
CLASSIFICATION, ORIGIN, AND DIVERSIFICATION OF THE NEW ZEALAND HEBES (SCROPHULARIACEAE)¹

Steven J. Wagstaff,² Michael J. Bayly,³
Philip J. Garnock-Jones,⁴
and Dirk C. Albach⁵

ABSTRACT

The New Zealand hebes (Scrophulariaceae) are members of a large Southern Hemisphere clade nested within *Veronica*. Analysis of ITS and *rbcL* sequences suggests that the New Zealand species are derived from a single common ancestor that arrived via long-distance dispersal. After the establishment of this initial founder population in New Zealand, the hebes have undergone at least two major episodes of diversification, giving rise to six clades. The great degree of morphological diversity in the New Zealand hebes contrasts with a corresponding low level of sequence divergence. New Zealand was a source of new emigrants to other regions in the South Pacific that were preadapted to high mountains or forest margins. Our results suggest that two instances of long-distance dispersal from New Zealand to South America, at least one instance from New Zealand to Australia, and one instance from New Zealand to New Guinea have occurred relatively recently. Shorter hops to the Chatham Islands and the subantarctic islands are also supported by the sequence data.

Key words: *Hebe*, ITS, New Zealand, phylogenetic analysis, *rbcL*, Scrophulariaceae, *Veronica*.

Long-distance dispersal has a profound influence on the evolution of insular floras (Carlquist, 1974), and there is substantial evidence suggesting that it occurs relatively frequently (Godley, 1967; Pole, 1994). One of the most remarkable examples of dispersal followed by adaptive evolution on islands is the New Zealand hebes (Scrophulariaceae). Wagstaff and Garnock-Jones (1998, 2000) suggested that the New Zealand hebes are the descendants of a small founder population that may have been derived from a single seed. They proposed that combined influences of inbreeding, genetic drift, and strong selection acting upon small populations have probably played a major role in the rapid diversification of the group.

The hebes are one of the largest and most ecologically diverse plant groups in New Zealand, including over 120 species, with outlier populations in eastern Australia, Tasmania, New Guinea, Rapa Island, and South America. They range from alpine cushion-forming plants (Fig. 5D) to lowland woody shrubs or small trees (Fig. 5M, R, S), and

in New Zealand are conspicuous elements in most terrestrial ecosystems except forests and wetlands. Species such as *Hebe armstrongii*, *H. cupressoides*, and *H. speciosa* have patchy or localized distributions and are considered rare or endangered; about 70% of the species are confined to small regions within New Zealand.

The New Zealand hebes were formerly included in a broadly defined circumscription of the genus *Veronica* (Wettstein, 1891; Cheeseman, 1925), but recent flora and taxonomic treatments (Ashwin & Moore in Allan, 1961; Garnock-Jones, 1993a, b; Heads, 1994a, b) recognize less inclusive groups (see Table 1), usually accepting four genera in New Zealand: *Chionohebe*, *Hebe*, *Heliohebe*, and *Parahеbe* (Garnock-Jones, 1993a, b). Heads (1987) described an additional genus, *Leonohebe*. Although we do not accept his wide circumscription of that genus, the name *Leonohebe* could be applied to a small clade of four or five species that is supported by the analyses of Wagstaff and Garnock-Jones (1998, 2000).

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²Landcare Research, P.O. Box 69, Lincoln 8152, New Zealand. wagstaffs@landcare.cri.nz.

³Museum of New Zealand Te Papa Tongarewa, P.O. Box 467, Wellington, New Zealand.

⁴School of Biological Sciences and Island Biology Research Programme, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand.

⁵Botanisches Institut der Universität Wien, Rennweg 14, 1030 Wien, Austria.

Table 1. Classifications of New Zealand hebes. The New Zealand species were placed in three sections of Wettstein's (1891) treatment of *Veronica*, and Cheeseman (1925) placed them in two divisions of *Veronica*.

Wettstein (1891)	Cheeseman (1925)	Ashwin & Moore in Allan (1961) ¹	Heads (1987, 1994b)	Garnock-Jones (1993a, b)
Veronica	Veronica			
sect. <i>Pygmea</i>	Division <i>Pygmea</i>	Pygmea	Chionohebe	Chionohebe Including <i>Parahebe</i> "Group B")
sect. <i>Hebe</i>			Leonohebe sect. <i>Densifoliae</i>	
	Division <i>Hebe</i>	Hebe		Hebe
		"Semiflagriformes"	sect. <i>Leonohebe</i>	"Semiflagriformes"
		"Connatae"	sect. <i>Connatae</i>	"Connatae"
			sect. <i>Apiti</i>	
		"Flagriformes"	sect. <i>Flagriformes</i>	"Flagriformes"
			sect. <i>Aromaticae</i>	
			sect. <i>Salicornioides</i>	
		"Buxifoliatae"	sect. <i>Buxifoliatae</i>	"Buxifoliatae"
			Hebe	
		"Subdistichae"	sect. <i>Subdistichae</i>	sect. <i>Subdistichae</i>
		"Subcarnosae"	sect. <i>Glaucæ</i>	sect. <i>Glaucæ</i>
			sect. <i>Hebe</i>	sect. <i>Hebe</i>
		"Apertae"	ser. <i>Hebe</i>	ser. <i>Hebe</i>
		"Occlusae"	ser. <i>Occlusae</i>	ser. <i>Occlusae</i>
			Parahebe	
		"Grandiflorae"		"Grandiflorae"
		"Paniculatae"	sect. <i>Paniculatae</i>	Heliohebe
sect. <i>Chamaedrys</i>	Division <i>Euveronica</i>	Parahebe		Parahebe
		"Group A, B, C"		"Group A, C"
sect. <i>Labiatooides</i>	—	—		Derwentia
sect. <i>Paederota</i>	—	—	—	—
sect. <i>Paederotooides</i>	—	—	—	—
sect. <i>Pseudolysimachia</i>	—	—	—	—
sect. <i>Veronicastrum</i>	—	—	—	—
sect. <i>Omphalospora</i>	—	—	—	—
sect. <i>Beccabunga</i>	—	—	—	—

¹ In the *Flora of New Zealand* Volume 1 (Allan, 1961), M. B. Ashwin prepared the treatment of *Parahebe*, *Pygmea*, and the informal grouping "Flagriformes" of *Hebe*. The remainder of the *Hebe* treatment, including the informal synopsis, was prepared by L. B. Moore.

This research contributes to ongoing efforts to create a phylogenetic classification of Scrophulariaceae. Olmstead and Reeves (1995) and Olmstead et al. (2001) showed that the Scrophulariaceae, as traditionally circumscribed, are not monophyletic. They identify clades from a dismembered Scrophulariaceae s.l. that could merit formal recognition. In their studies *Veronica* was nested within a large clade they called the Antirrhinaceae *nom. cons. prop.* (Reveal et al., 1999). This large clade was recognized by Olmstead and Reeves (1995) and includes part or all of Bentham's (1876) tribes Digitalaleae, Antirrhineae, Cheloneae, and Gratiroleae, the small tribe Angelonieae, and the small families Callitrichaceae, Globulariaceae (excluding Selaginaceae), Hippuridaceae, and Plantaginaceae.

The aim of this research is to identify well-sup-

ported monophyletic groups among the New Zealand hebes, to improve their classification, infer their origin, and explore underlying processes of diversification. We propose that diversification in the group reflects transoceanic dispersal and adaptive radiation. The hebes have successfully exploited a diversity of ecological niches that were probably created during the recent uplift and glaciation of the mountains of New Zealand.

MATERIALS AND METHODS

Our sampling strategy capitalized on the unique characteristics of *rbcL* and ITS sequences. The plastid encoded gene *rbcL* has relatively few variable sites, which allowed sequence comparisons among distantly related outgroups, and placement

of the hebes within Scrophulariaceae. It is also useful in that a large number of published *rbcL* sequences are available for comparison (see Chase et al., 1993; Källersjö et al., 1998; Olmstead et al., 2001, and references therein). Finally, Albert et al. (1994) and Bremer and Gustafsson (1997) suggested that the gene *rbcL* approaches clock-like behavior in its evolution, and hence the amount of sequence divergence could be used to estimate divergence times. By comparison, the nuclear encoded ITS-region has many more variable sites than *rbcL*, which provides more informative characters to resolve relationships at lower taxonomic levels (Baldwin et al., 1995).

STUDY GROUP

The *rbcL* study group consisted of 33 species including 12 of the New Zealand hebes with at least 1 representative from each of the currently recognized genera, 5 species of *Veronica*, and 1 species of *Veronicastrum*. Nineteen *rbcL* sequences were newly published herein along with 13 published sequences of Antirrhinaceae from Olmstead et al. (2001), and *Nicotiana tabacum* (Solanaceae) was designated as the outgroup (Lin et al., 1986). Seven sequences were considered redundant; even though they were not identical, the resolution of missing data could potentially make them identical. We therefore excluded *Derwentia derwentiana* and *D. perfoliata*, and the New Zealand accessions of *Hebe elliptica* and *H. salicifolia*, from subsequent analyses. Nineteen of the 37 species included in the *rbcL* analysis were also included in the ITS survey.

The ITS study group included 78 sequences, 19 of which were newly published. Among these are 58 representatives of *Chionohebe*, *Derwentia*, *Heliohebe*, and *Parahebe*, including conspecific accessions of *Chionohebe ciliolata* and *C. densifolia* from Australia and New Zealand, *Parahebe lithophila* from Australia, and *P. vandewateri* from New Guinea. Thirty-five species of *Hebe* were also included, and among these were: at least one representative from each of Moore's (in Allan, 1961) informal groups; *H. formosa* from Tasmania; *H. benthamii* from the New Zealand subantarctic islands; *H. barkeri*, *H. chathamica*, and *H. dieffenbachii* from the Chatham Islands (east of the main islands of New Zealand); accessions of *H. elliptica* from both New Zealand and the Falkland Islands; and *H. salicifolia* from both New Zealand and Chile. *Pseudolysimachion*, *Veronica*, *Veronicastrum*, and *Wulfenia* emerged as potential sister groups of the hebes in the analysis of Hong (1984) and Albach and Chase (2001); therefore a total of 19 species representing

these genera were included in our analysis. The Asiatic species *Veronicastrum sibiricum* was designated as the outgroup for the analysis of ITS sequences.

Voucher specimens are listed in Appendix 1, along with collection information, literature citations, and GenBank (<<http://www.ncbi.nlm.nih.gov>>) accession numbers. The complete data sets are available upon request from the first author, and they were deposited in TreeBASE (<<http://www.herbaria.harvard.edu/treebase>>). The study accession number is S623, and the matrix accession numbers are M961 (*rbcL*) and M962 (ITS).

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

Total DNA was extracted from either fresh leaves or leaf fragments dried with silica gel using a modification of the hot CTAB method of Doyle and Doyle (1987). The cpDNA gene *rbcL* and the nrDNA ITS-region [the 3' end of the 18S rDNA gene; internal transcribed spacer -1 (ITS-1); the 5.8S rDNA gene; internal transcribed spacer -2 (ITS-2); and the 5' end of the 28S rDNA gene] were amplified by PCR. Primer sequences and our amplification and sequencing techniques follow Olmstead et al. (1992) for *rbcL*, and Wagstaff and Garnock-Jones (1998) for the ITS-region. Excess primers and unincorporated nucleotides were removed from the PCR products by spin column centrifugation (QIAquick PCR purification kit, QIAGEN Inc.). The purified DNA samples were then labeled with Big Dye terminators (PE Applied Biosystems, The Perkin-Elmer Corp.). Both the forward and reverse DNA strands were sequenced by the Waikato University DNA Sequencing Facility. Contig editing and assembly was accomplished using Sequencher version 3.0 (Gene Codes Corp.).

SEQUENCE ALIGNMENT

The sequence alignment for the ITS-region was facilitated by ClustalX (Thompson et al., 1997). A gap penalty setting of 75 and a gap extension penalty of 6.6 were initially used to identify and position large gaps in the sequence data; then low-scoring segments were realigned using a gap penalty setting of 15 and a gap extension penalty of 6.6 with the removing new gaps option turned on. These settings opened and positioned small gaps. The final alignment was inspected and minor revisions were made manually.

DATA ANALYSIS

The phylogenetic analyses were accomplished using PAUP* version 4.0d65 (Swofford, 1998). The analyses were conducted using the PAUP* settings random addition sequence with 100 replicates, TBR branch swapping, mulpars in effect, and steepest descent. The characters were all unordered and weighted equally, and gaps were treated as missing data.

Support for the inferred clades is given by jackknife percentages (Farris et al., 1996) and by the number of synapomorphies for each group. Jackknife analysis investigates the structure, or phylogenetic signal, in a matrix without permutation, but excludes an assigned fraction of characters, here set to 30%. The jackknife searches were performed with 1000 replications excluding uninformative sites, maxtrees = 10 for each replication; the starting trees were obtained by random addition with one replication for each jackknife replication, TBR branch-swapping, and mulpars in effect.

The relationship between sequence divergence and time for the gene *rbcL* was discussed by Albert et al. (1994) and Bremer and Gustafsson (1997) and was calculated using the equation:

$$\text{substitution rate} = \text{patristic distance}(D_p) / \text{number of nucleotides} / \text{inferred time since cladogenesis.}$$

RESULTS

The *rbcL* sequences were 1402 nucleotides in length (positions 27–1428 in tobacco). Among the 1402 sites included in the *rbcL* matrix, 1103 sites were invariant; 144 were parsimony-uninformative, and 155 characters were parsimony-informative. Missing data accounted for 4.7% of the matrix. Most of the missing data fell in a region at the 5' end of *rbcL*, upstream from the conserved EcoRV restriction site used in cloning some sequences (Olmstead et al., 1992), and in a region downstream from position 1325, the location of a PCR primer site used to amplify some sequences. Most changes (calculated across the maximum parsimony tree shown in Fig. 2) occurred in the third codon position (369); substantially fewer changes occurred in the first (116) and second (47) codon positions. Changes in the third codon position are generally synonymous, and hence are more likely to evolve in a clock-like manner.

The analysis of *rbcL* sequences recovered 9408 maximum parsimony trees distributed in a single island of 529 steps (consistency index = 0.52 excluding uninformative characters, retention index = 0.73); a strict consensus tree is shown in Figure

1, and one of the maximum parsimony trees is shown in Figure 2. Most members of the Antirrhinoaceae form a basal grade in our analysis with *Chionohebe*, *Derwentia*, *Hebe*, *Heliohebe*, *Parahebe*, and *Veronica* forming a clade that receives 100% jackknife support. *V. anagallis-aquatica* is sister to a largely Australasian clade (98% jackknife support) that includes the New Zealand hebes along with *Derwentia*, *Veronica arguta*, and *V. persica*. Relationships within this clade are poorly resolved (Figs. 1, 2).

The mean absolute distance and standard deviation from *Veronicastrum sibiricum* to the *Chionohebe*, *Derwentia*, *Hebe*, *Heliohebe*, *Parahebe*, and *Veronica* terminals is 29.1 ± 7.7 (see Fig. 2). *Veronicastrum* is reported in the fossil record (Tiffney, 1985) from the mid Miocene some 15 million years before present (mybp). The substitution rate in the *Veronicastrum* lineage was estimated by dividing $29.1 \pm 7.7/15 = 1.9 \pm 0.5$ substitutions for the entire gene *rbcL*. The mean distance from the terminals to the ancestral node of the Australasian species (including *V. persica*, which is Eurasian) is 18.8 changes, which corresponds to an upper Miocene divergence estimate of about 9.9 mybp. The mean distance from the terminals to the ancestral node of the *H. salicifolia* lineage is 7.4 changes, which corresponds to a Pliocene divergence estimate of about 3.9 mybp (Fig. 2).

The aligned ITS matrix was 695 nucleotides in length with gaps created to account for insertions and deletions, among which 364 sites were constant, 109 were parsimony-uninformative, and 222 were potentially parsimony-informative. Missing data accounted for 1.2% and gaps accounted for 9.6% of the ITS data matrix. The 5.8S gene was uniformly 165 nucleotides; ITS-1 varied between 175 and 224 nucleotides and ITS-2 between 203 and 215 nucleotides. Most of the variation in the ITS region was observed in ITS-1 and ITS-2. The 5.8S gene was more conserved. Conserved motifs identified by Liu and Shardt (1994) and Hershkovitz and Zimmer (1996) were identified in the ITS-1 and ITS-2 sequences in our survey.

Thirty-eight insertions and deletions (indels) were inferred in the ITS-1 and ITS-2 spacer regions (Table 2). Mostly these were relatively small, ranging from 1 to 3 bp, but two large insertions of 27 and 44 bp and three deletions of 7 or 8 bp were also inferred. Most of the indels were unique to a single sample, but 13 were shared by two or more species, sometimes uniting groups supported by substitutions in the sequence data alone. Species of *Derwentia* are characterized by a one-base deletion. Species of *Heliohebe* are characterized by a

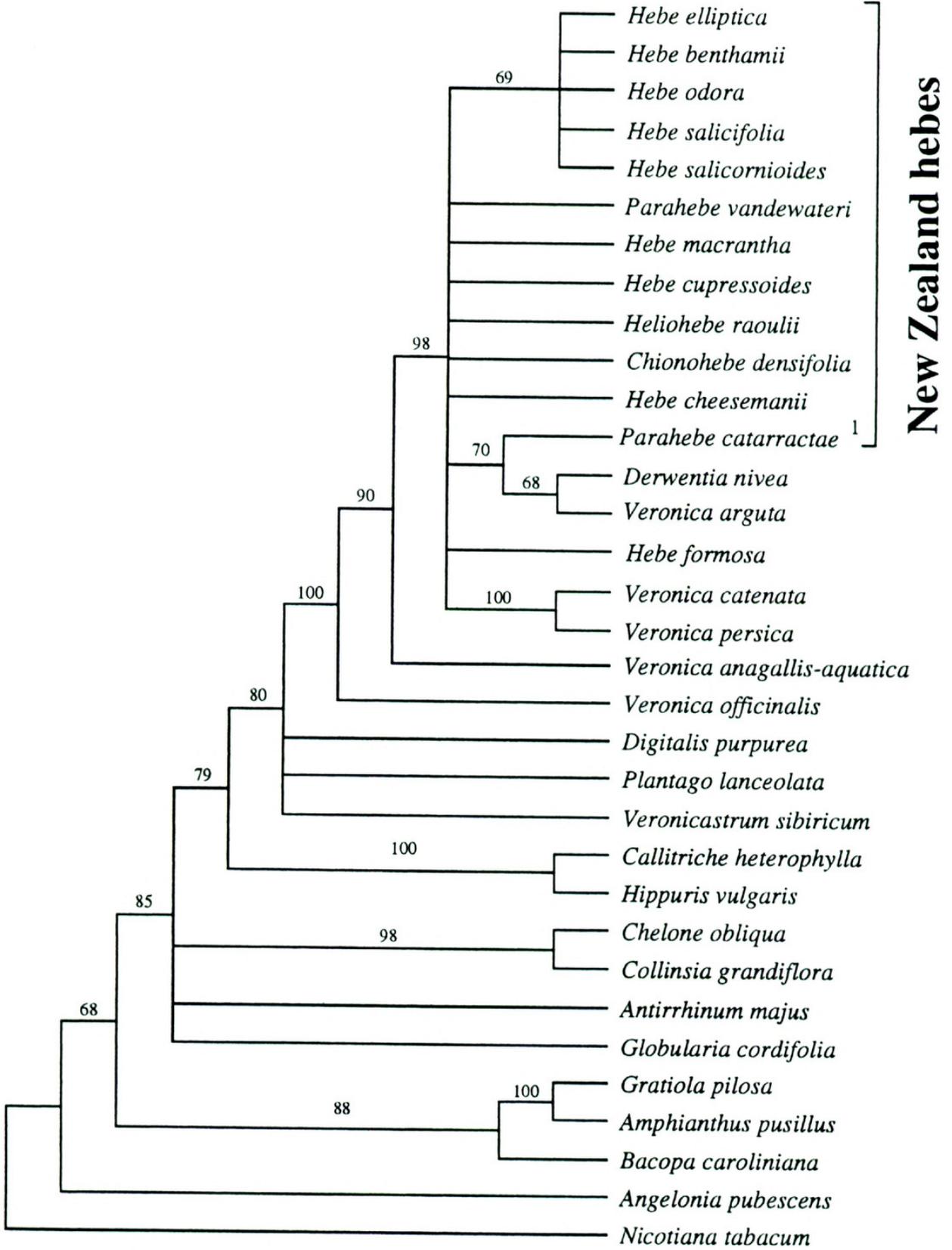


Figure 1. Strict consensus of 9408 minimal length trees produced by parsimony analysis of *rbcL* sequences. This tree shows the placement of New Zealand hebes within the Antirrhinaceae sensu Olmstead et al. (2001), using *Nicotiana tabacum* as an outgroup. Jackknife values > 50% are given above each node.

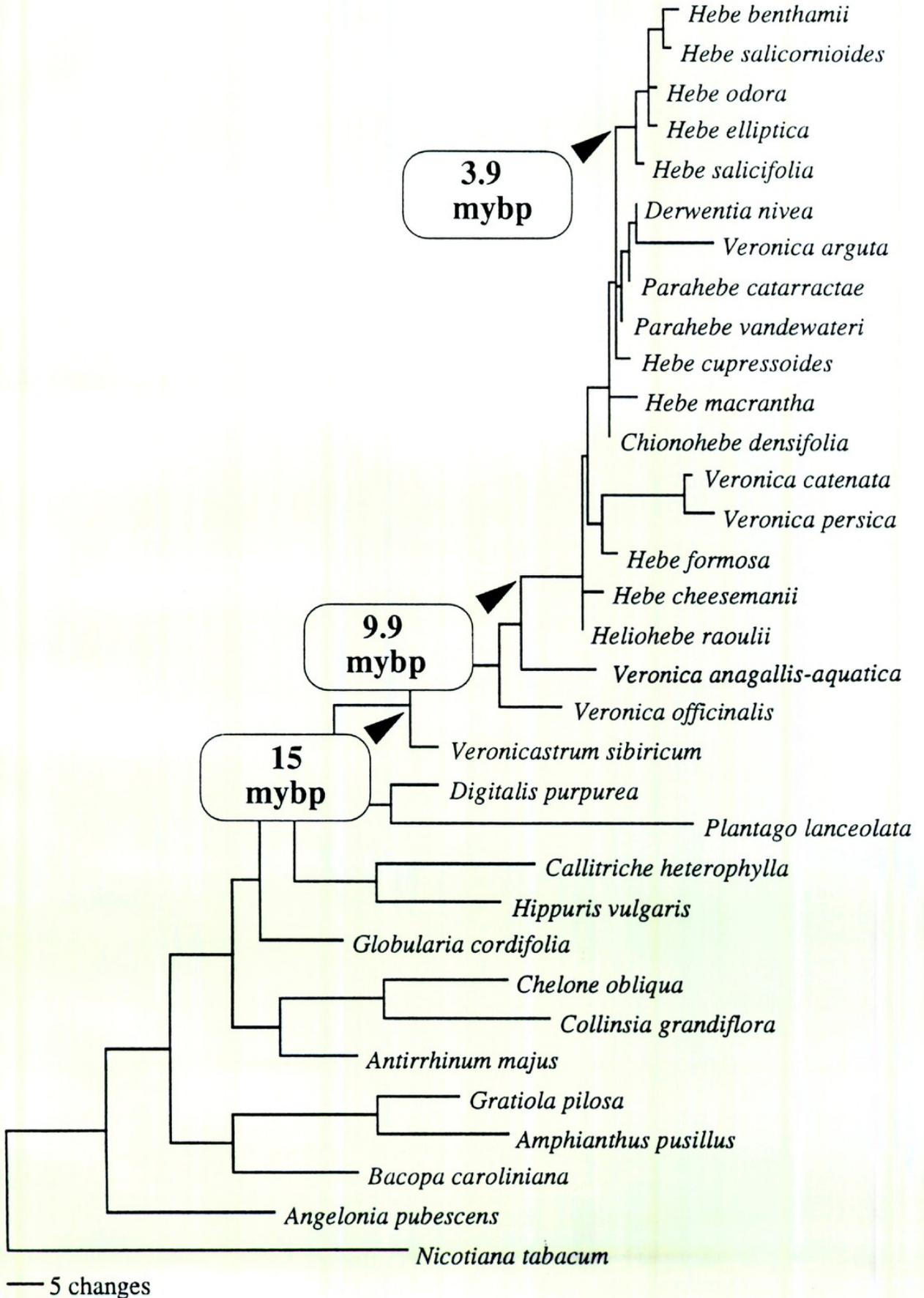


Figure 2. One of the maximum parsimony trees recovered from a parsimony analysis of *rbcL* sequences. The branch lengths are proportional to the number of changes along each branch. See scale at bottom. Fossils of *Veronicastrum sibiricum* are reported from the mid Miocene about 15 mybp. Divergence estimates are provided at the ancestral node of Australasian species (*V. persica* is Eurasian) and the ancestral node of the *Hebe* clade.

Table 2. Insertions and deletions inferred from ITS sequence comparison.

Taxon	Insertion/ deletion	Size	Position	Sequence
<i>Veronicastrum sibiricum</i>	Deletion	1	41	t/c
<i>Veronicastrum sibiricum</i> , <i>Wulfenia carinthiaca</i>	Insertion	1	54	c
<i>Veronica glandulosa</i>	Deletion	1	67	t/g
<i>Hebe vernicosa</i>	Insertion	3	68–79	gta
<i>Veronica calycina</i>	Insertion	1	77	t
<i>Veronica chamaedrys</i>	Deletion	1	78	c/g
<i>Veronicastrum sibiricum</i>	Deletion	1	89	c
<i>Wulfenia carinthiaca</i>	Insertion	44	90–134	aatctaggtgtgcaagcccccttgtgagag- tccgcgcctgctc
<i>Pseudolysimachion spicata</i> , <i>Veronica anagallis-aquatica</i> , <i>V. bellidioides</i> , <i>V. glandulosa</i> , <i>V. glauca</i> , <i>V. officinalis</i> , <i>V. serpyllifolia</i> , <i>V. urticifolia</i>	Insertion	27	108–134	gactagtcgagtgccgcctcctc
<i>Veronica bellidioides</i> , <i>V. officinalis</i> , <i>V. urticifolia</i>	Insertion	1	162	a
<i>Derwentia derwentiana</i> , <i>D. nivea</i> , <i>D. perfoliata</i> , <i>Parahebe lithophila</i> , <i>Veronica arguta</i>	Insertion	1	207	a
<i>Veronica macrostachya</i>	Deletion	3	208–209	cc
<i>Hebe salicifolia</i>	Insertion	1	217	c
<i>Veronica bellidioides</i> , <i>V. glandulosa</i> , <i>V. officinalis</i> , <i>V. urticifolia</i> , <i>Wulfenia carinthiaca</i>	Insertion	1	234	c/g
<i>Veronica persica</i>	Deletion	1	248	a
<i>Veronica chamaedrys</i> , <i>V. anagallis-aquatica</i>	Insertion	1	260	a
<i>Pseudolysimachion spicata</i> , <i>Veronica chamaedrys</i> , <i>V. macrostachya</i> , <i>V. oltensis</i>	Insertion	1	442	a
<i>Veronica urticifolia</i>	Insertion	1	454	c
<i>Veronica anagallis-aquatica</i>	Insertion	1	467	t
<i>Pseudolysimachion spicata</i> , <i>Veronica anagallis-aquatica</i> , <i>V. bellidioides</i> , <i>V. fruticulosa</i> , <i>V. glandulosa</i> , <i>V. glauca</i> , <i>V. officinalis</i> , <i>V. saturejoides</i> , <i>V. serpyllifolia</i> , <i>V. urticifolia</i> , <i>Veronicastrum sibiricum</i> , <i>Wulfenia carinthiaca</i>	Deletion	1	474	g
<i>Parahebe canescens</i>	Insertion	1	475	g
<i>Veronica bellidioides</i>	Insertion	2	501	cc
<i>Wulfenia carinthiaca</i>	Deletion	1	503	t
<i>Heliohebe hulkeana</i> , <i>H. laudiana</i> , <i>H. raoulii</i>	Insertion	1	508	t
<i>Veronica persica</i>	Deletion	1	573	t
<i>Hebe elliptica</i> , <i>H. elliptica</i> , <i>Parahebe birleyi</i> , <i>P. brevistylis</i> , <i>P. decora</i> , <i>P. lyallii</i> , <i>P. spathulata</i> , <i>P. vandewateri</i>	Deletion	8	583–590	tctcgtgc
<i>Parahebe planopetiolata</i>	Deletion	7	590–596	catctcc
<i>Parahebe canescens</i>	Deletion	8	591–598	atctcgc
<i>Veronica persica</i>	Deletion	3	592–594	tea
<i>Heliohebe hulkeana</i> , <i>H. laudiana</i> , <i>H. raoulii</i>	Deletion	1	606	g
<i>Parahebe vandewateri</i>	Deletion	1	609	a
<i>Veronica chamaedrys</i>	Deletion	2	609–610	ag

Table 2. Continued.

Taxon	Insertion/ deletion	Size	Position	Sequence
<i>Parahebe canescens</i>	Insertion	3	615–616	cat
<i>Veronica chamaedrys</i>	Deletion	2	620–621	tc
<i>Pseudolysimachion spicata</i>	Deletion	2	625–626	ac
<i>Veronica chamaedrys</i> , <i>V. serpyllifolia</i>	Insertion	1	631	a
<i>Veronica austriaca</i> , <i>V. oltensis</i>	Insertion	2	638–639	gc
<i>Veronica arguta</i>	Insertion	1	640	c

one-base insertion and a one-base deletion. Both accessions of *Hebe elliptica* and nine species of *Parahebe* have an eight-base deletion that appears to have evolved independently at least three times (Table 2). This deletion is lacking in *Parahebe linifolia* and in *P. catarractae* subsp. *catarractae* and subspecies *martinii*. The South American accession of *Hebe salicifolia* has a unique one-base insertion that is lacking in the accession of *Hebe salicifolia* from New Zealand.

The ITS sequences in our study were evolving at a faster rate than *rbcL*. The average rate of change per variable site for *rbcL* was 1.7 (tree length of 532/number of variable sites 144 + 155). The aligned ITS sequences were shorter than *rbcL*, there were more variable sites (331), and the average rate of change per variable site was 3.6 for the ITS region.

Parsimony analysis of the ITS-region recovered 6931 maximum parsimony trees distributed in at least two islands of 1213 steps (consistency index = 0.41 excluding uninformative characters, retention index = 0.73); a strict consensus tree is shown in Figure 3 and one of the maximum parsimony trees in Figure 4. Based upon the results from analysis of *rbcL* sequences (Figs. 1, 2), *Veronicastrum sibiricum* was designated as the outgroup. The earliest divergence within the ingroup is between *Wulfenia carinthiaca* and all other taxa. The Northern Hemisphere species of *Veronica* are found in five clades that form a grade basal to a Southern Hemisphere clade comprising the New Zealand hebes and their relatives. A heterogeneous Australian clade comprised of *Derwentia*, *Hebe formosa*, *Parahebe lithophila*, *Veronica arguta*, and *V. calycina* (82% jackknife; 18 synapomorphies) is sister to the New Zealand hebes, though there is relatively little support for this relationship (70% jackknife; 10 synapomorphies) (Figs. 3, 4).

Six well-supported clades are identified among the New Zealand hebes, but the relationships among these clades are unclear (Figs. 3, 4). The

first is a clade that comprises *Leonohebe* s. str. including a well-supported group, *Hebe tetrasticha*, *H. cheesemani*, and *H. ciliolata* (99% jackknife; 6 synapomorphies) with *Hebe cupressoides* weakly supported as their sister (61% jackknife; 3 synapomorphies). The *Chionohebe* A clade (98% jackknife; 5 synapomorphies) includes *Parahebe planopetiolata* and the cushion-forming species of *Chionohebe* with both the New Zealand and Australian accessions of *C. ciliolata*. The *Chionohebe* B clade consists of *Parahebe trifida* and both the New Zealand and Australian accessions of *Chionohebe densifolia* (91% jackknife; 4 synapomorphies). The fourth clade includes 6 species of *Parahebe* (93% jackknife; 7 synapomorphies) and accommodates the informal "Groups A & C" of Ashwin (in Allan, 1961; Table 1) and *P. spathulata*. The fifth clade includes all the species of *Heliohebe* in our analysis (100% jackknife; 13 synapomorphies). The sixth includes the remaining species of *Hebe* with both New Zealand and South American accessions of *Hebe salicifolia* and *Hebe elliptica* (100% jackknife; 11 synapomorphies). *Hebe macrantha* is weakly supported as the sister to the rest of this clade (50% jackknife; 4 synapomorphies) (Figs. 3, 4).

DISCUSSION

Large, unwieldy genera with a cosmopolitan distribution such as *Veronica* pose among the most difficult taxonomic problems for plant systematists, whose opinions are often strongly held. One of the most vexing of these problems is the inconsistent means by which taxonomists define generic boundaries and the recognition of rank within a hierarchical classification scheme. Recent taxonomic treatments in the Southern Hemisphere have favored narrow circumscriptions, and several new genera have been segregated from *Veronica* (see Table 1), whereas taxonomists in Europe and North America have traditionally embraced a broad ge-

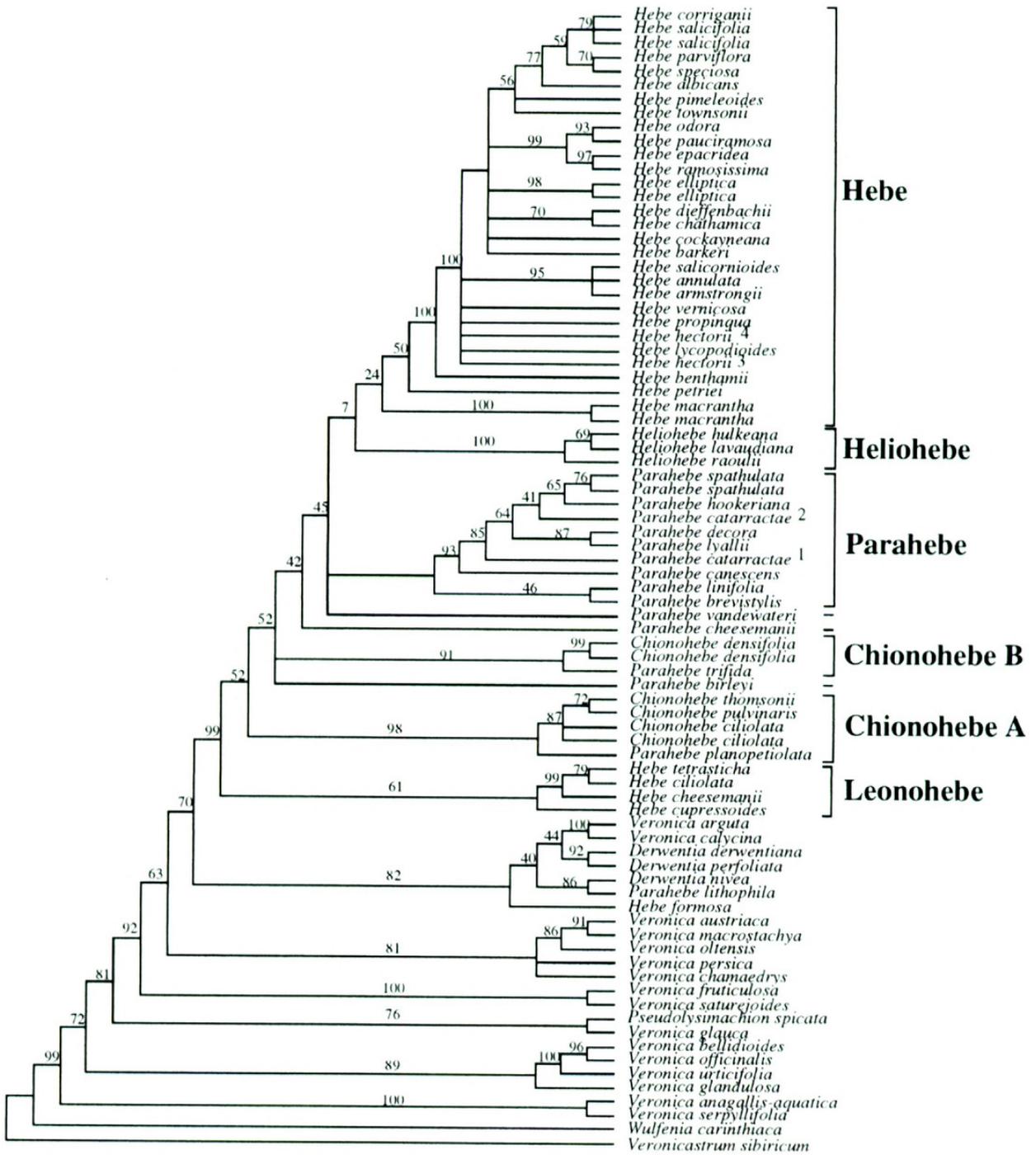


Figure 3. Strict consensus of 6931 minimal length trees produced by parsimony analysis of the entire ITS-region. Notable clades are identified with brackets. Jackknife values > 50% are given above each node. ¹*Parahebe cataractae* subsp. *martinii*, ²*Parahebe cataractae* subsp. *catarractae*, ³*Hebe hectorii* subsp. *subsimilis*, ⁴*Hebe hectorii* subsp. *hectorii*.

neric definition of *Veronica*, e.g., Wettstein (1891). This discrepancy of opinion contributes to taxonomic ambiguity and instability.

Our results support those of Albach and Chase (2001), implying that the genus *Veronica* is at best paraphyletic by exclusion of the Southern Hemisphere genera *Chionohebe*, *Derwentia*, *Hebe*, *Heliohebe*, *Leonohebe*, and *Parahebe* (Figs. 1, 3), as

well as the Eurasian genera *Paederota* and *Pseudolysimachion*, and the North American genera *Synthyris* and *Besseyia*. One possible solution is to lump them all in a broad circumscription of *Veronica*. This move, however, would create a cascade of nomenclatural changes requiring the recognition of many new combinations and the adoption of old combinations within *Veronica*. We

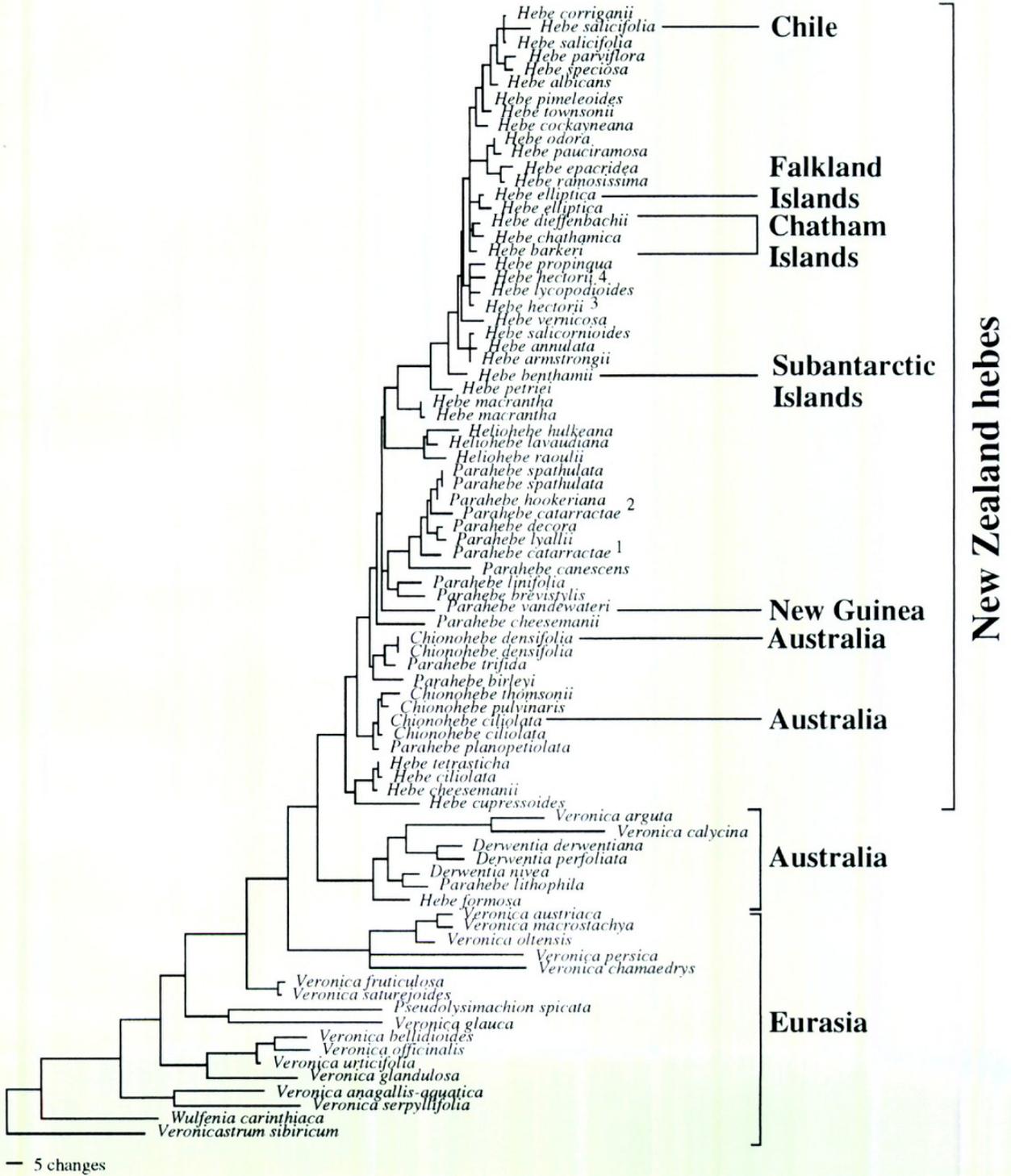


Figure 4. One of the maximum parsimony trees recovered from a parsimony analysis of the ITS-region. The New Zealand hebes comprise a well-supported monophyletic group with outliers on the offshore islands and in Australia, New Guinea, and South America. Dispersal away from the main islands of New Zealand is inferred in nine species. Branch lengths are proportional to the number of changes along each branch. See scale at bottom. ¹*Parahebe catarractae* subsp. *martinii*, ²*Parahebe catarractae* subsp. *catarractae*, ³*Hebe hectorii* subsp. *subsimilis*, ⁴*Hebe hectorii* subsp. *hectorii*.

accept that retaining a paraphyletic *Veronica* obscures phylogenetic relationships; however, an alternative approach is to recognize smaller, less inclusive clades as generic segregates of *Veronica*. This approach was adopted by Hong (1984). Here we identify major clades supported by the DNA

sequences and describe patterns of diversification in the New Zealand hebes.

MAJOR CLADES OF NEW ZEALAND HEBES

A heterogeneous clade composed of *Derwentia*, *Hebe formosa*, *Parahebe lithophila*, *Veronica arguta*,

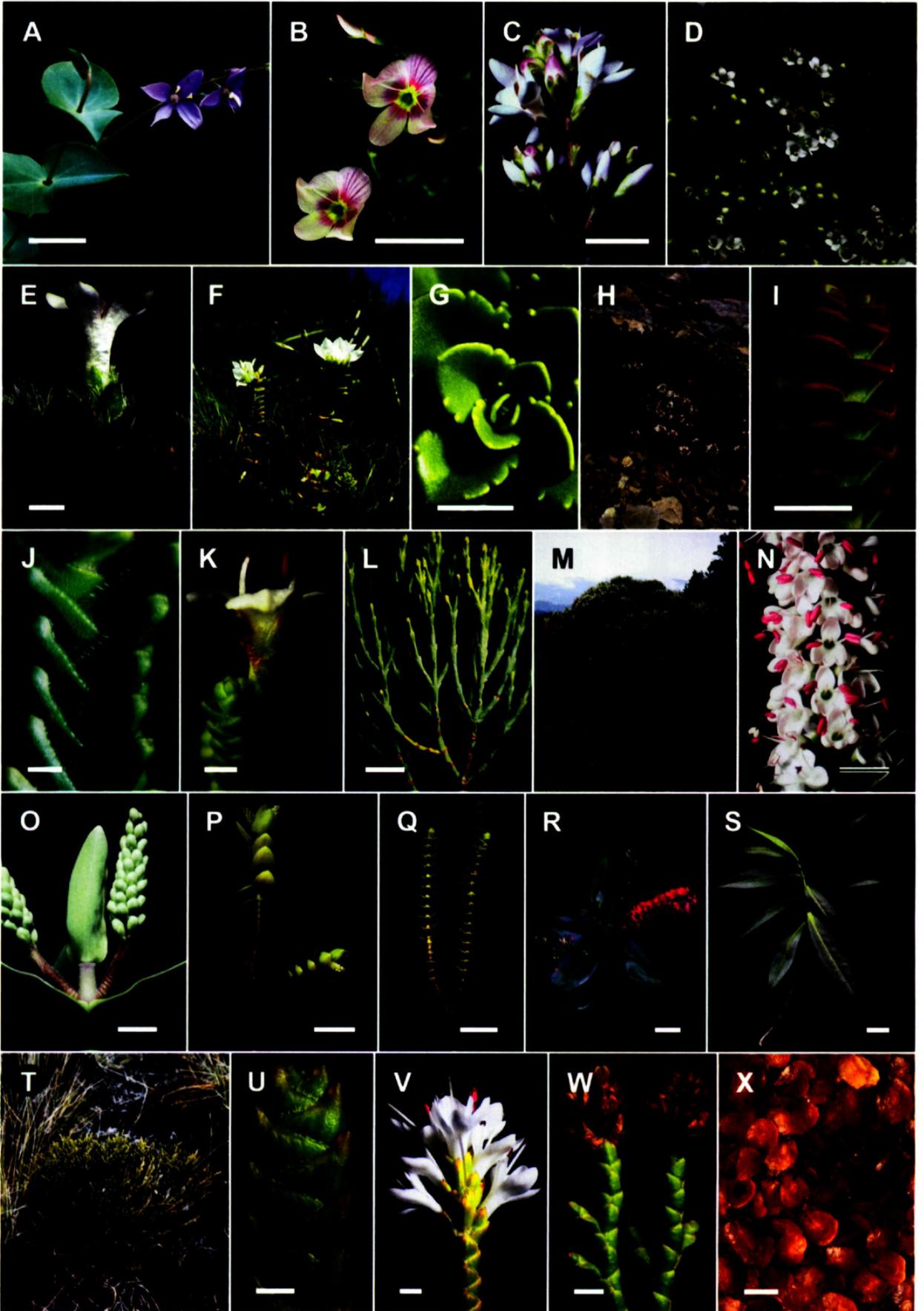


Figure 5. Plate illustrating some of the morphological diversity in the New Zealand hebes. —A. Flowering shoot of *Derwentia perfoliata* with toothed leaves obscure in this picture. —B. Flowers of *Parahebe catarractae*. —C. Panicle and terminal inflorescence of *Heliohebe raoulii* subsp. *maccaskillii*, P. J. Garnock-Jones 2123. —D. Cushion habit

and *V. calycina* is sister to the New Zealand hebes (Figs. 3, 4). The genus *Derwentia* includes nine currently accepted species that are endemic to Australia, from southeastern Queensland to Tasmania and west to Kangaroo Island in South Australia, where they are found mostly in tableland or cool temperate regions (Briggs & Ehrendorfer, 1992). Toothed leaves [only on the lower branches of *H. formosa* and often obscure in *D. perfoliata* (Fig. 5A)], and a dense ring of hairs in the corolla throat (glabrous in *H. formosa*) are possible synapomorphies that unite the clade. *Derwentia* and *Hebe formosa* also have similar growth forms; their new shoots are initiated at the base of the plant, overtopping older, short-lived branches. *Hebe formosa* is distinguished from *Derwentia* by the occurrence of a one-base insertion (Table 2). The chromosome number of *Hebe formosa* is $n = 21$, this possibly being the ancestral state within the *Derwentia* clade; chromosome numbers of $n = 19$ or 20 are published for *Derwentia* (Briggs & Ehrendorfer, 1992).

We identify six major clades within the New Zealand hebes that are supported by the sequence data, which we refer to as the *Leonohebe* clade, the *Chionohebe* A clade, the *Chionohebe* B clade, the *Parahebe* clade, the *Heliohebe* clade, and the *Hebe* clade (Fig. 3). ITS sequences provide strong support for the *Leonohebe* clade (Figs. 3, 4), comprising *Hebe cheesemani* (Fig. 5K), *H. ciliolata* (Fig. 5J), and *H. tetrasticha*. *Hebe cupressoides* (Fig. 5L) is weakly supported as sister to this clade. These species are endemic to the South Island of New Zealand. They have traditionally been included in

Hebe, but here, as in previous analyses (Wagstaff & Garnock-Jones, 1998, 2000), are far removed from the other species that Moore (in Allan, 1961) included in that genus. *Hebe cupressoides* and members of the *Leonohebe* clade lack the dorsal capsule compression typically found in members of *Hebe*, and a potential synapomorphy for the group is possession of a distinctive cupressoid growth habit, which has apparently evolved independently from that in the whipcord hebes [e.g., *H. annulata*, *H. armstrongii*, *H. hectorii*, *H. lycopodioides*, *H. propinqua*, and *H. salicornioides*, which have a similar growth form (Figs. 5T–W)]. *Hebe cheesemani*, *H. ciliolata*, and *H. tetrasticha*, along with *H. tumida*, comprise the informal group “Semiflagriformes” of Moore (in Allan, 1961). These similar species are subshrubs that occur in rocky areas at high altitude and are characterized by possession of lateral inflorescences (Fig. 5K), dioecious breeding system, and sour-scented flowers. We refer to this group as the *Leonohebe* clade, because *Leonohebe ciliolata* (*H. ciliolata*) was designated as the nomenclatural type for that genus by Heads (1987). If the group, including *H. cupressoides*, is treated as generically distinct from *Hebe* (and other genera of the *Hebe* complex; see Garnock-Jones, 1993a), then the use of the name *Leonohebe* seems warranted, though this is a much more restricted use of the name than the clearly polyphyletic circumscription originally employed by Heads (1987).

The *Chionohebe* A clade encompasses the cushion-forming species of *Chionohebe*. All of these species occur in the South Island where they are high-alpine plants of rock and scree. The cushion-forming species

←

of *Chionohebe thomsonii*, male plant, Eyre Mts., South Island, *P. J. Garnock-Jones* 1906. —E. Lateral view of erect tubular flower of *Chionohebe pulvinaris*, from Takitimu Range, South Island, F. G. *Hebe macrantha* var. *brachyphylla*. —F. Habit of a plant ca. 15 cm tall from same population as *M. J. Bayly* 560, Mt. Arthur, South Island. —G. Apex of vegetative shoot from Mt. Arthur, WELT 82554. H, I. *Hebe epacridea*. —H. Habit of a plant ca. 10 cm tall, same population as *M. J. Bayly* 795, Mt. St. Patrick, South Island. —I. Branchlet of plant from unknown locality. —J. *Hebe ciliolata*, branchlet showing ciliate leaf margins, plant from Mt. Arthur, WELT 82556. —K. *Hebe cheesemani*, male plant, from same population as *M. J. Bayly* 756–757, Black Birch Ra., South Island. —L. *Hebe cupressoides*, branchlet, cultivated Atawhai, Nelson, South Island, WELT 82553. M, N. *Hebe parviflora*. —M. Habit of a plant ca. 2.5 m tall from same population as *P. J. Garnock-Jones* 2258, Hauhangaroa Ra., North Island. —N. Inflorescence, *P. J. Garnock-Jones* 2257. O, P. *Hebe albicans*. —O. Shoot apex showing young lateral inflorescences and large apical vegetative bud, from Mt. Arthur, South Island, WELT 82555. —P. Shoot of plant from Cobb Valley, South Island, *M. J. Bayly* S-31. —Q. *Hebe pauciramosa*, shoot of plant from Mt. Brewster, South Island, *M. J. Bayly* 1478. —R. *Hebe speciosa*, shoot from a plant cultivated at Otari-Wiltons Bush, Wellington, originally from Maunganui Bluff, North Island. —S. *Hebe salicifolia*, shoot of plant from Upper Wairau Valley, South Island, *M. J. Bayly* S-70. T–V. *Hebe lycopodioides* subsp. *lycopodioides*. —T. Habit of plant from same population as *M. J. Bayly* 1512, Mt. Nimrod, South Island. —U. Apical portion of vegetative branchlet, cultivated in Landcare Research Gardens, Lincoln, originally from Fish Lake, Tarndale, South Island, WELT 82551. —V. Terminal inflorescence of a plant from same population as *M. J. Bayly* 771–773, Lake Tennyson, South Island. —W. Branchlets of *Hebe armstrongii* showing terminal infructescences, cultivated in Landcare Research Gardens, Lincoln, originally from Nigger Stream, Canterbury, South Island, WELT 82552. —X. Small, light seeds of *Hebe elliptica* (typical of those of most *Hebe*), cultivated, Otari-Wiltons Bush, Wellington, North Island. Scale bars: A, B, = 1 cm; C, G, I, L, N = 5 mm; E, V, W = 2 mm; J, K, U, X = 1 mm; O, P, Q, R, S = 2 cm.

of *Chionohebe* (e.g., Fig. 5D) are united by several synapomorphies, including cushion habit with the decussate leaf pairs slightly offset to form a pseudospiral (Heads, 1994b), thick-walled bristle-like eglandular hairs, solitary flowers with erect long corolla tubes (e.g., Fig. 5E), and corolla veins branching distally in the tube (Garnock-Jones, 1993a). The *Chionohebe* A clade is sister to *Parahebe planopetiolata*, one of the species of *Parahebe* "Group B" of Ashwin (in Allan, 1961). With *Parahebe planopetiolata* they share a five-lobed corolla and hygrochastic capsule dehiscence, but the species in the *Chionohebe* B clade also have these features.

The *Chionohebe* B clade includes *C. densifolia* (Australian and New Zealand populations), plus *Parahebe trifida* from the informal *Parahebe* "Group B" of Ashwin (in Allan, 1961) (Figs. 3, 4). *Parahebe birleyi* is not included in this clade in all trees, and in the consensus tree forms a polytomy with it and several other clades in the complex. The species of the *Chionohebe* B clade are all alpine plants found in the southern region of the South Island. *Parahebe trifida* occurs in alpine flushes and snowbanks, *P. birleyi* is a plant of nival rock ledges, and *C. densifolia* is found in a range of stony alpine habitats. *Chionohebe densifolia* is also found in the Kosciusco National Park in Australia. *Chionohebe densifolia*, *P. trifida*, and *P. birleyi* are all similar in appearance. Several of their shared characters are likely to be synapomorphies, including few-flowered inflorescences, large flowers with purple anthers, and presence of long glandular hairs on leaves. Other shared characters are also shared with the *Chionohebe* A clade, including old leaves withering and fading but retained on stems. All three species of the *Chionohebe* B clade are thought to form hybrids with cushion-forming species of *Chionohebe* A clade (Wagstaff & Garnock-Jones, 2000). There is little evidence from morphology to separate the *Chionohebe* A and B clades. Garnock-Jones (1993a), from a cladistic analysis of morphological and flavonoid data, proposed a more inclusive "*Chionohebe*" clade incorporating all the species of *Chionohebe* and *Parahebe* "Group B" of Ashwin (in Allan, 1961). Such a grouping appears paraphyletic at best in this and earlier ITS studies (Wagstaff & Garnock-Jones, 2000).

The *Parahebe* clade includes all the representatives of the informal *Parahebe* "Group A" of Ashwin (in Allan, 1961) plus *P. spathulata*. *Parahebe spathulata* is anomalous in this clade, which otherwise has morphological support from inflorescence, floral, and flavonoid characters (Garnock-Jones, 1993a). A sister relationship between this clade and *P. canescens*, the sole species of Ashwin's

"Group C," has 93% jackknife support. The informal "*Parahebe* Groups A and C" share several floral apomorphies (Garnock-Jones, 1993a). *Parahebe brevistylis* and *P. linifolia* (from Ashwin's "Group B") form a weakly supported small clade, which is sister to the "Group A and C" species. The clade is represented in both the North and South Islands of New Zealand, where species occur in well-drained soils associated with river banks, cliffs, and screes. *Parahebe canescens* is a creeping diminutive herb of South Island lake shores; its reduced features match convergent similarities seen in other plants associated with this habitat. The entire clade except for *P. brevistylis* and *P. spathulata* is united by floral features such as short corolla tubes, colored nectar guides (Fig. 5B), and stamen filaments narrowed at the base. In the case of *P. brevistylis*, the differences can be explained as losses of adaptations for insect pollination (Garnock-Jones, 1976b). *Parahebe spathulata* shares some features of habit and flower morphology with *P. cheesemanii* and might have an allopolyploid origin involving species from the *Parahebe* clade and the *P. cheesemanii* lineage.

The *Heliohebe* clade (Figs. 3, 4) was formerly recognized as *Hebe* "Paniculatae" in the informal classification of Moore (in Allan, 1961), and later segregated as a distinct genus by Garnock-Jones (1993b) (Table 1). It was also previously recognized as a distinct group in the key of Cheeseman (1925). *Heliohebe* includes five species that are found in northeastern parts of the South Island on rock outcrops, cliffs, and sometimes in grassland. Monophyly is well supported by two unique indels and several possible morphological apomorphies including an inflorescence that is a terminal, compound raceme or spike (Fig. 5C), protogyny (also evident in Fig. 5C, where styles are protruding from buds on the lowest inflorescence branches), stamens erect, anthers cream or yellow, seeds fusiform to irregular in shape and winged, and hemitropous ovules (Garnock-Jones, 1993b).

The *Hebe* clade corresponds to *Hebe* sensu Moore (in Allan, 1961) with the exclusion of *Heliohebe* and members of the *Leonohebe* clade. The majority of species within the *Hebe* clade form a well-supported group (100% jackknife value), with weaker support for *Hebe macrantha* (Fig. 5F, G) and *H. petriei* as sisters to this group (Figs. 3, 4). The *Hebe* clade is largely endemic to New Zealand, including many of its surrounding islands, with two species also extending to South America, and one species (*H. rapensis*, not included in this analysis) endemic to Rapa Island (Fig. 6). The clade is large and morphologically diverse; unambiguous morphological

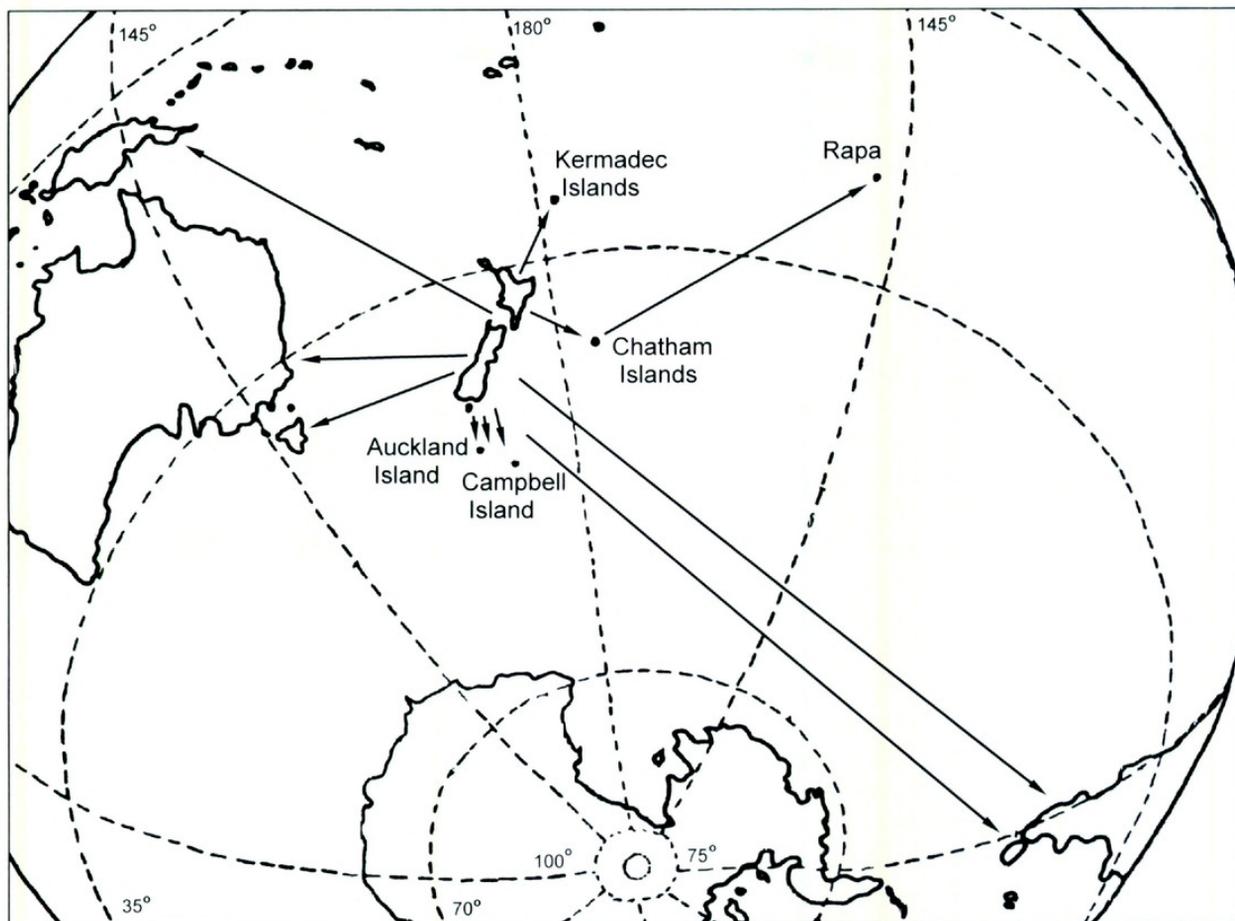


Figure 6. Map showing postulated dispersal of hebes from the main islands of New Zealand.

synapomorphies are difficult to identify, with absences or reversals in some taxa. Wagstaff and Garnock-Jones (1998) suggest that synapomorphies may include: a shrubby or arborescent habit (e.g., Fig. 5M, R, S), large leaf bud (e.g., Fig. 5O), entire leaf margins, protandrous flowers, peltate placentas, acute capsule apices, 3/5 or 5/8 inflorescence phyllotaxis. Within the *Hebe* clade there is little resolution, but several relationships are worthy of note. Firstly, the "Connatae" of Moore [in Allan, 1961, represented by *H. benthamii*, *H. petriei*, *H. epacridea*, (Fig. 5H, I) and *H. ramosissima*] are polyphyletic, with some members closely related to "Buxifoliatae" (*H. odora* and *H. pauciramosa*). These relationships were first suggested by Wagstaff and Garnock-Jones (1998), and the addition of further taxa in this study continues to support this earlier assessment. Secondly, as found by Wagstaff and Wardle (1999), three of the cupressoid species, *H. salicornioides*, *H. armstrongii* (Fig. 5W), and *H. annulata* (which share possession of fused anterior calyx lobes and chromosome number of $n = 21$), form a well-supported clade. Thirdly, two of the Chatham Island endemics, *H. chathamica* and *H. dieffenbachii*, are sister species (Figs. 3, 4), with

the third Chatham Island endemic, *H. barkeri*, being placed in a large polytomy that includes this grouping. *Hebe macrantha*, placed with weak jack-knife support at the base of the *Hebe* clade, lacks many of the previously mentioned synapomorphies for the group. This species has long held an isolated or ambiguous position, being placed by Moore (in Allan, 1961) in its own grouping, *Hebe* "Grandiflorae," and was included in *Parahebe* by Heads (1987, 1994b). For the present we suggest its retention in *Hebe*, which still leaves the genus, with the exclusion of *Heliohebe* (Garnock-Jones, 1993b) and the *Leonohebe* clade, monophyletic (see Table 1).

TAXA OF UNCERTAIN AFFINITIES

Many of the genera and subgeneric groupings historically recognized in the *Hebe* complex (e.g., *Heliohebe*, cushion-forming species of *Chionohebe*, and some *Hebe* groups) are shown to be monophyletic in this study. Significant exceptions are *Parahebe* "Group B" (of Ashwin in Allan, 1961) and species groups within *Hebe* [e.g., sects. *Hebe*, *Sub-*

distichae, *Glaucæ*, and the informal group “Connatae” of Moore (in Allan, 1961)] (see Table 1).

The species of *Parahebe* “Group B” are widely scattered, forming a grade among the New Zealand hebes, and few show any close relationship to other members within their informal group. Previous authors (Ashwin in Allan, 1961; Garnock-Jones, 1976b, 1993a) have suggested the *Parahebe* “Group B” species exhibit considerable morphological similarity, but now it seems this similarity might derive from plesiomorphic character states (relative to the *Hebe*–*Heliohebe* clade), from convergent evolution of floral features associated with self-pollination (Garnock-Jones, 1976b), and perhaps from reticulate evolution in *P. spathulata* (discussed above). Garnock-Jones (1993a) suggested that *Parahebe* “Group B” and *Chionohebe* should be united, but this view receives no support from the ITS analyses (Wagstaff & Garnock-Jones, 2000, and herein). Wagstaff and Garnock-Jones (2000) inferred that the ancestors of *Parahebe* and *Chionohebe* initially evolved in a montane or alpine environment, then subsequently radiated into lowland environments during episodes of Pleistocene glaciation. Extinction probably had a more profound effect on the basal lineages of *Parahebe* and *Chionohebe*, and this process further confounds our efforts to resolve relationships.

The relationships among species of *Hebe* remain uncertain after ITS analyses (Figs. 3, 4). Branch lengths are too short for us to confidently derive an infrageneric classification from this study. It may be that speciation and diversification in the *Hebe* clade is too recent for ITS divergence to reveal its phylogenetic pattern. Reticulate evolution might also have clouded the molecular signal either through diploid hybrid speciation or allopolyploidy in this group where about 32% of the species are polyploid.

ORIGIN, DIVERSIFICATION, AND DISPERSAL

Two widely differing opinions have been presented regarding the age and origins of the New Zealand hebes. Some authors (e.g., Skipworth, 1973; Heads, 1994a) have proposed a Gondwanan origin to account for the present distribution of the

group, whereas others (e.g., Raven, 1973; Garnock-Jones, 1993a; Wagstaff & Garnock-Jones, 1998) have suggested the group has arrived more recently in the Southern Hemisphere and that dispersal has played an important role in shaping its distribution. The data presented here lend support to the latter proposition.

A primary contribution of the present work is its assessment of relationships between *Veronica* and Australasian members of the *Hebe* complex. Although a close relationship between these two groups has long been assumed on morphological grounds (e.g., Wettstein, 1891; Cheeseman, 1925; Raven, 1973), some authors (e.g., Hong, 1984) have directly opposed the notion that Australasian taxa are derived directly from within *Veronica*. Our analysis of *rbcL* clearly supports a close relationship of *Veronica* to the Australasian genera, with the strict consensus including a well-supported (100% jack-knife) *Hebe*–*Veronica* clade (Fig. 3). Analysis of ITS sequences shows the Australasian members to form a clade nested within a paraphyletic *Veronica*. This pattern of relationships is congruent with the notion that the *Hebe* complex is an Australasian radiation of *Veronica*.

Our assessment of the time frame for the origin and radiation of the Australasian genera, and the New Zealand hebes in particular, relies on inferences from the fossil record, the geological and climatic history of New Zealand, and the distributions and ecological tolerances of extant species. For *Hebe*, the earliest appearance in the fossil record is in the Pliocene (Mildenhall, 1980), for Scrophulariaceae it is in the mid Miocene (Tiffney, 1985), and for the whole of the Lamiales (sensu APG, 1998) it is in the mid Eocene (Muller, 1981). Although there is always the possibility that older fossils will be found, it would be inconsistent with this record to assume that divergence, either within the Australasian *Hebe* complex, or between members of that group and *Veronica*, occurred in Gondwanan (Cretaceous) or earlier times.

We acknowledge that the divergence estimates presented in Figure 2 are crude and await further refinement. The paucity of the fossil record and the occurrence of undetected multiple substitutions on

Figure 7. Details of the natural elevational range of species of New Zealand hebes, overlaid on the strict consensus of trees produced by analysis of ITS sequences. Species are regarded as alpine if they occur predominantly in areas above the natural tree line. The other two elevational zones are less precisely defined with, on the two main islands of New Zealand, lowland corresponding to those areas below ca. 500 m above sea level, and montane being those between ca. 500 m and up to ca. 1000 m (but below natural tree line). Members of the basal grade of New Zealand hebes all occur in alpine or montane environments.

long branches are two potentially significant sources of error, both of which could lead to inaccurate estimates of divergence times. Though crude, the estimates nonetheless provide intriguing comparisons with patterns of ecological diversification and aspects of the geological history of New Zealand.

The geological and climatic history of New Zealand suggests that differentiation of the New Zealand hebes is likely to have occurred in the late Tertiary. Members of the basal grade of New Zealand hebes, in particular the *Leonohebe* clade, and the *Chionohebe* A and B clades (Fig. 3), are all alpine or montane plants, most occurring in areas above the natural tree line (Fig. 7). If the present ecological requirements of these groups are indicative of those of their past (i.e., assuming that each lineage has not independently and recently adapted to alpine habitats, or that each has not seen selective extinction of lowland members), it can be inferred that early differentiation of New Zealand hebes occurred in alpine environments, with colonization of the lowlands being a secondary event. The evidence is that alpine environments have only existed in New Zealand since the Pliocene or latest Miocene, subsequent to the onset of mountain building, in what was previously relatively low-lying land (Flemming, 1979; Ollier, 1986).

Prerequisite in any hypothesis of a late Tertiary origin for the New Zealand hebes is colonization of New Zealand by long-distance dispersal of ancestral form(s). Assuming a minimum number of dispersals or extinctions, the topology of cladograms derived from ITS sequences (Figs. 3, 4) suggests that differentiation of New Zealand hebes followed a single colonization from either Australia or Eurasia. This differentiation was succeeded by secondary dispersal from New Zealand.

As illustrated here and elsewhere (Wagstaff & Garnock-Jones, 1998, 2000) the morphology and ITS sequences (Fig. 3) of extant species with transoceanic distributions provide evidence of the capacity of New Zealand hebes for long-distance dispersal. Such transoceanic distributions are seen in four species, all of which are included in our ITS study group, and all of which are nested within the well-supported clade of New Zealand hebes. Of these species, *Hebe elliptica* and *H. salicifolia* naturally occur both in South America and southern New Zealand, whereas *Chionohebe ciliolata* and *C. densifolia* occur both in the South Island of New Zealand and southeastern Australia. Within each of these four species, populations separated by ocean gaps show no apparent morphological differentiation and only limited sequence divergence (Fig. 4). This suggests that the transoceanic disjunctions in

the distributions of these species are relatively recent phenomena, and given that these species and all of their closest relatives occur within New Zealand, that these disjunctions are products of long-distance dispersal of propagules from New Zealand.

Godley (1967) suggested oceanic birds as likely vectors for the dispersal of seeds of *H. elliptica* (Fig. 5X) and *H. salicifolia* from New Zealand to South America. Trans-Tasman dispersal of the two alpine *Chionohebe* species from New Zealand to Australia is less intuitively explained owing to the sexual dimorphism of one species (Delph, 1988, 1990), and their splash cup method of seed dispersal (Garnock-Jones, 1993a). The implied direction of dispersal from New Zealand to Australia is also against the prevailing westerly winds but, as noted by Wardle (1978), weather conditions sometimes occur in which the usual direction of winds across the Tasman Sea is reversed. The occurrence of two independent dispersals of *Chionohebe* from New Zealand to Australia may seem unlikely, but the alternative explanations are either an extended period of stasis in both morphology and ITS sequences (assuming distributions produced by fragmentation of Gondwana), or widespread extinction in Australia (assuming dispersal in the opposite direction).

Apart from the dispersal prerequisite to explain transoceanic species distributions, another six dispersal events from the main islands of New Zealand are required to explain the current distribution of *Hebe* (Fig. 6). Most of the postulated dispersals are to New Zealand's outlying islands, including one to the Pleistocene-age (Sykes, 1977) Kermadec Islands (where *Hebe brevitrachosa* is endemic), and three to islands of the New Zealand subantarctic (where *H. elliptica* and *H. odora* have populations disjunct from those on the main islands of New Zealand, and *H. benthamii* is endemic). One dispersal to the Chatham Islands has been postulated on morphological grounds (Moore in Allan, 1961; Garnock-Jones, 1976a; Wagstaff & Garnock-Jones, 1998). This is partially supported here by analysis of ITS sequences (Fig. 4), which places two of the endemic species, *H. chathamica* and *H. dieffenbachii*, as sister taxa, and the third, *H. barkeri*, in the polytomy that includes the branch uniting the other two. A final dispersal, probably from the Chatham Islands (Garnock-Jones, 1976a, 1993a), is also postulated to account for the distribution of *H. rapensis* (not included in our analysis), which is endemic on Rapa Island in French Polynesia.

The presence of *Parahebe* in New Guinea is difficult to explain. Here, as in the analysis of Wagstaff and Garnock-Jones (2000), ITS sequence data for

only one New Guinean species of *Parahebe* were included. That species, *P. vanderwateri*, is nested within the New Zealand hebes (Fig. 3) with 99% jackknife support. The most parsimonious interpretation of the present data (assuming a minimum number of dispersals or extinctions) is long-distance dispersal from New Zealand to New Guinea, as proposed by Wagstaff and Garnock-Jones (2000). Further sequence data for New Guinean *Parahebe* (of which 12 species are described) and *Detzneria* (monotypic and endemic) might provide a clearer picture of relationships between taxa from the two areas.

Literature Cited

Albach, D. C. & M. W. Chase. 2001. Paraphyly of *Veronica* (Veroniceae: Scrophulariaceae): Evidence from internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA. *J. Pl. Res.* 114: 9–18.

Albert, V. A., A. Backlund, K. Bremer, M. W. Chase, J. R. Manhart, B. D. Mishler & K. C. Nixon. 1994. Functional constraints and *rbcL* evidence for land plant phylogeny. *Ann. Missouri Bot. Gard.* 81: 534–567.

Allan, H. H. 1961. *Flora of New Zealand*, Vol. I. Government Printer, Wellington.

APG. 1998 [1999]. An ordinal classification for the families of flowering plants. *Ann. Missouri Bot. Gard.* 85: 531–553.

Baldwin, B. G., M. J. Sanderson, J. M. Porter, M. F. Wojciechowski, C. S. Campbell & M. J. Donoghue. 1995. The ITS region of nuclear ribosomal DNA: A valuable source of evidence on angiosperm phylogeny. *Ann. Missouri Bot. Gard.* 82: 247–277.

Bentham, G. 1876. Scrophulariaceae. Pp. 913–980 in G. Bentham & J. D. Hooker (editors), *Genera Plantarum*, Vol. 2. Reeve, London.

Bremer, K. & M. H. G. Gustafsson. 1997. East Gondwana ancestry of the sunflower alliance of families. *Proc. Natl. Acad. Sci. U.S.A.* 94: 9188–9190.

Briggs, B. G. & F. Ehrendorfer. 1992. A revision of the Australian species of *Derwentia* and *Parahebe* (Scrophulariaceae). *Telopea* 5: 241–287.

Carlquist, S. 1974. *Island Biology*. Columbia Univ. Press, New York.

Chase, M. W., D. E. Soltis, R. G. Olmstead, D. Morgan, D. H. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hills, Y.-L. Qiu, K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sytsma, H. J. Michaels, W. J. Kress, K. G. Karol, W. D. Clark, M. Hedrén, B. S. Gaut, R. K. Jansen, K.-J. Kim, C. F. Wimpee, J. F. Smith, G. R. Furnier, S. H. Strauss, Q.-Y. Xiang, G. M. Plunkett, P. S. Soltis, S. M. Swensen, S. E. Williams, P. A. Gadek, C. J. Quinn, L. E. Eguiarte, E. Golenberg, G. H. Learn, Jr., S. W. Graham, S. C. H. Barrett, S. Sayanandan & V. A. Albert. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbcL*. *Ann. Missouri Bot. Gard.* 80: 528–580.

Cheeseman, T. F. 1925. *Manual of the New Zealand Flora*, 2nd ed. Government Printer, Wellington.

Delph, L. F. 1988. The Evolution and Maintenance of Gender Dimorphism in New Zealand *Hebe* (Scrophular-

iaceae). Unpublished Ph.D. Thesis, University of Canterbury, Christchurch.

———. 1990. The evolution of gender dimorphism in New Zealand *Hebe* (Scrophulariaceae). *Evol. Trends Pl.* 4: 85–97.

Doyle, J. J. & J. L. Doyle. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull. Bot. Soc. Ames* 19: 11–15.

Farris, J. S., V. A. Albert, M. Källersjö, D. Lipscomb & A. G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 11: 99–124.

Flemming, C. A. 1979. *The Geological History of New Zealand and Its Life*. Auckland Univ. Press, Auckland.

Garnock-Jones, P. J. 1976a. *Hebe rapensis* (F. Brown) Garn-Jones comb. nov. and its relationships. *New Zealand J. Bot.* 14: 79–83.

———. 1976b. Breeding systems and pollination in New Zealand *Parahebe* (Scrophulariaceae). *New Zealand J. Bot.* 14: 291–298.

———. 1993a. Phylogeny of the *Hebe* complex (Scrophulariaceae: Veroniceae). *Austral. Syst. Bot.* 6: 457–479.

———. 1993b. *Heliohebe* (Scrophulariaceae–Veroniceae), a new genus segregated from *Hebe*. *New Zealand J. Bot.* 31: 323–339.

Godley, E. J. 1967. Widely distributed species, land bridges and continental drift. *Nature* 214: 74–75.

Heads, M. J. 1987. New names in New Zealand Scrophulariaceae. *Bot. Soc. Otago News* 5: 4–11.

———. 1994a. Morphology, architecture and taxonomy in the *Hebe* complex (Scrophulariaceae). *Bull. Mus. Natl. Hist. Nat., B. Adansonia* 16: 163–191.

———. 1994b. A biogeographic review of *Parahebe* (Scrophulariaceae). *Bot. J. Linn. Soc.* 115: 65–89.

Hershkovitz, M. A. & E. A. Zimmer. 1996. Conservation patterns in angiosperm rDNA sequences. *Nucl. Acids Res.* 24: 2857–2867.

Holmgren, P. K., N. H. Holmgren & L. C. Barnett. 1990. *Index Herbariorum*, Part 1, The Herbaria of the World, 8th ed. Regnum Veg. 120.

Hong, D. 1984. Taxonomy and evolution of the Veroniceae (Scrophulariaceae) with special reference to palynology. *Opera Bot.* 75: 5–60.

Källersjö, M., J. S. Farris, M. W. Chase, B. Bremer, M. F. Fay, C. J. Humphries, G. Petersen, O. Seberg & K. Bremer. 1998. Simultaneous parsimony jackknife analysis of 2538 *rbcL* DNA sequences reveals support for major clades of green plants, land plants, seed plants and flowering plants. *Pl. Syst. Evol.* 213: 259–287.

Lin, C. M., Z. Q. Liu & S. D. King. 1986. *Nicotiana* chloroplast genome: Correlation between the DNA sequences and the isoelectric focusing pattern of the LS of rubisco. *Pl. Molec. Biol.* 6: 81–87.

Liu Jih-Shiou & C. L. Schardl. 1994. A conserved sequence in internal transcribed spacer I of plant nuclear rRNA genes. *Pl. Molec. Biol.* 26: 775–778.

Mildenhall, D. C. 1980. New Zealand Late Cretaceous and Cenozoic plant biogeography: A contribution. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 31: 197–233.

Muller, J. 1981. Fossil pollen records of extant angiosperms. *Bot. Rev. (London)* 47: 1–142.

Ollier, C. D. 1986. The origin of alpine landforms in Australasia. Pp. 3–25 in B. A. Barlow (editor), *Flora and Fauna of Alpine Australasia: Ages and Origins*. CSIRO Australia, Melbourne.

Olmstead, R. G. & P. A. Reeves. 1995. Polyphyletic origin of the Scrophulariaceae: Evidence from *rbcL* and *ndhF* sequences. *Ann. Missouri Bot. Gard.* 82: 176–193.

- , H. J. Michaels, K. M. Scott & J. D. Palmer. 1992. Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbcL*. *Ann. Missouri Bot. Gard.* 79: 249–265.
- , B. Bremer, K. M. Scott & J. D. Palmer. 1993. A parsimony analysis of the Asteridae sensu lato based on *rbcL* sequences. *Ann. Missouri Bot. Gard.* 80: 700–722.
- , C. W. DePamphilis, A. D. Wolfe, N. D. Young & P. A. Reeves. 2001. Disintegration of the Scrophulariaceae. *Amer. J. Bot.* 88: 163–212.
- Pole, M. 1994. The New Zealand flora—Entirely long-distance dispersal? *J. Biogeogr.* 21: 625–635.
- Raven, P. H. 1973. Evolution of the subalpine and alpine plant groups in New Zealand. *New Zealand J. Bot.* 11: 177–200.
- Reveal, J. L., W. S. Judd & R. G. Olmstead. 1999. Proposal to conserve the name Antirrhinaceae and with a superconservation proposal to maintain Antirrhinaceae over Plantaginaceae (Magnoliophyta). *Taxon* 48: 182.
- Skipworth, J. P. 1973. Continental drift and the New Zealand biota. *New Zealand J. Geogr.* 57: 1–13.
- Swofford, D. L. 1998. PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), Vers. 4. Sinauer, Sunderland, Massachusetts.
- Sykes, W. R. 1977. Kermadec Island Flora, an Annotated Checklist. New Zealand Department of Scientific and Industrial Research, Bull. 219. Government Printer, Wellington.
- Thompson, J. D., T. J. Gibson, F. Plewniak, F. Jeanmougin & D. G. Higgins. 1997. The CLUSTAL_X windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucl. Acids Res.* 25: 4876–4882.
- Tiffney, B. H. 1985. Perspectives on the origin of the floristic similarity between Eastern Asia and eastern North America. *J. Arnold Arbor.* 66: 73–94.
- Wagstaff, S. J. & P. J. Garnock-Jones. 1998. Evolution and biogeography of the *Hebe* complex (Scrophulariaceae) inferred from ITS sequences. *New Zealand J. Bot.* 36: 425–437.
- & ———. 2000. Patterns of diversification in *Chionohebe* and *Parahebe* (Scrophulariaceae) inferred from ITS sequences. *New Zealand J. Bot.* 38: 389–407.
- & P. Wardle. 1999. Whipcord hebes—Systematics, distribution, ecology and evolution. *New Zealand J. Bot.* 37: 17–39.
- Wardle, P. 1978. Origin of the New Zealand mountain flora, with special reference to trans-Tasman relationships. *New Zealand J. Bot.* 16: 535–550.
- Wettstein, R. von. 1891. Scrophulariaceae. Pp. 39–107 in A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien*, Vol. 4, part 3a. W. Engelmann, Leipzig.

Appendix 1. Voucher information and GenBank accession numbers for the species of Scrophulariaceae included in our study. Herbarium abbreviations, in parentheses, follow *Index Herbariorum* (Holmgren et al., 1990). Specimens in the CHR herbarium receive a unique accession number (see fourth column) with complete collection information retrievable from this.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession	
					ITS	<i>rbcL</i>
<i>Amphicanthus pusillus</i> Torr.	<i>C. W. dePamphilis</i> 90.33 (PAC)			Olmstead et al. (2000)		AF123673
<i>Angelonia pubescens</i> Benth.	<i>C. W. dePamphilis</i> 94.03 (PAC)			Olmstead et al. (2000)		AF123672
<i>Antirrhinum majus</i> L.	<i>C. W. dePamphilis</i> 90.204 ex hort., University of Michigan (PSU)			Olmstead et al. (1992)		L11688
<i>Bucopa caroliniana</i> B. L. Rob.	<i>C. W. dePamphilis</i> 90.137 (PAC)			Olmstead et al. (2000)		AF123670
<i>Callitriche heterophylla</i> Pursh emend. Darby	<i>Philbrick</i> 2152 (CONN)			Olmstead et al. (1992)		L11681
<i>Chelone obliqua</i> L.	<i>C. W. dePamphilis</i> SS15 (<i>C. W. Morden</i> 853) ex hort., Indiana University (PSU)			Olmstead et al. (2000)		AF026824
<i>Chionohebe ciliolata</i> (Hook. f.) B. G. Briggs & Ehrend.	AUSTRALIA, Tasmania, Ben Lomond, Hamilton Crags, <i>M. J. A. Simpson</i> 8200		CHR 308581	Wagstaff & Garnock-Jones (2000)	AF229037	
<i>Chionohebe ciliolata</i> (Hook. f.) B. G. Briggs & Ehrend.	NEW ZEALAND, Westland, Wilberg Range, <i>P. Wardle, R. Buxton, K. Ford</i> , 27 Apr. 93		CHR 499838	Wagstaff & Garnock-Jones (2000)	AF229037	
<i>Chionohebe densifolia</i> (F. Muell.) B. G. Briggs & Ehrend.	AUSTRALIA, Northcote Pass, Main Range, Kosciusco Alpine Area at 2100 m, <i>T. Armstrong</i>		CHR 536185	this paper	AY034849	
<i>Chionohebe densifolia</i> (F. Muell.) B. G. Briggs & Ehrend.	NEW ZEALAND, 'Hokonui Alpines,' <i>P. Heenan</i> 9.3.90	G 19236	CHR 512454	Wagstaff & Garnock-Jones (1998)	AF037375	AY034007
<i>Chionohebe pulvinaris</i> (Hook. f.) B. G. Briggs & Ehrend.	NEW ZEALAND, Nelson, Mt. Arthur, summit trig point, <i>W. R. Sykes</i> 551/93	551/93	CHR 496926	Wagstaff & Garnock-Jones (2000)	AF229038	
<i>Chionohebe thomsonii</i> (Buchanan) B. G. Briggs & Ehrend.	NEW ZEALAND, Fog Peak, <i>P. Heenan, P. J. Garnock-Jones</i> 8.12.89	G 18586	CHR 512485	Wagstaff & Garnock-Jones (2000)	AF229039	
<i>Collinsia grandiflora</i> Lindl.	AUSTRALIA, Tasmania, <i>A. T. Dobson</i> 77180	G 11573	CHR 512469	Olmstead et al. (2000)	AF037381	AF026825
<i>Derwentia derwentiana</i> (Andrews) B. G. Briggs & Ehrend.	AUSTRALIA, Cultivated Landcare Research Experimental Garden <i>Wagstaff</i> 94.105	G 19629	CHR 512486	Wagstaff & Garnock-Jones (1998)	AF037382	AY034010
<i>Derwentia nivea</i> (Lindl.) B. G. Briggs & Ehrend.	AUSTRALIA, Cultivated Landcare Research Experimental Garden <i>Wagstaff</i> 94.40		CHR 512493	Wagstaff & Garnock-Jones (2000)	AF229040	—

Appendix I. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession	
					ITS	<i>rbcL</i>
<i>Digitalis purpurea</i> L.	unknown			Olmstead et al. (1993)	L01902	
<i>Globularia cordifolia</i> L.	<i>L. Hufford</i> , no voucher			Olmstead et al. (2000)	AF124558	
<i>Gratiola pilosa</i> Michx.	<i>C. W. dePamphilis 90.34</i>			Olmstead et al. (2000)	AF026827	
<i>Hebe albicans</i> (Petrie) Cockayne	NEW ZEALAND, Northwest Nelson, Boulder Lake, <i>D. Rooney 5.2.88</i>	G17134	CHR 512448	Wagstaff & Garnock-Jones (1998)	AF037373	
<i>Hebe annulata</i> (Petrie) Cockayne & Allan	NEW ZEALAND, Southland, Wye River near Lake Wakatipu, <i>P. Wardle, N. Simpson</i> , Dec. 1994	366/94	CHR 512497	Wagstaff & Wardle (1999)	AF069464	
<i>Hebe armstrongii</i> (J. B. Armstr.) Cockayne & Allan	NEW ZEALAND, Canterbury, Enys Reserve, <i>B. Molloy 20.3.85</i>	G16006	CHR 512483	Wagstaff & Wardle (1999)	AF069463	
<i>Hebe barkeri</i> (Cockayne) Cockayne	NEW ZEALAND, Chatham Island, <i>D. R. Given 121-85</i>	G16061	CHR 512496	Wagstaff & Garnock-Jones (1998)	AF037374	
<i>Hebe benthamii</i> (Hook. f.) Cockayne & Allan	NEW ZEALAND, Campbell Island, Bee-man Hill, <i>B. D. Rance 17 Nov. 1990</i>		CHR 468050	this paper; Wagstaff & Garnock-Jones (2000)	AF229041	AY034013
<i>Hebe chathamica</i> (Buchanan) Cockayne & Allan	NEW ZEALAND, Chatham Islands, Kaingaroa, <i>D. R. Given 12830, P. A. Williams</i>	G14675	CHR 512434	Wagstaff & Garnock-Jones (1998)	AF037387	
<i>Hebe cheesemanii</i> (Buchanan) Cockayne & Allan	NEW ZEALAND, Marlborough, George Stream, <i>P. Heenan, P. J. Garnock-Jones 1999</i>	49/91	CHR 512472	Wagstaff & Garnock-Jones (1998)	AF037377	AY034008
<i>Hebe ciliolata</i> (Hook. f.) Cockayne & Allan	NEW ZEALAND, Nelson, Havelock Valley, <i>D. Rooney 15.4.99</i>	292/91	CHR 512474	this paper	AY034851	—
<i>Hebe cockayneana</i> (Cheeseman) Cockayne & Allan	NEW ZEALAND, Southland, Gertrude Valley, <i>P. J. Garnock-Jones 1883</i>	G17527B	CHR 512443	Wagstaff & Garnock-Jones (1998)	AF037399	
<i>Hebe corriganii</i> Carse	NEW ZEALAND, South Auckland, McLaren Falls, <i>P. J. Garnock-Jones, B. D. Clarkson 1984</i>	G1/09B	CHR 512458	Wagstaff & Garnock-Jones (1998)	AF037384	
<i>Hebe cupressoides</i> (Hook. f.) Cockayne & Allan	NEW ZEALAND, Canterbury, Rakaia Gorge, <i>R. Buxton, 15 Dec. 1989</i>	G18637	CHR 512449	Wagstaff & Garnock-Jones (1998)	AF037378	AY034014
<i>Hebe dieffenbachii</i> (Benth.) Cockayne & Allan	NEW ZEALAND, Chatham Islands, Kaingaroa, <i>D. R. Given 14015</i>	G15933	CHR 512462	this paper	AY034852	—
<i>Hebe elliptica</i> (G. Forst.) Pennell	ARGENTINA, Falkland Island, Carcass Id., <i>U. McHardy</i>		WELTU 16897	Wagstaff & Garnock-Jones (1998)	AF037392	AY034011

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession	
					ITS	<i>rbcL</i>
<i>Hebe elliptica</i> (G. Forst.) Pennell	NEW ZEALAND. Cultivated Landcare Research experimental garden, originally from Mt. Peel Nursery, <i>P. Heenan</i> , 12.9.89		CHR 512484	Wagstaff & Garmock-Jones (1998)	AF037393	—
<i>Hebe epacridea</i> (Hook. f.) Cockayne & Allan	NEW ZEALAND. Canterbury, Mt. Terako, <i>S. J. Wagstaff</i> 95.01		CHR 512479	Wagstaff & Garmock-Jones (1998)	AF037389	
<i>Hebe formosa</i> (R. Br.) Cockayne	AUSTRALIA. Botanic Gardens, Canberra 186/94		CHR 512490	Wagstaff & Garmock-Jones (1998)	AF037383	AY034015
<i>Hebe hectorii</i> (Hook. f.) Cockayne & Allan subsp. <i>hectorii</i>	NEW ZEALAND. Southland, Takitimu Range, <i>P. J. Garmock-Jones</i> 1925	G18884	CHR 512450	Wagstaff & Wardle (1999)	AF069460	
<i>Hebe hectorii</i> subsp. <i>subsimilis</i> (Colenso) Wagstaff & Wardle	NEW ZEALAND. Hawkes Bay, Ngamoko Range (spur of Ruahine Range), <i>A. P. Druce</i> Apr. 1978		CHR 323681	Wagstaff & Garmock-Jones (1998)	AF037390	
<i>Hebe lycopodioides</i> (Hook. f.) Cockayne & Allan subsp. <i>lycopodioides</i>	NEW ZEALAND. Canterbury, Mt. Terako, <i>S. J. Wagstaff</i> 95.03		CHR 512480	Wagstaff & Wardle (1999)	AF069456	
<i>Hebe macrantha</i> (Hook. f.) Cockayne & Allan	NEW ZEALAND. Nelson, Maitiri Plateau <i>D. Glenn</i> , <i>S. J. Wagstaff</i> 95.09		CHR 512468	this paper	AY034853	—
<i>Hebe macrantha</i> (Hook. f.) Cockayne & Allan	NEW ZEALAND. Cultivated Landcare Research experimental garden, originally from Christchurch Botanic Garden, <i>P. Heenan</i> 17.11.89	G18370	CHR 512444	Wagstaff & Garmock-Jones (1998)	AF037391	AY034016
<i>Hebe odora</i> (Hook. f.) Cockayne	NEW ZEALAND. Mt. Peel Nursery, <i>P. J. Garmock-Jones</i> 4 Dec. 1990	G17812	CHR 512441	Wagstaff & Garmock-Jones (1998)	AF037388	AF034017
<i>Hebe parviflora</i> (Vahl) Cockayne & Allan	NEW ZEALAND. Cultivated Landcare Research Experimental Garden, originally from Mt. Peel Nursery, <i>P. Heenan</i> 12.9.89	G17820	CHR 512447	this paper	AY034854	—
<i>Hebe pauciflora</i> (Cockayne & Allan) L. B. Moore	NEW ZEALAND. Canterbury, Mt. Somers, <i>D. Rooney</i> 5.5.88	G17158	CHR 512461	Wagstaff & Wardle (1999)	AF069466	
<i>Hebe petrici</i> (Buchanan) Cockayne & Allan	NEW ZEALAND. Southland, Eyre Creek, <i>P. J. Garmock-Jones</i> 1965	G18708B	CHR 512498	Wagstaff & Garmock-Jones (2000)	AF229042	
<i>Hebe pineleoides</i> (Hook. f.) Cockayne & Allan	NEW ZEALAND. Cultivated Landcare Research Experimental Garden, ex. <i>J. Cartman</i> 19.9.89	G17906		this paper	AY034855	—

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession	
					ITS	<i>rbcL</i>
<i>Hebe propinqua</i> (Cheeseman) Cockayne & Allan	NEW ZEALAND. Southland, South Mavora Lake, <i>P. Wardle</i> 30.3.95	107/93B	CHR 512478	Wagstaff & Wardle (1999)	AF069458	
<i>Hebe ramosissima</i> G. Simpson & J. S. Thomson	NEW ZEALAND. Marlborough, Mt. Tapuaenuku, <i>J. Cartman</i> 9.1.90	G18659	CHR 512628	this paper	AY034856	
<i>Hebe salicifolia</i> (G. Forst.) Pennell	CHILE. San Rafael, <i>R. Buxton</i> 1992		WELTU 16898	Wagstaff & Garnock-Jones (1998)	AF037386	AY034018
<i>Hebe salicifolia</i> (G. Forst.) Pennell	NEW ZEALAND. Nelson, Matri Plateau, <i>S. J. Wagstaff</i> 95.10		CHR 512466	Wagstaff & Garnock-Jones (1998)	AF037385	
<i>Hebe salicornioides</i> (Hook. f) Cockayne & Allan	NEW ZEALAND. Canterbury, Jacks Pass, <i>Hammer, J. B. Hair</i> 26.10.66	G6602	CHR 512475	Wagstaff & Wardle (1999)	AF069465	AY034019
<i>Hebe speciosa</i> (A. Cunn.) Cockayne & Allan	NEW ZEALAND. North Auckland, Maungani Bluff, <i>D. R. Given, J. Bartlett</i> 11571	G12051	CHR 512457	this paper	AY034864 AY034865	
<i>Hebe tetrasticha</i> (Hook. f) Cockayne & Allan	NEW ZEALAND. Canterbury, Mt. Cheeseman, <i>A. P. Druce</i> 20.10.89	G18476	CHR 512451	this paper	AY034866 AY034867	
<i>Hebe townsonii</i> (Cheeseman) Cockayne & Allan	NEW ZEALAND. Northwest Nelson, Coastal, <i>A. W. Purdie</i> 29.1.88.	G17111	CHR 152489	this paper	AY034857	
<i>Hebe vernicosa</i> (Hook. f) Cockayne & Allan	NEW ZEALAND. Nelson, Maungatapu Summit, <i>P. J. Garnock-Jones</i> 1888	G17557E	CHR 465635	this paper	AY034858	
<i>Heliohebe hulkeana</i> (F. Muell.) Garn.-Jones	NEW ZEALAND. Marlborough, Ure River, <i>D. Given</i> 31.1.1966	G17113	CHR 512460	Wagstaff & Garnock-Jones (1998)	AF037379	
<i>Heliohebe laudiana</i> (Raoul) Garn.-Jones	NEW ZEALAND. Canterbury, Banks Peninsula, Summit Road, <i>B. Molloy</i> 8.9.82	G14806	CHR 512487	Wagstaff & Garnock-Jones (2000)	AF229043	
<i>Heliohebe raoulitii</i> (Hook. f.) Garn.-Jones	NEW ZEALAND. Marlborough, Mt. Fyffe, <i>L. Decourtye</i> 22.2.86	G16285	CHR 512459	Wagstaff & Garnock-Jones (1998)	AF037380	AY034009
<i>Hippuris vulgaris</i> L.	<i>Olmstead & Reeves</i> 92-127			<i>Olmstead & Reeves</i> (1995)		L36443
<i>Parahebe birleyi</i> (N. E. Br.) W. R. B. Oliv.	NEW ZEALAND. Southland, Takitimu Range, above tarn in cirque E of Tower Peak, 1340 m, <i>P. J. Garnock-Jones</i> 2039, <i>W. M. Malcolm</i>		CHR 470104	Wagstaff & Garnock-Jones (2000)	AF229044	
<i>Parahebe brevistylis</i> (Garn.-Jones) Heads	NEW ZEALAND. Southland Eyre Mountain, Upper Eyre Creek, <i>P. J. Garnock-Jones</i> 1910	G18892	CHR 512452	Wagstaff & Garnock-Jones (2000)	AF229045	

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession	
					ITS	<i>rbcL</i>
<i>Parahebe canescens</i> W. R. B. Oliv.	NEW ZEALAND, Canterbury, S end of Lake Lyndon, <i>P. J. Garnock-Jones</i> , Aug. 1990	264/90	CHR 512446	Wagstaff & Garnock-Jones (1998)	AF037394	AY034020
<i>Parahebe cataractae</i> subsp. <i>martinii</i> Garn.-Jones	NEW ZEALAND, Marlborough, Waima River, <i>P. A. William</i> 15.4.1976s	G11359	CHR 512456	Wagstaff & Garnock-Jones (1998) this paper	AF037396	AY034859
<i>Parahebe cataractae</i> (G. Forst.) W. R. B. Oliv. subsp. <i>catarractae</i>	NEW ZEALAND, Otago, Manapouri Wildlife Pass Rd., <i>P. J. Garnock-Jones</i> 24/03					
<i>Parahebe cheesemanii</i> (Benth.) W. R. B. Oliv.	NEW ZEALAND, Nelson, St. Arnaud Range, basin W of Rainbow Snowfield, <i>B. D. Rance, L. Leicington</i> 2 Apr. 1994		CHR 509212	Wagstaff & Garnock-Jones (2000)	AF229046	
<i>Parahebe decora</i> Ashwin	NEW ZEALAND, Nelson, Matiri Plateau, <i>D. Glenn, S. J. Wagstaff</i> 95.08		CHR 512467	Wagstaff & Garnock-Jones (2000) this paper	A229047	AY034860
<i>Parahebe hookeriana</i> (Walp.) W. R. B. Oliv.	NEW ZEALAND, Wellington, Mt. Ruapehu, <i>P. J. Garnock-Jones</i> 24/6					
<i>Parahebe linifolia</i> (Hook. f.) W. R. B. Oliv.	NEW ZEALAND, Canterbury, Havelock Valley, Carney's Creek Hut, <i>B. P. J. Molloy, A. P. Druce</i> 22 Feb. 1991	182/91	CHR 470347	Wagstaff & Garnock-Jones (2000)	AF229047	
<i>Parahebe lithophila</i> B. G. Briggs & Ehrend.	AUSTRALIA, New South Wales, 1 km on track below McMahons Lookout, ca. 5 km S of Wentworth Falls, Blue Mountains Natl. Park, <i>B. G. Briggs, B. Wiecek, L. Johnson</i> 2.5.92		CHR 454303	Wagstaff & Garnock-Jones (2000)	AF229048	
<i>Parahebe lyallii</i> (Hook f.) W. R. B. Oliv.	NEW ZEALAND, North Canterbury, Mt. Percival, <i>A. W. Purdie</i> 11.5.89	G17594	CHR 512440	Wagstaff & Garnock-Jones (1998)	AF037395	
<i>Parahebe planopetiolata</i> (G. Simpson & J. S. Thomson) W. R. B. Oliv.	NEW ZEALAND, Southland, Kingston, Mt. Dick, Lake Wakatipu, <i>N. Simpson</i> 15.5.95	147/95	CHR 512626	Wagstaff & Garnock-Jones (2000)	AF229050	
<i>Parahebe spathulata</i> (Benth.) W. R. B. Oliv.	NEW ZEALAND, Cultivated Victoria University, <i>P. J. Garnock-Jones</i> 24/04			this paper	AY034861	
<i>Parahebe spathulata</i> (Benth.) W. R. B. Oliv.	NEW ZEALAND, Volcanic Plateau, Mt. Ruapehu, Turoa Skifield, beside buildings at top of road, 1600 m, <i>P. J. Garnock-Jones</i> 22/63		WELTU 16860	Wagstaff & Garnock-Jones (2000)	AF229051	

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession	
					ITS	<i>rbcL</i>
<i>Parabebe trifida</i> W. R. B. Oliv.	NEW ZEALAND. Southland, Garvie Mts. Mt. Tennyson, E slope near summit, 1460 m, <i>P. J. Garnock-Jones 2161</i>		CHR 512442	Wagstaff & Garnock-Jones (1998)	AF037376	
<i>Parabebe vandewateri</i> (Pennell) P. Roy-en	NEW GUINEA. Neren Valley, M3, 4180 m, near clear-colored lake, <i>R. Buxton</i> , 12 Sep. 1998		CHR 530002	Wagstaff & Garnock-Jones (2000)	AF229052	AY034023
<i>Plantago lanceolata</i> L.	<i>Olmstead s.n.</i>			Olmstead & Reeves (1995)		L36454
<i>Pseudolysimachion spicatum</i> Opiz	Unknown, Bot. Garden Bonn		s.n., BONN	Albach & Chase (2001)	AF313022	
<i>Veronica anagallis-aquatica</i> L.	NEW ZEALAND. Canterbury, Harts Creek, <i>S. J. Wagstaff 94.09</i>		CHR 512465	Wagstaff & Garnock-Jones (1998)	AF037397	AY034021
<i>Veronica arguta</i> R. Br.	AUSTRALIA. Cultivated Landcare Research Experimental Garden, originally from Botanic Gardens, Canberra, 8704379	186/94	CHR 512625	this paper	AY034862	AY034025
<i>Veronica austriaca</i> L.	Unknown, Bot. Garden Bonn		s.n., BONN	Albach & Chase (2001)	AF313000	
<i>Veronica bellidoides</i> L.	AUSTRIA. Kärnten: Nockberge Hoher Falkert, <i>J. P. Grube</i> , MWC 7416 (K)	KEW 1996-761		Albach & Chase (2001)	AF313010	
<i>Veronica calycina</i> R. Br.	AUSTRALIA. Cultivated Landcare Research Experimental Garden, originally from Botanic Gardens, Canberra 8602018	187/94	CHR 512627	this paper	AY034863	
<i>Veronica chamaedrys</i> L.	NORWAY. Hørsland: Os, Hattvik, MWC 7419 (K)	KEW 1970-1438		Albach & Chase (2001)	AF313003	
<i>Veronica fruticulosa</i> L.	Unknown, Bot. Garden Bonn		s.n., BONN	Albach & Chase (2001)	AF313004	
<i>Veronica glandulosa</i> Hochst.	KENYA. <i>Fischer 713/98</i>	Bot. Garden Bonn		Albach & Chase (2001)	AF313008	
<i>Veronica glauca</i> Sibth. & Sm.	GREECE. RBG Kew, MWC 8922 (K)	KEW 1973-14554		Albach & Chase (2001)	AF313006	
<i>Veronica macrostachya</i> Vahl	Unknown, RBG Kew, MWC 7417 (K)	KEW 1969-50547		Albach & Chase (2001)	AF312999	
<i>Veronica officinalis</i> L.	ITALY. Reg. Calabria, Prov. Cosenza, <i>S. P. Brooks 23 July 1984</i>		CHR 423831	this paper		AY034024
<i>Veronica officinalis</i> L.	GREAT BRITAIN. Farthing Downs, MWC 7385 (K)	KEW 1978-1342		Albach & Chase (2001)	AF313024	
<i>Veronica oltensis</i> Woron.	TURKEY. NYBG, <i>L. Struwe 1405</i> (WU)	NYBG		Albach & Chase (2001)	AF312995	

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession	
					ITS	<i>rbcL</i>
<i>Veronica persica</i> Poir.	NEW ZEALAND. Canterbury, Lincoln, Agricultural and Science Research Centre, adventive, <i>S. J. Wagstaff 94.04 Olmstead 92-144</i>	CHR 512455		this paper	AY036878	AY034023
<i>Veronica persica</i> Poir.				Olmstead & Reeves (1995)		L36453
<i>Veronica satutarejoides</i> Vis.	Unknown, NYBG, <i>L. Struce 1408</i> (WU)			Albach & Chase (2001)	AF313005	
<i>Veronica serpyllifolia</i> L.	NEW ZEALAND. Canterbury, Groynes Nature Reserve, adventive along lake shore, <i>S. J. Wagstaff 95.55</i>	CHR 518833		this paper	AY036879	
<i>Veronica urticifolia</i> Jacq.	Unknown, Bot. Garden Bonn	s.n., BONN		Albach & Chase (2001)	AF313011	
<i>Veronicastrum sibiricum</i> (L.) Pennell	NEW ZEALAND. Cultivated Landcare Research Experimental Garden, <i>S. J. Wagstaff, P. J. Garnock-Jones 94.09</i>	CHR 512445		Wagstaff & Garnock-Jones (1998)	AF307398	AY034012
<i>Wulfenia carinthiaca</i> Jacq.	AUSTRIA. Karnten, Gartnerkofel	Bot. Garden Bonn s.n., BONN		Albach & Chase (2001)	AF313025	



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