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New Zealand sub-Antarctic phytoliths and their potential for past vegetation reconstruction

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Abstract: Phytoliths in the modern vegetation of sub-Antarctic Campbell Island are compared with those in the soil beneath to assess the accuracy of vegetation reconstructions made from dispersed phytolith assemblages. The soil phytoliths alone suggest the source vegetation is a grassland association for all study sites, which reflects none of the herb, fern or shrub component of the overlying vegetation. It is concluded that at this locality dispersed phytoliths on their own are not reliable indicators of source vegetation and should be used with caution in this context for palaeoecological studies. However, they can provide useful botanical information where all other organic material is absent. With further research, based on the abundance and diversity of Poaceae phytoliths observed in this and other studies, dispersed phytoliths from the fossil record have the potential to contribute significantly to the understanding of grassland ecosystem development in the geological past.

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Introduction

The study of southern high latitude vegetation contributes to the search for modern analogues for the sparse Cenozoic palaeobotanical record around the Antarctic margin (e.g. Edwards 1921, Cookson 1947, Askin 2000, Raine & Askin 2001, Thorn 2001, Ashworth & Cantrill 2004, Truswell *et al.* 2005, MacPhail & Cantrill 2006, Prebble *et al*. 2006). Understanding these fossil deposits has been an important pursuit for decades, in conjunction with interest in the development of the Antarctic Ice Sheet, its processes and response to global climate change (e.g. Francis 1999). Established 'nearest modern relative' or 'nearest modern equivalent' techniques compare the composition of the fossil flora with that of similar modern day vegetation associations which, by extrapolation, allow assumptions to be made about the past vegetation stature and environmental conditions of growth. The fern-bush communities of the southern oceanic islands, e.g. the New Zealand sub-Antarctic islands, have been suggested as modern analogues for late Eocene floras (e.g. the Cytadela and Petrified Forest Creek floras of King George Island) (Birkenmajer & Zastawniak 1989, Askin 1992, Birkenmajer 1997). These floras were growing in cool, humid climates in the Antarctic Peninsula region as climate deteriorated before the permanent establishment of a significant East Antarctic Ice Sheet.

This investigation contributes to the analogue reference collection of phytoliths from the high southern latitudes first described in Thorn (2004) by studying phytoliths in the modern plants and soil of sub-Antarctic Campbell Island, south of New Zealand. This investigation also provides a case study for a preliminary assessment of the likely accuracy of reconstructing past vegetation using dispersed phytoliths alone.

Phytoliths are microscopic particles formed from the solidification of biogenic silica (biosilica) gel within and between the cells of many plants. They have a varied morphology depending upon the plant species and host cell type, can be isolated idioblastic forms or skeletal structures, and are commonly between 5 and 200 μm in size. Due to the multiplicity and redundancy of phytolith forms (Rovner 1971) the taxonomic affinity of individual phytoliths, when separated from their source plant, is complex. However, ongoing studies on phytolith production in modern plants can identify the parent plant to generic and sometimes species level (e.g. Piperno & Pearsall 1998, Carnelli *et al*. 2004). Due to their siliceous composition, they can survive in oxidizing conditions and commonly provide an *in situ* record of vegetation composition. Phytoliths therefore have the potential to both complement and supplement plant macrofossil and terrestrial palynology records and are becoming increasingly used in palaeoecological studies.

Campbell Island is located *c.* 600 km SSE of South Island, New Zealand, and comprises the remains of a dissected Pliocene volcanic cone (Fig. 1; Oliver *et al.* 1950, Beggs 1978, Michaux & Leschen 2005). The majority of the island is covered in vegetation and peat soils (blanket peats average up to four metres thick), which began to accumulate after the last glaciation *c.* 13 000 BP (Fig. 2; Campbell 1980, McGlone *et al.* 1997, McGlone 2002). Prevailing winds are from the west to west–north-west and the climate is generally cloudy, moist and cool with minimal sunshine.

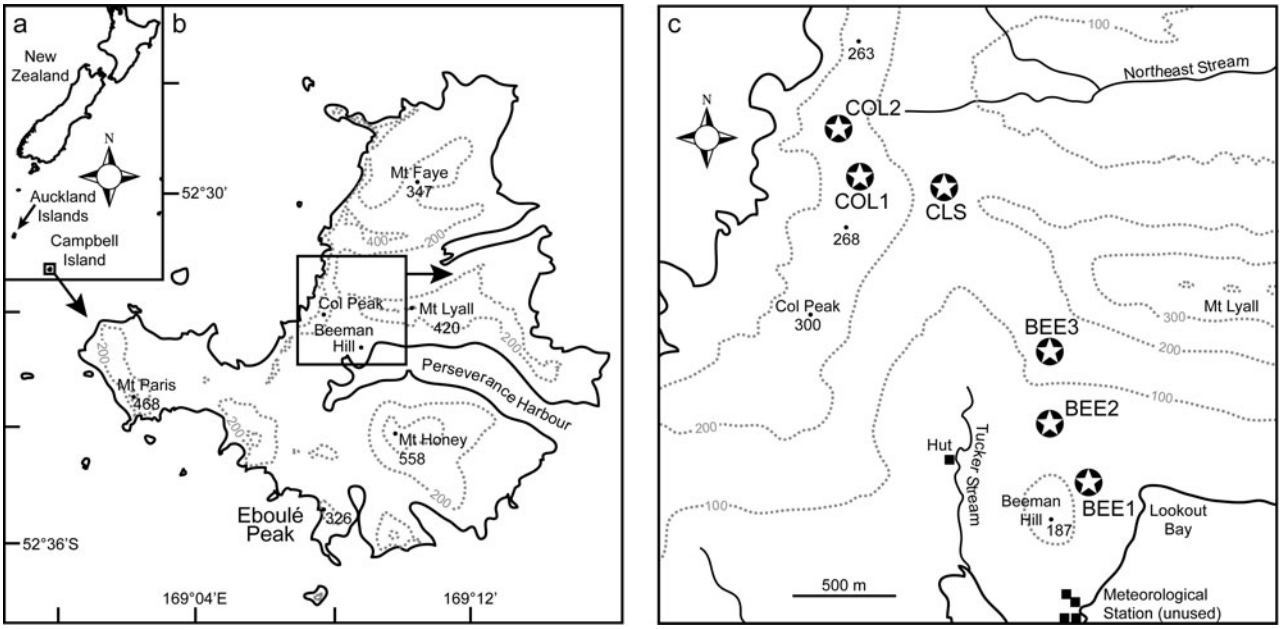

Fig. 1. Campbell Island locality maps. Contour and spot heights in metres above sea level. **a.** Location of Campbell Island in relation to New Zealand, also indicating the Auckland Islands where two plant specimens used in this study were collected. **b.** Campbell Island with general topography. Boxed in area is enlarged in c. **c.** Locations of quadrats named in the text. GPS co-ordinates and altitudes for each are in Table I.

Mean monthly temperatures vary little throughout the year, ranging from 6.5°C in August to 9°C in February (De Lisle 1965, New Zealand Meteorological Service 1973). The modern vegetation is a mosaic, ranging from near-pristine to communities heavily modified by grazing and burning during farming between 1895 and 1931. The island is no longer settled and domestic sheep and cattle were eliminated in 1991 (Bestic *et al.* 2005). The vegetation is a relatively depauperate flora of *c.* 132 indigenous vascular plants and 39 naturalised adventives including *Dracophyllum* (up to 5 m in height), and *Coprosma-Myrsine* scrub and tussock grasslands beyond the immediate coastal zone (Meurk & Given 1990, Meurk *et al.* 1994a, Rogers & Walker 2005). A notable feature of the island flora are the distinctive and impressive macrophyllous forbs, commonly referred to as "megaherbs", which prefer the cliff tops and, except for *Stilbocarpa polaris*, are endemic to New Zealand's southern oceanic islands (Fig. 2; McGlone 2002). Floristic structure and productivity on the island has been shown to be influenced by spatial variations in marine ionic input from precipitation (Meurk *et al.* 1994b).

Methods

Fieldwork for this project was undertaken during March 2004 (austral autumn). Six sites within different vegetation associations (BEE1, BEE2, BEE3, CLS, COL1 and COL2) were located across central Campbell Island from the

Fig. 2. Landscape and vegetation views of Campbell Island. **a.** From Col-Lyall saddle looking south across Beeman Hill to Mount Honey. Tussock grassland in the foreground. **b.** From Tucker Cove at the base of Beeman Hill looking west across *Dracophyllum* scrub towards Menhir. **c.** Close-up of a megaherb field association at the cliff-top near quadrat COL2. Al = *Anisotome latifolia*, Ps = *Pleurophyllum speciosum*, Br = end of season *Bulbinella rossii*, Pv = *Polystichum vestitum*.

Table I. Location and ground cover characteristics of quadrats on Campbell Island. Latitude, longitude and altitude are GPS data. Vegetation association and ground cover type, overlapping, therefore ≥ 100% at each site, as observed in the field. m.a.s.l. = metres above sea level.

Locality	Latitude (S)	Longitude (E)	m.a.s.l.	Observed vegetation association	Ground cover type (%)				
					Vascular vegetation	Moss	Leaf litter	Bare ground	Rock
BEE1	52°32'38.4"	169°09'07.9"	80	*Dracophyllum/Coprosma/Blechnum* scrub	100	–	100	–	–
BEE2	52°32'30.2"	169°08'58.9"	78	*Dracophyllum/Sphagnum* tussock	70	20	15	5	–
BEE3	52°32'15.9"	169°09'00.3"	125	*Coprosma/Bulbinella/Polystichum* low scrub	100	1	–	–	–
CLS	52°31'47.5"	169°08'33.5"	186	*Polystichum/Bulbinella* tussock	80	20	–	–	–
COL1	52°31'44.9"	169°08'10.3"	238	Stony subalpine herbfield	60	5	< 1	15	20
COL2	52°31'37.9"	169°08'06.9"	257	Megaherb field	60	< 1	40	< 1	–

north-eastern slopes of Beeman Hill, north–north-west to the cliff tops of Col Ridge on the western side of the island (Table I, Fig. 1). Temporary quadrats (4 m^2) were used at each site (except at COL1 where a 1 m^2 quadrat was more appropriate due to the small size and low-lying nature of the vegetation, Fig. 3). At each site the soil surface was sampled, plant specimens collected and canopy cover surveyed. The peat soils were of varying depths (several centimetres to over three metres), and generally poorly drained. Peat slips were avoided, and the geomorphic

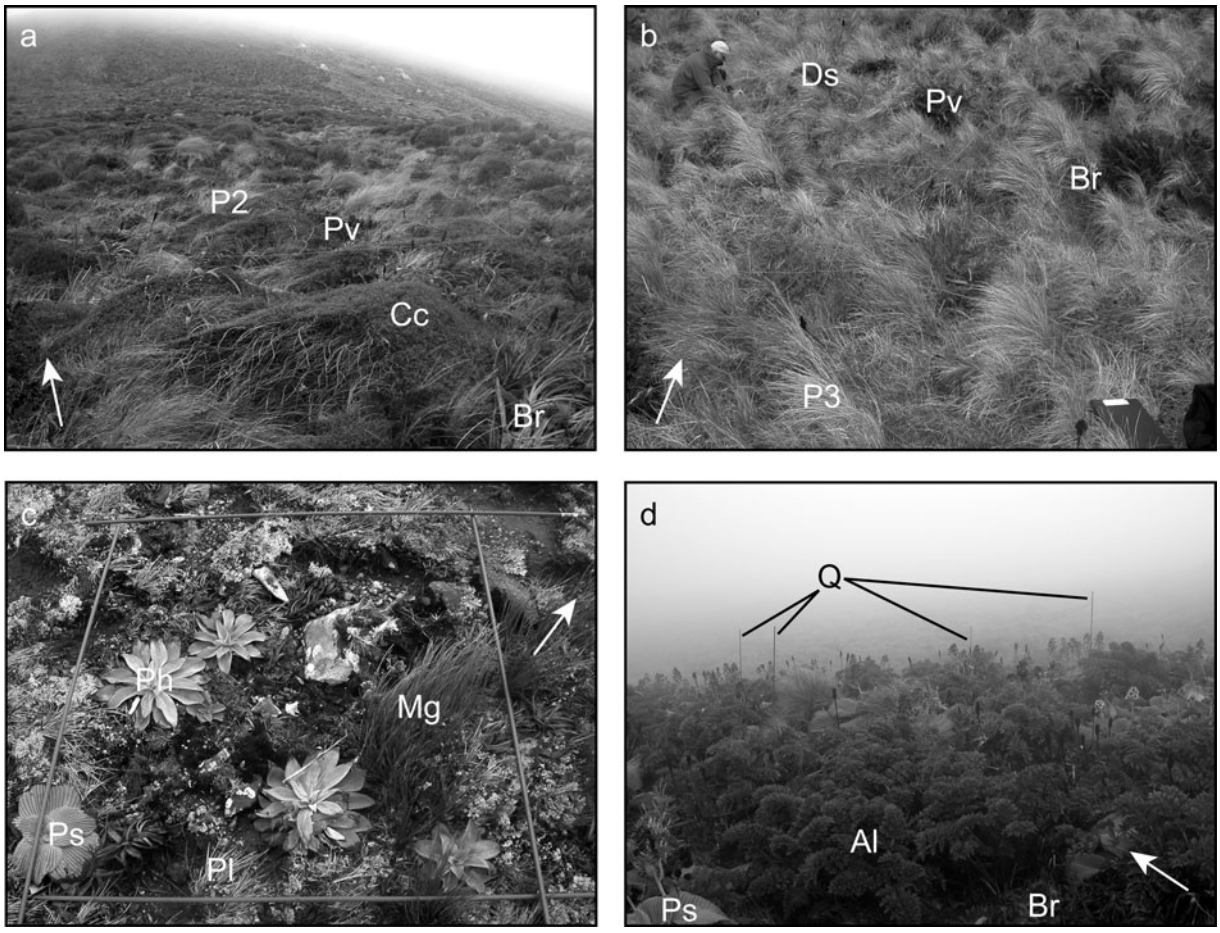

Fig. 3. Photographs of the four main survey sites. Arrows indicate north. All quadrats measured 4 m x 4 m, except COL1 at 1 m x 1 m. Q, quadrat poles. **a.** BEE3, *Coprosma/Bulbinella/Polystichum* low scrub. **b.** CLS, *Polystichum/Bulbinella* tussock. **c.** OL1, Stony subalpine herbfield. **d.** COL2, Megaherb field. Al = *Anisotome latifolia*, Br = *Bulbinella rossii*, Cc = *Coprosma cuneata* or *C. ciliata*, Ds = *Dracophyllum scoparium*, Mg = *Marsippospermum gracile*, Ph = *Pleurophyllum hookeri*, Ps = *Pleurophyllum speciosum*, Pl = *Poa litorosa*, P2 = *Poa* sp.2, P3 = *Poa* sp.3, Pv = *Polystichum vestitum*.

Table II. Species list and canopy cover for each surveyed quadrat at Campbell Island. Plant organs analysed: F = non-fertile fronds, L = leaves, R = roots, Se = seeds, Fl = flowers; S = herbaceous stems, W = woody stems, [MF] = macrophyllous forb, * = analysed for phytoliths in Thorn (2004), ? = not collected. Data in *italics* refer to the quadrat from which a specimen was collected (and processed if in ***bold italics***). [#] = specimen collected from Enderby Island in the Auckland Islands, [∝] = specimen collected from Skua Gull Flat, south Auckland Island (Fig.1). For specimen collection numbers refer to Turnbull *et al.* (2004).

Family	Species	Organs	Phytolith producer?	Normalized canopy cover (%) within each quadrat					
				BEE1	BEE2	BEE3	CLS	COL1	COL2
Grasses:									
Poaceae	*Chionochloa antarctica* (Hook.f.) Zotov*	L	Y		*21*				
	Hierochloe sp.	L,Fl	Y				***5***		
	Poa ?*antipoda* Petrie	L	Y						***1***
	Poa litorosa Cheeseman*	L,R	Y					*10*	4
	Poa sp. 2	L,R,Se	Y			***9***			
	Poa sp. 3	L,R	Y				***65***		
Rushes:									
Juncaceae	*Luzula* sp.	L,R,Se	N				1	***4***	
	Marsippospermum gracile (Hook.f.) Buchenau	L	N					***16***	
Sedges:									
Cyperaceae	*Carex trifida Cav.**	L	Y	***1***					
	Isolepis aucklandica Hook.f.	L,R	N		***28***				
	Uncinia sp.	L,R,Se	Y						***1***
Herbs:									
Apiaceae	[MF]*Anisotome latifolia* Hook.f.*	L	N						21
Asteraceae									
	Abrotanella sp.	–	?					*4*	
	Anaphalioides bellidioides (G.Forst.) Glenny*	L	Y			1	1	6	
	Damnamenia vernicosa (Hook.f.) Given	L	N					***4***	
	[MF]*Pleurophyllum hookeri* Buchanan*	L	N					*30*	
	[MF]*Pleurophyllum speciosum* Hook.f.*	L	N					*2*	35
Boraginaceae	*Myosotis capitata* Hook.f.*	L	Y						1
Brassicaceae	*Cardamine corymbosa* Hook.f.	–	?						1
Caryophyllaceae	*Cerastium fontanum* Baumg.	–	?						1
	Cerastium sp.	–	?			1			
Droseraceae	*Drosera stenopetala* Hook.f.	–	?		1				
Gentianaceae	*Gentiana antarctica* Kirk	–	?					2	
Geraniaceae	*Geranium* sp.	–	?			1	1	2	
Liliaceae	*Astelia subulata* (Hook.f.) Cheeseman in Chilton	L,R,S	N		***4***				
	[MF]*Bulbinella rossii* (Hook.f.) Cheeseman*	L	N	*1*		6	6	8	32
Onagraceae	*Epilobium* sp. 1	–	?			1			1
	Epilobium sp. 2	–	?					2	
Orchidaceae	*Chiloglottis* sp.	–	?				1		
Rosaceae	*Acaena anserinifolia* (J.R.Forst. & G. Forst.) J.B. Armstr.*[#]	L	Y			1	1		
	Acaena minor (Hook.f.) Allan[#]	L,S,Se	N					2	
Stylidiaceae	*Phyllachne clavigera* (Hook.f.) F. Muell.	L	N		1			***8***	
Ferns:									
Blechnaceae	*Blechnum novae-zelandiae* T.C. Chambers & P.A. Farrant	F	N	***31***					
Dryopteridaceae	*Polystichum vestitum* (G.Forst.) C. Presl*	F	N			21	8		2
Pallaviciniaceae	*Hymenophyllum* sp.	–	?			*1*	3		
Schizaceae	*Schizaea* sp.	–	?		1				
Shrubs:									
Epacridaceae	*Dracophyllum longifolium* (J.R.Forst. & G.Forst.) R.Br.*	L,W	N	*2*	3				
	Dracophyllum scoparium Hook.f.*	L,W	N	*45*	36	1	1		
Myrsinaceae	*Myrsine divaricata* A. Cunn.*	L,W	N	*9*	1				
Rubiaceae	*Coprosma ciliata* Hook.f.	L,W	N	***11***	1	16			
	Coprosma cuneata Hook.f.	L,W	N			**41**			
	Coprosma perpusilla Colenso[∝]	L,W	N		3		7		

settings of each site appeared relatively stable, so it is assumed that there would be neglible transport of phytoliths into and out of the quadrats through aeolian or run-off processes.

Each site was characterized by estimating the overall per cent cover of vascular vegetation, moss, leaf litter, bare ground and rock. All vascular plants within the boundaries were then identified and the per cent cover of their canopies estimated to the nearest 5% in two different height bands (< 30 cm and 30–200 cm, based on Allen 1992). Overlapping canopies allowed the total canopy cover to be greater than 100%. Per cent canopy cover of

Table III. Plant phytolith production summarized by morphotype category. Morphotype diversity (when > 1) within each category is indicated in brackets. *Carex trifida* was counted quantitatively for this study in comparison to the qualitative presence/absence data recorded for this species in Thorn (2004). $^{\phi}$ = count data from Thorn (2004). *Anaphalioides bellidioides*, *Myosotis capitata* and *Acaena anserinifolia* produced few forms, so counts were not practical and presence only is noted*. Stomate morphotypes were noted in the *Hierochloe* sp. specimen beyond the formal count. Equivalent morphotype terminology used in Thorn (2004) for comparison with the more recent International Code for Phytolith Nomenclature (Madella *et al.* 2005): Acicular (this study), Trichome (hair) (Thorn 2004); Bilobe, Bilobate; Conical, Hat-shaped; Elongate, Elongate; Globular, Mesophyll; Polygonal, Plate (polygonal); Rondel, Rondel; Saddle, Saddle; Tabular, Plate (rectangular).

		Grasses						Sedges		Herbs		
	Includes fragile forms	*Chionochloa antarctica*$^{\phi}$	*Hierochloe* sp.	*Poa ?antipoda*	*Poa litorosa*$^{\phi}$	*Poa* sp. 2	*Poa* sp. 3	*Carex tridifa*	*Uncinia* sp.	*Anaphalioides bellidioides*$^{\phi}$	*Myosotis capitata*$^{\phi}$	*Acaena anserinifolia*$^{\phi}$
Acicular	Y		37(2)	5		27(2)	24	2	2(2)		*	*
Bilobe	N	1	2	5		1	1	1				
Conical	Y		1					61(4)	207(9)			
Elongate	Y	8(3)	120(6)	15(4)	115(3)	16(3)	28(3)	26(2)	55			
Globular	Y			4		1	2(2)	9	1	*	*	
Hair base	Y										*	*
Parallelepipedal	N	3(2)			3(2)		3		7(2)			
Polygonal	Y								3			
Rondel	N	279	47(2)	32	78	181	158		4			
Saddle	N	9		7	106	2	14					
Stomate	Y		*						2			
Tabular	N		48(2)				5	2	14			*
Trapeziform	N		45(3)	233(2)		71(3)	67(2)		1			
Vascular tissue	Y					1			4	*		*
Sum		300	300	301	302	300	302	101	300	–	–	–
Biosilica by dry weight (%)		0.61	1.27	4.71	2.29	2.04	2.81	0.50	0.22	3.10	0.50	5.44

Table IV. Relative contribution of biosilica (Y) by each phytolith-producing species to the vegetation phytolith assemblage at each quadrat. C, normalized canopy cover. Refer to Eq. (1) in text.

		Grasses						Sedges		Herbs		
	%	*Chionochloa antarctica*	*Hierochloe* sp.	*Poa ?antipoda*	*Poa litorosa*	*Poa* sp. 2	*Poa* sp. 3	*Carex tridifa*	*Uncinia* sp.	*Anaphalioides bellidioides*	*Myosotis capitata*	*Acaena anserinifolia*
BEE1	C							1				
	Y							100				
BEE2	C	21										
	Y	100										
BEE3	C					9				1		1
	Y					76				2		22
CLS	C		5				65			1		1
	Y		3				94			0.3		2.7
COL1	C				10					6		
	Y				88					12		
COL2	C			1	4				1		1	
	Y			27	52				18		3	

each species from both height bands was then summed, normalized and used to represent an estimate of the quantity of phytolith-producing plant organs at the site. To constrain the study, it is assumed that no plants beyond the quadrat boundaries contribute to the phytolith assemblages within. Specimens of each plant species were then collected (to include as many different organs from each plant as possible) from the site in which they were first encountered. The individuals collected are assumed to be representative of their species on Campbell Island. Voucher specimens of phytolith-producing species are stored in the Victoria University of Wellington herbarium in New Zealand (WELTU).

Soil sub-samples (*c.* 50 g each) were collected from the centre and all quarters of each quadrat, then amalgamated to provide a representative sample for that site. It is assumed that accumulation of phytoliths in the soil surface may be only several decades old, on the basis of work on the peaty soils at Mount Hauhungatahi (Tongariro National Park, central North Island, New Zealand; Horrocks & Ogden 2000), which suggests a soil accumulation rate of 0.8–1.5 cm per century. The soil samples were collected from 2–5 cm below the current leaf litter, which removes the bias of the immediately overlying plant.

To compare the vegetation and underlying soil phytoliths, overall phytolith production of the vegetation within each quadrat has to be in the form of a list of morphotype proportions reflecting the species canopy cover, phytolith production rate and preservation potential. This is achieved by weighting the proportion of each morphotype from each phytolith-producing species using the following formula (Thorn 2006):

For example, for phytolith-producing species A:

$$Y_A = \frac{W_A C_A}{\sum_{D}^{A} WC} \times 100 \quad (1)$$

where Y = relative biosilica contribution to site (%), W = biosilica production by dry weight (%), C = canopy

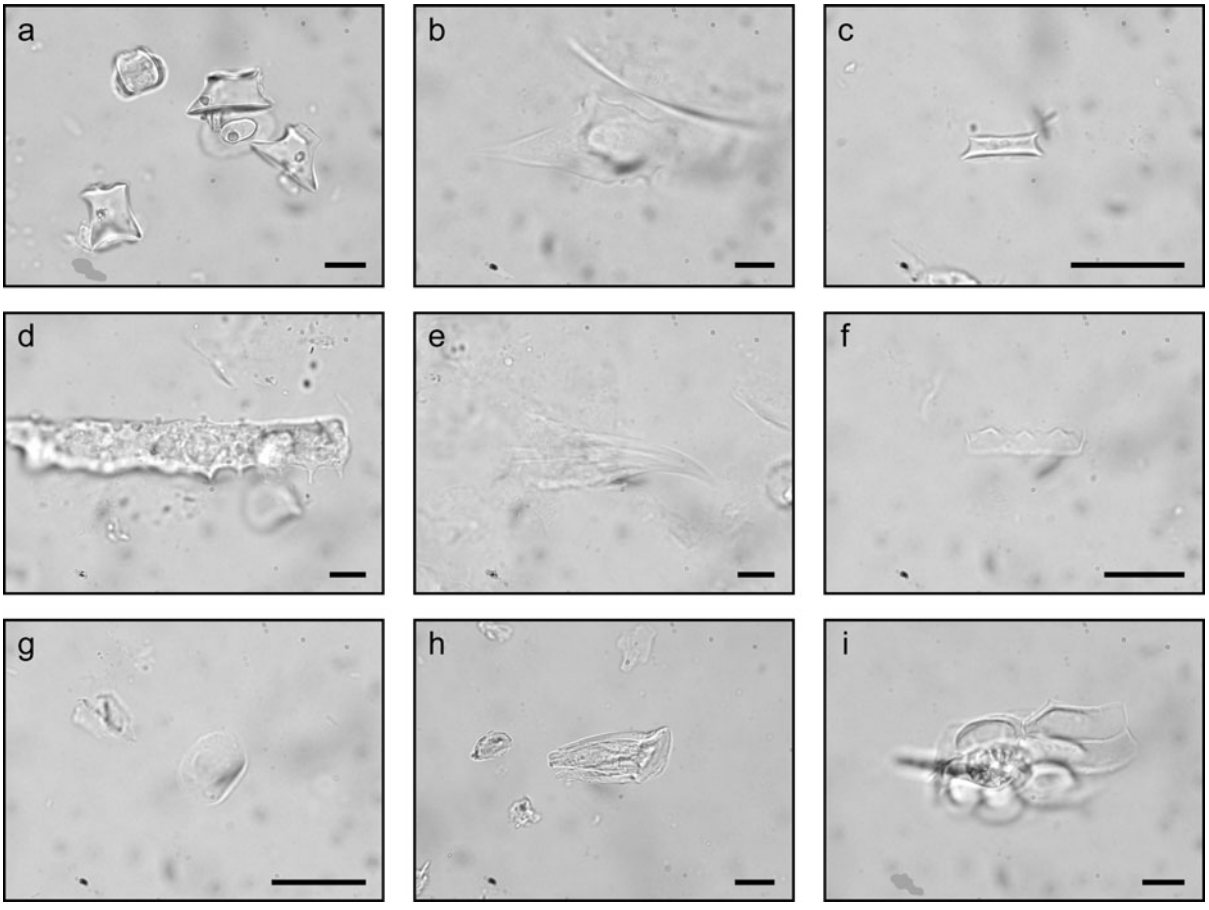

Fig. 4. Selected phytoliths from plant species recorded within the study quadrats on Campbell Island. All scale bars = 10 μm. * = previously discussed in Thorn (2004). Acicular types compare to those described by Carnelli *et al.* (2004). **a.** Rondel, *Chionochloa antarctica**, **b.** Acicular [Type 1], *Hierochloe* sp. (CLS), **c.** Trapeziform polylobate, *Poa* ?*antipoda* (COL2), **d.** Elongate columellate, *Poa litorosa**, **e.** Acicular [Type 1], Poa sp. 2 (BEE3), **f.** Conical square verrucate 3, *Carex trifida* (BEE1), **g.** Conical square verrucate 1, *Uncinia* sp. (COL2), **h.** Acicular myosotis, *Myosotis capitata**, **i.** Acicular [Type 16] and Tabular epidermal, *Acaena anserinifolia**.

cover (%). *Species A* to *D* contribute phytoliths to the soil at this theoretical site.

If the same morphotype occurs in more than one species (conservative forms reflecting phytolith redundancy) the weighted proportion from each species in which it occurs are summed for that morphotype.

Phytoliths were extracted from plants and soils using a wet oxidation technique outlined in Thorn (2004). Plant material was cleaned using dilute hydrochloric acid and an ultrasonic tank. Concentrated sulphuric acid and hydrogen peroxide (an exothermic and effervescent reaction) removed the organic matter from the siliceous residue. Extraction of phytoliths from the soil samples followed a modified method of Pearsall (2000). Treatment with dilute hydrochloric acid removed carbonates and concentrated sulphuric acid and hydrogen peroxide were added, as in the plant processing procedure, to remove the organic material. Inorganic siliceous grains were separated from the less dense biosilica using sodium polytungstate heavy liquid at specific gravity 2.3. Quantitative processing for both plants and soil samples allowed the calculation of per cent biosilica content by dry weight of each sample. The biosilica residues were mounted in Canada Balsam and analysed on a Leica DMLB transmitted light microscope. A count of 300 phytoliths was the target for each sample and morphotypes classified using the recent International Code of Phytolith Nomenclature (ICPN; Madella *et al*. 2005). This resulted in a slightly different terminology than a previous study on Campbell Island phytoliths (Thorn 2004), in particular the grouping of all rondel forms.

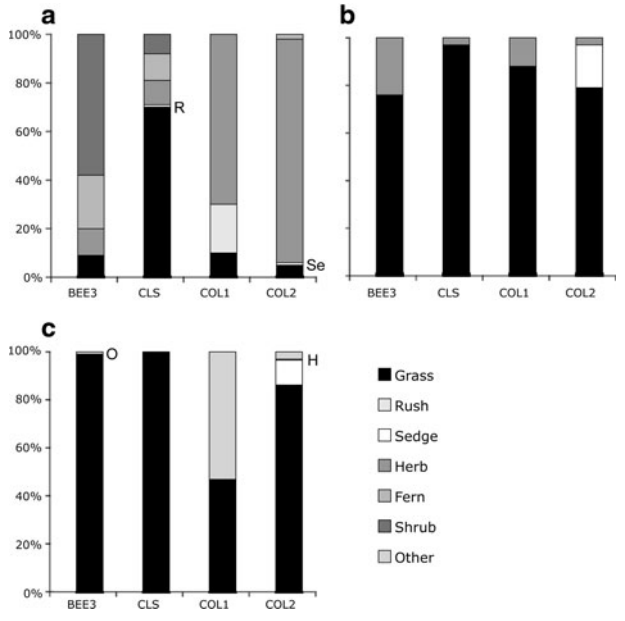

Fig. 5. Graphs to compare summary aspects of the canopy cover and phytolith assemblages for the four main survey sites. **a.** canopy cover, **b.** vegetation phytolith assemblages, **c.** soil phytolith assemblages. Narrow bars are clarified with the following notation: R = rush, Se = sedge, H = herb, O = other.

Results

Vascular vegetation covered between 60 and 100% of each quadrat, with the sparser sites being those at higher altitude. Sites on Beeman Hill were at the lowest altitudes, relatively sheltered from the prevailing westerlies and consisted mainly of shrub and fern vegetation associations (Tables I & II, Fig. 3). Sites BEE1 and BEE2 were dominated by *Dracophyllum scoparium* together with *Blechnum novae-zelandiae* at BEE1, and *Isolepis aucklandica* and *Chionochloa antarctica* at BEE2 (Table II). BEE3 was dominated by *Coprosma*, with a high proportion of *Polystichum vestitum*. Site CLS was dominated by *Poa* sp. 3 on the Col-Lyall saddle. Site COL1 was the most exposed cliff-top site, the smallest area analysed, and had the highest diversity with 14 species, despite a low vascular plant cover of 60% and very thin soil (evident by the 20% exposure of bare rock, Table I, Fig. 3). There were no ferns or shrubs at this site, with most of the vegetation consisting of low-lying herbs and a small proportion of grass (*Poa litorosa*). Site COL2 was in the middle of a megaherb field, also at the cliff top and highly exposed. The canopy mainly comprised *Anisotome latifolia*, *Pleurophyllum speciosum* and *Bulbinella rossii* with a minor proportion of grasses.

Each quadrat had between one and four phytolith-producing species and varied in overall vascular plant diversity between seven and 14. Grass (six species), rush (two), sedge (three), herb (17, plus four macrophyllous forbs), fern (four) and shrub (six) species were recorded (Table II). In total, 30 species have been analysed for their phytolith production, of which 16 were processed for this study and 14 had been analysed in a previous study (Thorn 2004; Table III, Fig. 4). Some species collections were not processed due to their small size and rarity in the vegetation (e.g. *Abrotanella* sp.). If they later prove to be phytolith producers, it is likely they would make only a negligible contribution to the soil phytolith floras in this study. Two species had also been collected from the sub-Antarctic Auckland Islands (Table II, Fig. 1) *en route* to Campbell Island, so collections were not duplicated. In summary, 11 of the 30 species (37%) were found to be phytolith producers and 19 are non-producers (Table II).

Of the grasses, all were shown to be abundant phytolith producers (between 0.61 and 4.71% biosilica by dry weight) and all produced elongate and rondel forms (Table III). Form diversity in the grasses is high (eight to 18 broad morphotype categories). Many acicular and trapeziform forms were also produced by *Hierochloe* sp., *Poa* ?*antipoda*, *Poa* sp.2 and *Poa* sp.3. *Poa* sp.2 and *Poa* sp.3 have similar assemblages, so may be the same species. Identification of the grasses was not always possible to

species level due to the lack of flowering heads or seeds in the collected specimen. *Poa litorosa* differs from the other three *Poa* spp. by the absence of acicular, bilobe, globular and trapeziform forms in particular, producing instead relatively more elongate and saddle forms. *Poa* ?*antipoda* produces the greatest relative abundance of trapeziform forms of all the grasses. *Chionochloa antarctica* is markedly different from the other grasses as its phytoliths are dominantly rondel in form. Two of the three sedge species are phytolith producers. Both *Carex trifida* and *Uncinia* sp. produce characteristically high relative abundances of conical phytoliths, which distinguish the sedges from the other species. Elongate forms are also common with morphotype category diversity higher in *Uncinia* sp. Of the herbs only *Anaphalioides bellidioides*, *Acaena anserinifolia* and *Myosotis capitata* produced any biosilica, and so few morphotypes or rare phytoliths that counts were unrealistic. Despite this, acicular, globular, hair base, tabular and vascular tissue forms were noted as present with spectacular hairs and hair bases in *Myosotis capitata* (Thorn 2004). There are 17 conservative morphotypes between the phytolith-producing plants. The ferns, rushes, majority of herbs (including the macrophyllous forbs) and the shrubs were non-producers.

Fragile forms include several acicular, all conical, thin elongate, stomate, vascular tissue and thin-walled globular forms. Species with a high abundance of fragile forms are the sedges (*Carex trifida*, 74%; *Uncinia* sp., 91%) and the herb *Anaphalioides bellidioides*, which produces almost entirely thin-walled globular orbicular psilate forms. In comparison, the grasses have relatively low proportions of fragile phytoliths from 0% (*Poa litorosa* and *Chionochloa antarctica*) to 17% (*Hierochloe* sp.). The proportions of each morphotype category within the vegetation phytolith assemblage (calculated using count data weighted by relative biosilica contribution per species from Eq. (1)) are compared to the directly observed soil phytolith assemblage for sites BEE3, CLS, COL1 and COL2 (Tables IV–VI).

Table V. Soil phytolith assemblages summarized by morphotype category. Morphotype diversity (when > 1) within each category is indicated in brackets. Soils at quadrats BEE1 and BEE2 contained rare phytoliths, so counts were not undertaken.

	Soil (S) assemblages					
	S_{BEE1}	S_{BEE2}	S_{BEE3}	S_{CLS}	S_{COL1}	S_{COL2}
Acicular	*		8(2)	1	1	4(2)
Bilobe			1	5	1	6
Conical			1		1	
Cuneiform						
Elongate	*	*	20(4)	8(5)	32(6)	63(6)
Globular	*		1		1	9
Parallelepipedal					4	1
Reniform						
Rondel		*	154	134	106	92
Saddle		*	21	8	16	18
Tabular						
Tracheid						
Trapeziform		*	94(3)	140(3)	138(3)	107(3)
Vascular tissue						
Sum	–	–	300	296	300	300

Sites BEE1 and BEE2 each had only one phytolith-producing species from diversities of seven and 11 species respectively (Table IV). *Carex trifida* had only a 1% canopy cover at BEE1 representing all of the phytolith contribution to that site. *Chionochloa antarctica* produced all the phytoliths for site BEE2 with a canopy cover of 21%. Vegetation reconstruction from the phytolith assemblages was not therefore possible for quadrats BEE1 and BEE2 due to insufficient phytolith content in the soil (Table V). This is unsurprising at BEE1 as the only phytolith-producing species at this site was *Carex trifida*, which had a canopy cover of only 1% and produces only fragile, conical forms. *Chionochloa antarctica* morphotypes are of generally robust morphology in the BEE2 soil assemblage, but rarely occur, despite this species having a relatively high canopy cover of 21% (Tables IV & V). This may be explained by sampling if the *Chionochloa* plants were sufficiently distant from the actual soil collection localities within the quadrat.

Table VI. Comparative table of vegetation (V) and soil (S) phytolith assemblages for each quadrat.

	Vegetation (V) vs Soil (S) assemblages (%)							
	V_{BEE3}	S_{BEE3}	V_{CLS}	S_{CLS}	V_{COL1}	S_{COL1}	V_{COL2}	S_{COL2}
Acicular	9.7	2.7	8.2	0.3		0.3	0.5	1.3
Bilobe	0.2	0.3	0.3	1.7		0.3	0.4	2.0
Conical		0.3				0.3	11.1	
Elongate	4.0	6.6	9.9	2.7	33.6	10.7	26.7	21.0
Globular	2.3	0.3	0.8		11.1	0.3	0.4	3.0
Parallelepipedal			0.9		0.9	1.3	1.0	0.3
Polygonal							0.2	
Rondel	44.8	51.4	49.9	45.3	22.8	35.3	18.2	30.7
Saddle	0.5	7.1	4.4	2.7	31.0	5.4	21.4	6.0
Stomate							0.1	
Tabular	20.1		4.1				0.8	
Trapeziform	17.6	31.3	21.4	47.3		46.1	19.0	35.7
Vascular tissue	0.8		0.1		0.6		0.2	

At BEE3 (diversity 12) phytolith-producing species comprised only 11% of the canopy and although there is a significant (24%) phytolith contribution from the herb canopy (*Acaena anserinifolia* and *Anaphalioides bellidioides*), grass phytoliths dominate the vegetation input (*Poa* spp., 76%) and comprise 99% of the soil phytoliths (Tables IV & V, Fig. 4). The remaining 1% consists of forms not produced by the plants at this site. The lack of *Acaena* phytoliths is probably due to their fragility, despite their abundant production (5.44% biosilica by dry weight). Taken on its own, the soil assemblage suggests a grassland source vegetation. In fact, grass comprised only 9% of the canopy cover and the soil assemblage indicates none of the shrub (58%), fern (22%) or herb (11%) components of the source vegetation, which was noted as '*Coprosma*/*Bulbinella*/*Polystichum* low scrub'. The grass morphotypes in the soil at this site are conservative forms, so recognizing the species of grass represented is not currently possible. However, the overall *Poa*-type assemblage dominated by elongate and rondel morphotypes is evident. Comparing the morphotype relative abundances between the vegetation and soil assemblages suggests that there is some phytolith accumulation (mainly of robust forms) as the proportions of, in particular, rondel and trapeziform phytoliths are higher in the latter (Table VI). Overall, if a *Poa* grass is the only species recognized in the source vegetation from the dispersed soil assemblage at this site, then 91% of the original vegetation canopy (e.g. herbs, ferns and shrubs) at the site will have no lasting phytolith record (Fig. 4).

Poa sp. 3 dominated the phytolith contribution at site CLS (diversity 12) at 94% with minor additions from *Hierochloe* sp., *Acaena anserinifolia* and *Anaphalioides bellidioides* (Table IV). At this site only phytoliths produced by grasses are observed in the soil (with some conservative forms that are also produced in sedges), hence a grassland vegetation community again seems the only possible source compared with the observed '*Polystichum*/*Bulbinella* tussock' association (Tables II & V). *Hierochloe* and *Poa* have many common morphotypes, so the two grasses cannot be distinguished from the soil assemblage, and the soil and vegetation assemblages cannot be directly compared. There is no record in the soil assemblage of the fern (11%), herb (10%), rush (1%) or shrub (8%) canopy components due to non-production or non-preservation (Fig. 5). Higher proportions of some morphotypes in the vegetation than the soil suggests the non-preservation of some fragile forms (Table VI).

At COL1 despite the highest species diversity of all the sites (14), only two species are phytolith-producers with grass phytoliths dominating (*Poa litorosa*, 88%), in addition to herb production (*Anaphalioides bellidioides*, 12%) (Table IV). Again, only grass phytoliths from the vegetation above are observed in the soil, suggesting a grassland source, with no record of the significant herb (70%) or rush (20%) canopy cover at this 'stony subalpine herbfield' site. Only 47% of the phytoliths observed in the soil were forms produced by the overlying vegetation (Fig. 5). COL1 is extremely exposed suggesting that, contrary to the assumption made, there is aeolian transport of phytoliths at this site. This quadrat was also smaller than other sites including bare ground and rock, with a thin and stony soil and slow accumulation of leaf litter (Fig. 3).

Finally, COL2 is located within a megaherb field association and had the highest number of phytolith-producing species (4, diversity 11) with biosilica contributions from *Poa litorosa* (52%), *Poa* ?*antipoda* (27%), *Uncinia* sp. (18%) and *Myosotis capitata* (3%) (Table IV). *Poa* spp. and *Uncinia* sp. are significant phytolith contributors, despite their low canopy cover, but share many conservative forms. None of the distinctive, but fragile, *Uncinia* sp. conical forms survived in the soil, so the majority of the soil assemblage consists of grass morphotypes (including some conservative forms also produced by sedges) (Fig. 5). A grassland interpretation is the inevitable result, with no record of the significant macrophyllous forbs (88%) or minor other herbs (4%) and fern (2%) components of the source canopy.

Discussion

Of the species recorded in the extant vegetation at the Campbell Island quadrats only 37% were found to produce phytoliths and hence there would only ever be the potential to reconstruct up to 37% of the source vegetation diversity from dispersed soil phytoliths alone. Further, this 37% is overwhelming biased by grass phytoliths of predominantly robust morphotypes, with the sedges also producing abundant, but fragile morphotypes of a lower preservation potential. Meurk *et al.* (1994b) found that the high altitude herbfields had a relatively high soil pH due to a mineral-rich soil and lower levels of nutrient input from aerosols due to the height above sea level. These conditions affect phytolith preservation by enhancing dissolution. However, mechanical damage or dissolution in the study sites is likely to be low due to the acidic nature and relative stability of the peaty soils. Therefore, the soil phytolith record is inevitably diluted by lack of production in the majority of herbs, ferns and shrubs, preservation potential and in certain sedimentary settings, phytolith transport. An additional complication arises with the difficulty of differentiating taxonomically characteristic morphotypes in the dispersed soil assemblages, even at Family level. For example, conical forms reflect the presence of at least two members of the Cyperaceae, and rondel forms are consistently present in abundance throughout the Poaceae (mainly *Poa* spp.). Many conservative phytoliths, e.g. elongate morphotypes, are produced by two or more species, sometimes from different Families or even broader taxonomic divisions. Individual species can only easily be

defined when there are no conservative forms present, e.g. in this study at COL1.

The above complications in the interpretation of dispersed soil phytolith assemblages, here including 17 conservative morphotypes, allow only the reconstruction of the overlying source vegetation to a broad grassland community level for all sites. Overall, there is disagreement between the soil phytolith assemblage and the character of the overlying source vegetation canopy, with both the vegetation phytolith production and soil phytolith content reflecting the dominance of grass phytolith production and preservation.

A pilot study on soil surface samples from Campbell Island also recorded the dominance of grass phytoliths and, although conical forms were rare in the soil samples during the current study, two samples in this previous study contained significant abundances, suggesting that soil phytolith assemblages are indeed localized with minimal homogenization of assemblages over large areas (Thorn 2004). The grassland interpretation for the quadrats in this study is only really applicable to that at CLS with a 70% grass canopy cover. This overall result reflects a previous observation during a similar study at Tongariro National Park, central North Island, New Zealand, that the presence of grass in the source vegetation is likely to be over-represented in general, and the proportion of grasses in the source vegetation association cannot be estimated from the dispersed phytolith assemblage alone (Thorn 2006).

The nature of the pollen record on Campbell Island has been investigated through studies on the modern pollen rain (McGlone & Meurk 2000) and Holocene peat profiles (McGlone *et al.* 1997), but little is currently known about the pre-Quaternary terrestrial palynology record. The terrestrial palynology and phytolith content of Neogene samples collected during this fieldwork will be discussed in a future publication. Similarly, the pollen rain, in agreement with this phytolith study, is dominated by Poaceae, but, in contrast to this phytolith study, was found to correspond approximately with canopy cover interpreted as a result of restricted dispersal and low canopies in the central part of the island (McGlone & Meurk 2000). The diversity and abundance of Poaceae phytolith morphotypes observed during this and studies by other authors suggests that, with further detailed taxonomic work on modern grasses involving cluster analysis in the future, differentiation to generic or even species level may be possible (e.g. Marx *et al.* 2004). Therefore, dispersed phytoliths in the sedimentary record, despite the apparent poor reflection of overall source vegetation character as shown in this study, have the potential to provide a significant contribution to the interpretation of past grass-rich floras, particularly as Poaceae pollen is conservative in morphology. This study has shown that previous terrestrial palynology work provides the most useful reconstruction of source vegetation compared with that of the dispersed soil phytolith record (McGlone *et al.* 1997, McGlone & Meurk 2000). However, in sedimentary situations where organics are absent, such a phytolith record would provide presence/absence data on plant types, at least to Family level when no other palaeobotanical information was available.

Conclusions

At four quadrats on sub-Antarctic Campbell Island phytoliths produced by the extant vegetation have been compared with the dispersed soil assemblages accumulating directly beneath. The results indicate that the soil record is dominantly composed of grass phytoliths and provides a poor representation of the overlying source vegetation. The over-representation of grass phytoliths implies ubiquitous grassland at all of the study sites suggesting the apparent absence of significant plant types, e.g. ferns and shubs, in the canopy. The abundance and diversity of phytolith production from grass species is high, even if the canopy cover of grass is low. Taphonomic problems have been highlighted, which result in the loss and blurring of ecological information through time: differential production by different plant species (in phytolith abundance and diversity of form, as well as presence or absence of any biosilica), the occurrence of conservative morphologies produced by several plant species, and the apparently biased preservation of 'robust' solid, idioblastic forms in preference to the fragile, thinner-walled and more planar morphotypes. However, taking these issues into account, the dispersed phytolith record can still confirm the presence of grasses (and to a lesser extent sedges and rushes). However, overall, a lack of phytolith production in many key species of the modern flora within these quadrats (e.g. shrubs, ferns and macrophyllous forbs) prevent detailed reconstructions of the source vegetation composition as is possible from the terrestrial palynology record.

The derivation of detailed source vegetation composition from dispersed fossil phytolith assemblages has not been possible at these Campbell Island localities. The implication is that similar difficulties are likely in any such study of dispersed phytoliths from assemblages in the fossil record. Such vegetation reconstructions should be treated with due caution and with reference to the particular taphonomic issues that phytoliths present. However, the dominance of grass phytoliths in the soil assemblages at Campbell Island, and their varied and often robust morphology emphasises the potential importance of phytoliths as evidence of grasses in the geological past. Future statistical analyses on grass phytolith taxonomy will also refine their modern analogue potential in Cenozoic palaeoecological studies of high latitude floras. Grass macrofossils are rare, and grass pollen is of conservative morphology, therefore attention to the fossil record of grass

phytoliths can contribute significantly to our understanding of past grassland ecosystems.

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References

Allen, R.B. 1992. RECCE - an inventory method for describing New Zealand vegetation: a field manual. *Forest Research Institute Bulletin*, No. 176, 25 pp.

Ashworth, A.C. & Cantrill, D.J. 2004. Neogene vegetation of the Meyer Desert Formation (Sirius Group) Transantarctic Mountains, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **213**, 65–82.

Askin, R.A. 1992. Late Cretaceous–Early Tertiary Antarctic outcrop evidence for past vegetation and climate. *Antarctic Research Series*, **56**, 61–75.

Askin, R.A. 2000. Spores and pollen from the McMurdo Sound Erratics, Antarctica. *Antarctic Research Series*, **76**, 161–181.

Beggs, J.M. 1978. Geology of the metamorphic basement and Late Cretaceous to Oligocene sedimentary sequence of Campbell Island, southwest Pacific Ocean. *Journal of the Royal Society of New Zealand*, **8**, 161–177.

Bestic, K.L., Duncan, R.P., McGlone, M.S., Wilmshurst, J.M. & Meurk, C.D. 2005. Population age structure and recent *Dracophyllum* spread on subantarctic Campbell Island. *New Zealand Journal of Ecology*, **29**, 291–297.

Birkenmajer, K. 1997. Tertiary glacial/interglacial palaeoenvironments and sea-level changes, King George Island, West Antarctica: an overview. *Bulletin of the Polish Academy of Sciences - Earth Sciences*, **44**, 157–181.

Birkenmajer, K. & Zastawniak, E. 1989. Late Cretaceous–early Tertiary floras of King George Island, West Antarctica: their stratigraphic distribution and palaeoclimatic significance. *In* Crame, J.A., *ed*. *Origins and evolution of the Antarctic biota*. *Geological Society of London Special Publication*, **147**, 227–240.

Campbell, I.B. 1980. Soil pattern of Campbell Island. *New Zealand Journal of Science*, **24**, 111–135.

Carnelli, A.L., Theurillat, J.-P. & Madella, M. 2004. Phytolith types and type-frequencies in subalpine-alpine plant species of the European Alps. *Review of Palaeobotany and Palynology*, **129**, 39–65.

Cookson, I.C. 1947. Plant microfossils from the lignites of Kerguelen Archipelago. *British, Australian and New Zealand Antarctic Research Expedition, 1929–1931, Reports Series A*, **2**(8), 127–142.

De Lisle, J.F. 1965. The climate of the Auckland Islands, Campbell Island and Macquarie Island. *Proceedings of the New Zealand Ecological Society*, **12**, 37–44.

Edwards, W.N. 1921. Fossil coniferous wood from Kerguelen Island. *Annals of Botany*, **35**, 609–617.

Francis, J.E. 1999. Evidence from fossil plants for Antarctic palaeoclimates over the past 100 million years. *Terra Antartica Reports*, **3**, 43–52.

Horrocks, M. & Ogden, J. 2000. Evidence for Late-glacial and Holocene tree-line fluctuations from pollen diagrams from the Subalpine zone on Mt Hauhungatahi, Tongariro National Park, New Zealand. *The Holocene*, **10**, 61–73.

MacPhail, M.K. & Cantrill, D.J. 2006. Age and implications of the Forest Bed, Falkland Islands, southwest Atlantic Ocean: evidence from fossil pollen and spores. *Palaeogeography, Palaeoecology, Palaeoclimatology*, **240**, 602–629.

Madella, M., Alexandre, A. & Ball, T. 2005. International code for phytolith nomenclature 1.0. *Annals of Botany*, **96**, 253–260.

Marx, R., Lee, D.E., Lloyd, K.M. & Lee, W.G. 2004. Phytolith morphology and biogenic silica concentrations and abundance in leaves of *Chionochloa* (Danthonieae) and *Festuca* (Poeae) in New Zealand. *New Zealand Journal of Botany*, **42**, 677–691.

McGlone, M.S. 2002. The late Quaternary peat, vegetation and climate history of the Southern Oceanic Islands of New Zealand. *Quaternary Science Reviews*, **21**, 683–707.

McGlone, M.S. & Meurk, C.D. 2000. Modern pollen rain, subantarctic Campbell Island, New Zealand. *New Zealand Journal of Ecology*, **24**, 181–194.

McGlone, M.S., Wardle, P. & Meurk, C.D. 1997. Late-glacial and Holocene vegetation and environment of Campbell Island, far southern New Zealand. *The Holocene*, **7**, 1–12.

Meurk, C.D. & Given, D.R. 1990. *Vegetation map of Campbell Island, 1:25000*. Christchurch, New Zealand: DSIR Land Resources.

Meurk, C.D., Foggo, N.M. & Bastow, W.J. 1994a. The vegetation of subantarctic Campbell Island. *New Zealand Journal of Ecology*, **18**, 123–168.

Meurk, C.D., Foggo, M.N., Thomson, B.M., Bathurst, E.T.J. & Crompton, M.B. 1994b. Ion-rich precipitation and vegetation pattern on subantarctic Campbell Island. *Arctic and Alpine Research*, **26**, 281–289.

Michaux, B. & Leschen, R.A.B. 2005. East meets west: biogeology of the Campbell Plateau. *Biological Journal of the Linnean Society*, **86**, 95–115.

New Zealand Meteorological Service. 1973. Summaries of observations to 1970. *New Zealand Meteorological Service Miscellaneous Publication*, No. 143, 77 pp.

Oliver, R.L., Finlay, H.J. & Fleming, C.A. 1950. The geology of Campbell Island. *Cape Expedition Series Bulletin*, **3**, 62 pp.

Pearsall, D.M. 2000. *Paleoethnobotany - a handbook of procedures*. San Diego, CA: Academic Press, 700 pp.

Piperno, D.R. & Pearsall, D.M. 1998. The silica bodies of tropical American grasses: morphology, taxonomy, and implications for grass systematics and fossil phytolith identification. *Smithsonian Contributions to Botany*, **85**, 1–40.

Prebble, J.G., Raine, J.I., Barrett, P.J. & Hannah, M.J. 2006. Vegetation and climate from two Oligocene glacioeustatic sedimentary cycles (31 and 24 Ma) cored by the Cape Roberts Drilling Project, Victoria Land Basin, Antarctica. *Palaeogeography Palaeoclimatology Palaeoecology*, **231**, 41–57.

Raine, J.I. & Askin, R.A. 2001. Vegetation history and climate from the Early Oligocene to Early Miocene, Cape Roberts, Ross Sea region, Antarctica. *Terra Antartica*, **5**, 539–548.

Rogers, G. & Walker, S. 2005. Evolution of the New Zealand vascular flora: regional and provincial patterns of richness, radiation and endemism. *New Zealand Journal of Botany*, **43**, 381–414.

Rovner, I. 1971. Potential of opal phytoliths for use in paleoecological reconstruction. *Quaternary Research*, **1**, 343–359.

THORN, V.C. 2001. Oligocene and early Miocene phytoliths from CRP-2/2A & CRP-3, Victoria Land Basin, Antarctica. *Terra Antartica*, **8**, 407–422.

THORN, V.C. 2004. Phytoliths from subantarctic Campbell Island: plant production & soil surface spectra. *Review of Palaeobotany and Palynology*, **132**, 37–59.

THORN, V.C. 2006. Vegetation reconstruction from soil phytoliths, Tongariro National Park, New Zealand. *New Zealand Journal of Botany*, **44**, 397–413.

TRUSWELL, E.M., QUILTY, P.G., MCMINN, A., MACPHAIL, M.K. & WHELLER, G.E. 2005. Late Miocene vegetation and palaeoenvironments of the Drygalski Formation, Heard Island, Indian Ocean: evidence from palynology. *Antarctic Science*, **17**, 427–442.

TURNBULL, I.M., ADAMS, C.J., BEAVAN, J., FORSYTH, P.J., GARNOCK-JONES, P.J., HAYWARD, B.W., RAINE, J.I., THORN, V.C. & VAJDA, V. 2004. Report on visit to subantarctic islands, March 2004. *Institute of Geological and Nuclear Sciences Limited Science Report*, **2004/09**, 34 pp.