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Recircumscription and revision of the genus *Vanoverberghia* (*Zingiberaceae*)

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Key words

Alpinia
ITS
Lanyu
Luzon
new species record
*trn*K/*mat*K

Abstract The genus *Vanoverberghia* currently includes three species namely *V. sepulchrei* and *V. rubrobracteata* from the Philippines and *V. sasakiana* from Taiwan. New material targeting the *Alpinia eubractea* clade of the tribe *Alpinieae* was used to test the monophyly of *Vanoverberghia*. A combined analysis of the ITS and *trn*K/*mat*K regions reveals that these three species form a strongly supported monophyletic clade with *Alpinia diversifolia* and *Alpinia vanoverberghii*. The morphological descriptions of all species were updated after examining recent collections and comparing with types and protologues. The original description of *A. diversifolia* did not include information on the flowers which are described here. The morphology of *A. diversifolia* and *A. vanoverberghii* is for most parts in accordance with the previous perception of the genus but a few characters are added and a recircumscription of *Vanoverberghia* is subsequently provided here. *Vanoverberghia diversifolia* is reinstated and *A. vanoverberghii* is combined in *Vanoverberghia*. Furthermore, collections from northern Luzon documents the presence of *V. sasakiana* and all species of *Vanoverberghia* thus occur in the Philippines. A key to the five species is provided including a comprehensive taxonomic revision and designation of three lectotypes.

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INTRODUCTION

Vanoverberghia Merr. is a small genus in the family *Zingiberaceae* with three accepted species namely *V. sepulchrei* Merr. (Fig. 7, 8) and *V. rubrobracteata* Docot & Ambida (Fig. 5) both from the Philippines and *V. sasakiana* Funak. & H.Ohashi from Taiwan (Fig. 6). The genus was named in honour of Father Morice Vanoverbergh (1885–1982), a Belgian priest who made extensive collections of plants alongside his missionary work in Mountain Province, Philippines, from 1910–1914 (Merrill 1912). In the tribe *Alpinieae*, *Vanoverberghia* is considered exceptional by its pendulous inflorescence, single flower per bract, absence of bracteoles, lateral corolla lobes that are basally connate to each other and to the labellum, and filiform lateral staminodes (Merrill 1912, Burtt & Smith 1972, Smith 1990, Larsen et al. 1998, Funakoshi & Ohashi 2000, Docot et al. 2016). Species of *Vanoverberghia* are rarely encountered in the forest but can be easily recognised even when sterile by their reddish coriaceous ligules and flagellate leaf apices. They occur in lowland and montane forest near streams and ravines, forming loose clumps of leafy shoots 2–8 m long.

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When describing the monotypic genus *Vanoverberghia*, Merrill (1912) emphasised its affinity to *Riedelia* Oliv. and *Alpinia* Roxb. Elmer described the second species, *Vanoverberghia diversifolia* Elmer (Fig. 3, 4) in 1915 but in 1919, however, Elmer changed his mind and combined it in *Alpinia* without any explanation. Moreover, Smith (1990) did not place this species in her classification of *Alpinia* and regarded it as an imperfectly known species. As Funakoshi & Ohashi (2000) described *V. sasakiana* in Taiwan, the monotypic and endemic status of *Vanoverberghia* to the Philippines was gone.

Merrill (1912) described *Alpinia vanoverberghii* Merr. (Fig. 9, 10) from northern Luzon and placed it in *Alpinia* subg. *Probolocalyx* K.Schum. Merrill considered it unique among *Alpinia* species by its racemose inflorescence, large flowers, crestless anthers, and in the complete absence of bracts and bracteoles. Smith (1990), however, placed this species in sect. *Kolowratia* (C.Presl) Loes. noting that the bracts and bracteoles are minute and soon deciduous, and the flower being so similar to *Alpinia elegans* (C.Presl) K.Schum. that it would be inappropriate to separate these two species.

In the phylogenetic analyses of Kress et al. (2002, 2005, 2007) and De Boer et al. (2018), *Alpinia* appeared to be highly polyphyletic and Kress et al. (2005, 2007) suggested that *Alpinia* should be split into several genera reflecting evolutionary history. These phylogenetic analyses, and that of Funakoshi et al. (2005) revealed that *Vanoverberghia* was nested in the *Alpinia eubractea* clade of the *Alpinieae* and was more closely related to *Alpinia* species in the Philippines than to *Riedelia* in New Guinea. In addition, Kress et al. (2005, 2007) also stated that the species in the *Alpinia eubractea* clade are highly polymorphic with no apomorphic character shared to circumscribe them as a genus.

The aim of the present study was to address the placement of *Alpinia diversifolia* (Elmer) Elmer and *A. vanoverberghii* in relation to *Vanoverberghia* using a combined analysis of the

ITS and *trn*K/*mat*K regions, and to provide a comprehensive taxonomic revision of *Vanoverberghia*. In addition, after examining and comparing recent collections to types and protologues, the morphological descriptions of these species were revised and amplified. A taxonomic treatment is presented below including the recircumscription of *Vanoverberghia* and a key to five species.

MATERIALS AND METHOD

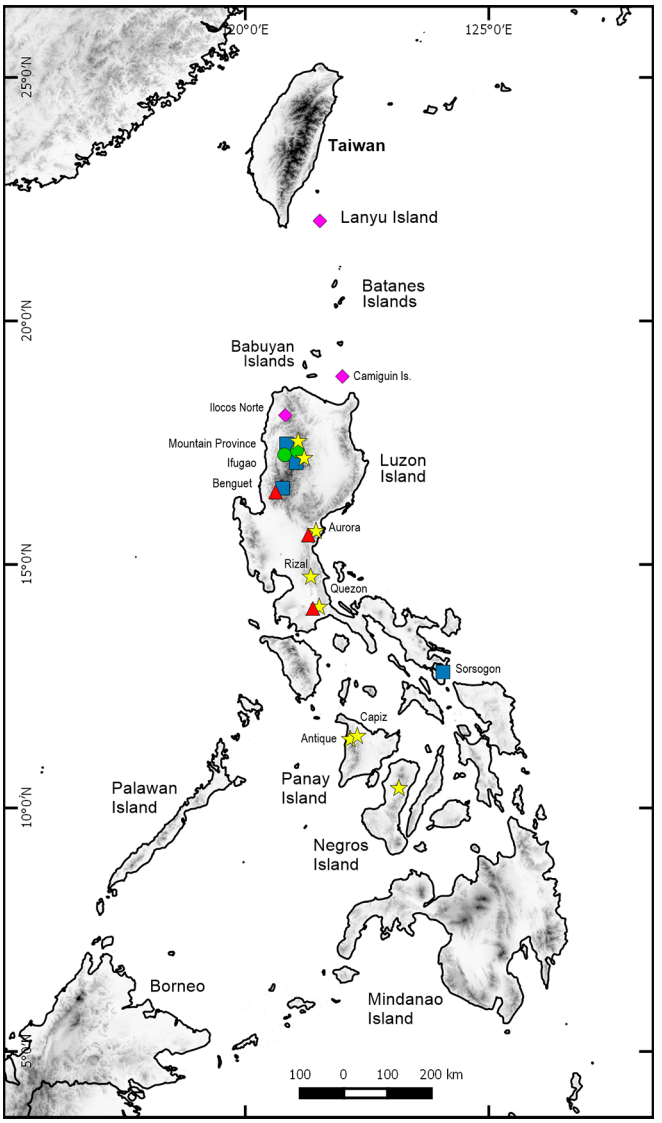
Plant material and morphological examination

This study is based on herbarium specimens including types deposited at AAU, BISH, BM, E, F, FEUH, G, GH, HAST, K, L, LD, MO, NY, P, PNH, S, SING, TAI, TAIF, TI, U, US, USTH and Z. Herbarium acronyms follow Thiers (continuously updated). Specimens seen only as digital images available online (e.g., specimens deposited at HAST and Z) are denoted with an asterisk (*). The silica-dried leaf material used to generate the new sequences in this study was obtained from recent collections. Collections with reproductive parts preserved in 70 % ethanol were dissected and examined using an OLYMPUS CX21 Stereomicroscope. The local names of Philippine species gathered from the literature (e.g., Madulid 2001), interviews and herbarium labels are given for each species with the name of the local dialect in parentheses.

Conservation status and distribution map

Conservation status assessments are available for *Vanoverberghia diversifolia*, which was assessed as Critically Endangered (CR) by Contu (2013, as *Alpinia diversifolia*), for *V. rubrobracteata*, which was assessed as Least Concern (LC) by Ambida et al. (2018), for *V. sasakiana*, assessed as Vulnerable (VU) by The Editorial Committee of the Red List of Taiwan Plants (2017) and for *Vanoverberghia sepulchrei* which was assessed as Near Threatened (NT) by Fernando et al. (2008). However, as all of these assessments were based on a different number of occurrences than we report here, we have made new assessments for all *Vanoverberghia* species using the International Union for Conservation of Nature (IUCN) criteria (IUCN 2016). The extent of occurrence (EOO) and area of occupancy (AOO) of each species were calculated using the Geospatial Conservation Assessment Tool (GeoCAT) (Bachman et al. 2011: http://geocat.kew.org/). The assessments are currently under review and will be available at http://www.iucnredlist.org/.

For the geographic distribution of *Vanoverberghia*, the coordinates of the localities based on information on herbarium labels were collected and generated in QGIS v. 2.18 (Quantum GIS Development Team 2016), to create a distribution map (Map 1).



Map 1 Distribution of *Vanoverberghia diversifolia* Elmer (▲), *V. rubrobracteata* Docot & Ambida (★), *V. sasakiana* Funak. & H.Ohashi (◆); *V. sepulchrei* Merr. (■) and *V. vanoverberghii* (Merr.) Funak. & Docot (●).

DNA extraction, amplification and sequencing

Total genomic DNA was extracted using DNeasy Plant Mini Kit (Qiagen®, Germany) following the manufacturer's protocol. Amplification of the ITS region was accomplished using ITS4 and ITS5 primers (White et al. 1990) in 25 µL volumes and mix as follows: 15.8 µL of dH_2O; 2.5 µL of 10 by PCR buffer; 2 µL of 25 mM $MgCl_2$; 2 µL of 10 mM dNTP; 1 µL each of 10 mM forward and reverse primers; 0.5 µL Kapa Taq (KAPA Biosystems©); and 1 µL DNA. The thermal cycling profile for the ITS region was set under initial denaturation at 94 °C for 5 min, followed by 30 cycles of denaturation at 94 °C for 1 min, primer annealing at 55 °C for 1 min, and DNA strand extension at 72 °C for 1 min with a final extension of 10 min at 72 °C. The chloroplast *trn*K intron and *mat*K gene were amplified in short sections using primers from Leong-Škorničková et al. (2011: table 2) in 50 µL volumes and mix as follows: 24.25 µL of dH_2O; 5 µL of 10× PCR buffer; 5 µL of 25 mM $MgCl_2$; 4 µL of 10 mM dNTP; 0.5 µL of 0.1 mg/ml bovine serum albumin (BSA); 5 µL of 5 mM tertramethylammonium chloride (TMACl); 0.5 µL each of 10 mM forward and reverse primers; 0.25 µL Kapa Taq; and 5 µL of DNA. PCR thermal profile for the *trn*K/*mat*K region was set under initial denaturation at 95 °C for 5 min, followed by 40 cycles of denaturation at 95 °C for 30 s, primer annealing from 50–60 °C for 40 s and DNA strand extension at 72 °C for 1 min with a final extension of 7 min at 72 °C. All PCR reactions were performed in Biometra T-Gradient thermocycler. PCR products were purified using QIA-quick Purification Kit (Qiagen®, Germany) following manufacturer's protocol and were sent to Macrogen© (Seoul, Korea) for sequencing.

Sequence assembly, alignment, and phylogenetic analyses

A total of sixteen newly generated sequences (ITS = 8; *trn*K/*mat*K = 8) was edited and assembled in Codon Code Aligner v. 4.1.1 (Codon-Code 2013). The sequences were then aligned, using Mesquite v. 3.04 (Maddison & Maddison 2016), to sequence data from previous phylogenetic studies on *Zingiberaceae* downloaded from GenBank (see Table 1 for complete accession details of sequences). A total of 61 accessions from the ITS and 58 for the *trn*K/*mat*K region (59 taxa) were used to construct the phylogenetic tree of the tribe *Alpinieae* with

emphasis on the *Alpinia eubractea* clade. Genera with only one taxon in the analysis, including *Aframomum* K.Schum., *Amomum* Roxb., *Etlingera* Giseke, *Geocharis* (K.Schum.) Ridl., *Geostachys* (Baker) Ridl., *Hornstedtia* Retz., *Lanxangia* M.F.Newman & Škorničk., *Leptosolena* C.Presl, *Plagiostachys* Ridl., *Siliquamomum* Baill., *Renealmia* L.f. and *Wurfbainia* Giseke, were included to demonstrate generic boundaries inside the tribe *Alpinieae*. Moreover, six outgroups from the tribes *Globbeae*, *Riedelieae*, *Siphonochiloideae*, *Tamijioideae* and *Zingiberoideae* were included.

The phylogeny of the tribe *Alpinieae* was constructed using Maximum likelihood (ML) for bootstrap supports and Bayesian inference analysis (BI) for posterior probabilities. Modeltest

Table 1 List of GenBank accession details of ITS and *trn*K/*mat*K regions, vouchers, and references used in the phylogenetic analyses. Taxa with an asterisk (*) are new sequences.

Species	ITS	*trn*K/*mat*K	Reference / Voucher
Tribe *Alpinieae*			
Aframomum angustifolium (Sonn.) K.Schum.	AF478704	AF478804	*Kress #92-3403* (US)
Alpinia abundiflora B.L.Burtt & R.M.Sm.	AY742334	AY742393	Rangsiruji et al. (2000)
Alpinia arctiflora (F.Muell.) Benth.	AY742336	AY742395	Rangsiruji et al. (2000)
Alpinia argentea (B.L.Burtt & R.M.Sm.) R.M.Sm.	AY742337	AY742396	*CS 02-303* (HLA)
Alpinia arundelliana (F.M.Bailey) K.Schum.	AY742338	AY742397	Rangsiruji et al. (2000)
Alpinia bilamellata Makino	AY742339	AY742398	*L-97.0268* (HLA)
Alpinia brevilabris C.Presl	AY742339	AY742399	Rangsiruji et al. (2000)
Alpinia caerulea (R.Br.) Benth.	AY742342	AY742400	Rangsiruji et al. (2000)
Alpinia calcarata (Haw.) Roscoe	AF478710	AF478810	*Kress #94-3657* (US)
Alpinia carolinensis Koidz.	AF478711	AF478811	*Kress #99-6404* (US)
Alpinia conchigera Griff.	AF478712	AF478812	*Kress #00-6706* (US)
Alpinia congesta Elmer*	LT717106	LT717120	*R.V.A. Docot 0018* (USTH)
Alpinia diversifolia (Elmer) Elmer*	LT717105	LT717122	*R.V.A. Docot 0034* (USTH)
Alpinia elegans (C.Presl) K.Schum.	AF478713	AF478813	*Kress #99-6412* (US)
Alpinia eremochlamys K.Schum.	AY742346	AY742404	*SUL02-68* (E)
Alpinia eubractea K.Schum.	AY742347	–	Rangsiruji et al. (2000)
Alpinia fax B.L.Burtt & R.M.Sm.	AY742348	AY742405	Rangsiruji et al. (2000)
Alpinia flabellata Ridl.	AY742349	AY742406	Rangsiruji et al. (2000)
Alpinia galanga (L.) Willd.	AF478715	AF478815	*Kress #94-5263* (US)
Alpinia haenkei C.Presl	AY742354	AY742410	*L-82.0072* (HLA)
Alpinia javanica Blume	AY742358	AY742413	Rangsiruji et al. (2000)
Alpinia ligulata K.Schum.	AY742361	AY742415	Rangsiruji et al. (2000)
Alpinia luteocarpa Elmer	AF478717	AF478817	*Kress #99-6403* (US)
Alpinia modesta F.Muell. ex K.Schum.	AY742364	AY742418	Rangsiruji et al. (2000)
Alpinia monopleura K.Schum.	AY742363	AY742419	*SUL143* (E)
Alpinia murdochii Ridl.	KY438007	KY620260	*O. Šída, T. Fér & E. Záveská M-11-1* (PR)
Alpinia nutans (L.) Roscoe	AY742369	AY742423	*CS 02-337* (HLA)
Alpinia oceanica Burkill	AY742370	AY742424	Rangsiruji et al. (2000)
Alpinia officinarum Hance	AF478718	AF478818	*Kress #00-6614* (US)
Alpinia oxyphylla Miq.	AY742372	AY742425	Rangsiruji et al. (2000)
Alpinia pinetorum (Ridl.) Loes.	AY742373	AY742426	*CS 02-300* (HLA)
Alpinia purpurata (Vieill.) K.Schum.	AY742375	AY742429	Rangsiruji et al. (2000)
Alpinia rafflesiana Wall. ex Baker	AY742376	AY742430	Rangsiruji et al. (2000)
Alpinia rufa (C.Presl) K.Schum.	LT717109	LT717125	*R.V.A. Docot 0063* (USTH)
Alpinia sibuyanensis Elmer	AY742381	AY742434	*L-99.0098* (HLA)
Alpinia vanoverberghii Merr.*	LT717107	LT717123	*R.V.A. Docot 0005* (USTH)
Alpinia vittata W.Bull	AF478720	AF478820	Rangsiruji et al. (2000)
Alpinia warburgii K.Schum.	AY742388	AY742442	*SUL02-169* (E)
Alpinia zerumbet (Pers.) B.L.Burtt & R.M.Sm.	AY742389	AY742443	Rangsiruji et al. (2000)
Amomum maximum Roxb.	AY351995	AY352025	*Xia-725* (HITBC)
Etlingera littoralis (J.Koenig) Giseke	AF478750	AF478849	*Kress #99-6323* (US)
Geocharis fusiformis (Ridl.) R.M.Sm. var. *borneensis* R.M.Sm.	AF414487	–	*L.B. Pedersen 1141* (C)
Geostachys densiflora Ridl.	KY438011	KY620238	*O. Šída, T. Fér & E. Záveská M-11-2* (PR)
Hornstedtia scyphifera (J.Koenig) Steud.	KY438021	–	*J. Škorničk. et al. SNG-21* (SING)
Lanxangia tsaoko (Crevost & Lemarié) M.F.Newman & Škorničk.	AY352007	AY352037	*Xia-734* (HITBC)
Leptosolena haenkei C.Presl	AY742331	AY742390	*Funakoshi & Co 2006* (US)
Plagiostachys sp.	AF478773	AF478873	*Kress #00-6745* (US)
Renealmia battenbergiana Cummins ex Baker	AF478779	AF478880	*Kress #94-5277* (US)
Vanoverberghia rubrobracteata Docot & Ambida (1)*	MH270333	MH286066	*R.V.A. Docot 0118* (USTH)
Vanoverberghia rubrobracteata Docot & Ambida (2)*	MH270334	MH286067	*R.V.A. Docot 0123* (USTH)
Vanoverberghia sasakiana Funak. & H.Ohashi*	MH270332	MH286065	*Sekiguchi 23* (TI)
Vanoverberghia sepulchrei Merr. (1)	AF478798	AF478899	*Kress #95-5562* (US)
Vanoverberghia sepulchrei Merr. (2)*	MH270331	MH286064	*R.V.A. Docot 0027* (USTH)
Wurfbainia uliginosa (J.Koenig) Škorničk. & A.D.Poulsen	AY352008	AY352038	*99.0474* (HLA)
Incertae sedis			
Siliquamomum oreodoxa N.S.Lý & Škorničk.	KY438093	KY620221	*S. Hul & N.S. Lý 3583* (E)
Tribe *Riedelieae*			
Burbidgea schizochelia Hackett	AF478729	AF478828	*Kress #01-6867* (US)
Pleuranthodium schlechteri (K.Schum.) R.M.Sm.	AF478775	AF478876	*Kress #00-6725* (US)
Tribe *Globbeae*			
Globba curtisii Holttum	AF478754	AF478853	*Kress #99-6347* (US)
Tribe *Zingibereae*			
Zingiber wrayi Ridl.	AF478802	AF478905	*Kress #00-6721* (US)
Tribe *Tamijieae*			
Tamijia flagellaris S.Sakai & Nagam.	AF47879	AF478898	*K. Ooi #S55* (KYO)
Tribe *Siphonochileae*			
Siphonochilus decorus (Druten) Lock	AF478793	AF478894	*GH #00-135* (US)

v. 3.06 (Posada & Crandall 1998) determined the most appropriate molecular model for each dataset. A general time reversible model (GTR+I+Γ) was used for both ITS and *trn*K/*mat*K in ML and BI analysis. Maximum likelihood tree searches and bootstrapping of the combined data were obtained by running 1 000 replicates using RaxML-HPC2 v. 8.2.10 (Stamatakis 2014), while BI analysis was carried out using MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001), both on the CIPRES portal (Miller et al. 2010). For ML analysis, bootstrap values were categorised according to Kress et al.'s (2002) standard cut-off values. For BI analysis, data was partitioned in order to accommodate differing evolutionary rates for the respective datasets. Four Markov Chain Monte Carlo (MCMC) were performed for ten million generations with trees sampled every 1 000th generations. Values for Potential Scale Reduction Factor (PSRF) and standard deviation of the split frequencies between two runs were considered to confirm convergence. Additional convergence diagnostics was performed using Tracer v. 1.7.1 (Rambaut et al. 2018) to check if each parameter had an effective sample size (ESS) > 100. Trees saved prior to convergence were discarded as burn-in (10 000 trees), creating a 50 % majority rule consensus tree constructed from the remaining trees.

RESULTS AND DISCUSSION

Phylogenetic analyses of the ITS and trnK/matK regions

The combined ITS and *trn*K/*mat*K dataset is comprised of 3 888 characters, of which 13.01 % (506 bp) were parsimony informative. The ITS region yielded the highest number of parsimony informative characters with 31.74 % (233 bp out of 734), while the *trn*K/*mat*K region obtained 8.66 % (273 out of 3 154 bp). The six clades of *Alpinia* scattered within tribe *Alpinieae* namely *A. galanga*, *A. fax*, *A. rafflesiana*, *A. carolinensis*, *A. zerumbet* and *A. eubractea* clade recognised in Kress et al. (2005, 2007)

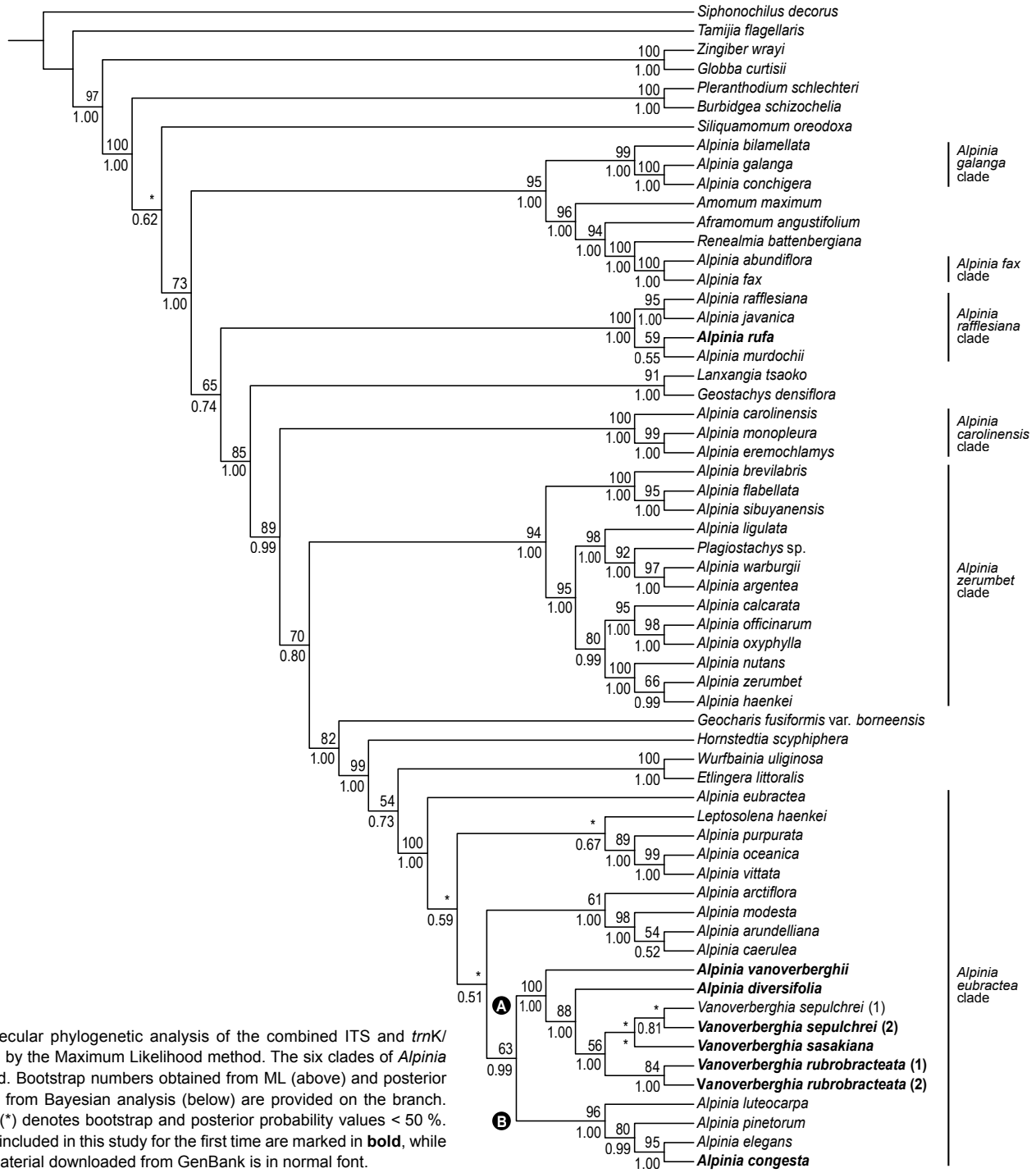


Fig. 1 Molecular phylogenetic analysis of the combined ITS and *trn*K/*mat*K region by the Maximum Likelihood method. The six clades of *Alpinia* are indicated. Bootstrap numbers obtained from ML (above) and posterior probabilities from Bayesian analysis (below) are provided on the branch. An asterisk (*) denotes bootstrap and posterior probability values < 50 %. Accessions included in this study for the first time are marked in **bold**, while additional material downloaded from GenBank is in normal font.

Table 2 Comparative morphology of the five *Vanoverberghia* species focusing on distinguishing characters (key characters states in **bold**).

Morphological characters	*Vanoverberghia diversifolia*	*Vanoverberghia rubrobracteata*	*Vanoverberghia sasakiana*	*Vanoverberghia sepulchrei*	*Vanoverberghia vanoverberghii*
Height	1–1.5 m	4–6 m	2–3 m	4–8 m	2–5 m
Ligule	**bilobed**, the lobes ovate, 1–1.5 mm long, **densely pubescent**, greenish brown, apex rounded	ovate, 10–25 mm long, glabrous, coriaceous, red, **apex unevenly truncate**	ovate, 3–5 mm long, glabrous, coriaceous, reddish brown, apex rounded	ovate, 7–13 mm long, glabrous, coriaceous, red, apex rounded	**oblong**, 10–15 mm long, glabrous, **subcoriaceous**, mid-green, apex rounded
Sheath	**pubescent**	glabrous	glabrous	glabrous	glabrous
Petiole	**0.5–1 mm (subsessile)**	10–13 mm long	3–5 mm long	8–10 mm long	15–20 mm long
Leaf margin	**pubescent**	glabrous	glabrous	glabrous	glabrous
Bracts	spathaceous, 13–15 by 4–5 mm, **brown**	spathaceous, 35–40 by 5–10 mm when flattened, **red**	spathaceous, 25–27 by 10–12 mm when flattened, **translucent white at the base** and brown at the apex	spathaceous, 25–30 by 15–20 mm when flattened, **pinkish white at the base** and brown at the apex	**absent**
Peduncle color	mid-green	red	mid-green	red	mid-green
Peduncle, rachis, pedicel	pubescent	glabrous	glabrous	glabrous	pubescent
Calyx	spathaceous (laterally split to the base), 37–40 by 7–10 mm, light green, **apex 1-dentate**	funnel-shaped, 15–18 mm long, glabrous, **red**, apex 2–3-dentate	funnel-shaped, 12–13 mm long, glabrous, white, apex 3-dentate	funnel-shaped, 15–20 mm long, glabrous, white, apex 2–3-dentate	spathaceous (laterally split to the base), 35–40 by 20–23 mm, mid-green, apex 3-dentate
Corolla tube and lobes color	white	white to **pink**	white	white	white
Dorsal corolla and lobe apex	glabrous	glabrous	glabrous	glabrous	**pubescent**
Labellum	bifid, the lobes subulate, apex entire and acute	bifid, the lobes subulate, apex entire and acute	bifid, the lobes subulate, **apex slightly bifid**, the lobes acute	bifid, the lobes subulate, apex entire and acute	bifid, the lobes **deltate and petaloid**, apex entire
Anther shape	linear	oblong	oblong	oblong	linear
Anther crest	absent	absent	absent	absent	**present**
Style	pubescent spotless	glabrous, spotless	glabrous, spotless	glabrous, **spots present**	pubescent, spotless
Ovary	pubescent	glabrous	glabrous	glabrous	pubescent
Fruits	ellipsoid to subglobose, 12–15 by 15–17 mm, pubescent, **dark green when mature**	ellipsoid to subglobose, 20–25 by 15–20 mm, glabrous, deep red when mature	ellipsoid to subglobose, 15 by 12 cm, glabrous, mid-green when mature	ellipsoid to subglobose, 21–26 by 13–18 mm, glabrous, deep red when mature	**oblong**, 35–40 by 10–20 mm, pubescent, mid-green when mature

and De Boer et al. (2018) analyses are well represented, and these clades are all strongly supported with bootstrap support ranging from 94–100 % and posterior probability value of 1.00 (Fig. 1). The ML and Bayesian tree topologies are consistent with each other and with those obtained from previous studies (e.g., Kress et al. 2005, 2007, Funakoshi et al. 2005, De Boer et al. 2018).

Alpinia diversifolia and *A. vanoverberghii* appeared within the *Alpinia eubractea* clade and formed a strongly supported monophyletic group with the three *Vanoverberghia* species (PP = 1.00; BS = 100, subclade A in Fig. 1). The molecular data also supports the observation of Smith (1990) that *A. vanoverberghii* and *A. elegans* are related to each other because subclade A, where *A. vanoverberghii* belongs, forms a sister taxon relationship to subclade B (PP = 96; BS = 100), which is composed of *Alpinia* species distributed in the Philippines, and among them is *A. elegans*. Furthermore, the clade consisting the subclades A and B is weakly supported (PP = 0.99; BS = 63) and their morphology differs greatly. For example, species within subclade A has pendulous inflorescence (vs erect in subclade B), no bracteoles (vs tubular in subclade B), and single flower per bract (vs 2–3 in subclade B). In fact, Kress et al. (2005) already noted that no good characters define *Alpinia eubractea* clade as a whole.

Recircumscription of Vanoverberghia

The circumscription of *Vanoverberghia* by Merrill (1912) includes limited information because *V. sepulchrei* was monotypic at that time. The molecular and morphological data presented in this study highly justify the reinstatement of *V. diversifolia* and combination of *A. vanoverberghii* in *Vanoverberghia*. Both species share the following morphological characters with the three species currently included in *Vanoverberghia*:

1. terminal raceme and pendulous inflorescence;
2. spathaceous calyx;
3. lateral corolla lobes that are basally connate to the base of the bifid labellum;
4. filiform and ciliate lateral staminodes; and
5. canaliculate filament

(see Table 2 for morphological comparison between the five species of *Vanoverberghia*).

Since this study now includes five species, the circumscription of the genus must be widened. The following characters of Merrill's circumscription agree with the recent data:

1. inflorescence a terminal raceme;
2. bracteoles absent;
3. flowers single;
4. calyx in bud cylindrical, at anthesis spathaceous;
5. labellum connate to the base of lateral corolla lobes;
6. lateral staminodes filiform;
7. ovary trilocular; and
8. two compressed epigynous glands.

Table 3 enumerates characters by Merrill (1912), the variation of which needs to be updated. In addition, the canaliculate filament is recognised here as a new diagnostic character of *Vanoverberghia*.

Table 3 Morphological characters used by Merrill (1912) to circumscribe *Vanoverberghia* and updated information provided in the present paper.

Characters	Merrill (1912)	Updated circumscription
Habit	tall herb	1–8 m tall
Rhizome	robust	7–40 mm wide
Inflorescence	sub-erect	pendulous
Bracts	present	absent or present
Calyx apex	tridentate	1–3-dentate
Corolla lobes	narrowly-oblong	linear-oblong
Labellum lobes	linear	subulate or deltate
Anther crest	broad and semi-cylindrical	absent or emarginate
Style	filiform	slender

Morphological distinction of Vanoverberghia within Alpinia s.lat.

Since it was published, *Vanoverberghia* has been consistently associated with *Alpinia* in taxonomic revisions (e.g., Smith 1990) because of its terminal inflorescence. Recent phylogenetic studies have revealed that *Vanoverberghia* is indeed related to *Alpinia*, especially to species distributed in the Philippines (Kress et al. 2002, 2005, 2007, Funakoshi et al. 2005). Despite this evidence, *Vanoverberghia* has never been sunk in *Alpinia* because of its distinct morphology.

The molecular result of this study demonstrates that Smith (1990) was correct in placing *A. vanoverberghii* near *A. elegans* that is also included in the *Alpinia eubractea* clade (Fig. 1). The latter species is, however, distinct by having flowers in cincinni. In fact, *Vanoverberghia* is unique within this clade by having a single flower per bract (vs in cincinni for all species currently known to belong here). The closest clade of *Alpinia* s.lat. to *Vanoverberghia* that has a single flower per bract is the *Alpinia zerumbet* clade, particularly species belonging to *Alpinia* subsect. *Cenolophon* (Blume) R.M.Sm. (Smith 1990), e.g., *Alpinia officinarum* Hance. These species are, however, distinct from *Vanoverberghia* by having erect inflorescences (vs pendulous) and an entire labellum (vs bifid). Furthermore, the pendulous habit of the inflorescence is also a characteristic feature of *Vanoverberghia* within the *Alpinia eubractea* clade, but this character is also observed elsewhere within the clade (e.g., *Alpinia vittata* W.Bull and some populations of *Alpinia oceanica* Burkill). These are, however, distinct from *Vanoverberghia* by the presence of bracteoles (vs absence) and having flowers in cincinni. It is also worth mentioning the filiform lateral staminodes of *Vanoverberghia* which, in most species of *Alpinia* s.lat., are greatly reduced (e.g., tooth-like) or entirely absent (Smith 1990, Kress et al. 2005).

New species record of Vanoverberghia in the Philippines

Examination of recent collections from northern Luzon initially identified as *V. sepulchrei* including *J.R. Callado s.n* (PNH) from Solsona, Ilocos Norte (Fig. 2a) and *R.V.A. Docot 0182* (FEUH) from Camiguin Island, Cagayan (not to be confused with Camiguin Island of Mindanao) revealed that these are in fact *V. sasakiana*, the type locality which is Lanyu Island, a small volcanic island located c. 70 km SE of Taiwan proper, c. 350 km N of Camiguin and c. 400 km N of Luzon Island (Map 1). The significantly shorter leafy shoot and ligule, mid-green peduncle and fruit, and translucent white floral bract separate it clearly from *V. sepulchrei*. The inflorescence length of *J.R. Callado s.n.*, however, is significantly longer than specimens from Lanyu

Fig. 2 a. *Vanoverberghia sasakiana* Funak. & H.Ohashi. from Solsona, Ilocos Norte; b. *Vanoverberghia sepulchrei* Merr. from Mount Bulusan, Sorsogon (a: *J.R. Callado s.n.*; b: *R.V.A. Docot 0209*). — Photos: a. J.R. Callado; b. R.V.A Docot.

Island (40 vs 8–25 cm long). Accepting this variation extends its distribution to the Philippines and the species is thus no longer endemic in Taiwan. Furthermore, we also recognise a fruiting collection also from Camiguin Island (*G. Edaño 79204*), previously identified as *Languas glabrescens* (Ridl.) Merr. (= *Alpinia glabrescens* Ridl.), as *V. sasakiana* by its pendulous infructescence and subglobose fruits (vs erect and globose in *A. glabrescens*).

At 10 Ma (late Miocene), Lanyu Island was much nearer to Luzon Island than to Taiwan proper but at 5 Ma (early Pliocene), however, Luzon and Lanyu together with Batanes and Babuyan Islands on the Philippine Sea Plate moved north-westward tectonically, positioning Lanyu Island much nearer to Taiwan proper than to the Philippines (Wang 1990, Funakoshi & Ohashi 2000, Hall 2000). Lanyu Island contains c. 850 indigenous vascular plants species of which almost 13 % occur in the Philippines but not in Taiwan proper (Lin & Lu 1982). These plants, including *V. sasakiana*, may have dispersed from Luzon to Lanyu Island or vice versa in a period when they were nearer to each other and the sea level was lower than at present. This geological scenario, however, must be supported by a proper biogeographical analysis (which is beyond the scope of the present study) in order to determine the dispersal timing and route, and possible dispersal methods of *V. sasakiana*.

TAXONOMIC TREATMENT

Vanoverberghia

Vanoverberghia Merr. (1912) 76. — Type: *Vanoverberghia sepulchrei* Merr.

Terrestrial herb in loose clumps. *Rhizome* 1–4 cm across, red or reddish green to yellowish brown, scales thick or thin, brown. *Leafy shoot* erect to arching, pseudostem terete, base bulbose; sheath glabrous or pubescent, mid-green to reddish; ligule ovate to oblong, if ovate, entire or bilobed, coriaceous to subcoriaceous, glabrous to densely pubescent; lamina subsessile to petiolate, oblong, apex caudate. *Inflorescence* a terminal raceme, pendulous, with 1–3 persistent brown bracts; floral bract absent or spathaceous, if spathaceous, tubular at the base; bracteole absent; flowers one per fertile bract, congested or laxly arranged along the rachis, pedicellate, opening in succession from base to top; calyx in bud cylindrical, at anthesis funnel-shaped or spathaceous, if spathaceous, laterally split to the base, apex 1–3-dentate; corolla lobes linear-oblong, white or mid-green, apices rounded, cucullate, glabrous to pubescent; labellum connate to base of lateral corolla lobes, free part bifid, the lobes subulate or deltate, if deltate, petaloid and crisped, white; lateral staminodes filiform, pubescent; stamen curved at anthesis; filament canaliculate and enclosing the style up to almost half its length, spirally coiled after anthesis; anther oblong or linear, sericeous, thecae dehiscing throughout their entire length, pubescent, crest absent or present, if present, emarginate and pubescent; style glabrous to pubescent; stigma cupular, ostiole elliptic, margin pubescent or hispid; epigynous glands two, compressed, oblong or subglobose; ovary subglobose to globose, glabrous or densely pubescent, green, yellow, or deep red, trilocular with axile placentation. *Fruit* ellipsoid to subglobose to oblong, indehiscent, calyx persistent. *Seed* subglobose, black or brown with white aril.

Distribution, habitat, and species richness

Vanoverberghia was endemic to the Philippines until *V. sasakiana* was described based on a collection from Lanyu Island, Taiwan. The extension of distribution of *V. sasakiana* to the Philippines supports Luzon Island as the center of diversity of *Vanoverberghia*, specifically within the Cordillera Mountains, a 320 km long mountain range in Luzon Island situated from the province of Ilocos Norte down to Pangasinan (Map 1). The type species, *V. sepulchrei*, as well as *V. diversifolia*, and *V. vanoverberghii* were actually discovered within this mountain range. *Vanoverberghia rubrobracteata* occurs in eight provinces in the Philippines, making it the most widespread species of the genus. In fact, *V. rubrobracteata* distribution extends to the Visayas including the islands of Negros and Panay (Map 1).

Vanoverberghia species usually inhabit shaded montane forest above 800 m but some also favour lowland forest (e.g., *V. diversifolia* was recorded as low as at 100 m). Their most preferred habitat appears to be near streams and ravines where the soil is humid, although some species occupy pine forest (e.g., *V. sepulchrei*).

Floral biology, pollination and seed dispersal

Observation in the field and data gathered from herbarium sheets and photographs with dates from the internet (e.g., Pelser et al. 2011 onwards: 'Co's Digital Flora website') document that flowering occurs between September and January (wet season) while their closely related *Alpinia* species (subclade B in Fig. 1) flower in the dry season between March and May.

The epigynous glands of *Vanoverberghia* are located at the base of the 12–20 mm long corolla tube, and therefore the pollinator needs to have a long proboscis. Those species flowering at night (e.g., *V. sepulchrei*) are most likely to be pollinated by moths but butterflies and bees are also likely when anthesis occurs by day. Furthermore, the fruits of *Vanoverberghia* are indehiscent and contain arillate seeds with a sweet-sour flavour. This indicates that seed dispersal may be by birds or bats but this needs further field observation.

KEY TO THE SPECIES OF VANOVERBERGHIA

1. Peduncle, rachis, style, ovary and fruit pubescent; flowers laxly arranged along the rachis; calyx spathaceous; anther linear 2
1. Peduncle, rachis, style, ovary and fruit glabrous; flowers congested along the rachis; calyx funnel-shaped; anther oblong 3
2. Rhizomes 7–8 mm across; ligules bilobed and densely pubescent; leaf margin pubescent; petiole 0.5–1 mm long; bracts present; calyx glabrous, apex 1-dentate; flower buds claw-like; corolla tube glabrous; dorsal corolla lobe apex glabrous; labellum lobes subulate; anther crest absent; fruits globose to subglobose . . . . . *V. diversifolia*
2. Rhizomes 3–4 cm across; ligules entire and glabrous; leaf margin glabrous; petiole 10–15 mm long; bracts absent; calyx slightly pubescent, apex 3-dentate; flower buds cylindrical; corolla tube slightly pubescent; dorsal corolla lobe apex pubescent; labellum lobes deltate; anther crest present; fruits oblong . . . . . *V. vanoverberghii*
3. Pseudostem 4–8 m long; petiole 3–4 mm long; peduncle, rachis and pedicel red; apices of labellum lobes entire; mature fruits deep red 4
3. Pseudostem 2–3 m long; petiole 8–10 mm long; peduncle, rachis and pedicel yellowish green; apices of labellum lobes bifid; mature fruits mid-green . . . . . *V. sasakiana*
4. Lamina oblong; ligule apex rounded; bracts pubescent and pinkish white; calyx pinkish white; corolla tube and lobes white; style with spots . . . . . *V. sepulchrei*
4. Lamina oblong to narrowly elliptic; ligule apex unevenly truncate; bracts glabrous and red; calyx red; corolla tube and lobes white to pink; style without spots . . . . . *V. rubrobracteata*

Vanoverberghia diversifolia Elmer — Fig. 3, 4; Map 1

Vanoverberghia diversifolia Elmer (1915) 2913 (as '*diversifolium*'). — *Alpinia diversifolia* (Elmer) Elmer (1919) 2991. — *Languas diversifolia* (Elmer) Merr. (1923) 231. — Type: *A.D.E. Elmer 8853* (lecto SING barcode SING0044093, designated here; isolecto BISH, BO, F, G, K, L, MO, NY, US), Philippines, Luzon, Benguet, Baguio, Mar. 1907.

Etymology. The specific epithet refers to the varying leaf size.

Terrestrial herb in loose clumps. *Rhizome* 10–12 mm across, reddish green, scales thin, brown. *Leafy shoot* arching, pseudostem 1–1.5 m long, terete, base bulbose; sheaths pubescent, mid-green; ligule bilobed, greenish brown, lobes ovate, 1–1.5 by 3–5 mm, pubescent, apices rounded; petiole 0.5–1 mm long (subsessile); lamina oblong, 18–20 by 6.5–8 cm, slightly plicate, glabrous on both sides except the pubescent base and midrib beneath, coriaceous and dark green above, lighter beneath, base obtuse, margin entire and pubescent, apex caudate, flagellate tip 8–15 mm long. *Inflorescence* 10–25 cm long; peduncle terete, 3–4 cm long, pubescent, mid-green, subtended by one persistent bract; rachis terete, 8–20 cm long, pubescent, mid-green; pedicel terete, 7–10 mm long, pubescent, mid-green; floral bract spathaceous, tubular at base, 13–15 by 4–7 mm when flattened, brown, apex acute and pubescent; flower bud claw-like; flowers laxly arranged along rachis, white; calyx spathaceous, laterally split to base, 37–40 by 7–10 mm, glabrous, mid-green, angled at up to 90° to axis of flower, apex acute and pubescent; corolla tube 2–2.5 cm long, glabrous, white; dorsal corolla lobe linear-oblong, 33–40 by 5–8 mm, glabrous, white, margin translucent white, apex rounded and cucullate; lateral corolla lobes linear-oblong, 18–22 by 3–5 mm, glabrous, white, margin translucent white, apex rounded and cucullate; labellum connate to base of lateral corolla lobes, free part bifid, lobes subulate, 30–35 by 1–1.5 mm, white, base glabrous, apices entire and acute; lateral staminodes filiform, 1.5–2 cm long, pubescent, white; filament enclosing style for almost half its length above labellum, 27–30 by 3–3.5 mm, glandular, white; anther linear, 15–17 by 4–5 mm, cream, crestless; style 3.7–4 cm long, pubescent, white; stigma cupular, 1–2 mm wide, white, ostiole elliptic, margin pubescent; epigynous glands compressed, subglobose, 1.6–2 by 1–1.2 mm; ovary subglobose, 18–20 by 4–5 mm, pubescent, mid-green. *Fruit* ellipsoid to subglobose, 12–15 by 15–17 mm, dark green when mature, pubescent, calyx persistent. *Seed* subglobose, brown with white aril.

Local names & Uses — Kagda-opot (Igorot language), buntotpusa (Tagalog), and oplay (Tagalog). *Vanoverberghia diversifolia* is often associated by the locals of Maria Aurora, Aurora as the white form of *Strongylodon elmeri* Merr., commonly known as the 'jade vine' because of its claw-like flower buds. In addition, the bulbose base of the pseudostem is reported to be eaten by the Igorots living in Sablan, Benguet (Elmer 1915).

Phenology — Flowering occurs between November and January but a few individuals may bloom between February and April, which is also the fruiting season.

Distribution & Habitat — *Vanoverberghia diversifolia* is endemic to Luzon Island, particularly in the provinces of Aurora, Benguet, and Quezon. The species inhabits deeply shaded ravines and stream sides at 100–1100 m.

Additional specimens examined. Philippines. *D.N. Tandang s.n.* (PNH [2 sheets]), Aurora, Maria Aurora, Barangay Bazal, Bazal-Baubo Watershed, N15°48'37.5" E121°24'33.3", 300 m, 10 Apr. 2010; *R.V.A. Docot 0034* (PNH, USTH [4 sheets] incl. spirit), Aurora, Maria Aurora, Barangay Bazal, Bazal-Baubo Watershed, 9 Apr. 2016; *R.V.A. Docot 0085* (USTH), Quezon, Tayabas, Barangay Lalo, Mount Banahaw, N14°03'00.4" E121°32'29.1", 1010 m, 26 June 2016.

Note — In describing this species, Elmer (1915) did not mention a holotype, so, we designate *A.D.E. Elmer 8853* (SING) as the lectotype since this is the only specimen with reproductive material. The protologue of *V. diversifolia* does not include a description of a flower and the type at SING is the only duplicate with fruits; all others are sterile. Recent collections of *V. diversifolia* were obtained in Aurora and Quezon provinces, 127–300 km from the type locality (Sablan, Benguet) on the same island (Luzon). These collections match the vegetative and fruiting characters of the type of *V. diversifolia* well and agree with most of the morphological characters indicated in the

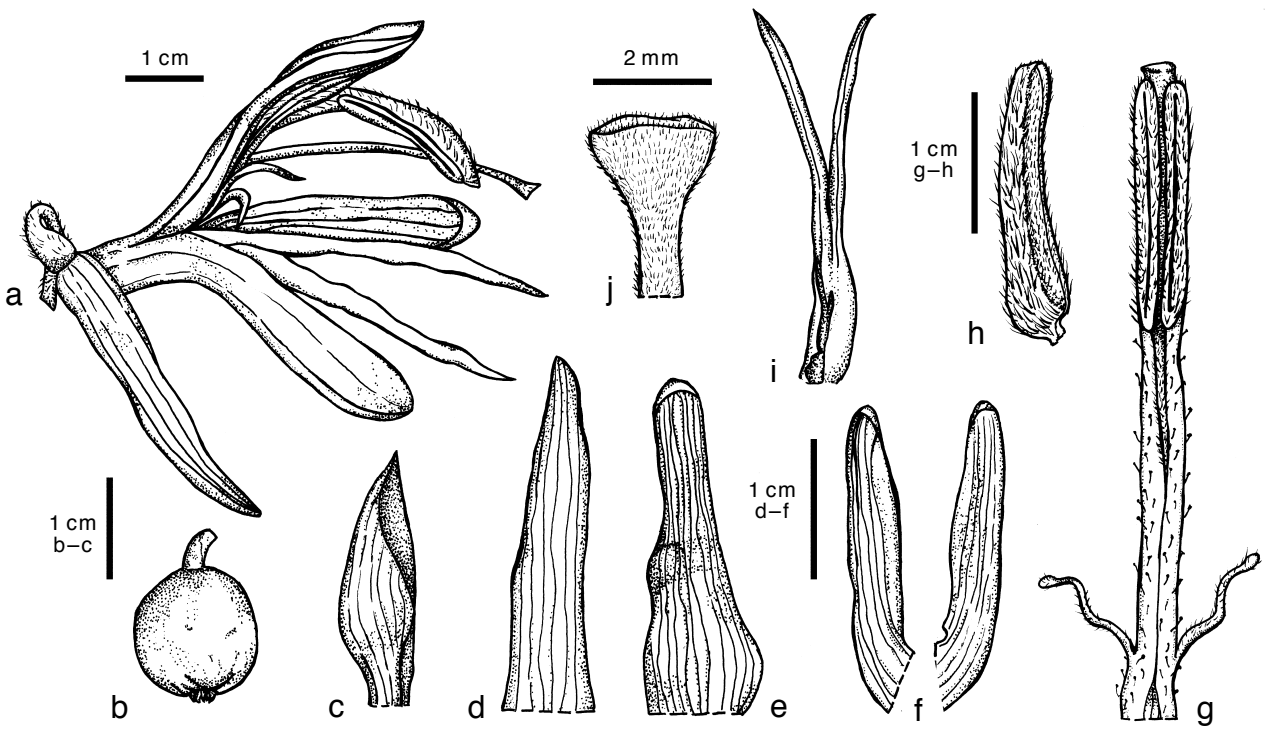


Fig. 3 *Vanoverberghia diversifolia* Elmer. a. Flower at anthesis; b. fruit; c. bract; d. calyx; e. dorsal corolla lobe; f. lateral corolla lobes; g. stamen with lateral staminodes; h. anther (side view); i. labellum; j. stigma (all: *R.V.A. Docot 0032*). — Drawn from material in spirit: a, c–j. P.G. Campos; b. R. Campos.

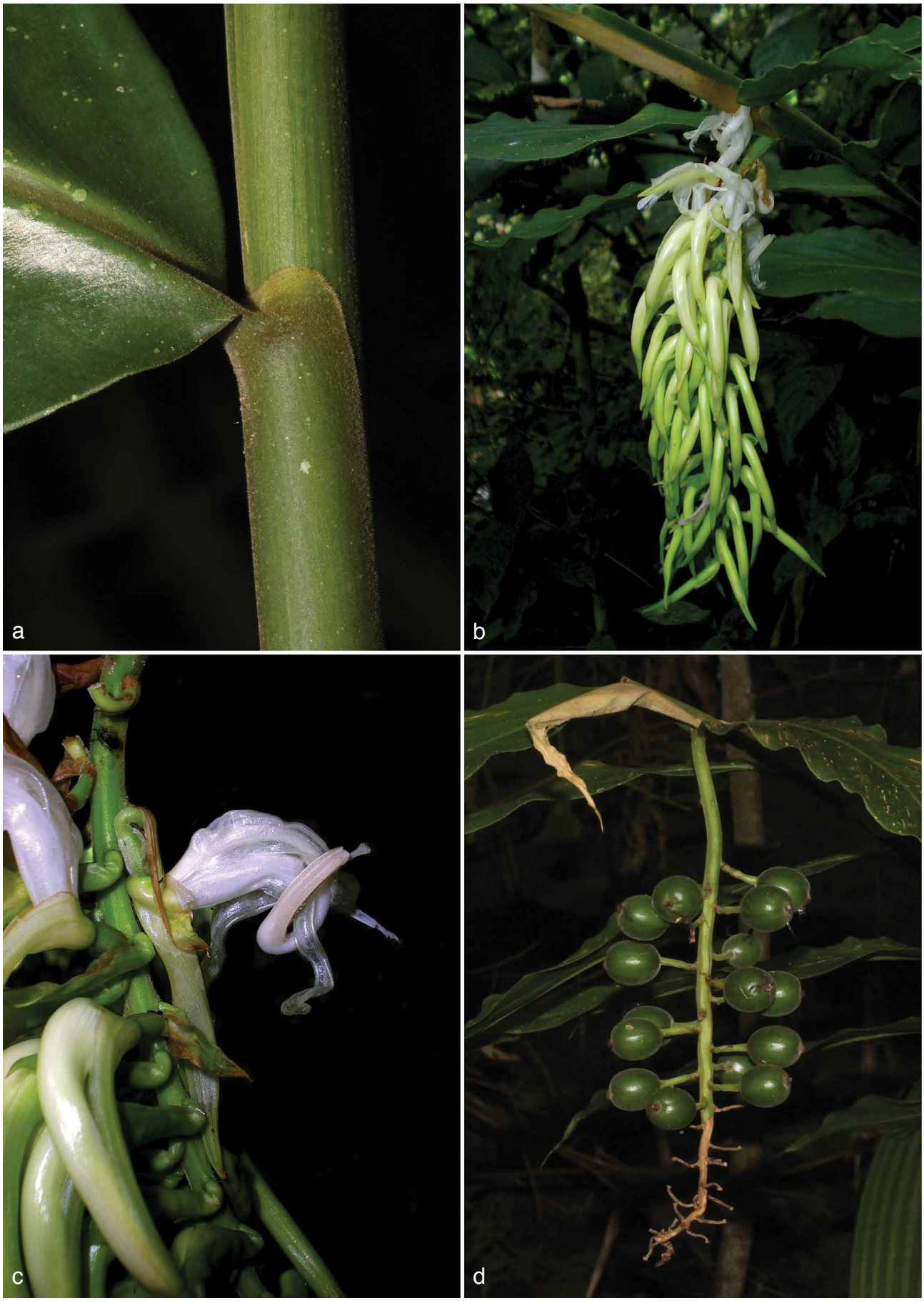


Fig. 4 *Vanoverberghia diversifolia* Elmer. a. Ligule; b. inflorescence; c. flower after anthesis; d. infructescence (a, d: *R.V.A. Docot 0032*; b, c: *D.N. Tandang s.n.*). — Photos: a, d. R.V.A. Docot; b, c. D.N. Tandang.

protologue (e.g., densely pubescent ligules; terminal pendulous infructescence). Interestingly, upon careful examination of the type material, some of the characters included in the protologue did not match well with the type and our collections. For example, Elmer (1915) described the ligule as entire, but our observation of the type and recent collections revealed that it is bilobed (Fig. 4a). In addition, Elmer described the infructescence as a spike, but our examination suggests that the infructescence is a raceme since the fruits are rather pedicellate (Fig. 4d). Recent collections including flowers allowed us to amplify the description of *V. diversifolia* as well as make it more accurate regarding vegetative and fruit characters.

Vanoverberghia rubrobracteata Docot & Ambida — Fig. 5; Map 1

Vanoverberghia rubrobracteata Docot & Ambida (in Ambida 2018) 130. — Type: *R.V.A. Docot 0123* (holo PNH accession no. 256337; iso E, NY, SING, USTH), Philippines, Luzon. Quezon, Tayabas, Barangay Lalo, Mount Banahaw, N14°03'43.9" E121°29'34.1", 1432 m, 12 Nov. 2017.

Etymology. The specific epithet refers to the red floral bracts.

Terrestrial herb in loose or dense clumps. *Rhizome* 25–50 mm across, red, strongly aromatic when cut, scales thick, brown. *Leafy shoot* arching at various degrees, pseudostem 4–6 m long, base bulbose, red; sheaths glabrous, green; ligule ovate, 20–30 mm long, coriaceous, glabrous, red, apex unevenly truncate and entire; petiole terete, 10–13 mm long; lamina oblong to narrowly elliptic, 50–51 by 11–15 cm, veins obscure, dark green above, lighter beneath, glabrous on both sides, base rounded, margin entire, apex caudate with a 20–30 mm long flagellate tip. *Inflorescence* 25–35 cm long; peduncle terete, 10–20 cm long, glabrous, deep red, subtended by 2–3 persistent bracts; rachis 7–15 cm long, glabrous, deep red; pedicel terete, 3–5 mm long, puberulous, red; floral bract spathaceous, tubular at base, glabrous, 35–40 by 5–10 mm when flattened, red, apex pubescent; flower bud cylindrical; flowers congested along rachis; calyx funnel-shaped, 15–18 mm long, glabrous, coriaceous, red, apex tridentate; corolla tube 10–15 mm long, glabrous, coriaceous, white or pink; dorsal corolla lobe linear-oblong, 55–60 by 6–8 mm, glabrous, white or pink, apex rounded and cucullate; lateral corolla lobes linear-oblong, 55–60 by 3–5 mm, glabrous, white or pink, apex rounded and cucullate; labellum connate to base of lateral corolla lobes, free part bifid, lobes subulate, 30–40 by 3–5 mm, white, base pubescent, apices of lobes entire; lateral staminodes filiform, 2–3 mm long, pubescent, white; filament enclosing style for almost half its length above labellum, 53–55 by 2–3 mm, slightly glandular, cream-white; anther oblong, 15–16 by 2–3 mm, sericeous, crestless, thecae pubescent; style 4–6 cm long, glabrous, white; stigma cupular, 1–2 mm wide, white, ostiole elliptic, margin hispid; epigynous glands compressed, subglobose, 1–2 mm long; ovary subglobose, 4–7 by 2–3 mm, coriaceous, glabrous, deep red. *Fruit* ellipsoid to subglobose, 20–25 by 15–20 mm, coriaceous, glabrous, deep red when mature, calyx persistent. *Seed* subglobose, brown with white aril.

Local names & Uses — Akbab (Igorot language), bagombong (Tagalog) and tagbak (Bisaya). The fruits are eaten by the locals and reported to have a sweet and sour flavour.

Phenology — Flowering takes place between October and January. Fruiting is between February and May.

Distribution & Habitat — *Vanoverberghia rubrobracteata* is endemic in the Philippines where it is distributed in the provinces of Antique, Aurora, Capiz, Ifugao, Mountain Province, Quezon, Negros Occidental and Rizal. It inhabits primary forests along streams and ravines from 800–1600 m.

Additional specimens examined. Philippines, **Luzon**, *R.V.A. Docot 0089* (USTH [2 sheets] incl. spirit), Aurora, Dingalan, Barangay Davil-Davilan, Mingan Mountains, Mount Mingan, 8 June 2016; *R.V.A. Docot 0106* (NY, USTH incl. spirit), Aurora, Dingalan, Barangay Davil-Davilan, Mingan Mountains, Mount Mingan, N15°26'25.6" E121°24'04.2", 1339 m, 17 June 2017; *D.N. Tandang & R.T. Angeles s.n.* (PNH), Ifugao**,** Banaue, 22 Jan. 2013; *R.V.A. Docot 0049* (USTH [2 sheets] incl. spirit), Quezon, Tayabas, Barangay Lalo, Mount Banahaw, 25 Apr. 2016; *A. Loher 7028* (K), Rizal, 1906; *A. Loher 7006* (K), Rizal, Montalban, 1906; *B.F. Herman 5452* (CAHUP), Sorsogon, Bacon, Pocdol Mountains, PNOC Geothermal Project site, 5 Jan. 2001; **Visayas**, *R.V.A. Docot 0118* (L, NY, USTH incl. spirit), Antique, Culasi, Barangay Flores, Mount Madjaas, 17 Oct. 2017; *M. Ramos & G. Edaño 30734* (BM, BO, K, P), Capiz, Mount Madjaas, Apr.-May 1918.

Note — Ambida et al. (2018) listed *A.D.E. Elmer 17095* and *17383* from Mount Bulusan, Sorsogon under this species. Examination of recent collections (*R.V.A. Docot 0133*, *0198* & *0209*; Fig. 2b) with flowering material from this locality reveals that this population belongs rather to *V. sepulchrei* than to *V. rubrobracteata*. The populations of *V. sepulchrei* in Mount Bulusan, however, differ only slightly from the northern Luzon populations by having subsessile leaves (vs petiolate). Accepting this variation extends the distribution of *V. sepulchrei* to the far south of Luzon (see Map 1). The fruiting specimen *B.F. Herman 5452*, also from Sorsogon, needs to be compared with new collections from its locality to confirm whether it is also *V. sepulchrei.* This specimen is here placed, tentatively, under *V. rubrobracteata.*

Vanoverberghia sasakiana Funak. & H.Ohashi — Fig. 6; Map 1

Vanoverberghia sasakiana Funak. & H.Ohashi (2000) 270. — Type: *H. Funakoshi & T.-T. Chen 1936* (holo TI; iso AAU [2 sheets], K [2 sheets], TAIF [2 sheets]), Taiwan, Taitung County, Lanyu Island, Yehyou Village, Mount Hontou, 350 m, 30 Sept. 1998.

Etymology. The specific epithet honours Shun'ichi Sasaki (1888–1960), a plant collector of the Taiwan Forestry Department, who first collected this species in July 1912.

Terrestrial herb in clumps. *Leafy shoot* erect then arching, pseudostem 2–3 m long, base bulbose; sheath glabrous, reddish; ligule ovate, 4–5 mm long, coriaceous, glabrous, reddish brown, apex rounded and entire; petiole terete, 3–4 mm long, glabrous, mid-green; lamina oblong, 50–55 by 11–13 cm, veins obscure, glabrous on both sides, base attenuate, margin entire, apex caudate with flagellate tip. *Inflorescence* 12–40 cm long; peduncle terete, 30–50 mm long, glabrous, mid-green, subtended by 2–3 persistent bracts; rachis terete, 5–20 cm long, glabrous, yellowish red or yellow; pedicel terete, 8–9 mm long, yellowish red to yellow; floral bract spathaceous, tubular at base, 25–27 by 10–12 mm when flattened, translucent white to yellow with brownish apex; flowers congested along rachis, white; calyx funnel-shaped, 12–13 mm long, yellowish white, apex tridentate; corolla tube 6–7 mm long, glabrous, white; corolla lobes oblong, linear-oblong, 22 by 6 mm, glabrous, white, apex rounded, cucullate; labellum connate to base of lateral corolla lobes, free part bifid or split into two subulate lobes, 12 by 2.5 mm, white, base pubescent, apices of lobes slightly bifid; lateral staminodes filiform, 10 mm long, pubescent, white; filament enclosing style for almost half its length above labellum, 25–35 mm long, white; anther oblong, 6–2.5 mm, sericeous, white, crestless; ovary subglobose, 4–5 by 3–4 mm, glabrous, yellowish white. *Fruit* subglobose, 15–17 by 12–15 mm, glabrous, mid-green when mature, calyx persistent. *Seed* subglobose, angular, black with white aril.

Phenology — Flowering occurs between September and November although some populations bloom in June. Fruiting is between January and March.

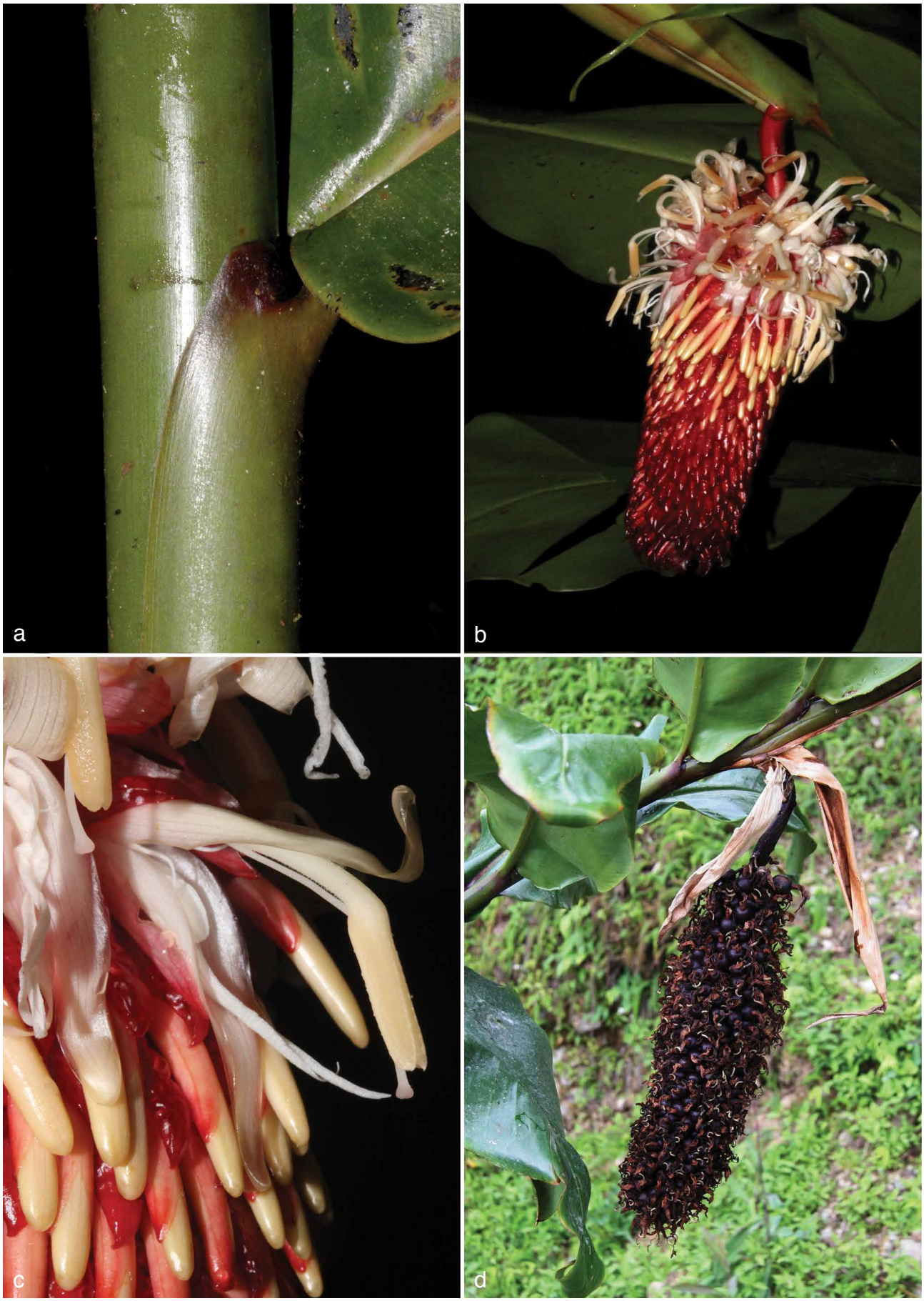


Fig. 5 *Vanoverberghia rubrobracteata* Docot & Ambida. a. Ligule; b. inflorescence; c. flower at anthesis; d. infructescence (a–c: *R.V.A. Docot 0123*; d: without voucher) — Photos: a–c. R.V.A. Docot; d. H. Funakoshi.

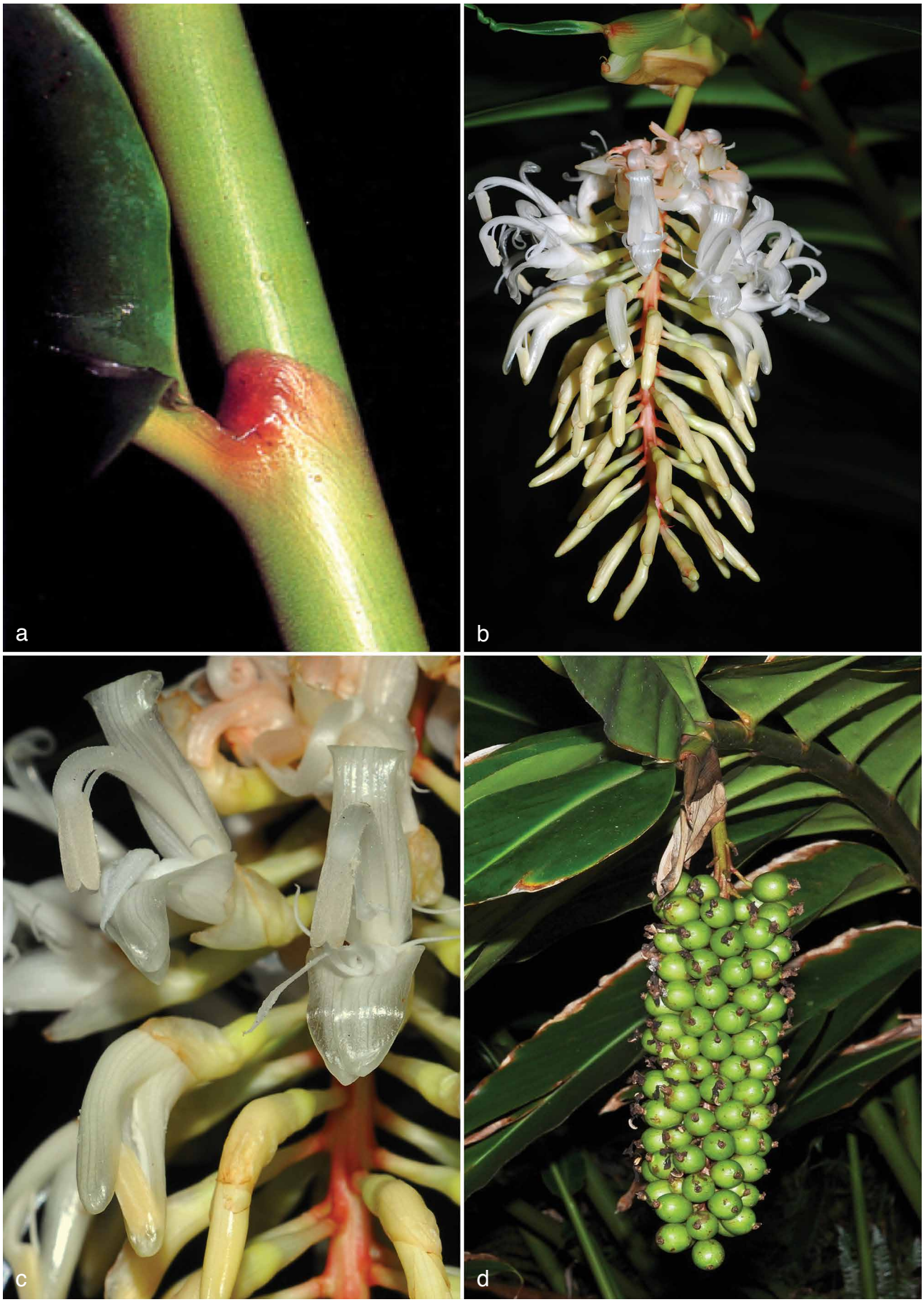


Fig. 6 *Vanoverberghia sasakiana* Funak. & H.Ohashi. a. Ligule; b. inflorescence; c. flower at anthesis; d. infructescence (a: *H. Funakoshi & T.-T. Chen 1936*; b–d: without voucher) — Photos: a. H. Funakoshi; b–d. S.-W. Chung.

Distribution & Habitat — *Vanoverberghia sasakiana* is distributed in the Philippines and Taiwan where it inhabits primary forest at 300–1400 m.

Additional specimens examined. Philippines, Luzon, *G. Edaño 79204* (NY), Cagayan, Calayan, Camiguin Island, Mount Malabsing, Mar. 1930; *R.V.A. Docot 0182* (FEUH), Cagayan, Calayan, Camiguin Island, Mount Camiguin de Babuyanes, 500 m, 9 Aug. 2018; *J.R. Callado s.n.* (PNH), Solsona, Ilocos Norte, 1400 m, 16 June 2014. – Taiwan, Taitung County, Lanyu Island. *S. Sasaki s.n.* (TAI), July 1912; *S. Sasaki s.n.* (TAI), 7 Feb. 1920; *S. Sasaki s.n.* (TAI), 20 Sept. 1933; *C.-T. Moo 1230* (TAI), 30 Oct. 1934; *C.-T. Moo 2339* (TAI! [3 sheets]), 20 Sept. 1972; *C.-E. Chang 16878* (K), 5 Apr. 1974; *S.-Y. Chung 18474* (TAIF [2 sheets]), 22 Feb. 1986; *Tateishi et al. 15306* (TAI), 20–350 m, 12 Nov. 1982; *C.-I. Huang 2452* (HAST*), 28 Mar. 2006; *T.C. Huang & M.-T. Kao 5205* (TAI), Mount Hongtou, 29 Aug. 1969; *T.C. Huang & M.T. Kao 6200* (TAI), Mount Hongtou, 20 Sept. 1972; *T.C. Huang & M.T. Kao 6268* (TAI), Mount Hongtou; *T.C. Huang & M.T. Kao 6200* (TAI), Mount Hongtou; *C.-S. Kuoh 4851* (TAI), Mount Hongtou; *S.-Y. Lu 17613* (TAIF [3 sheets]), Mount Hongtou, 24 Oct. 1985; *W.-C. Leong 2481* (HAST*), Mount Hongtou, 12 Oct. 2001; *S.-W. Chung 8418* (TAIF!), Mount Hongtou, 12 Nov. 2006; *W.-Y. Wang 1846* (TAIF), Mount Hongtou, 7 Oct. 2013; *P.-F. Lu 12731* (HAST*, TAIF [2 sheets]), Tienchih, 22 Oct. 1985; *M.-J. Jung 5146* (TAIF), Tien Pond, 27 Sept. 2010; *M.-J. Jung 5338* (TAIF), 5 Jan. 2011; Tungching Stream, 11 Nov. 2006; *T.-C. Hsu 654* (TAIF), Tungching Stream; *M.-J. Jung 5170* (TAIF), Tungching Stream, 20 Sept. 2010; *S.-Y. Lu 17540* (TAIF [2 sheets]), 22 Oct. 1985.

Note — The species is believed to occur also in Batan Island, Batanes (between Camiguin and Lanyu Islands) based on field observation but a proper collection is needed to validate this.

Vanoverberghia sepulchrei Merr. — Fig. 7, 8; Map 1

Vanoverberghia sepulchrei Merr. (1912) 76. — Type: *M. Vanoverbergh 956* (lecto BM barcode BM001209990, designated here; isolecto US), Philippines, Luzon, Mountain Province, Bontoc, 19 Oct. 1910.

Etymology. The specific epithet honours Father Jules Sepulchre (1880–1912), who established the Bauko Mission, and rendered assistance to Father Vanoverbergh during his botanical explorations in Mountain Province.

Terrestrial herb in loose or dense clumps. *Rhizome* 3–4 cm across, red, strongly aromatic when cut, scales thick, brown. *Leafy shoot* erect to drooping, pseudostem 4–8 m long, base bulbose, red; sheaths glabrous, mid-green; ligule ovate, 7–13 by 6–10 mm, coriaceous, glabrous, red, apex rounded and entire; petiole terete, subsessile or c. 10 mm long, red, glabrous; lamina oblong, 30–45 by 12–17 cm, largest are located in the superior portion, obscure, dark green above, lighter beneath, glabrous on both side, base rounded, margin entire, apex caudate with 3–5 cm long flagellate tip. *Inflorescence* 18–30 cm long; peduncle terete, 8–20 cm long, glabrous, deep red, subtended by 2–3 persistent bracts; rachis 6–12 cm long, glabrous, deep red; pedicel 2–5 mm long, glabrous, red to pink; floral bract spathaceous, tubular and pubescent at base, 25–30 by 15–20 mm when flattened, pinkish white at base and brown at pubescent apex; flower bud cylindrical; flowers congested along rachis, numerous, white; calyx funnel-shaped, 15–20 mm long, glabrous, white, apex 2–3-dentate, pubescent; corolla tube 12–16 mm long, glabrous, white; dorsal corolla lobe linear-oblong, 22–27 by 5–6 mm, glabrous, white, apex rounded, cucullate with a small cleft in the middle; lateral corolla lobes linear-oblong, 20–32 by 4–5 mm, glabrous, white, apex rounded and cucullate; labellum connate to base of lateral corolla lobes, free part bifid, lobes subulate, 17–23 by 1–2 mm, glabrous, white, base pubescent, apices of lobes entire; lateral staminodes filiform, 5–8 mm long, pubescent, white; filament enclosing style for almost half its length above labellum, 30–35 by 3–6 mm, glandular, white; anther oblong, 15–20 by 4–5 mm, cream-white, crestless; style 4–5 cm long, glabrous, white with spots; stigma cupular, 1–2 mm wide, white, ostiole elliptic, margin hispid; epigynous glands compressed, subglobose, c. 1 mm long; ovary subglobose, 4–5 by 2–3 mm, coriaceous, glabrous, deep red. *Fruit* ellipsoid to subglobose, 21–26 by 13–18 mm, coriaceous, glabrous, deep red when mature, calyx persistent. *Seed* subglobose, brown with white aril.

Local names & Uses — Agbab (Bontoc language), akbab (Bontoc), barapat (Igorot), paddapad (Igorot) and chakchakil (Igorot). The fruits of *V. sepulchrei* are eaten by the locals of Mountain Province and reported to have a sweet and sour flavour (Docot et al. 2016).

Phenology & Ecology — Flowering is between September and January. Fruiting starts in February. Anthesis occurs by day, pollination is by bees (pers. obs.).

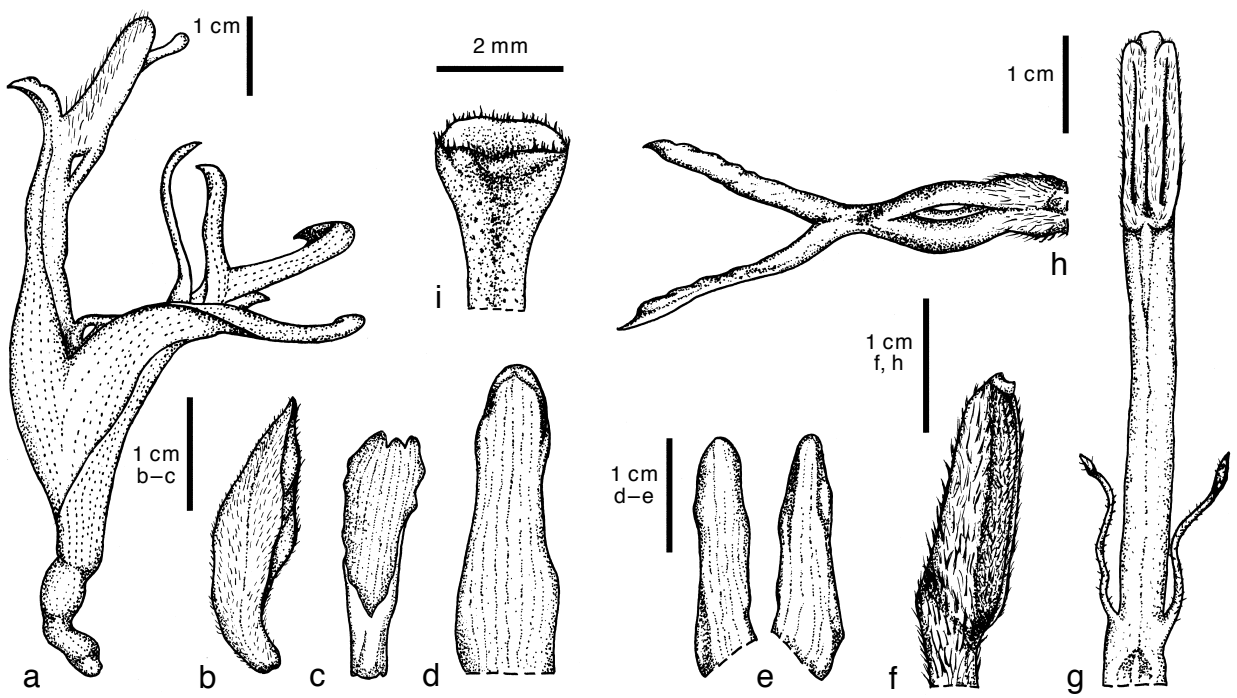


Fig. 7 *Vanoverberghia sepulchrei* Merr. a. Flower at anthesis; b. bract; c. calyx; d. dorsal corolla lobe; e. lateral corolla lobes; f. anther (side view); g. stamen with lateral staminodes; h. labellum; i. stigma (all: *R.V.A. Docot 0122*). — Drawn from material in spirit by P.G. Campos.

Fig. 8 *Vanoverberghia sepulchrei* Merr. a. Ligule; b. inflorescence; c. flower at anthesis; d. infructescence (all: *R.V.A. Docot 0027*). — Photos: a–d. R.V.A. Docot.

Distribution & Habitat — *Vanoverberghia sepulchrei* is endemic in the Philippines, and particularly abundant in the provinces of Benguet, Ifugao, Mountain Province and Sorsogon within primary forests along streams and ravines at 700–1600 m.

Additional specimens examined. Philippines, Luzon, *A.D.E. Elmer s.n.* (NY), *s.lat.*; *P.T. Barnes 947* (SING), Benguet, May-June 1904; *A.D.E. Elmer 8560* (BO, K, SING, US), Benguet, Baguio, Mar. 1907; *E. Fenix 12913* (K), Benguet, Baguio, Dec. 1910; *M. Ramos & G. Edaño 45045* (BM, BO, P, SING), Benguet, Baguio, Mar. 1925; *H.C. Conklin & Buwaya I-984* (K, L [2 sheets], PNH), Ifugao, Banaue, Bayninan, 6 Mar. 1963; *M. Vanoverbergh 956* (BM), Mountain Province, Bontoc, Aug. 1911; *M. Vanoverbergh 956* (P [2 sheets]), Mountain Province, Bontoc, Sept. 1913; *R.V.A. Docot 0001* (USTH [2 sheets]), Mountain Province, Bontoc, Barangay Alab Oriente, Mount Data, 1 Nov. 2013; *R.V.A. Docot 0027* (USTH [3 sheets] incl. spirit), Mountain Province, Bontoc, Barangay Alab Oriente, Mount Data, N17°03'57.6" E120°57'12.1", 1430 m, 9 Jan. 2016; *R.V.A. Docot 0122* (NY, PNH, USTH incl. spirit), Mountain Province, Bontoc, Barangay Alab Oriente, Mount Data, 5 Nov. 2017; *A.D.E. Elmer 17095* (BM [2 sheets], BO, K, P, S, US), Sorsogon, Irosin, Mount Bulusan, Aug. 1916; *A.D.E. Elmer 17383* (BM [3 sheets], BO, K, P, US), Sorsogon, Irosin, Mount Bulusan, Sept. 1916; *R.V.A. Docot 0133* (USTH), Sorsogon, Irosin, Barangay Cogon, Mount Bulusan, N12°45'51.0" E124°02'01.7", 801 m, 6 June 2018; *R.V.A. Docot 0198* (FEUH, USTH), Sorsogon, Casiguran, Barangay Inalgadian, Mount Bulusan, N12°47'26.5" E124°03'44.5", 700 m, 27 Oct. 2018; *R.V.A. Docot 0209* (FEUH incl. spirit, USTH), Sorsogon, Casiguran, Barangay Inalgadian, Mount Bulusan, N12°46'37.9" E124°04'07.7", 860 m, 27 Oct. 2018. – Cultivated material: Hawaii, Honolulu, Lyon Arboretum. *Anon L-87.0651* (E [4 sheets], US), 1995; *J. Mood 46* (E), 15 June 1998; *J. Mood 47* (E), 15 June 1998; *W.J. Kress 95-5562* (US [2 sheets]), 16 July 1995.

Note — Like *V. vanoverberghii*, the type (*M. Vanoverbergh 953*) does not represent a single gathering. Merrill (1912) mentioned two dates in the protologue, 19 October 1910 (flowering specimen) and 17 August 1911 (fruiting specimen). We have located flowering material with non-conflicting collecting dates at two herbaria and designated the type at BM as the lectotype since this specimen has superior vegetative and flowering material. It also has what appears to be an original label whereas the carpological collection at the same herbarium has a written label also saying 'October 1910'. These clearly mature fruits obviously must originate from a different sheet and because the protologue mentions the mature fruits being of a different gathering, it will remain as a syntype, together with specimens at P with a label saying 'September 1913'.

Vanoverberghia vanoverberghii (Merr.) Funak. & Docot, *comb. nov.* — Fig. 9, 10; Map 1

Alpinia vanoverberghii Merr. in Philipp. J. Sci., C 7 (1912) 75. — *Languas vanoverberghii* (Merr.) Merr. (1923) 234 — Type: *M. Vanoverbergh 573* (lecto K barcode K000292453, designated here; isolecto BM, E, K [3 sheets], P, US, Z*), Philippines, Luzon, Mountain Province, Bontoc, 11 June 1910.

Etymology. The specific epithet is in honour of Father Morice Vanoverbergh.

Terrestrial herb in loose or dense clumps. *Rhizome* robust, 2–3 cm wide, yellowish brown, scales thick, brown. *Leafy shoot* erect then drooping, pseudostem 2–5 m long, base bulbose; sheath glabrous, waxy white when young, light green; ligule oblong, 10–15 by 5–7 mm, subcoriaceous, glabrous, mid-green, apex rounded and entire; petiole terete, 10–15 mm long, glabrous, mid-green; lamina oblong, 26–32 by 11–13 cm, veins obscure, glabrous on both sides except pubescent midrib beneath, mid-green above, lighter beneath, base rounded to cuneate, margin entire, apex caudate, flagellate tip 5–6 mm long. *Inflorescence* 35–40 cm long; peduncle terete, 8–10 cm long, pubescent, mid-green, subtended by 1–2 persistent bracts; rachis terete, 28–30 cm long, pubescent, mid-green; pedicel terete, 2–2.5 cm long, pubescent, mid-green, a bud-like protuberance present near base; floral bracts absent; flower bud cylindrical; flowers laxly arranged along the rachis, white; calyx in bud cylindrical, at anthesis spathaceous, laterally split to base, 35–40 by 20–23 mm, subcoriaceous, slightly pubescent, mid-green, angled at up to 90° to axis of the flower, apex tridentate and pubescent; corolla tube 2–2.5 cm long, subcoriaceous, puberulous, white; dorsal corolla lobe linear-oblong, 40–45 by 8–11 mm, glabrous, mid-green, apex rounded, cucullate, slightly pubescent; lateral corolla lobes linear-oblong, 30–37 by 5–8 mm, glabrous, mid-green, apex rounded and cucullate; labellum connate to base of lateral corolla lobes, free part bifid, lobes deltate and petaloid, 5–5.5 by 4–4.3 cm, crisped, glabrous, white, base glabrous, margin repand; lateral staminodes filiform, 1.5–2 cm long, pubescent, white; filament enclosing the style 5–7 mm above the labellum, 20–25 by 10–13 mm, slightly glandular, white; anther linear, 25–30 by 5–6 mm, white, crest emarginated, 0.5–1 by 1.5–2.5 mm, pubescent, mid-green; style 4–5 cm long, pubescent white; stigma cupular, c. 2 mm wide, white, ostiole elliptic, margin pubescent; epigynous glands compressed, subglobose, 1–2 by 2–3 mm; ovary ovoid to subovoid, 7–10 by 8–10 mm,

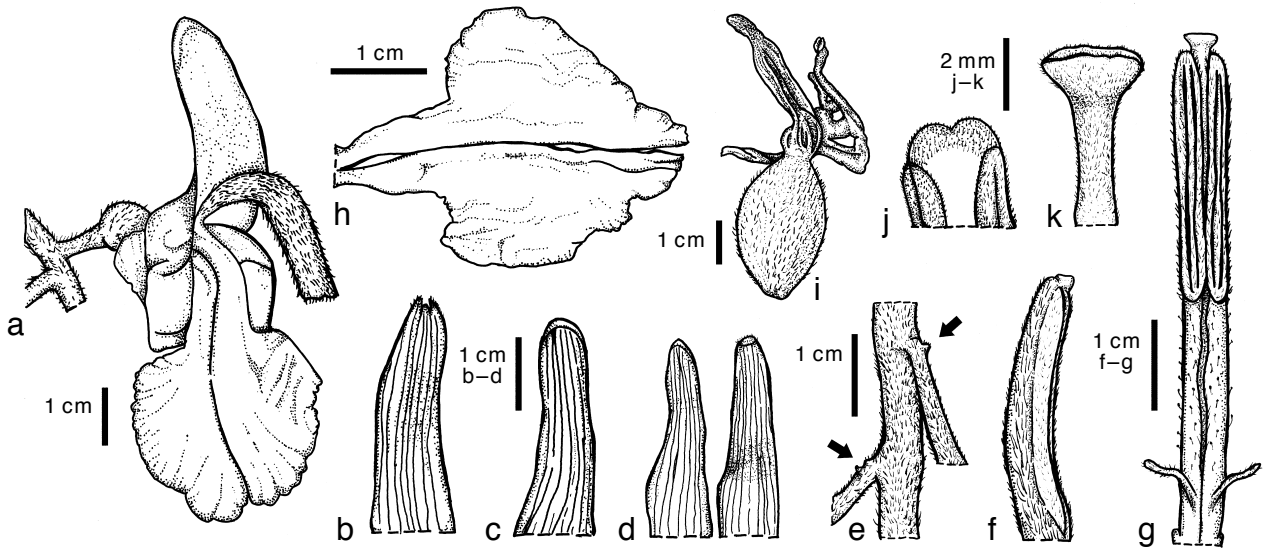


Fig. 9 *Vanoverberghia vanoverberghii* (Merr.) Funak. & Docot. a. Flower at anthesis; b. calyx; c. dorsal corolla lobe; d. lateral corolla lobes; e. pedicel (note the bud-like protuberance indicated by the arrow); f. anther (side view); g. stamen with lateral staminodes; h. labellum; i. fruit; j. anther crest; k. stigma (a–k: *R.V.A. Docot 0032*). — Drawn from material in spirit by: a–h, j–k. P.G. Campos; i. R. Campos.

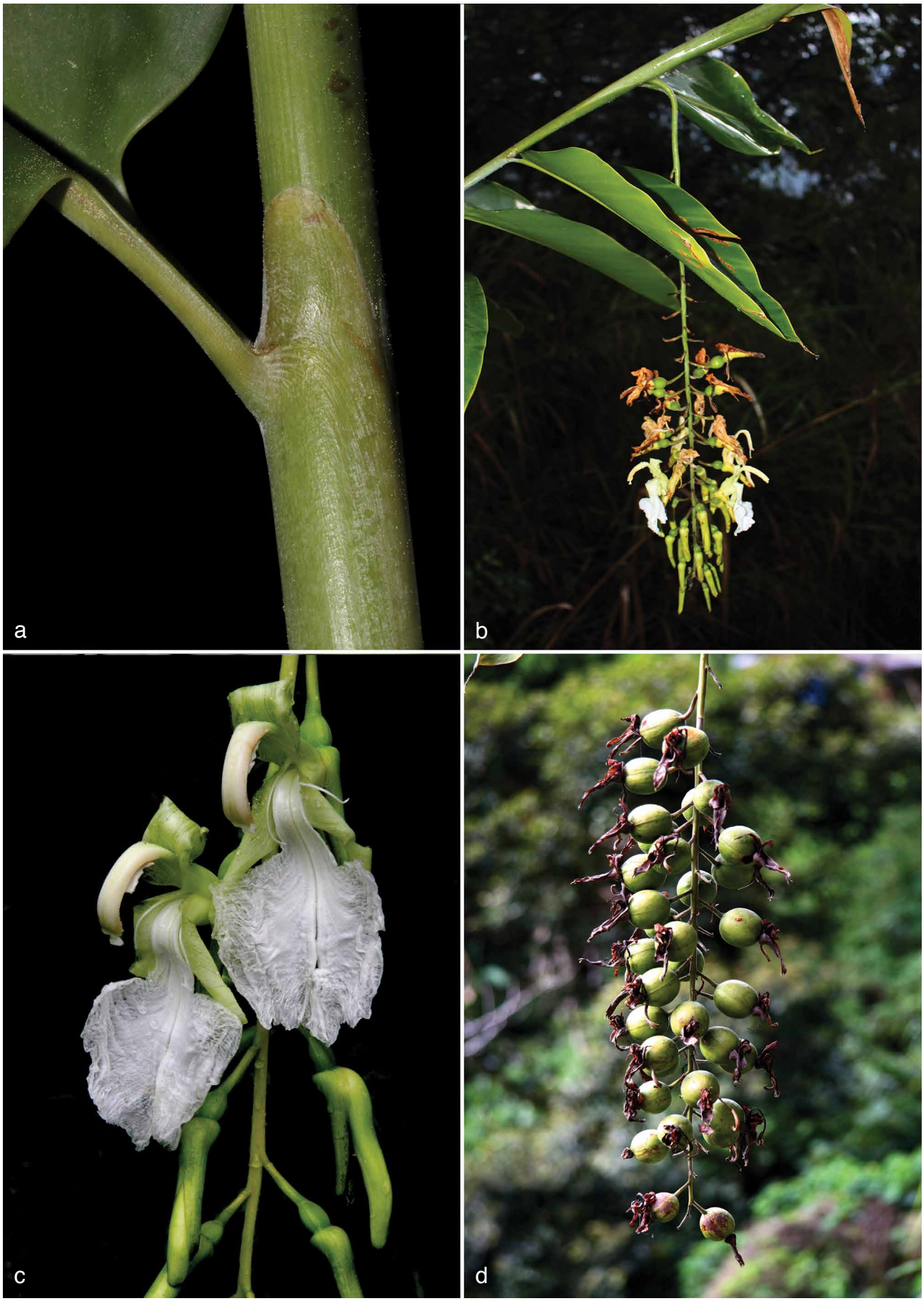


Fig. 10 *Vanoverberghia vanoverberghii* (Merr.) Funak. & Docot. a. Ligule; b. inflorescence; c. flower at anthesis; d. infructescence (a: *R.V.A. Docot 0031*; b: *R.V.A. Docot 0005*; c–d: without voucher). — Photos: a–b. R.V.A. Docot; c–d. H. Funakoshi.

densely pubescent, mid-green. *Fruit* oblong, 35–40 by 10–20 mm, pubescent, mid-green when mature, calyx persistent. *Seed* subglobose, brown with white aril.

Local names & Uses — Akbab (Bontoc language), kalawin (Igorot) and paluyyapuy (Igorot). The locals of Bontoc, Mountain Province consider this species as the female form of *V. sepulchrei*. The fruits are also eaten and reported to have a sweet-sour flavour.

Phenology — Flowering is between March and July, while fruiting starts in August.

Distribution & Habitat — *Vanoverberghia vanoverberghii* is endemic to Luzon Island, particularly in the provinces of Ifugao and Mountain Province. The species inhabits forests on hillsides and open slopes at 900–1300 m.

Additional specimens examined. Philippines, Luzon, *H.C. Conklin & Buwaya 80463* (K), Ifugao, Banaue, Bayninan, 28 Apr. 1963; *M. Vanoverbergh 573* (GH), Mountain Province, Bontoc; *M. Vanoverbergh 573* (LD, MO, S), Mountain Province, Bontoc, 28 Apr. 1914; *R.V.A. Docot 0005* (USTH [2 sheets] incl. spirit), Mountain Province, Bontoc, Barangay Alab Oriente, Mount Data, 3 July 2015; *R.V.A. Docot 0031* (USTH incl. spirit), Mountain Province, Bontoc, Barangay Alab Oriente, Mount Data, N17°03'55.8" E120°56'59.8", 1116 m, 29 Mar. 2016.

Notes — The type of *V. vanoverberghii* does not represent a single gathering. In the protologue, Merrill (1912) mentioned only one date, 11 June 1910, but the sets of *M. Vanoverbergh 573* have varying information: [1] June 1910 (K barcode K000292455, K000292456, US); [2] May–June 1910 (K barcode K000292454); [3] May–June 1911 (BM, E, K barcode K000292453, P); and [4] 28 April 1914 (LD, MO, S, Z). Unfortunately, the specimen at GH does not have a date. The date of the specimen at K (barcode K000292454) was altered from 1911 to 1910, and thus specimens from BM, E, K (barcode K000292453) and P are also from 1910, and are thus not in conflict with the information provided in the protologue. Therefore, the lectotype must be chosen from the BM, E, K, P and US collections. Since the specimen at K (barcode K000292453) has good vegetative and reproductive material, we designate it as the lectotype, and the specimens with 28 April 1914 label and the GH specimen with no date will remain as syntypes.

Recent collections from the type locality match the type and the protologue well for most characters with a few exceptions. Merrill (1912) described the anther of the species as crestless but in recent collected material, the anther has an emarginate and puberulent crest which is 0.5–1 by 1.5–2.5 mm (Fig. 9j). The original description of the labellum lacks detail, which is most likely because the labellum becomes fragile after drying and easily breaks off (Larsen & Larsen 2006). Smith (1990: f. 3Ab) illustrated the labellum of *V. vanoverberghii* as ovate and entire but recent collections demonstrate that the labellum is rather bifid with deltate and petaloid lobes (Fig. 9h). Smith (1975) when examining a collection (*A.D.E. Elmer 7396* at E) of *Alpinia paradoxa* (Ridl.) Loes. explained that, as the flower of a dry specimen ages, the labellum tends to curl and split. This is perhaps the reason why Smith concluded and illustrated the labellum of *V. vanoverberghii* as entire rather than bifid. Also, Smith (1990) mentioned that the bracts and bracteoles are minute and soon dehisce but our observation of young inflorescences reveals that the bracts and bracteoles are only present as bud-like protuberances near the base of pedicel (Fig. 9e). It is also worth mentioning that *V. vanoverberghii* has a robust rhizome, which is also observed in *V. sepulchrei* (Merrill 1912, Docot et al. 2016).

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