species (*H. pilosella*, *H. praealtum*, *H. caespitosum*, *H. aurantiacum*, *H.*
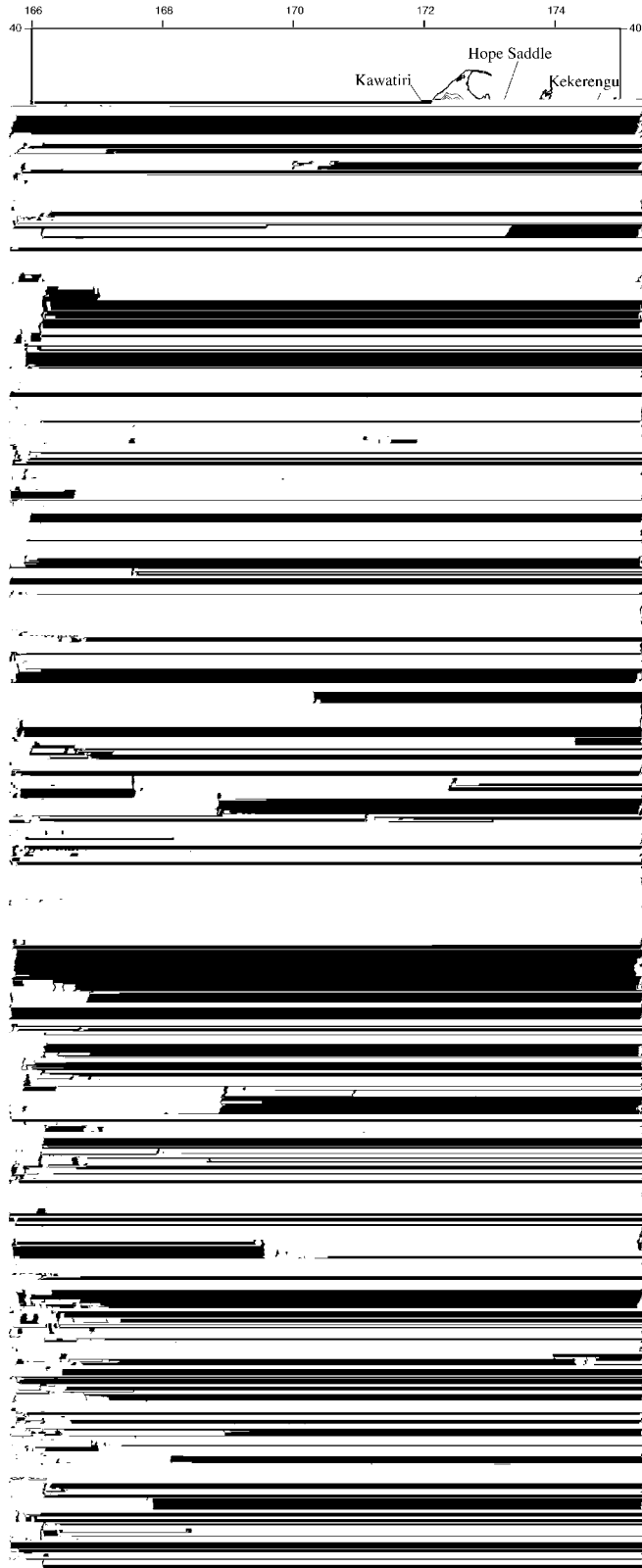
Fig. 1.   Collection locations and occurrence of cpDNA haplotypes in *Hieracium pilosella* in South Island, New Zealand. This species is scarce in North Island.
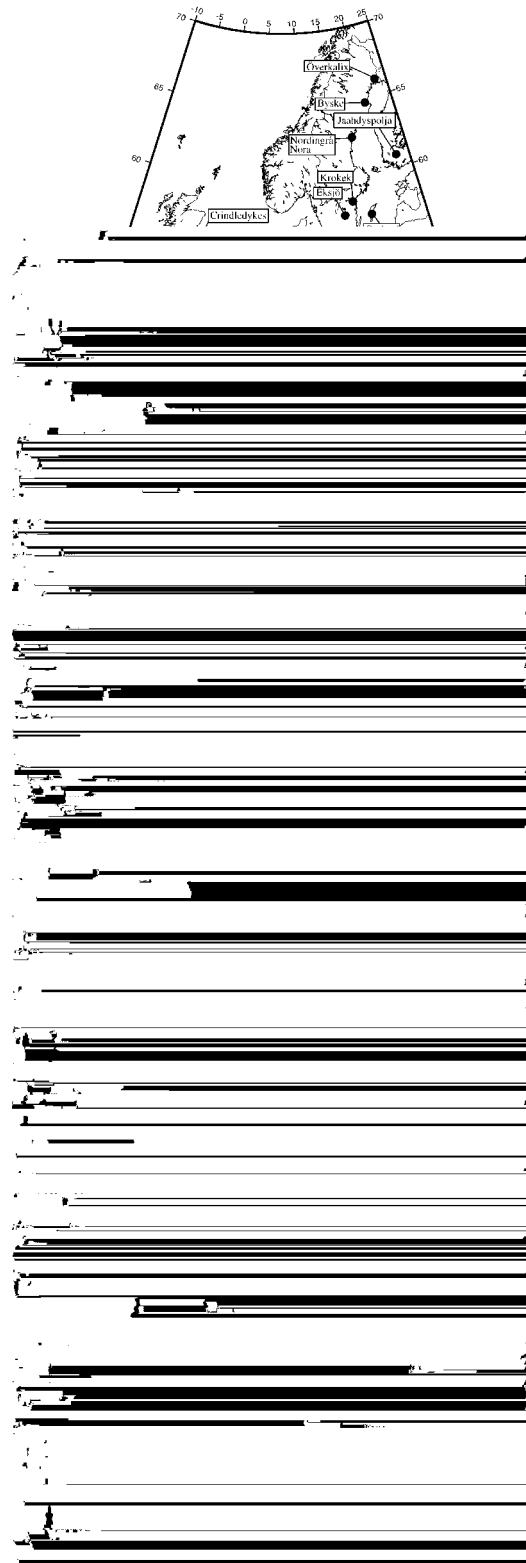

Fig. 2.   Collection locations and occurrence of cpDNA haplotypes in *Hieracium pilosella* in Europe.

TABLE 2. Summary of variation encountered among chloroplast DNA sequences for the *trnL–trnF* region. Numbers indicate position of variable sites among 900 bp of 11 aligned *Hieracium* subgenus *Pilosella* haplotype sequences.

Haplotype	98	117	241	250	300	394	406	520	533	569	597	622	666	690	755	839	869
A	A	A	G	A	G	A	C	C	-----	C	T	TATTCT	A	-------------	T	AATGAG	A
B	A	A	A	A	T	A	C	C	-----	C	T	TATTCT	A	-------------	T	AATGAG	A
C	A	A	G	A	G	A	C	C	-----	C	T	------	A	-------------	T	AATGAG	G
D	-	A	G	G	G	A	C	C	TTATC	C	G	TATTCT	A	CAAGGAATCCCCA	G	-----	A
G	-	C	G	A	G	G	C	C	-----	A	G	TATTCT	A	-------------	G	AATGAG	A
H	-	A	G	A	G	A	C	C	-----	C	G	TATTCT	A	CAAGGAATCCCCA	G	-----	A
I	A	A	G	A	G	A	T	C	-----	C	T	TATTCT	A	-------------	T	AATGAG	A
J	-	C	G	A	G	G	C	C	-----	A	G	TATTCT	G	-------------	G	AATGAG	A
L	-	C	G	A	G	A	C	C	-----	C	G	TATTCT	A	-------------	G	AATGAG	A
M	-	A	G	A	G	A	C	C	-----	C	T	TATTCT	A	-------------	T	AATGAG	A
N	-	C	G	A	G	G	C	A	-----	A	G	TATTCT	A	-------------	G	AATGAG	A

types were found in a number of taxa: I in two *H. caespitosum* (of eight), J in a single *H. lactucella*, and H in a single *H. auricula*.

Phylogeny—The relationship among these haplotypes was inferred using a fully resolved parsimony spanning tree. Many of the haplotypes we encountered appear as internal nodes in our tree, consistent with shallow or recent splitting (Fig. 3a). Interestingly, four of the five internal nodes consisted of haplotypes found in *H. pilosella*.

DISCUSSION

Considering the number of taxa surveyed, we found a high level of haplotype diversity, but we also found a high level of haplotype sharing among taxa. This might reflect two distinct processes: incomplete lineage sorting or interspecies hybridization (Comes and Abbott, 2001). Both are consistent with recent speciation. Our data do not allow us to study the phylogenetics nor the systematics of species, but our data do demonstrate the complex recent history of the group and help explain taxonomic difficulties. *Hieracium pilosella* introduced to New Zealand brought with it much of the European chloroplast variation. It has not increased cpDNA diversity via hybridization since introduction, but hybridization may nevertheless have a significant impact on invasiveness in New Zealand.

Reticulate evolution—We found six haplotypes within *H. pilosella* and extensive sharing among ploidal levels and sharing among species. Despite the predominance of apomixis the sharing of haplotypes can be explained by reticulate evolution. In New Zealand *Hieracium pilosella*, a low level of residual sex has been demonstrated in pentaploid apomicts (Houliston and Chapman, 2001) and a breakdown in microspecies boundaries has been observed (Chapman and Brown, 2001). Fur-

TABLE 3. Locations in the South Island, New Zealand, sampled for *Hieracium* subgenus *Pilosella*, with occurrence of haplotypes indicated by location, taxon, and ploidy. Frequency of haplotypes in *H. pilosella* are shown as *n*.

Location	*n*	H. pilosella 4×	5×	6×	?	H. praealtum 4×	5×	H. caespltosum 4×	H. × stoloniflorum 6×	aurantiacum 4×
Brockville	6		B							
Burke Pass	2,1		AB				A			
Chilton	2,2		AB							
Coalgate	1		A							
Cowans Hill	2		A			A				
Daisy Bank	1		A			A				
Drac Flat	9,13,1	C	AB			A	A	A	G	
Dunstan Range	1,1		AB							
Fairlie dom.	1,1		A	A						
Glen Tanner						A				
Godley	1		B			A				
Hanmer										D
Holbrook	1		B							
Hooker Flat						A				
Hope Saddle						A	D			
Hope Saddle top	1		B							
Idaburn	1		A							
Kakanui	3		A							
Kawatiri	1		B							
Kekerengu	2,2		AB							
Klondye shelter	2		A							
Kurinui	5		A			A				
Lake Tennyson										D
Lindis Pass	2		A			A				
Lions Head	6		A							
Lyndon	5,1,10,2	AC	AB			A				
Maryburn								A		
Mt. Bee	1		A							
Mt. Fyffe	2		B							
Mt. Somers	1		A							
Omarama	1		A							
Porters Pass										D
Pudding Hill	1		A							
Raggedy Range	1		B							
Rakaia	7,2,6	AC	A							
Saddle Hill	1		B							
Sawdon							A			
Seymour	1		A							
Shannon	2		A							
St. James ww	3,1		AB							
Tekapo										D
Temuka dom.	8		A							
Twizel dom.	1,2			AM						
Waitaki	1		A							
Waitohi memorial	1		A							
Balmoral herb.	1				A					
Cave Stream herb.	1				B					
Hanmer herb.	1				B					
Hope Valley herb.					A					
Rakaia herb.	1,1				AB					
Tekapo herb.	1				A					
Temuka dom. herb.	1				B					

TABLE 4. Frequency of three haplotypes among tetraploid and pentaploid *Hieracium pilosella* and tetraploid putative hybrids, at three sites in South Island, New Zealand.

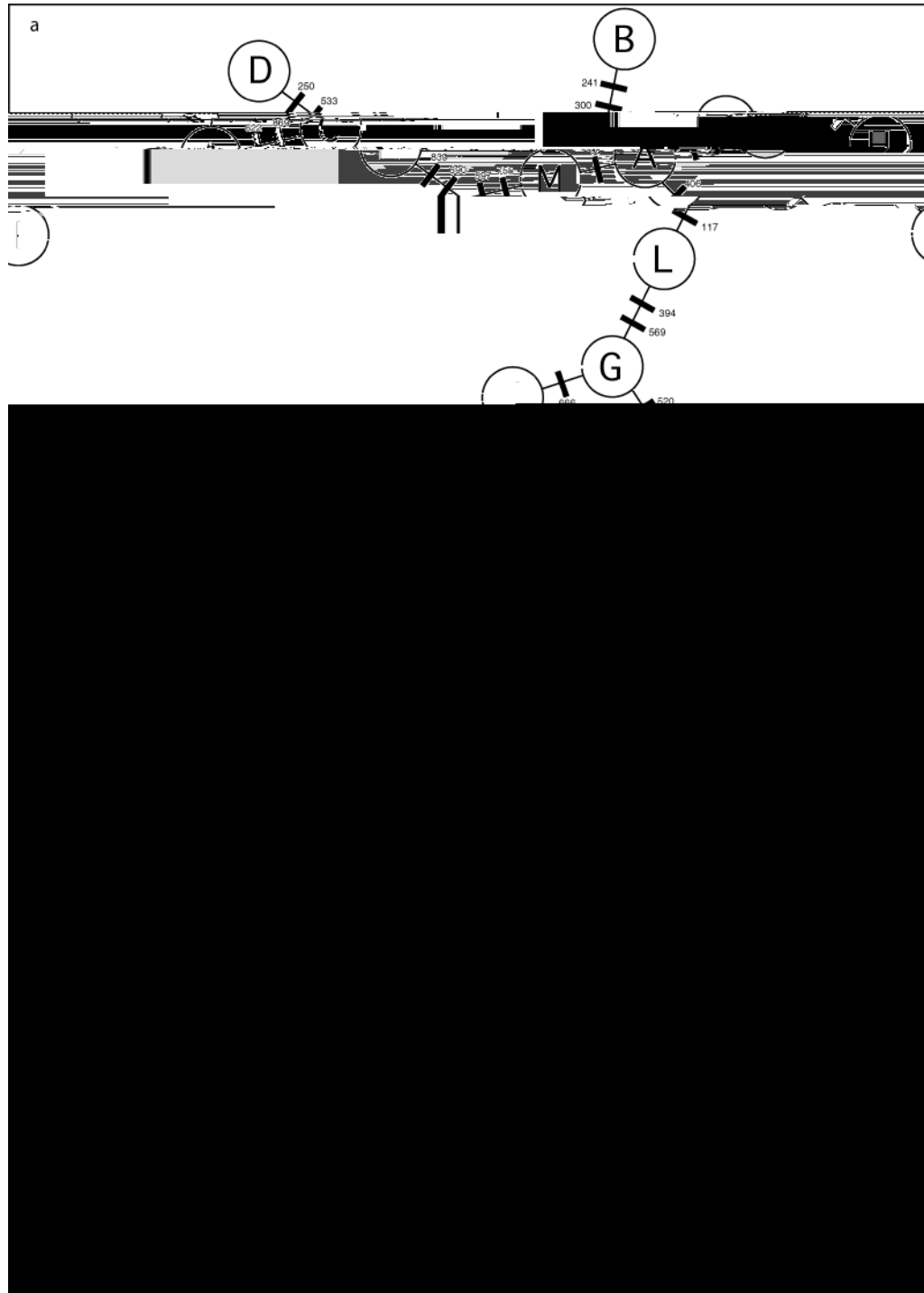| Site	4× A	B	C	5× A	B	C	6× A	M	4× hybrids A	B	C	Total
Drac Flat			9	13	1				2		7	32
Lyndon	5		1	10	2				3	1	1	23
Rakaia	7		2	6								15
Other				54	23		2	2	4			85
Total	12		12	83	26		2	2	9	1	8	155

Fig. 3. Minimum spanning tree of 11 *Hieracium* subgenus *Pilosella* cpDNA haplotypes, with point mutations and tandem repeats scored equally as single events. (a) Bars indicate character state changes at 17 variable sites, numbered according to position in aligned sequence (see Table 1). (b) The species, in which the haplotypes were found, and their ploidy (where known). Grey fill indicates haplotypes found only in *H. pilosella*.

New Zealand arrived sometime in the mid-1800s (Travers, 1884). Introduction probably resulted from seed accidentally harvested with European grass seed used for development of New Zealand pastureland. It is assumed that the United Kingdom was the source of this seed but this is not supported by our data. We found more cpDNA haplotypes in New Zealand *H. pilosella* than in the United Kingdom. The two haplotypes in the United Kingdom (A, B) were ubiquitous throughout Europe. In particular, we did not find haplotype C in the United Kingdom, despite sampling from several populations. However, haplotype C was present in our smaller sample from eastern/northern Europe (Czech Republic, Finland). Also in our central European sample were *H. pilosella* and *H. aurantiacum* with haplotype G (Austria). Although G was not found in ei-

ther of these species sampled in New Zealand, it was present in samples of the hybrid taxon derived from these parentals (*H. × stoloniflorum*). We note, too, that New Zealand *H. × stoloniflorum*, which are evidently derived from introduced hybrids rather than arising here, are hexaploid (Jenkins and Jong, 1997; Morgan-Richards et al., in press), and this ploidy is reported from Bavaria (Germany) and the Czech Republic but not the United Kingdom (Krahulcova et al., 2000). It is significant too that all of the subgenus *Pilosella* taxa in New Zealand, except *H. pilosella*, exist only as garden escapes in the United Kingdom (Stace, 1997). The combined evidence unexpectedly indicates that some, if not all, extant New Zealand *Hieracium* taxa came from central Europe rather than the United Kingdom.

Invasion—Why some introduced taxa succeed in founding persistent populations is not well understood. Acclimatization societies in New Zealand actively introduced foreign organisms and thus supplemented the large number that arrived accidentally (Travers, 1884). A study of bird introductions to New Zealand revealed that colonization success might have as much to do with management as ecological characteristics of individual species (Veltman et al., 1996). In the case of *Hieracium pilosella*, it cannot be known which, and in what relative frequencies, lineages (genotypes) were initially introduced. Initial studies of *H. pilosella* ploidy in New Zealand indicated most plants were pentaploids and tetraploids were absent (Makepeace, 1981; Jenkins and Jong, 1997). Sexual tetraploids have since been found (Chapman et al., 2003), but so has evidence that apomict pentaploids are able to generate other ploidies through residual sex (Chapman and Bicknell, 2000; Houliston and Chapman, 2001). It has been inferred that tetraploid sexuals may have evolved in New Zealand (Chapman et al., 2003).

The present study indicates that at least one sexual tetraploid lineage (4× C) was introduced directly from Europe. To have evolved in New Zealand would require a population of haplotype C pentaploids and given that the level of residual sex in apomicts is low (up to 2.3%; Houliston and Chapman,

APPENDIX 1. Locations in Europe sampled for *Hieracium* subgenus *Pilosella*, with details of incidence of haplotypes among locations and taxa.

APPENDIX 1.   Extended.

praealtum	caespitosum	aurantiacum	pilosselloides	glomeratum	glabrum	glaciale	florentinum	auricula	× stoioniflorum
AD	AI	ADGN	A	A	A	D	G	H	—
AD	A	D	—	—	—	—	—	—	G
		G							
			A						
						D			
A									
A									
		D							
				A					
		N							
		D		A	A				
		D							
	A							H	
		D							
	I								
	A								
	I								
	A								
A			A						
			A						
		D							
	A			A					
		A							
	A								
	A								
								G	
D									
								G	
		D							
		D							
	A								

APPENDIX 1.   Continued.

Country	Region	Location	Collector/ID	*pilosella*	*peleterianum*	*lactucella*
United Kingdom	Cornwall	Nare Head	CS	B		
United Kingdom	Cornwall	New Down Head	CS	A		
United Kingdom	Glamorgan	Cilibion	CS	A		
United Kingdom	Glamorgan	Connelly	CS	B		
United Kingdom	Glamorgan	Cwm Ivy Tor	CS	B		
United Kingdom	Glamorgan	Maesteg	CS	B		
United Kingdom	Gwyned	Criccieth	HC	B		
United Kingdom	Worcestershire	Coombe Green Common	CS	B		
United Kingdom	Worcestershire	Knightwick-on-Teme	CS	A		
United Kingdom	Worcestershire	Windmill Hill	CS	B		
United Kingdom	Worcestershire	Worcester Beacon	CS	B		

APPENDIX 1. Extended continued.

praealtum	*caespitosum*	*aurantiacum*	*pilosselloides*	*glomeratum*	*glabrum*	*glaciale*	*florentinum*	*auricula*