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Molecular phylogeny of the genus *Philodendron* (Araceae): delimitation and infrageneric classification

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The genus *Philodendron* (Araceae) is a large neotropical group whose classification remains unclear. Previous classifications are based on morphological characters, mainly from the inflorescence, flower and leaf shape. The classification by Krause, with few modifications, is still the most commonly used system. To examine phylogenetic relationships in the genus, two ribosomal DNA nuclear markers, internal transcribed spacer (ITS) and external transcribed spacer (ETS), and the chloroplast intron *rpl*16, were sequenced and analysed for more than 80 species of *Philodendron* and its close relative *Homalomena*. According to the resulting phylogeny, the genus *Homalomena* may be paraphyletic to the genus *Philodendron*. The inclusion of the American *Homalomena* species within the genus *Philodendron* might resolve this taxonomic problem. All three subgenera of *Philodendron* were revealed as monophyletic. Below the subgeneric level, the groups obtained in our phylogeny globally correspond to sections recognized in previous classifications. Among the morphological characters used by previous taxonomists to build their classifications, and which we optimized onto one of the most parsimonious trees, most characters were found to be homoplasious. However, leaf shape, characteristics of the sterile zone on the spadix and venation patterns are useful for delimiting subgenera and sections within the genus.

ADDITIONAL KEYWORDS: external transcribed spacer (ETS) – *Homalomena* – internal transcribed spacer (ITS) – morphology – *rpl*16 intron.

INTRODUCTION

With more than 700 species, the genus *Philodendron* is, after *Anthurium*, the largest genus in the family Araceae (Croat, 1997). This morphologically and ecologically diverse genus is strictly New World, occurring from northern Mexico to southern Uruguay (Mayo, Bogner & Boyce, 1997). The genus, first divided into four subgenera (Schott, 1832), and later into two subgenera (Engler, 1899; Krause, 1913), is now subdivided into three subgenera, two of which are morphologically well defined (Mayo, 1986, 1990, 1991). In 1986, Mayo (1986) conducted cladistic and phenetic analyses showing the monophyly of these subgenera. Today, the subgenera, *Pteromischum* with 75 species (Grayum, 1996), *Meconostigma* with 15 species (Mayo, 1986, 1988, 1991; Croat, 1997) and *Philodendron* with more than 600 species (Croat, 1997), are accepted worldwide (Mayo, 1988; Grayum, 1990, 1996; Mayo *et al*., 1997; Croat, 1997; Sakuragui, Mayo & Zappi, 2005). Recently, subgenus *Meconostigma* was revised (Mayo, 1991; Gonçalves, 2002), and partial revisions of the subgenera *Pteromischum* (Grayum, 1996) and *Philodendron* (Croat, 1997) have also been published. However, no complete revision of the genus has been undertaken since the classification of Krause (1913), which included 222 species of *Philodendron*.

Since the advent of molecular data, taxonomic changes have occurred in other Araceae genera (e.g. Grob *et al*., 2002; Jung *et al*., 2004), highlighting the morphological plasticity of the family by the impressive number of homoplasious characters used in previous classifications. Molecular phylogenies at the family level have also changed our concept of

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Table 1. Significant morphological differences between *Homalomena* and *Philodendron* (Mayo *et al*., 1997; S. J. Mayo, pers. comm.)

Homalomena	*Philodendron*
Always terrestrial to rheophytic, never epiphytic or climbing	Most species are epiphytes or climbers
Inflorescence not secreting resin (although tissues have resin canals)	Inflorescence secretes resin at anthesis, either from spathe or spadix or sometimes both
Staminodes occur generally throughout the female zone of the inflorescence (staminodes not always present)	Staminodes are grouped into a clear sterile zone between the pistillate and staminate flower zones
Anther endothecium with cell wall thickenings	Anther endothecium lacking except in 2 species
Ovary 1 locular to incompletely 2–5 locular	Ovary completely 2–8 (–47) locular
Ovules hemianatropous	Ovules usually hemiorthotropous

relationships among genera (French, Chung & Hur, 1995; Barabé *et al*., 2002; Tam *et al*., 2004). For example, according to the results of Barabé *et al*. (2002) and Tam *et al*. (2004), the genus *Philodendron* would be paraphyletic because the genus *Homalomena* occurs nested within *Philodendron* in their phylogenetic analyses based on chloroplast DNA sequences. The genus *Homalomena*, which comprises approximately 110 species (Mayo *et al*., 1997), is morphologically very similar to *Philodendron*. The principal differences between the two genera lie, among others, in type of habit, secretion of resin at anthesis, and presence or absence of staminodes in the intermediate or female zone of the spadix (Table 1). The geographical distribution of the genus *Homalomena* overlaps with the distribution of *Philodendron* in the northern part of South America. However, most species of *Homalomena* are Asian, whereas only a small number are American (Mayo *et al*., 1997).

Mayo (1986) proposed a phylogenetic hypothesis of relationships within the genus *Philodendron* based mostly on floral anatomic characters from a sample of 15 representative species (Fig. 1). However, no genus level study of *Philodendron*, including species from all three subgenera of *Philodendron* as well as American and Asian *Homalomena* species, has been published to test this hypothesis. The species of *Homalomena* included in the study by Barabé *et al*. (2002) were all from Asia and grouped with members of subgenus *Meconostigma* in their phylogenetic analyses. However, relationships in the *Philodendron*/*Homalomena* clade were not well resolved, nor well supported. Similarly, no resolution was found at this level in the Tam *et al*. (2004) study. In this paper, we present a phylogenetic analysis of the genus *Philodendron* based on chloroplast and nuclear markers in order to evaluate the infrageneric classification and to resolve its relationships with the genus *Homalomena*. To better understand the morphological characters used to elaborate the previous classifications of the genus, some of those characters are studied in the nine sections of subgenus *Philodendron*, partially revised by Croat (1997) (Table 2).

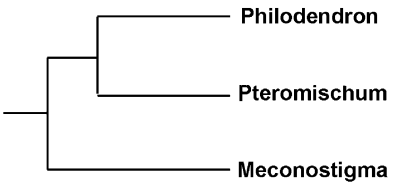

Figure 1. Phylogenetic relationship of the three *Philodendon* subgenera based on Mayo (1986).

MATERIAL AND METHODS

Taxon sampling

For this study, 72 *Philodendron* species and nine *Homalomena* species were examined. Of the nine species of *Homalomena* sampled, five were from America and four from Asia. We included species from all three subgenera of *Philodendron*. For subgenus *Philodendron*, representatives from eight of the nine sections recognized by Croat (1997) were included. Section *Macrogynium* is not represented because no samples were available for study. Samples were obtained from the greenhouses of the Montreal Botanical Garden, the Montreal Biodôme and the Missouri Botanical Garden (with the collaboration of Dr Thomas Croat). These samples generally originated from natural populations collected in southern Mexico, Central America and French Guiana (Table 3). Silica gel dried leaves from French Guiana were also used.

Morphological methods

The taxon sampling for the morphological analyses was carried out using specimens from the greenhouses at the Montreal Botanical Garden and Montreal Biodôme. A total of four inflorescences was sampled for each species studied and special attention was taken to survey different individuals when possible. A total of 15 characters was studied, 10 of which were inflorescence characters used to define inflorescence types by Mayo (1986). To study characters evo-

Table 2. Division of *Philodendron* subgenus *Philodendron* following the classification of Croat (1997)

Sections	Subsections	Series
Baursia (Rchb. ex Schott) Engler		
Philopsammos G. S. Bunting		
Philodendron	*Macrolonchium* (Schott) Engler	
	Canniphyllum (Schott) Mayo	
	Platypodium (Schott) Engler	
	Psoropodium (Schott) Engler	
	Solenosterigma (Klotzsch ex Schott) Engler	
	Philodendron	*Philodendron*
		Impolita Croat
		Velutina Croat
		Fibrosa Croat
		Albisuccosa Croat
	Achyropodium (Schott) Engler	
**Calostigma* (Schott) Pfeiffer	*Macrobelium* (Schott) Engler	*Macrobelium* (Schott) Croat
		Ecordata Croat
		Reticulata Croat
		Pachycaulia Croat
	Glossophyllum (Schott) Croat	*Glossophyllum* Croat
		Ovata Croat
	Oligocarpidium (Engler) Mayo	
	Bulaoana Mayo	
	Eucardium (Engler) Mayo	
Tritomophyllum (Schott) Engler		
Schizophyllum (Schott) Engler		
Polytomium (Schott) Engler		
Macrogynium Engler		
Camptogynum K. Krause		

*Now called Sect. *Macrobelium* according to Sakuragui *et al*. (2006).

lution, we optimized on the most parsimonious tree obtained from the phylogenetic analysis. The following characters were evaluated:

Resin secretion in the inflorescence (absence 0/presence 1). In all but a few species, resin canals within the inflorescence (spathe or spadix) secrete a sticky, usually orange, yellow to cherry-coloured, substance similar to resin. In some species, secretion is from the inner surface of the spathe, usually in the lower half of the spathe. In others, the resin is exuded from the spadix. The female zone never exudes resin. There are three possibilities:

1. Resin secretion from the spathe.
2. Resin secretion from the staminate spadix zone.
3. Resin secretion from both staminate and staminodial zones.

Certain species do not secrete resin at all, although resin canals are present. They can be seen by sectioning the spathe or spadix transversally.

4. Resin canal present on the adaxial side of the spathe (absence 0/presence 1).
5. Resin canals present in the spadix (absence 0/presence 1).
6. In the genus *Philodendron* the inflorescences are terminal on their respective shoot. A system of inflorescences clustered in the sheath of a leaf correspond to a sympodial unit (see Fig. 2 in Mayo, 1991). A sympodium may comprise one to several inflorescences (one coded as 0/two or more coded as 1).
7. The length of the sterile flower zone in comparison with the length of the pistillate flower zone is a character used to separate species of *Philodendron* subgenus *Meconostigma* from the other subgenera. The character is coded as the sterile zone shorter (0) or longer (1) than the pistillate zone.
8. Some species of *Philodendron* have a second sterile flower zone at the apex of the spadix (presence coded as 1). However, the majority of the species of *Philodendron* only have a few staminodes at the apex of the inflorescence rather than a clear sterile zone (absence coded as 0).
9. A constriction in the middle of the spathe is observed, corresponding to the upper part of the

Table 3. Collection and voucher information for species of *Homalomena* and *Philodendron* studied

Species	Collection and reference number	Voucher	GenBank *rpl*16	GenBank ITS	GenBank ETS
Homalomena					
Homalomena aff. *panamense* Croat & Marcell	MBG 90162	*Croat 90162* (MO)	DQ866155	DQ866880	DQ870563
Homalomena cochinchinensis Engl.	MBG 77907d	*Croat 77907* (MO)	DQ866152	DQ866877	DQ870560
Homalomena crinipes Engl.	MBG 81956c	*Croat 81956* (MO)	DQ866153	DQ866878	DQ870561
Homalomena erythropus Engl. ssp. *allenii* Croat	MBG 79249	*Croat 79249* (MO)	DQ866154	DQ866879	DQ870562
Homalomena sp.	MBG 77079a	*Croat 77079* (MO)	DQ866151		DQ870559
Homalomena philippinensis Engl.	MBG 52988	*Croat 52988* (MO)	DQ866202	DQ866881	DQ870564
Homalomena picturata Regel	MBG 90199	*Croat 90199* (MO)	DQ866156	DQ866882	DQ870565
Homalomena rubescens Kunth	JBM 1721-1955	*Gauthier 40* (MT)			DQ870566
Homalomena wendlandii Schott	MBG 85114a	*Croat 85114* (MO)	DQ866157	DQ866883	DQ870567
Philodendron subgenus *Philodendron*					
Philodendron sp_1	JBM 2188-1986	*Gauthier 14* (MT)	DQ866201		DQ870570
Philodendron angustisectum Engl.	JBM 2801-1950	*Gauthier 2* (MT)	DQ866158	DQ866884	DQ870576
Philodendron angustisecum Engl.	JBM 6380-1939	*Gauthier 5* (MT)	DQ866191		DQ870622
Philodendron anisotomum Schott	MBG 82-124	*Croat 82–124* (MO)		DQ866884	
Philodendron anisotomum Schott	JBM 2803-1950	*Gauthier 38* (MT)	DQ866200	DQ866885	
Philodendron barrosoanum G.S. Bunting	MBG 81932a	*Croat 81932* (MO)		DQ866886	DQ870577
Philodendron billietiae Croat	FG	*Barabé 36* (MT)	DQ866159		DQ870578
Philodendron brevispathum Schott	JBM 1518-2003	No voucher	DQ866161	DQ866887	DQ870579
Philodendron callosum K. Krause	FG	*Barabé 63* (MT)	DQ866162		DQ870580
Philodendron martianum Engl.	JBM 2424-1946	*Chouteau 6* (MT)	DQ866163	DQ866888	DQ870581
Philodendron crassinervium Lindl.	JBM 2119-1951	*Gauthier 8* (MT)	DQ866164		DQ870582
Philodendron davidsonii Croat	MBG 38177a	*Croat 38177* (MO)			DQ870583
Philodendron distantilobum Krause	JBM 2601-1999	*Gauthier 12* (MT)	DQ866199	DQ866889	DQ870584
Philodendron ecordatum Schott	JBM 145-2003	*Gauthier 1* (MT)		DQ866890	
Philodendron erubescens K. Koch & Augustin	JBM 1892-1957	*Gauthier 25* (MT)	DQ866194		DQ870585
Philodendron findens Croat & Grayum	MBG 38218	*Croat 38218* (MO)	DQ866204	DQ866892	DQ870586
Philodendron fragrantissimum Kunth	FG	*Barabé 77* (MT)	DQ866167	DQ866893	DQ870587
Philodendron glaziovii Hook. f.	BM 7014-1998	*Gauthier 26* (MT)	DQ866168	DQ866894	DQ870588
Philodendron gloriosum Andre	BM 7168-1995	*Chouteau 7* (MT)			DQ870589
Philodendron grandifolium Schott	JBM 3549-1987	*Gauthier 15* (MT)			DQ870590
Philodendron grandipes Krause	MBG 79244	*Croat 79244* (MO)		DQ866896	DQ870591
Philodendron grazielae Bunting	JBM 2602-1959	*Gauthier 7* (MT)	DQ866170		
Philodendron sp_5	JBM 1130-1952	*Gauthier 20* (MT)	DQ866181	DQ866910	DQ870613
Philodendron heleniae Croat	MBG 83278	*Croat 83278* (MO)		DQ866897	DQ870592
Philodendron hylaeae Bunting	MBG 84578a	*Croat 84578* (MO)		DQ866897	DQ870593
Philodendron ilsemannii Hort.	BM 7068-1998	*Gauthier 28* (MT)	DQ866171		DQ870594
Philodendron imbe Schott	JBM 2123-1951	*Gauthier 29* (MT)	DQ866172		DQ870595
Philodendron insigne Schott	FG	*Barabé 75* (MT)		DQ866899	DQ870596

Table 3. *Continued*

Species	Collection and reference number	Voucher	GenBank *rpl*16	GenBank ITS	GenBank ETS
Philodendron lazorii Croat	MBG 69833	*Croat 69833* (MO)			DQ870597
Philodendron lindenii Wallis	JBM 7064-1998	*Gauthier 31* (MT)	DQ866173	DQ866900	DQ870598
Philodendron linnaei Kunht	FG	*Barabé 76* (MT)		DQ866901	DQ870599
Philodendron sp_2 Engl.	BM 2970-1959	*Gauthier 17* (MT)	DQ866198		DQ870600
Philodendron longistilum Krause	MBG-11-17-78	No voucher	DQ866174	DQ866902	DQ870601
Philodendron malesevichiae Croat	JBM 76707	*Croat 76707* (MO)			DQ870602
Philodendron mamei Andre	BM 7224-1992	*Gauthier 39* (MT)		DQ866904	
Philodendron martianum Engl.	JBM 2424-1946	*Chouteau 6* (MT)	DQ866163	DQ866888	DQ870581
Philodendron megalophyllum Schott	JBM 194-1997	*Gauthier 20* (MT)	DQ866197		
Philodendron aff. *megalophyllum* Schott	JBM 2415-1992	*Gauthier 16* (MT)			
Philodendron melinonii Brongn.	JBM 1535-1994	*Gauthier 13* (MT)			DQ870603
Philodendron ornatum Schott	FG	*Barabé 30* (MT)	DQ866176		
Philodendron ornatum Schott	JBM 1511-1996	*Gauthier 33* (MT)	DQ866166	DQ866891	DQ870604
Philodendron panamense Krause	MBG 55184c	*Croat 55184* (MO)	DQ866196	DQ866905	DQ870605
Philodendron panduriforme Schott	MBG 85311b	*Croat 85311* (MO)			DQ870606
Philodendron pedatum Kunth	JBM 2043-1997	*Gauthier 44* (MT)	DQ866195	DQ866906	DQ870607
Philodendron pinnatifidum Schott	JBM 1131-1952	*Gauthier 41* (MT)	DQ866177		DQ870608
Philodendron pterotum K. Koch & Augustin	JBM 1840-1955	*Gauthier 42* (MT)		DQ866907	
Philodendron radiatum Schott	JBM 2740-1951	*Gauthier 6* (MT)	DQ866178	DQ866908	DQ870609
Philodendron aff. *radiatum* Schott	JBM 2802-1950	*Gauthier 9* (MT)	DQ866182		DQ870614
Philodendron rothschuhianum Engl. & Krause	MBG 57199	*Croat 57199* (MO)			
Philodendron rubens Schott	BM 7070-1998	*Gauthier 34* (MT)			
Philodendron ruizii Schott	JBM 1638-1953	*Chouteau 10* (MT)	DQ866179		DQ870609
Philodendron sagittifolium Liebm	JBM 3402-1983	*Gauthier 46* (MT)	DQ866180	DQ866909	DQ870612
Philodendron serpens Hook.	MBG 97-100	*Croat 97–100* (MO)	DQ866193	DQ866911	
Philodendron simsii (Hook.) Don	JBM 1893-1957	*Gauthier 35* (MT)			DQ870615
Philodendron smithii Engl.	MBG 64524	*Croat 64524* (MO)	DQ866183	DQ866912	DQ870615
Philodendron sodiroi Hort.	BM 7163-1995	*Gauthier 36* (MT)	DQ866192	DQ866913	
Philodendron squamiferum Poepp. & Endl.	JBM 7009-1998	*Gauthier 45* (MT)		DQ866916	DQ870617
Philodendron sp_4	JBM 1659-1953	*Gauthier 19* (MT)	DQ866186	DQ866917	DQ870618
Philodendron sp_3	JBM 2576-1954	*Gauthier 18* (MT)	DQ866187		DQ870619
Philodendron tripartitum Schott	JBM 2347-1992	*Gauthier 3* (MT)	DQ866188		DQ870620
Philodendron verrucosum Schott	JBM 6382-1939	No voucher			DQ870621
Philodendron victoriae Bunting	MBG 54758c	*Croat 54758* (MO)			
Philodendron subgenus *Pteromischum*					
Philodendron duckei Croat & Grayum	FG	*Barabé 269* (MT)	DQ866165		
Philodendron rudgeanum Schott	FG	*Barabé 37* (MT)			DQ870568
Philodendron sp. (*pteromischa*)	MBG 84914	*Croat 84914* (MO)	DQ866185	DQ866915	DQ870573
Philodendron surinamense (Miq. ex Schott) Engl.	FG	*Haig et al. 14* (KW)		DQ866918	

Table 3. *Continued*

Species	Collection and reference number	Voucher	GenBank *rpl*16	GenBank ITS	GenBank ETS
Philodendron subgenus *Meconostigma*					
Philodendron bipinnatifidum Schott ex Endl.	JBM 1836-1955	*Gauthier 4* (MT)	DQ866160		DQ870569
Philodendron goeldii Barroso	JBM 1699-1996	*Gauthier 27* (MT)	DQ866169	DQ866895	DQ870571
Philodendron lundii Warm.	MBG 82932	*Croat 82932* (MO)	DQ866175	DQ866903	
Philodendron solimoesense A.C. Smith	FG	*Barabé 60* (MT)	DQ866184	DQ866914	DQ870572
Philodendron undulatum Engl.	JBM 1930-52	*Gauthier 37* (MT)	DQ866189	DQ866919	DQ870574
Philodendron xanadu Croat, Mayo & J. Boos «winterbourne»	MBG 71897	*Croat 71897* (MO)	DQ866190	DQ866920	DQ870575
Out-group taxa					
Anchomanes difformis (Blume) Engl.	JBM 3991-84	*Barabé & Archambault 191* (MT)	DQ866203		
Culcasia saxatilis A. Chev.	JBM 4094-84	*Barabé & Chantha 91* (MT)			

GenBank accession numbers are given for the chloroplast *rpl*16 intron, and the nuclear ITS and ETS regions.
BM, Montreal Biodôme; ETS, external internal transcribed spacer; FG, French Guiana, wild collected; ITS, internal transcribed spacer; JBM, Montreal Botanical Garden; MBG, Missouri Botanical Garden.

pistillate flower zone in the spadix. Some species have a strong hourglass shape while other are almost straight (weak constriction coded 0, moderate coded 1, strong coded 2).

10. Nectar glands can be found on the external part of the spathe in some *Philodendron* species (absence 0/presence 1).

Only a few vegetative characters were surveyed although they were used extensively by Engler and Krause (see Figs 1, 2 in Mayo, 1991).

11. Conspicuous primary lateral veins on the leaf blade (absence 0/presence 1).
12. Leaf type: lanceolate (coded as 0), trisect (coded as 1), sagittate (coded as 2), cordate (coded as 3), and pinnatifid and bipinnatifid (coded as 4).
13. Internode length grouped by class: 1–5 cm (1), 6–10 cm (2), 11–15 cm (3), 16–20 cm (4), 21–25 cm (5).
14. Petiole shape (Croat, 1985) basically terete ranging from round to elliptical (coded as 0), flat adaxially with marginal and medial ribs (coded as 1), and shallowly sulcate, cresecent shape in section (coded as 2).
15. Glands on the petiole (absence 0/presence 1).

MOLECULAR METHODS

Total genomic DNA was isolated using the Doyle & Doyle (1987) extraction protocol as modified by Philipps & Morden (2001), or DNeasy kit (Qiagen, Mississauga, ON, Canada) for problematic specimens. The chloroplast *rpl*16 intron and the nuclear rDNA internal transcribed spacer (ITS) and external transcribed spacer (ETS) regions were sequenced. New *rpl*16 primers were designed for the group: a forward primer *rpl*16-FA (CAACTTATGGTTCATATTG) and a reverse primer *rpl*16-RA (TCGCGGGCGAATATTG). For the ITS region, we used the universal primer ITS4 from White *et al*. (1990) and a modified ITS-5A primer (GGAAGGAGAAGTCGTAACAAG) designed for the genus *Philodendron*. For the ETS region, amplifications were carried out with universal primer 18S from Starr, Harris & Simpson (2003) and a new forward primer ETS-AF (GACCGTGACGGYACGT GAG), specifically designed for the group.

We used the following amplification programme for both the chloroplast and nuclear regions: melting step at 95 °C for 2 min, followed by 35 cycles (chloroplast DNA) or 40 cycles (nuclear DNA) at 95 °C for 30 s, 30 s at 48 °C to 56 °C depending on the specimen, then 72 °C for 30 s to 2 min, and a final extension step of 7 min at 72 °C.

Amplified fragments were purified using 20% polyethylene glycol (PEG) with 2.5 M NaCl. Sequencing amplifications were performed with the Big Dye terminator cycle sequencing kit V.1.1 (Applied Biosystems, Foster City, CA, USA). Non-incorporated dyes were removed using 2 µL 3 M pH 4.6 NaOAc and 50 µL 95% ethanol precipitation followed by two 70%

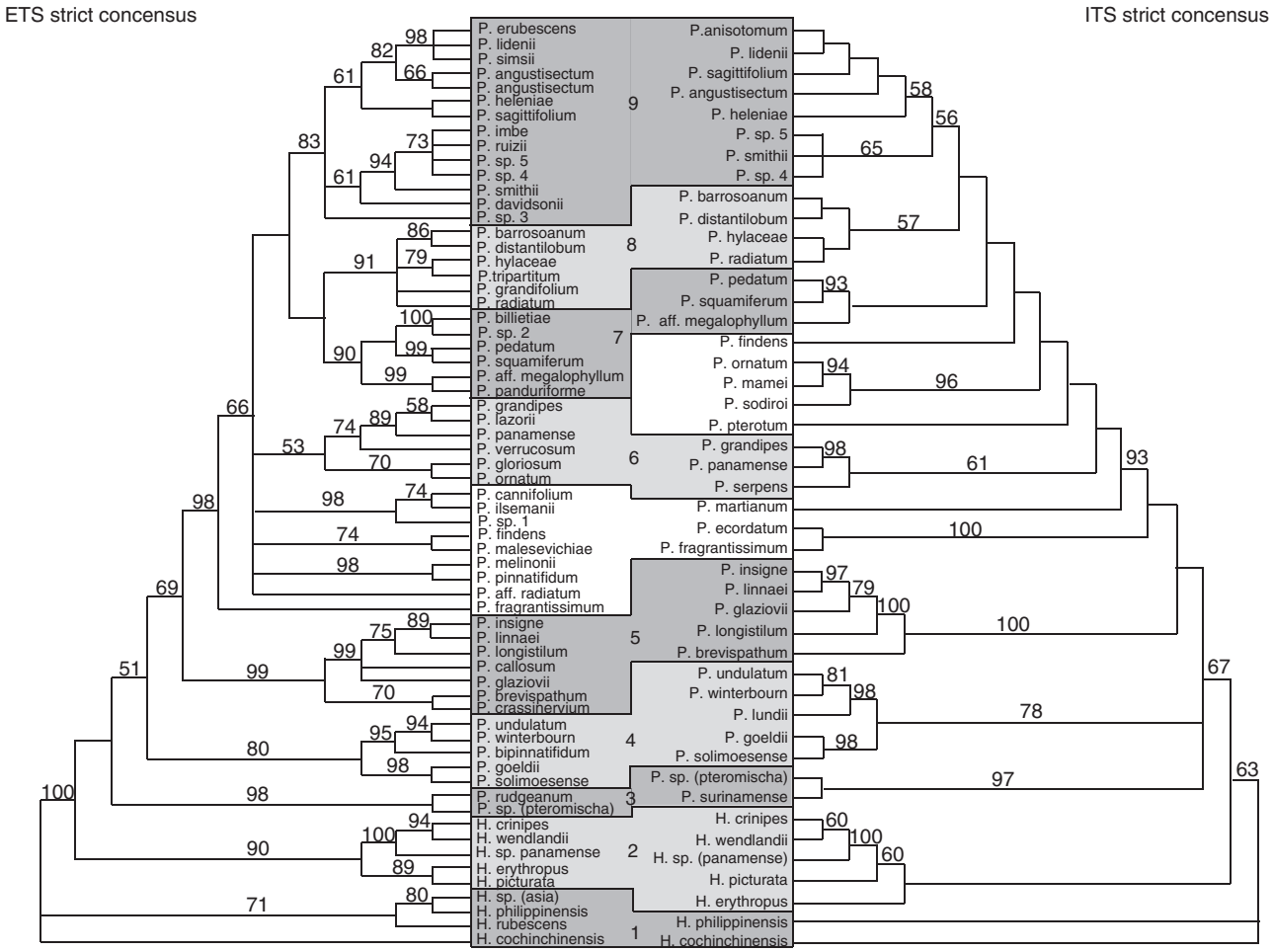

Figure 2. Strict consensus of the 15 036 most parsimonious trees of 64 species for the external transcribed spacer (ETS) data. Strict consensus of the 19 most parsimonious trees of 45 species for the internal transcribed spacer (ITS) data. Bootstrap values are given on the topology. **1**. *Homalomena* from Asia; **2**. *Homalomena* from America; **3**. *Philodendron* subgenus *Pteromischum*; **4**. *Philodendron* subgenus *Meconostigma*; **5, 6, 7, 8, 9**. *Philodendron* subgenus *Philodendron*. Species that do not form monophyletic groups in one of the two data sets are not shaded.

ethanol washes. Sequencing was performed with an Applied Biosystem 3100-avant automated sequencer. Polymorphic nuclear DNA sequences were cloned using a cloning kit from Invitrogen (Invitrogen, Carlsbad, CA, USA) or Qiagen. Eight colonies were sampled for each cloned species and accuracy of the insert sequence was determined by amplification of the ribosomal DNA insert, using the same protocol as for amplification, but with 1 μL bacteria in the culture media (last step before plasmid purification). Amplicons were run on 1% agarose gels and length discriminated. Four plasmids per species were purified using Qiagen MiniPrep. Samples were sequenced using the same protocol as noted previously. Both strands were sequenced. Sequences were assembled and edited with SEQUENCHER 3.1 (Gene Codes Corp., Ann Arbor, MI, USA). Alignments were performed with Clustal X (version 1.83, Thompson *et al*., 1997), verified by eye with Se-Al (Rambaut, 1996) and exported as NEXUS files for phylogenetic analyses.

PHYLOGENETIC ANALYSES

Maximum parsimony searches were conducted with PAUP* version 4.0b.10 (Swofford, 2002). Heuristic searches with 1000 taxon addition replicates were conducted. Bootstrap values were obtained with PAUP* with full heuristic searches, tree bisection-reconnection (TBR) branch swapping and 1000 replicates. Gaps were treated as missing data and indels (insertions or deletions) were recoded as separate presence/absence characters. The analyses were performed separately for the three regions sequenced, and the two nuclear (ITS and ETS) regions also were

Table 4. Alignment information for the three regions sequenced

Region	No. of species included	Length with gaps (bp)	No. of informative characters	% hypervariable regions (removed)	No. of characters	No. of informative characters
ITS	45	1225	539	24.9%	920	373
ETS	64	1307	671	34.8%	853	344
*rpl*16	58	926	60	0	914	60

ETS, external internal transcribed spacer; ITS, internal internal transcribed spacer.

concatenated in a combined analysis. Partition homogeneity tests (Farris *et al*., 1994) were implemented using PAUP* to look for incongruence among the three regions studied.

To root the phylogeny, we included *Anchomanes* and *Culcasia* as out-group taxa. The out-group taxon differed between the chloroplast and nuclear sequence analyses because of difficulties in amplification. Both genera were found to be close relatives of the genus *Philodendron* in the Barabé *et al*. (2002) study. Only the genus *Anchomanes* was used as the out-group taxon in the chloroplast DNA analysis. For the ITS analyses, we performed a preliminary analysis with all *Philodendron* and *Homalomena* species and included *Culcasia* as the out-group taxon, but only for the more conserved 5.8S ITS region that could be aligned. Because this phylogeny lacked resolution among terminals, we then rooted the subsequent ITS analyses with the sister species of *Culcasia* found in the preliminary analysis: *Homalomena cochinchinensis*. For the ETS analyses, no out-group taxon could be aligned because of the extreme variation in the region. Thus, *H. cochinchinensis*, found to be sister to the remainder of the group in the 5.8S ITS analysis, was also used to root the ETS topology.

Bayesian analyses were performed using Mr Bayes (Huelsenbeck & Ronquist, 2003) with the combined ITS and ETS matrix, under a GTR+G model determined using Model Test (Posada & Crandall, 1998). Bayesian analyses were carried out with four independent Markov chains run for 1 000 000 MCMC generations with tree sampling every 100 generations and a burn-in of 1000 trees. The analyses were run twice using different starting trees to evaluate the convergence of likelihood values and posterior clade probabilities.

RESULTS

Molecular analyses

Nuclear markers

Alignment of the nuclear ITS and ETS sequences was difficult as a result of the presence of numerous indels. The hypervariable sections that could not be aligned because of difficulties in assessing homology were removed in the final analyses, but initial analyses were performed with and without these hypervariable regions (Table 4). For ITS, almost a quarter of the data was removed from the alignment because of problematic hypervariable regions. With ETS, the number of unaligned regions represented a little more than a third of the data set.

With the hypervariable regions, over 10 000 trees were found with the parsimony analysis for both nuclear markers. The consensus trees were not well resolved and clades were poorly supported by bootstrap values (not shown). Without the problematic regions, 19 trees were obtained with ITS (1443 steps, CI = 0.628, RI = 0.704) and 15036 trees with the ETS data (1235 steps, CI = 0.633, RI = 0.770). The strict consensus trees from these analyses were well resolved and clades were relatively well supported by bootstrap values (Fig. 2). The groups observed in the ETS and ITS strict consensus trees are similar. Although the species sampled are not exactly the same in the two analyses, almost all groups supported in one analysis also are supported in the other. In both analyses, the genus *Homalomena* is paraphyletic and basal to the genus *Philodendron*. American *Homalomena* (group 2) are monophyletic and sister to the genus *Philodendron*, while the Asian *Homalomena* (group 1) are sister to both these groups. The three subgenera of *Philodendron*, *Pteromischum* (group 3), *Meconostigma* (group 4) and *Philodendron* (groups 5–9), are supported as monophyletic. In subgenus *Philodendron* five clades (groups 5–9) are resolved in the analyses.

The partition homogeneity test for the ITS and ETS matrices gave a *P*-value of 0.8700, suggesting that the two partitions are congruent. The topology of the strict consensus tree resulting from the analysis of combined data (not shown) is less resolved than those from the separate analyses. This is because of the large proportion of missing data (about 35%) in the combined matrix.

The topology obtained from the Bayesian analysis (not shown) is similar to that obtained with maximum parsimony, with the exception of the position of *Philodendron* subgenus *Pteromischum* (group 3), which is

sister to the American *Homalomena* (posterior probability of 98%) in the Bayesian analysis, making the genus *Philodendron* paraphyletic. No parsimony analysis, separate or combined yielded this topology. One of the groups of *Philodendron* subgenus *Philodendron* (clade 8 in Fig. 2) also occurs in a different position in the Bayesian analysis.

Chloroplast marker

The results obtained with the chloroplast marker are different from those obtained with the nuclear markers. The alignment of that region was less problematic than for the nuclear markers and no hypervariable region was found. The strict consensus tree (not shown) is not well resolved and clades are generally poorly supported. This likely is as a result of the low level of variation in the *rpl*16 region (Table 4) and is evident by the short branch lengths seen in one of the most parsimonious trees. Species of the genus *Homalomena* do not group together and nor do those of *Philodendron* subgenus *Meconostigma*, groups that are well supported with the nuclear markers. Moreover, one species of *Philodendron* subgenus *Philodendron* (*P. anistomum*) and one species of the subgenus *Pteromischum* (*P. duckei*) occur as the first branch in the topology, conflicting with the findings of the nuclear analysis that subgenera *Philodendron* and *Pteromischum* are monophyletic (Fig. 3). No group in *Philodendron* subgenus *Philodendron* is consistent between the chloroplast and nuclear analyses.

The homogeneity test between the chloroplast and nuclear markers (two partitions) indicates that ETS and ITS are not congruent with the *rpl*16 analysis (P-value = 0.01, with 100 replicates). For this reason, and because of the low levels of variation obtained with the *rpl*16 analyses, the chloroplast and nuclear data were not combined.

Morphology

The morphological characters (Table 5) were optimized onto one of the most parsimonious trees, similar to the Bayesian tree, obtained from the analysis of the combined ITS and ETS regions for all species studied. However, because of the low proportion of species that were studied morphologically, the optimization is not illustrated; instead the distribution of these characters is given in Table 5. A total of 74 species were included in the phylogeny, but of these only 40 were studied morphologically. The 23 species from the Missouri Botanical Garden, as well as 14 immature specimens from the Montreal Botanical Garden and the Montreal Biodôme, could not be surveyed.

Finally, the classification of each species according to the morphologically based sections from Croat (1997) is indicated for subgenus *Philodendron* on one of the most parsimonious trees found with combined nuclear data (Fig. 4). Some species are represented by two sectional symbols because their assignation is not clear.

DISCUSSION

The relationship between *Philodendron* and *Homalomena*

The relationships observed between *Philodendron* and *Homalomena* are equivocal in the analyses. With the chloroplast marker, *Homalomena* is nested within *Philodendron*. In addition, two species of *Philodendron* (*P. anisotomum* and *P. duckei*) are supported, with bootstrap values above 95%, as distinct from the rest of *Homalomena* and *Philodendron*, which together group with low internal resolution (Fig. 3). Without these two problematic species, *Philodendron* appears monophyletic in the chloroplast analyses. The Bayesian analysis of the combined nuclear markers places the American *Homalomena* as sister to *Philodendron* subgenus *Pteromischum*. *Philodendron* is therefore paraphyletic in this analysis. These findings may be congruent with a previous study at the family level where *Homalomena* was nested in *Philodendron* (Barabé *et al*., 2002). In contrast, the parsimony analyses of both separate and combined nuclear markers yielded a monophyletic *Philodendron* as sister to American *Homalomena*, agreeing with morphologically based classifications (Mayo, 1986; Grayum, 1990; Croat, 1997). In the parsimony analyses, the support values for the *Philodendron* clade are always above 50% and in the ETS only analysis the clade support is above 95%. Two synapomorphies, both in the ITS region, are shared by American *Homalomena* and *Philodendron* subgenus *Pteromischum*. The present results suggest a close relationship between the American species.

Homalomena and subgenus *Pteromischum*

Two possible hypotheses of relationship are evident from our analyses. The first, suggested by the parsimony analysis of the nuclear data, is that *Philodendron* is monophyletic and sister to American *Homalomena* (Fig. 5A). The second, found with the Bayesian analysis, suggests that subgenus *Pteromischum* is sister to American *Homalomena* and that this group is sister to all other *Philodendron* (Fig. 5B). The second hypothesis would imply the inclusion of American *Homalomena* in the genus *Philodendron*. Our analyses do not allow us to discriminate between these two patterns of relationship. Because the chloroplast data lack resolution, no strong hypothesis of relationships can be obtained from those analyses. Although more data are needed to resolve this ambi-

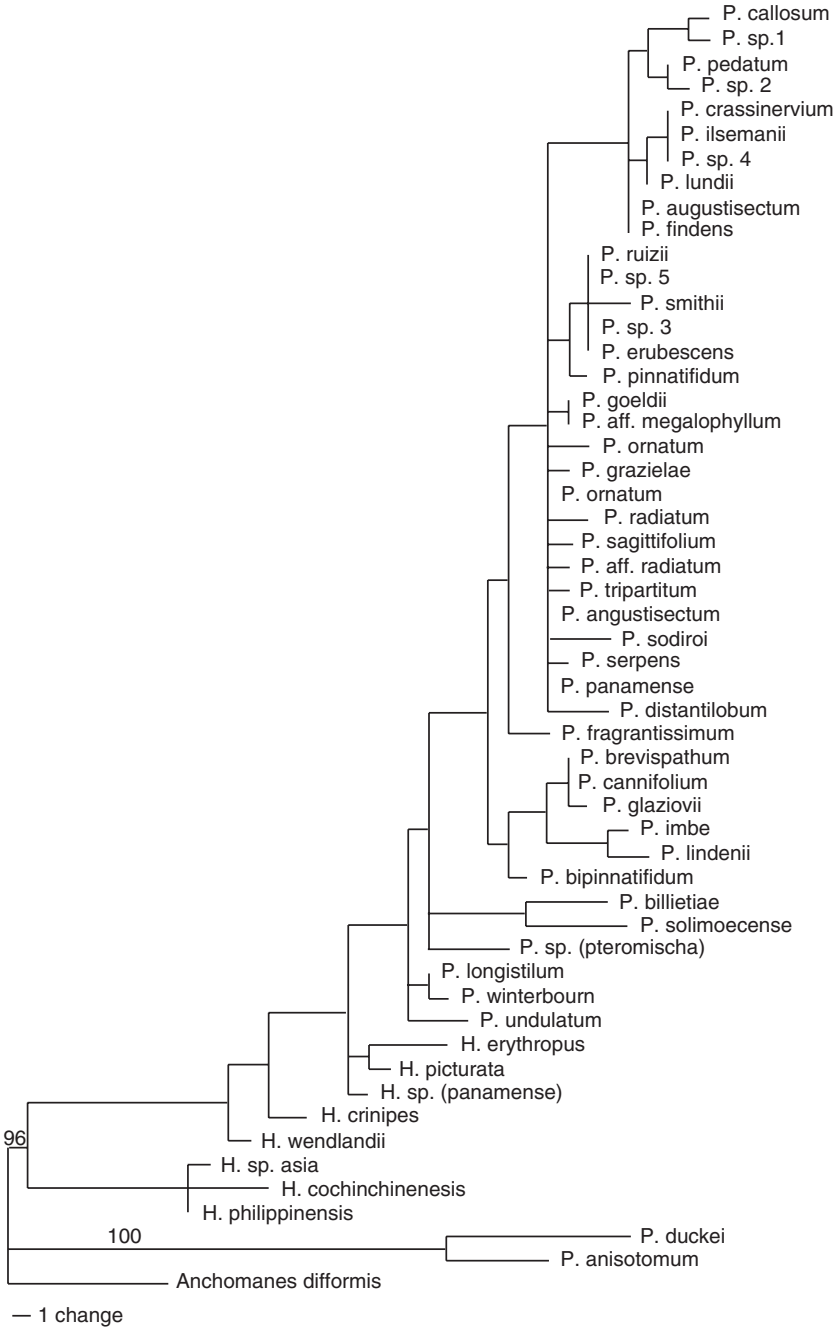

Figure 3. One of the 10 000 most parsimonious trees with 58 species resulting from the analysis of the chloroplast *rpl*16 intron.

guity, all analyses seem to indicate that *Homalomena* is not monophyletic, with a clear separation of the Asian and American species.

Relationship among subgenera

Contrary to the chloroplast marker analysis, in the analyses of the nuclear data, the three subgenera were always supported as monophyletic (Fig. 2). In our study, *Philodendron* subgenus *Pteromischum* is always the sister clade to subgenus *Meconostigma*, which is the sister clade to subgenus *Philodendron*. This pattern of relationships conflicts with Mayo's (1986) hypothesis that subgenus *Meconostigma* was the sister clade to the subgenera *Philodendron* and *Pteromischum* (Fig. 1). The chloroplast marker data

Table 5. Morphological characters surveyed in species of subgenus *Philodendron* present at the Montreal Botanical Garden and Montreal Biodôme collections. See text for character descriptions. Dashed lines indicate that the character was not surveyed. The species grouping corresponds to Figure 4

Species	1. Resin on spathe	2. Resin on male flowers zone	3. Resin on sterile flowers zone	4. Resin canal in spathe (abaxial side)	5. Resin canal in spadix	6. Number of inflorescences per axil	7. Length of spadix sterile zone	8. Spadix terminal sterile zone	9. Spathe constriction	10. Production of extrafloral nectar	11. Conspicuous primary lateral veins	12. Leaf type	13. Internode distance	14. Petiole shape	15. Glandular petiole
Homalomena rubescens	0	0	0	0	0	0	–	0	0	0	–	–	–	–	–
Subg.***Pteromischum***	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Subg. ***Meconostigma***															
Philodendron bipinnatifidum	1	0	0	1	1	1	1	1	0	1	–	–	–	–	–
Philodendron undulatum	0	1	1	1	1	1	1	1	0	1	–	–	–	–	–
Subg. ***Philodendron***															
Clade 1															
Philodendron callosum	0	1	0	1	1	1	0	0	2	1	0	0	1	2	0
Philodendron crassinervium	0	0	–	–	–	1	0	–	–	1	0	0	1	0	0
Philodendron glaziovii	0	0	0	1	1	1	0	0	1	1	0	0	–	1	0
Philodendron insigne	0	0	0	1	1	0,1	0	0	1	1	0	0	–	0	0
Philodendron linnaei	0	0	0	0	0	1	0	0	1	1	0	0	1	2	0
Group A															
Philodendron cannifolium	–	–	–	–	–	–	–	–	–	–	0	0	0	2	0
Philodendron ecordatum	–	–	–	–	–	–	–	–	–	–	?	1	2	0	0
Philodendron fragrantissimum	0	1	0	1	1	1	0	0	2	1	1	0	1	2	0
Philodendron gloriosum	–	–	–	1	1	1	0	–	0	0	1	3	1	1	0
Philodendron ilsemannii	–	–	–	–	–	–	–	–	–	–	1	3	1	0	0
Philodendron mamei	–	–	–	–	–	–	–	–	–	–	1	3	1	2	0
Philodendron melinonii	0	1	1	1	1	0,1	0	0	1	1	1	3	1	2	0
Philodendron ornatum	–	–	–	–	–	–	–	–	–	–	1	3	1	0	1
Philodendron pinnatifidum	–	–	–	–	–	–	–	–	–	–	1	2	1	1	0
Philodendron sodiroi	–	–	–	–	–	–	–	–	–	–	1	3	2	2	1
Philodendron sp1	–	–	–	–	–	–	–	–	–	–	1	3	2	0	0
Clade 2															
Philodendron aff. *megalophyllum*	1	0	0	1	1	0,1	0	0	0	1	1	3	–	0	0
Philodendron pedatum	0	1	1	1	1	0,1	0	0	1	1	1	4	1	0	0
Philodendron squamiferum	0,1	1	1	1	1	0,1	0	0,1	2	1	1	3	1	0	1
Philodendron sp2	–	–	–	–	–	–	–	–	–	–	1	3	4	0	0
Clade 3															
Philodendron distantilobum	1	1	0	1	1	0,1	0	0	1	1	1	2	1	0	0
Philodendron grandifolium	0	1	1	1	1	0,1	0	0	0	1	1	3	1	0	0
Philodendron radiatum	0	1	1	1	1	0,1	0	0	1	0,1	1	3	1	0	0
Philodendron tripartitum	0	1	1	1	1	0,1	0	0	1	1	1	1	5	0	0
Clade 4															
Philodendron angustisectum	–	–	–	–	–	–	–	–	–	–	1	4	1	0	0
Philodendron angustisectum	–	–	–	1	1	1	0	–	1	1	–	–	–	–	–
Philodendron erubescens	1	0	0	1	1	1	0	0	0	0,1	1	3	2	0	0
Philodendron imbe	0	1	0	1	1	1	0	0	1	0	1	3	2	2	0
Philodendron lindenii	–	–	–	–	–	–	–	–	–	–	1	3	2	0	0
Philodendron melanochrysum	0	1	1	1	1	0,1	0	0,1	0	0	–	–	–	–	–
Philodendron microstictum	0	0	0	1	1	0	1	0	1	0	–	–	–	–	–
Philodendron ruizii	0,1	1	1	1	1	1	0	0	1	1	1	3	1	0	0
Philodendron sagittifolium	0,1	0	0	1	1	0,1	0	0,1	1	1	1	3	1	0	0
Philodendron simsii	–	–	–	–	–	–	–	–	–	–	1	3	2	0	0
Philodendron sp3	–	–	–	–	–	–	–	–	–	–	1	3	2	0	0
Philodendron sp4	0	1	1	1	1	1	–	0	1	1	1	3	1	2	0
Philodendron sp5	0	1	1	1	1	0,1	0	0	1	1	1	3	–	2	0

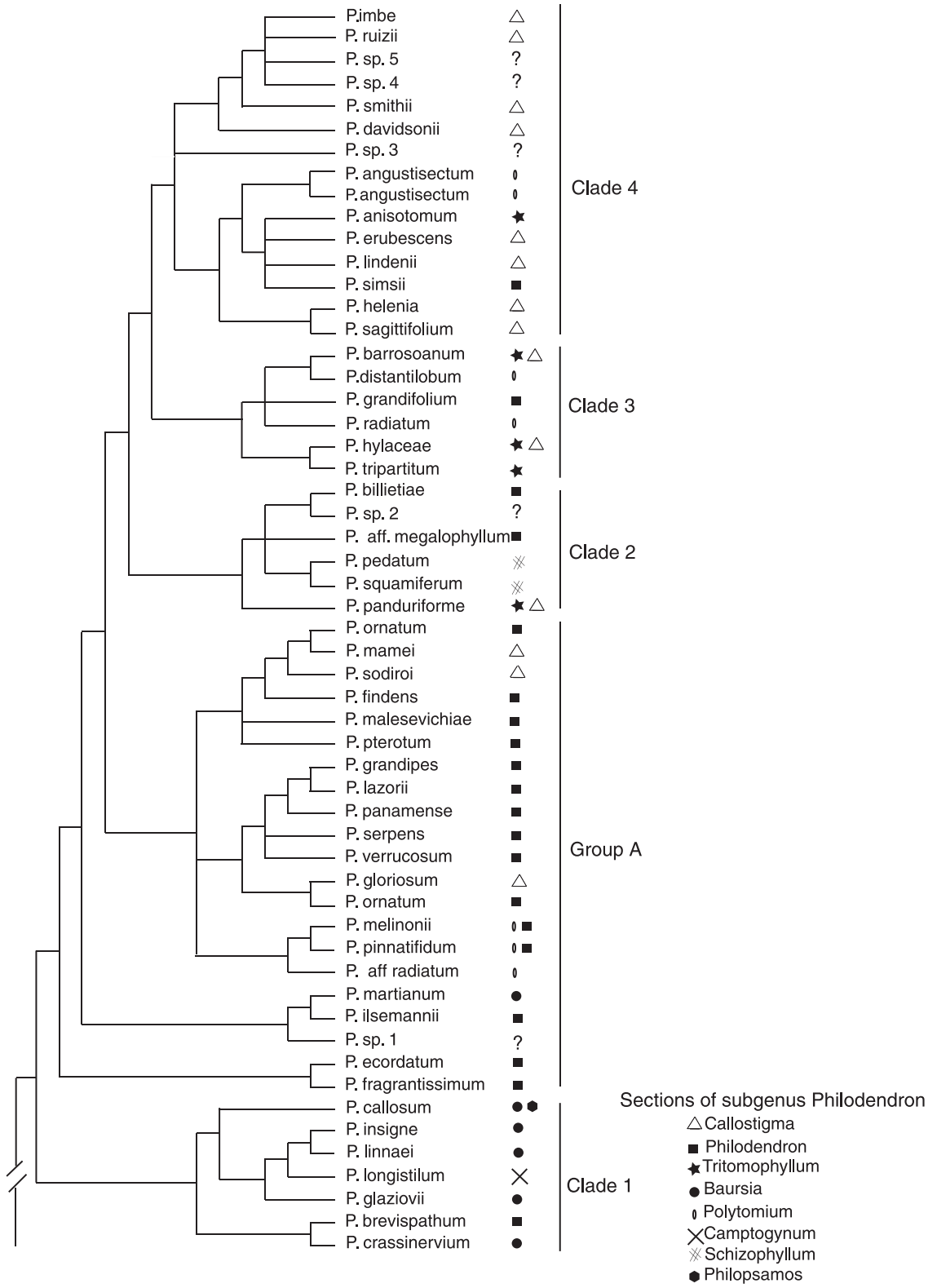

Figure 4. Sections of subgenus *Philodendron* are noted on one of the most parsimonious trees, most similar to the Bayesian analysis obtained from the combination of internal transcribed spacer (ITS) and external transcribed spacer (ETS) sequences. Two sectional pictograms for one species indicate sectional ambiguity. ?, Species belonging to the section *Philodendron* or *Callostigma*.

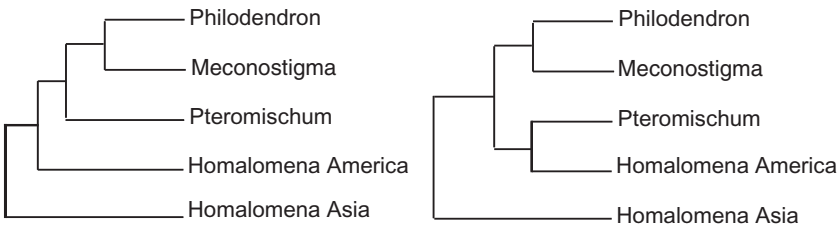

Figure 5. Two evolutionary hypotheses of *Philodendron* subgenus *Pteromischum* and *Homalomena* from America as suggested by the nuclear markers. A, parsimony analysis; B, Bayesian analysis.

showed insufficient resolution to define relationships among the *Philodendron* subgenera. More resolution was found in the analysis of the *trn*L region by Barabé *et al*. (2002), possibly because only six species of *Philodendron* and two of *Homalomena* were included. However, the relationships found in that study seem to be in conflict with our results. A rooting problem, low variability in the marker and the few species sampled, could explain the difference observed between the *trn*L region analysis and our nuclear ITS and ETS analysis.

The morphological characters surveyed for the study were mainly those used by Mayo (1986) to study the classification of the genus *Philodendron*, and diagnostic characters for the sections of subgenus *Philodendron* used by Croat (1997). Molecular data support the three subgenera as monophyletic. However the morphological data presented in Table 4 do not clearly support the monophyly of subgenera *Pteromischum* and *Meconostigma*. The principal morphological characters used to distinguish subgenus *Pteromischum* are the presence of polyphyllus sympodial growth in the adult vegetative shoots, with many leaves per stem article, the absence of cataphylls (or inconspicuous) and leaves that have extensively sheathed petioles and are usually lanceolate to elliptical (Grayum, 1996). According to Croat (1997), except for the axile placentation and many ovules per locule, there are no other characters that completely characterized subgenus *Philodendron*. In contrast in the cladistic analysis (based on 15 species) of morphological characters by Mayo (1986: 430–431, fig. 9.2), subgenus *Philodedron* is supported as by the presence of adjacent thecae and of secreting resin in the spadix with large lumens and strongly papillose epithelia. Of the 15 morphological characters surveyed in our analysis, two synapomorphies are evident (Table 5): the long spadix middle sterile zone (character 7) and the presence of a sterile zone at the apex of the spadix (character 9), both diagnostic for subgenus *Meconostigma*, which is defined in part by its arborescent stem and its staminodial zone on the spadix equal to or longer than the pistillate zone (Mayo, 1991).

Subgenus Philodendron

Even if there is little resolution in the topologies, our results show some agreement between the molecular results and the classification of Croat (1997) (Fig. 4).

Clade 1 groups nearly all sampled members of section *Baursia* (Fig. 4). The absence of conspicuous primary lateral veins (character 11) and lanceolate leaves (character 12) are the main defining characters for this section: all species surveyed in this group have them (Table 5). For these two characters, there are, respectively, one (*P. martianum*) and two (*P. martianum* and *P. fragrantissimum*) species with the same character state elsewhere in the phylogeny, and all are phylogenetically close to the *Baursia* clade.

These molecular results support the observations of Mayo (1986) who found that in two species of sect *Baursia* (*P. insigne*, *P. longilaminatum*) the anatomy of the gynoecium and of resin canal in the spadix is very distinct from other species studied. This reinforces the traditional taxonomic recognition of the section *Baursia* (Mayo, 1991). Our results support the inclusion of *P. callosum* in section *Baursia* as initially proposed by Krause (1913). This interpretation is also supported by a similar mode of growth between *P. callosum* and *P. insigne* (D. Barabé, unpubl. results).

Group A, which is paraphyletic, contains a majority of species of section *Philodendron*, the largest section of the subgenus and morphologically very diverse. This group includes clusters that are not supported by bootstrap values, and not present in the strict consensus tree (Fig. 2). *Philodendron pinnatifidum,* tentatively placed in section *Polytomium* (Croat, 1997) because of its pinnatifid leaves, groups with species from section *Philodendron* in our analyses, as originally proposed by Krause (1913). There are some other problematic species. *Philodendron mamei* and *P. sodiroi* are known to be closely related to *P. gloriosum* in section *Calostigma* (Croat, 1997). Our analyses suggest a close association of *P. mamei*, *P. sodiroi* and *P. gloriosum* with typical members of section *Philodendron*, such as *P. findens* and *P. ornatum*. Many problematic species that occur in Group A were sequenced for only one of the two nuclear markers.

The large proportion of missing data in the combined matrix might explain the weak bootstrap values and, consequently, the problematical position of certain species as for the disjoint position of the two samples of *P. ornatum* (Fig. 4). More molecular and morphological data are needed to confirm the sectional affiliation of certain species.

There is no clear trend in clade 2. Although species from clade 2 look alike morphologically (Table 5), they do not seem to share particular characters among those surveyed. The sections in which they have been placed by previous authors are not known to be particularly close. Let us mention, however, that the two samples species of the section *Schizophyllum* are grouped in the same clade.

Clade 3 contains almost all and only species from sections *Tritomophyllum* and *Polytomium*. Section *Tritomophyllum* is characterized by trisected or ternate leaves and 1–2 ovules per locules and section *Polytomium* by pinnatifid or bipinnatifid leaves with somewhat terete petioles. *Philodendron grandifolium* with its cordate leaves and terete petiole doubtfully belongs to the group according to our molecular analyses. As section *Tritomophyllum* is morphologically similar to subsection *Bulaoana* of section *Calostigma*, it is very difficult, or impossible, to distinguish the two groups (Croat, 1997). This could explain why *P. anisotomum* (section *Tritomophyllum*) with its three-lobed leaves and great resemblance to *P. tripartitum*, is not included in this clade based on the molecular data, but with section *Calostigma* species (clade 5) [*Philodendron barrosoanum* and *P. hylaeae* have been placed by previous taxonomists in either *Calostigma* or *Tritomophyllum*. Our results preclude their assignment to section *Calostigma*, now called *Macrobelium* (Sakuragui *et al*., 2005)].

Clade 4 is dominated by species of section *Calostigma*. This section is a large group with basal or subbasal placentation and many ovules per locules (Sakuragui, 2001). Sections *Calostigma* and *Philodendron* share many characteristics and there are no clear characters to differentiate between these two sections. The two species from another section that are included in the *Calostigma* clade are *P. angustisectum* and *P. simsii*, respectively, from section *Polytonium* and *Philodendron*, two sections that are not very well defined in our cladogramm. However, our results are not strongly supported and more molecular data, along with a morphological revision of these species, are needed to confirm our results.

CONCLUSION

Although the chloroplast marker was not variable enough to resolve the phylogeny, the analyses of the two ribosomal DNA regions resulted in well-resolved and -supported topologies. Because the position of the genus *Homalomena* is still ambiguous, both *Philodendron* and *Homalomena* should be revised together to clarify their relationship. Relationships in the genus *Philodendron* are mostly congruent with previous classifications based on morphological characters. All three subgenera as defined by morphological characters are monophyletic in our molecular analyses. In subgenus *Philodendron*, the species that are not grouped with members of the same section were generally those that were difficult to place in one section or another using morphological characters or species where only one of the two nuclear markers was sequenced. As no revision of the entire genus *Philodendron* has been published since Krause (1913), it would be interesting to undertake a global phylogenetic revision. Until this work is performed, we consider that the morphological characters used as diagnostic for the three subgenera and for the sections in subgenus *Philodendron* are useful but not infallible. Investigation of more molecular markers would help to better resolve relationships between the genera *Philodendron* and *Homalomena*, and among species of subgenus *Philodendron*.

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