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**A molecular and morphological survey of generic limits of *Acsmithia* and
Spiraeanthemum (Cunoniaceae)**

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Abstract—A phylogenetic analysis was conducted on the tribe Spiraeanthemeae (Cunoniaceae) to clarify relationships of the genera *Acsmithia* and *Spiraeanthemum*. Three molecular markers, one plastid region (*trnL* intron and *trnL-trnF* intergenic spacer) and two nuclear-single copy genes (*ncpGS* and *PHYC*), were sequenced for this purpose. The independent analysis of the three markers and a combined analysis all showed that the genus *Acsmithia* is paraphyletic since the genus *Spiraeanthemum* is nested within it. A morphological survey of all species in the tribe confirmed the existence of two groups within *Acsmithia*. One comprises the species from Australia, New Guinea, and *A. densiflora* from New Caledonia and is characterised by multiple ovules per carpel. The other group contains all the remaining New Caledonian species plus *A. vitiensis* from Fiji and is characterised by a single ovule per carpel. The study shows that characters previously used to distinguish *Acsmithia* and *Spiraeanthemum*, phyllotaxy and sexual system, are homoplasious as in several other groups of Cunoniaceae. A broad circumscription of the genus *Spiraeanthemum* is

adopted here that includes the species formerly placed in *Acsmithia*. Two new combinations are proposed: *Spiraeanthemum collinum* and *Spiraeanthemum meridionale*.

Spiraeanthemum austrocaledonicum is considered a synonym of *Spiraeanthemum densiflorum*.

Keywords— glutamine synthetase, Melanesia, New Caledonia, nuclear-single copy gene, phyllotaxy, sexual system.

Cunoniaceae (Oxalidales) are a predominantly Southern Hemisphere family of trees and shrubs consisting of 27 genera and ca. 300 species (Bradford et al. 2004). Molecular phylogenetic studies of the family (Bradford and Barnes 2001) allowed circumscription of a number of monophyletic tribes within the family for several groups of genera that had been allied previously on morphological grounds (Hufford and Dickison 1992). Tribe Spiraeanthemeae was shown to be sister to the remainder of the family (Bradford and Barnes 2001; Sweeney et al. 2004) and consists of two genera : *Acsmithia* Hoogland and *Spiraeanthemum* A. Gray. The members of this tribe are unique in the family in being apocarpous (but see the recently described *Hooglandia* McPherson & Lowry which is monomerous, McPherson and Lowry 2004) and a close relationship has been suggested with *Brunellia* Ruiz & Pavón (Hufford and Dickison 1992), the only genus of Brunelliaceae, a closely related family within Oxalidales. Synapomorphies of Spiraeanthemeae include epidermal glands, pocket domatia along the midvein, and synchronously maturing flowers (Bradford and Barnes 2001). Within Cunoniaceae, none of these characters is unique to this tribe; the combination is, however, unique.

As currently circumscribed *Acsmithia*, consists of 14 species from eastern Malesia, Australia, New Caledonia, and Fiji; and *Spiraeanthemum* comprises six species from the Bismarck Archipelago, Bougainville, Solomon Islands, Vanuatu, Fiji, and Samoa. *Acsmithia*, named after Albert C. Smith, an authority of the flora of Fiji, was described in 1979 by R.D. Hoogland to accommodate species formerly included in *Spiraeanthemum* which have whorled leaves and hermaphroditic flowers, whereas *Spiraeanthemum* s.s. is characterized by opposite leaves and unisexual flowers (dioecious). Although recognition of two genera was questioned by Hufford and Dickison (1992), they have been considered as distinct in all regional treatments of the family published since 1979 (Smith 1985; Hopkins and Hoogland 2002), in Hoogland (unpublished manuscript for the Flore de la Nouvelle-Calédonie et Dépendances) and in the generic survey of the family by Bradford et al. (Bradford and Barnes 2001; Bradford et al. 2004). As part of a study on the evolution of the family in New Caledonia and Vanuatu, a molecular phylogeny of the tribe Spiraeanthemeae in this region is presented here, along with a survey of morphological characters. We were interested in assessing the monophyly *Acsmithia* in New Caledonia and the biogeographical patterns of both *Acsmithia* and *Spiraeanthemum*.

MATERIAL AND METHODS

Molecular analysis—Leaf material of *Acsmithia* and *Spiraeanthemum* was dried in the field in silica gel (Chase and Hills 1991) and DNA was extracted following a modified CTAB protocol (Csiba and Powell 2006). *Brunellia* (Brunelliaceae), *Hooglandia* (Cunoniaceae, unplaced to tribe) and *Platylophus* D. Don (Cunoniaceae, tribe Schizomerieae) were also included as outgroups. The plastid *trnL-F* region (*trnL* intron and *trnL-trnF* spacer) was amplified with the primers c and f from Taberlet et al. (1991) using a standard protocol (e.g. Pillon et al. 2007). A portion of the chloroplast-expressed glutamine synthetase

(*nepGS*), a nuclear single-copy gene, was amplified using the primers 687F and 994R of Emshwiller and Doyle (1999). PCR reaction mix included 45 μ L of 2.5 mM $MgCl_2$ Reddy PCR Master Mix 1.1 \times (ABgene Ltd, Surrey, U.K.), 1 μ L of 0.4% bovine serum albumin (BSA), 0.5 μ L of each primer (100 ng/ μ L) and 3 μ L of template DNA. The following PCR program was used: 2 min at 94°C, 38 cycles of 1 min at 94°C, 1 min at 50°C, 1 min 30 sec at 72°C and a final extension of 5 min at 72°C. A portion of the first exon of phytochrome C (*PHYC*), another nuclear single-copy gene, was amplified using the primers PhyC-F and PhyC-R from Samuel et al.(2005). The PCR reaction mix included 45 μ L of 1.5 mM $MgCl_2$ Reddy PCR Master Mix 1.1 \times (ABgene Ltd), 1.5 μ L of 0.4% bovine serum albumin (BSA), 0.5 μ L of each primer (100 ng/ μ L), 1 μ L of DMSO and 2 μ L of template DNA. The following PCR program was used: 3 min at 94°C, 38 cycles of 1 min at 94°C, 1 min at 50°C, 1 min at 72°C and a final extension of 10 min at 72°C. For nuclear genes, cloning for some accessions was necessary to separate alleles. Alignment and phylogenetic analyses were carried out with PAUP*4.01b10 (Swofford 2002). To recover the most parsimonious trees, we used branch and bound searches. Robustness of tree topology was assessed using bootstrapping with 100 replicates, also with branch and bound searches. For the combined analysis, a single allele was retained for each accession; we chose the allele that appeared as the most ancestral (the one on the shortest branch). For *Brunellia* the sequences from two different species were combined. The list of species, vouchers and GenBank accession numbers are provided in the appendix. Sequence datasets and phylogenetic trees were deposited in Treebase (study accession number: S2119, matrix accession numbers: M4005, M4006, M4007).

Morphology—Morphological characters either observed by us or mentioned in the literature as differing between *Spiraeanthemum* and *Acsmithia* or varying among *Acsmithia*

species were scored with the aid of a binocular microscope ($\times 10$ -40 magnification) for all species in both genera in the herbaria at Kew (K) and Nouméa (NOU). The only character not scored by us was the number of ovules per carpel, for which data were taken from Hoogland (1979, unpublished manuscript, and in Hopkins and Hoogland 2002). Literature sources used to suggest possible characters included these works by Hoogland as well as Bradford and Barnes (2001), Bradford et al. (2004), Dickison (1984), Rutishauser and Dickison (1989), Hufford and Dickison (1992), Hyland and Whiffin (1993), and Smith (1952; 1985).

RESULTS

Molecular analysis— Detailed statistics for each DNA regions studied are provided in Table 1. The two nuclear-single copy genes both had a greater proportion of variable and parsimony informative characters than the plastid *trnL* region. The *ncpGS* region was particularly informative, with nearly 20% of sites variable, over ca. 1,200 base pairs. It is thus a promising tool for phylogenetic studies in Cunoniaceae and Oxalidales in general.

Analysis of *trnL-F* sequences (Fig. 1) indicates that the two accessions of *Acsmithia densiflora* from New Caledonia form a monophyletic group that is sister to a well-supported group (94 bootstrap percentage, BP) consisting of all other species of the tribe. In this group we can distinguish *Spiraeanthemum s.s.* as well supported (91 BP); it is represented by *S. macgillivrayi* (Vanuatu) and *S. samoense* (Samoa). The sister group of *Spiraeanthemum s.s.* is a moderately supported clade (67 BP) consisting of four species of New Caledonian *Acsmithia*: *A. brongniartiana*, *A. elliptica*, *A. meridionalis*, and *A. pubescens* (hereafter referred to as the brongniartiana group).

Analysis of *ncpGS* (Fig. 1) also recovered *A. densiflora* as sister to the remaining members of Spiraeanthemeae, and *Spiraeanthemum s.s.* as sister to the brongniartiana group

represented by *A. brongniartiana* and *A. pubescens*. Monophyly of the brongniartiana group and of the clade *Spiraeanthemum* s.s.- brongniartiana group are both well supported (99 and 100 BP).

In the *PHYC* analysis (Fig. 1), *A. densiflora* is again sister to the remaining members of the tribe. *Spiraeanthemum macgillivrayi* is sister to the brongniartiana group represented by *A. brongniartiana*, *A. collina*, *A. elliptica*, *A. pedunculata* and *A. pubescens*.

In the combined analysis (Fig. 1), we recovered the same topology as for the three separate analyses, with a strongly supported (100 BP) *Spiraeanthemeae* structured as followed (*A. densiflora* (*Spiraeanthemum* s.s.; brongniartiana group)) with 100 BP for the brongniartiana group and *Spiraeanthemum* s.s. plus the brongniartiana group. A combined analysis including all taxa for which at least one of the loci was available was also conducted. The topology recovered was identical to the one recovered in the reduced dataset with no missing loci, but bootstrap supports were lower, it is therefore not shown here.

Morphology—Since the phylogenetic analysis suggested that three groups of species could be recognised within *Spiraeanthemum-Acsmithia* (see discussion), morphology is described largely in terms of these groups. Species of *Acsmithia* not included in the phylogenetic analysis were assigned initially to either the brongniartiana group or the densiflora group on the basis of their ovule number.

STIPULES AND APICAL BUDS—Two types of interpetiolar stipules were found, and among the species with small, linear stipules, two types of apical buds occur.

In *Spiraeanthemum* s.s., interpetiolar stipules are large, ovate to oblong-elliptic, and attached broadly at the base. In dormant apical buds, opposite stipules are adpressed around their margins to enclose the developing leaves; after separating, they are caducous or sometimes briefly persistent, and leave a long, curved scar.

In both the *brongniartiana* and *densiflora* groups, interpetiolar stipules are narrowly triangular to linear, with a small attachment at the base (see Rutishauser and Dickison 1989, Figs. 80-82, *A. densiflora*, given as *A. undulata*). Although stipules overtop leaves in small buds (Rutishauser and Dickison 1989), in dormant apical buds they are not contiguous with one another and do not enclose the developing leaves, which are visible between them and larger; as the apical bud starts to develop, stipules are usually fugaceous, leaving a small round or elliptic scar. It appears that stipules are not smaller in these two groups only because whorled phyllotaxis means that more stipules and petioles are present at each node; their shape and persistence differs from those in *Spiraeanthemum s.s.*

Apical buds in both *Spiraeanthemum s.s.* and the *densiflora* group are hairy, whereas in the *brongniartiana* group they are glabrous and varnished except in *A. pubescens*, with some rare exceptions (e.g. *A. pubescens*: *Pancher Mus. Neocal. 191*, some apical buds glabrous and varnished; *A. meridionalis*: *Bernardi 12434*, apical bud hairy with some varnish).

LEAVES—These have either toothed margins and craspedodromous or semicraspedodromous venation, or entire margins with brochidodromous venation. Although distinctive patterns of venation can be picked out, some species or individuals within each group have a more generalized type of venation, so these categories are of only limited use.

Three species in *Spiraeanthemum s.s.* (*S. serratum*, *S. samoensis*, and *S. macgillivrayi*) have markedly serrate margins with numerous teeth and semicraspedodromous venation in which branches of the secondary veins reach the margin at the sinus of a tooth. The secondary veins are numerous, regularly spaced along the midrib, parallel to one another across the blade, and prominent on the abaxial surface; leaf blades are flat. In *S. bougainvillense*, teeth are much smaller and the pattern of secondary veins is less marked, whereas in *S. graeffei* and *S. katakata* margins can be entire or toothed, in which case teeth are small.

In the brongniartiana group, all species have entire margins and brochidodromous venation. Secondary veins are not especially numerous, but they are usually regularly spaced and parallel and either flat or prominent on the abaxial surface; leaf blades are flat or slightly bullate.

In the densiflora group, especially in New Guinea, the leaf margin is commonly entire or sometimes weakly toothed, especially in *A. reticulata*, and venation is brochidodromous to craspedodromous, in which case secondary veins reach the margin at the tip of a tooth. The secondary veins are typically few and irregularly spaced along the midrib, sometimes with weaker veins between them, and they are often not parallel to one another across the blade. Veins are prominent on the abaxial surface, and leaf blades are flat to bullate. Only in *A. davidsonii* are leaves sometimes strongly toothed.

INFLORESCENCES—In all species except *A. davidsonii*, panicles are typically axillary, and in most species they are exclusively axillary, although, especially in the densiflora group in New Guinea, median panicles are also found occasionally. *Acsmithia davidsonii* has predominantly median panicles.

The branching pattern within panicles changes acropetally. In general, branching initially follows the phyllotaxis of the leaves (opposite and decussate in *Spiraeanthemum s.s.* and whorled in *Acsmithia*, but see comments for densiflora group) and switches distally to become \pm alternate or irregular.

Considering only axillary panicles, first branches on the main axis are produced well above the base in *Spiraeanthemum s.s.* and the brongniartiana group. However, in *S. macgillivrayi* subsp. *macgillivrayi*, axillary buds or panicles are occasionally accompanied by additional axillary buds (e.g. *Pillon 570*, *Wheatley 341*), and in the brongniartiana group, leaf axils occasionally contain two panicles in series (e.g. *A. brongniartiana*: *Balansa 2303*, *MacKee 4432*, *15327*, *30991*; *A. meridionalis*: *Bernardi 12434*, *Pancher s.n.*; *A. pubescens*:

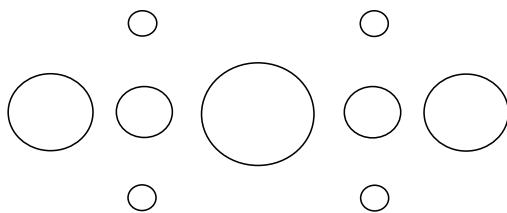
MacKee 37894; A. vitiensis : Horne 1104, 1113). Usually one of these panicles is much larger than the other, giving the appearance of a single panicle that is branched at the base of its main axis.

In the densiflora group (except *A. davidsonii*), first branches of axillary panicles are usually at or just above the base of the main axis, one on either side of it, i.e. these branches appear \pm opposite (possibly by abortion of other branches), rather than whorled. More distal branching is usually whorled and then eventually alternate to irregular. In median panicles in this group, including those of *A. davidsonii*, first branches are well above the base.

The difference between basally branched panicles in the densiflora group and additional axillary panicles in the brongniartiana group is that in the former, first branches are \pm lateral, in a plane perpendicular to that of the leaf axil, whereas in the latter additional axes arising near the base are in the same plane as the axil. However, this difference can only be seen with a binocular microscope.

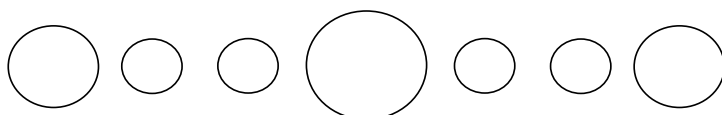
This could be shown diagrammatically (leaves shown as opposite for simplicity) as:

densiflora group:



sequence: petiole, axillary bud with lateral branches, main stem, axillary bud with lateral branches, petiole.

brongniartiana group:



sequence: petiole, 2 axillary buds in series, main stem, 2 axillary buds in series, petiole.

FLOWERS—Although flowers in *Acsmithia* are normally bisexual, some rare exceptions have been found in *A. meridionalis*, in MacKee 42518 and 42993, in which 5 and 15% respectively of flowers lacked carpels (Hoogland ms), as in the male flowers of *Spiraeanthemum s.s.* (fide Smith, 1985).

OVULES AND SEEDS—The number of ovules per carpel correlates strongly with seed morphology (one ovule per carpel and seeds with a flattened wing, or, more than one ovule per carpel and seeds ellipsoid to spindle-shaped).

Species in the brongniartiana group have one ovule per carpel, and mature seeds are ellipsoid or flattened-ellipsoid with a flat, membranous wing at one end or obliquely at one end (see Dickison 1984, Fig. 54 – *A. elliptica*, Fig. 55-56 – *A. pubescens*).

In the densiflora group, the number of ovules is usually two or four (rarely three, five or six), and mature seeds are ellipsoid with a small, thin tail at each end that is easily detached (see Dickison 1984, Fig. 57 – *A. reticulata*). A similar picture is seen in *Spiraeanthemum s.s.* in which number of ovules per carpel is two and mature seeds are spindle-shaped, ellipsoid in middle and tapering gradually towards either end (see Dickison 1984, Fig. 52 – *S. katakata*). However, no real difference exists between seeds in *Spiraeanthemum s.s.* and the densiflora group, although tails are perhaps more ephemeral in the latter.

REJECTED CHARACTERS—Gland dots on the intervenium appear to be present in all species, although they are not always easily seen in old leaves and on old specimens. Domatia occur in the angle between secondary veins and the midrib in all species, although not necessarily on all leaves or all specimens, and in a few species they are small. Some species have additional domatia in the angle between major branches of the secondary veins towards the margin. Domatia vary from simple hair-tufts to pits and pouches (Hopkins and Hoogland 2002, Fig. 3), and, although certain types are more common in certain species, they are too variable to be taxonomically useful. The number of calyx lobes and carpels, form of disc, and

extent to which carpels are connate towards their bases all appear to show more variation within species than between them.

DISCUSSION

Separate and combined analyses of the three DNA regions all showed that two groups can clearly be distinguished within New Caledonian *Acsmithia*. The first consists of *A. densiflora* only and the second (the brongniartiana group) of the remaining species. The brongniartiana group is a well supported, and a more complete analysis (Pillon et al., in prep.) shows that it includes all New Caledonian taxa except *A. densiflora* and *A. austrocaledonica*, which is in fact conspecific with *A. densiflora* (see below). The brongniartiana group and *Spiraeanthemum* s.s. form a well-supported clade to which *A. densiflora* is sister.

Acsmithia densiflora can be distinguished from species of the brongniartiana group by a number of morphological features (Table 2) including number of ovules per carpel. This character was the first used in Hoogland's key to the species of *Acsmithia* (Hoogland 1979) and allows placement of non-New Caledonian species of *Acsmithia* in one or the other group, even though material was not available for molecular analysis.

Acsmithia vitiensis, the only species of *Acsmithia* in Fiji, is morphologically similar to *A. brongniartiana* and like all species of the brongniartiana group has a single ovule per carpel. *Acsmithia pulleana* (type of *Acsmithia*), *A. parvifolia*, *A. integrifolia*, *A. reticulata* (all from New Guinea), and *A. davidsonii* (Australia) have several (two to four or rarely six) ovules per carpel, as in *A. densiflora*.

The two groups within *Acsmithia* also differ in other characters. Members of the densiflora group all have hairy apical buds, whereas in the brongniartiana group apical buds are glabrous and often resinous, with the notable exception of *A. pubescens*. Axillary panicles in the densiflora group are ramified at, or close to, the base (within the first few millimetres),

whereas those in the *brongniartiana* group have a marked peduncle, often extending a third or more of the total length of the panicles. Seeds in the *densiflora* group are ellipsoid with a small tail at either end, whereas those in the *brongniartiana* group are flattened to ellipsoid with a membranous wing at one end.

Within the *densiflora* group, *Acsmithia davidsonii* has several characters that are unusual: leaves are sometimes strongly toothed; panicles are mostly median, and even in axillary ones, the lowest branches are above the base. However, the number of ovules, shape of the seeds, and secondary venation are all consistent with other members of the *densiflora* group.

The morphological survey also confirmed a character shared by the two groups within *Acsmithia* but not by *Spiraeanthemum* that was first noted briefly by Smith (1952). In *Acsmithia* stipules are small and narrowly triangular, whereas in *Spiraeanthemum* s.s. they are larger and broadly ovate to oblong-elliptic. This second type of stipule is common, although not universal, throughout Cunoniaceae (Rutishauser and Dickison 1989).

Evolution of the different characters observed can be tracked by comparing them with the topology observed in the molecular trees. The following characters are homoplasious in *Spiraeanthemeae* and have either evolved twice or are ancestral in the tribe but show a reversal: narrowly triangular stipules, hairy apical buds, whorled leaves, bisexual flowers, multiple ovules per carpel and spindle-shape/ellipsoid seeds. The *densiflora* group has a single autapomorphy, panicles branched near the base, and the clade *Spiraeanthemum* s.s. – *brongniartiana* group is also only characterised by a single character, a clearly pedunculate inflorescence. Autapomorphies for *Spiraeanthemum* s.s. include opposite leaves, ovate-elliptic stipules and dioecy. Autapomorphies for the *brongniartiana* group include glabrous apical buds, a single ovule per carpel, seeds with membranous wings and adaptation to ultramafic soils in New Caledonia. Future biochemical studies may provide further characters

to support these groups, as bioactivity and taxonomy are well correlated within Cunoniaceae (Pillon and Fogliani 2009)

In terms of biogeography, the densiflora group is restricted to the relatively ancient landmasses of New Guinea, Australia and New Caledonia (Fig. 2) and has a distribution comparable to *Dubouzetia* Brong. & Gris (Elaeocarpaceae, Coode 2004) or *Sphenostemon* Baill. (Sphenostemonaceae, Jérémie 1997). The brongniartiana group, restricted to New Caledonia and Fiji (Fig. 2), can be compared to *Acmopyle* Pilg. (Podocarpaceae, de Laubenfels 1996) and can be considered as a typical eastern Melanesia endemic, like *Cyphosperma* H. Wendl. (Arecaceae, Dowe and Cabalion 1996) or *Geissois* Labill. s.s. (Cunoniaceae, Hopkins 2006). *Spiraeanthemum* s.s. has a relatively large distribution covering most islands of the Melanesian arc from New Britain to Fiji and extending to western Polynesia (Samoa) but excluding New Caledonia (Fig. 2): most of these islands have a volcanic origin. Several palm genera show similar distributions, e.g. *Metroxylon* Rottb., *Clinostigma* H. Wendl., and *Physokentia* Becc. (Dowe and Cabalion 1996). *Spiraeanthemum* s.s. reaches its western limit in the Bismarck Archipelago and the Solomon Islands. Another group of Cunoniaceae that reaches its distributional limit here is the Pacific section of *Weinmannia*, sect. *Leiospermum* (D. Don) Engl., but its distribution is wider than that of *Spiraeanthemum* s.s. as it extends eastwards to French Polynesia and southwards to New Caledonia and New Zealand (Hopkins and Bradford 1998).

Acsmithia was created to accommodate species of *Spiraeanthemum* with whorled leaves and hermaphroditic flowers, as opposed to those with opposite leaves and a dioecious sexual system in *Spiraeanthemum* s.s. However, it seems that whorled leaves and hermaphroditism are ancestral characters within the tribe Spiraeanthemeae, and transitions between opposite and whorled leaves have occurred several times in the course of the evolution of Cunoniaceae. For instance, in the New Caledonian endemic genus *Pancheria*

Brong. & Gris, all species have whorled leaves with the exception of *P. confusa* Guillaumin, which has opposite ones. Conversely, all species of *Codia* J.R. Forst. & G. Forst., which is also endemic to New Caledonia, usually have opposite leaves except for *C. albifrons* (Brongn. ex Schinz & Guillaumin) Baker f. and *C. triverticillata* H.C. Hopkins & Pillon in which they are whorled (Hopkins et al. 2007). Whorled leaves are clearly derived when mapped onto a phylogenetic tree of *Codia* (Pillon et al., unpublished), and they have been recorded as a rare occurrence in most taxa in this genus. In *Pullea glabra* Schltr. in New Guinea, both opposite and verticillate leaves occur regularly within a single species, in var. *glabra* and var. *verticillata* Hoogland respectively. Teratological cases are not uncommon in Cunoniaceae, and for example in *Cunonia* L., in which all species normally have opposite leaves, twigs with whorled leaves have been observed on a potted plant of *C. pterophylla* Schltr. (Pillon, pers. obs.). Sexual systems are also labile characters that can show great variability, as seen for instance in *Weinmannia* L. (Hopkins and Bradford 1998), and, furthermore, sexual systems are capable of evolving quickly (e.g. Sakai et al. 1997). Thus phyllotaxis and sexual system, even in combination, can be misleading characters in classification of Cunoniaceae.

The paraphyly of *Acsmithia* implies that taxonomic changes need to be made. Two alternatives are possible: either we could treat tribe Spiraeanthemeae as a single genus, *Spiraeanthemum* s.l., or as three distinct genera: *Spiraeanthemum* s.s., a narrowly defined *Acsmithia* comprising the densiflora group, and an undescribed genus which would contain all New Caledonian and Fijian species except for *A. densiflora*. The first alternative is preferred for several reasons. Firstly, the densiflora and brongniartiana groups are morphologically similar, and differences between them are in characters that are difficult to observe; splitting *Acsmithia* into two would not aid generic identification by a non-specialist nor by anyone without a microscope. Secondly, although *Spiraeanthemum* s.s. and the brongniartiana group each have several synapomorphies, the densiflora group has only one (axillary panicle

branching near base), which is absent in one of its members and can be confused with a similar, though rare, character-state in the *brongniartiana* group. A broad circumscription of *Spiraeanthemum* requires two new combinations, which are proposed below.

TAXONOMIC TREATMENT

SPIRAEANTHEMUM A.Gray, Proc. Amer. Acad. Arts Sci. 3: 128 (1854). —LECTOTYPE (of Smith 1952): *Spiraeanthemum samoense* A.Gray.

Acsmithia Hoogland, Blumea 25: 493 (1979). —TYPE: *Acsmithia pulleana* (Schltr.) Hoogland, *syn. nov.*

Spiraeanthemum collinum (Hoogland) Pillon *comb. nov.* Basionym: *Acsmithia collina*

Hoogland, Bull. Mus. Natl. Hist. Nat. B, Adansonia, 9: 396 (dated 1987, published 1988). —TYPE: NEW CALEDONIA, Mé Maoya, contrefort sud du Djiaouma, 800m, 7 March 1976, *MacKee 30809* (holotype: P!; isotype: CANB, L, MO, NOU!, P, Z).

Spiraeanthemum meridionale (Hoogland) Pillon *comb. nov.* Basionym: *Acsmithia*

meridionalis Hoogland, Bull. Mus. Natl. Hist. Nat. B, Adansonia, 9: 396 (dated 1987, published 1988). —TYPE: NEW CALEDONIA, haute Yaté, Rivière Bleue, 150m, 15 March 1981, *MacKee 388821* (holotype: P!; isotype: L, MO, NOU!, P, Z).

Examination of herbarium material determined by Hoogland as *Acsmithia densiflora* and *A. austrocaledonica* failed to reveal any consistent characters to distinguish between them. In his unpublished manuscript for the “Flore de la Nouvelle-Calédonie et Dépendances” Hoogland mentioned two characters: number of ovules per carpel, given as four or sometimes

three or six in *A. densiflora* and two or sometimes three in *A. austrocaledonica*, and, the stamens, which are generally twice as many as the sepals in *A. densiflora* and generally fewer than twice as many in *A. austrocaledonica*. Both characters are overlapping and difficult to observe. Furthermore both species have the same ecology, distribution, and type locality. We propose here to consider the two species as synonyms.

SPIRAEANTHEMUM DENSIFLORUM Brongn. & Gris, Bull. Soc. Bot. France 9: 74 (1862).

—TYPE: NEW CALEDONIA, Balade, 1855-60, *Vieillard 566* (holotype: P!; isotype: P!).

Spiraeanthemum austrocaledonicum Brongn. & Gris, Bull. Soc. Bot. France 9: 74 (1862). —TYPE: NEW CALEDONIA, Balade, 1855-60, *Vieillard 568* (holotype: P!; isotype: BM, G, K, P), *syn. nov.*

As newly circumscribed, *Spiraeanthemum*, sole genus of Spiraeanthemeae, consists of 19 species, distributed in Australia, Melanesia, and western Polynesia (Table 3).

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LITERATURE CITED

- Bradford, J. C. and R. W. Barnes. 2001. Phylogenetics and classification of Cunoniaceae (Oxalidales) using chloroplast DNA sequences and morphology. *Systematic Botany* 26: 354-385.
- Bradford, J. C., H. C. F. Hopkins, and R. W. Barnes. 2004. Cunoniaceae. *In* K. Kubitzki [ed.], The families and genera of vascular plants, 91-111. Springer, Berlin.
- 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.
- Coode, M. J. E. 2004. Elaeocarpaceae. *In* K. Kubitzki [ed.], The families and genera of vascular plants, 135-144. Springer, Berlin.
- Csiba, L. and M. P. Powell. 2006. DNA extraction protocols. *In* V. Savolainen, M. P. Powell, K. Davis, G. Reeves, and A. Corthals [eds.], DNA and tissue banking for biodiversity and conservation: theory, practice and uses, 48-51. Royal Botanic Gardens, Kew, Richmond.
- De Laubenfels, D. J. 1996. Gondwanan conifers on the Pacific Rim. *In* A. Keast and S. E. Miller [eds.], The origin and evolution of Pacific Islands biotas, New Guinea to Eastern Polynesia: patterns and processes, 261-265. SPB Academic Publishing, Amsterdam.
- Dickison, W. C. 1984. Fruits and seeds of the Cunoniaceae. *Journal of the Arnold Arboretum* 65: 149-190.

- Dowe, J. L. and P. Cabalion. 1996. A taxonomic account of Arecaceae in Vanuatu, with descriptions of three new species. *Australian Systematic Botany* 9: 1-60.
- Emshwiller, E. and J. J. Doyle. 1999. Chloroplast-expressed glutamine synthetase (ncpGS): potential utility for phylogenetic studies with an example from *Oxalis* (Oxalidaceae). *Molecular Phylogenetics and Evolution* 12: 310-319.
- Hoogland, R. D. 1979. Studies in the Cunoniaceae. II. The genera *Caldcluvia*, *Pullea*, *Acsmithia* and *Spiraeanthemum*. *Blumea* 25: 481-505.
- Hopkins, H. C. F. 2006. Nomenclature and typification in *Geissois* (Cunoniaceae) in the South-West Pacific. *Adansonia* 28: 311-327.
- Hopkins, H. C. F. and J. C. Bradford. 1998. A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific. 1. Introduction and an account of the species of Western Malesia, the Lesser Sunda Islands and the Moluccas. *Adansonia* 20: 5-41.
- Hopkins, H. C. F. and R. D. Hoogland. 2002. Cunoniaceae. In H. P. Neteboom [ed.], *Flora Malesiana*, 53-165. Nationaal Herbarium Nederland, Leiden.
- Hopkins, H. C. F., B. Fogliani, and Y. Pillon. 2007. Four new species in the endemic genus *Codia* (Cunoniaceae) from New Caledonia. *Kew Bulletin* 62: 259-274.
- Hufford, L. and W. C. Dickison. 1992. A phylogenetic analysis of Cunoniaceae. *Systematic Botany* 17: 181-200.
- Hyland, B. P. and T. Whiffin. 1993. Australian Tropical Rain Forest Trees, an interactive identification system, vol. 2 : Cunoniaceae. CSIRO, Australia.
- Jérémie, J. 1997. Sphenostemonaceae. In P. Morat [ed.], *Flore de la Nouvelle-Calédonie et Dépendances*, 3-21. Muséum National d'Histoire Naturelle, Paris.
- Mcpherson, G. and P. P. Lowry. 2004. *Hooglandia*, a newly discovered genus of Cunoniaceae from New Caledonia. *Annals of the Missouri Botanical Garden* 91: 260-265.

- Pillon, Y. and B. Fogliani. 2009. Evidence for a correlation between phylogeny and bioactivity in New Caledonian Cunoniaceae and its implications for screening and conservation. *Pacific Science* 63: 97-103.
- Pillon, Y., M. F. Fay, M. Hedrén, R. M. Bateman, D. S. Devey, A. B. Shipunov, M. Van Der Bank, and M. W. Chase. 2007. Evolution and temporal diversification of western European polyploid species complexes in *Dactylorhiza* (Orchidaceae). *Taxon* 56: 1185-1208.
- Rutishauser, R. and W. C. Dickison. 1989. Developmental morphology of stipules and systematics of the Cunoniaceae and presumed allies. I. Taxa with interpetiolar stipules. *Botanica Helvetica* 99: 147-169.
- Sakai, A. K., S. G. Weller, W. L. Wagner, P. S. Soltis, and D. E. Soltis. 1997. Phylogenetic perspectives on the evolution of dioecy: adaptive radiation in the endemic Hawaiian genera *Schiedea* and *Alsinosdendron* (Caryophyllaceae: Alsinoideae). In T. J. Givnish and K. J. Sytsma [eds.], *Molecular Evolution and Adaptive Radiation*. Cambridge University Press, Cambridge.
- Samuel, R., H. Kathriarachchi, P. Hoffmann, M. H. J. Barfuss, K. J. Wurdack, C. C. Davis, and M. W. Chase. 2005. Molecular phylogenetics of Phyllanthaceae: evidence from plastid *matK* and nuclear *PHYC* sequences. *American Journal of Botany* 92: 132-141.
- Smith, A. C. 1952. Studies of Pacific Island plants, XII, the Cunoniaceae of Fiji and Samoa. *Journal of the Arnold Arboretum* 33: 119-149.
- Smith, A. C. 1985. Cunoniaceae. In A. C. Smith [ed.], *Flora Vitiensis Nova*. A new flora of Fiji, 5-26. Pacific Tropical Botanical Garden, Kauai.
- Sweeney, P. W., J. C. Bradford, and P. P. Lowry II. 2004. Phylogenetic position of the New Caledonian endemic genus *Hooglandia* (Cunoniaceae) as determined by maximum

parsimony analysis of chloroplast DNA. *Annals of the Missouri Botanical Garden* 91: 266-274.

Swofford, D. L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (and Other Methods) 4.0 Beta. Florida State University.

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.

APPENDIX. List of taxa, country of collection, voucher reference (voucher location) and GenBank accession number for *trnL*, *PHYC* and *ncpGS*.

Brunellia colombiana Cuatrec., Colombia, *Bradford* 753 (MO), AF299187 & AF299240, —, —; *Brunellia mexicana* Standl., Mexico, *Salazar s.n.* (MEXU), —, EU867237, EU867247; *Hooglandia ignambiensis* McPherson & Lowry, New Caledonia, *Lowry* 5767 [Type] (CANB,G,MO,NOU,P), AY549639 & AY549640, EU867229, EU867239; *Platylophus trifolius* (L. f.) D. Don, South Africa, *Goldblatt* 10888 (MO), AF299177 & AF299230, —, —; *Platylophus trifolius* (L. f.) D. Don, South Africa, *Chase* 5726 (K), —, EU867228, EU867238; *Spiraeanthemum brongniartianum* Schltr., New Caledonia, *Pillon et al.* 87 (K,MO,NOU,P), EU867221, EU867231, EU867240; *Spiraeanthemum collinum* (Hoogland) Pillon, New Caledonia, *Pillon et al.* 464 (K,NOU,P), —, EU867233, —; *Spiraeanthemum densiflorum* Brongn. & Gris, New Caledonia, *Pillon* 667 (NOU), EU867225, EU867235, EU867243 & EU867244; *Spiraeanthemum densiflorum* Brongn. & Gris, New Caledonia, *Munzinger et al.* 4575 (K,MO,NOU,P), EU867226, —, —; *Spiraeanthemum ellipticum* Vieill. ex Pamp., New Caledonia, *Pillon et al.* 20 (K,NOU,P), EU867222, EU867230, —; *Spiraeanthemum macgillivrayi* Seem. subsp. *macgillivrayi*, Vanuatu, *Pillon et al.* 570 (K,MO,NOU,P,PVNH), EU867227, EU867236, EU867245; *Spiraeanthemum macgillivrayi* Seem. subsp. *macgillivrayi*, Vanuatu, *Pillon et al.* 525 (NOU,P), —, —, EU867246; *Spiraeanthemum meridionale* (Hoogland) Pillon, New Caledonia, *Pillon et al.* 1 (NOU), EU867223, —, —; *Spiraeanthemum pedunculatum* Schltr., New Caledonia, *Pillon et al.* 437 (NOU), —, EU867234, —; *Spiraeanthemum pubescens* Pamp., New Caledonia, *Pillon & Munzinger* 82 (K,NOU,P), EU867224, EU867232, EU867241 & EU867242; *Spiraeanthemum samoense* A. Gray, Samoa, *Bradford* 809 (MO,NOU), AF299160 & AF299213, —, —

TABLE 1. Statistics for each DNA sequences used in the phylogenetic analysis of the tribe Spiraeanthemeae.

	<i>trnL</i>	<i>PHYC</i>	<i>ncpGS</i>	combined
# Taxa	11	10	10	7
# Characters	952	650	1254	2856
# Constant characters	880	586	1022	2503
# Variable characters	72 (7.5%)	64 (9.8%)	232 (18.5%)	353 (12.6%)
# Parsimony informative characters	20 (2.1%)	21 (3.1%)	107 (8.5%)	114 (4%)
# Tree	13	2	1	1
Consistency Index	0.988	0.985	0.953	0.969
Retention Index	0.97	0.979	0.93	0.928

TABLE 2. Comparative morphology between the different species and species group of *Acsmithia* and *Spiraeanthemum*. Rare occurrences are given in brackets. A=axillary, M=median. ?=see text.

species	stipules	apical bud	Number of leaves per node	leaf margin	position of panicles	branching in axillary panicles	additional axillary buds	sexual expression	Number ovules per carpel	seed shape
densiflora group										
densiflora	narrowly triangular	hairy	3	entire	A	near base	no	bisexual	4 (to 6)	ellipsoid with tails
integrifolia	narrowly triangular	hairy	3 or 4	entire	A + M	near base	no	bisexual	4	not seen
parvifolia	narrowly triangular	hairy	3 (4)	entire	A + M	near base	no	bisexual	2	ellipsoid with tails
pulleana	narrowly triangular	hairy	3 or 4	mostly entire toothed to \pm	A (M)	near base	no	bisexual	2 (3)	ellipsoid with tails
reticulata	narrowly triangular	hairy	3 or 4	entire	A	near base above	no	bisexual	2 (3)	ellipsoid with tails
davidsonii	narrowly triangular	hairy	3 (4)	toothed	M (A)	base	no	bisexual	2 to 4	ellipsoid with tails
brongniartiana group										
brongniartiana	narrowly triangular	glabrous/varnished	3 (4)	entire	A	above base	yes?	bisexual	1	with membranous wing
collina	narrowly triangular	glabrous/varnished	3 to 5	entire	A	above base	no	bisexual	1	with membranous wing
elliptica	narrowly triangular	glabrous/varnished	4	entire	A	above base	no	bisexual	1	with membranous wing
meridionalis	narrowly triangular	glabrous/varnished	4 (5)	entire	A	above base	yes?	bisexual	1	with membranous wing
pedunculata	narrowly triangular	glabrous/varnished	4	entire	A	above base	no	bisexual	1	with membranous wing
pubescens	narrowly triangular	hairy	4	entire	A	above base	no	bisexual	1	with membranous wing
vitiensis	narrowly triangular	glabrous/varnished	3 or 4 (5)	entire	A	base	yes?	bisexual	1	with membranous wing
Spiraeanthemum s.s.										

bougainvillense	ovate-elliptic	hairy	2	toothed	A	above base	no	dioecious	2	spindle-shaped / ellipsoid
macgillivrayi	ovate-elliptic	hairy	2	toothed	A	above base	yes	dioecious	2	spindle-shaped / ellipsoid
graeffei	ovate-elliptic	hairy	2	toothed to entire entire to \pm	A	above base	no	dioecious	2	spindle-shaped / ellipsoid
katakata	ovate-elliptic	hairy	2	toothed	A (M)	above base	no	dioecious	2	spindle-shaped / ellipsoid
serratum	ovate-elliptic	hairy	2	toothed	A	above base	no	dioecious	2	spindle-shaped / ellipsoid
samoensis	ovate-elliptic	hairy	2	toothed	A	above base	no	dioecious	2	spindle-shaped / ellipsoid

TABLE 3. List of taxa currently accepted in the genus *Spiraeanthemum*. Species belonging to *Spiraeanthemum s.s.*, the *densiflorum* and *brongniartianum* group are marked with a S, D and B respectively.

Australia
<i>Spiraeanthemum davidsonii</i> F. Muell. [D]
New Guinea and Moluccas
<i>Spiraeanthemum integrifolium</i> Pulle [D]
<i>Spiraeanthemum parvifolium</i> Schltr. [D]
<i>Spiraeanthemum pulleana</i> Schltr. [D]
<i>Spiraeanthemum reticulatum</i> Schltr. [D]
Solomon Islands, New Britain, New Ireland and Bougainville
<i>Spiraeanthemum bougainvillense</i> Hoogland [S]
<i>Spiraeanthemum macgillivrayi</i> Seem. subsp. <i>kajewskii</i> (Perry) Hoogland [S]
Vanuatu
<i>Spiraeanthemum macgillivrayi</i> Seem. subsp. <i>macgillivrayi</i> [S]
New Caledonia
<i>Spiraeanthemum brongniartianum</i> Schltr. [B]
<i>Spiraeanthemum collinum</i> (Hoogland) Pillon [B]
<i>Spiraeanthemum densiflorum</i> Brongn. & Gris [D]
<i>Spiraeanthemum ellipticum</i> Vieill. ex Pamp. [B]
<i>Spiraeanthemum meridionale</i> (Hoogland) Pillon [B]

Spiraeanthemum pedunculatum Schltr. [B]

Spiraeanthemum pubescens Pamp. [B]

Fiji

Spiraeanthemum graeffei Seem. [S]

Spiraeanthemum katakata Seem. [S]

Spiraeanthemum serratum Gillespie [S]

Spiraeanthemum vitiense A. Gray [B]

Samoa

Spiraeanthemum samoense A. Gray [S]

trnL

8 *Platylophus trifolius*
6 99 15 *Hooglandia ignambiensis*
1 *Acsmithia brongniartiana*
1 *Acsmithia elliptica*
1 67 1 *Acsmithia meridionalis*
3 94 *Acsmithia pubescens*
2 *Spiraeanthemum macgillivrayi*
2 91 4 *Spiraeanthemum samoense*
1 *Acsmithia densiflora* YP667
2 89 5 *Acsmithia densiflora* JM4575
22 7 100
Brunellia colombiana

ncpGS

40 *Platylophus trifolius*
18 100 41 *Hooglandia ignambiensis*
6 *Acsmithia brongniartiana*
4 99 8 *Acsmithia pubescens* allele 1
100 3 *Acsmithia pubescens* allele 2
12 100 1 *Spiraeanthemum macgillivrayi* YP570
11 100 2 *Spiraeanthemum macgillivrayi* YP525
16 100 *Acsmithia densiflora* allele 1
1 *Acsmithia densiflora* allele 2
47 40 100
Brunellia mexicana

PHYC

8 *Platylophus trifolius*
3 96 10 *Hooglandia ignambiensis*
1 *Acsmithia elliptica*
1 *Acsmithia brongniartiana*
5 98 2 *Acsmithia pedunculata*
1 *Acsmithia pubescens*
2 86 1 *Acsmithia collina*
7 *Spiraeanthemum macgillivrayi*
4 *Acsmithia densiflora*
13 11 100
Brunellia mexicana

Combined

56 *Platylophus trifolius*
27 100 66 *Hooglandia ignambiensis*
8 *Acsmithia brongniartiana*
10 100 9 *Acsmithia pubescens*
18 100 23 *Spiraeanthemum macgillivrayi*
23 *Acsmithia densiflora*
80 57 100
Brunellia

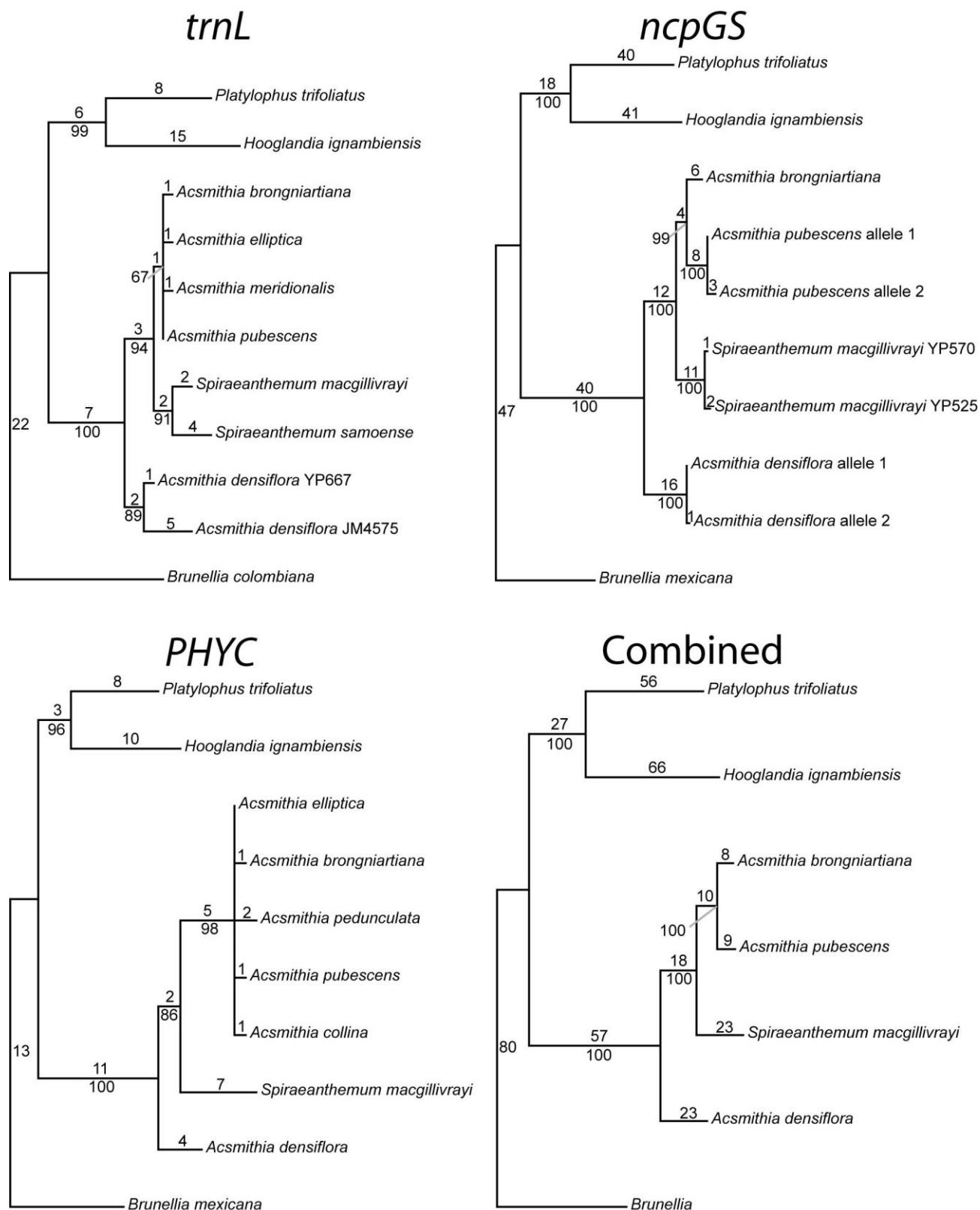


FIG. 2. Distribution of the *Acsmithia densiflora* group, the *Acsmithia brongniartiana* group and *Spiraeanthemum* s.s.

