tildenia* sensu Dahlstedt (1900), forming a distinct monophyletic clade which correctly should be named as *Peperomia* subgenus *Tildenia* (Miq.) Miq. (Wanke et al. 2006, 2007, Samain et al. 2007, 2009).

The last detailed studies dealing exclusively with *Tildenia* date back more than a century (Hill 1906, 1907). First, Hill (1906) published a detailed description of the morphology and seedling structure of this group. Next, he treated twelve South American and ten Mexican species (Hill 1907), some of which were later excluded or synonymized. Since this revision (Hill 1907), six taxa belonging to *Tildenia* in South America were newly described (Trelease 1936, Rauh & Kimnach 1987, Pino 2004, 2008, Pino et al. 2005). Similar to the species described in this paper, all species (except *P. polycephala* Trel.) were based on fresh field collections, generally made by the author himself, and clearly are separate species. These species are not only supported by distinct morphological characters but also by our ongoing molecular investigations, which in addition confirm the relatively narrow species concept which is applied in the whole genus *Peperomia*.

The similar habit of many *Tildenia* species hinders their identification and makes observations of living plants in their natural environment, as well as meticulous reinvestigation of existing herbarium material, a prerequisite for correct identification. Indeed, since the phenotype within *Tildenia* is superficially very similar, many collections were often identified under a few common better known names, which led to a wrong estimation of species number and distribution. A comprehensive reinvestigation of this group has largely been prevented by fragmentary and insufficiently documented herbarium material. The study of *Tildenia* especially suffers from 1) fragmentary herbarium specimens with missing tubers or inflorescences, 2) the plants being above-ground for part of the year only, usually during the rainy season, and 3) the plants being quite small and inconspicuous. The latter two problems also account for the fact that this group has been overlooked and undercollected all over its distribution area. Field work and observation of the plants during their life cycle in a living collection is necessary for accurate description of the characters of each species.

In close collaboration with local botanists, field work, dedicated nearly exclusively to this group, was carried out in the past years in all countries of high diversity of *Tildenia*. In total more than one year of intensive field work in South America has been accumulated by the authors of this paper, complemented by important long-term observation by local collaborators. The information obtained from intensive field-work in combination with screening of available herbarium specimens allowed for a detailed treatment of the species of Bolivia and Peru and the discovery of species new to science. During this study it became obvious that subgenus *Tildenia* in the Andean hotspot includes much more species than initially assumed. In this study fourteen species are newly described and shortly discussed in a phylogenetic framework, two former varieties are raised to species rank and for one name, basionym rejection and lectotypification are proposed. An emended description of *Peperomia* subgenus *Tildenia* is also provided.

## MATERIALS AND METHODS

### Field work and herbarium study

During field work in Bolivia (2008) and Peru (since the 1990s, and more intensively in 2009–2010), specimens of different developmental stages and longitudinal sections of tubers were preserved. When possible, infructescences with mature fruits were stored in 70% alcohol. After careful cleaning and digital imaging of all aerial and subterranean parts, plants were immediately pressed and dried using a hot air drier that kept the temperature of the specimens below 50°C. This study is based on 300 of our own recent collections and approximately 400 additional specimens from 57 herbaria (see acknowledgements for an enumeration of these herbaria).

### Sampling for molecular phylogeny

Our molecular phylogeny includes all currently known species of subgenus *Tildenia* reported from South America, with the exception of *P. minuta* Hill due to its uncertain taxonomic status. Whenever possible we used material from the type locality of the respective species. The outgroup consists of *P. pinoi* G.Mathieu, belonging to a yet unnamed subgenus closely related to *Tildenia*, *Piper crocatum* Ruiz & Pav. from the sister genus of *Peperomia*, and *Saururus chinensis* from Saururaceae, sister family to Piperaceae (Wanke et al. 2007). The plant material used for DNA extraction mainly comes from living plants collected in the field. Freshly harvested leaves were directly dried in silica gel. If silica dried material was not available, sampling was completed by material originating from herbarium specimens. The taxa used to generate the molecular data are listed in table 1 with detailed origin information, and Genbank accession numbers.

### DNA-isolation, amplification, and sequencing

We extracted genomic DNA following the modified miniprep procedure (Liang & Hilu 1996), published in Borsch et al. (2003). The final cleaning steps by ammonium acetate and sodium acetate were replaced by a single purification by col-

Table 1 – List of sampled taxa included in the present study.

species	lab number	voucher	field/garden origin (country, state/department)	geographical coordinates	altitude	Genbank accession
<i>P. andina</i> Pino	284	Pino 284 (USM)	Perú, Cajamarca	7°10'23"S 78°31'51"W	3,050 m	HQ331483
<i>P. ayacuchoana</i> Pino & Samain sp. nov.	Pe428	Samain et al. 2009-040 (BR, GENT, USM)	Perú, Ayacucho	12°56'37.0"S 74°01'15.0"W	3,190 m	HQ331493
<i>P. cerrateae</i> Pino sp. nov.	Pe408	Samain et al. 2009-002 (BR, GENT, USM)	Perú, Lima	11°26'51"S 76°36'57"W	2,750 m	HQ331484
<i>P. chutanka</i> Pino	Pe436	Samain et al. 2009-076 (GENT, USM)	Perú, Lima	12°09'17"S 76°23'40"W	3,320 m	HQ331485
<i>P. cyclaminoides</i> Hill	Pe110	Samain et al. 2008-080 (BR, GENT, LPB)	Bolivia, Tarija	21°09'16.5"S 64°41'32.0"W	2,940 m	HQ331486
<i>P. dolabella</i> Rauh & Kimmach	885	Pino 885 (USM)	Perú, Cajamarca	7°12'19"S 78°30'24"W	3,000 m	HQ331487
<i>P. gigantea</i> G.Mathieu & Pino sp. nov.	Pe358	Mathieu et al. 2009-158 (BR, GENT, USM)	Perú, Cajamarca	07°09'25.5"S 78°50'30.4"W	1,770 m	HQ331488
<i>P. jalcaensis</i> Pino sp. nov.	Pe394	Mathieu et al. 2009-120 (GENT)	Peru, Cajamarca	07°11'19.8"S 78°34'32.3"W	3,639 m	HQ331489
<i>P. klopfensteinii</i> Pino sp. nov.	Pe397	Mathieu et al. 2009-130 (BR, GENT, USM)	Perú, Cajamarca	06°39'32.3"S 78°44'01.4"W	2,450 m	HQ331490
<i>P. tilliputiana</i> (Pino & Cieza) Pino stat. nov.	Pe361	Mathieu & Symmank 2009-024 (BR, GENT, USM)	Perú, La Libertad	07°53'03.1"S 78°07'21.2"W	3,350 m	HQ331491
<i>P. macrorrhiza</i> Kunth	RM275	Pino 327 (USM)	Perú, Cajamarca	7°11'24"S 78°21'27"W	2,800 m	HQ331492
<i>P. oerosensis</i> G.Mathieu sp. nov.	Pe355	Mathieu et al. 2009-042 (USM, BR, GENT, K, MO)	Perú, Ancash	10°27'32.4"S 77°24'29.6"W	3,104 m	HQ331494
<i>P. parvifolia</i> C.DC.	Pe420	Samain et al. 2009-027 (GENT)	Perú, Huancavelica	12°20'40.8"S 74°56'13.0"W	4,180 m	HQ331495
<i>P. parvisagittata</i> G.Mathieu & Pino sp. nov.	Pe352	Mathieu & Symmank 2009-020 (BR, GENT, USM)	Perú, Ancash	10°09'31.4"S 77°21'13.3"W	3,480 m	HQ331496
<i>P. peruviana</i> Dahlist.	Pe168	Symmank et al. 2008-036 (BR, GENT, LPB, MO)	Bolivia, La Paz	15°44'14.8"S 68°41'54.0"W	2,250 m	HQ331497
<i>P. polycephala</i> Trel.	Pe446	Samain et al. 2009-113 (BR, GENT, USM)	Perú, Cuzco	13°20'33.7"S 71°56'40.3"W	2,950 m	HQ331498
<i>P. pseudoperuviana</i> (Pino) Pino stat. nov.	P151	Pino 894 (USM)	Perú, Cajamarca	7°17'31"S 78°29'27"W	2,370 m	HQ331499

Table 1 (continued) – List of sampled taxa included in the present study.

species	lab number	voucher	field/garden origin (country, state/department)	geographical coordinates	altitude	Genbank accession
<i>P. pseudoverruculosa</i> G.Mathieu sp. nov.	Pe432	Samain et al. 2009-052 (BR, GENT, USM)	Perú, Ayacucho	13°18'55.7"S 73°58'48.8"W	3,450 m	HQ331500
<i>P. pugnicaudex</i> Pino sp. nov.	Pe412	Samain et al. 2009-007 (BR, GENT, USM)	Perú, Lima	11°44'24.4"S 76°16'48.7"W	3,430 m	HQ331501
<i>P. purpureoneervosa</i> G.Mathieu sp. nov.	Pe174	Symank et al. 2008-051 (BR, GENT, LPB, MO)	Bolivia, La Paz	16°18'54.8"S 67°55'28.4"W	3,270 m	HQ331502
<i>P. quercocochana</i> G.Mathieu & Pino sp. nov.	Pe372	Mathieu et al. 2009-043 (BR, GENT, MO, USM)	Perú, Ancash	10°20'08.1"S 77°20'88.0"W	3,956 m	HQ331503
<i>P. radiatinervosa</i> G.Mathieu sp. nov.	Pe121	Samain et al. 2008-090 (BR, G, GENT, K, LPB, MO)	Bolivia, Chuquisaca	19°05'11.2"S 65°13'14.5"W	2,900 m	HQ331504
<i>P. rupiseda</i> C.DC.	Pe413	Samain et al. 2009-008 (GENT, USM)	Perú, Lima	11°08'52.8"S 76°21'25.6"W	2,680 m	HQ331505
<i>P. scutellifolia</i> Ruiz & Pav.	Pe579	Pino 2439 (USM)	Perú, Arequipa	15°46'56"S 74°23'13"W	1,016 m	HQ331506
<i>P. umbilicata</i> Ruiz & Pav.	Pe324	Pino 1375 (USM)	Perú, Lima	11°21'17"S 77°21'56"W	590 m	HQ331507
<i>P. umbrosa</i> G.Mathieu sp. nov.	Pe395	Mathieu et al. 2009-122 (BR, GENT, USM)	Perú, Cajamarca	07°11'29.7"S 78°34'48.0"W	3,557 m	HQ331508
<i>P. verruculosa</i> Dahlst. ex Hill	Pe456	Samain et al. 2009-123 (BR, GENT, USM)	Perú, Cuzco	13°30'08.3"S 71°58'48.2"W	3,660 m	HQ331509
<i>P. wernerrauhii</i> Pino & Samain sp. nov.	Pe482	Samain et al. 2009-214 (BR, GENT, USM)	Perú, Huánuco	09°53'36.8"S 76°09'03.2"W	2,470 m	HQ331510
<b>Outgroup</b>						
<i>Piper crocatum</i> Ruiz & Pav.		Wanke 070 (DR)	BG Bonn, 18143	-	-	DQ212714
<i>Saururus chinensis</i> Hort. ex Loudon		Wanke 001 (DR)	BG Bonn, 00312	-	-	DQ212713
<i>P. pinoi</i> G.Mathieu aff.	Pe474	Samain et al. 2009-230 (GENT, USM)	Perú, Huánuco	12°22'02.4"S 74°48'20.7"W	3,560 m	HQ331482

**Table 2 – Primers used in present study.**

primer	direction	sequence 5'–3'	reference
MG15	for.	ATC TGG GTT GCT AAC TCA ATG	Liang & Hilu (1996)
Pe-matK-2000F	for.	TTC CTT ACG AAT CCA TAG A	Wanke et al. (2006)
Pe-matK-2500R	rev.	TTC GCA ATA AAT GCA AAG AGG	Wanke et al. (2006)
Pe-matK-2140F	for.	ACTTTATCTATTTATGGCAATG	this study
Pe-matK-2340R	rev.	TTTCTCTTTGACATTGAACCAA	this study
psbA-R	rev.	CGCGTCTCTCTAAAATTGCAGTCAT	Steele & Vilgalys (1994)

umns using the NucleoSpin®-Extract II kit (MachereyNagel). We amplified the whole gene cluster (*trnK* intron, *matK* gene and the *trnK-psbA* spacer) in two parts with an overlapping region of 200 to 400 bp depending on the primer sets employed (table 2).

The Polymerase Chain Reaction (PCR) consisted of an initial denaturation for 5 min at 94°C and 34 cycles of the following steps: (1) denaturation for 1 min at 95°C, (2) annealing for 1 min at 48°C, (3) elongation for 2 min at 68°C. Finally, the reaction was treated at 68°C for 20 min and subsequently stored at 4°C. The PCR was carried out in 50 µl reactions, containing 1 µl DNA template of total genomic DNA (~ 10–50 ng), 10 µl dNTP mix (1.25mM each), 2 µl of each primer (20 pmol/µl) and 1 µl Taq Polymerase (PeqLab). After gel electrophoresis we cleaned the PCR products by NucleoSpin®-Extract II purification kit (MachereyNagel). The DNA sequencing was carried out on a Perkin Elmer automated sequencer (ABI Prism 377) or by MacroGen Inc. sequencing service (MacroGen, Seoul, Korea). We manually edited and aligned the sequences using PhyDE® (Müller et al. 2005).

### Phylogenetic analyses

Phylogenetic analyses were conducted on the aligned sequence matrix after exclusion of five small regions of uncertain sequence homology assessment in the noncoding parts (table 3). Additionally, indels were coded at the end of the sequence matrix applying the simple coding algorithm of Simmons & Ochoterena (2000), implemented in the program SeqState (Müller 2005). We used jModeltest 0.1.1 (Posada 2008) to detect the optimal evolutionary models for our se-

quence data. Bayesian inference was applied using MrBayes v3.1 (Ronquist & Huelsenbeck 2003) with the 'model of best fit', GTR+G (-lnL=10.479,161) for the sequence partition. Ten runs with four chains each were executed simultaneously, initiated from random starting trees. Four million MCMC generations were run with a sampling frequency of 100. We assessed the burn-in using the program Tracer v1.5 (Rambaut & Drummond 2009). After exclusion of the first 10% of the sampled trees we constructed a majority rule consensus tree with posterior probabilities ≥ 0.5. The resulting phylogenetic hypothesis was graphically displayed using TreeGraph 2 (Stöver & Müller 2010; fig. 1).

## RESULTS AND DISCUSSION

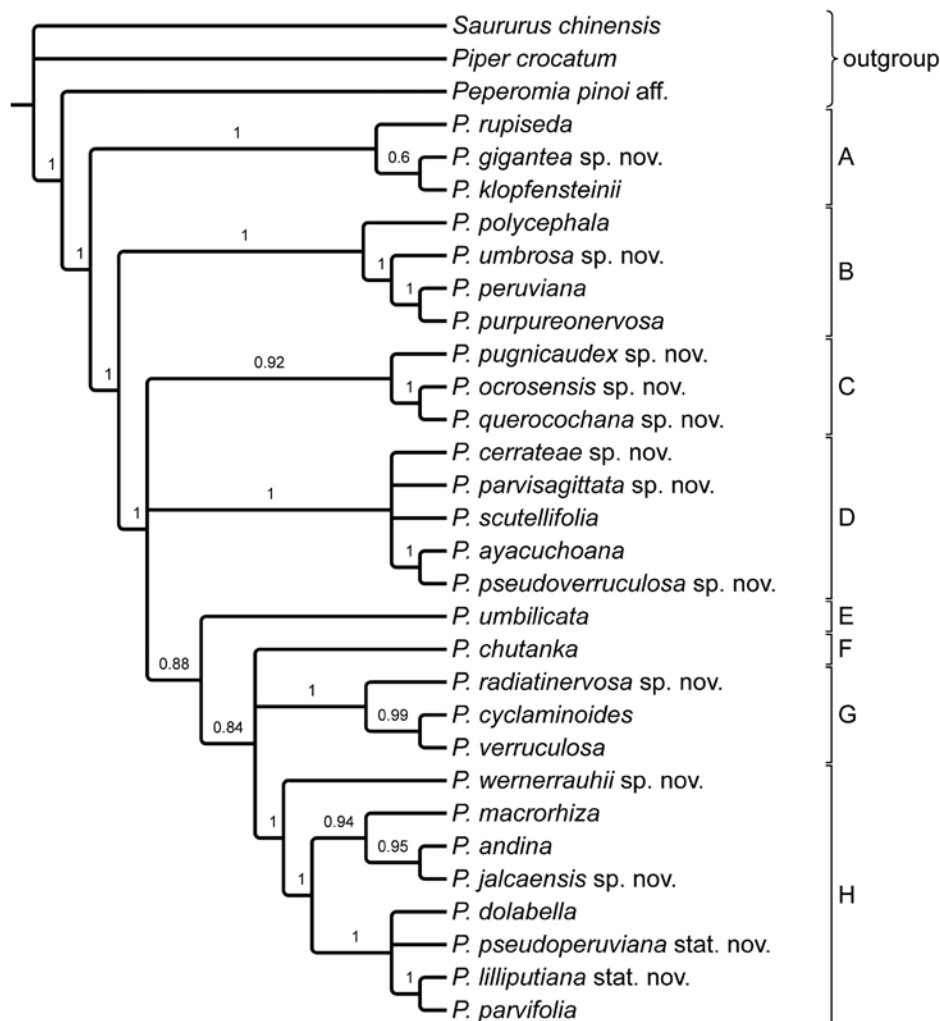
### Species concept and morphological variation

The species concept in *Peperomia* is quite narrow and intra-specific variation has not been investigated. This narrow concept of morphospecies hinders research within the genus, as it is very difficult to get familiar with such a large number of (sometimes highly similar) species within a relatively short period of time. The large species number is the direct reason for maintaining the morphological species concept, as a different and perhaps more convenient concept could only be introduced after a review of the whole genus or of at least a well-delineated group within the genus, such as a subgenus (Samain 2008). However, this morphological species concept is not problematic in *Tildenia* as, compared to some other subgenera, it consists of a relatively small number of species which are generally easy to distinguish and key out on the basis of conspicuous macromorphological characters. According to our observations, intraspecific variation is also quite limited in this group and is mainly restricted to a change in tuber shape (e.g. branching) with increasing age. Nevertheless, it remains difficult to include such variation into some species descriptions as a consequence of the very slow growth rate of the tuber.

The biology of *Tildenia* is also entirely unknown. Whereas extensive research was performed for some common epiphytic *Peperomia* species, e.g. *P. macrophylla* (Youngsteadt et al. 2008), terrestrial species have not yet been seriously investigated with regard to pollination, fruit distribution, etc., perhaps as a consequence of the generally accepted idea that most *Peperomia* species are epiphytes. Data on hybridisation and cytology are also not available for *Tildenia*.

**Table 3 – Position of hotspots excluded from analyses in the *trnK-psbA* alignment.**

hotspot	position	
H1	406–409	<i>trnK5'</i> -intron
H2	444–452	<i>trnK5'</i> -intron
H3	510–518	<i>trnK5'</i> -intron
H4	2448–2467	<i>trnK3'</i> -intron
H5	2589–2594	<i>trnK3'</i> -intron
H6	2661–2664	<i>trnK3'</i> -intron
H7	2848–2855	<i>trnK-psbA</i> spacer
H8	2933–3052	<i>trnK-psbA</i> spacer



**Figure 1** – Phylogenetic tree derived from Bayesian inference based on *trnK-psbA* gene cluster. The phylogenetic position of the newly described species is shown with respect to the remaining South American species of *Peperomia* subgenus *Tildenia*. Posterior probabilities (PP) are shown above branches. See text for explanation of brackets along the tree.

### Phylogeny and classification

Our phylogenetic hypothesis lends support to the morphological species concept employed within the Andean *Tildenia* species. Figure 1 shows the phylogenetic relationships based on the chloroplast *trnK-psbA* gene cluster of these species, each represented by one accession, the type specimen, or in case of previously described species, a collection from the type locality. Most of the currently accepted species and all described species hereafter are supported by these molecular data.

Hill (1907) distinguished four rankless groups in his subsection *Geophila* Hill, mainly based on tuber morphology: *Parvifoliae*, *Umbilicatae*, *Campylotropae* and *Rhizomatosae* (Samain et al. 2007). However, as two species are each mentioned in two different groups, it is likely he did not want to give any taxonomical value to these groups. Our results show that these groups do not correspond to any of the monophyletic clades recognized based on the *Tildenia* molecular phylogeny. Instead, there is a geographical pattern with eight

Andean clades consisting of all included South American species. In addition to this parallelism between phylogenetic relationships and distribution, there also is a morphological evolution pattern with regard to the position of the roots on the tuber. The first branching Andean clades (fig. 1A–D) mainly consist of species with tubers with roots growing at the apex or all over their surface and rarely at the base whereas it is exactly the opposite in the last branching clades (fig. 1E–H). A detailed study of character evolution in the whole subgenus elucidating the possible correlation of root position as well as other characters with habitat variables will be published elsewhere.

### Distribution in the Andes

The diversity of *Tildenia* species is highest in the Central Andes, defined by e.g. Weigend (2002) as the area between the Huancabamba Depression in Northern Peru (at 4–6°S) and central Bolivia (near Santa Cruz, at 18°S), followed by the Southern Andes (up to approximately 26°S in northern

Argentina) and the northern Andes (between approximately 2°N in Ecuador up to nearly 11°N in Venezuela). All species included in the analysis of figure 1 occur in the Central Andes. The highest species diversity as well as the highest number of endemics of the clade is encountered in Cajamarca, S. Amazonas and La Libertad. This area coincides with the surroundings of the so-called Amotape-Huancabamba Zone, an east-west depression made by the Río Chamaya/Río Marañón drainage system. This zone forms at the one hand a biogeographic barrier to montane taxa between the Northern Andes and the Central Andes of Northern Peru, and at the other hand a biogeographic connection between the lowland forests of the Pacific coast and the Amazon basin through its lowest point at the Western Cordillera at the Paso de Porculla (2,145 m). It is considered as an important biodiversity centre (e.g. Young & Reynel 1997, Knapp 2002, Stern et al. 2008, Weigend 2002, 2004, Weigend et al. 2010a, 2010b).

Within the phylogenetic tree, a certain geographical pattern can be distinguished. The distribution core of clade A is in the southern portion of the Amotape-Huancabamba Zone with the rare species *P. klopfensteinii* and *P. gigantea* in the southern part and slightly south of this zone. The third species, *P. rupiseda* is wider spread and also ranges to the south until the department of Lima. Clade B consists of four species with main distribution ranging from central and southern Peru (*P. umbrosa* and *P. polycephala*) to Bolivia (*P. purpureonervosa* and *P. peruviana*) and up to northern Argentina (*P. peruviana*). Clade C consists of three rare species occurring in the western Cordillera in the Peruvian departments Lima and Ancash. Clade D does not show a clear geographical pattern. *Peperomia scutellifolia* is one of the two coastal loma species described by Ruiz and Pavón from the department of Arequipa. The other species in this clade are more widespread although *P. parvisagittata* is only known from three localities. Within this clade, *P. cerrateae* has a remarkably large distribution area ranging from central Peru to southern Bolivia. Branch E refers to the single species *P. umbilicata*, the second loma species from the Peruvian departments of Lima, Ancash and La Libertad. Branch F equally consists of the single species *P. chutanka* known from few localities of the department of Lima. Clade G consists of three species with core distribution of *P. radiatinervosa* and *P. cyclaminoides* from central to south Bolivia and *P. verruculosa* which is widespread in central and south Peru. Finally, clade H consists of eight species, six of which are restricted to the Amotape-Huancabamba Zone. The two other species do not occur in this zone: *P. wernerrauhii* is known from the central Peruvian department of Huánuco whereas *P. parvifolia* occurs from central Peru to northern Argentina.

The species from the Amotape-Huancabamba Zone occur in different clades within the phylogeny, potentially indicating multiple parallel species radiations in this area. Also, the rest of the Central Andes is species-rich for *Tildenia* and has several rare endemic species scattered over the whole area. So far, we did not yet find a particular pattern in occurrence of these endemics. However, with the exception of the coastal species, *P. scutellifolia* and *P. umbilicata*, which grow on few remaining localities in the loma vegetation – habitats which are suffering heavily from human pressure – it should be emphasized that a large portion of the central Andes is undercol-

lected for *Tildenia*. As a consequence, we do not yet know whether the pattern of narrow endemics we observe here is an artifact because of undercollecting or a genuine biogeographical pattern.

The Central Andes share several species with the southern Andes. Several of these are growing only in the southernmost portion of the Central Andes and the extreme northern part of the southern Andes, e.g. *P. cyclaminoides*, *P. radiatinervosa*. In contrast, some species have a much broader range, e.g. *P. parvifolia* and *P. peruviana*. The latter is probably the species with the southernmost occurrence on the American continent, as it has been collected at up to 26°S in the Argentinian province Tucumán. *Peperomia peruviana* is sister to an endemic species from the Bolivian department La Paz, *P. purpureonervosa*. It is important to note here that the herbarium specimens of the northern Andes in Ecuador, Colombia and Venezuela which are identified as *P. peruviana* probably belong to a different yet undescribed species. However, recent attempts to collect this species in Colombia were not successful due to the extreme drought as a consequence of the El Niño weather phenomenon in the second half of 2009 and the first months of 2010. A detailed biogeographical study including extensive analyses for the whole subgenus will be published elsewhere.

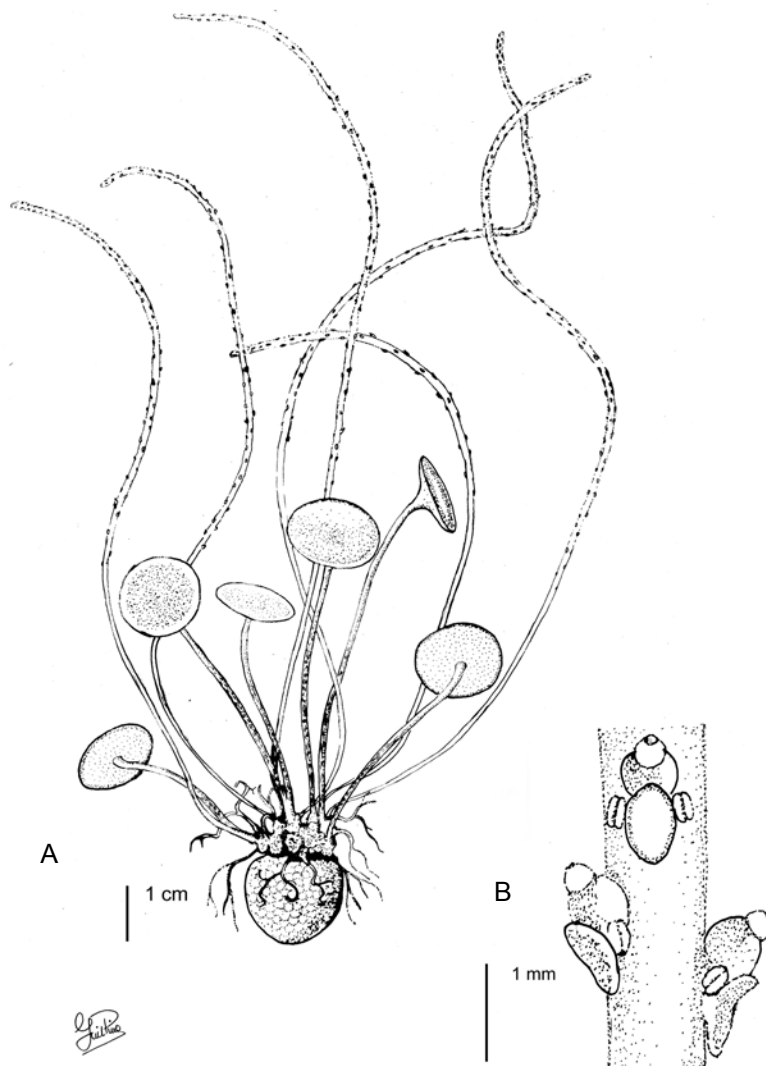
## TAXONOMIC TREATMENT

The present treatment covers seventeen Andean species of *Peperomia* subgenus *Tildenia* of which fourteen new species, two former varieties which are raised to species rank and basionym rejection and lectotypification for one name.

***Peperomia* subgenus *Tildenia* (Miq.) Miq.** (Miquel 1843c–1844: 69). – Type: *Tildenia mexicana* Miq., nom. cons. prop. (Mathieu 2009: 1374) (accepted name *Peperomia mexicana* (Miq.) Miq.)

Geophytic herbs with a perennial tuber and annual leaves and peduncles of inflorescences directly originating from the tuber.

**Geophytic herbs**, minute to large, 2–50 cm tall, entirely glabrous. **Tuber** entirely to partially buried, (sub)globose to ellipsoid, sometimes flattened or irregularly shaped, sometimes apically lobed, or rarely rhizomatous, rooting at apex, at base, or with roots all over its surface, whitish, yellowish or brownish. **Leaves** 1–20 per plant; petioles originating apically or rarely laterally on tuber; lamina often orbicular, occasionally (ob-)ovate, cordate, deltoid, or reniform, membranous to coriaceous, rarely succulent, generally peltate, rarely non-peltate, often conspicuously palmatinerved. **Inflorescences** simple spadices, rarely compound; peduncles developing from the apical part of the tuber; spadices 1–20, peduncle and rachis generally slender, peduncle usually shorter than the often loosely flowered rachis. **Floral bracts** generally peltate, rarely non-peltate, orbicular, ovate or elliptic, apex rounded, acute or acuminate, occasionally glandularly dotted. **Stamens** with (sub-)globose anthers, often very small, filaments short, occasionally long, caducous or persistent but wilting during fructification. **Ovary** ellipsoid, ovoid or conical, generally larger than the style; style conical, ellipsoid, obovoid, mam-



**Figure 2** – *Peperomia ayacuchoana*: A, general habit; B, part of fruiting rachis. Drawn by G. Pino.

miform or cylindrical, sometimes glandularly dotted; stigma terminal, sometimes fimbriate, occasionally cone-shaped, sometimes on a stigmal plateau, rarely flabelliform. Fruit (sub)globose, ellipsoid, ovoid, (sub)sessile or pedicellate, pericarp completely or partially granulose, (minutely) papillate or verruculose, rarely partially smooth.

The concept of *Peperomia* subg. *Tildenia* is here recircumscribed according to phylogenetic relationships determined by Wanke et al. (2006) and Samain et al. (2009). In contrast to Dahlstedt (1900), who expanded the circumscription to include all species with peltate leaves, the clade is restricted to the geophytic species exhibiting a perennial tuber from which petioles and peduncles of seasonal leaves and inflorescences directly originate. As such, the current circumscription largely corresponds to subsection *Geophila* A.W.Hill (1907). *Peperomia cotyledon* Benth. is excluded while the species described herein are included.

### 1. *Peperomia ayacuchoana* Pino & Samain, *sp. nov.*

Planta tubere globoso obovoideo supra excrescentia more capituli obtecto, foliis petiolatis peltatis rotundatis, spadicebus longissimis laxifloris pedunculo rachidi aequanti. Differt a *P. peruviana* Dahlst. forma, magnitudine coloreque tuberis, stylo quoque doliiformi (in illa elongato); a *P. pseudoverruculosa* G.Mathieu proxima, sed differt tubere majore rubrobrunneo, foliis majoribus et fructibus haud verruculosus. – Type: Peru, Ayacucho, prov. La Mar, dist. Tambo, along road Ayacucho–San Francisco, km 65–66, near Tambo, on rocks, 12°56'37"S 74°01'15"W, alt. 3,190 m, 24 Jan. 2009, Samain et al. 2009-040 (holo-: USM; iso-: BR, GENT).

Small herb, 9–16(–20) cm tall. Tuber entirely buried, globose to obovoid, light reddish brown, obscurely tessellate, 0.6–1.5 × 0.5–1.7 cm diam., base rounded, rooting at apex, which forms an irregular hemispherical excrescence, 0.4–0.9 × 0.6–1.3 cm diam., developing with age. Leaves 3–7 per plant; petiole 3–6 cm × 0.9–1.0 mm, terete, light



green with reddish longitudinal lines near base, lighter and slightly thicker near insertion to lamina, erect to slightly curved; lamina orbicular, coriaceous, flat to slightly concave, centrally peltate, 1.2–1.9 cm diam., margin entire, adaxially glossy green, nerves obscure, abaxially greenish white, only main nerve conspicuous. *Spadices* 6–17 per plant, initially erect, then slightly curved; peduncle 3.5–9 cm × 0.8–0.9 mm diam., light green or pink near base; rachis 4–9 cm × 0.9–1.1 mm diam., light green, loosely flowered. *Floral bracts* elliptic, 0.7–0.8 × 0.5–0.6 mm, peltate, dark green, brown when old. *Stamens* with filaments 0.1–0.2 mm long, terete, white; anthers subglobose 0.3–0.4 mm wide, white when young, dark brown when drying. *Ovary* widely ovoid, 0.7 × 0.5 mm, bright green to brownish, stigma brown. *Fruit* ovoid, body 0.8–0.9 × 0.6–0.7 mm; pericarp papillate, shiny dark brown; style cylindrical to conical, 0.15–0.25 × 0.25–0.35 mm, brown. Fig. 2.

**Other representative specimens examined** – Peru: Ayacucho, prov. La Mar, dist. Tambo, along road Ayacucho–San Francisco, km 65–66, near Tambo, 12°56'37.9"S 74°01'16.8"W, alt. 3,180 m, 24 Jan. 2009, *Samain et al.* 2009-041 (GENT, USM); loc. cit., km 72, 12°55'51"S 74°00'19"W, alt. 3,290 m, 24 Jan. 2009, *Samain et al.* 2009-042 (GENT, USM); loc. cit., km 64, 12°57'05"S 74°01'21"W, alt. 3,410 m, 24 Jan. 2009, *Samain et al.* 2009-044 (GENT, USM); prov. San Miguel, 'Hatun Wayqo' 50 km E of Ayacucho, road to the jungle, 27 Mar. 2003, *Pino* 1114 (photographs).

**Etymology** – This species is named after the Peruvian department of Ayacucho, where it was collected first. Note: This name is different from *P. ayacuchoana* Trel., which is a herbarium name referring to *P. serpens* (Sw.) Loudon (Mathieu 2007: 44).

**Relationships** – This new species has a very particular apical outgrowth upon the tuber, from where roots, petioles and spadices grow. Plants resemble *P. peruviana* Dahlst. but this latter species has smaller irregularly globose tubers developing the upper appendage only in old plants, and its fruits have a prolonged style compared to the short, barrel-like style of *P. ayacuchoana*. *Peperomia ayacuchoana* also resembles *P. pseudoverruculosa* G.Mathieu but has larger, reddish brown and minutely tessellated tubers, longer spadices and non verruculose fruits. According to our phylogenetic analysis, *P. ayacuchoana* is sister to *P. pseudoverruculosa* (fig. 1).

**Phenology** – Leaves are present from November to April, spadices appear from January to March, and fruits ripe from February to March.

**Distribution and habitat** – This species has only been collected in the department of Ayacucho in rocky places where it tolerates sun exposure, drought and human disturbance.

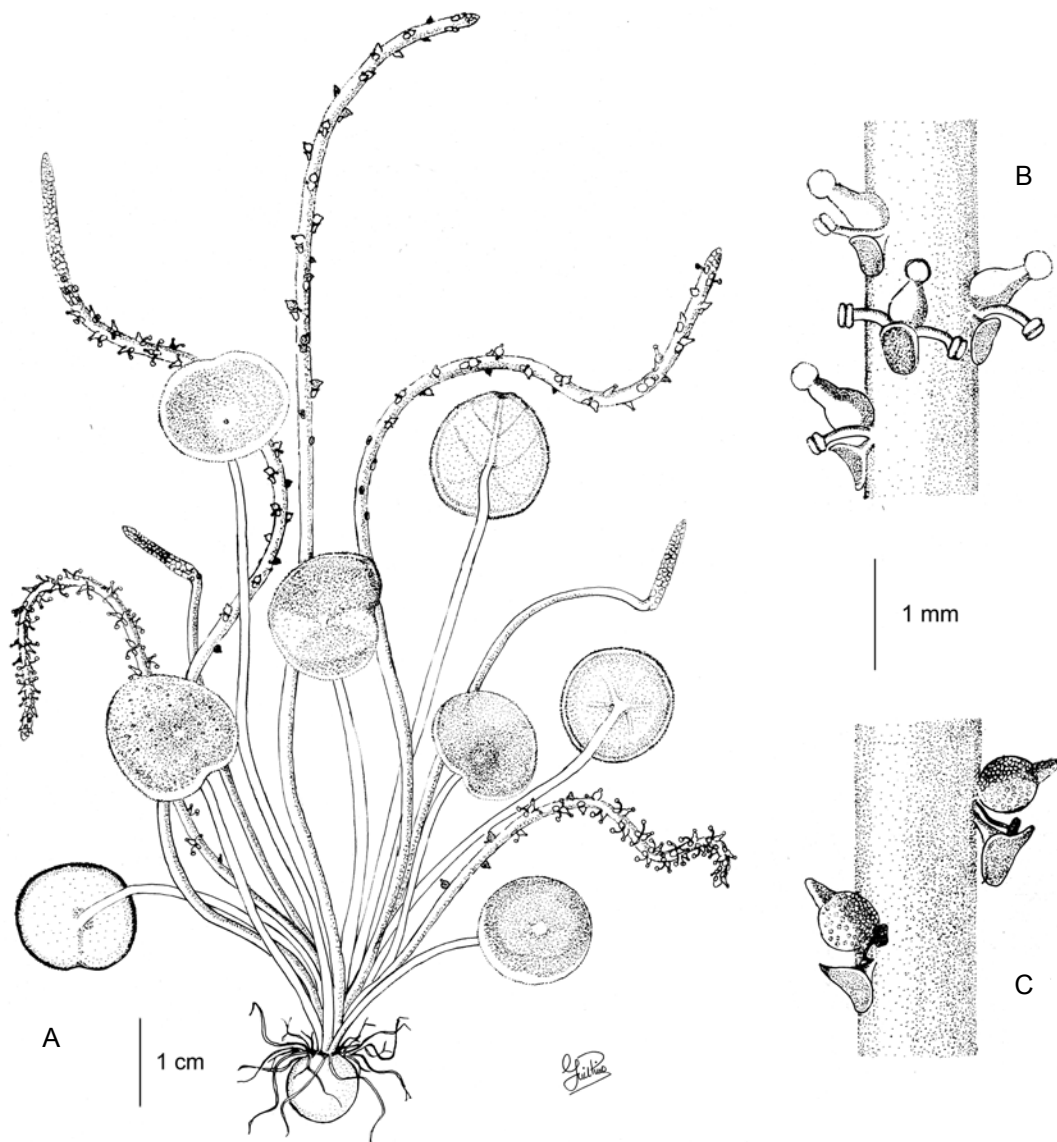
## 2. *Peperomia cerrateae* Pino & G.Mathieu, sp. nov.

Planta geophila a *P. scutellifolia* Ruiz et Pavón similis sed differt rachidibus spadicum decumbentibus longioribus angustioribusque; ab ea crescit in locis frigidis simulque humidis in montibus altis apud 3,000–4,000 m, foliis spadicibusque tantum a Novembre ad Aprilem praesentibus. – Type: Peru, Lima, prov. Huarochirí, dist. Mariatana, Huancalasila, under rocks, 12°14'S 76°23'W, alt. 3,750 m, 4 Apr. 1968, *Cerrate et al.* 4436 (holo-: USM 210992).

Small herb, 3–7 cm tall. Tuber entirely buried, globose, very light yellow, greenish when exposed to daylight, brown when old, smooth, rooting from the apex, base rounded, 0.6–0.9 cm diam. *Leaves* 4–8 per plant; petiole (2–)3–6(–8) cm × 0.7–1.4 mm, terete, whitish, straight to slightly curved; lamina orbicular, chartaceous, flat to slightly concave, centrally peltate, 9–20 mm long, 11–22 mm wide, base rounded to subcordate, very rarely with overlapping lobes, apex widely emarginate (90% of the leaves) or rounded, margin entire, adaxially glossy green, minutely pitted, minutely centrally umbilicate, obscurely 5-palmatinerved, abaxially greenish white, only central nerve conspicuous from insertion of petiole to apex. *Spadices* 4–9(–14) per plant; peduncle 2–5 cm × 0.6–0.8 mm, whitish, initially peduncle erect with nutant rachis, then the whole inflorescence erect or slightly curved; rachis (1–)6–9(–12) cm × 0.7–1.1 mm, very light green, flowered every 0.5–1 mm. *Floral bracts* 0.6–0.7 × 0.4–0.5 mm peltate, ovate, green, brown when old. *Stamens* with filaments 0.3–0.4 × 0.12 mm, terete, white; anthers subglobose 0.3–0.4 mm diam., white when young, dark brown when drying. *Ovary* narrowly ovoid to conical, bright green, 0.5–0.6 × 0.3 mm; stigma white, flabelliform. *Fruit* ovoid, 0.5–0.6 × 0.4–0.5 mm; pericarp papillate, olive green-brownish; style narrowly cylindrical to conical, 0.15–0.25 × 0.08–0.09 mm, brown. Fig. 3.

**Other representative specimens examined** – Bolivia: La Paz, prov. Inquisivi, along 'Jucumarini Trail' between Chichipata and Jucumarini, Condor Conuña area, sandstone cliffs 2 km N of Quime, very fragile, growing entwined with the moss *Thuidium yungarum*, 16°58'S 67°13'W, alt. 3,300–3,400 m, 23 Feb. 1990, *Lewis* 37133 (LPB); prov. Larecacha, 11 km from Sorata on road to Consata, 15°43'40.9"S 68°39'26.2"W, alt. 3,200 m, 17 Jan. 2008, *Symmank et al.* 2008-041 (BR, GENT, K, LPB, MO); prov. Murillo, 1 km N (below) the dam of Lake Zongo, wet puna vegetation, at the base of rocks, 16°17'S 68°07'W, alt. 4,600 m, *Solomon* 15839 (LPB, MO); valley of the Rio Zongo, 20 km N of the pass, shrubby vegetation (3–4 m) along creeks flanked by pastures, in moss mats in shady spots, 16°09'S 68°07'W, alt. 3,400 m, 17 Nov. 1987, *Solomon* 17433 (BR, LPB); Cochabamba, prov. Quillacollo, Cerro Tunari, 17°15'47.8"S 66°20'59.3"W, alt. 4,080 m, 12 Feb. 2008, *Samain & Bates* 2008-146 (GENT, LPB); Tarija, prov. Eustaquio Méndez, near León Canche, 21°06'50.2"S 64°41'42.1"W, alt. 3,000 m, 30 Jan. 2008, *Samain et al.* 2008-081 (BR, GENT, LPB).

**Peru:** Ancash, prov. Bolognesi, dist. Cajacay, road Huaraz–Pativilca, km 103, 1 km above Majoralca, c. 250 m uphill Cerro Huansharury, 10°09'33"S 77°21'06"W, alt. 3,560 m, 25 Jan. 2009, *Mathieu & Symmank* 2009-021 (BR, GENT, USM); prov. Ocos, dist. Ocos, road Paramonga–Conococha (via Ocos), km 24, 10°20'31"S 77°24'20"W, alt. 2,360 m, 3 Feb. 2009, *Mathieu et al.* 2009-041 (BR, GENT, USM); road Huaraz–Paramonga, km 98, rock wall next to road, 10°00'32.7"S 77°23'15.1"W, alt. 2,975 m, 3 Feb. 2009, *Mathieu et al.* 2009-044 (BR, GENT, USM); Ayacucho, prov. Huamanga, dist. Acocro, along road Ayacucho–Chincheros km 79, 13°23'18.5"S 73°57'38.1"W, alt. 4,090 m, 26 Jan. 2009, *Samain et al.* 2009-055 (GENT, USM); along road Ayacucho–Chincheros km 82, 13°23'57.4"S 73°56'52.3"W, alt. 4,020 m, 26 Jan. 2009, *Samain et al.* 2009-056 (GENT, USM); loc. cit., *Samain et al.* 2009-057 (GENT, USM); Junín, prov. Chupaca, along road Huancayo–Yauyos, 27 km from Huancayo, 500 m before Roncia, 12°01'38"S 75°24'29"W, alt. 3,350 m, 21 Jan. 2009, *Samain et al.* 2009-016 (GENT, USM); Lima, prov. Huarochirí, dist. San Mateo, central highway km 98, beyond Infiernillo railroad bridge, N bank of Rimac river, before Cacray tunnel, aside waterfall, 11°44'21"S 76°16'45"W, alt. 3,300 m, 29 Mar. 2002, *Pino* 836 (USM); central



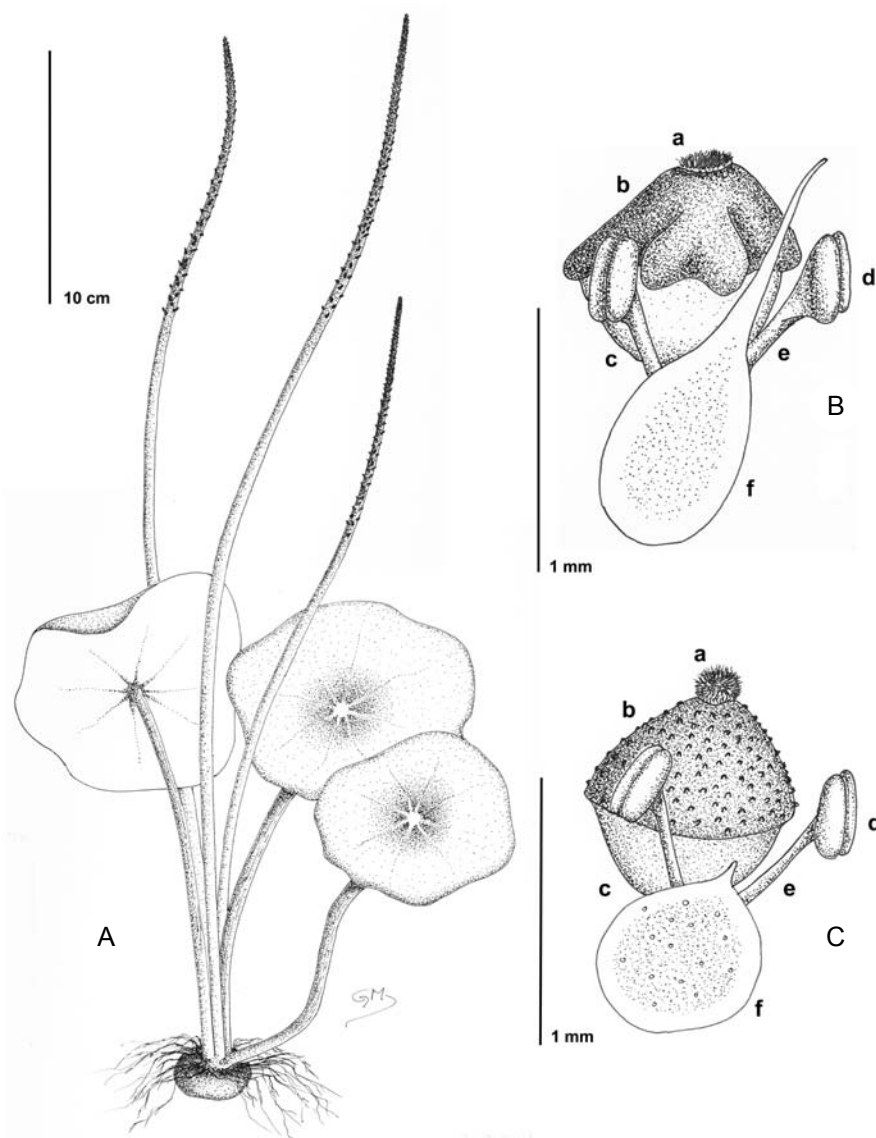
**Figure 3** – *Peperomia cerrateae*: A, general habit; B, part of flowering rachis; C, part of fruiting rachis. Drawn by G. Pino.

highway km 99, Anchi II bridge, W bank of Anchi river (flowing into the Rimac river from the S), on rocks, 11°42'46"S 76°16'13"W, alt. 3,680 m, 21 Mar. 2004, *Pino* 1294 (USM); loc. cit., 8 Jan. 2005, *Pino* 1446 (USM); loc. cit., 6 Apr. 2006, *Pino* 1650 (USM); E bank of Anchi river, 11°43'56"S 76°16'05"W, alt. 3,440 m, 18 Jan. 2009, *Samain et al.* 2009-006 (BR, GENT, USM); dist. Chicla, central highway km 110, in small N exposed canyon, 11°40'26"S 76°12'20"W, alt. 3,900 m, 15 Dec. 2003, *Pino* 1254 (USM); central highway km 111, on rocks, 11°40'02"S 76°14'51"W, alt. 3,950 m, 1 May 2005, *Pino* 1441 (USM); central highway km 108, slope next to road and opposite church tower of Chicla, 11°42'16"S 76°16'05"W, alt. 3,790 m, 18 Jan. 2009, *Samain et al.* 2009-005 (BR, GENT, USM); dist. San Damián, road Santiago de Tuna–San Damián, before the town, on rocks, 12°00'22"S 76°24'12"W, alt. 3,200 m, 23 Jan. 2005, *Pino* 1581 (USM); prov. Canta, dist. Canta, above Obrajillo waterfall, 11°26'51"S 76°36'57"W, alt. 2,750 m, 17 Jan. 2009, *Samain et al.* 2009-002 (BR, GENT, USM); dist. Huaros, road Canta–La Viuda pass, N detour towards Huaros, with *P. galioides*, 11°24'31"S 76°33'05"W, alt. 3,300 m, 19 Feb. 2005, *Pino* 1596 (USM); dist. Lachaki, road Canta–Lachaki, banks of Chacallayqui river, 11°31'58"S 76°37'11"W, alt. 3,630 m, 12 Apr.

2008, *Pino* 1960 (USM); prov. Oyón, dist. Caujul, road Sayán–Caujul, 10°48'37"S 76°59'03.7"W, alt. 3,170 m, 21 Mar. 2008, *Pino* 1936 (USM); prov. Yauyos, dist. Tomas, along road Huancayo–Yauyos, 103 km from Huancayo, 2 km beyond Tinco, 12°16'55.4"S 75°42'06.4"W, alt. 4,010 m, 21 Jan. 2009, *Samain et al.* 2009-023 (GENT, USM).

**Etymology** – The specific epithet is chosen in honour of Emma Cerrate, collector of the type. She specialized in ethnobotany and is, after her husband Ramón Ferreyra, the Peruvian researcher who made the highest number of *Peperomia* collections in the 20<sup>th</sup> century, mainly in Peru.

**Relationships** – At first sight, *P. cerrateae* resembles *P. umbilicata* Ruiz & Pav. However, *P. cerrateae* has larger leaves and inflorescences. It also has smaller fruits and white anthers instead of red or brown ones. The phylogeny shows this species to be in a polytomy of *P. scutellifolia*, *P. parvisagittata*, *P. ayacuchoana* and *P. pseudoverruculosa* (fig. 1). The spadices of *P. scutellifolia* tend to be erect and are shorter than the long trailing spadices of *P. cerrateae*. *P. umbilicata* as well as



**Figure 4** – A & B, *Peperomia gigantea*; C, *P. rupiseda*: A, general habit; B, flower; C, flower; a, stigma; b, style; c, ovary; d, anther; e, filament; f, floral bract. Drawn by G. Mathieu.

*P. scutellifolia* differ in phenology, appearing above-ground during the South American winter months (May–August). These two species occur in dry W facing coastal mountains at relatively low elevations between 300 and 1,000 m.

**Phenology** – Leaves are present from November to April, spadices appear from January to March, and fruits ripen from February to April.

**Distribution and habitat** – This species is a widespread Andean geophyte occurring at elevations between 2,750 and 4,600 m, reported from the Peruvian department of Ancash down to the department of Tarija in Bolivia. It grows in clayish soil between rocks, together with mosses, in moderately shaded places.

### 3. *Peperomia gigantea* G.Mathieu, **sp. nov.**

*A. P. rupiseda* C.DC. differt statura magna, bracteibus floralibus junioribus apice caudato, stylo lobato laevique, stigmatibus

plano. – Type: Peru, Cajamarca, prov. San Pablo, dist. San Bernardino, road Chilate–San Pablo, 23.9 km from Chilate, ‘Boladera La Cueva’, rock wall 50 m left from the cave, 07°09’25.2”S 78°50’30.4”W, alt. 1,780 m, 28 Feb. 2009, *Mathieu & Symmank* 2009-158 (holo-:USM; iso-: BR, GENT).

Large herb, up to 50 cm tall when flowering. Tuber more or less globose, slightly flattened, usually small for size of plant, up to 2 cm diam., surface yellow or greenish yellow when partially exposed to daylight, white on cross section, rooting at apex. Leaves 1–3 per plant; petiole (8–)15–20 cm, terete, whitish green to green or pinkish/purplish red, minutely longitudinally striate; lamina irregularly orbicular, (4–)6–10(–13) cm diam., slightly undulate and minutely sunken in the middle, vivid green adaxially, dull whitish green abaxially, 8-palmatinerved, main nerves contrasting yellowish adaxially, not reaching margin. Spadices 1–5 per plant; peduncle up to 35 cm, terete, usually more reddish than petiole; rachis up to 15 cm, usually less than half length

of peduncle, not wider than peduncle. **Floral bracts** elliptic, 1.5 mm long, apex caudate and comprising  $\frac{1}{2}$  to  $\frac{2}{3}$  of total length of young floral bract, long acuminate when growing older. **Stamens** with short, apically widening filaments; anthers c. 0.4 mm long. **Ovary** lighter than style, apical part of ovary covered by irregularly lobed, smooth cap; stigma terminal, usually flat, exceptionally divided. **Fruit** globose when young, mature fruit not seen. Fig. 4.

**Other representative specimens examined** – Peru: Cajamarca, prov. Contumazá, road Cascas–Contumazá, Plantanar Electrical power plant, alt. 1,400 m, 31 Mar. 1994, *Sagástegui et al.* 15197 (F, MO).

**Etymology** – The specific epithet refers to the size of the species as it is the largest known geophytic *Peperomia*.

**Relationships** – Small specimens of *P. gigantea* resemble *P. rupiseda* C.DC. Tubers of *P. gigantea* are solitary, yellow to greenish yellow and root from the apex whereas in *P. rupiseda* they tend to form clusters, are light brown and root from the base or occasionally from all over its surface. Both species show subglobose fruits, which differ however in the shape of their style. The differences are most clear in the young pistil before the style deforms and shrinks concurrent with the growth of the fruit. In *P. gigantea* it is an irregularly lobed, smooth cap usually bearing a flat stigma whereas in *P. rupiseda* it is a minutely papillate dome bearing a globose stigma. *P. gigantea* also differs in the young floral bract with distinct caudate apex. Based on molecular data, *P. gigantea* and *P. rupiseda* form a clade together with *P. klopfensteinii* Pino & Cieza (fig. 1). Within this clade, *P. gigantea* appears to be related more closely to *P. klopfensteinii* than to *P. rupiseda*. The two known collections of *P. gigantea* are from 1,400 and 1,780 m, substantially lower than *P. rupiseda* which is commonly found above 2,500 m.

**Phenology** – The plant has been found above-ground in February and March, flowering and with immature fruits.

**Distribution and habitat** – *Peperomia gigantea* seems to be a rather rare species occurring in western Cajamarca whereas the more common *P. rupiseda* is reported from Ancash, La Libertad and Lima.

#### 4. *Peperomia jalcaensis* Pino, sp. nov.

Planta geophila a *P. parvifolia* C.DC. differt spadicibus laxioribus, bracteis albidis antherisque rubris, fructibus angustioribus stylis pro ratione majoribus. A *P. macrorhiza* Kunth differt tubere infosso minore nec multilobato nec nitido, spadicibus brevioribus et fructibus longioribus. – Type: Peru, Cajamarca, prov. Cajamarca, dist. Cajamarca, Cumbemayo, on rocky wall among mosses and foliose lichens, 07°11'19"S 78°33'32"W, alt. 3,650 m, 17 May 2001, *Pino* 663 (holo: USM 184604).

Small **herb**, 3.5–4.5 cm tall above surface. **Tuber** usually buried among mosses in shadowed places, globose to depressed, grayish brown or yellowish, 1.2–2.3 cm high, 1.2–1.5(–2.5) cm diam., apex flat with one to several buds, rooting at base. **Leaves** 7–9 per plant; petiole (0.8–)2.2–3.2 cm × 0.5–0.6 mm, terete, light green with reddish stripes or totally reddish, straight to slightly curved; lamina orbicular to subdeltoid, succulent, funnel-shaped, peltate a little below

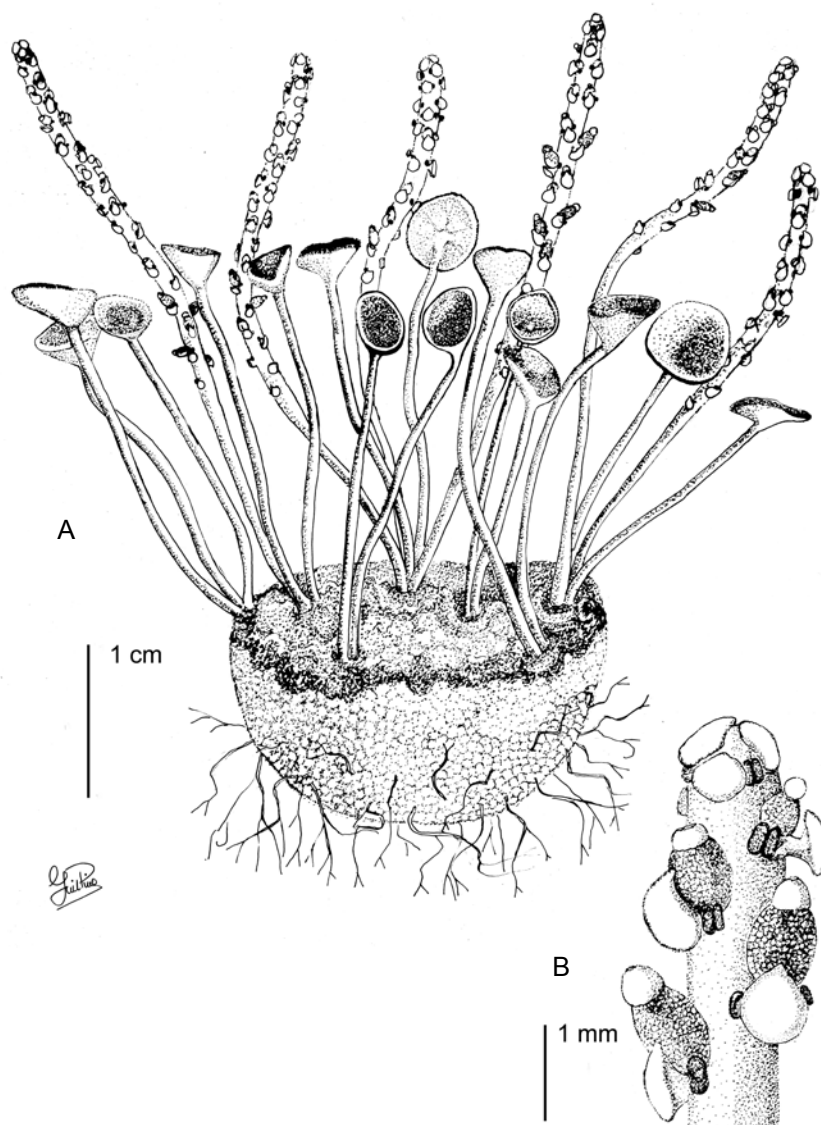
middle, 0.4–0.6 cm long, 0.35–0.5 cm wide, margin entire, obtuse to subemarginate, base rounded, adaxially concave, dark green, nerves not visible, abaxially greenish white, obscurely 5–7-palmatinerved. **Spadices** 8–20 per plant, 2–4 from each bud, erect to slightly curved; peduncle 2.8–3.5 cm × 0.6–0.9 mm, light green or with reddish stripes; rachis (1.4–)1.8–2.4 cm long × 1.2–1.4 mm wide, light green or reddish when exposed. **Floral bracts** peltate, orbicular, acuminate, white, diam. 0.6–0.7 mm. **Stamens** with filaments 0.2–0.3 mm long; anthers subglobose 0.2–0.25 mm diam., dark red when young, then brown. **Ovary** ovoid, light green to reddish, 0.5–0.6 mm × 0.3–0.4 mm. **Fruit** narrowly ovoid, body 0.9–1 mm × 0.6–0.7 mm, brown, papillate; style widely conical with flat top, 0.2–0.3 mm long × 0.3–0.4 mm diam., dull yellowish green. Fig. 5.

**Other representative specimens examined** – Peru: Cajamarca, prov. Cajamarca, dist. Cajamarca, around the city of Cajamarca, alt. 3,700 m, 31 May 1986, *Becker & Terrones* 1836 (USM 76415); Cumbemayo, c. 20 km SW of Cajamarca, on solitary rock, 07°11'19.8"S 78°34'32.3"W, alt. 3,640 m, 18 Feb. 2009, *Mathieu et al.* 2009-120 (BR, GENT, K, MO, USM); Cumbemayo, on rocky formations 'Frailones', 07°11'17"S 78°34'32"W, alt. 3,500 m, 12 Apr. 2002, *Pino* 926 (USM); Maqui-Maqui mountain, N of Cajamarca, route to Shanta Alta, on grassy 'Jalca' upon rocks, alt. 3,900 m, 15 Jan. 1994, *Sánchez-Vega & Cabanillas* 6666 (CPUN 4314); lower slope of Baúl mountain, alt. 3,900 m, 5 Feb. 1994, *Sánchez-Vega & Cabanillas* 6719 (CPUN 19137); prov. San Marcos, dist. Gregorio Pita, Las Pajas, 07°11'46"S 78°09'60"W, alt. 3,765 m, 10 Dec. 2002, *RRP* 360 (photographs).

**Etymology** – The epithet stands for the habitat of this species: 'jalca' is the common name of the moist rocky and shrubby highlands above 3600 m in northern Peru, which is intermediate between 'páramo' from the northern hemisphere and 'puna', the open, seasonally dry grassland above 4000 m from Central and Southern Peru, Bolivia and Argentina.

**Relationships** – Several collections mentioned here were erroneously cited by Pino (2004: 31) as *P. parvifolia*. However, leaves in *P. jalcaensis* are somewhat more succulent, glossy, darker and funnel-shaped, with the petiole less excentrically inserted; spadices of *P. jalcaensis* are longer, less compact on anthesis, with white bracts and red anthers instead of green as seen in *P. parvifolia*. Fruits are somewhat smaller but much narrower in *P. jalcaensis* with a relatively larger style, light green in contrast.

Large tubers of *P. jalcaensis* could also be confused with *P. macrorhiza*, a species that grows in the same area although 1,000 m lower and in drier places. However, the tubers of *P. jalcaensis* are smaller, generally covered by organic matter, brownish, coarse, globose or discoid instead of the large, exposed, glossy grayish and flat irregularly lobed tubers of *P. macrorhiza* and *P. lilliputiana* (Pino & Cieza) Pino. Leaves in *P. macrorhiza* are usually orbicular and peltate at the middle, flat to slightly concave and very rarely funnel-shaped, in *P. jalcaensis* they are more succulent, consistently funnel-shaped and peltate below the middle. Spadices of *P. jalcaensis* are stouter, shorter and appear and remain at the same time as the leaves, similar to those of *P. lilliputiana*, while in *P. macrorhiza* they are longer, more laxly flowered and precede the leaves being short-lived. The most important difference is the shape of the fruit, which in *P. jalcaensis* is very narrowly ovoid, with a large conical style, overall much



**Figure 5** – *Peperomia jalcaensis*: A, general habit; B, part of flowering rachis. Drawn by G. Pino.

longer than the fruits of the other species growing nearby that have mainly globose and smaller fruits (*P. macrorhiza* Kunth, *P. andina* Pino, *P. dolabella* Rauh & Kimmach, *P. lilliputiana* (Pino & Cieza) Pino). In the molecular phylogeny, *P. jalcaensis* is most closely related to *P. andina* (fig. 1).

**Phenology** – Leaves are present from November to May, spadices appear from December to May, fruits ripen from December to June.

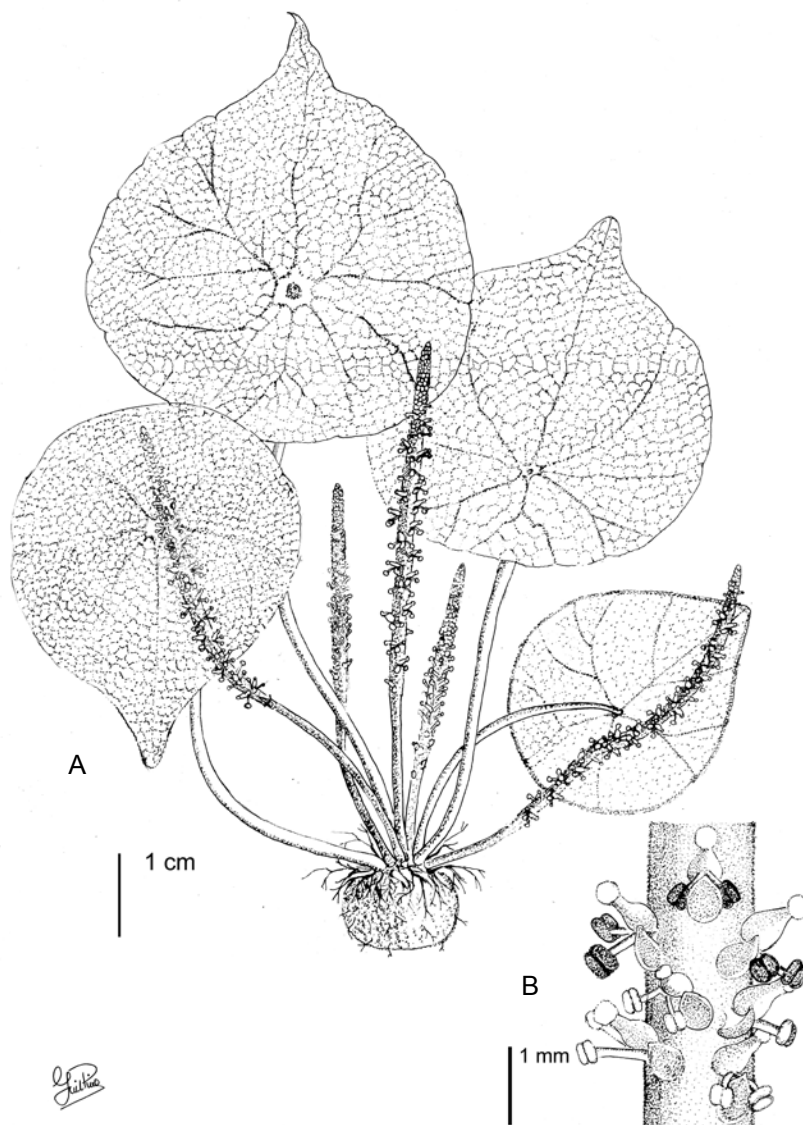
**Distribution and habitat** – This species occurs in ‘jalca’ formations of the Peruvian department of Cajamarca where it grows on rocks with a very thin layer of substrate, together with mosses and lichens that hide the tubers.

##### 5. *Peperomia klopfensteinii* Pino & Cieza, sp. nov.

Planta geophila tubere globoso apice radicibus instructo; folia longe petiolata lamina tenui iridescenti, rotundata, apice acuto vel acuminato, sub medio peltata; spadices erectae staminibus longissimis antheris rubris; habitat in cryptis perum-

brosis humidis Peruviae septentrionalis. – Type: Peru, Cajamarca, prov. Hualgayoc, dist. Chugur, Perlamayo, road Hualgayoc–Chugur, very shaded, wet places on rocks, growing with *Masdevallia* sp., *Lycaste* sp., 06°39'16"S 78°43'71"W, alt. 2,557 m, 16 Nov. 2002, *Klopfenstein* RRP-343 (holo: USM 230318).

Medium sized herb, 10–20 cm tall. Tuber entirely buried, globose to slightly flattened, yellowish brown to light brown, 1.2–1.6 cm diam., rooting at apex. Leaves 2–5 per plant; petiole 5–8(–15) cm × 1.8–2 mm, terete, light green to pinkish flushed with red, straight to slightly curved; lamina orbicular to widely obovate, membranous, flat, peltate a little below middle, 4–8(–11) × 3–7 cm, apex obtuse to acute, frequently slightly acuminate, base rounded, margin entire, adaxially vivid green to iridescent, (5–)7–9-palmatinerved, nerves lighter, reticulately nerved in between, abaxially greenish white to reddish when more exposed, nerves same as adaxially but slightly darker. Spadices (1–)6–11 per plant, erect or slightly curved but tips erect; peduncle 3–5 cm × 1–1.4



**Figure 6** – *Peperomia klopfensteinii*: A, general habit; B, part of flowering rachis. Drawn by G. Pino.

mm, whitish or pinkish flushed with red; rachis 3.5–6 cm × 1.2–1.6 mm, light green to reddish, densely flowered. **Floral bracts** peltate, orbicular, 0.6 mm diam., same colour as rachis, inconspicuous. **Stamens** with filaments 0.9–1.2 × 0.15–0.2 mm, terete, transparent; anthers subglobose 0.4–0.5 mm diam., reddish when young, then bright white. **Ovary** cylindrical, 0.7–0.8 mm × 0.3–0.4 mm, bright green; stigma white. **Fruit** not seen. Fig. 6.

**Other representative specimens examined** – Peru: Amazonas, prov. Luya, dist. Lamud, ‘Caverna de Quiocta’, entrance to the cave, 06°08’21.0”S 77°59’26.1”W, alt. 2,800 m, 14 Feb. 2009, *Mathieu et al.* 2009-104 (BR, GENT, MO, USM); Cajamarca: prov. Chota, dist. Conchán, road Chota–Conchán, km 13.6, in cave along the road, 6°29’36.4”S 78°37’26.9”W, alt. 2,852 m, 4 Nov. 2010, *Samain et al.* 2010-168 (GENT, USM); prov. Cutervo, dist. San Andrés de Cutervo, 2.5 km from San Andrés, ‘Gruta de Guacharo’, at the entrance of the cave, dripping rock wall next to torrent, 06°13’44.4”S 78°45’15.0”W, alt. 1,550 m, 22 Feb. 2009, *Mathieu et al.* 2009-135 (BR, GENT, USM); prov. Hualgayoc, dist. Chugur, road Chugur–Hualgayoc, track to Rio Grande, 2.5 km from Chugur, 200 m down-

hill by trail, 30 m upstream from bridge, in side canyon, ‘La Palma’, soil pockets on shady rock wall, 06°39’32.3”S 78°44’01.4”W, alt. 2,450 m, 20 Feb. 2009, *Mathieu et al.* 2009-130 (BR, GENT, MO, USM); prov. San Ignacio, dist. Tabaconas, road Tabaconas–Huanabamba 40.9 km, at the entrance of very steep canyon with waterfall, in mosses on vertical rock wall, 05°19’28”S 79°21’38”W, alt. 2,670 m, 6 Feb. 2009, *Mathieu et al.* 2009-049 (BR, GENT, USM).

**Etymology** – The species is named after Olivier Klopferstein, collector of the type. He is a Swiss ranger and amateur botanist, founder of the Botanical Garden of San Marcos in Cajamarca, a tireless researcher of the Peruvian flora during his stay in Peru (1998–2004).

**Relationships** – This species is delicate and easily disintegrates when touched. Leaves are large, papery, ovate, acuminate, easily breakable and with an iridescent colour. Spadices are conspicuous, straight or slightly curved but with erect tips, reddish rachides with very long stamens and red anthers. Based on molecular data, *P. klopfensteinii* is sister to *P. gigantea* G. Mathieu (fig. 1).

**Phenology** – Leaves present from November to April. Spadices appear at the same time as the leaves.

**Distribution and habitat** – The species thrives in very shady, humid places preferably near water courses, frequently at cave entrances or very steep canyons. It grows with mosses in clayish soil in rock crevices.

#### 6. *Peperomia lilliputiana* (Pino & Cieza) Pino, **stat. nov.**

*Peperomia macrorhiza* var. *lilliputiana* Pino & Cieza, Haseltonia 11: 110. 2005 (Pino et al. 2005) – Type: Peru, La Libertad, prov. Sanchez Carrión, dist. Huamachuco, Sausacocha lagoon, 7°47'24"S 77°59'11"W, alt. 3,290 m, Klopfenstein & Cieza AJABOSAM-593 (holo.: USM 184605).

The species was described as a variety of *P. macrorhiza* Kunth with similar reproductive organs and large exposed tubers growing on rocks. However, *P. lilliputiana* has much smaller leaves that are glaucous, cordate and quite succulent contrasting with the orbicular, centrally peltate leaves of *P. macrorhiza*. Phylogenetic analyses show this species to be most closely related to *P. parvifolia* (fig. 1).

#### 7. *Peperomia ocrosensis* G.Mathieu & Pino, **sp. nov.**

A *P. rupiseda* C.DC. differt rachidi graciliore et floris morphologia, bractea florali elliptica vel interdum parum obovate, epunctulata, ovario minute papillato, stylo glabro, stigmatum stipitato tholiformi; tubere interiore aliquantum fibroso haud succulento colore pallide stramineo. – Type: Peru, Ancash, prov. Ocros, dist. Ocros, road Paramonga–Conococha (via Ocros), km mark 29, 10°27'32.4"S 77°24'29.6"W, alt. 3,105 m, 3 Feb. 2009, Mathieu et al. 2009-042 (holo.: USM; iso.: BR, GENT, K, MO).

Rather robust herb, 10–15 cm tall. Tuber globose, up to 3.5 cm diam., slightly flattened, developing irregular outgrowths from apex when becoming older, then becoming higher than wide, surface brown, slightly rough, yellowish beige on cross section, internal texture rather dry and fibrous, rooting at apex. Leaves 5–12 per plant; petiole 9–12 cm × 1.5–2.4 mm, terete, whitish green to whitish pink with red striae; lamina orbicular, to 4 cm diam., rather firm, undulate, centrally peltate, 8(–9)-palmatinerved, nerves branched. Spadices (1)–5–12(–17) per plant; peduncle 9–11 cm × 1.4–1.6 mm, light green or with a reddish tinge; rachis 4.5–6.5 cm × 1.4–1.8 mm, light green, moderate-densely flowered. Floral bracts elliptic to sometimes slightly obovate, 0.75–0.85 × 0.5–0.65 mm, centrally peltate, apex short acuminate, light green. Stamens with slender filaments 0.3–0.6 × 0.16–0.18 mm, perpendicular to rachis; anthers ellipsoid, 0.4–0.6 mm, white, brown and collapsed when dry. Ovary globose to broad ellipsoid, 0.3–0.4 × 0.3–0.35 mm, short pedicellate, intense green, entirely minutely papillate; style broad conical to ob-ovoid, 0.52–0.3 × 0.3–0.35 mm, yellowish green, lighter than ovary; stigma terminal, pedicellate, dome-shaped, 0.2–0.25 mm diam., stigmatal fimbriae white, surpassing edge of stigmatal plateau. Fruit not seen. Figs 7 & 8.

**Etymology** – The specific epithet refers to Ocros, the nearest village, c. 6 km N of the type locality.

**Relationships** – *Peperomia ocrosensis* exhibits the robust general habit of *P. rupiseda* C.DC. Both species show rather

large, slightly undulate leaves. *P. ocrosensis*, however, has much thinner inflorescences (rachis 1.5 mm diam. vs. 3.5 mm in *P. rupiseda*). They also differ in the characters of the style, most clear in young carpels. In *P. ocrosensis*, the smooth style is lighter than the body of the ovary and apically positioned on the minutely papillate ovary. In *P. rupiseda* on the contrary, the minutely papillate style is darker than the ovary and dome-shaped 'over' the ovary, thus covering its apical part. *P. ocrosensis* shows a pedicellate, dome-shaped stigma that surpasses the limits of the stigmatal plateau whereas in *P. rupiseda* the stigma is sessile and globose. The tuber of *P. ocrosensis* is yellowish beige on cross section whereas in *P. rupiseda* it is creamy white with a darker brownish peripheral zone (fig. 8). Inside, the tuber of *P. ocrosensis* is rather dry and fibrous, juicy in *P. rupiseda*. Also their root position is different (rooting from the apex in *P. ocrosensis* versus from all over the surface in *P. rupiseda*). In a phylogenetic analysis, *P. ocrosensis* is sister of *P. querocochana* G.Mathieu & Pino (fig. 1).

**Phenology** – The plant has been found above-ground in February, flowering but not fruiting.

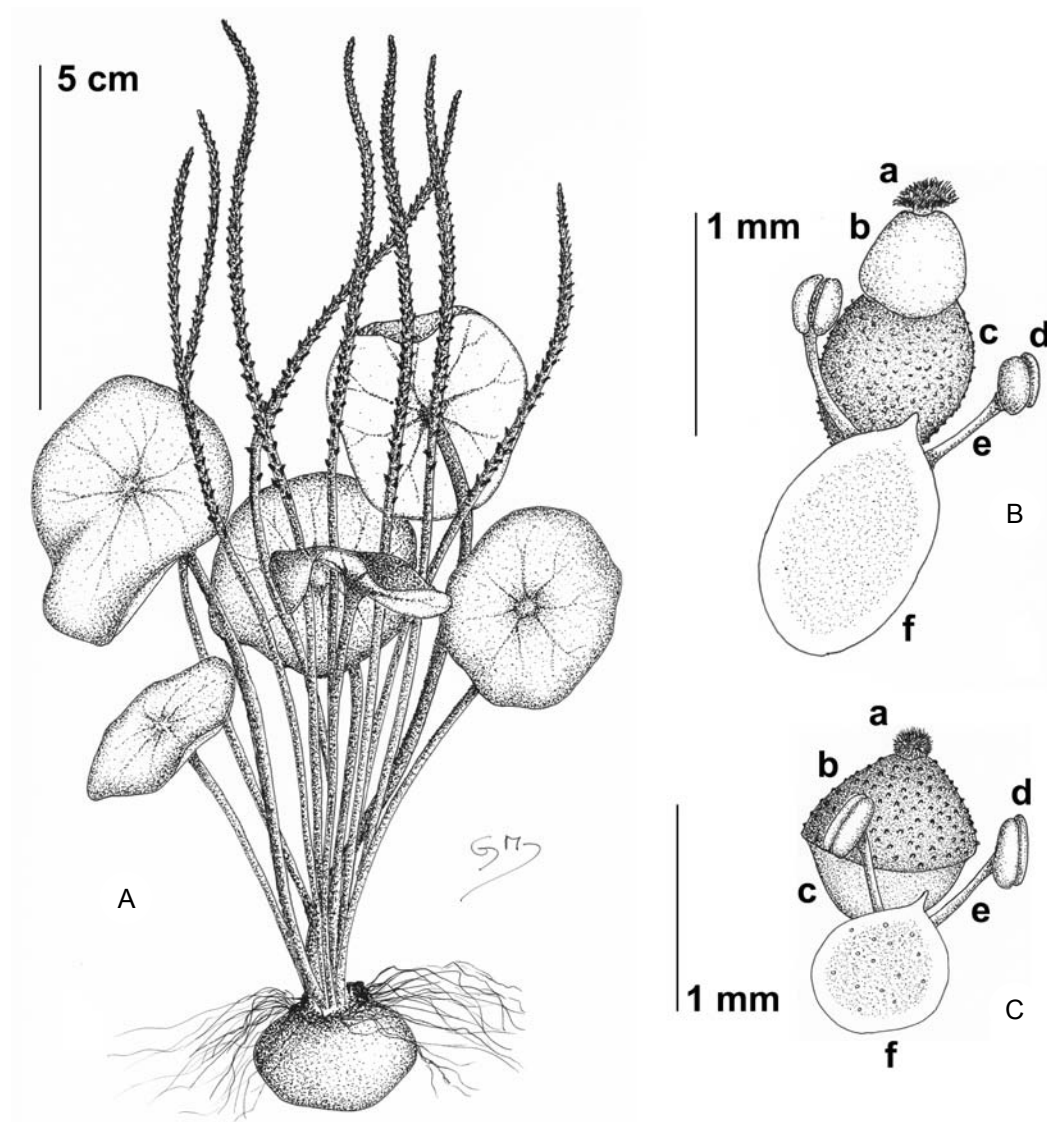
**Distribution and habitat** – *Peperomia ocrosensis* is only known from its type locality in the Peruvian department of Ancash. It was found at an elevation of 3,105 m, growing in clayish soil, at the base of an exposed but overhanging rock wall.

#### 8. *Peperomia parvisagittata* G.Mathieu & Pino, **sp. nov.**

A speciebus geophilis australo-americanis notis distincta lamina ovata vel deltoidea, cordata, vulgo non-peltata vel minute peltata. – Type: Peru, Ancash, prov. Bolognesi, dist. Cajacay, road Huaraz–Pativilca km 103, 940 m before Majoralca, c. 250 m uphill Cerro Huansharury, in mosses on vertical sandy rock wall above *Eucalyptus* plantation, 10°09'31.4"S 77°21'13.3"W, alt. 3,480 m, 25 Jan. 2009, Mathieu & Symmank 2009-020 (holo.: USM; iso.: BR, GENT).

Delicate herb, up to 2–3.5 cm tall in vegetative stage. Tuber usually buried, up to 0.8 cm diam., globose or slightly higher than wide, rooting at base, surface yellowish-green to light brown or reddish. Leaves 2–6(–13) per plant; petiole 1–3 cm × 0.25–0.4 mm, terete, light green, often whitish at the base; lamina chartaceous, flat or slightly folded upward along the main nerve, cordiform, ovate to deltoid or, more rarely, almost orbicular, 4–8 × 4–6 mm, apex acute to obtuse, rarely emarginate, base usually cordate, rarely rounded, usually non-peltate or slightly peltate, rather dark green adaxially, lighter, whitish green abaxially, nervation obscure, usually only main nerve noticeable. Spadices (1)–2–5 per plant; peduncle 2–6 cm × 0.35–0.45 mm, light green, often whitish at the base, sparsely minutely dotted, usually twice as long as petiole; rachis 1.5–5 cm × 0.55–0.85 mm, same length or a little shorter than peduncle, towards the apex gradually becoming wider, apically up to twice as thick as peduncle, light green, more intense towards apex, sparsely minutely dotted, loosely flowered. Floral bracts orbicular to elliptic, (0.5)–0.8–0.9 × (0.3)–0.5–0.6 mm, centrally peltate, abaxially convex, apex acute to acuminate, base rounded, pedicel thick, 0.2–0.25 mm diam. Stamens with short filaments, c. 0.2 mm long; anthers 0.2–0.25 mm long, rapidly becoming





**Figure 7** – A & B, *Peperomia ocrosensis*; C, *P. rupiseda*: A, general habit; B, flower; C, flower; a, stigma; b, style; c, ovary; d, anther; e, filament; f, floral bract. Drawn by G. Mathieu.



**Figure 8** – Tubers on cross section: *P. ocrosensis*, young tuber (left), older tuber (middle), *P. rupiseda* (right).

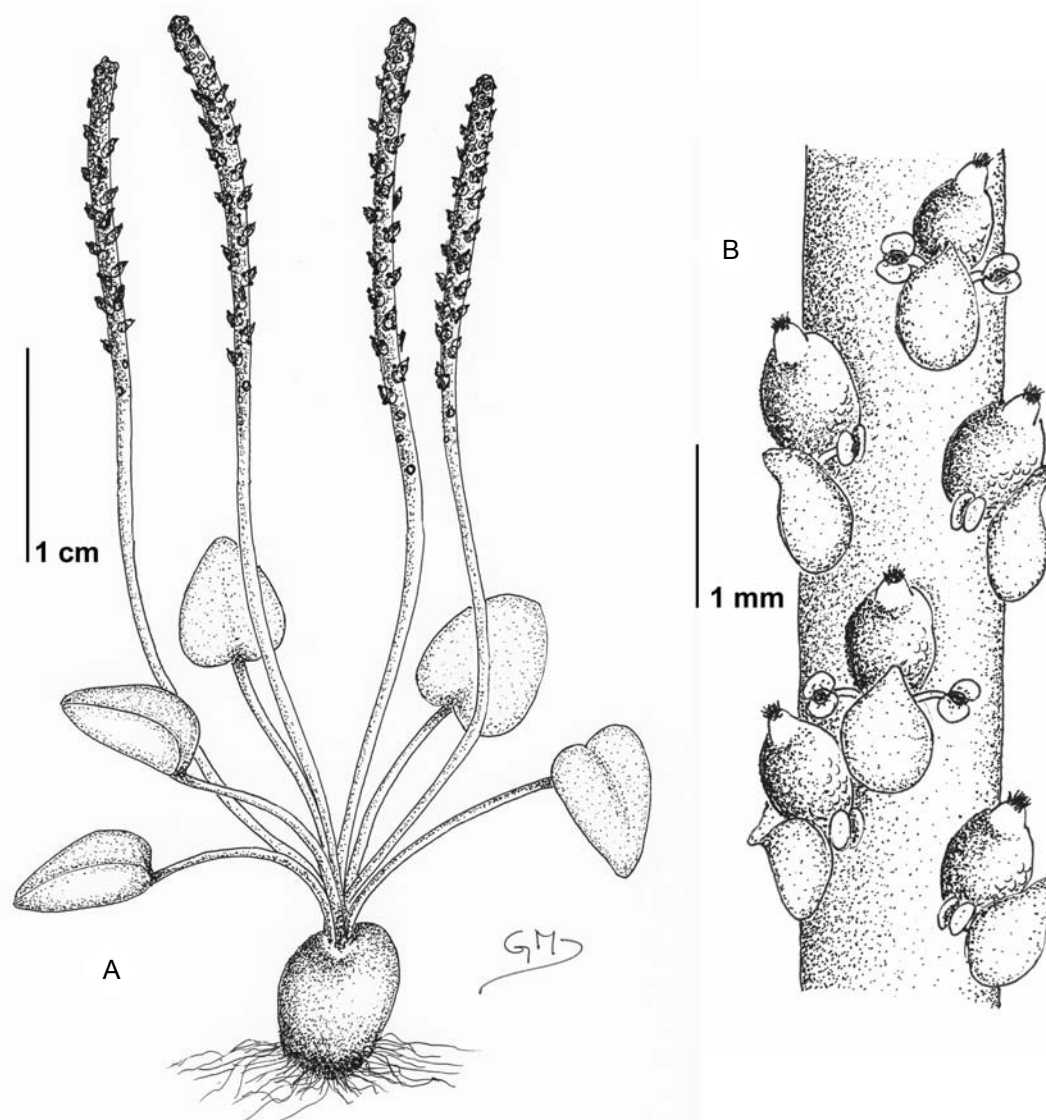
brown. Ovary globose to ellipsoid, 0.25–0.30 mm diam., intense green; stigma terminal, flabelliform spherical, 0.2–0.3 mm diam., white. Fruit ellipsoid, 0.9 × 0.6 mm, sessile, centrally attached at the base; pericarp minutely papillate; style wide conical to mammiform. Fig. 9.

**Other representative specimens examined** – **Bolivia**: Tarija, prov. Méndez, near Colorado Norte, 21°11'14.6"S 64°46'18.9"W, alt. 3,060 m, 30 Jan. 2008, *Samain et al.* 2008-083 (GENT, LPB).

**Peru**: Lima, prov. Canta, dist. Lachaki, Panamericana Norte, near km 95, 11°29'10.8"S 76°38'37.6"W, alt. 2,400 m, 17 Jan. 2009, *Samain et al.* 2009-003 (GENT, USM); prov. Huarochirí, dist. San Mateo, E slope of the Cerros de San Mateo, alt. 3,000 m, 3 Feb. 1968, *Cerrate* 4318 (USM 67220).

**Etymology** – The specific epithet refers to the leaf shape, the most characteristic feature of this species.





**Figure 9** – *Peperomia parvisagittata*: A, general habit; B, part of fruiting rachis. Drawn by G. Mathieu.

**Relationships** – Although non-peltate leaves do occur in several Central American geophytes, *P. parvisagitta* is, together with *P. lilliputiana* (Pino & Cieza) Pino, the only South American geophytic species showing non-peltate leaves. The latter species shows succulent leaves and a large irregular tuber. Phylogenetic analysis reveals *P. parvisagittata* to be related to *P. scutellifolia* Ruiz & Pav., *P. cerrateae* Pino & G.Mathieu, *P. ayacuchoana* Pino & Samain and *P. pseudoverruculosa* G.Mathieu (fig. 1).

**Phenology** – The plant has been found above-ground in January and February, flowering and fruiting.

**Distribution and habitat** – Although the species is known from only four collections, it seems to have a quite wide distribution: from the Peruvian departments of Ancash and Lima down to the department of Tarija in southern Bolivia. The elevation range covers more than 1,000 m, growing between mosses on vertical rock walls.

#### **9. *Peperomia peruviana* Dahlst. (Dahlstedt 1900: 92)**

**Basionym rejection and lectotypification** – Describing the genus *Tildenia*, Miquel included a single species: *Tildenia mexicana* Miq. (Miquel 1843a: 82). Shortly afterwards, Miquel transferred *Peperomia umbilicata* Ruiz & Pav. to the new genus but named it *Tildenia peruviana* Miq., not upholding the epithet of the basionym (Miquel 1843b: 483). There was no reason not to use the epithet *umbilicata* in *Tildenia* and therefore, *Tildenia peruviana* has to be considered as superfluous.

Subsequently, *Tildenia* was reclassified at subgeneric rank [‘sectio’] within *Peperomia*. Miquel correctly revived *Peperomia umbilicata* Ruiz & Pav. and cited *Tildenia peruviana* Miq. as its synonym (Miquel 1843c–1844: 69). Hence, it is clear that *Tildenia peruviana* Miq.  $\equiv$  *Peperomia umbilicata* Ruiz & Pav.

Dahlstedt (1900) observed correctly that the specimen at B from “St. Franco de Hay circa Lacum Titicaca”, cited by

Miquel as “St. Franco de Ary circa Lacum Titicacum. Apr. 1831. Meyen” under *P. umbilicata*, could not be considered as belonging to that species. Apart from the differences in fruit morphology he mentioned *P. umbilicata* as a coastal Peruvian species occurring below 800 m whereas the Meyen collection is a different species from the high Andes. Unfortunately, Dahlstedt published the new species as *Peperomia peruviana* (Miq.) Dahlst. but he made a nomenclatural mistake (Dahlstedt 1900: 32) as there was no objection against the use of the epithet *peruviana*. Miquel did not introduce the name *Peperomia peruviana* and the epithet was still available in *Peperomia*. The error is not the choice of the epithet but the citation of the basionym. If Dahlstedt wanted to distinguish *P. peruviana* from *P. umbilicata* he could not, at the same time, refer to *Tildenia peruviana* (superfluous for *P. umbilicata*) as the basionym. This error is corrected herewith according to ICBN art. 48.1 “when an author who adopts a name refers to an apparent basionym but explicitly excludes its type, a new name is considered to have been published that must be attributed solely to that author” (McNeill et al. 2006).

**Lectotype designation** – In his protologue Dahlstedt (1900) refers to five collections of which Meyen’s specimen at B is mentioned first. That specimen was destroyed during World War II and a lectotype has to be chosen from other material cited. Also mentioned is *Gaudichaud* 150 at G-DC, but that collection (G, G-DC, MO, NY, P [3], U) has to be excluded. In 1936 it became the type of *Peperomia hillii* Trel., a synonym of *P. umbilicata*. Dahlstedt already cited it under the latter name (Dahlstedt 1900: 31), although it was included at the same time under *P. peruviana*. Neither the B nor the Hb Gris. (currently GOET) specimen of *Lorentz & Hieronymus* Fl. arg. no 658 could be found. Of the two remaining collections, *Lorentz & Hieronymus* 2 and *Schickendantz* 165, a specimen is extant at GOET. Both specimens bear the annotation: “det. H. Dahlstedt 1901”. *Schickendantz* 165 is chosen as the lectotype because it best exhibits the morphology of the species and mentions a precise collection site.

Although a lectotype is designated herewith, the locality of the lost Meyen type is still important in the view of future collections that might provide support for the current *P. peruviana* concept. The locality “St. Franco de Hay” (by Dahlstedt) or “St. Franco de Ary” (by Miquel) has puzzled many botanists. The difference in spelling suggests that the writing of the original label might have been obscure. We assume that it was actually meant “St. Franco de Anq.”, standing for San Francisco de Anquac, already in 1831 an abandoned mission station, about 2½ hours walking distance from Lake Titicaca and 3 hours W of the small town of Jull [apparently Juli]. In his travel reports, Meyen pointed to a series of conspicuous parallel rock walls, running in SW-NE direction, 20–30 feet high and 4–5 feet wide, just before reaching the mission station [coming from the south] on April 7<sup>th</sup> and he especially mentioned the many small but very attractive plants that were growing on these walls (Meyen 1834: 478). This is very likely a direct reference to *P. peruviana* and the precise location where it was collected.

# 10. *Peperomia pseudoperuviana* (Pino) Pino, stat. nov.

*Peperomia andina* var. *pseudoperuviana* Pino, *Peperomias* de Cajamarca: 14. 2004. (Pino 2004). – Type: Peru, Cajamarca, prov. Cajamarca, dist. San Juan, road Cajamarca–San Juan km 146, in crevices on rock wall, in mosses, together with *Oxalis* sp., *Peperomia cymbifolia* Pino and *Peperomia galioides* Kunth (Pino 2010), 7°17′32″S 78°29′27″W, alt. 2,370 m, 4 Oct. 2002, *Pino* 894 (holo-: USM 184602).

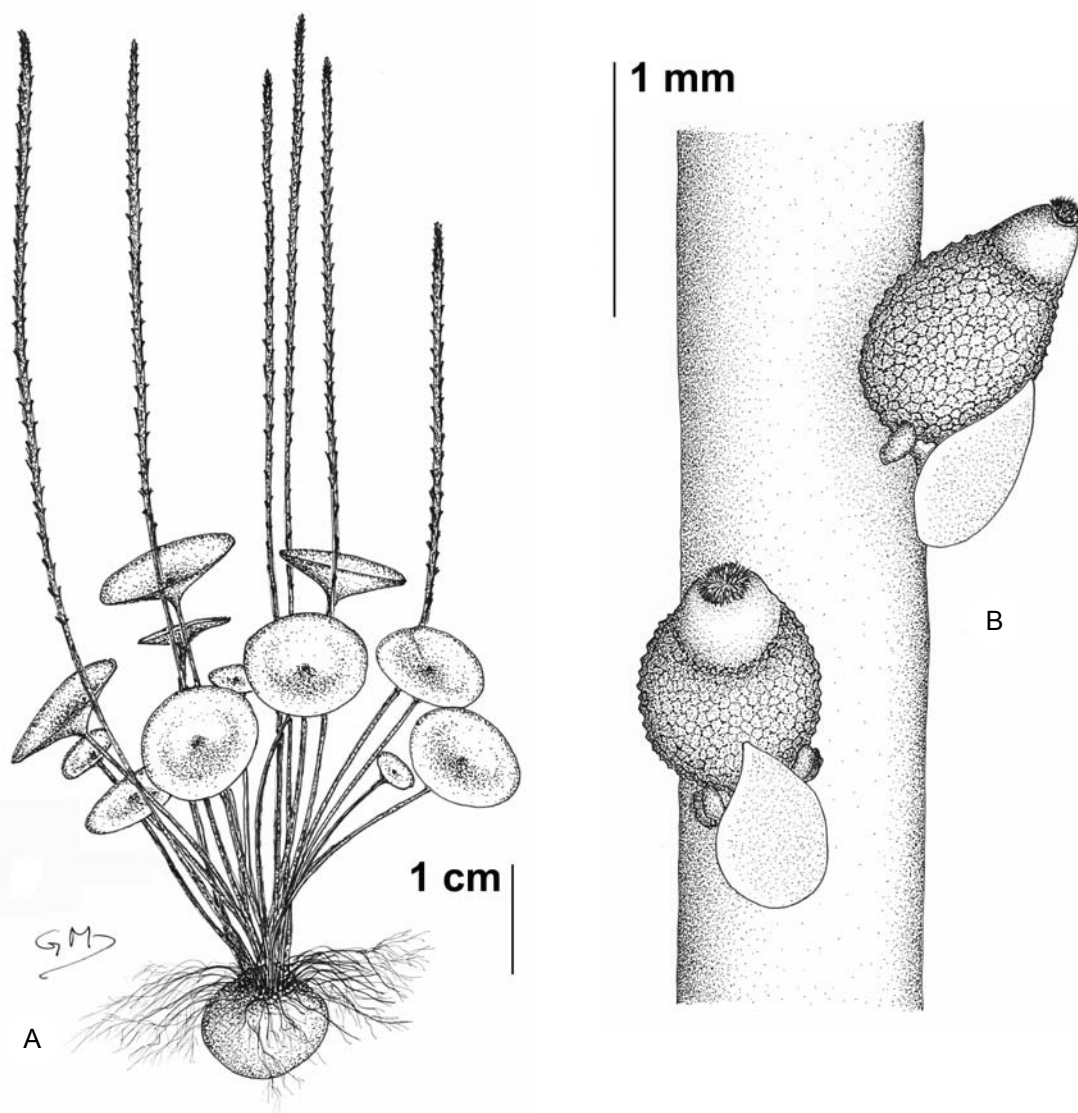
The species was first described as a variety of *P. andina* but it proved to have several morphological differences. It grows in the same region although it prefers lower elevations and more sheltered places in the shade. Distinct are the orbicular and flat leaves, peltate in the middle, whereas *P. andina* shows larger, oval or subtriangular funnel-shaped leaves. The tubers of *P. pseudoperuviana*, usually buried under moss, remain quite small.

**Other representative specimens examined** – Peru: Cajamarca, prov. Cajamarca, dist. San Juan, Road Cajamarca–San Juan km 148.5, between rocks, 7°15′58″S 78°30′39″W, alt. 2,660 m, 3 May 2002, *Pino* 298 (USM); road San Juan–Huacraruco, on rock wall, 7°17′35″S 78°29′18″W, alt. 2,400 m, 16 May 2000, *Pino* 642 (USM).

# 11. *Peperomia pseudoverruculosa* G.Mathieu, sp. nov.

A *P. verruculosa* Dahlst. ex Hill differt tubere ex apice radicante, spadicibus longioribus et laminis orbicularibus; a *P. ayacuchoana* Pino & Samain differt tubere minore, foliis majoribus et fructibus verruculosus. – Type: Peru, Ayacucho, prov. Huamanga, dist. Acocro, road Ayacucho–Chincheros, km 62, 13°18′55.7″S 73°58′48.8″W, alt. 3,450 m, 26 Jan. 2009, *Samain et al.* 2009-052 (holo-: USM; iso-: BR, GENT).

Small herb, up to 10 cm tall. **Tuber** globose, up to 1 cm diam., forming apical outgrowth half the size of tuber when growing older, surface smooth, yellowish to light brown, rooting at apex. **Leaves** (3–)5–13 per plant; petiole (1.5–)3–5(–7) cm × 1 mm, terete, whitish translucent green, sometimes slightly tinged pink-purple, often whitish at base; lamina membranous but not translucent except for peripheral 0.2 mm, orbicular, (0.5–)0.7–1.0(–1.2) cm diam., apex often minutely emarginate, flat but centrally slightly depressed, centrally peltate, vivid green adaxially, dull whitish green abaxially, nervation obscure, only main nerve distinct, especially in dried specimens, slightly protruding abaxially, slightly depressed adaxially, minutely yellow-brown glandularly dotted abaxially when dried. **Spadices** 4–12 per plant; peduncle same length as petiole or a little longer, 4–6(–8) cm × 1 mm, whitish at base, becoming green more apically; rachis same length or longer than peduncle, up to 8 cm × 1.5 mm, about same diam. as peduncle, usually slightly darker green than peduncle, loosely flowered. **Floral bracts** elliptic, 0.7–0.8 × 0.5–0.6 mm, apex acuminate, base rounded, centrally peltate, succulent and a little convex adaxially, margin membranous. **Stamens** with short filaments, 0.1–0.2 mm long; anthers c. 0.3 mm long. **Ovary** ellipsoid, surface granulose; style ovoid to mammiform, larger than ovary in young carpels; stigma terminal, dome-shaped or a little flatter, stigmatal fimbriae surpassing the edges of stigmatal plateau. **Fruit** ovoid, body 0.7 × 0.6 mm, sessile and slightly sunken in rachial pit, cen-



**Figure 10** – *Peperomia pseudoverruculosa*: A, general habit; B, part of fruiting rachis. Drawn by G. Mathieu.

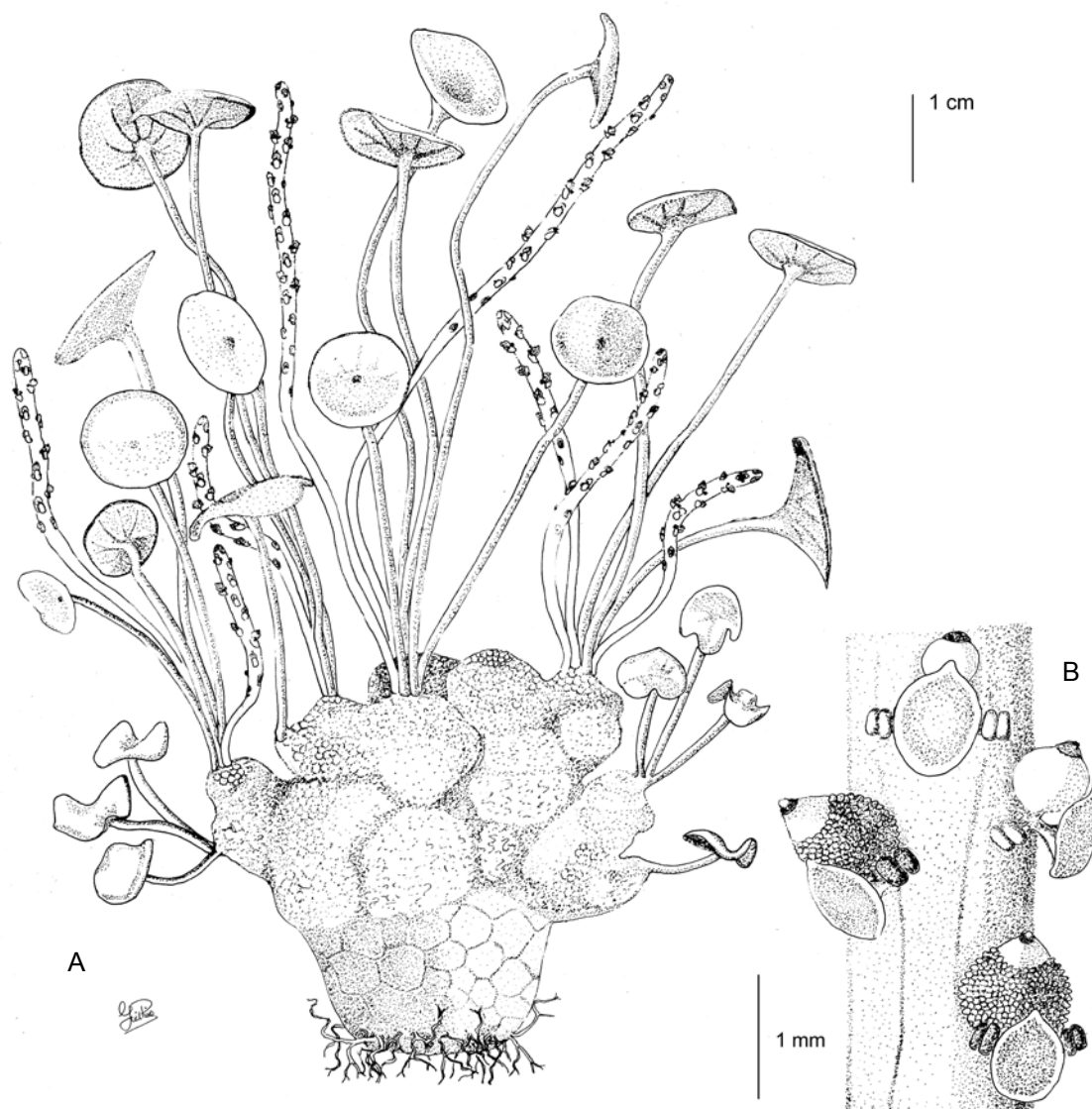
trally attached at the base, pericarp polygonal verruculose; style short conical to mammiform, 0.2–0.3 mm long. Fig. 10.

**Other representative specimens examined** – **Peru**: Apurímac, prov. Chincheros, dist. Ocobamba, along road Chincheros–Abancay, km 165, 13°32'22.3"S 73°40'24.2"W, alt. 3,290 m, 26 Jan. 2009, *Samain et al.* 2009-061 (GENT, USM); loc. cit., km 175, 13°32'48.4"S 73°37'43.2"W, alt. 3,760 m, 27 Jan. 2009, *Samain et al.* 2009-062 (BR, GENT, USM); prov. Andahuaylas, dist. Huancarama, along road Chincheros–Abancay, km 328, 13°42'01.3"S 73°02'47.4"W, alt. 3,470 m, 27 Jan. 2009, *Samain et al.* 2009-072 (GENT, USM); Ayacucho, prov. Huamanga, dist. Quinua, along the 'Via Los Libertadores' Pisco–Ayacucho, 13°16'52.3"S 74°18'25.7"W, alt. 3,730 m, 23 Jan. 2009, *Samain et al.* 2009-036 (BR, GENT, USM); Cuzco, prov. Cuzco, dist. Cuzco, 6 km from San Jerónimo Huaccoto, 13°31'05.5"S 71°52'14.0"W, alt. 3,890 m, 13 Feb. 2009, *Samain et al.* 2009-122 (BR, GENT, USM); behind the ruins of Sacsayhuamán, near the road Cuzco–Calca km 7–8, 13°30'08.3"S 71°58'48.2"W, alt. 3,660 m, 13 Feb. 2009, *Samain et al.* 2009-123 (BR, GENT, USM); along the road Cuzco–Calca km 8–9, 13°29'47.8"S 71°58'24.1"W, alt. 3,740 m, 13 Feb. 2009, *Samain et al.* 2009-124 [fruits with gals] (BR, GENT, USM).

**Etymology** – The specific epithet refers to the verruculose fruit pericarp. In this respect, the species resembles *P. verruculosa* Dahlst. ex Hill.

**Relationships** – *Peperomia pseudoverruculosa* can be distinguished from the three other Peruvian species with fruits with a verruculose pericarp (*P. verruculosa*, *P. parvifolia* C.DC. and *P. pugnicaudex* Pino). These three species have tubers rooting at the base whereas the tuber of *P. pseudoverruculosa* roots at the apex. The Bolivian *Peperomia radiatinervosa* G.Mathieu also shows verruculose fruits and a tuber rooting from the apex but this species has much larger, distinctly nerved leaves.

At its type locality, *P. pseudoverruculosa* grows together with *P. verruculosa* and both species apparently prefer the same habitat. However, *P. pseudoverruculosa* can easily be distinguished morphologically by the tuber (lighter colour, smooth surface, apical root position), the longer inflorescences and the orbicular leaves. Its floral bracts show a more acute



**Figure 11** – *Peperomia pugnicaudex*: A, general habit; B, part of rachis. Drawn by G. Pino.

to acuminate apex and are more slenderly stalked. Finally, the fruits do not show the almost discoid style of *P. verruculosa*. According to phylogenetic analysis, *P. pseudoverruculosa* is not closely related to any of the species mentioned. Its closest relative appears to be *P. ayacuchoana* Pino & Samain (fig. 1).

**Phenology** – The plant has been found above-ground in January and February, flowering and fruiting.

**Distribution and habitat** – *P. pseudoverruculosa* occurs in the Peruvian departments of Apurímac, Ayacucho and Cuzco, at rather high elevations (3,000–4,000 m) on eastern Andean slopes. It prefers an exposed, grassy and shrubby habitat where it grows in soil pockets and crevices between and on rocks.

## 12. *Peperomia pugnicaudex* Pino, sp. nov.

Planta geophila tubere epigaeo basi radicibus instructo; caudex expositus, globosus vel late infundibuliformis, obscure lobatus; folia petiolata sub medio peltata, lamina rotundata

coriacea 1.2–1.8 cm diam., supra concava, subtus purpurascens, marginibus saepe undulatis; a *P. chutanka* Pino differt caudice crassiore breviorique, foliis minoribus, spadicibus brevioribus et baccis ovoideis verruculosis. – Type: Peru, Lima, prov. Huarochiri, dist. San Mateo, central highway km 98, beyond Infiernillo railroad bridge, S bank of Rimac river, before Cacray tunnel, in front of waterfall, 11°44'45"S 76°17'35"W, alt. 3,300 m, 24 Feb. 2002, Pino 792 (holo: USM 230319).

Medium sized herb, 7–15 cm tall. Tuber exposed, globose when young, then funnel-shaped, branching after each flowering, light brown to grayish, rooting at base, 1.5–3 cm diam. at base, 6–7 cm diam. at apex, 4–5 cm tall, with knuckle-like projections on top, 0.8–1.5 cm diam. Leaves up to 50 or more per plant, 12–15 from each projection; petiole 6–12 cm × 1–1.3 mm, terete, light green with reddish longitudinal lines when exposed, straight to slightly curved; lamina orbicular, 1.2–1.8 cm diam., coriaceous, peltate slightly below middle, base and apex rounded, margin entire, induplicate or

undulate in young leaves, flat to sometimes revolute in older leaves, adaxially flat to concave, umbilicate at petiole insertion, dark green, nerves invisible, abaxially funnel-shaped, reddish to purplish when more exposed, 7–9-palmatinerved, nerves darker red or purple. Spadices 3–6 from each tuberos projection, erect or slightly curved with upward apices; peduncle 1.2–3 cm × 1–1.4 mm, whitish or very light green; rachis 1.5–3 cm × 1.3–1.6 mm, light green. Floral bracts peltate, ovate, slightly more red than rachis, 0.8 × 0.6 mm. Stamens with short filaments; anthers globose, 0.4–0.5 mm diam., white, drying brownish gray. Ovary 0.6–0.7 × 0.4–0.5 mm, ovoid, bright green. Fruit ovoid, 1–1.1 × 0.7–0.8 mm; pericarp minutely verruculose, reddish brown; style widely conical, bright green. Fig. 11.

**Other representative specimens examined – Peru:** Lima, prov. Huarochirí, dist. San Mateo, central highway km 98, beyond Infierillo railroad bridge, N bank of Rimac river before waterfall, 11°44'24"S 76°16'49"W, alt. 3,430 m, 18 Jan. 2009, *Samain et al.* 2009-007 (GENT, USM).

**Etymology** – The aerial tuber parts of this species look like a closed hand, ‘pugnus’ = ‘fist’ in Latin.

**Relationships** – The tubers of *P. pugnicaudex* produce irregularly branching outgrowths only comparable with those of *P. chutanka* Pino, with which it shares the vernacular name ‘chutanka’. However, tubers in *P. pugnicaudex* are smaller and thicker, and definitely do not look like stems like in *P. chutanka*. The leaves are reddish, coriaceous and funnel-shaped like they are in *P. chutanka*, but they are much smaller, constantly orbicular and with more undulate margins. Spadices are more abundant but shorter and fruits are ovoid and verruculose compared to the odd cylindrical drupes of *P. chutanka*. According to molecular data this species is most closely related to the clade consisting of *P. ocosensis* G.Mathieu & Pino and *P. querocochana* G.Mathieu & Pino (fig. 1).

**Phenology** – Leaves are present from December to April, spadices appear from October to January and fruits ripen from December to February.

**Distribution and habitat** – It grows in clayish soil among rocks, in half shaded places. *P. pugnicaudex* appears to be rare and very few specimens have been found at the only known locality. Careful efforts have to be made for its conservation.

### 13. *Peperomia purpureonervosa* G.Mathieu, sp. nov.

A speciebus geophilis notis distincta nervis laminae, supra reticulatis atro-viridibus, infra purpureis. – Type: Bolivia, La Paz, prov. Nor Yungas, road Unduavi–La Paz, 2.7 km from La Paz, on rocks along the road, shaded by shrubs, 16°18'54.8"S 67°55'28.4"W, alt. 3,270 m, 20 Jan. 2008, *Symmank et al.* 2008-051 (holo-: BR; iso-: GENT, LPB, MO).

Delicate herb, usually not more than 5–8 cm tall due to decumbent petioles. Tuber globose when young, c. 1 cm diam., developing apical outgrowths and becoming irregular when growing older, rooting all over its surface, dark brown to almost black, creamy white on cross section with a rather thick peripheral dark brown zone. Leaves 2–8 per plant; petiole 5–11 cm long, whitish near base, rest purplish, longitudinally striate distally; lamina membranous, translucent, slightly irregularly orbicular, 1–4 cm diam., apex rounded or often emarginate, centrally peltate, (4–5–)6-palmatinerved, main

nerves profusely branching and anastomosing near margin, reticulately nerved in between, nerves and small zone along them usually distinctly contrasting with remainder of lamina, dark green on light green background adaxially, purple (or slightly magenta) on whitish green or purplish tinged background abaxially, umbilicus yellowish with dark centre. Spadices 1–6 per plant, filiform; peduncle 2–12 cm long, whitish green to purplish, longitudinally striate; rachis usually longer than peduncle, except in young spadices, about same diam. as peduncle, whitish green to purplish, longitudinally striate, very loosely flowered, individual flowers up to 3 mm apart. Floral bracts short elliptic, 0.7 × 0.5 mm, centrally peltate, apex acuminate. Stamens with filaments 0.4 mm long; anthers 0.2 × 0.15 mm. Ovary ellipsoid, 0.4 mm long; stigma terminal. Fruit long ellipsoid, body 0.8 × 0.5 mm, shortly pedicellate; pericarp granulose; style long conical, 0.4 mm. Figs 12 & 13.

**Other representative specimens examined – Bolivia:** La Paz, prov. Franz Tamayo, Integrated Management Natural Area (ANMI) Apolobamba, sector Laitiki–Piara, between Pelechuco and Apolo, saxiculous herb in shade, spadices purple-red, 14°47'01"S 69°01'08"W, alt. 2,659 m, 20 Apr. 2006, *Fuentes et al.* 10409 (BR, LPB, MO).

**Etymology** – The specific epithet refers to the purple colour at and along the nerves abaxially.

**Relationships** – Phylogenetically *P. purpureonervosa* appears to be related to *P. peruviana* Dahlst. (fig. 1). Morphologically *P. purpureonervosa* is quite distinct in the colour at and along the nerves (dark green adaxially, purple abaxially) (fig. 13), which is, due to the translucent leaves, also clearly visible in the herbarium specimens. However, as it is evident from *Fuentes et al.* 10409, the purple colour may not be that prominently present in every population or can even lack completely in individual specimens. In those cases, the reticulate nervation pattern remains diagnostic as the secondary nerves in the leaves of *P. peruviana* are nearly invisible. The leaves of *P. purpureonervosa* can be twice as wide as in *P. peruviana* and are also more translucent.

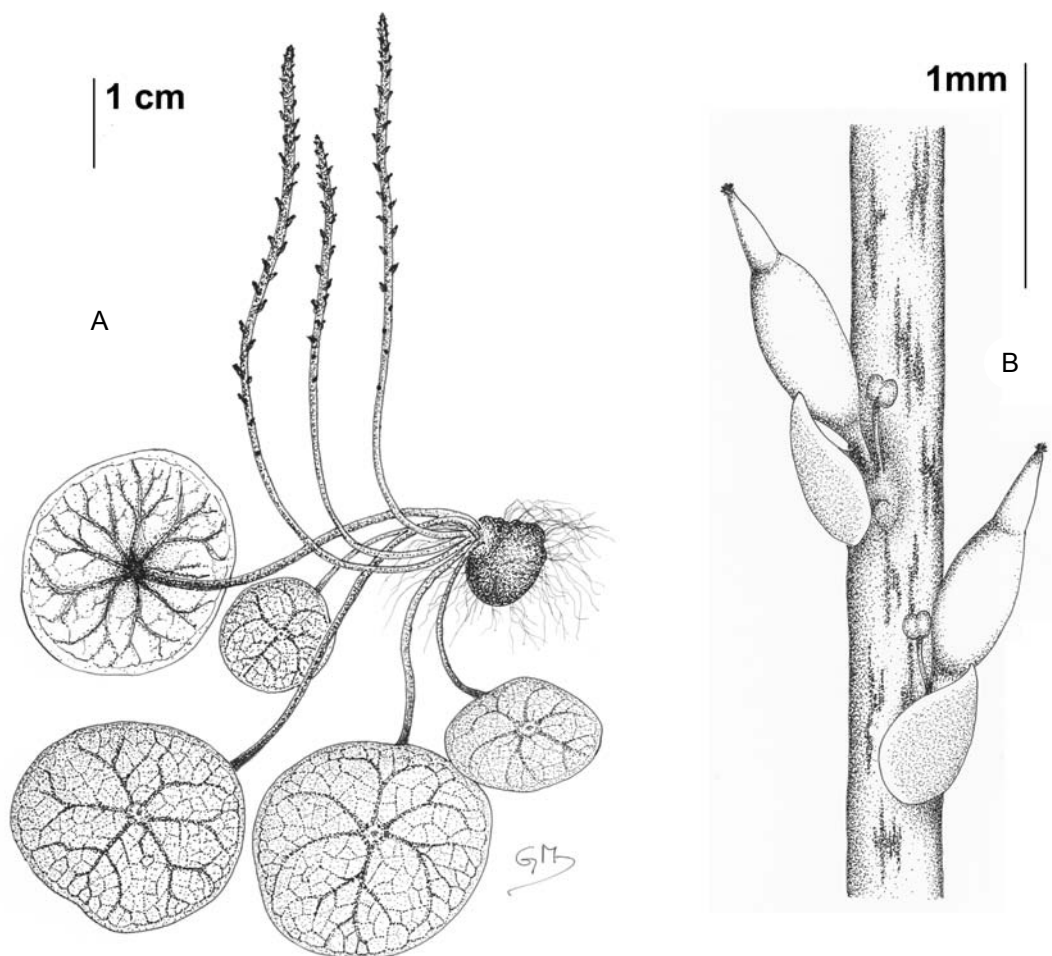
**Phenology** – The plant is above-ground at least from January to April, flowering and fruiting.

**Distribution and habitat** – Growing in moss on rock walls in the Bolivian department of La Paz.

### 14. *Peperomia querocochana* G.Mathieu & Pino, sp. nov.

A *P. umbrosa* G.Mathieu differt lamina distincte nervosa et tubere e basi radicante, parte basali laevi flavaque, parte apicali aspera brunneaque, ramificanti ubi vetusto. – Type: Peru, Ancash, prov. Recuay, dist. Recuay, Cordillera Blanca, road Ticapampa–Chavin de Huántar, near Lake Querococha, along brooklet uphill from road, in mosses, 09°43'40.2"S 77°19'40.5"W, alt. 4,100 m, 22 Jan. 2009, *Mathieu & Symmank* 2009-017a (holo-: USM; iso-: BR, GENT, MO).

Delicate herb, 8–12 cm tall. Tuber globose, surface entirely smooth and yellowish when young, gradually developing apically brown and rough zone, distinctly separated from remaining yellowish basal part, finally completely replacing yellowish part, losing globose aspect when becoming older by forming two or more thick outgrowths, apically bearing buds from which leaves and inflorescences develop, rooting



**Figure 12** – *Peperomia purpureonervosa*: A, general habit; B, part of rachis. Drawn by G. Mathieu.



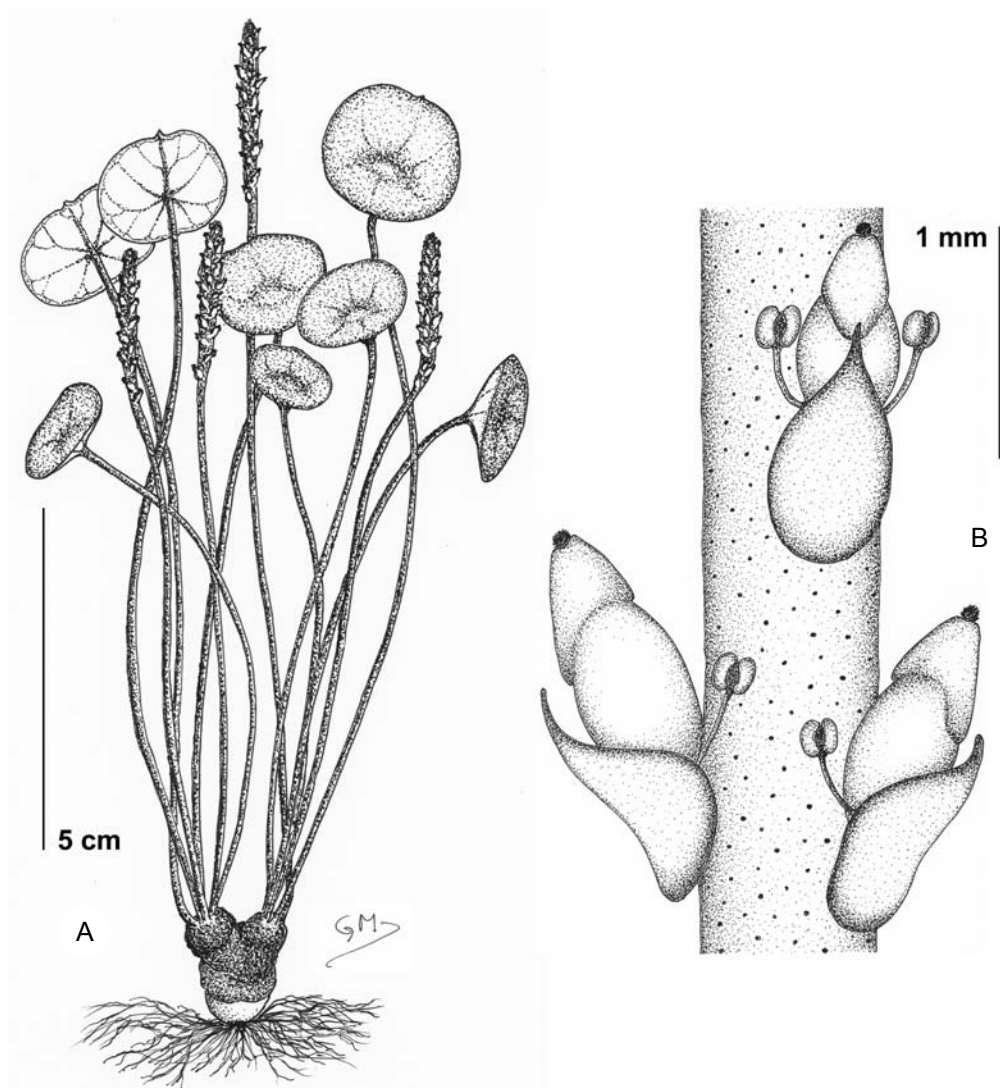
**Figure 13** – *Peperomia purpureonervosa*, leaf nervation (pattern and colour): A, adaxially; B, abaxially.

at base, creamy white to yellowish on cross section. **Leaves** 2–12 per plant; petiole slender, 5–10(–11) × 0.05 cm, white or whitish-green; lamina membranous, orbicular, (0.5–)0.8–1.3(–2) cm diam., flat or sometimes slightly funnel-shaped in centre, peltate in middle or slightly below, base sometimes slightly truncate, apex often widely emarginate with very tip minutely acuminate, distinctly nerved abaxially, 5–7-palmatinerved, main nerves distally anastomosing by perimarginal nerve, main nerve often slightly protruding abaxially. **Spadices** 1–4 per plant; peduncle 5–10 cm, white or whitish-green; rachis 1.5–2 cm × 1.2–1.5 mm, 2 times as thick as peduncle, loosely flowered, green, minutely dark dotted. **Floral bracts** elliptic, 1–1.1 × 0.5–0.7 mm, centrally peltate,

apex acuminate to long acuminate, intense green. **Stamens** with filaments 0.3–0.5 × 0.08–0.09 mm, perpendicular to rachis; anthers subglobose, 0.4 × 0.3 mm, white, brown when dry. **Ovary** ellipsoid, 0.6–0.65 × 0.5–0.55 mm, intense green; stigma terminal, subglobose, fimbriate, 0.3–0.4 mm diam., white. **Fruit** ellipsoid, 0.9–1 × 0.6–0.7 mm, sessile, centrally attached at the base, pericarp granulose; style conical, slightly asymmetrical, reaching further towards base abaxially than adaxially (best visible in younger fruits), 0.2–0.25(–0.4) mm long, 0.35–0.45 mm wide, brownish. Figs 14 & 15.

**Other representative specimens examined** – Peru: Ancash, prov. Ocos, dist. Ocos, road Ocos–Cerro Chunto km 15.5, rocky slope,





**Figure 14** – *Peperomia querocochana*: A, general habit; B, part of flowering rachis. Drawn by G. Mathieu.



**Figure 15** – *Peperomia querocochana*: tubers of different ages and developmental stages (young to the left, older to the right).

c. 200 m uphill from road, 10°20'08.1"S 77°20'88.0"W, alt. 3,955 m, 3 Feb. 2009, Mathieu *et al.* 2009-043 (BR, GENT, USM).

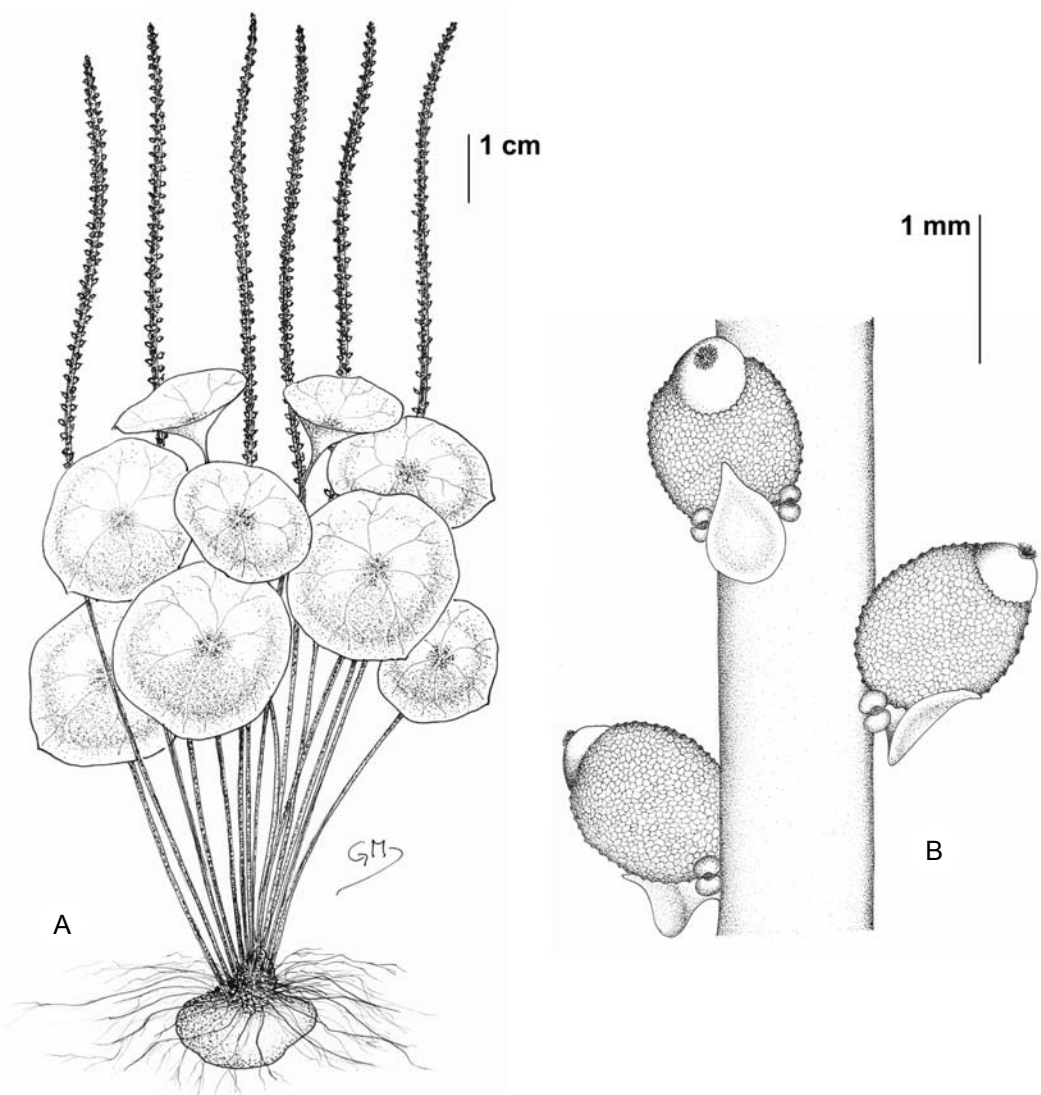
**Etymology** – The specific epithet refers to the locality where the type was found, near lake Querococha.

**Relationships** – The species resembles *P. umbrosa* to some extent. However, the latter species has obscurely nerved leaves and a tuber rooting all over its surface. That species is also lacking the particular tuber development observed in

*P. querocochana* (fig. 15). According to phylogenetic analysis, this species is most closely related to *P. ocrosensis* G. Mathieu & Pino (fig. 1).

**Phenology** – The plant has been found above-ground in January and February, flowering and fruiting.

**Distribution and habitat** – Both known collections were made near 4,000 m. Therefore, it seems that the species is restricted to rather high locations.



**Figure 16** – *Peperomia radiatinervosa*: A, general habit; B, part of fruiting rachis. Drawn by G. Mathieu.

**15. *Peperomia radiatinervosa* G.Mathieu, sp. nov.**

A *P. polycephala* Trel. differt tubere ex apice radicante, lamina leviter undulata infundibuliformique, petiolo longiore, spadice robustiore, bacca majore sed bractea florali minore, crescit in saxis gramineis nec rupibus muscosis. – Type: Bolivia, Chuquisaca, prov. Oropesa, hillside along road Sucre–Tarabuco, 8 km from Sucre, together with grasses in rock crevices, 19°05'11.2"S 65°13'14.5"W, alt. 2,900 m, 3 Feb. 2008, Samain et al. 2008-090 (holo-: BR; iso-: G, GENT, K, LPB, MO).

Rather robust herb, 10–20 cm tall. Tuber flattened globose or slightly irregular, to 4 cm diam. but usually smaller, forming apical outgrowths when growing older, surface dark brown, rather smooth except for the outgrowths, rooting at apex, sometimes a few lateral roots. Leaves 5–12 per plant; petiole (5–)10–12(–20) cm × 2–2.5 mm, terete, whitish at the base and pinkish purple more apically, or entirely purple; lamina orbicular or irregularly orbicular, 2–4 cm diam., centrally peltate, usually undulate and centrally slightly funnel-shaped, apex rarely obtuse, usually rounded and exhibiting

a very discrete, acuminate, whitish or yellowish tip, chartaceous, shiny green adaxially, dull whitish green or purple tinged abaxially, distinctly 6-palminerved, main nerves branching, almost reaching margin, adaxially protruding and usually lighter than remainder of lamina. Spadices (1–)3–10 per plant; peduncle usually a little shorter and thinner than petiole; rachis a little shorter than peduncle, to 10 cm × 2 mm, moderate-densely flowered. Floral bracts orbicular to ovate, 0.7–0.8 × 0.5–0.6 mm, fleshy, adaxially concave, apex acuminate, c. 0.5 mm distant from rachis on firm stalk. Stamens minute, filaments c. 0.3 mm long; anthers 0.2 mm long. Ovary ellipsoid, surface granulose; style prominent, globose to dome-shaped, larger than the ovary; stigma globose to dome-shaped. Fruit large, fruit body broadly ellipsoid, c. 1.4 × 1.1 mm, pericarp verruculose, centrally attached at base, base somewhat sunken in rachis; style flat dome-shaped, 0.2 mm high; stigma terminal, sessile or slightly sunken, dome-shaped. Fig. 16.

**Other representative specimens examined** – **Bolivia**: Chuquisaca, prov. Zudañez, Mojocoya, near Buenavista, in thick humus layer,



together with grasses and sedges, 18°42'14.1"S 64°41'41.5"W, alt. 2,535 m, 4 Feb. 2008, *Samain et al.* 2008-101 (BR, GENT, LPB, MO); loc. cit., together with mosses and grasses in rock crevices, dry habitat, 18°41'36.3"S 64°41'37.3"W, alt. 2,670 m, 4 Feb. 2008, *Samain et al.* 2008-105A (BR, GENT, LPB); near Villa Redencio Pampa, together with ferns, grasses, mosses and Cactaceae in rock crevices below cliff with *Puya*, 18°49'43.6"S 64°34'57.2"W, alt. 2,625 m, 4 Feb. 2008, *Samain et al.* 2008-110 (BR, GENT, LPB); Cochabamba, prov. Cervado, Cochabamba, Cerro San Pedro, along path from El Cristo to the Botanical Garden, steep rocky slope with *Puya* near the top of the hill, 17°24'03.3"S 65°48'24.9"W, alt. 3,180 m, 15 Jan. 2008, *Samain & Bates* 2008-014 (BR, GENT, LPB, MO); prov. Arani, hillside along old road Cochabamba–Santa Cruz, 6 km W of Monte Punku, together with mosses in thin soil layer between *Puya* sp. and small rocks, 17°33'35.6"S 65°20'25.4"W, alt. 3,030 m, 17 Jan. 2008, *Samain & Bates* 2008-028 (BR, GENT, LPB); prov. Arani, hillside along old road Cochabamba–Santa Cruz, km 328, 17°44'38.2"S 64°58'33.4"W, alt. 3,015 m, 17 Jan. 2008, *Samain & Bates* 2008-029 (BR, GENT, LPB); prov. Campero, along road Aiquile–Santiago, together with grasses, mosses and *Puya* in shallow clayish soil in rocky area, 18°11'46.3"S 65°16'14.0"W, alt. 2,890 m, 9 Feb. 2008, *Samain et al.* 2008-127 (BR, GENT, LPB).

**Etymology** – The specific epithet refers to the usually distinct main nerves radiating from the petiole insertion. The palminerved pattern is always present in the orbicular-leaved species of subgenus *Tildenia* but often the nervation is obscure or the nerves are only distinct to halfway between the petiole insertion and the margin.

**Relationships** – Phylogenetic analysis reveals *P. radiatinervosa* to be related to *P. cyclaminoides* Kunth and *P. verruculosa* Dahlst. ex Hill., both distinctly smaller species with ovate, not centrally peltate leaves (fig. 1). Morphologically *P. radiatinervosa* is closer to the Peruvian *P. polycephala* Trel. Although the leaves of *P. polycephala* can reach the same diam., the usually shorter petioles, (2.5–)3–5(–7) cm, make this species appear smaller. Leaves of *P. polycephala* are usually not undulate, flat instead of slightly funnel-shaped and thinner. The leaf apex is rounded without a minute acuminate tip. Spadices of *P. polycephala* are more slender but usually conspicuously long, 3–4(–5) times as long as the petioles. The tubers of *P. polycephala* are not larger than 10–15 mm and root from all over their surface. This species also has smaller fruits but larger floral bracts. *P. polycephala* occurs at a similar elevation but prefers a more humid habitat. It is observed on rock walls, growing together with mosses.

**Phenology** – The plant has been found above-ground in January and February, flowering and fruiting.

**Distribution and habitat** – *Peperomia radiatinervosa* is apparently abundant in dry rocky and grassy habitats at an elevation of 2500–3200 m.

## 16. *Peperomia umbrosa* G.Mathieu, sp. nov.

A *P. cerrateae* Pino & G.Mathieu differt tubere, e superficie tota radicante, aspera brunneaque; a *P. querocochana* G.Mathieu & Pino differt tubere, e superficie tota radicante, lamina obscuro nervosa. – Type: Peru, Cajamarca, prov. Cajamarca, dist. Cajamarca, Cumbemayo, c. 20 km SW of Cajamarca, trail along (partly) underground creek, 07°11'29.7"S 78°34'48.0"W, alt. 3,560 m, 18 Feb. 2009, *Mathieu et al.* 2009-122 (holo-: USM; iso-: BR, GENT).

Delicate herb, up to 8 cm but often not more than 3–5 cm tall due to decumbent petioles and peduncles. Tuber 0.6–0.8 cm diam., globose or slightly higher than wide when growing older, rooting all over its surface but mainly at the base, surface dark brown, rough, creamy white on cross section with distinct brown peripheral zone. Leaves 3–6 per plant; petiole terete, filiform, up to 12 cm long, whitish, uncommonly slightly tinged pink-red; lamina membranous, orbicular, 0.8–1.5 cm diam., sometimes slightly emarginate, centrally peltate, vivid green adaxially, whitish green abaxially, obscurely 6-palminerved, nerves only visible abaxially. Spadices (1–)2–5 per plant; peduncle up to 9 cm long, shorter than petiole, whitish, rarely slightly tinged pink-red; rachis 1.5–2.5 cm long, 1.5 times as thick as peduncle, loosely flowered, whitish green, little darker apically. Floral bracts elliptic, 0.7–0.8 mm long, apex acute to acuminate, base rounded, centrally peltate, translucent, minutely vividly glandular-dotted. Stamens with filaments 0.3 mm long; anthers 0.2 mm long. Ovary shortly ellipsoid, stigma terminal. Fruit shortly ellipsoid, 0.8 mm long, sessile, centrally attached at the base; pericarp granulose, partially covered with minute papillae, hardly visible when dried; style mammiform when fresh, narrowly conical when dried. Fig. 17.

**Other representative specimens examined** – Peru: Apurimac, prov. Andahuaylas, dist. Kishuara, along road Chincheros–Abancay, km 290.5, beyond Andahuaylas, 13°40'20.3"S 73°11'48.4"W, alt. 4,160 m, 27 Jan. 2009, *Samain et al.* 2009-067 (BR, GENT, USM); Junin, prov. Junin, along road La Oroya–Pasco, km 138, 11°17'27.9"S 75°54'47.6"W, alt. 4,190 m, 26 Feb. 2009, *Samain et al.* 2009-210a (USM).

**Etymology** – The specific epithet refers to the shady habitat where the type collection was made.

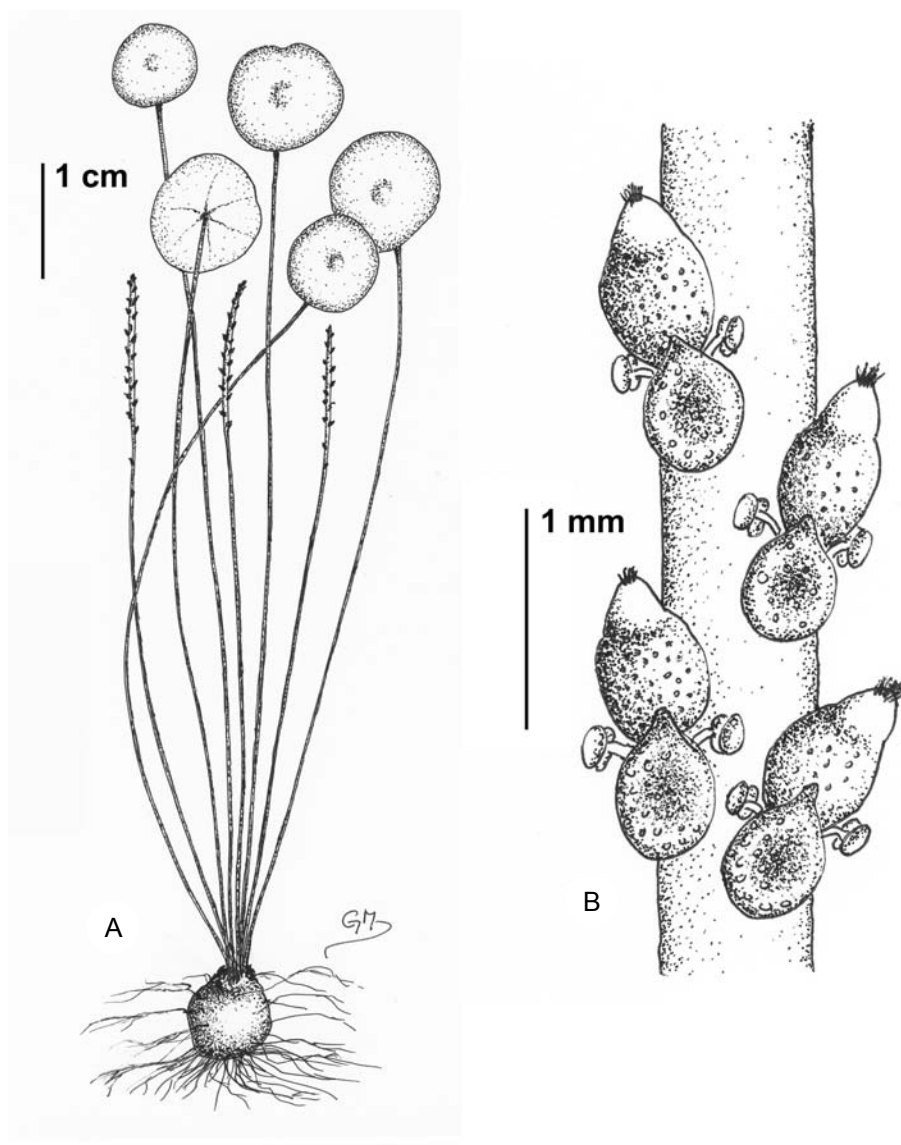
**Relationships** – This species is distinct in its slender general habit, its small, dark brown tubers with rough surface and the long petioles of the small obscurely nerved leaves. Also *P. cerrateae* is characterized by small tubers but these have a yellowish and smooth surface and root at the apex. This species resembles *P. querocochana* to some extent. However, the leaves of the latter species have a distinct nervation and a tuber rooting only at the base. Phylogenetically *P. umbrosa* appears to be related to *P. polycephala* Trel., *P. peruviana* Dahlst. and to *P. purpureonervosa* G.Mathieu (fig. 1). *P. andina* Pino and *P. jalcaensis* Pino, two other geophytic *Peperomia* species, are growing abundantly on exposed spots near the *P. umbrosa* type locality.

**Phenology** – The plant has been found above-ground in February.

**Distribution and habitat** – The localities of the mentioned collections (departments of Cajamarca, Apurimac and Junin) suggest a rather wide Peruvian distribution. The type collection was made from a population growing in a cave-like rock formation, dark and wet, in loamy soil together with liverworts. Additional collections mentioned herewith were found in crevices and at the base of rocks, in shady conditions but not as extreme as the type collection.

## 17. *Peperomia wernerrauhii* Pino & Samain, sp. nov.

Planta geophila a *P. andina* Pino differt tubere minore supra non caulescente, laminis foliorum minoribus subtus non pur-



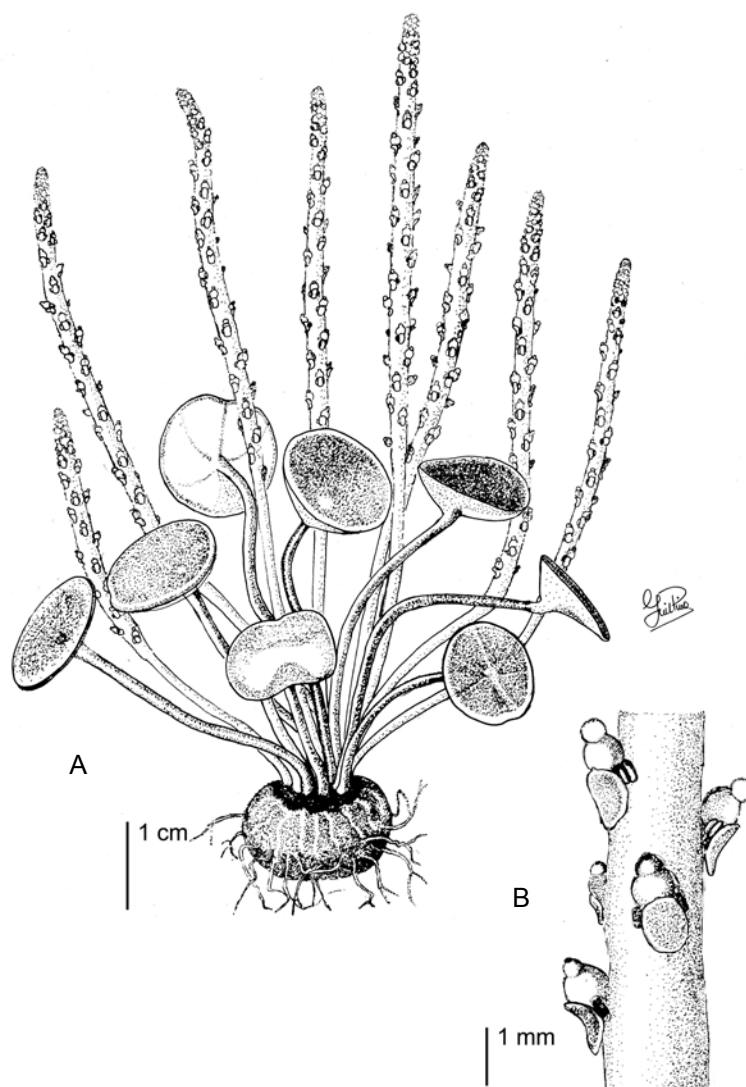
**Figure 17** – *Peperomia umbrosa*: A, general habit; B, part of fruiting rachis. Drawn by G. Mathieu.

purascensibus. – Type: Peru, Huánuco, prov. Huánuco, dist. Santa María del Valle, Cochabamba, near Marambuco, on rocks of steep canyon aside fields of Gregorio Espíritu, growing together with *P. naviculifolia* Trel. and *Echeveria andicola* Pino, 09°53'37"S 76°09'03"W, alt. 2,470 m, 27 Feb. 2009, Samain et al. 2009-214 (holo-: USM; iso-: BR, GENT).

Small herb, 5–14(–20) cm tall. Tuber usually buried or partially exposed, globose, depressed, light grayish brown, 7–11 mm high, (0.7–)1.1–1.5(–2.2) cm diam., rooting at base, apex flat forming a darker central ring 3–7 mm diam. Leaves 6–9(–12) per plant; petiole terete, light green with reddish longitudinal lines, 2.5–5(–9) cm × 0.9–1.2 mm diam., erect to slightly curved; lamina orbicular to widely ovoid, chartaceous, peltate a little below middle, (0.8–)1.2–2.2 cm diam., margin entire, apex minutely emarginate, adaxially concave or flat, centrally umbilicate, glossy green, obscurely 7-palmatinerved, nerves lighter in colour and not reaching margin, only central nerve from insertion of petiole to apex conspicuous, darker and sometimes there induplicate, abaxially green-

ish white. Spadices 8–14(–20) per plant, initially erect, then slightly curved; peduncle 4–8 cm × 0.8–0.9 mm, light green or reddish; rachis 4–10(–14) cm × 1–1.6 mm, light yellowish green. Floral bracts peltate, elliptic, green, 0.8–0.9 mm long, 0.6–0.7 mm wide. Stamens with filaments 0.15 × 0.1 mm, terete, transparent; anthers ellipsoid 0.35–0.4 × 0.25–0.3 mm, red when young, dark brown when drying. Ovary ovoid, bright green, 0.6–0.7 × 0.5–0.6 mm; stigma globose, yellowish green 0.3 × 0.35 mm. Fruit ovoid, body 0.8–0.9 × 0.7–0.8 mm, brown; style widely conical, green, 0.3–0.4 × 0.35–0.45 mm; stigma dark. Fig. 18.

**Other representative specimens examined** – Peru: Huánuco, prov. Huánuco, dist. Chinchao, along road Pachachupan–Pillao, 4.5 km from the crossing with the road Huánuco–Chinchao km 34, 09°47'59"S 76°03'27"W, alt. 2,380 m, 1 Mar. 2009, Samain et al. 2009-248 (BR, GENT, USM); dist. Churubamba, Chinchobamba, 10°04'S 76°11'W, alt. 2,200 m, 9 Apr. 2005, Pino & Novoa 1623 (Photos); prov. Huamalíes, dist. Chavín de Pariarca, Chavín, s.d., alt. 2,800 m, Rauh 53869a (HEID).



**Figure 18** – *Peperomia wernerrauhii*: A, general habit; B, part of flowering rachis. Drawn by G. Pino.

**Etymology** – The name stands for Werner Rauh (1914–2000), the German botanist who discovered this plant and described several *Peperomia* species from Peru and Ecuador. The name *P. wernerrauhii* differs from *P. rauhii* Hutchison, a herbarium name of *P. congesta* Kunth (Mathieu 2007: 419).

**Relationships** – This species was discovered in 1983 by Werner Rauh in Chavín de Parí and was cultivated in Heidelberg Botanical Garden where he primarily identified it as *P. peruviana* and with that name he published a photo of this plant in 1989 (Rauh 1989). Since then it was not collected until we found it in several places of the department of Huánuco immediately pointing out its relationship with *P. andina*. Both species form identical depressed globose or discoid tubers with a black ring on the top where petioles and spadices emerge, although *P. andina* has larger tubers and eventually this ring can grow as a short conical stem in very old plants. The leaves of this new species are smaller, less markedly ovate, slightly concave instead of infundibuliform and they lack the purple hue of the abaxial side of *P. andina*.

*P. wernerrauhii* is closely related to several other Andean species, amongst others *P. andina* (fig. 1).

**Phenology** – Leaves are present from November to April, spadices appear from January to March, fruits ripen from February to March.

**Distribution and habitat** – It grows on rocks partially hidden by mosses or exposed, in the department of Huánuco at 2200–2800 m.

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