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

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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 from 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 2000 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 ten 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.

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Introduction

Generic limits in Campanulaceae subfamily Lobelioideae are notoriously difficult, particularly because of the wide paraphyly of the genus *Lobelia* L. (Antonelli 2008, 2009; Givnish et al. 2009; Lammers 2011). The family includes probably the largest plant radiation on a single archipelago: the Hawaiian lobeliads with six 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, 2007b; Figure 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 have only recently been discovered and described (Florence 1996; Raynal 1976). They are two of the 12 angiosperm genera considered to be endemic to south-eastern 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 2200 m elevation (in Tahiti), except in Rapa which is characterized by a more subtropical climate. 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, and 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 (Garnock-Jones 2014; Pillon, Barrabé, and Buerki 2017; Stuessy, König, and Sepulveda 2014).

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. margaretae*, *S. forsteri*, and *S. jayorum*, in an analysis based on seven plastid loci and recovered a monophyletic *Sclerotheca*, with *A. margaretae* 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 a study investigating the geographical origin of giant Lobelias (Knox and Li 2017), complete plastid genomes for *A. longistigmata* and *S. viridiflora* were sequenced, and the two species were recovered as

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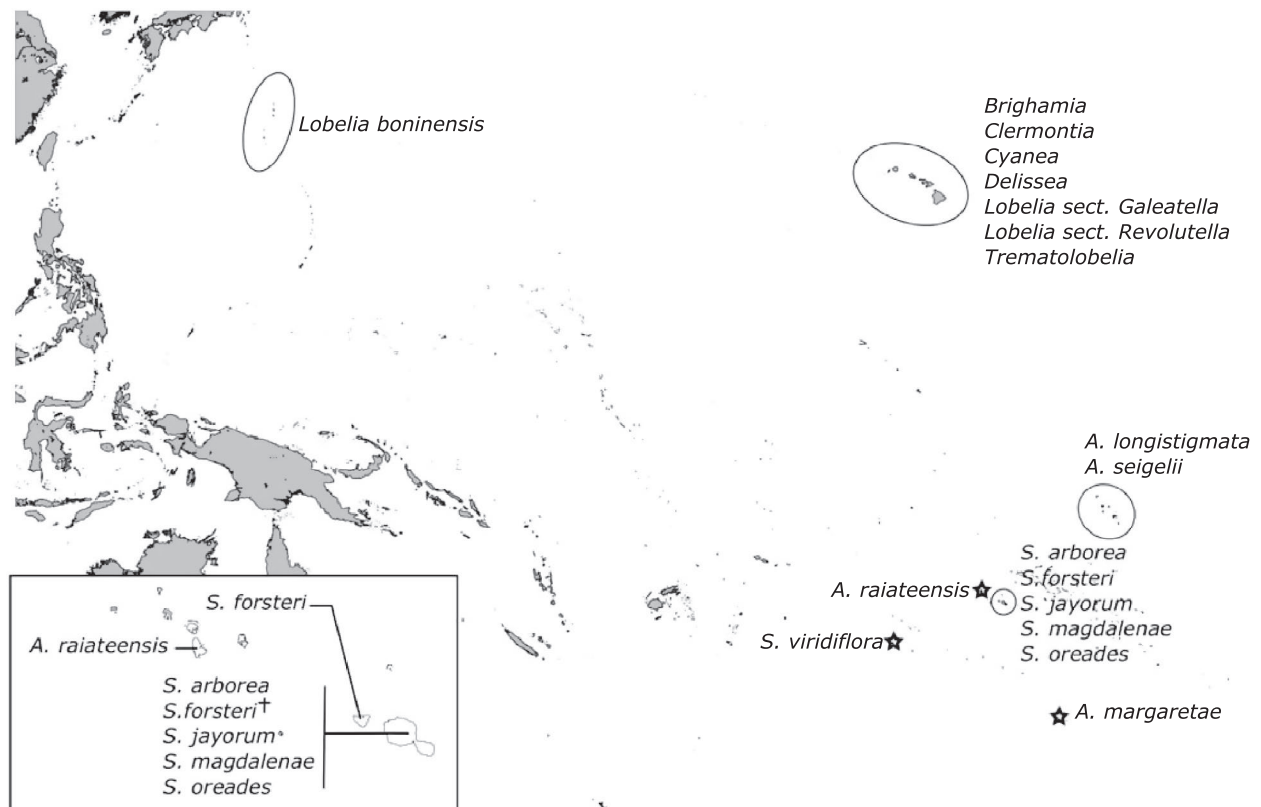


Figure 1. Geographical distributions of the species of *Apetahia* and *Sclerotheca* and related lineages of woody Lobelioideae. Inset shows a detailed view of the Society Islands.

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 and 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 and 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 and Hills 1991).

This material 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, Gielly, and Bouvet (1991) for *trnL-F*.

The four plastid DNA regions were amplified using the following mix: 12.3 μ L of H₂O, 4 μ L of GoTaq 5 \times (PROMEGA), 2 μ L of MgCl₂ 25 mM, 1 μ L of BSA (4 mg/mL), 0.4 μ L of dNTP 1.25 μ M, 0.2 μ L of each primer 10 μ M, 0.1 μ L of GoTaq Flexi DNA polymerase 5u/ μ L (PROMEGA) and 0.8 μ L 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 and 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 (Darriba et al. 2012; Guindon and Gascuel 2003). We ran one million generations of Markov Chain Monte Carlo (MCMC) in MrBayes (Ronquist and Huelsenbeck 2003) on a combined dataset, sampling one tree every 1000 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 (Figure 2). 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. seigelii* (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 a single genus, *Sclerotheca* s.l., the older of the two names.

With the discovery and description of *Apetahia seigelii*, 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 versus 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.

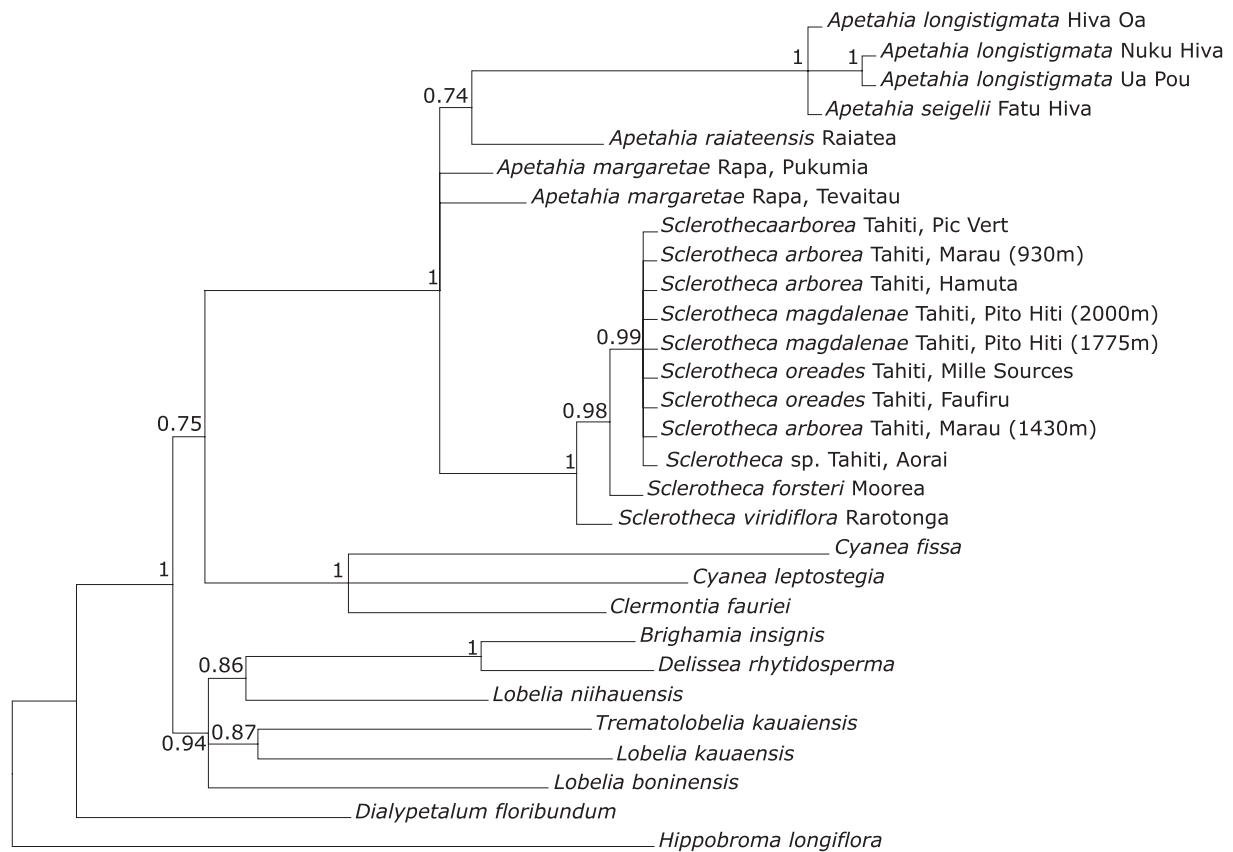


Figure 2. Half-compatible Bayesian phylogenetic tree of *Apetahia* and *Sclerotheca* with selected representatives of other lineages of Campanulaceae subfam. Lobelioideae from the Pacific Islands. Numbers at nodes are posterior probabilities.

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 and 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 (Barraclough and Humphreys 2015; Chase, Fay, and Savolainen 2000), 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 and 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

versus Windward Society Islands and Marquesas versus 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 (Prebble and Dowe 2008), but also before, possibly associated with changes in climatic conditions (Prebble et al. 2016). Currently, species of *Apetahia* and *Sclerotheca* are relatively rare locally and in decline (Jacq and 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, IUCN France, MNHN, and DIREN Polynésie française 2015) and should be urgently targeted by *in situ* and *ex situ* conservation efforts, including seed conservation.

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 Iiti”, joined by a low and narrow isthmus.

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 Teava-haakiti	Montane shrubland	
<i>Apetahia seigelii</i> Florence	Tahuata	800–950	Mt Haaioiputeomo	Montane shrubland	
	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 cloud-forest	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 Iiti	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 cloud-forest	CR

*From Sykes (2016).

Taxonomic treatment

SCLEROTHERCA 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 longistigmata* 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 and Fosberg (2003, 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 P06234613 is 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. Wimm., 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.** ≡ *Apetahia seigelii* Florence, Allertonia 7(4): 248 (1997) – Type: Marquesas Islands, Fatu-Hiva, trail to Mounanui from Teavepuhiau 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, P!, 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.

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Disclosure statement

The authors declare no conflict of interests.

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Notes on contributors

Yohan Pillon studies the ecology and evolution of plants, with a broad interest in the flora of the Pacific islands. He performed the molecular work and data analyses, and all three authors wrote the manuscript.

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. He collected and identified the plant material.

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