Is There Such a Thing as *Kalmia* × *Rhododendron*?

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ABSTRACT. Two putative hybrids between *Kalmia* and *Rhododendron*, their suspected progenitor species and related taxa were submitted to DNA sequencing of cpDNA trnL-F and nrDNA ITS regions in order to test whether there was DNA sequence evidence both for hybridization per se and for the direction of the cross should one be evident. Comparison of eight DNA sequences from these putative hybrids with *Rhododendron* and *Kalmia* species showed clear evidence of origin within *Rhododendron*. No evidence of *Kalmia* DNA was detected. These putative intergeneric hybrids appear to be mutants of *Rhododendron* and not of hybrid origin.

The hybrid of *Kalmia* and *Rhododendron* is the most genetically distant cross recorded in the *Ericaceae*. Three selections are attributed to this intergeneric hybrid. To date there have been no investigations into the status of these hybrids although the plants persist in cultivation.

Of several claimed intergeneric hybrids in the *Ericaceae*, the only ones that stand up to rigorous inspection are within tribe *Phyllodoceae* Drude, Engl. & Prantl. These are × *Kalmiothamnus*, × *Phylliopsis* and × *Phyllothamnus* and they represent crosses between *Kalmiopsis*, *Phyllodoce* and *Rhodothamnus*. This interfertility reflects the close relationship between these three genera. The only cross in this group that has not yet been performed successfully is that between *Kalmiopsis* and *Phyllodoce* (Starling, 1982).

Intergeneric crosses in other sections of the *Ericaceae* have all proved to be less resilient to taxonomic re-alignments. × *Gaulnettya* resides in *Gaultheria* now that *Pernettya* is sunk, × *Ledodendron* resides in *Rhododendron* now that *Ledum* is sunk and *Bruckenthalia* × *Erica* resides in *Erica* now that *Bruckenthalia* is sunk. × *Ericalluna* merely proved to be an abnormal *Erica*, not a hybrid

with *Calluna*. This leaves us with one outstanding putative hybrid, that between *Kalmia* and *Rhododendron*. The former belongs to tribe *Phyllodoceae* and the latter to tribe *Rhodoreae* DC. ex Duby. Kron et al. (2002) show that these two tribes are quite distantly related. For example, they are no more related to each other than either is to *Empetreae* D. Don (which includes *Empetrum*). However, a hybrid between the two genera has been reported on two occasions with different *Rhododendron* parents.

The first reputed cross between *Kalmia* and *Rhododendron* was made in the 1950s by Halfdan Lem (1885–1969) in the USA, allegedly between *K. latifolia* and *R. williamsianum* (Pierce, 1974). The hybrid was reported as having “pinkish-white, cup-like flowers of all kalmias, but with a larger leaf resembling the male parent, *R. williamsianum*.” (Pierce, 1974). This established both the diagnostic characters of the hybrid and the direction of the cross. The one plant resulting from the hybridization was named ‘No Suchianum’ (sometimes styled as ‘Nosuchianum’) in jest by Warren Berg in 1973. Unfortunately, when the cultivar name was brought to the attention of International Cultivar Registration Authority for *Rhododendron* in 1996 it was noted that it fell foul of Article 17.9 of the *International Code of Nomenclature for Cultivated Plants* (Trehane et al., 1995) because it is styled in Latin. Therefore a new name, ‘Everlasting’, was coined by Pierce (Murray, 1996 in litt.). It is quite widely cultivated by enthusiasts in north-west USA (Halligan, 1994) and is favored for its long flowering season, perhaps caused by its apparent sterility, and its seemingly curious origin. ‘Everlasting’ is widely regarded as

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Table 1. Accession data for plant material used in DNA sequencing.

Name	Source	Origin	Accession no.	EMBL ID no.	
				ITS	trnL-F
‘Everlasting’ a and b	RHS Garden, Wisley	Cult.	W20012690	AJ626912, AJ626913	AJ626918, AJ626919
Hillier taxon a and b	Hillier Gardens & Arboretum	Cult.	H19841501	AJ626914, AJ626915	AJ626920, AJ626921
<i>K. latifolia</i> a	RHS Garden, Wisley	Cult.	W951916	AJ626905	AJ626916
<i>K. latifolia</i> b	RHS Garden, Wisley	Cult.	W960618	AJ626906, AJ626907	AJ626917
<i>R. williamsianum</i> a	RHS Garden, Rosemoor	Cult.	R960393	AJ626909	AJ626923
<i>R. williamsianum</i> b	RHS Garden, Rosemoor	Cult.	R888391	AJ626910	AJ626924
<i>R. williamsianum</i> c	Glendoick Gardens	Wild	None	AJ626911	AJ626925
<i>R. maximum</i>	Glendoick Gardens	Wild	None	AJ626908	AJ626922

Table 2. EMBL accessions used in analysis of the cpDNA trnL-F region

Species	EMBL ID	Source
<i>Bejaria aestuans</i>	AF394264	Gao et al., 2003
<i>Cassiope fastigiata</i>	AF394265	Gao et al., 2003
<i>Ledum palustre</i> var. <i>palustre</i>	AF394252	Gao et al., 2003
<i>Menziesia ciliicalyx</i> var. <i>multiflora</i>	AF452223	Gao et al., 2003
<i>Menziesia pilosa</i>	AF452224	Gao et al., 2003
<i>Rhododendron albiflorum</i>	AF394266	Gao et al., 2003
<i>Rhododendron albrechtii</i>	AF452214	Gao et al., 2003
<i>Rhododendron boninense</i>	AB038835, AB038885	Ikenoue H.
<i>Rhododendron brachycarpum</i>	AB038847, AB038897	Ikenoue H.
<i>Rhododendron camtschaticum</i>	AF394258	Gao et al., 2003
<i>Rhododendron championae</i> var. <i>ovatifolium</i>	AF452189	Gao et al., 2003
<i>Rhododendron chilanshanense</i>	AB038825, AB038875	Ikenoue H.
<i>Rhododendron decandrum</i>	AB038809, AB038859	Ikenoue H.
<i>Rhododendron degronianum</i>	AB038845, AB038895	Ikenoue H.
<i>Rhododendron dilatatum</i>	AB038807, AB038857	Ikenoue H.
<i>Rhododendron duclouxii</i>	AF452210	Gao et al., 2003
<i>Rhododendron ellipticum</i>	AF288670	Hwang S.-Y., Hsu K.-K.
<i>Rhododendron farrerae</i>	AB038799, AB038849	Ikenoue H.
<i>Rhododendron ferrugineum</i>	AF394254	Gao et al., 2003
<i>Rhododendron fortunei</i>	AF394247	Gao L.M.
<i>Rhododendron hancockii</i>	AF452192	Gao et al., 2003
<i>Rhododendron henryi</i>	AF452193	Gao et al., 2003
<i>Rhododendron hongkongense</i>	AF394260	Gao et al., 2003
<i>Rhododendron indicum</i>	AB038829, AB038879	Ikenoue H.
<i>Rhododendron javanicum</i>	AF394256	Gao L.M.
<i>Rhododendron kaempferi</i>	AB038828, AB038878	Ikenoue H.
<i>Rhododendron keiskei</i>	AB038842, AB038892	Ikenoue H.
<i>Rhododendron kiusianum</i>	AF394267	Gao et al., 2003
<i>Rhododendron kiyosumense</i>	AB038822, AB038872	Ikenoue H.
<i>Rhododendron latouchiae</i>	AF394262	Gao L.M.
<i>Rhododendron luteum</i>	AF394263	Gao et al., 2003
<i>Rhododendron mackenzianum</i>	AF452196	Gao et al., 2003
<i>Rhododendron mariesii</i>	AB038800, AB038850	Ikenoue H.
<i>Rhododendron micranthum</i>	AB038843, AB038893	Ikenoue H.
<i>Rhododendron molle</i>	AB038841, AB038891	Ikenoue H.
<i>Rhododendron moulmainense</i>	AF452194	Gao et al., 2003
<i>Rhododendron mucronulatum</i>	AB038894	Ikenoue H.
<i>Rhododendron neriiflorum</i>	AF394248	Gao et al., 2003
<i>Rhododendron nipponicum</i>	AF452215	Gao et al., 2003
<i>Rhododendron occidentale</i>	AF396216, AF396215	Fritsch P.W., Morton C.M., Chen T., Meldrum C.
<i>Rhododendron oldhamii</i>	AB038832, AB038882	Ikenoue H., Kurashige Y., Ueda K.
<i>Rhododendron ovatum</i>	AF452204	Gao et al., 2003
<i>Rhododendron pachypodum</i>	AF394249	Gao L.M.
<i>Rhododendron pentaphyllum</i>	AB038840, AB038890	Ikenoue H., Kurashige Y., Ueda K.
<i>Rhododendron ponticum</i>	AF452222	Gao et al., 2003
<i>Rhododendron primuliflorum</i>	AF394255	Gao et al., 2003
<i>Rhododendron quinquefolium</i>	AB038838, AB038888	Ikenoue H.
<i>Rhododendron racemosum</i>	AF394250	Gao L.M.
<i>Rhododendron redowskianum</i>	AF394257	Gao et al., 2003
<i>Rhododendron reticulatum</i>	AB038824, AB038874	Ikenoue H., Kurashige Y., Ueda K.
<i>Rhododendron rubropilosum</i>	AB038830, AB038880	Ikenoue H., Kurashige Y., Ueda K.
<i>Rhododendron sanctum</i>	AB038804, AB038853	Ikenoue H.
<i>Rhododendron santapaui</i>	AF452207	Gao et al., 2003
<i>Rhododendron schlippenbachii</i>	AF452213	Gao et al., 2003
<i>Rhododendron semibarbatum</i>	AF452206	Gao et al., 2003
<i>Rhododendron serpyllifolium</i>	AB038834, AB038884	Ikenoue H., Kurashige Y., Ueda K.
<i>Rhododendron simsii</i>	AF452216	Gao et al., 2003
<i>Rhododendron spiciferum</i>	AF452208	Gao et al., 2003
<i>Rhododendron spinuliferum</i>	AF452209	Gao et al., 2003
<i>Rhododendron stamineum</i>	AF394261	Gao L.M.
<i>Rhododendron stamineum</i> var. <i>gaozhaiense</i>	AF452197	Gao et al., 2003
<i>Rhododendron subestipitatum</i>	AF452190	Gao et al., 2003
<i>Rhododendron trichocladum</i>	AF394253	Gao et al., 2003
<i>Rhododendron tsurugisanense</i>	AB038871, AB038821	Ikenoue H.
<i>Rhododendron tsusiophyllum</i>	AF452217	Gao et al., 2003
<i>Rhododendron vialii</i>	AF452205	Gao et al., 2003
<i>Rhododendron wadanum</i>	AF452218	Gao et al., 2003
<i>Rhododendron weyrichii</i>	AB038802, AB038852	Ikenoue H.
<i>Rhododendron yakumontanum</i>	AB038820, AB038870	Ikenoue H.

Table 3. EMBL accessions used in analysis of nrDNA ITS region

Species	EMBL ID	Source
<i>Gaultheria itoana</i>	AF432430	Tsai C.C., Chen C.H., Chou C.H.
<i>Gaultheria taiwaniana</i>	AF432429	Tsai C.C., Chen C.H., Chou C.H.
<i>Kalmia angustifolia</i>	U48599	Kron K.A., King J.M.
<i>Kalmia cuneata</i>	U48603	Kron K.A., King J.M.
<i>Kalmia hirsuta</i>	U48601	Kron K.A., King J.M.
<i>Kalmia latifolia</i>	U48600	Kron K.A., King J.M.
<i>Kalmia microphylla</i>	U48598	Kron K.A., King J.M.
<i>Kalmia occidentalis</i>	U48602	Kron K.A., King J.M.
<i>Rhododendron alabamense</i>	AF072478	Scheiber S.M., Jarret R.L., Robacker C.D.
<i>Rhododendron albiflorum</i>	RA28S58S	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron albrechtii</i>	RARRNAIT7	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron anthopogon</i>	RA58S28SR	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron arborescens</i>	AF072477	Scheiber S.M., Jarret R.L., Robacker C.D.
<i>Rhododendron argyrophyllum</i>	RA58S28S	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron atlanticum</i>	AF072479	Scheiber S.M., Jarret R.L., Robacker C.D.
<i>Rhododendron breviperulatum</i>	AF285853	Tsai C.C., Chen C.H., Huang S.C.
<i>Rhododendron camtschaticum</i>	RC58S28S	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron canadense</i>	RCRRNAIT9	Volckaert G.
<i>Rhododendron ellipticum</i>	AF285841	Tsai C.C., Chen C.H., Huang S.C.
<i>Rhododendron ferrugineum</i>	RF58S28S1	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron flammeum</i>	AF072483	Scheiber S.M., Jarret R.L., Robacker C.D.
<i>Rhododendron formosanum</i>	AF297190	Shih B.-L., Yang Y.-P., Chaw S.-M.
<i>Rhododendron hongkongense</i>	RH58S28S	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron hyperythrum</i>	AF297192	Shih B.-L., Yang Y.-P., Chaw S.-M.
<i>Rhododendron javanicum</i>	RJ58S28S	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron kaempferi</i>	AB080082	Scheiber S.M., Jarret R.L., Robacker C.D.
<i>Rhododendron kawakamii</i>	AF432420	Tsai C.C., Chen C.H., Huang S.C.
<i>Rhododendron kiusianum</i>	RKRRNAIT3	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron lamprophyllum</i>	AF285855	Tsai C.C., Chen C.H., Huang S.C.
<i>Rhododendron lasiostylum</i>	AF285845	Tsai C.C., Chen C.H., Huang S.C.
<i>Rhododendron leptanthum</i>	RL58S28S	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron luteum</i>	AF072485	Scheiber S.M., Jarret R.L., Robacker C.D.
<i>Rhododendron mariesii</i>	AF285844	Tsai C.C., Chen C.H., Huang S.C.
<i>Rhododendron molle</i>	RM58S28SR	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron morii</i>	AF297198	Shih B.-L., Yang Y.-P., Chaw S.-M.
<i>Rhododendron moulmainense</i>	RM58S28S	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron occidentale</i>	AF072487	Scheiber S.M., Jarret R.L., Robacker C.D.
<i>Rhododendron oldhamii</i>	AF285843	Tsai C.C., Chen C.H., Huang S.C.
<i>Rhododendron ovatum</i>	AF393424	Gao L.M., Li D.L., Yang J.B.
<i>Rhododendron ponticum</i>	RP58S28S	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron pseudochrysanthum</i>	AF297196	Shih B.-L., Yang Y.-P., Chaw S.-M.
<i>Rhododendron reticulatum</i>	RRRRNAIT6	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron rubropilosum</i>	AF285849	Tsai C.C., Chen C.H., Huang S.C.
<i>Rhododendron rubropunctatum</i>	AF432442	Tsai C.C., Chen C.H., Chou C.H.
<i>Rhododendron schlippenbachii</i>	RSRRNAIT8	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron semibarbatum</i>	AB080083	Scheiber S.M., Jarret R.L., Robacker C.D.
<i>Rhododendron simsii</i>	AF285848	Tsai C.C., Chen C.H., Huang S.C.
<i>Rhododendron taiwanalpinum</i>	AF432479	Tsai C.C., Chen C.H., Huang S.C.
<i>Rhododendron tschonoskii</i>	RTRRNAIT4	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron tsusiophyllum</i>	RT58S28S	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.
<i>Rhododendron vaseyi</i>	AF072491	Scheiber S.M., Jarret R.L., Robacker C.D.
<i>Rhododendron viscosum</i>	AF072492	Scheiber S.M., Jarret R.L., Robacker C.D.
<i>Rhododendron wadanum</i>	RWRRNAIT5	Volckaert G.
<i>Rhododendron yedoense</i>	RYRRNAIT1	Aert R., Hyam R., Chamberlain D., Karp A., Volckaert G.

being an intergeneric hybrid on the basis of its claimed parentage, apparent sterility and the seemingly *Kalmia*-like characters of a shallow saucer-shaped corolla and widely spreading stamens. Despite the corolla and stamen characters there do not appear to be any other features of the flower that suggest an affinity with *Kalmia*. 'Everlasting' was reputedly crossed with *R. arboreum* subsp. *delavayi* resulting in a cultivar called 'Brilliant Abbé' (Anon, 1985). The latter reference erroneously lists one parent as 'Brilliantcy' (Murray, 1996 in litt.).

The second reputed cross between *Kalmia* and *Rhododendron* is represented by a plant (hereafter referred to as the Hillier taxon) in the collection at the Sir Harold Hillier Gardens and Arboretum in England. It was thought to represent a hybrid between *K. latifolia* and *R. maximum* originating in America (Hillier and Sons, 1981) but subsequent editions (e.g., Hillier and Coombes, 2002) have been more cautious and listed it under *R. maximum*. Likewise, Jaynes (1997) has questioned its intergeneric status. The Hillier taxon is also grown at Arboretum Trompenburg in the Netherlands where it is listed as an intergeneric hybrid (van Hoey Smith, 2001) and at the US National Arboretum (Jaynes, 1997). The reported evidence for hybridity is on the basis of the tendency of its flower buds to abort (Coombes, pers. comm.; Fortgens, pers. comm.) and its long petiole relative to length of leaf lamina, the latter character is reminiscent of *K. latifolia*. It has been suggested that its reluctance to flower is because *Rhododendron* flower buds develop on shoots of the previous season whereas those of *Kalmia* develop on shoots of the current season.

Claims for intergeneric status of various hybrids are made on a fairly regular basis by horticulturists. Such pronouncements are usually worth investigating, not least because of what they may tell us about the relatedness of the genera in question. These two cases demand investigation because, if their parental status could be proved, they would represent the most distant intergeneric hybrids in *Ericaceae* and this would have important taxonomic implications. Additionally, as *Kalmia* and *Rhododendron* are widely grown and appreciated in ornamental horticulture, there would be interesting potential breeding consequences between these two attractive woody genera. As International Cultivar Registration Authority for the genus *Rhododendron*, the Royal Horticultural Society has an interest in putative hybrids between *Rhododendron* and other genera. We therefore decided to submit material of the two available cultivars and related species to DNA sequencing of the trnL-F region and ITS regions in order to test whether there was DNA sequence evidence both for hybridization per se and for the direction of the cross should one be evident.

Materials and Methods

Plant material was obtained from the Royal Horticultural Society's gardens at Wisley and Rosemoor (England), the Sir Harold Hillier

Gardens and Arboretum (England) and Glendoick Gardens (Scotland) (Table 1). Leaves were collected on to silica gel and stored at room temperature.

DNA was extracted using the CTAB technique (Doyle and Doyle, 1987) and stored in TE buffer at 5 °C while in use. PCR amplification of the nrDNA ITS regions followed Compton et al. (1998a) and cpDNA trnL-F followed Compton et al. (1998b). DNA sequencing, sequence editing and DNA sequence alignment was performed following Compton et al. (1998b).

Additional DNA sequences were available for both ITS and trnL-F regions from the EMBL/Genbank/DBJ database of nucleotide sequences. The analysis of these sequences, in addition to our own new sequences, was necessary in order to answer the question of relationships in the absence of a published phylogeny. Species and identification numbers are given in Tables 2 and 3.

Alignments were saved as Nexus files and analyzed in PAUP*4.0b10 (Swofford, 2002) under Parsimony. The trnL-F

Fig. 1. One of 1440 most parsimonious trees resulting from analysis of the cpDNA trnL-F sequence data. Heavy lines indicate bootstrap support >50%

analysis consisted of 79 taxa including 2 outgroups (*Cassiope fastigiata* and *Bejaria aestuans*) and 930 characters. The ITS analysis consisted of 64 taxa including two outgroups (*Gaultheria itoana* and *G. taiwaniana*) and 709 characters. Analyses were conducted separately because the relationship of hybrid material would differ with the pattern of inheritance of the DNA region and conflict would result in artifactually low resolution of the cladogram. Heuristic searches were performed using 100 sequence addition replicates and TBR. Most parsimonious trees were stored and a strict consensus established. Clade support was established using 1000 Bootstrap replicates using the fast swapping option.

Results

The cpDNA trnL-F analysis resulted in 1440 most parsimonious trees of 329 steps (C.I.0.805, R.I. 0.908) differing in the placement of a small number of species within groups that showed very little sequence divergence. The first most parsimonious tree is shown here (Fig. 1) with bootstrap support marked on appropriate branches. *Rhododendron* is a paraphyletic group that contains three species (*R. camtschaticum*, *R. redowskianum*, *R. albrechtii*) distantly related to the main generic diversification (clade A). Within this clade species of *Ledum* and *Menziesia* are nested. Clade A contains two main groups one of which includes both putative intergeneric hybrids. 'Everlasting' is identical in sequence to *R. brachycarpum* and the Hillier taxon is identical in sequence to *R. maximum*.

The nrDNA ITS analysis resulted in 231655 most parsimonious trees of 532 steps (C.I. 0.742, R.I. 0.847) differing in the placement of a small number of species within groups that showed very little sequence divergence. The first most parsimonious tree is shown here (Fig. 2) with bootstrap support marked on appropriate branches. *Rhododendron* forms a monophyletic group in which *R. camtschaticum* is a sister lineage to the rest of the genus. The same two major groups can be identified within *Rhododendron* even though the species sampling is somewhat different. Again, both putative hybrids occur in the same clade. 'Everlasting' has no exact match (note *R. brachycarpum* was not available for this analysis) but groups with *R. williamsianum* and its close relatives. The Hillier taxon again shows an exact match to *R. maximum*.

In both analyses the *Kalmia* samples showed very high sequence divergence and formed a group separate from *Rhododendron* and sister to the outgroups. Within the genus *Rhododendron* the level of sequence divergence was low compared with *Kalmia*. The analysis demonstrated that current sections within *Rhododendron* do not match the infrageneric groups found using molecular analysis. The consequence of this is that we could not use the current classification to direct our sampling.

Discussion

'EVERLASTING'. Pierce (1974) records *Kalmia latifolia* as the seed parent of 'Everlasting', although he is not the originator of this cultivar. Evidence from cpDNA trnL-F sequence data indicates a seed parent in *Rhododendron* and an exact match with *R. brachycarpum* for one replicate of 'Everlasting'. The inference is that at least the seed parent was either *R. brachycarpum*, a close relative, or hybrid, of it. This indicates that the record of the direction of the hybrid by Pierce can not be correct without unusual inheritance of the cpDNA from the male parent. The evidence from nrDNA ITS again shows very close affinity with *Rhododendron* species, particularly the *R. williamsianum* group. The ITS analysis lacked *R. brachycarpum* as material was not available. The combination of both chloroplast and nuclear DNA

Fig. 2. One of 231655 most parsimonious trees resulting from analysis of the nrDNA ITS data. Heavy lines indicate bootstrap support >50%

evidence indicates that *Kalmia* has not contributed to the genetic makeup of 'Everlasting' but that the cultivar is derived from within a group of closely related *Rhododendron* species.

HILLIER TAXON. The Hillier taxon is of putative *R. maximum* × *K. latifolia* origin (Hillier and Sons, 1981). Both samples of this material group with *R. maximum* in the cpDNA trnL-F analysis and have identical sequence to it. This would allow *R. maximum* as the putative seed parent. The evidence from nrDNA ITS again shows very close affinity with *Rhododendron* species and again an exact match of one sample (Hillier taxon a) with *R. maximum*. The ITS data show no evidence of hybridization with *Kalmia* and indicate strongly that this taxon is not of hybrid origin. Like 'Everlasting' only *Rhododendron* shows evidence of genetic contribution to this taxon.

HYBRID STATUS. Evidence of female parentage for each of the two putative hybrids was established using cpDNA trnL-F sequencing based on the usual female-only mode of inheritance of this DNA (Palmer, 1985) and a neutral pattern of nucleotide substitution (Bakker et al., 2000). It is evident that the putative hybrids both are nested well within the genus *Rhododendron* and consequently are inferred to have had a *Rhododendron* seed parent. The sequence divergence among closely related species is very low and sometimes zero. The consequence is that we can be sure of the female *Rhododendron* origin of each putative hybrid but can confirm the identity only to species group with confidence. The nrDNA ITS sequences can be expected to show inheritance from both parents, particularly as these plants are the F1 generation and there has been no chance of segregation. *Kalmia* and *Rhododendron* show considerable divergence in ITS sequence and recombination of these differing ITS types would be easily detected. In the Hillier taxon and 'Everlasting' the nrDNA ITS sequence shows a close match with species in *Rhododendron*. Again, the levels of sequence divergence allow identification of the parents to species group only.

The stated origin of 'Everlasting' as *Kalmia latifolia* (female) and *Rhododendron williamsianum* (male) (Pierce, 1974) is refuted by the DNA sequence evidence. Neither sequence shows origin in *Kalmia* and both show identity with at least one species of *Rhododendron* that was sampled. The Hillier taxon also shows no sign of *Kalmia* in either DNA sequence and a match to *Rhododendron maximum* in both sequences.

When treated as a *Rhododendron*, 'Everlasting' can be identified to subsection *Pontica* Sleumer in section *Ponticum* G. Don in the key to subgenus *Hymenanthes* (Blume) K. Koch (Chamberlain, 1982), except for the corolla lobe to tube ratio. The morphology of this plant fits the placement of the cultivar into subsection *Pontica* very well. Thus we see concordance of the molecular and morphological evidence. The open corolla tube is probably the result of a mutation in the genes controlling floral development. The Hillier taxon sometimes produces flower buds but these abort, therefore the lack of available flowers prevents this being keyed out. The evidence suggests that this, like 'Everlasting', is a chance mutant of a *Rhododendron*.

The balance of evidence, both direct and indirect, supports the recognition of these unusual plants as *Rhododendron* mutants. The desire to see new and novel hybrids between two genera of the spectacular shrubby *Ericaceae* may have influenced uncritical reports of hybridization. It is notable that in neither case has anyone directly claimed in print to have made the hybrid. The driving evidence to suggest hybridity has been minor changes in floral structure, leaf shape and lack of seed production.

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