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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 Spiraeantheae (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 australocaledonicum* 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 *Spiraeanthemaeae* 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
(ncpGS), a nuclear single-copy gene, was amplified using the primers 687F and 994R of Emshwiller and Doyle (1999). PCR reaction mix included 45 μL of 2.5 mM MgCl$_2$ Reddy PCR Master Mix 1.1× (ABgene Ltd, Surrey, U.K.), 1 μL of 0.4% bovine serum albumin (BSA), 0.5 μL of each primer (100 ng/μL) and 3 μL 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 μL of 1.5 mM MgCl$_2$ Reddy PCR Master Mix 1.1× (ABgene Ltd), 1.5 μL of 0.4% bovine serum albumin (BSA), 0.5 μL of each primer (100 ng/μL), 1 μL of DMSO and 2 μL 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 (Swoford 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 (× 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 Spiraeanthemaeae, 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) *Spiraeanthemeeae* structured as followed (*A. densiflora* (*Spiraeanthemum s.s.;* brongniartiana group)) with 100 BP for the brongniartiana group and *Spiraeanthemum s.s.* plus the brongnartiana 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 ± 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 ± 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 ± 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:

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

brongniartiana group:

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    o o o o o o o
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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 Spiraeanthemaeae 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 *brongniatiana* 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 Spiraeanthemeeae, 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. al bifrons* (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 *Spiraeanthemae* 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**


Hoogland, syn. nov.

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


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.


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


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

**Acknowledgments**—We wish to thank all staff and students of the Botanical Laboratory at IRD for assistance in the field. We also thank the organisers of the Santo 2006 expedition in Vanuatu during which material of *Spiraeanthemum macgillivrayi* was collected, Gerardo Salazar for collecting *Brunellia*, and Pete Lowry and the Missouri DNA bank for providing material of *Hooglandia*. We are grateful to Edith Kapinos, Laszlo Csiba, Olivier Maurin, Dion Devey, and Martyn Powell for their help in the Jodrell Laboratory and to Laura Kelly, Maria Vorontsova, and Jim Clarkson for discussion on nuclear-single copy genes. Completion of the study in Nouméa was made possible by Michel Lebrun, who allowed access to the molecular platform, and the help of Céline Gomez and Emeline Lhuillier. Anaïs Cardineau and Cyril Poullain (CNRS) provided a Macintosh computer to complete data
analysis. We thank two anonymous reviewers and the editors for their helpful comments on this manuscript.

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


*Platylophus trifoliatus* (L. f.) D. Don, South Africa, *Goldblatt 10888* (MO), AF299177 & AF299230, —, —; *Platylophus trifoliatus* (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, —, —;

Table 1. Statistics for each DNA sequences used in the phylogenetic analysis of the tribe Spiraeanthemae.

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

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

*Spiraeanthemum s.s.*
<table>
<thead>
<tr>
<th>Species</th>
<th>Leaf Shape</th>
<th>Leaf Margin</th>
<th>Leaves</th>
<th>Stamen</th>
<th>Anther Location</th>
<th>Sex</th>
<th>Stamens</th>
<th>Petal Shape</th>
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<tbody>
<tr>
<td>bougainvillense</td>
<td>ovate-elliptic</td>
<td>hairy</td>
<td>2</td>
<td>toothed</td>
<td>A</td>
<td>no</td>
<td>dioecious</td>
<td>spindle-shaped / ellipsoid</td>
</tr>
<tr>
<td>macgilivrayi</td>
<td>ovate-elliptic</td>
<td>hairy</td>
<td>2</td>
<td>toothed</td>
<td>A</td>
<td>yes</td>
<td>dioecious</td>
<td>spindle-shaped / ellipsoid</td>
</tr>
<tr>
<td>graeffei</td>
<td>ovate-elliptic</td>
<td>hairy</td>
<td>2</td>
<td>toothed to entire</td>
<td>A</td>
<td>no</td>
<td>dioecious</td>
<td>spindle-shaped / ellipsoid</td>
</tr>
<tr>
<td>katakata</td>
<td>ovate-elliptic</td>
<td>hairy</td>
<td>2</td>
<td>toothed</td>
<td>A (M)</td>
<td>no</td>
<td>dioecious</td>
<td>spindle-shaped / ellipsoid</td>
</tr>
<tr>
<td>serratum</td>
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<td>2</td>
<td>toothed</td>
<td>A</td>
<td>no</td>
<td>dioecious</td>
<td>spindle-shaped / ellipsoid</td>
</tr>
<tr>
<td>samoensis</td>
<td>ovate-elliptic</td>
<td>hairy</td>
<td>2</td>
<td>toothed</td>
<td>A</td>
<td>no</td>
<td>dioecious</td>
<td>spindle-shaped / ellipsoid</td>
</tr>
</tbody>
</table>
TABLE 3. List of taxa currently accepted in the genus *Spiraeanthemum*. Species belonging to *Spiraeanthemum s.s.*, the *densiflorum* and *brongniarianum* group are marked with a S, D and B respectively.

Australia

*Spiraeanthemum davidsonii* F. Muell. [D]

New Guinea and Moluccas

*Spiraeanthemum integrifolium* Pulle [D]
*Spiraeanthemum parvifolium* Schltr. [D]
*Spiraeanthemum pulleana* Schltr. [D]
*Spiraeanthemum reticulatum* Schltr. [D]

Solomon Islands, New Britain, New Ireland and Bougainville

*Spiraeanthemum bougainvillense* Hoogland [S]
*Spiraeanthemum macgillivrayi* Seem. subsp. *kajewskii* (Perry) Hoogland [S]

Vanuatu

*Spiraeanthemum macgillivrayi* Seem. subsp. *macgillivrayi* [S]

New Caledonia

*Spiraeanthemum brongniarianum* Schltr. [B]
*Spiraeanthemum collinum* (Hoogland) Pillon [B]
*Spiraeanthemum densiflorum* Brongn. & Gris [D]
*Spiraeanthemum ellipticum* Vieill. ex Pamp. [B]
*Spiraeanthemum meridionale* (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]
FIG 1. Strict consensus trees of most parsimonious trees resulting from phylogenetic analyses of *trnL*, *ncpGS*, *PHYC*, and combined data. Numbers above branches are branch lengths, and numbers below branches are bootstrap percentages.
FIG. 2. Distribution of the *Acsmithia densiflora* group, the *Acsmithia brongniartiana* group and *Spiraeanthemum s.s.*