



HAL
open science

Phylogenetics and systematics of the South Polynesian genera *Apetahia* and *Sclerotheca* (Campanulaceae subfam. Lobelioideae)

Elizabeth Stacy, Jean-Yves Meyer, Yohan Pillon

► To cite this version:

Elizabeth Stacy, Jean-Yves Meyer, Yohan Pillon. Phylogenetics and systematics of the South Polynesian genera *Apetahia* and *Sclerotheca* (Campanulaceae subfam. Lobelioideae). *Botany Letters*, 2018, *Botany Letters*, 165 (2), pp.186-192. 10.1080/23818107.2018.1452792 . ird-03644823

HAL Id: ird-03644823

<https://ird.hal.science/ird-03644823>

Submitted on 19 Apr 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Phylogenetics and systematics of the South Polynesian genera *Apetahia* and *Sclerotheca*
(Campanulaceae subfam. Lobelioideae)

Yohan Pillon^{1,4}, Elizabeth Stacy² & Jean-Yves Meyer³

¹ LSTM, IRD, INRA, CIRAD, Montpellier SupAgro, Univ. Montpellier, Montpellier, France.
yohan.pillon@ird.fr

² School of Life Sciences, University of Nevada Las Vegas, 4505 S. Maryland Parkway, Las Vegas, NV 89154, USA. elizabeth.stacy@unlv.edu

³ Délégation à la Recherche de la Polynésie française, Bâtiment du Gouvernement, avenue Pouvanaa a Oopa, B.P. 20981, 98713 Papeete, Tahiti, French Polynesia. jean-yves.meyer@recherche.gov.pf

⁴ Author for correspondance

Running title: *Apetahia* and *Sclerotheca* (Campanulaceae)

Abstract

Apetahia and *Sclerotheca* are two small genera of Campanulaceae (subfam. Lobelioideae) endemic to South East Polynesia (French Polynesia and the Cook Islands). These groups comprise small shrubs to small trees (up to 3 m tall) that are restricted to upland tropical rainforests and montane cloud forests, where they are generally found between 400 and 2,000 m above sea level. We investigated their molecular phylogenetics by sequencing four plastid loci. We found that the two genera together form a well-supported clade but did not find support for their reciprocal monophyly. The genus *Sclerotheca* is supported as monophyletic clade that may be nested within a paraphyletic *Apetahia*. Because of their morphological similarities, we opted to treat them as a single genus, *Sclerotheca* s.l., comprising 10 species, and here provide the necessary new combinations, *Sclerotheca raiateensis* comb. nov. and *Sclerotheca seigellii* comb. nov. The expanded genus *Sclerotheca* has a patchy geographical distribution with remarkable disjunctions and may be undergoing a long-term decline. Conservation efforts to protect these highly threatened endemic species (all classified CR or EN according to the IUCN red List) are urgently needed, as they may be also considered as indicators of long-term ecological changes.

Keywords: Austral Islands, biogeography, conservation, endemic, Marquesas, Tahiti, Cook Islands

Résumé

Apetahia et *Sclerotheca* sont deux petits genres de Campanulaceae (subfam. Lobelioideae) endémiques de Polynésie (Polynésie Française et îles Cook). Ce sont des petits arbustes ou des petits arbres (jusqu'à 3 m) confinés aux forêts tropicales humides et aux forêts nuageuses des montagnes, que l'on rencontre à des altitudes de 400 à 2000 m. Quatre gènes chloroplastiques ont été séquencés pour une phylogénie moléculaire. Les deux genres forment ensemble un clade bien soutenu mais nous n'avons pas trouvé de soutien pour leur monophylie réciproque. Le genre *Sclerotheca* est un clade monophylétique soutenu qui semble dérivé du genre *Apetahia* qui serait paraphylétique. En raison de leur similarité morphologique, nous choisissons ici de les traiter comme un seul genre, *Sclerotheca* s.l., de 10 espèces, en faisant deux nouvelles combinaisons, *Sclerotheca raiateensis* comb. nov. et *Sclerotheca seigelii* comb. nov. Le genre *Sclerotheca* dans son concept élargi présente des disjonctions remarquables et une répartition géographique sporadique où il semble partout en déclin. Des efforts de conservation pour préserver ces espèces endémiques menacées (toutes classées CR ou EN sur la liste rouge de l'UICN) sont urgents, car ces plantes pourraient être des indicateurs de changements écologiques à long terme.

Introduction

Generic limits in Campanulaceae subfamily Lobelioideae are notoriously difficult, particularly because of the wide paraphyly of the genus *Lobelia* L. (Antonelli 2008; Antonelli 2009; Givnish et al. 2009; Lammers 2011). The family includes probably the largest plant radiation on a single archipelago: the Hawaiian lobeliads with 6 genera and c. 126 species descended from a single ancestor that reach the islands c. 13 million years ago (Givnish et al. 2009). There are also two other lobelioid genera restricted to Polynesia (Lammers 2007a; Lammers 2007b, Fig. 1): *Apetahia* Baill. with four species [two in the Marquesas, one in Raiatea (Society Islands), and one in Rapa (Austral Islands)] and *Sclerotheca* DC. with six species [four in Tahiti, one in Moorea, and one in Rarotonga (Cook Islands)], some of which are only recently discovered and described (Raynal 1976; Florence 1996). They are two of the 12 angiosperm genera considered to be endemic to southeastern Polynesia (French Polynesia and the Cook Islands, Meyer 2004). These small shrubs to small trees (up to 3 m tall) are restricted to tropical upland rainforests and montane cloud forests where they are generally found between 400 m (in Rarotonga) and 2,200 m elevation (in Tahiti), except in Rapa which is characterized by a more subtropical climate (Tab. 1). Generic concepts in insular flora require particular scrutiny; a pattern commonly observed is that genera restricted to islands are phylogenetically nested in larger more widespread genera (Stuessy, König, et Sepulveda 2014). As a result, several recent reviews have indicated that the number of plant genera reported as endemic to a given island or archipelago is typically overestimated (Stuessy, König, et Sepulveda 2014; Garnock-Jones 2014; Pillon, Barrabé, et Buerki 2017).

Few species of the genera *Apetahia* and *Sclerotheca* have been included in phylogenetic analyses to date, and the relationships of these genera to others within subfamily Lobelioideae are not known. Givnish et al. (2009) included *A. longistigmata*, *A. margeretae*, *S. forsteri*, and *S. jayorum*, in an analysis based on seven plastid loci and recovered a monophyletic *Sclerotheca*, with *A. margeretae* and *A. longistigmata* as successive sister groups, making *Apetahia* paraphyletic. The analysis by Antonelli (2009), which was based on the same DNA sequences and accessions, including fewer loci but broader sampling within Lobelioideae, also recovered a monophyletic *Sclerotheca* but no support for the monophyly of *Apetahia*. As part of study investigating the geographical origin of giant Lobelias (Knox et Li 2017), complete plastid genomes for *A. longistigmata* and *S.*

viridiflora were sequenced, and the two species were recovered as sister with strong support. Despite these efforts, the position of *Apetahia/Sclerotheca* within Lobelioideae remains unknown. Two alternative hypotheses seem possible: *Sclerotheca* and *Apetahia* may be either sister to the entire Hawaiian lobeliad clade or nested within it and sister to *Cyanea* Gaudich. + *Clermontia* Gaudich. (Knox et Li 2017). *Apetahia raiateensis* shares the same chromosome number as all of the Hawaiian lobeliads (Lammers 1993).

The relationships among species within *Apetahia/Sclerotheca* are not resolved. No study to date has provided phylogenetic evidence to support the reciprocal monophyly of these two genera, and no study to date has included their type species. The distribution of the two genera is somewhat overlapping, although they do not occur anywhere in sympatry. The morphological distinctness of the two genera has also been confused and questioned, since two species of *Apetahia* were first described in *Sclerotheca* (Brown 1935), and the distinction based on the number of ovary locules has been questioned (Florence 1997). To better resolve the relationships within *Apetahia* and *Sclerotheca*, we conducted a molecular phylogenetic analysis on these genera to test their generic limit, using near-complete species-level sampling.

MATERIALS & METHODS

Leaf material for all species of *Apetahia* and *Sclerotheca* of French Polynesia was collected in the wild, dried and preserved in silica-gel (Chase et Hills 1991). These included *A. longistigmata* (accessions from three islands of the Marquesas, namely Nuku Hiva, Hiva Oa and Ua Pou), *A. seigelii* (Fatu Hiva in the Marquesas), *A. raiateensis* (Raiatea, Leeward Society Islands), *A. margaretae* (Rapa, Austral Islands), *S. forsteri* (Moorea, considered to be extinct in Tahiti, Windward Society Islands), *S. arborea*, *S. oreades*, and *S. magdalenae* (Tahiti). No material was available for *S. jayorum* (Tahiti), which is now extremely rare on Mt. Marau. Voucher (herbarium) specimens were not collected for all of the accessions because of the rarity of some of the species and their sensitivity to injury and disease when their stems are broken. Instead, digital pictures were taken and are available in supplementary material. Genomic DNA was extracted using the Nucleospin® Plant II Kit (MACHEREY-NAGEL). Because some of our accessions had relatively degraded DNA, we selected four relatively short plastid DNA regions that could be amplified successfully in all accessions: *rbcl*, *trnD-trnE*, *trnH-psbA*, and *trnL-F* (*trnL* intron and *trnL-trnF* spacer amplified separately).

We used primers from Shaw et al. (2005) for *trnD-trnE* and *trnH-psbA*, Fazekas et al. (2012) for *rbcl*, and Taberlet et al. (1991) for *trnL-F*.

The four plastid DNA regions were amplified using the following mix: 12.3 μL of H_2O , 4 μL of GoTaq 5 \times (PROMEGA), 2 μL of MgCl_2 25mM, 1 μL of BSA (4 mg/mL), 0.4 μL of dNTP 1.25 μM , 0.2 μL of each primer 10 μM , 0.1 μL of GoTaq Flexi DNA polymerase 5u/ μL (PROMEGA) and 0.8 μL of genomic DNA. The following amplification program was used: 5 min at 80°C, 35 cycles of 1 min at 95°C, 1 min at 50°C, 1 min at 65°C and a final extension of 5 min at 65°C. All DNA sequences were deposited in Genbank (MG03314-MG053376, supplementary material).

To complete our sampling, we obtained the sequences of the four DNA regions from complete plastid genomes available in Genbank (Knox et Li 2017), including another accession each of *Apetahia longistigmata* (Marquesas, Ua Pou, MF061165) and *Sclerotheca viridiflora* (Rarotonga, Cook Islands, MF061223). We also included representatives of Hawaiian Lobeliads: *Brighamia insignis* A.Gray (KT372780), *Clermontia fauriei* H.Lév. (MF061167), *Cyanea fissa* Hillebr. (K354213), *C. leptostegia* A.Gray (MF061168), *Delissea rhytidosperma* H.Mann (KY354214), *Lobelia kauaensis* (A.Gray) A.Heller (MF061196), *L. niihauensis* St John (MF061202), *Trematolobelia kauaiensis* (Rock) Skottsb. (MF061225) and *L. boninensis* Koidz. (K354217) from Ogasawara Islands (Bonin islands) and two more distant outgroups: *Dialypetalum floribundum* Benth. (MF061169) and *Hippobroma longiflora* (L.) G.Don (MF061173).

Best-fit substitution models for *trnD-trnE*, *trnH-psbA*, *trnL-F*, and *rbcl* were respectively GTR+ γ , GTR+I ; JC+ γ , and GTR, according to JModeltest 2.1.10 analyses (Guindon et Gascuel 2003; Darriba et al. 2012). We ran one million generations of Markov Chain Monte Carlo (MCMC) in MrBayes (Ronquist et Huelsenbeck 2003) on a combined dataset, sampling one tree every 1,000 generations, unlinking substitution models, and with a 250,000-generation burnin; convergence was checked in Tracer.

RESULTS

The species of *Apetahia* and *Sclerotheca* formed a well-supported clade (posterior probability of 1), and the genus *Sclerotheca* was recovered as monophyletic with strong support. All accessions from Tahiti (*S. arborea*, *S. madgalenae* and *S. oreades*, and one undetermined specimen from Mt. Aorai), had identical sequences at the four loci examined,

thus forming a well-supported clade. Relationships within this clade were thus not resolved. The extremely rare *S. jayorum* was not included here, but previously published sequences (Givnish et al. 2009) are either identical (*trnL*) or nearly identical (*trnH-psbA*, with a single-base difference) to the Tahitian clade. The single accession of *S. forsteri* from the island of Moorea was sister to the Tahitian group, forming a Windward Society Island clade. *Sclerotheca viridiflora* (Rarotonga, Cook Islands) was sister to this entire clade.

The two species of *Apetahia* from the Marquesas Islands formed a well-supported clade, with the two accessions from the northern islands (Nuku Hiva and Ua Pou) forming a subclade within it. The relationship between *A. seigelia* (restricted to the southernmost Fatu Hiva) and the more widespread *A. longistigmata* was not resolved. *Apetahia raiateensis* (Raiatea, Leeward Society Island) was recovered as sister to the Marquesas clade, but with only moderate support (0.74). The position of *A. margaretae* (Rapa, Austral Islands) was unresolved between the *Sclerotheca* clade and the clade formed by *A. raiateensis* + Marquesas *Apetahia*. Even when excluding the accession of *A. margaretae* from Mt Tevaitau that lacks a *trnL* sequence, no further resolution was obtained (not shown). Finally, our analysis recovered *Apetahia* + *Sclerotheca* as sister to the Hawaiian *Clermontia* + *Cyanea*; however, support was only moderate (0.75).

DISCUSSION

We found strong support for the monophyly of South East Polynesian Lobeliads, including all species of *Apetahia* and *Sclerotheca*. There was also strong support for the monophyly of *Sclerotheca* but no evidence for a monophyletic *Apetahia*. The relationships among *Sclerotheca*, *A. margaretae* and the species of *Apetahia* from Raiatea and the Marquesas were unresolved, and the sister relationship between the species from Raiatea and the species from the Marquesas was only weakly supported. Because *Apetahia* and *Sclerotheca* together form a strongly supported clade and current phylogenetic evidence does not allow exclusion of the possible paraphyly of *Apetahia* relative to *Sclerotheca*, we propose treating them as single genus, *Sclerotheca* s.l., the older of the two names.

With the discovery and description of *Apetahia seigelia*, Florence (1997) had already questioned the distinction between *Apetahia* and *Sclerotheca* based on the number of ovary locules. The ovary of *Sclerotheca* is bilocular whereas a certain variation is observed in *Apetahia*. In the type species, *A. raiateensis*, the ovary is unilocular with non-intrusive

parietal placentation. In *A. margaretae*, carpellary intrusions can be observed in the chamber of the ovary. There is variation with *A. longistigmata* from non-intrusive placenta to placenta expansions that make contact in the axial part of the locule. In *A. seigelii*, the ovary is bilocular basally and apically because of the fusion of the carpels, and pseudo-bilocular in the middle part where the placentas are joined in the axial region (Florence 1997). Thus the number of locules in the ovary (strictly bilocular vs. unilocular to pseudobilocular) does not seem to be a very reliable character to distinguish *Sclerotheca* and *Apetahia*. The only reliable character left to distinguish them is the dehiscence of the fruit: via two apical pores in *Sclerotheca* and septically by valves in *Apetahia*. If *Apetahia* species indeed form a basal grade in the lineage, though, septical dehiscence by valves would be the ancestral (plesiomorphic) character that later evolved into apical pores.

The two genera are relatively small in species number (four and six species), and two of the species of *Apetahia* were initially described as *Sclerotheca* (Brown 1935). Merging the two genera requires only two new combinations (see below). The genetic divergence between *Apetahia* and *Sclerotheca* is also moderate and recent. Givnish et al. (2009) estimated the divergence between *A. longistigmata* and (*A. margaretae* + *S. forsteri* + *S. jayorum*) at 6.4 Mya; and Knox & Li (2017) estimated the divergence between *A. longistigmata* and *S. viridiflora* at 4.4 Mya. These divergence times are similar in range to the crown age of the Hawaiian-endemic Lobelioid genera (Givnish et al. 2009), all of which are members of a remarkable and recent adaptive radiation. Thus, when using divergence times or tree topology as criteria for genus delimitation (Chase, Fay, et Savolainen 2000; Barraclough et Humphreys 2015), the *Apetahia-Sclerotheca* clade may be better treated as a single genus rather than two.

Although our phylogenetic tree is not entirely resolved, *Sclerotheca* s.l. displays some biogeographical patterns commonly observed in other Polynesian groups (reviewed in Hembry et Balukjian 2016): a sister relationship between species from Moorea and Tahiti, a phylogeographical division between the Leeward and Windward Society Islands, and a relationship between the Society Islands and the Cook Islands. Some of the disjunctions observed within this genus span a broad geographic distance: Rarotonga vs. Windward Society Islands and Marquesas vs. Raiatea. These may be explained by direct, long-distance dispersal from one archipelago to another, but other hypotheses may be possible. For example, it may be that the genus used to be more widespread and the currently known

species represent only a small fraction of the past diversity of the group. *Sclerotheca* is absent from many islands in French Polynesia where apparently suitable habitats occur (e.g. the summital ridges of Bora Bora in the Leeward Society Islands, between 600 and 730 m elevation, or Raivavae in the Austral Islands with a summit up to 480 m elevation). More generally, Campanulaceae subfamily Lobelioideae is curiously absent from major Pacific archipelagos including Fiji, New Caledonia and Samoa in spite of their impressive dispersability. There is growing evidence that there have been many plant extinctions on Pacific islands during the Quaternary, probably concomitant with the first human arrivals (M Prebble et Dowe 2008), but also before, possibly associated with changes in climatic conditions (Matthew Prebble et al. 2016). Currently, species of *Apetahia* and *Sclerotheca* are relatively rare locally and in decline (Jacq et Meyer 2012; Sykes 2016), as they face a range of threats including rat predation and fungal pathogens. All of the island-endemic species are classified CR or EN according to IUCN Red Lists (table 1, UICN France, MNHN, et DIREN Polynésie française 2015) and should be urgently targeted by *in situ* and *ex situ* conservation efforts, including seed conservation.

TAXONOMIC TREATMENT

SCLEROTHECA A.DC. in DC., Prodrumus 7(2): 356 (1839) — Type: *Sclerotheca arborea* (G.Forst.) A.DC.

= *Apetahia* Baill. **syn. nov.**, Bull. Mens. Soc. Linn. Paris 1: 310 (1882) — Type: *Apetahia raiateensis* Baill.

non *Sclerotheca* Bubák & Vleugel (1908) (fungi)

Binomes for two names of *Apetahia* already exist in *Sclerotheca*: *Sclerotheca longstigmata* F.Br. and *Sclerotheca margaretae* F.Br. Two new combinations and three new lectotypifications are provided below.

Sclerotheca arborea (G.Forst.) A.DC. in DC., Prodrumus 7(2): 357 (1839) ≡ *Lobelia arborea* G. Forst. — Type *G. Forster 210*, in Hb. Montin (lecto-: S), designated by Nicolson & Fosberg (2003; p. 349).

Sclerotheca forsteri Drake, Ill. Fl. Ins. Pacif. 1: 26, pl. 8 (1886); 7: 222 (1892); Fl. Polynésie Franç.: 114 (1892) — Type (**designated here** by Florence & Pillon): Société, Tahiti, Faūtaūa, 700 m, *J.N. Vesco s.n* (lecto-: P00641770!; isolecto-: P06234612!, P06234613!, US00516689!)

In his diagnosis, Drake wrote: “Crescit in insula Tahiti, inter rupes vallis Fautahua, 700 altidine Vesco”. There are three sheets from this collector at P, none bears the name given by Drake (which is common for him), or the indication of a type. One sheet, P00641770, bears the names *Sclerotheca* and *Lobelia arborea* Forst. with two different handwritings. The other two sheets P06234612 and P06234613 have the name *Sclerotheca arborea*; the generic name of P06234612 has the same handwriting as P00641770 and the binomial name on P006234613 the same as the species epithet of the other two sheets. A sheet at US (00516689) bearing the name *Sclerotheca* (F.R. Fosberg handwriting?) was annotated by D.H. Nicolson as “Type material of *Sclerotheca forsteri* Drake, Ill. Fl. Ins. Pac. 1: 24, T.8 1886”. We select the sheet P00641770 as the lectotype, which has a detailed description written in Vesco’s hand, locality, phenology and the vernacular name *aa-rai-fau* (cited by Drake); the other sheets P06234612, P06234613 and US00516689 are duplicates of the first one.

Sclerotheca oreades E. Wimmer., Ann. Naturhist. Mus. Wien 56: 373 (1948) — Type (**designated here** by Florence & Pillon): Society Islands, Tahiti, Orofena, east side of south ridge, 1400 m, 20 Sept. 1934, *St. John & Fosberg 17022* (lecto-: K!; isolecto-: BISH!, P00641809!)

Wimmer cited two collections: *St. John & Fosberg 17022* and *17023*. The sheet of *St. John & Fosberg 17022* at K is chosen as a lectotype because this is the only specimen we have seen with flowers, although it does not bear Wimmer’s handwritten determination. No syntype has been located at W, where Wimmer worked.

Sclerotheca raiateensis (Baill.) Pillon & Florence, **comb. nov.** ≡ *Apetahia raiateensis* Baill., Bull. Mens. Soc. Linn. Paris 1: 311 (1882) — Type: Raiatea, *Vesco s.n.* (lecto-: P00641768!, designated by Florence (1997) ; isolecto-: P00641769!, P-BAILLON).

Sclerotheca seigelii (Florence) Pillon & Florence, **comb. nov.** \equiv *Apetahia seigelii* Florence, Allertonia 7(4): 248 (1997) — Type: Marquesas Islands, Fatu-Hiva, trail to Mounanui from Teavepuhia pass, ½ way to Mounanui, then west up ridge crest, 2200 ft (671 m), 18 Aug. 1988 (fl, fr), S. Perlman 10268 (holo-: BISH ; iso-: AD, BISH, E, F, K, MO, NY, PI, PAP, PTBG, US).

Sclerotheca viridiflora Cheeseman, Trans. Linn. Soc. London, Bot. (ser.2) 6(6): 285, pl. 33 (1903) — Type (**designated here** by Florence & Pillon): Rarotonga, 1899, *Cheeseman s.n.* (lecto-: AK92672!).

There are four sheets at Auckland Museum Herbarium that are Cheeseman's collections of this species. AK46015 bears the handwritten name *Sclerotheca viridiflora* Cheeseman and is annotated cotype, with handwritten elements of the diagnosis on a recent label. It seems to be the mixture of two plants: a fertile branch with elliptic leaf blades, 7.5-11 × 2.5-3.5 cm, with acute-acuminate tip and an open flower, the other sterile, with elliptic to obovate leaf blades, 11.5-15 × 4.5-6 cm, with pointed to rounded tips. A similar sterile branch is found on the sheet AK92673 with two handwritten determinations: *Apetahia* ? (crossed) and *Sclerotheca viridiflora*, not clearly signed: [MC]. The sheet AK92672 is fertile with a first branch bearing a flower and the second a bud. A handwritten label (probably by Cheeseman) bears the name *Sclerotheca* and a label of Auckland Museum Herbarium with the indication: *Sclerotheca viridiflora* Cheesem. n.sp. Rarotonga, 1899. It is a single collection, with leaves similar to that of the fertile branch of the sheet AK46015, with elliptic leaf blades 8.5-11 × 3-4 cm, but the margin is more strongly toothed, which suggests they are distinct collections. Finally AK92674 also has two branches from a single collection, with the same handwritten determination and label as AK92672; but this collection is probably the same as the fertile branch of AK46015, as suggested by the marginal teeth that are less pronounced than on AK92672. Considering that none of the sheet bears the indication of a type or name by Cheeseman, a lectotype needs to be chosen and we select here AK92672.

Acknowledgments

We are grateful to Jacques Florence for the lectotypifications and discussion. We also thank Tomoko Sakishima for assistance in the lab, Eric Knox for information on specimens and

discussion, the curators of the herbaria P, K (Aurélie Grall) and BISH (Barbara Kennedy, Nicolas Walvoord) for access to their collections. Two anonymous reviewers and the editor Arnaud Mouly provided constructive comments on an earlier version of the manuscript.

Disclosure statement

The authors declare no conflict of interests.

Funding

This research was funded by the Gordon and Betty Moore Foundation and NSF award HRD 0833211.

Notes on contributors

Yohan Pillon studies the ecology and evolution of plants with a broad interest in the Pacific islands flora.

Elizabeth Stacy is an evolutionary biologist who studies population divergence and speciation in plants.

Jean-Yves Meyer is a plant ecologist and botanist studying the flora of French Polynesia and South Pacific Islands.

Jean-Yves Meyer collected and identified the plant material, Yohan Pillon performed the molecular work and data analyses, and all three authors wrote the manuscript.

References

- Antonelli, A. 2008. « Higher levels phylogeny and evolutionary trends in Campanulaceae subfam. Lobelioideae: Molecular signal overshadows morphology ». *Molecular Phylogenetics and Evolution* 46: 1- 18.
- Antonelli, A. 2009. « Have giant lobelias evolved several times independently? Life forms shift and historical biogeography of the cosmopolitan and highly diverse subfamily Lobelioideae (Campanulaceae) ». *BMC Biology* 7: 82.
- Barracough, T. G., and A. M. Humphreys. 2015. « The evolutionary reality of species and higher taxa in plants: a survey of post-modern opinion and evidence ». *New Phytologist* 207 (2): 291- 296.
- Brown, F. B. H. 1935. *Flora of Southeastern Polynesia III. Dicotyledons*. Vol. 130. Honolulu: Bernice P. Bishop Museum.

- Chase, M. W., M. F. Fay, and V. Savolainen. 2000. « Higher-level classification in the angiosperms: new insights from the perspective of DNA sequence data ». *Taxon* 49: 685- 703.
- Chase, M. W., and H. G. Hills. 1991. « Silica gel: an ideal material for field preservation of leaf samples for DNA studies ». *Taxon* 40: 215- 220.
- Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. « jModelTest 2: more models, new heuristics and parallel computing ». *Nature Methods* 9 (8): 772- 772.
- Fazekas, A. J., M. L. Kuzmina, S. G. Newmaster, and P. M. Hollingsworth. 2012. « DNA Barcoding Methods for Land Plants ». In *DNA Barcodes*, édité par W. John Kress and David L. Erickson, 858:223- 252. Totowa, NJ: Humana Press.
- Florence, J. 1996. « *Sertum polynesianum* V. Une nouvelle espèce de *Sclerotheca* (Campanulaceae-Lobelioideae), endémique de Tahiti, Polynésie Française ». *Adansonia* 18: 97- 101.
- Florence, J. 1997. « New species of *Plakothira* (Loasaceae), *Melicope* (Rutaceae), and *Apetahia* (Campanulaceae) from the Marquesas islands ». *Allertonia* 7 (4): 238- 253.
- Garnock-Jones, P. J. 2014. « Evidence-based review of the taxonomic status of New Zealand's endemic seed plant genera ». *New Zealand Journal of Botany* 52 (2): 163- 212.
- Givnish, T. J., K. C. William, A. R. Mast, T. B. Paterson, T. J. Theim, A. L. Hipp, J. M. Henss, J. F. Smith, K. R. Wood, and K. J. Sytsma. 2009. « Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae) ». *Proceedings of the Royal Society of London B* 276: 407- 416.
- Guindon, S., and O. Gascuel. 2003. « A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood ». *Systematic Biology* 52 (5): 696- 704.
- Hembry, D. H., and B. Balukjian. 2016. « Molecular Phylogeography of the Society Islands (Tahiti; South Pacific) Reveals Departures from Hotspot Archipelago Models ». *Journal of Biogeography* 43 (7): 1372- 1387.
- Jacq, F. A., and J. Y. Meyer. 2012. « Taux de mortalité et causes de disparition de *Apetahia raiateensis* (Campanulaceae), une plante endémique de l'île de Raiatea (Polynésie française) ». *Revue d'écologie (Terre Vie) Supplément* 11: 57- 72.
- Knox, E. B., and C. Li. 2017. « The East Asian Origin of the Giant Lobelias ». *American Journal of Botany* 104 (6): 924- 938. doi:10.3732/ajb.1700025.
- Lammers, T. G. 1993. « Chromosomes numbers of Campanulaceae. III. Review and integration of data for subfamily Lobelioideae ». *American Journal of Botany* 80 (6): 660- 675.
- Lammers, T. G. 2011. « Revision of the infrageneric classification of *Lobelia* L. (Campanulaceae: Lobelioideae) ». *Annals of the Missouri Botanical Garden* 98 (1): 37- 62.
- Lammers, T.G. 2007a. *World Checklist and Bibliography of Campanulaceae*. Kew: Royal Botanic Gardens.
- Lammers, T.G. 2007b. « Campanulaceae ». In *The Families and Genra of Vascular Plants*, édité par K. Kubitzki, 8:26- 56. Berlin: Springer-Verlag.
- Meyer, J.-Y. 2004. « Threat of invasive alien plants to native flora and forest vegetation of eastern Polynesia ». *Pacific Science* 58 (3): 357- 375.
- Nicolson, D. H., and F. R. Fosberg. 2003. *The Forsters and the Botany of the Second Cook Expedition (1772 - 1775)*. Regnum Vegetabile 139. Ruggell: Gantner.

- Pillon, Y., L. Barrabé, and S. Buerki. 2017. « How Many Genera of Vascular Plants Are Endemic to New Caledonia? A Critical Review Based on Phylogenetic Evidence ». *Botanical Journal of the Linnean Society* 183 (2): 177- 198.
- Prebble, M, and J Dowe. 2008. « The Late Quaternary Decline and Extinction of Palms on Oceanic Pacific Islands ». *Quaternary Science Reviews* 27 (27- 28): 2546- 2567.
- Prebble, M., R. Whitau, J.-Y. Meyer, L. Sibley-Punnett, S. Fallon, and N. Porch. 2016. « Abrupt Late Pleistocene Ecological and Climate Change on Tahiti (French Polynesia) ». *Journal of Biogeography* 43 (12): 2438- 2453.
- Raynal, J. 1976. « Une Lobéliacée polynésienne nouvelle ». *Adansonia* 16 (3): 379- 382.
- Ronquist, F., and J. P. Huelsenbeck. 2003. « MrBayes 3: Bayesian phylogenetic inference under mixed models ». *Bioinformatics* 19 (12): 1572- 1574.
- Shaw, J., E. D. Lickey, J. T. Beck, S. B. Farmer, W. Liu, J. Miller, K. C. Sirupun, C. T. Winder, E. E. Schilling, and R. L. Small. 2005. « The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis ». *American Journal of Botany* 92 (1): 142- 166.
- Stuessy, T. F., C. König, and P. L. Sepulveda. 2014. « Paraphyly and endemic genera of oceanic islands: implications for conservation ». *Annals of the Missouri Botanical Garden* 100 (1- 2): 50- 78.
- Sykes, William Russell. 2016. *Flora of the Cook Islands*. Kalaheo, Kaua'i, Hawai'i: National Tropical Botanical Garden.
- Taberlet, P., G. Gielly, and J. Bouvet. 1991. « Universal primers for amplification of three non-coding regions of chloroplast DNA ». *Plant Molecular Biology* 17: 1105- 1109.
- UICN France, MNHN, and DIREN Polynésie française. 2015. *La liste rouge des espèces menacées en France -Chapitre Flore vasculaire endémique de Polynésie française*. Paris, France. http://uicn.fr/wp-content/uploads/2015/12/Liste_rouge_Flore_vasculaire_endemique_de_Polynesie_francaise.pdf.

Figure 1. Geographical distributions of the species of *Apetahia* and *Sclerotheca* and related lineages of woody Lobelioideae. Inset shows a detailed view of the Society Islands.

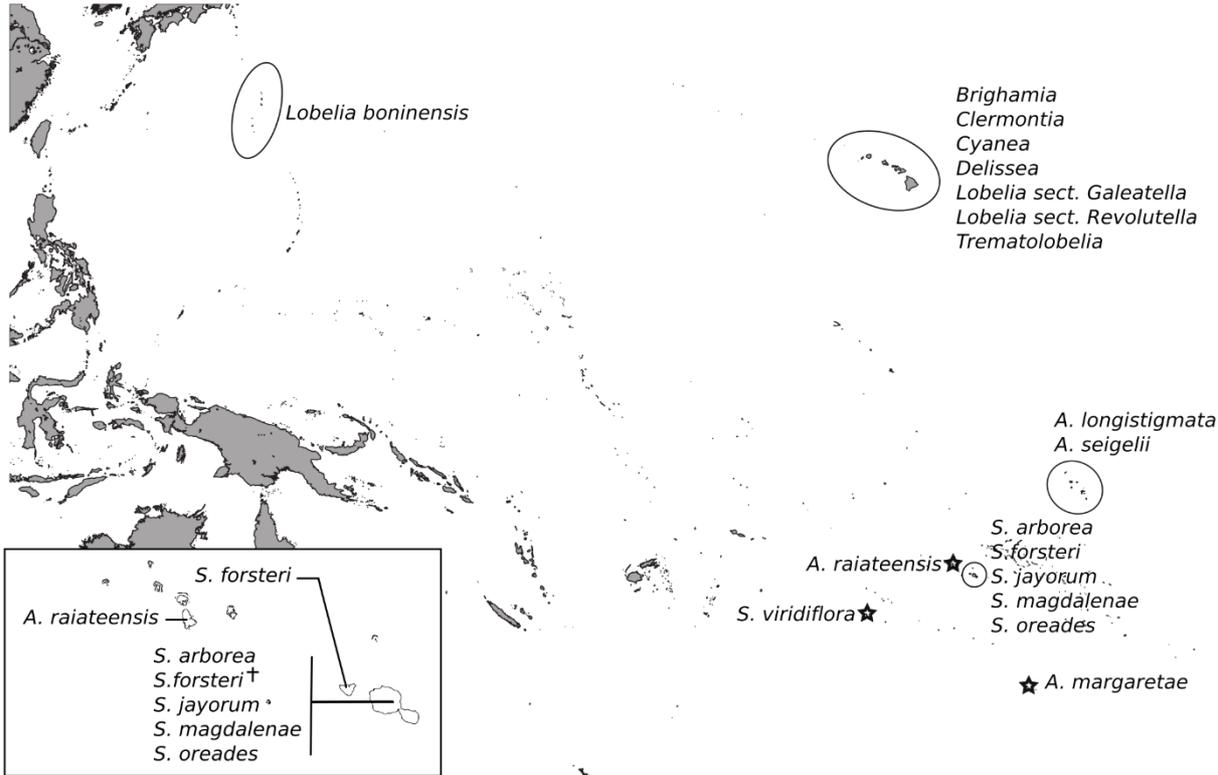


Figure 2. Half-compatible Bayesian phylogenetic tree of *Apetahia* and *Sclerotheca* with selected representatives of other lineages of Campanulaceae subfam. Lobelioideae from the Pacific Islands. Numbers at nodes are posterior probabilities.

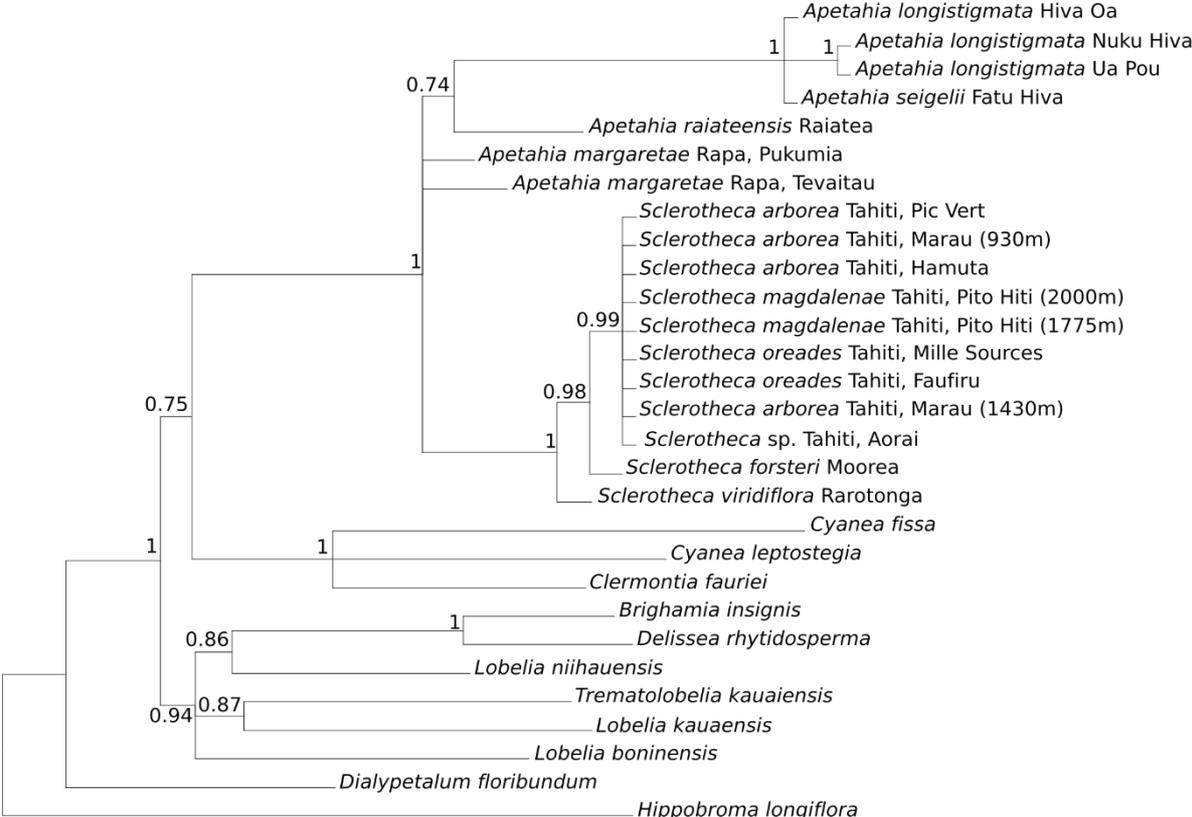


Table 1. Distribution and ecology of the species of *Apetahia* and *Sclerotheca* based on field observation (J.-Y.Meyer) and conservation status. Tahiti is formed by two ancient volcanoes, the larger and older (0.8 My old) being “Tahiti Nui”, the smaller and younger (0.4 My) “Tahiti Iti” joined by a low and narrow isthmus. *from Sykes (2016)

Species	Island	elevation range (m)	Localities	Habitat type(s)	IUCN Red List
<i>Apetahia raiateensis</i> Baill.	Raiatea	500-800	Temehani Plateaus	montane shrubland	CR
<i>Apetahia longistigmata</i> F.Br.	Nuku Hiva	900-1100	Col Toovii, Mt Tekao	montane shrubland and cloud forest	CR
	Hiva Oa	780-890	Mt Ootua	montane shrubland	
	Ua Pou	670-920	Poumaka, Mt Oave, Mt Teavahaakiti	montane shrubland	
	Tahuata	800-950	Mt Haaioputeomo	montane shrubland	
<i>Apetahia seigellii</i> Florence	Fatu Hiva (Fatu Iva)	650-720	Mt Mounanui	montane shrubland	CR
<i>Apetahia margaretae</i> (F.Br.) E.Zimm.	Rapa	160-550	Mt Pukumia, Mt Maugaoa, Mt Namuere	upland rainforest	EN
<i>Sclerotheca arborea</i> DC.	Tahiti Nui	930-1400	Col Hamuta, Mt Marau, Pic Vert	upland rainforest & montane cloudforest	EN
<i>Sclerotheca forsteri</i> Drake	Moorea	680-870	Mt Tohiea, Mt Rotui, Mt Fairurani	upland rainforest & cloudforest	EN
<i>Sclerotheca jayorum</i> J.Raynal	Tahiti Nui	1100-1300	Mt Marau	montane cloudforest	CR
<i>Sclerotheca magdalenae</i> Florence	Tahiti Nui	1775-2200	Mt Pito Hiti, Mt Orohena	montane shrubland & cloudforest	CR
<i>Sclerotheca oreades</i> E.Wimm.	Tahiti Nui and Tahiti Iti	800-1210	Faufiru, Orofero, Mt Aorai, Mt Ivirairai, Mt Pihaiateta (Mille Sources), Mt Mauru, Mt Atara, Vaihiria	montane cloudforest	EN
<i>Sclerotheca</i> sp.	Tahiti Nui	1690-1700	Mt Aorai	montane cloudforest	
<i>Sclerotheca viridiflora</i> Cheeseman	Rarotonga	400-450*		upland rainforest & montane cloudforest	CR