

2. Methods

2.1 SAMPLING

Grasshoppers were collected by hand at sites with suitable habitat (Figs 4 & 5). Taxonomic identification primarily followed Bigelow (1967). Most material is held in ethanol at Massey University, although voucher specimens will ultimately be deposited at Museum of New Zealand Te Papa Tongarewa on completion of the research.

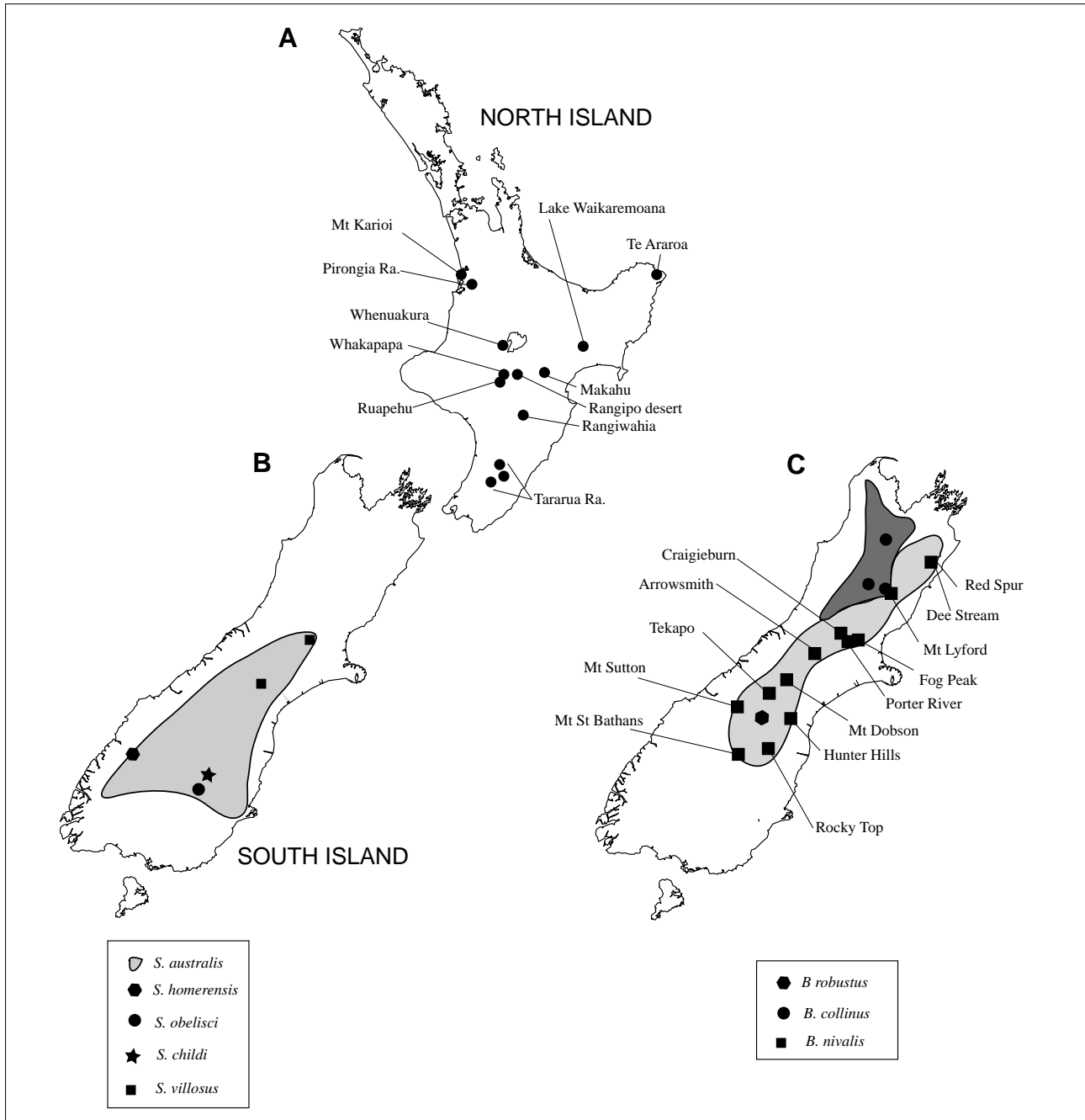


Figure 4. Ranges and sampling locations for grasshoppers. A. Locations in North Island sampled for *Sigaus piliferus*; B. approximate taxon ranges of South Island *Sigaus*; C. ranges and sampling for *Brachaspsis* taxa.

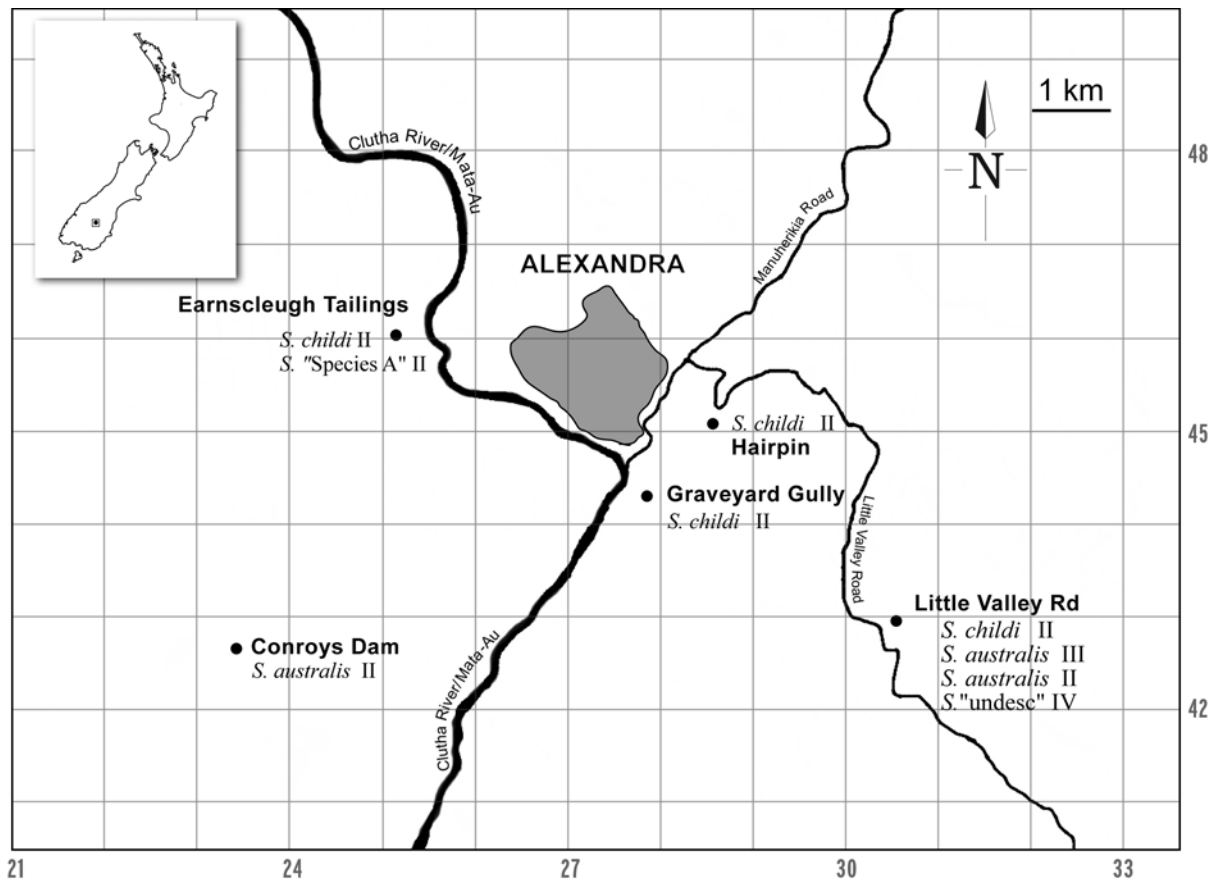


Figure 5. Sampling locations around Alexandra, and details of morphospecies found and DNA sequence haplogroup.

2.2 MOLECULAR METHODS

Single stranded conformational polymorphism (SSCP) was used to screen for variant haplotypes (combinations of alleles) prior to DNA sequencing (Trewick et al. 2000). For this purpose, the primers SR-J-14233 and SR-N-14588 (Simon et al. 1994) were used to amplify a c. 380 bp fragment of the 3' end of mitochondrial 12S rRNA. PCR (polymerase chain reaction) products were labelled with a radio isotope by incorporation of α ATP³³P. Amplification products were denatured for 5 min at 95°C in the presence of an equal volume (10 μ L) of 95% formamide loading buffer. These were loaded from ice into vertical, non-denaturing polyacrylamide gels consisting of 6% 37.5:1 bis/acrylamide, 5% glycerol and 0.5 \times TBE. Gels were electrophoresed at 4°C for 200 W/h at approximately 13 W and then lifted on blotting paper, dried and exposed with Biomax (Kodak) film for 24–48 h. Individuals were scored for haplotype by comparison of re-natured single strand DNA migration patterns (Sunnucks et al. 2000).

Representatives of each haplotype that was resolved by SSCP were subjected to further PCR to amplify and sequence a larger fragment comprising the 3' end of the 12S rRNA, the tRNA valine and the 5' end of the 16S rRNA, using primers LR-J-13417 and SR-N-14588 (Simon et al. 1994). The 12S-16S fragment of at least one individual of each population presenting a particular SSCP pattern was sequenced to confirm that sequences matched. In addition, a fragment from the 3' end of the mitochondrial COI was amplified and sequenced using primers C1-N-2195 and C1-J-3014 (Simon et al. 1994). PCR reactions for sequencing were

performed in 25 µL volumes using the same conditions as for SSCP. Products were purified using High Pure purification columns (Roche). Cycle sequencing used Perkin Elmer Bigdye chemistry following the manufacturer's protocols and were analysed on a Prism 377 DNA sequencer (Applied Biosystems, Inc., Foster City, California). Sequences were checked against the ABI trace file and aligned manually using SeqEd v1.0.3 (Applied Biosystems, Inc., Foster City, California), Sequencher v4.1 (Applied Biosystems, Inc., Foster City, California) and SeAL v2.0 (Rambaut 1996).

2.3 ANALYSIS

Two types of haplotype data were obtained (as reported in Trewick 2001a): initially, multiple individuals of the *B. nivalis* and *S. australis* complexes were screened using SSCP, which provides a rapid means of identifying DNA sequence variants; secondly, individuals representing the sequence diversity indicated by SSCP were sequenced to provide DNA nucleotide data for phylogenetic reconstruction. For *S. piliferus*, all individuals surveyed were sequenced for the COI mtDNA gene without prior screening. Distance estimation and phylogenetic analyses (maximum parsimony (MP), neighbor-joining (NJ), and maximum likelihood (ML)) were performed using PAUP*4.0b10 (Swofford 2002). Character evolution was assessed using McClade version 3.07 (Maddison & Maddison 1997). Further details of the analyses undertaken are reported in Trewick (2008).

3. Results and discussion

DNA sequences representing those obtained for each of the taxon groups detailed below were deposited on GenBank (accession numbers AY42370-AY42390, EF544487-EF544562). Pairwise genetic distances among sequence variants (haplotypes) are given in Appendix 1.

All phylogenetic analyses resulted in similar trees, and there was consistent support for the existence of the three taxon groups in question (*Sigauss piliferus*, the *Brachaspis nivalis* complex and the *Sigauss australis* complex), with each forming a separate clade. The overall level of genetic diversity within each taxon group is within a range that, for these genes, allows confidence in phylogenetic reconstruction, i.e. exhibits sufficient sequence variation to be sensitive enough to reveal within-species variation, yet does not reach a point of mutational substitution that would mask a deeper phylogenetic signal (> 13% in COI; Szymura et al. 1996). This confidence is reflected in the high statistical support from bootstrap resampling for each of the three target groups (see Trewick 2001, 2008).

The analyses reported here used COI mtDNA sequence alignments of between 540 and 780 nucleotides in length depending on the samples involved. The use of fairly short gene fragments was the result of a compromise between the number

of individuals surveyed and the quantity of data per individual; however, these fragments are sufficient to provide the necessary haplotypic data for our study.

The extent of genetic divergence among sequences from individuals within each group was in the typical range for insect species. In several instances, genetic distances (expressed here as percentage difference using Kimura two parameter correction) within existing grasshopper species complexes were higher than those found in even the most highly diverse New Zealand orthopterans (c. 8% in scree weta *Deinacrida connectens* (Trewick et al. 2000); and 9.5% in Auckland tree weta *Hemideina thoracica* (Morgan-Richards et al. 2001)). This degree of mtDNA sequence diversity within a species is unusual, and other studies of insects report divergences of as little as 2% between species (e.g. Langor & Sperling 1997). For convenience, we present trees generated using the neighbor-joining clustering method, which utilises the pairwise genetic distances determined from mtDNA sequence data (Appendix 1). Phylogenetic trees were inferred for each of the taxon groups in question, as this is the simplest means of expressing the distribution of haplotypes among sampling locations, morphospecies and the overall phylogeny.

A pattern of spatial structuring of genetic diversity was evident in all three taxon groups examined. Not surprisingly, where total genetic diversity was lowest (*Sigaus piliferus*), spatial structuring was least pronounced. An approximate indication of the likely time since the last common ancestor of a set of sequences can be inferred using a standard rate calibration of 2–2.3% per million years (Brower 1994; Juan et al. 1995; Fleischer et al. 1998). Such rates are generalised for a number of genes and taxa, and variation of gene and taxon specific rates is known.

The results for each taxon group are presented below, together with a discussion of any conservation implications or considerations. Table 1 summarises the combined spatial, morphological (current taxonomic) and haplotype (mtDNA) evidence for the grasshopper populations examined here. A set of management units have also been identified, based upon the available information. Note that this should be viewed as a working evolutionary/taxonomic hypothesis.

3.1 *Sigaus piliferus*

3.1.1 Genetic structure

Analysis of *S. piliferus* diversity used an alignment of 780 bp for a total of 51 grasshoppers from 14 locations in the North Island (Fig. 4). Two clades are evident among the data. One group (Sp.I; see Fig. 6) includes sequences from grasshoppers collected from the Ruahine Ranges northwards, including the isolated locations at Pirongia, Mt Karioi, Te Araroa and Lake Waikaremoana. The second group (Sp.II) is restricted to the Tararua Ranges. The maximum genetic divergence among samples of this species was 6.5%, and the mean divergence between the two clades was 5.4% (Table A1.1, Appendix 1). This is consistent with, but not proof of, these two groups having species status, and implies a common ancestor for the lineages during the Pliocene (2–5 mya). Within the main northern group (Sp.I), genetic diversity was distributed unevenly. The numerous samples from the Central Plateau area showed almost no DNA sequence variation,

TABLE 1. DIVERSITY AMONG *Sigaia pitliferus*, *Brachaspis nivalis* COMPLEX AND *Sigaia australis* COMPLEX.

Clade code refers to the designations made in Figs 6 and 7. Locations are those given in Figs 4 and 6 for *S. pitliferus* and *B. nivalis* complex, and Fig. 7 for *Sigaia australis* complex.

CURRENT TAXONOMY	PRINCIPLE CLADE CODE	TAXON/SPATIAL GROUP	MANAGEMENT UNITS	LOCATIONS SAMPLED	CURRENT EVIDENCE	
<i>Sigaia pitliferus</i> North Island	Sp.II	<i>S. pitliferus</i> Tararua	1 Peripheral	Tararua Range	MtDNA split and morphology (Bigelow 1967)	
	Sp.I	<i>S. pitliferus</i> northern	2 Central	Mt Karioi, Pirongia Range, Whenuakura frost flats, Te Araroa	Localised, unique mtDNA and morphology (Bigelow 1967)	
<i>Brachaspis nivalis</i> (complex) South Island	B.II	<i>B. nivalis</i> northern	3 Marlborough—subalpine	Kawekas, Central Plateau, Rualhines	Shared mtDNA and morphology (Bigelow 1967)	
			4 Canterbury —subalpine	Dee Stream	MtDNA split, habitat and size (Hutton 1897)	
			5 Sub-alpine	Fog Peak, Craigieburn, Arrowsmith	MtDNA split, habitat and size	
			6 Lowland (<i>B. robustus</i>)	Porter River	Mt DNA split, habitat and size	
		B.III	<i>B. nivalis</i> southern ("Hunter")	7 Typical form	MtDNA split, habitat and morphology (Morris 2001a)	
				8 Typical form	Habitat and morphology (Bigelow 1967)	
<i>Sigaia australis</i> (complex) South Island	Sa.I	<i>S. australis</i> northern	9 <i>S. species A</i>	Mt Sutton, Mt Dobson, Sealy Tarns, Craigieburn, Fog Peak, Mt St John	MtDNA split	
	Sa.II	<i>S. australis</i> south central	10 <i>S. chilti</i>	Alexandra, Mt St Bathans, Mt Sutton, Lindis Pass, Dunstan Mountains	MtDNA split, morphology	
			11 Typical form	Alexandra	Morphology (Jamieson 1999)	
		Sa.III	<i>S. australis</i> southwest	12 <i>S. obelisci</i>	Alexandra	Morphology (Jamieson 1999)
			13 <i>S. homerensis</i>	Rob Roy, Harris Saddle, Remarkables, Old Woman Range, Alexandra	MtDNA split (additional morphs likely; Morris 2003)	
		Sa.IV	<i>S. australis</i> southeast	14 Typical form	Old Man Range	Isolation, morphology (Bigelow 1967)
				15 <i>S. "undescribed"</i>	Earl Mountains	Isolation, morphology (Morris 2003)
					Danseys Pass, Rock & Pillar Range, Flagstaff Hill, Mt St Bathans, Kakanui Mountains, Rocky Top	MtDNA split
					Alexandra	Novel morphotypes, crypsis

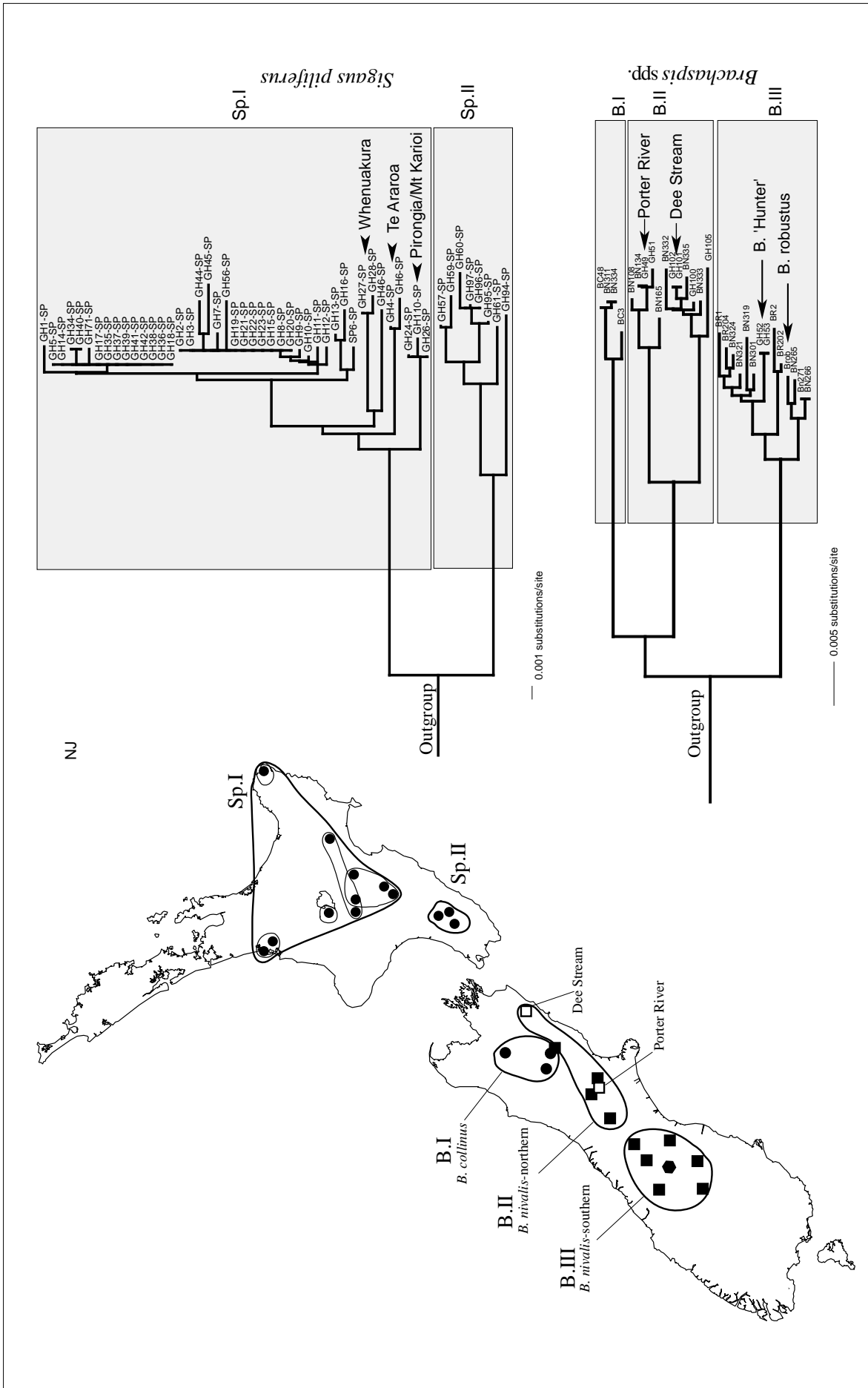


Figure 6. Neighbor-joining trees of mtDNA COI sequences from *Sigaus ptiliferus* (top), and *Brachasps* spp. (bottom). Clades inferred from phylogenetic analysis are labelled Sp.I-II and B.I-III, respectively. Contour plots on the map indicate the geographic distribution of grasshopper clades.

and haplotypes found there were also present in the Ruahines, Kaweka and Lake Waikaremoana samples. The few individuals from isolated sites at Te Araroa, Whenuakura (Lake Taupo) and Pirongia area showed a comparatively high level of sequence difference; each location had unique haplotypes that differed by c. 2.5% from those at other locations.

3.1.2 Conservation considerations

In his examination of *Sigauss piliferus*, Bigelow (1967:29) identified 'three morphological groups, corresponding with three broad geographical areas; a northern group from the Rotorua area and East cape Peninsula, a central group from Tongariro National Park and the Kaimanawa and Kaweka Ranges, and a southern group from the Tararua Range'. The present genetic analysis is broadly consistent with this, allowing for small differences in the locations sampled.

Two features of these genetic data are particularly significant for conservation. First, there is a distinct split between *S. piliferus* collected on the Tararuas and those collected from all other locations, which represents the minimum number of taxa deserving of conservation effort. Second, some populations outside the Tararuas and the central North Island area are probably very small, isolated and dependent on a vegetation type that may not be self-sustaining (see below). Furthermore, grasshoppers at several of these (northern) sites have distinct genetic identities (i.e. Te Araroa, Pirongia and Whenuakura). Further work to determine the status of these populations and their habitats should be considered. Two locations (Kaueranga Valley on the Coromandel Peninsula, and Mt Maungatautari) reported as having *S. piliferus* by Bigelow (1967) were not searched explicitly for the present work, but no grasshoppers have recently been reported from them. Given that Kaueranga Valley is transected by a road and is fairly accessible, it is reasonable to assume that grasshoppers might have been found there if present. No new information is available for Mt Maungatautari.

Many of the sites from which *S. piliferus* was collected for the present study did not have typical subalpine vegetation. North Kaweka, Ruahine, Whakapapa and Tararua locations were above the treeline in tussock grasslands, whereas Pirongia, Mt Karioi, Lake Waikaremoana, Te Araroa, Rangipo Desert and Whenuakura sites were in areas where the combination of low altitude and low latitude would not normally support subalpine vegetation. However, grasshoppers were typically collected from seral tussock grassland or flax/manuka shrubland habitats. The flax shrublands appear to have developed in exposed areas of poor or thin soil. Whether or not such habitats are natural and permanent or products of past habitat modification by humans is not clear, but Rogers (1994, and references therein) concluded that seral grasslands in central North Island are unlikely to have existed in pre-human times. From the perspective of conservation, some active management role may be required to maintain grasshopper habitat at some of these small but widely spaced sites.

3.2 *Brachaspis nivalis* COMPLEX

3.2.1 Genetic structure

The genetic structure of the *Brachaspis nivalis* complex has previously been reported, with an emphasis on the status of the protected species *B. robustus* (Trewick 2001a). Here we used the same DNA sequence data with the addition of sequences from individuals representing three additional locations and forms. Trewick (2001a) reported a prominent split among sequences from individuals of *B. nivalis*, which corresponds with a spatial (north-south) split of populations in the South Island (see Fig. 6, B.II versus B.III; B.I corresponds to the species *B. collinus*, which is not a subject of this report). COI haplotypes from *B. robustus*, the rare, low-altitude species of the Mackenzie Basin area, are very closely related to haplotypes of *B. nivalis* (B.III) from montane locations in the southern part of the *Brachaspis* range. DNA sequence divergence in the B.III group is a maximum of 2.8% (Table A1.2, Appendix 1). Samples from the Hunter Hills that were added in the present study yielded haplotypes that also fell in this southern B.III clade. Sequence divergence between these two *B. nivalis* clades is relatively high (maximum 10.6%), and at a level more typical of interspecific divergence between insect species.

Haplotypes from both samples of small, low-altitude *Brachaspis* fell in the northern *B. nivalis* clade (B.II), which is consistent with their geographic position. However, a further split within the B.II clade is evident, which also shows a north-south geographic structure. Instead of the two small, low-altitude forms falling together on the tree, as might be predicted from their similar morphology, they fall into separate clades with sequences from individuals from montane sites that they are each geographically close to. Hence, haplotypes from the low-altitude Porter River *Brachaspis* are genetically most similar to Craigieburn and Fog Peak montane *Brachaspis*, and those from Dee Stream are genetically most similar to alpine *Brachaspis* from Mt Lyford and Red Spur (a montane location close to Dee Stream).

3.2.2 Conservation considerations

Three low-altitude *Brachaspis* populations were included in this study: two populations of small forms from Porter River and Dee Stream, and the large form *B. robustus* from Mackenzie Basin area. In all three cases, DNA sequences from these low-altitude forms indicate close genealogical relationships with typical nearby *B. nivalis* from montane habitats. This implies that the low-altitude forms have evolved recently under selective pressure that is specific to these habitats, as Bigelow (1967) suggested. The fact that the two small forms do not share a common ancestor indicates that the small form cannot be treated as a single separate species, and that Bigelow (1967) was, considering the information available to him, correct to group them with *B. nivalis*. However, when the genetic and morphological evidence are considered together, it is evident that this approach has clearly underestimated diversity within the group. *Brachaspis robustus* is accepted as a distinct taxon on the grounds of gross external morphological (male genitalia of this species have yet to be characterised) and habitat differences, despite the lack of neutral mtDNA sequence evidence to support it. There may be justification in similarly treating the small, low-altitude forms as distinct taxa (conservation units) as well, given that they are isolated

from one another and may be isolated from their nearest montane relatives, and occupy narrow and atypical habitat. Bigelow (1967) noted that the shape of the subgenital plate of females from low-altitude populations tended to differ from that of other populations and that ‘this may raise the question of a possible specific distinction’ (Bigelow 1967:70). Further population genetic research would be required to determine if this is, in fact, the case and what feature of the environment results in the reduced body size.

The southern *B. nivalis* clade (B.III) (*B. robustus** in Trewick 2001a) corresponds with the range delineated by Morris (2003) for *Brachaspis* “Hunter”. Preliminary examination of leg spines, colouration and epiphallus indicates that the southern and ‘Hunter’ group are one and the same, and formal delineation of this taxon is required.

Certainly, the possibility that the low-altitude forms have a greater susceptibility to extinction has to be considered. Low-altitude populations occupy extremely restricted habitats in braided rivers (which are themselves narrowly circumscribed). Flooding events, land development, weed invasion and introduced predators could, quite plausibly, extinguish a population rapidly.

3.3 *Sigauss australis* COMPLEX

3.3.1 Genetic structure

The genetic diversity of *Sigauss australis* complex grasshoppers was initially surveyed using SSCP with the 12S gene fragment. Shared banding patterns indicated a shared mtDNA nucleotide sequence. The alternative haplotypes (banding patterns) were coded alphabetically and their distribution is summarised in Table 2.

Populations of *S. australis* complex tend to have unique mtDNA haplotypes. The general pattern of low diversity at sites that was inferred from SSCP haplotyping was confirmed by sequence data. Most locations have a single and usually unique haplotype, although three closely related haplotypes are evident in the Mt Dobson sample (Table 2, Fig. 7). In contrast, three haplotypes (n, o, j) at Mt St Bathans correspond to two clades (Sa.II and Sa.IV), and five SSCP haplotypes (a, c, i, s, L) at Alexandra correspond to two groups (Sa.II and Sa.III), with the addition of the sequence from *S.* “undescribed” falling into Sa.IV.

Individuals that yielded Sa.I DNA sequences came from the northernmost extent of the *S. australis* complex in the central South Island (Fig. 7). Genetic distances between Sa.I and other *S. australis* complex haplotypes are relatively high (mean 10%) and above typical values for interspecific distances in insects (Table A1.3, Appendix 1). For further discussion, see Trewick (2008).

Each of the three southern groups comprised sequences from individuals that were collected in geographically distinct (but parapatric) ranges that meet at Alexandra (Fig. 5). Clade Sa.III comprises haplotypes (in brackets) from *S. australis* (c, d, g), *S. obelisci* (p) and *S. homerensis* distributed from Alexandra westwards. Haplotype p was unique to and shared by all 13 *S. obelisci* individuals collected on the Old Man Range (Table 2). In contrast, haplotype c was present in grasshoppers from three locations, including Alexandra. Clade

TABLE 2. MORPHOSPECIES, SAMPLING LOCATIONS, SSCP HAPLOTYPES, SAMPLE SIZES (*n*), NUMBERS OF INDIVIDUALS SEQUENCED FOR THE COI AND 12S mtDNA GENES, AND HAPLOGROUPS FOR *Sigaüs australis* COMPLEX GRASSHOPPERS.

SPECIES	LOCATION	12S-SSCP		SEQUENCE		HAPLOGROUP
		HAPLOTYPE	<i>n</i> *	COI	12S-16S	
<i>S. australis</i>	Mt Sutton	m	3	2	–	+
<i>S. australis</i>	Mt Dobson	e	3	1	1	Sa.I
<i>S. australis</i>	Sealy Tarns	e	7	2	1	Sa.I
<i>S. australis</i>	Mt Dobson	h	5	1	1	Sa.I
<i>S. australis</i>	Craigieburn	k	1	–	–	Sa.I
<i>S. australis</i>	Fog Peak/Torlesse	k	3	–	1	Sa.I
<i>S. australis</i>	Mt Dobson	t	2	–	1	Sa.I
<i>S. australis</i>	Mt Dobson	u	2	–	1	Sa.I
<i>S. australis</i>	Mt John		[1]	–	1	Sa.I
<i>S. australis</i>	Alexandra—Conroy Dam	a	1	–	1	Sa.II
<i>S. cbildi</i>	Alexandra—Earnsclough	a	2	1	–	Sa.II
<i>S. cbildi</i>	Alexandra—Hairpin Little Valley Rd	a	4	1	1	Sa.II
<i>S. cbildi</i>	Alexandra—Earnsclough	i	1	1	1	Sa.II
<i>S. cbildi</i>	Alexandra—Graveyard Gully	i	1	–	–	
<i>S. australis</i>	Alexandra—Little Valley Rd	i	2	2	1	Sa.II
<i>S. australis</i>	Alexandra—Conroy Dam	L	1	1	1	Sa.II
<i>S. australis</i>	Mt St Bathans	n	1	–	1	Sa.II
<i>S. australis</i>	Mt St Bathans	o	3	1	1	Sa.II
<i>S. australis</i>	Mt Sutton	q	1	1	1	Sa.II
<i>S. australis</i>	Dunstan Mountains		[1]	1	–	Sa.II
<i>S. australis</i>	Lindis Pass		[2]	2	–	Sa.II
<i>S. cbildi</i>	Alexandra—Graveyard Gully	s	3	–	1	Sa.II
<i>S. cbildi</i>	Alexandra—Little Valley Rd		[1]	–	1	Sa.II
<i>S. species A</i>	Alexandra—Earnsclough		[1]	1	–	Sa.II
<i>S. australis</i>	Rob Roy		[2]	2	–	Sa.III
<i>S. bomerensis</i>	Earl Mountains		[3]	3		Sa.III
<i>S. australis</i>	Harris Saddle	c	9	2	1	Sa.III
<i>S. australis</i>	Alexandra—Little Valley Rd	c	3	–	1	Sa.III
<i>S. australis</i>	Mt Scott	c	5	–	–	Sa.III
<i>S. australis</i>	Remarkables	d	8	1	1	Sa.III
<i>S. australis</i>	Old Woman Ra.	g	8	1	1	Sa.III
<i>S. obelisci</i>	Old Man Ra.	p	13	1	1	Sa.III
<i>S. australis</i>	Danseys Pass	b	15	1	1	Sa.IV
<i>S. australis</i>	Rock and Pillar Ra.	b	13	1	1	Sa.IV
<i>S. australis</i>	Flagstaff Hill	f	8	1	1	Sa.IV
<i>S. australis</i>	Mt St Bathans	j	5	1	1	Sa.IV
<i>S. australis</i>	Kakanui Mnts.	v	1	1	–	Sa.IV
<i>S. australis</i>	Rocky Top	w	8	1	1	Sa.IV
<i>S. australis</i>	Crawford Hills	r	2	1	–	Sa.IV
<i>S. australis</i>	Danseys Pass		[2]	2	1	Sa.IV
<i>S. australis</i>	Rock and Pillar Ra.		[2]	2	–	Sa.IV
<i>S. “undescribed”</i>	Alexandra—Little Valley Rd		[1]	1	1	Sa. IV
Ingroup—Total individuals SSCP screened			144			
—Total individuals including non-SSCP			160	40	29	
Outgroup				1	4	
Total sequences			41	33		

* Entries in square brackets [] indicate the number of individuals subjected to DNA sequencing but not SSCP haplotyping.

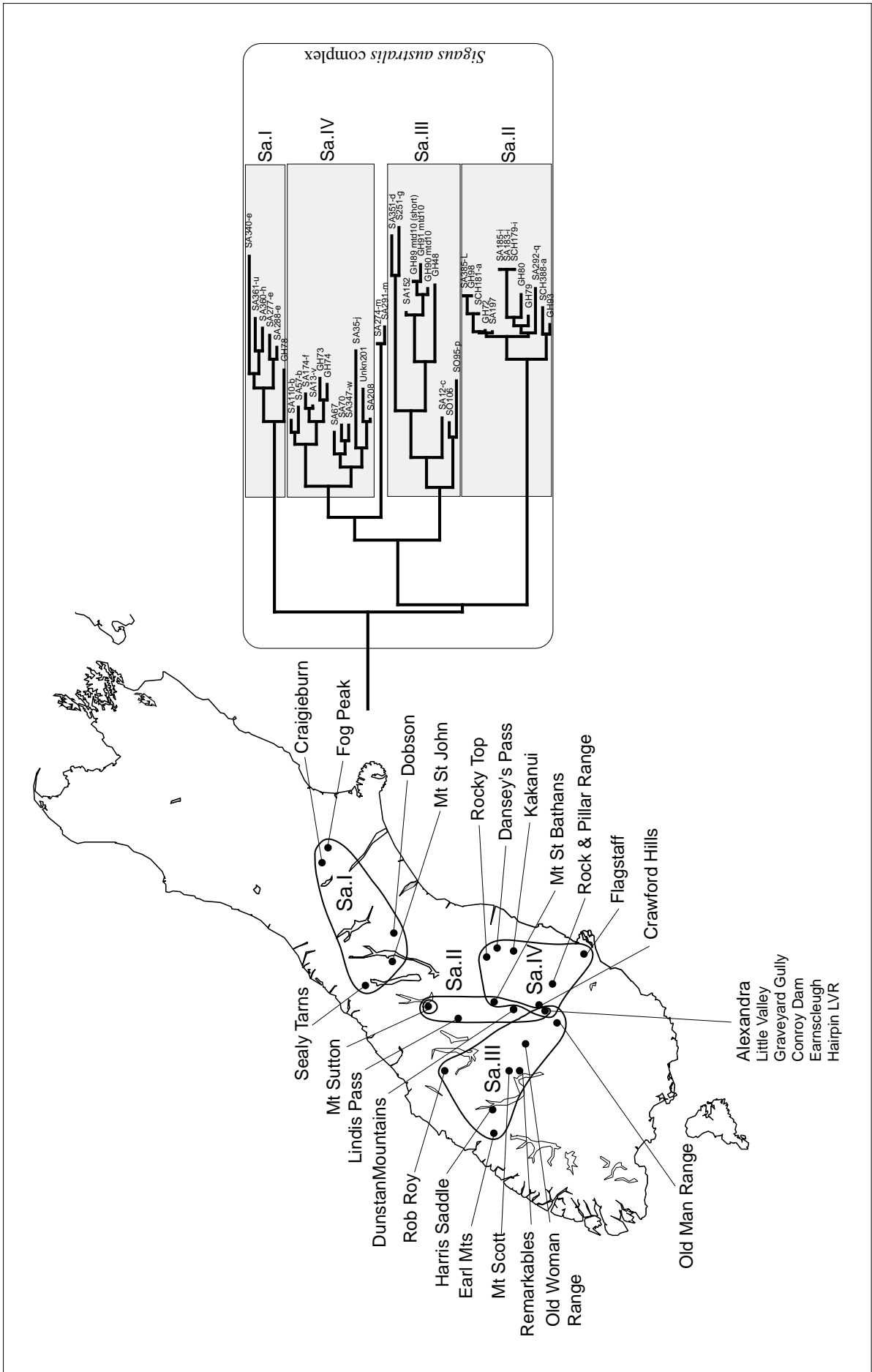


Figure 7. Neighbor-joining tree of mtDNA COI sequences from *Sigaus australis* complex. Clades inferred from phylogenetic analysis are labelled Sa.I-IV. Contour plots on the map indicate the geographic distribution of grasshopper clades. Sampling locations are labelled on the map.

Sa.IV comprised haplotypes from individuals of *S. australis* (b, f, j, v, w, r) and a single individual of *S. "undescribed"* that was collected north and east of Alexandra (see Fig. 3D). Clade Sa.II included all 12 *S. childi* (a, i, s) surveyed, plus *S. australis* (a, i, L, n, o, q) and the single sequence from *S. speciesA* (Fig. 7). Some individuals of *S. australis* and *S. childi* shared the same putative (SSCP) haplotypes (two *S. australis* and two *S. childi* had putative haplotype i, one *S. australis* and six *S. childi* had haplotype a). Furthermore, two *S. australis* from Little Valley Rd had the same COI sequence haplotype as an *S. childi* from Alexandra (Earnsclough), and an *S. australis* from the Dunstan Mountains had the same COI sequence haplotype as an *S. childi* from Alexandra (Hairpin, Little Valley Road; see Fig. 5).

3.3.2 Conservation considerations

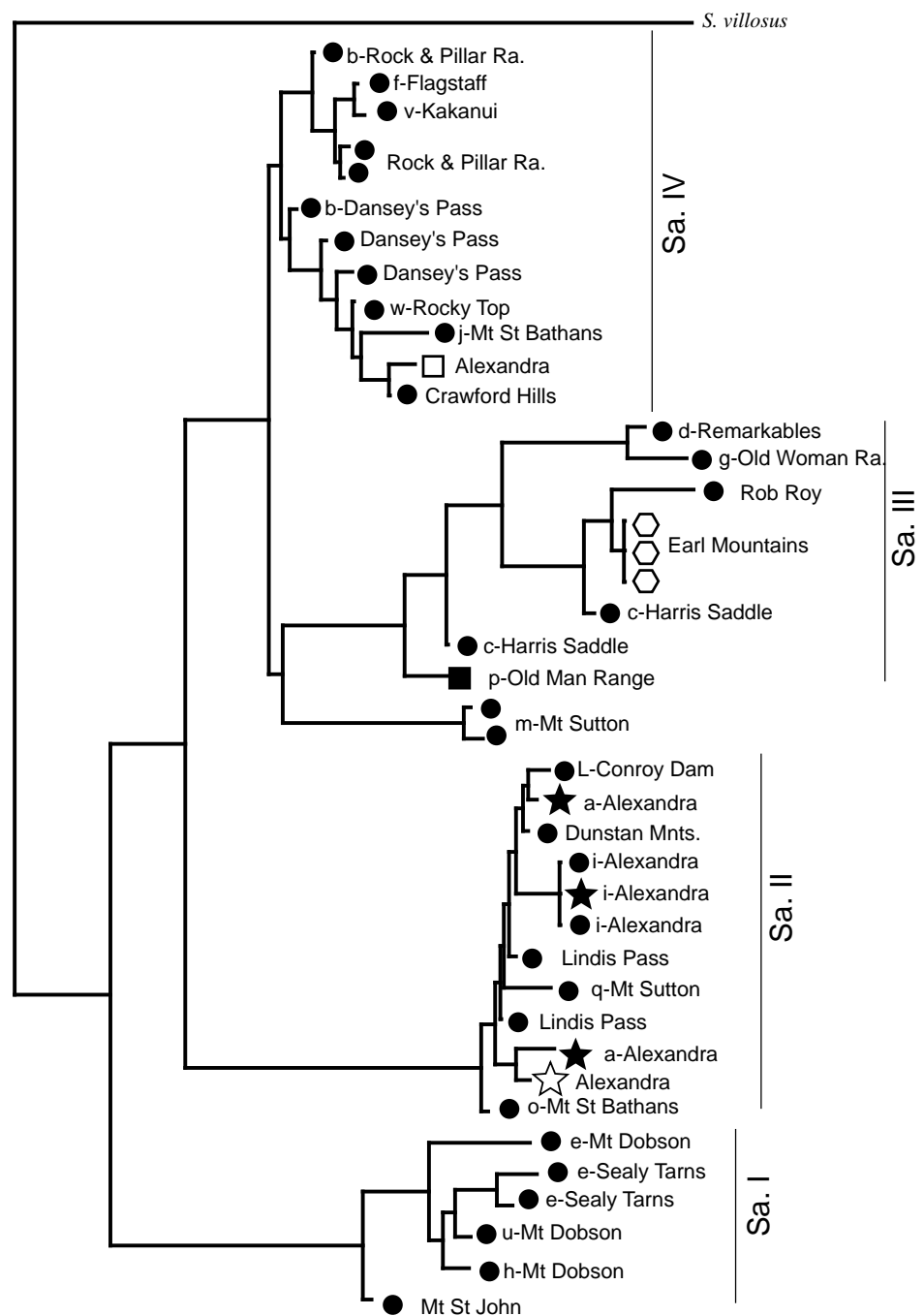
The *Sigaüs australis* complex contains comparatively high genetic and morphological (taxonomic) diversity. Three of the four main mtDNA clades comprise more than one morphotype. This is above and beyond the colour polymorphism that is known from single populations of typical *S. australis* in typical montane habitat. Further morphospecies have been proposed (Morris 2002a). Preliminary indications from ongoing morphological study are that additional diversity may exist. In particular, morphological and behavioural variation among grasshoppers on the Remarkables may mean that there are sympatric species there.

Of the four clades, Sa.I is the most clearly circumscribed spatially and genetically. The presence of a distinct *S. australis* lineage in central South Island suggests a protracted period of isolation throughout many episodes of Pleistocene climate change, rather than colonisation of the area at the end of the Pleistocene. On the basis of estimates of genetic distance between clade Sa.I and other *S. australis* COI haplotypes, this split may date back to the late Pliocene (5 mya). This spatial pattern and estimated time of divergence are similar to those identified for the alpine scree weta (*Deinacrida connectens*) in the same landscape (Trewick et al. 2000; Trewick 2001b).

Clade Sa.IV is also dominated by typical *S. australis* grasshoppers, with a single undescribed form (in our sample) being closely related to these (Fig. 8). Jamieson (1999) recorded a similar form to this undescribed specimen; both are highly cryptic on the tumbling lichen (*Chondropsis semiviridis*) (Fig. 3F). One of the authors (SM) has also observed this form on several occasions within the geographic range encompassed by Sa.IV. Further survey work is required, as there appears to be more morphological variation in this area, and it would be useful to determine whether this represents polymorphism or the existence of independent evolutionary lineages.

Clade Sa.III consists of the southwestern *S. australis* grasshoppers, and includes *S. homerensis* (Morris 2003), *S. obelisci* (Bigelow 1967) and *S. "Rob Roy"* (Morris 2002a). The group also includes specimens from the Remarkables, but whether these represent *S. "Remarkables"* (Morris 2002a) remains to be resolved. All of these taxa are very close in general form to typical *S. australis*. The existence of an additional haplotype at Mt Sutton that is weakly associated with Sa.IV (m; Fig. 8) indicates that this location may deserve further study.

Figure 8. Neighbor-joining tree of mtDNA COI sequences from grasshoppers of the *Sigaus australis* complex. Four clades are indicated: Sa.I–Sa.IV. Symbols at branch tips indicate morphospecies: ● = *S. australis*, ○ = *S. homerenensis*, ★ = *S. childi*, ■ = *S. obeliscus*, ☆ = *S. species A*, □ = *S.* “undescribed”.



Clade Sa.II is the south central *S. australis* group, and includes apparently typical *S. australis*, plus *S. childi* and *S. species A* grasshoppers. These taxa have similar or, in some instances, identical haplotypes and a rather narrow geographic range (Fig. 8). The sharing of haplotypes by species, and therefore their paraphyly, can be explained in two contrasting ways: either mitochondria have been exchanged recently via introgression (hybridisation) or they have been retained by incomplete lineage sorting through a recent speciation event (Funk & Omland 2003). In the case of Sa.II, if hybridisation has been involved, it was not restricted to a single ancestral event but rather has been extensive and recent, with multiple similar haplotypes being shared between species. Morris (2002c) noted that some individuals examined had characteristics of both *S. childi* and *S. species A*. Distinguishing these processes is beyond the scope of the present data.

4. Conclusions and recommendations

It is highly likely that some species (e.g. *S. obelisci*) represent small, geographically isolated populations of a more widely distributed taxon that have accumulated subtle morphological differences. Diversity in each of the groups studied has evolved relatively recently and probably during the late Pliocene/Pleistocene at the latest. As noted by Trewick (2001a), *B. robustus* may well have evolved after a population become isolated at the end of the last glacial maximum (LGM). Climate cycling was probably of broad significance in population structuring and speciation in New Zealand grasshoppers. Following each glaciation, the climate warmed and the lowest extent of the alpine zone was raised in altitude. Grasshopper populations presumably tracked this change, maintaining their association with open and predominantly grassland habitat above the treeline. Forest replaced most open country below the montane zone, extirpating grasshoppers. In some instances, successive glacial cycles probably reinforced regional differences. The relatively high genetic distances between *Brachaspis nivalis* groups (B.II versus B.III) and *Sigauss australis* groups (Sa.I versus others) are consistent with this (Appendix 1).

In some instances, it is likely that relict low-altitude populations survived climate and vegetation shifts, finding suitable habitat in braided riverbeds and the semi-arid environments of Central Otago and central Canterbury. Following the LGM, these semi-arid environments apparently did support some woodland (Clark et al. 1996; McGlone et al. 1995)—perhaps as much as 80% (Walker et al. 2004)—but it is unlikely that continuous dense forest developed.

The Alexandra area is of particular interest for conservation. It either represents a focus of speciation within the *S. australis* complex or it is an active contact area, where species and geographic populations meet and hybridise. In the same area, two species of *Phaulacridium* grasshoppers have narrowly circumscribed ecological ranges (Westman & Ritchie 1984) and the status of two *Prodontria* beetles has been debated (Emerson & Wallis 1994; Wallis 2001). Because mitochondrial DNA is inherited maternally, the use of mtDNA sequence data alone cannot distinguish between introgression or recent speciation (with incomplete lineage sorting), no matter how many data are collected. Any hope of understanding the state of gene flow among taxa at Alexandra will require the application of sufficiently variable biparentally inherited markers.

Application of a strict phylogenetic approach to the systematics of these grasshoppers would not be consistent with existing taxonomy and would be unhelpful. It is clear that, for the *S. australis* complex in particular, additional genetic markers are required to determine what process has resulted in the mismatch between mtDNA data and morphology. However, for the purposes of biodiversity conservation (as opposed to taxonomic revision), an optimal approach would be to incorporate both morphological and phylogenetic evidence to maximise the inclusion and retention of diversity. The molecular phylogenetic evidence is an indicator of historic boundaries among populations, while morphological/behavioural evidence may be indicative of adaptive responses to habitat and predators.

4.1 *Sigauss piliferus*

This species almost certainly consists of at least two diagnosable entities deserving species status. These will be referred to as *Sigauss* “Tararuas” for the Tararua lineage and *S. piliferus* for the remainder. However, for the purposes of conservation, additional populations should be accommodated in management policy. From the present survey, these include populations at Whenuakura, Pirongia area and Te Araroa (Table 1). It is likely that other populations exist, and effort needs to be given to find these as soon as possible. Anthropogenic habitat modification, vegetation succession and climate change are expected to impact on these populations in the short, medium and long term.

4.2 *Brachaspis nivalis* COMPLEX

Brachaspis “Hunter” as proposed by Morris (2002a) will, with additional morphological examination, very probably prove to be diagnosable as a separate species from *B. nivalis*. *Brachaspis* “Hunter” corresponds to the southern *B. nivalis* clade (B.III) identified as *B. robustus** by Trewick (2001). In addition, conservation managers need to give special attention to low-altitude populations, all of which are morphologically distinct (on size at least) from alpine populations (White 1994). The two populations of small, low-altitude *Brachaspis* examined in the present study have genealogical relationships in the northern (B.II) clade that are analogous to the pattern observed for *B. robustus* in the southern (B.III) clade. In these cases, morphologically distinct populations (species in the case of *B. robustus*) are allied to nearby montane populations of typical *B. nivalis* (Table 1). Further study will reveal whether there is justification for describing low-altitude forms (e.g. *B.* “low altitude”; Morris 2002a) as distinct species.

4.3 *Sigauss australis* COMPLEX

Recognition needs to be given to the spatial distribution of diversity within this group (Table 1). Further morphological study may support the splitting of one or more of the groups indicated by phylogenetic analysis of mtDNA sequences (i.e. Sa.I, etc.). There is, however, currently little evidence from the mtDNA to support *S.* “Remarkables” and *S.* “Rob Roy” as being distinct, although this may change with further sampling and analysis. Whilst *S. homerensis* and *S. obelisci* show distinct morphological characters, they are closely allied to the above and other Sa.III populations in the geographic area (Table 2). The status of *S. childi* and *S.* species A in Sa.II is of paramount concern in this group. There is little doubt that these and other cryptic forms are geographically localised and deserving of further study to determine to what extent they are threatened ecologically.

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7. Glossary

Allopatric Spatially separate populations or species.

Biogeography The study of the distribution of diversity over space and time.

Haplotypes A set of closely linked alleles (genes or DNA polymorphisms) inherited as a unit. In the case of mitochondrial data, haplotypes are DNA sequence variants identified at mitochondrial gene regions.

Introgression Gene flow between species.

Morphospecies A typological species distinguished solely on the basis of morphology.

Morphotype The morphological form of a species.

Neotype The single specimen designated as the name-bearing type of a nominal species or subspecies for which no holotype, etc. is available.

Parapatric Adjacent populations or closely related species.

Paraphyletic A group of organisms that contains its most recent common ancestor but does not contain *all* the descendants of that ancestor.

Phylogenetics The study of the evolutionary relationships of organisms.

Phylogeny The evolutionary relationships of organisms.

Phylogeography Biogeography as revealed by a comparison of estimated phylogenies of populations or species with their geographic distributions.

Sympatric Species inhabiting the same geographic area.

Appendix 1

PAIRWISE GENETIC DISTANCES FOR NEW ZEALAND GRASSHOPPERS

Pairwise genetic distances (Kimura 2 parameter model) among mitochondrial COI DNA sequences from *Sigaus piliferus*, *Brachaspis nivalis* complex and *Sigaus australis* complex. Values indicate genetic distance between pairs of individual grasshoppers (indicated by codes GH1, SP6, etc.); smaller values indicate greater similarity of individuals.

TABLE A.1.1. PAIRWISE GENETIC DISTANCES FOR *Sigaia pitiferus*. □ = CLADE Sp.I; ■ = Sp.II.

REGION	CLADE	CODE	GH1	SP6	GH2	GH56	GH3	GH5	GH19	GH21	GH22	GH23	GH13	GH14	GH15	GH17	GH18	GH34	GH35	GH36		
Central	Sp.I	GH1	0.000																			
		SP6	0.002	0.002																		
		GH2	0.002	0.002	0.000																	
		GH56	0.002	0.002	0.000	0.000																
		GH3	0.002	0.002	0.000	0.002	0.000															
		GH5	0.000	0.000	0.002	0.002	0.000	0.002														
		GH19	0.002	0.002	0.000	0.002	0.000	0.002	0.000													
		GH21	0.002	0.002	0.000	0.002	0.000	0.002	0.000	0.000												
		GH22	0.002	0.002	0.000	0.002	0.000	0.002	0.000	0.000	0.000											
		GH23	0.002	0.002	0.000	0.002	0.000	0.002	0.000	0.000	0.000	0.000										
		GH13	0.002	0.002	0.000	0.002	0.000	0.002	0.000	0.000	0.000	0.000	0.000									
		GH14	0.002	0.002	0.000	0.002	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000								
		GH15	0.002	0.002	0.000	0.002	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000							
		GH17	0.000	0.000	0.002	0.002	0.000	0.002	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.000						
		GH18	0.000	0.000	0.002	0.002	0.000	0.002	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.000	0.000					
		GH34	0.002	0.002	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.002	0.002	0.002				
		GH35	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.000	0.000	0.000	0.002			
		GH36	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.000	0.000	0.000	0.002	0.000		
		GH37	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.000	0.000	0.000	0.002	0.000	0.000	
		GH38	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.000	0.000	0.000	0.002	0.000	0.000	
		GH39	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.000	0.000	0.000	0.002	0.000	0.000	
		GH40	0.002	0.002	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.002	0.002	0.002	0.002	0.002	0.002	0.002
		GH41	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.000	0.000	0.000	0.002	0.000	0.000	
		GH42	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.000	0.000	0.000	0.002	0.000	0.000	
		GH44	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006
		GH45	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008
		GH10	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002
		GH9	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002
		GH8	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002
		GH7	0.004	0.004	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.004	0.004	0.004	0.004	0.004	0.004	0.004
		GH12	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002
		GH11	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.002	0.002	0.002	0.002	0.002
		GH16	0.002	0.002	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.002	0.002	0.002	0.002	0.002	0.002	0.002
		GH20	0.002	0.002	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.002	0.002	0.002	0.002	0.002	0.002	0.002
		GH24	0.012	0.012	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.012	0.012	0.012	0.012	0.012	0.012	0.012
		GH110	0.014	0.014	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.014	0.014	0.014	0.014	0.014	0.014	0.014
GH26	0.012	0.012	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.012	0.012	0.012	0.012	0.012	0.012	0.012		
GH46	0.008	0.008	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.008	0.008	0.008	0.008	0.008	0.008	0.008		
GH27	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012		
GH28	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014		
GH4	0.012	0.012	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.012	0.012	0.012	0.012	0.012	0.012	0.012		
GH6	0.014	0.014	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.014	0.014	0.014	0.014	0.014	0.014	0.014		
GH57	0.052	0.052	0.053	0.053	0.053	0.053	0.053	0.053	0.053	0.053	0.053	0.053	0.050	0.052	0.055	0.052	0.052	0.055	0.052	0.052		
GH59	0.057	0.057	0.058	0.058	0.058	0.058	0.058	0.058	0.058	0.058	0.058	0.058	0.055	0.057	0.059	0.057	0.057	0.055	0.057	0.057		
GH60	0.061	0.061	0.062	0.062	0.062	0.062	0.062	0.062	0.062	0.062	0.062	0.062	0.061	0.061	0.063	0.061	0.061	0.061	0.061	0.061		
GH97	0.059	0.059	0.060	0.060	0.060	0.060	0.060	0.060	0.060	0.060	0.060	0.060	0.059	0.059	0.061	0.059	0.059	0.059	0.059	0.059		
GH95	0.057	0.057	0.058	0.058	0.058	0.058	0.058	0.058	0.058	0.058	0.058	0.058	0.055	0.057	0.059	0.057	0.057	0.055	0.057	0.057		
GH96	0.059	0.059	0.060	0.060	0.060	0.060	0.060	0.060	0.060	0.060	0.060	0.060	0.057	0.059	0.061	0.059	0.059	0.057	0.059	0.059		
GH61	0.052	0.052	0.053	0.053	0.053	0.053	0.053	0.053	0.053	0.053	0.053	0.053	0.050	0.052	0.055	0.052	0.052	0.055	0.052	0.052		
GH94	0.052	0.052	0.055	0.055	0.055	0.055	0.055	0.055	0.055	0.055	0.055	0.055	0.050	0.052	0.054	0.052	0.052	0.054	0.052	0.052		

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Table A1.1—continued.

REGION	CLADE	CODE	GH37	GH38	GH39	GH40	GH41	GH42	GH44	GH45	GH10	GH9	GH8	GH7	GH12	GH11	GH16	GH20			
Central	Sp.I	GH1																	Sp.I		
		SP6																			
		GH2																			
		GH56																			
		GH3																			
		GH5																			
		GH19																			
		GH21																			
		GH22																			
		GH23																			
		GH13																			
		GH14																			
		GH15																			
		GH17																			
		GH18																			
		GH34																			
		GH35																			
		GH36																			
		GH37																			
		GH38																			
GH39			0.000																		
GH40			0.000																		
GH41			0.000		0.002																
GH42			0.000		0.000	0.002	0.000														
GH44			0.006	0.006	0.006	0.008	0.008	0.006													
GH45			0.008	0.008	0.008	0.010	0.008	0.006	0.006												
GH10			0.002	0.002	0.002	0.004	0.002	0.002	0.004	0.006											
GH9			0.002	0.002	0.002	0.004	0.002	0.002	0.004	0.006	0.000										
GH8			0.002	0.002	0.002	0.004	0.002	0.002	0.004	0.006	0.000	0.000									
GH7			0.004	0.004	0.004	0.006	0.004	0.006	0.006	0.008	0.002	0.002	0.002								
GH12			0.002	0.002	0.002	0.004	0.002	0.002	0.004	0.006	0.000	0.000	0.000	0.002							
GH11			0.002	0.002	0.002	0.004	0.002	0.002	0.004	0.006	0.000	0.000	0.000	0.002	0.000						
GH16			0.002	0.002	0.002	0.004	0.002	0.002	0.004	0.006	0.000	0.000	0.000	0.002	0.004	0.004					
GH20			0.002	0.002	0.002	0.004	0.002	0.002	0.004	0.006	0.000	0.000	0.000	0.002	0.000	0.000	0.004				
GH24	Pirongia		0.012	0.012	0.012	0.014	0.012	0.012	0.018	0.020	0.014	0.014	0.014	0.016	0.014	0.014	0.014	0.014			
GH110	Pirongia		0.014	0.014	0.014	0.016	0.014	0.014	0.020	0.022	0.016	0.016	0.016	0.018	0.016	0.016	0.016	0.016			
GH26	Pirongia		0.012	0.012	0.012	0.014	0.012	0.012	0.018	0.020	0.014	0.014	0.014	0.016	0.014	0.014	0.014	0.014			
GH46	Whenuakura		0.008	0.008	0.008	0.010	0.008	0.008	0.014	0.016	0.010	0.010	0.010	0.012	0.010	0.010	0.010	0.010			
GH27	Whenuakura		0.012	0.012	0.012	0.014	0.012	0.012	0.018	0.020	0.014	0.014	0.014	0.016	0.014	0.014	0.014	0.014			
GH28	Whenuakura		0.014	0.014	0.014	0.016	0.014	0.014	0.016	0.022	0.016	0.016	0.016	0.018	0.016	0.016	0.016	0.016			
GH4	Te Araroa		0.012	0.012	0.012	0.014	0.012	0.012	0.018	0.020	0.014	0.014	0.014	0.016	0.014	0.014	0.014	0.014			
GH6	Te Araroa		0.014	0.014	0.014	0.016	0.014	0.014	0.020	0.022	0.016	0.016	0.016	0.018	0.016	0.016	0.012	0.016			
GH57	Tararua	Sp.II	0.052	0.052	0.052	0.055	0.052	0.053	0.059	0.061	0.055	0.055	0.055	0.057	0.055	0.055	0.050	0.055			
GH59	Tararua	Sp.II	0.057	0.057	0.057	0.055	0.057	0.057	0.063	0.065	0.059	0.059	0.059	0.061	0.059	0.059	0.055	0.059			
GH60	Tararua	Sp.II	0.061	0.061	0.061	0.059	0.061	0.061	0.068	0.070	0.063	0.063	0.063	0.065	0.063	0.063	0.059	0.063			
GH97	Tararua	Sp.II	0.059	0.059	0.059	0.057	0.059	0.059	0.065	0.067	0.061	0.061	0.061	0.063	0.061	0.061	0.057	0.061			
GH95	Tararua	Sp.II	0.057	0.057	0.057	0.055	0.057	0.057	0.063	0.065	0.059	0.059	0.059	0.061	0.059	0.059	0.055	0.059			
GH96	Tararua	Sp.II	0.059	0.059	0.059	0.057	0.059	0.059	0.065	0.067	0.061	0.061	0.061	0.063	0.061	0.061	0.057	0.061			
GH61	Tararua	Sp.II	0.052	0.052	0.052	0.055	0.052	0.053	0.059	0.061	0.055	0.055	0.055	0.057	0.055	0.055	0.050	0.055			
GH94	Tararua	Sp.II	0.052	0.052	0.052	0.054	0.052	0.053	0.059	0.061	0.054	0.054	0.054	0.057	0.054	0.054	0.050	0.054			

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Table A1.1—continued.

REGION	CLADE	CODE	GH24	GH110	GH26	GH46	GH27	GH28	GH4	GH6	GH57	GH59	GH60	GH97	GH95	GH96	GH61	GH94	
Central	Sp.I	GH1																	
		SP6																	
		GH2																	
		GH56																	
		GH3																	
		GH5																	
		GH19																	
		GH21																	
		GH22																	
		GH23																	
		GH13																	
		GH14																	
		GH15																	
		GH17																	
		GH18																	
		GH34																	
		GH35																	
		GH36																	
		GH37																	
		GH38																	
GH39																			
GH40																			
GH41																			
GH42																			
GH44																			
GH45																			
GH10																			
GH9																			
GH8																			
GH7																			
GH12																			
GH11																			
GH16																			
GH20																			
GH24																			
GH110																			
GH26																			
GH46																			
GH27			0.002																
GH28			0.000	0.002															
GH4			0.008	0.010	0.008														
GH6			0.016	0.018	0.016	0.012													
GH27			0.018	0.020	0.018	0.014	0.002												
GH28			0.016	0.018	0.016	0.012	0.002												
GH4			0.018	0.020	0.018	0.012	0.016	0.018											
GH6			0.018	0.020	0.018	0.010	0.018	0.020	0.002										
GH27			0.057	0.059	0.057	0.057	0.053	0.055	0.048	0.050									
GH59			0.057	0.059	0.057	0.057	0.057	0.059	0.053	0.055	0.004								
GH60			0.061	0.064	0.061	0.061	0.061	0.063	0.057	0.059	0.012								
GH97			0.059	0.061	0.059	0.059	0.059	0.061	0.055	0.057	0.010	0.008							
GH95			0.061	0.064	0.061	0.061	0.057	0.059	0.053	0.055	0.010	0.006	0.002						
GH96			0.059	0.061	0.059	0.059	0.059	0.061	0.055	0.057	0.008	0.008	0.004	0.002					
GH61			0.057	0.059	0.057	0.057	0.057	0.059	0.053	0.055	0.010	0.006	0.002	0.000	0.002				
GH94			0.052	0.055	0.052	0.052	0.057	0.059	0.048	0.050	0.008	0.008	0.016	0.014	0.016	0.014	0.028		
											0.026	0.026	0.030	0.028	0.030	0.028	0.026		
Tararua	Sp.II	GH57																	
		GH59																	
		GH60																	
		GH97																	
		GH95																	
		GH96																	
		GH61																	
		GH94																	

TABLE A1.2. PAIRWISE GENETIC DISTANCES FOR *Brachaspis nivalis* COMPLEX. □ = CLADE B.I; ▒ = B.II; ■ = B.III.

TAXON/ REGION	CLADE	BC48	BN311	BN334	BC3	BN108	BN134	GH49	GH51	BN165	BN332	GH102	GH105	GH100	GH101	BN335	BN333	BR1	BR204	
<i>B. collinus</i>	B.I																			
	BC48																			
	BN311	0.002																		
	BN334	0.002	0.000																	
	BC3	0.004	0.004	0.004																
Northern <i>B. nivalis</i>	B.II																			
	BN108	0.080	0.083	0.083	0.066															
	BN134	0.080	0.083	0.083	0.066	0.004														
	GH49	0.080	0.083	0.083	0.066	0.004	0.000													
	GH51	0.083	0.085	0.085	0.069	0.006	0.002	0.002												
	BN165	0.083	0.086	0.086	0.069	0.010	0.010	0.010	0.012											
	BN332	0.063	0.065	0.065	0.053	0.044	0.040	0.040	0.042	0.048										
	GH102	0.063	0.065	0.065	0.053	0.044	0.040	0.040	0.042	0.048	0.008									
	GH105	0.069	0.067	0.067	0.057	0.046	0.042	0.042	0.044	0.051	0.010	0.014								
	GH100	0.061	0.063	0.063	0.051	0.042	0.038	0.038	0.040	0.046	0.006	0.002	0.012							
Dec	GH101	0.063	0.065	0.065	0.053	0.044	0.040	0.040	0.042	0.048	0.008	0.000	0.014	0.002						
	BN335	0.067	0.069	0.069	0.058	0.044	0.044	0.044	0.046	0.048	0.008	0.004	0.014	0.006	0.004					
BN333	0.061	0.063	0.063	0.051	0.044	0.040	0.040	0.042	0.044	0.008	0.004	0.014	0.002	0.004	0.008					
Southern <i>B. nivalis</i>	B.III																			
	BR1	0.076	0.074	0.074	0.069	0.082	0.078	0.078	0.080	0.083	0.065	0.065	0.067	0.063	0.065	0.069	0.065	0.067	0.067	0.065
	BR204	0.078	0.076	0.076	0.066	0.085	0.080	0.080	0.082	0.085	0.067	0.067	0.067	0.065	0.067	0.071	0.067	0.067	0.067	0.067
	BN319	0.074	0.072	0.072	0.062	0.080	0.076	0.076	0.078	0.081	0.067	0.067	0.067	0.065	0.067	0.071	0.067	0.067	0.067	0.067
	BN321	0.074	0.071	0.071	0.062	0.080	0.076	0.076	0.078	0.081	0.063	0.063	0.063	0.060	0.063	0.067	0.063	0.067	0.063	0.063
	BN301	0.074	0.072	0.072	0.062	0.076	0.071	0.071	0.074	0.076	0.063	0.063	0.063	0.061	0.063	0.067	0.063	0.067	0.063	0.063
	BN324	0.078	0.076	0.076	0.066	0.080	0.076	0.076	0.078	0.081	0.067	0.067	0.067	0.065	0.067	0.071	0.067	0.067	0.067	0.067
	GH52	0.083	0.080	0.080	0.071	0.085	0.080	0.080	0.082	0.085	0.067	0.067	0.067	0.065	0.067	0.071	0.067	0.067	0.067	0.067
	GH53	0.083	0.080	0.080	0.071	0.085	0.080	0.080	0.082	0.085	0.067	0.067	0.067	0.065	0.067	0.071	0.067	0.067	0.067	0.067
	BR2	0.073	0.071	0.071	0.062	0.078	0.078	0.078	0.080	0.082	0.069	0.069	0.069	0.073	0.073	0.078	0.069	0.069	0.069	0.069
	BR202	0.076	0.073	0.073	0.064	0.080	0.080	0.080	0.082	0.085	0.071	0.071	0.071	0.073	0.073	0.078	0.069	0.069	0.069	0.069
	BroB	0.080	0.078	0.078	0.069	0.082	0.078	0.078	0.080	0.082	0.069	0.069	0.069	0.073	0.073	0.078	0.069	0.069	0.069	0.069
BN271	0.071	0.069	0.069	0.060	0.074	0.069	0.069	0.071	0.070	0.061	0.061	0.061	0.065	0.065	0.069	0.065	0.065	0.065	0.065	
BN265	0.074	0.071	0.071	0.062	0.080	0.076	0.076	0.078	0.081	0.063	0.063	0.063	0.060	0.063	0.067	0.063	0.067	0.063	0.063	
BN266	0.071	0.069	0.069	0.060	0.074	0.069	0.069	0.071	0.070	0.061	0.061	0.061	0.065	0.065	0.069	0.065	0.065	0.065	0.065	

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Table A1.2—continued.

TAXON/ REGION	CLADE	CODE	BN319	BN321	BN301	BN324	GH52	GH53	BR2	BR202	BROB	BN271	BN265	BN266	
<i>B. collinus</i>	B.I	BC48													
		BN311													
		BN334													
			BC3												
	Northern		BN108												
		B.II	BN134												
	<i>B. nivalis</i>	Porter	GH49												
			GH51												
			BN165												
			BN332												
Dec		GH102													
		GH105													
Dec		GH100													
		GH101													
		BN335													
		BN333													
Southern	<i>B. nivalis</i>	B.III	BR1												
			BR204												
			BN319												
			BN321	0.012											
			BN301	0.008	0.004										
			BN324	0.008	0.004	0.004									
			GH52	0.012	0.012	0.008	0.008								
			GH53	0.012	0.012	0.008	0.008	0.000							
			BR2	0.024	0.022	0.018	0.020	0.024	0.024						
			BR202	0.018	0.016	0.012	0.014	0.018	0.018	0.018	0.006				
			Brob	0.022	0.018	0.014	0.018	0.022	0.022	0.026	0.020				
			Bn271	0.022	0.018	0.014	0.018	0.022	0.022	0.020	0.008				
			BN265	0.024	0.020	0.016	0.020	0.024	0.024	0.028	0.006	0.006			
			BN266	0.022	0.018	0.014	0.018	0.022	0.022	0.020	0.008	0.000	0.006		

TABLE A1.3. PAIRWISE GENETIC DISTANCES FOR *Sigaus australis* COMPLEX. □ = CLADE Sa.I; □ = Sa.II; □ = Sa.III; ■ = Sa.IV.

REGION	CLADE	CODE	SA340-e	SA277-e	SA288-e	SA361-u	SA360-h	GH78	SA110-b	SA57-b	SA174-f	SA13-v	GH73	GH74	SA67	SA70	SA347-w	
Northern	Sa.I	SA340-e																
		SA277-e	0.022															
		SA288-e	0.020	0.004														
		SA361-u	0.018	0.010	0.010													
		SA360-h	0.020	0.014	0.014	0.006												
	GH78	0.020	0.020	0.018	0.014	0.012												
	Southeastern	Sa.IV	SA110-b	0.061	0.062	0.055	0.057	0.057	0.047									
			SA57-b	0.063	0.068	0.061	0.059	0.059	0.046									
			SA174-f	0.069	0.065	0.059	0.063	0.063	0.052	0.012								
			SA13-v	0.067	0.063	0.057	0.060	0.061	0.050	0.010	0.014							
GH73			0.073	0.073	0.066	0.064	0.066	0.055	0.008	0.010	0.006							
GH74		0.068	0.069	0.069	0.062	0.062	0.051	0.004	0.010	0.006	0.008	0.004						
SA67		0.063	0.068	0.061	0.063	0.059	0.046	0.008	0.018	0.020	0.016	0.016	0.014					
SA70		0.066	0.070	0.064	0.066	0.062	0.049	0.010	0.006	0.018	0.020	0.014	0.016	0.016				
SA347-w		0.072	0.076	0.069	0.072	0.067	0.055	0.018	0.012	0.026	0.028	0.020	0.024	0.024	0.008	0.000		
SA35-j		0.074	0.074	0.067	0.069	0.069	0.057	0.024	0.018	0.028	0.030	0.026	0.030	0.030	0.018	0.012	0.014	
Unkn201		0.072	0.076	0.069	0.072	0.067	0.055	0.022	0.016	0.030	0.028	0.024	0.024	0.028	0.016	0.010	0.012	
SA208		0.069	0.073	0.066	0.067	0.064	0.051	0.018	0.012	0.026	0.024	0.020	0.020	0.024	0.012	0.006	0.008	
SA274-m		0.067	0.071	0.065	0.061	0.063	0.050	0.026	0.026	0.034	0.032	0.036	0.032	0.032	0.026	0.030	0.040	
SA291-m		0.069	0.074	0.067	0.063	0.065	0.052	0.028	0.028	0.036	0.034	0.039	0.039	0.034	0.028	0.032	0.042	
Southwestern		Sa.III	SA351-d	0.083	0.085	0.078	0.083	0.085	0.076	0.045	0.042	0.048	0.050	0.049	0.049	0.049	0.047	0.052
	S251-g		0.087	0.092	0.085	0.091	0.092	0.083	0.042	0.040	0.048	0.050	0.049	0.049	0.049	0.047	0.045	
	SA152		0.069	0.078	0.076	0.067	0.070	0.061	0.040	0.039	0.050	0.047	0.043	0.043	0.041	0.037	0.041	
	GH48		0.083	0.087	0.080	0.081	0.083	0.074	0.047	0.044	0.052	0.050	0.053	0.054	0.049	0.044	0.050	
	GH89		0.074	0.083	0.080	0.072	0.074	0.065	0.045	0.044	0.056	0.054	0.049	0.049	0.049	0.046	0.046	
	GH90	0.072	0.081	0.078	0.074	0.076	0.063	0.043	0.047	0.046	0.052	0.047	0.047	0.047	0.044	0.044		
	GH91	0.076	0.085	0.083	0.074	0.076	0.067	0.043	0.047	0.059	0.056	0.051	0.051	0.051	0.048	0.045		
	SA12-c	0.063	0.072	0.065	0.063	0.063	0.055	0.028	0.028	0.040	0.038	0.039	0.039	0.035	0.030	0.028		
	SO106	0.066	0.064	0.057	0.054	0.057	0.044	0.018	0.018	0.026	0.028	0.024	0.024	0.020	0.020	0.018		
	SO95-p	0.063	0.069	0.063	0.060	0.061	0.052	0.028	0.028	0.036	0.036	0.034	0.030	0.030	0.030	0.028		
	SA385-L	0.074	0.071	0.069	0.062	0.067	0.061	0.053	0.053	0.054	0.052	0.051	0.047	0.047	0.053	0.057		
	GH98	0.074	0.071	0.069	0.062	0.067	0.061	0.053	0.053	0.054	0.052	0.051	0.047	0.047	0.053	0.057		
	SCH181-a	0.072	0.069	0.067	0.060	0.065	0.059	0.051	0.050	0.052	0.050	0.049	0.049	0.045	0.051	0.055		
	SA185-i	0.072	0.072	0.069	0.065	0.069	0.067	0.053	0.053	0.055	0.054	0.052	0.051	0.047	0.055	0.059		
	SA183-i	0.072	0.072	0.069	0.065	0.069	0.067	0.053	0.053	0.055	0.054	0.052	0.051	0.047	0.055	0.059		
SCH179-i	0.072	0.072	0.069	0.065	0.069	0.067	0.053	0.053	0.055	0.054	0.052	0.051	0.047	0.055	0.059			
Central	Sa.II	GH79	0.071	0.069	0.066	0.062	0.069	0.058	0.050	0.051	0.049	0.049	0.049	0.045	0.050	0.054		
		GH80	0.075	0.073	0.071	0.067	0.073	0.062	0.050	0.050	0.051	0.049	0.049	0.045	0.050	0.054		
		GH72	0.069	0.066	0.064	0.060	0.067	0.056	0.048	0.047	0.049	0.047	0.047	0.043	0.048	0.052		
		SA197	0.069	0.066	0.064	0.060	0.067	0.056	0.048	0.047	0.049	0.047	0.047	0.043	0.048	0.052		
		SA292-q	0.076	0.074	0.072	0.067	0.074	0.063	0.049	0.050	0.052	0.050	0.049	0.045	0.051	0.055		
	SCH388-a	0.078	0.071	0.069	0.067	0.072	0.065	0.053	0.053	0.054	0.052	0.051	0.047	0.053	0.057			
	GH93	0.074	0.072	0.069	0.065	0.072	0.061	0.049	0.048	0.050	0.048	0.048	0.047	0.048	0.053			
	SV305	0.100	0.084	0.082	0.085	0.087	0.080	0.072	0.078	0.078	0.078	0.080	0.081	0.077	0.080			

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Table A1.3—continued.

REGION	CLADE	CODE	SA35-j	Unkn201	SA208	SA274-m	SA291-m	SA351-d	S251-g	SA152	GH48	GH89	GH90	GH91	SA12-c	SO106	SO95-p	
Northern	Sa.I	SA340-c																
		SA277-c																
		SA288-c																
		SA361-u																
		SA360-h																
		GH78																
		SA110-b																
		SA57-b																
		SA174-f																
		SA13-v																
Southeastern	Sa.IV	GH73																
		GH74																
		SA67																
		SA70																
		SA347-w																
		SA35-j																
		Unkn201	0.018															
		SA208	0.014	0.004														
		SA274-m	0.042	0.040	0.037													
		SA291-m	0.044	0.042	0.039	0.002												
Southwestern	Sa.III	SA351-d	0.063	0.061	0.056	0.057	0.059											
		S251-g	0.061	0.059	0.054	0.059	0.057											
		SA152	0.052	0.045	0.041	0.043	0.045											
		GH48	0.061	0.050	0.049	0.050	0.052											
		GH89	0.056	0.046	0.045	0.050	0.052											
		GH90	0.054	0.044	0.043	0.048	0.050											
		GH91	0.059	0.048	0.047	0.052	0.054											
		SA12-c	0.044	0.038	0.035	0.034	0.036											
		SO106	0.032	0.032	0.028	0.036	0.038											
		SO95-p	0.044	0.040	0.036	0.044	0.046											
Central	Sa.II	SA385-L	0.067	0.065	0.060	0.065	0.067	0.085	0.087	0.074	0.087	0.083	0.081	0.085	0.066	0.055	0.063	
		GH98	0.067	0.065	0.060	0.065	0.067	0.085	0.087	0.074	0.087	0.083	0.081	0.085	0.066	0.055	0.063	
		SCH181-a	0.065	0.063	0.058	0.063	0.065	0.083	0.085	0.072	0.085	0.081	0.078	0.083	0.064	0.053	0.061	
		SA185-i	0.069	0.067	0.062	0.067	0.069	0.083	0.085	0.076	0.090	0.085	0.083	0.087	0.068	0.058	0.065	
		SA183-i	0.069	0.067	0.062	0.067	0.069	0.083	0.085	0.076	0.090	0.085	0.083	0.087	0.068	0.058	0.065	
		SCH179-i	0.069	0.067	0.062	0.067	0.069	0.083	0.085	0.076	0.090	0.085	0.083	0.087	0.068	0.058	0.065	
		GH79	0.064	0.062	0.058	0.062	0.064	0.081	0.083	0.072	0.083	0.078	0.076	0.080	0.063	0.052	0.060	
		GH80	0.064	0.062	0.058	0.062	0.064	0.081	0.083	0.072	0.083	0.078	0.076	0.080	0.063	0.052	0.060	
		GH72	0.062	0.060	0.055	0.060	0.062	0.078	0.081	0.069	0.080	0.076	0.074	0.078	0.061	0.050	0.058	
		SA197	0.062	0.060	0.055	0.060	0.062	0.078	0.081	0.069	0.080	0.076	0.074	0.078	0.061	0.050	0.058	
SA292-q	0.065	0.063	0.058	0.063	0.065	0.083	0.085	0.072	0.085	0.081	0.078	0.083	0.064	0.053	0.061			
SCH388-a	0.067	0.065	0.060	0.065	0.067	0.085	0.087	0.074	0.087	0.080	0.081	0.083	0.066	0.055	0.063			
GH93	0.063	0.061	0.055	0.061	0.063	0.081	0.083	0.070	0.083	0.076	0.076	0.078	0.061	0.051	0.059			
SV305	0.075	0.089	0.088	0.089	0.091	0.107	0.109	0.101	0.105	0.102	0.103	0.105	0.089	0.078	0.087			

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Table A1.3—continued.

REGION	CLADE	CODE	SA385-l	GH98	SCH181-a	SA185-i	SA183-i	SCH179-i	GH79	GH80	GH72	SA197	SA292-q	SCH388-a	GH93	SV305	
Northern	Sa.I	SA340-e															
		SA277-e															
		SA288-e															
		SA361-u															
		SA360-h															
		GH78															
		SA110-b															
		SA57-b															
		SA174-f															
		SA13-v															
Southeastern	Sa.IV	GH73															
		GH74															
		SA67															
		SA70															
		SA347-w															
		SA35-j															
		Unkn201															
		SA208															
		SA274-m															
		SA291-m															
Southwestern	Sa.III	SA351-d															
		S251-g															
		SA152															
		GH48															
		GH89															
		GH90															
		GH91															
		SA12-c															
		SO106															
		SO95-p															
Central	Sa.II	SA385-L															
		GH98	0.000														
		SCH181-a	0.002	0.002													
		SA185-i	0.010	0.010	0.008												
		SA183-i	0.010	0.010	0.008	0.000											
		SCH179-i	0.010	0.010	0.008	0.000	0.000										
		GH79	0.006	0.006	0.004	0.008	0.008	0.008									
		GH80	0.010	0.010	0.008	0.008	0.008	0.008	0.004								
		GH72	0.004	0.004	0.002	0.010	0.010	0.010	0.002	0.006							
		SA197	0.004	0.004	0.002	0.010	0.010	0.010	0.002	0.006	0.006						
		SA292-q	0.010	0.010	0.008	0.012	0.012	0.012	0.008	0.006	0.006	0.000					
		SCH388-a	0.016	0.016	0.014	0.014	0.014	0.014	0.010	0.012	0.006	0.006	0.006	0.014			
		GH93	0.012	0.012	0.010	0.010	0.010	0.010	0.006	0.006	0.006	0.008	0.008	0.010	0.004		
		SV305	0.095	0.095	0.093	0.100	0.100	0.100	0.100	0.092	0.097	0.090	0.090	0.098	0.091	0.091	

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