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MOLECULAR STUDIES OF SUBFAMILY GILLIESIOIDEAE (ALLIACEAE)

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ABSTRACT

We present an analysis of relationships in Gilliesioideae (Alliaceae) based on a combined matrix of plastid *rbcL*, the *trnL* intron, the *trnL*-F intergenic spacer, and the *rps16* intron and nuclear ITS ribosomal DNA sequences. The results are generally congruent with previous analyses, indicating two well-supported groups: *Ipheion* plus allied genera (“*Ipheiae*” ined.) and Gilliesiae. They also provide higher bootstrap support for many patterns of relationships. Polyphyly of *Ipheion* and *Nothoscordum* is confirmed. Increased taxon sampling (particularly in Gilliesiae) and additional molecular data would be desirable to provide further resolution and to allow an appropriate taxonomic revision to be made.

Key words: *Ipheion*, *Leucocoryne*, *Nothoscordum*, *Tristagma*.

INTRODUCTION

Alliaceae Batsch ex Borkh. are a family of Asparagales Bromhead sensu Angiosperm Phylogeny Group (APG; 1998). They consist of ca. 14 genera and 600 species of bulbous or rhizomatous geophytes characterized by an umbel-like inflorescence subtended by two spathe-like bracts (sometimes fused), a superior ovary, a solid style, and the frequent occurrence of alliaceous chemistry. Alliaceae are most closely related to Amaryllidaceae J. St.-Hil. and the monogeneric Agapanthaceae F. Voigt. In APG II (2003) these three families were combined, with the three family names being “bracketed” under the oldest, Alliaceae. For bracketed names, APG II permits the recognition of the smaller units; here we use Alliaceae in the narrow sense (as in APG 1998) to allow more accurate descriptions of the clades.

Agapanthaceae have frequently been included in Alliaceae (e.g., Dahlgren et al. 1985), but phylogenetic analyses of molecular data from *rbcL* (Fay and Chase 1996), *rbcL* plus the *trnL* intron and the *trnL*-F intergenic spacer (together called *trnL*-F in this paper) (Meerow et al. 1999) and *rbcL*, *trnL*-F, and *atpB* (Fay et al. 2000) have demonstrated that *Agapanthus* L'Hér. falls outside Alliaceae. Fay and Chase (1996) transferred *Agapanthus* to Amaryllidaceae, with which it was placed in analyses of *rbcL* data alone. However, in combined molecular analyses (Fay et al. 2000), although the clade consisting of Alliaceae, Amaryllidaceae, and *Agapanthus* was strongly supported, and each of these three groups was also strongly supported, the relationships between them were not resolved, with *Agapanthus* placed as sister to either Amaryllidaceae or Alliaceae plus Amaryllidaceae. For these reasons, and because *Agapanthus* lacks some highly characteristic features of Alliaceae, such as the possession of a solid style (Rudall et al. 2002), we here exclude *Agapanthus* from Alliaceae.

The analyses of Fay and Chase (1996), Fay et al. (2000) and Pires et al. (2001) also indicated that the cormous taxa previously often treated as tribe Brodiaeae Traub of Alliaceae, e.g., by Dahlgren et al. (1985), were more closely related to other asparagalean families, including Hyacintha-

ceae Batsch ex Borkh. On the basis of these results, Fay and Chase (1996) resurrected Themidaceae Salisb. for this group. A suite of morphological and anatomical characters, including corms vs. bulbs, absence of membranous sheathing leaf bases, three or more spreading bracts vs. a spatheous involucre of two (sometimes fused) bracts, and hollow style vs. solid style, add support to this separation of Themidaceae from Alliaceae (e.g., Hoover 1939). Themidaceae have been recognized in most subsequent treatments (Rahn 1998a, b; APG 1998; Thorne 2000; Chase et al. 2000). In APG II (2003), Themidaceae were bracketed under Asparagaceae Juss. s.l. together with six other families.

On account of its alliaceous odor the enigmatic genus *Hesperocallis* A. Gray has been included either in Alliaceae (e.g., Traub 1968) or in a monotypic family Hesperocallidaceae Traub allied to Alliaceae (Traub 1972b, 1982). However, other authors (e.g., Cave 1948, 1970; Dahlgren et al. 1985) have suggested an affinity with Agavaceae Dumort. sensu APG (1998) or Hemerocallidaceae R. Br. (Hutchinson 1934, 1959). Molecular data have recently indicated a close relationship with *Agave* L. (Pires et al. 2004), and *Hesperocallis* is thus a member of Agavaceae or Asparagaceae sensu APG II (2003).

Fay and Chase (1996) subdivided Alliaceae s.s. (i.e., excluding *Agapanthus* and Brodiaeae) into three subfamilies: Allioideae Herb. (northern hemisphere), Gilliesioideae (Lindl.) Arn. (mostly southern South America, but with *Nothoscordum* Kunth extending into North America), and Tulbaghioidae (Endl. ex Meisn.) M. F. Fay & M. W. Chase, (southern Africa).

Allioideae consist of the north temperate *Allium* L. s.l. (including *Nectaroscordum* Lindl., *Caloscordum* Herb., and *Milula* Prain) and are sister to the other two subfamilies (Fay and Chase 1996; Fay et al. 1997; Meerow et al. 1999; Fay et al. 2000). *Allium dregeanum* Kunth from South Africa is the only member of the subfamily native to the southern hemisphere (e.g., De Sarker et al. 1997). Members of this subfamily differ from other Alliaceae in the possession of a gynobasic style (e.g., Di Fulvio 1973; Rudall et al. 2002). *Nectaroscordum* has been segregated from *Allium* by many

authors on the basis of a semi-inferior ovary, but some (e.g., Traub 1972a) have included it in *Allium*. Molecular analyses of plastid DNA (Fay and Chase 1996; Friesen et al. 2000) and the internal transcribed spacer (ITS) of nuclear ribosomal DNA (Dubouzet and Shinoda 1998) have shown *Nectoscordum* to be embedded within *Allium*. *Caloscordum* has been treated as a distinct genus on the basis of the shape of its floral tube, the deeply inserted filaments without membranous appendages, a withering style, recurring lobes of the perianth, and a lack of alliaceous chemistry (Herbert 1844; Lindley 1847). *Caloscordum* has been included in *Nothoscordum*, but anatomy indicates a relationship with *Allium* rather than to *Nothoscordum* as the style is gynobasic (Lindley 1847; Hanelt et al. 1991). Other authors have included *Caloscordum* in *Allium* (e.g., Li et al. 1996), and molecular studies supported this relationship (Dubouzet and Shinoda 1998). Molecular studies have also shown *Milula*, which possesses a dense raceme instead of the characteristic umbel-like inflorescence, to be embedded in *Allium* (Friesen et al. 2000).

Tulbaghioideae, consisting of *Tulbaghia* L. alone, are rhizomatous herbs from southern Africa. The flowers have a corona (e.g., Burbidge 1978; Snijman 2000). With the exception of *Allium dregeanum*, they are the only members of Alliaceae in sub-Saharan Africa. Tulbaghioideae are sister to Gilliesioideae (Fay and Chase 1996; Meerow et al. 1999; Fay et al. 2000).

Gilliesioideae, comprising all New World genera except *Allium*, are bulbous herbs. All genera are exclusively South American, with a concentration in southern Chile and Argentina, except *Nothoscordum*, which is widespread in South America but has some species that extend to North America. Most authors (e.g., Fay and Chase 1996; Rudall et al. 2002) have recognized two groups within Gilliesioideae: (1) a group with actinomorphic flowers, sometimes referred to as tribe Ipheieae although this name does not appear to have been published, including *Ipheion* Raf., *Nothoscordum*, and *Leucocoryne* s.l. (sensu Rahn 1998a; including *Pabellonia* Quezada & Martic. and *Stemmatium* Phil. sampled here); and (2) tribe Gilliesieae Lindl. (*Gilliesia* Lindl. and allies) with zygomorphic flowers. Gilliesieae are mostly Chilean endemics; they are relatively rarely represented in herbaria, and are generally not available in cultivation (Zöllner and Arriagada 1998; M. F. Fay unpubl. obs.).

Generic delimitation has been considered somewhat problematic in Gilliesioideae, and many species have been variously treated as members of several different genera. For example, *Ipheion uniflorum* (Lindl.) Raf. has been included in *Beauverdia* Herter, *Brodiaea* Sm., *Hookera* Salisb., *Leucocoryne* Lindl., *Milla* Cav., *Tristagma* Poepp., and *Triteleia* Douglas ex Lindl., and *Nothoscordum fragrans* Kunth has been included in *Allium*, *Geboscon* Raf., *Hesperocles* Salisb., *Maligia* Raf., *Milla*, *Ornithogalum* L., and *Sowerbaea* Sm. Referring to *Ipheion sellowianum* (Kunth) Traub and *I. dialystemon* Guaglianone, Mathew (1995) stated that "these differ most noticeably from the blue *I. uniflorum* in having bright yellow flowers and, in fact, these 'ipheions' are probably better referred to as species of *Nothoscordum*." Both *Ipheion* and *Nothoscordum* were shown to be polyphyletic by Fay et al. (1997) using combined sequence data for *rbcL* and the *trnL-F* region. The delimitation of genera in the

Ipheion/Nothoscordum complex remains one of the major unresolved issues in Alliaceae. In this paper we present further molecular studies of Alliaceae, with an emphasis on clarifying generic relationships within Gilliesioideae. Here we present an analysis of combined *rbcL*, *trnL-F*, *rps16* intron, and ITS sequence data with increased taxon sampling compared to our earlier analyses.

MATERIALS AND METHODS

Species used for this study are similar to those in previous papers (Chase et al. 1995; Fay and Chase 1996; Meerow et al. 1999; Chase et al. 2000; Fay et al. 2000). A full table of taxa including voucher information and GenBank accession numbers will be provided in a future paper. Methods of sequence production have varied greatly over time; primers and protocols can be found in studies of the individual loci (see Chase et al. [2006] for general comments, and Taberlet et al. [1991] for the *trnL-F* region, Oxelman et al. [1997] for *rps16*, and Baldwin [1992] for ITS). The combined matrix included 23 taxa (21 members of Gilliesioideae, *Tulbaghia*, and *Agapanthus*). *Agapanthus* was defined as the outgroup based on the results of Fay and Chase (1996), Meerow et al. (1999), and Fay et al. (2000). Allioideae were excluded from these analyses, due to problems with alignment of *trnL-F* and ITS sequences for this subfamily with Gilliesioideae, *Tulbaghia*, and *Agapanthus* (Fay et al. 2000 for *trnL-F*; this paper for ITS).

We analyzed the combined matrix using the branch and bound search option of PAUP* vers. 4.0b10 (Swofford 2001). We then used bootstrapping to estimate internal support with 1000 replicates of simple taxon addition, again using the branch and bound option. We show a randomly selected single tree to illustrate branch lengths (DELTRAN optimization due to problems with ACCTRAN optimization in PAUP* vers. 4.0b10) and indicate groups not found in the strict consensus with arrows. We report all bootstrap support (BS) >50%.

RESULTS

The combined matrix consisted of 4480 characters of which 232 were excluded (mostly at the beginnings and ends of the four loci). Of the remaining 4148 characters, 791 were variable and 454 were potentially parsimony informative. The combined analysis gave eight equally parsimonious trees of Fitch length 1249 steps, consistency index 0.77, and retention index 0.80. One of the trees is shown in Fig. 1 (with bootstrap percentages), with arrows indicating branches that do not occur in the strict consensus tree. The trees were generally well resolved, with the only polytomy being found in one clade of four species of *Nothoscordum*.

Agapanthus was defined as the outgroup, and *Tulbaghia* (Tulbaghioideae) fell as sister to Gilliesioideae. Gilliesioideae were strongly supported as monophyletic (100% BS). Within Gilliesioideae, the genera with zygomorphic flowers (tribe Gilliesieae, represented here by *Gilliesia* and *Solaria* Phil.) formed a well-supported clade (100% BS). The genera with actinomorphic flowers (*Ipheion* and allies) also formed a well-supported clade (100% BS), in which *Ipheion* and *Nothoscordum* were both shown to be biphyletic. One clade of *Ipheion* (the species with yellow flowers) was intercalated

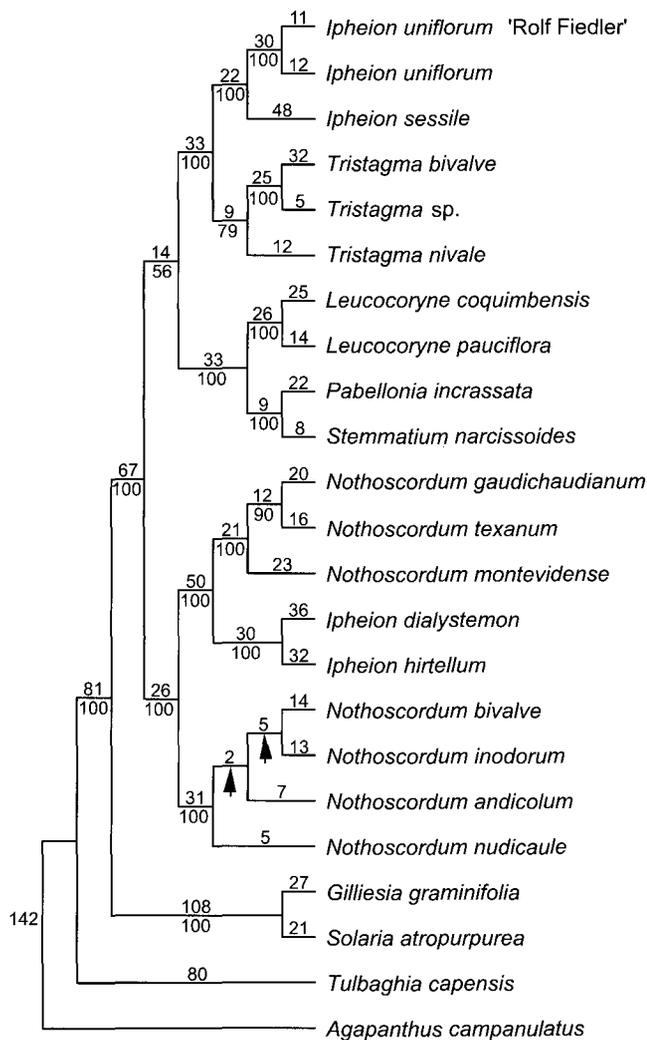


Fig. 1.—One of eight most-parsimonious trees from the combined analysis, tree length 1249 steps, consistency index 0.77, retention index 0.80. Branch lengths are given above the lines, bootstrap percentages >50% below. Arrows indicate the two branches that do not occur in the strict consensus tree.

between the two clades of *Nothoscordum*, and species of *Leucocoryne* s.l., *Nothoscordum*, and *Tristagma* were intercalated between the two clades of *Ipheion*. In both cases, the lack of monophyly was supported by high bootstrap percentages. *Tristagma* was shown to be monophyletic, with intermediate BS (79%). *Leucocoryne* s.l. was placed as sister to the blue/white flowered *Ipheion* spp. plus *Tristagma*, but this relationship gained only weak support (56%). At this level of sampling in *Leucocoryne* s.l., the taxa with six stamens (*Pabellonia* and *Stematium*) formed a clade sister to *Leucocoryne* s.s.

DISCUSSION

The regions of DNA used in this study were all easily alignable across the included taxa, but it was not possible to include *Allium* (Allioideae) due to a large insertion and a large deletion in the *trnL-trnF* intergenic spacer and markedly divergent ITS sequences in *Allium* relative to the other taxa in Alliaceae and *Agapanthus*. These features made se-

quence alignment difficult or impossible. However, other analyses with length-conserved regions of DNA demonstrate the monophyly of Alliaceae, with Allioideae sister to Tulbaghioideae plus Gilliesioideae (e.g., Fay and Chase 1996). Here we focus on relationships in Gilliesioideae.

Our results agree with those from other studies that demonstrate two clearly marked groups within Gilliesioideae. Sampling within Gilliesioideae remains poor, as a result of the difficulty in obtaining material of these little-known plants. Thus we are unable to comment on an appropriate taxonomic treatment for the members of this tribe. Some genera are of uncertain affinity within the subfamily, and increased sampling is necessary to resolve these questions. Despite some obvious differences in floral structure (Rudall et al. 2002), the level of sequence divergence between *Gilliesia* and *Solaria* is low compared to that found in the *Ipheion/Nothoscordum* group; increased sampling might improve our understanding of the number of genera that should be recognized. This is currently somewhat variable. For example, Rahn (1998a) treated *Ancrumia* Harvey ex Baker and *Gethyum* Phil. as synonyms of *Solaria*, in contrast to Zöllner and Arriagada (1998) and Rudall et al. (2002), who treated *Ancrumia* and *Gethyum* as separate genera. Inclusion of other South American genera of Alliaceae, such as *Schickendanziiella* (Speg.) Speg., *Speea* Loes., and *Trichlora* Baker (listed as Gilliesioideae of uncertain placement by Rudall et al. 2002) would aid our understanding of this subfamily if material becomes available.

As stated by Fay et al. (1997), neither *Ipheion* nor *Nothoscordum* as currently circumscribed is monophyletic, and this will result in some taxonomic rearrangements. All species with only one flower per umbel have been considered members of *Ipheion*, but this analysis shows the emphasis on this single character to be unjustified. With this level of sampling, flower color among these uniflorous species seems to be more important, with the blue-flowered species falling with *Tristagma* and the yellow-flowered species falling with one group of *Nothoscordum*, some of which are also yellow flowered. However, the relatively low taxon sampling combined with the lack of strong support for one critical branch defining relationships between the genera, namely the branch indicating a relationship between the blue-flowered *Ipheion* plus *Tristagma* with *Leucocoryne* s.l., means that taxonomic rearrangement may be premature. The taxonomic history of these taxa is already complex, and adding a further set of names at this stage would make it more so. Inclusion of other taxa (e.g., the genera treated as synonyms by Rahn (1998a) including *Zoellnerallium* Crosa [= *Nothoscordum*], and *Garaventia* Looser and *Steinmannia* Phil. [= *Tristagma*]) would be desirable. Taxonomic changes will be the subject of a future paper.

Lack of unambiguous morphological characters supporting the subgroups within the clade composed of *Ipheion*, *Nothoscordum*, and allies is also a problem. Single-flowered inflorescences have evolved at least twice, and reduction in stamen number appears to be a unique character in *Leucocoryne* s.s. Other species of *Leucocoryne* s.l. (e.g., *L. narcissoides* Phil. = *Stematium narcissoides* Phil.) possess six stamens. Stamen number also shows reduction in some members of Gilliesioideae, but this is related to floral zygomorphy encompassing both stamen whorls, and is indepen-

dent of the actinomorphic reduction involving a single stamen whorl in *Leucocoryne* (e.g., Zöllner and Arriagada 1998; Rudall et al. 2002). Some of the other characters that have been used to separate the genera in the clade composed of *Ipheion*, *Nothoscordum*, and allies include continuously variable characters such as the degree of fusion of tepals or spathe bracts; our analysis indicates that these are also ambiguous. Other characters that merit further investigation include seed coat texture, reported as pitted in *Ipheion* and smooth in the other genera (Rahn 1998a).

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