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The southernmost worm, *Scottnema lindsayae* (Nematoda): diversity, dispersal and ecological stability

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Abstract The nematode worm *Scottnema lindsayae* (Cephalobidae) was found near the base of the Beardmore Glacier in the Transantarctic Mountains 83.48°S, over 5° further south than previously recorded. Identification was confirmed using morphological analyses of males, females and juvenile stages, and by DNA sequencing of the ITS1 region of the ribosomal RNA tandem repeat unit. These data revealed no discernable morphological or ITS rDNA sequence variation between the extreme southern population of *S. lindsayae* and disparate populations from the McMurdo Dry Valleys in south Victoria Land (77–78°S). Based on these results, we suggest that broadcast dispersal, with accompanying high rates of gene flow, establish the extreme southern distribution of the phylum Nematoda. High abundance, low rates of diversification and lack of an apparent biogeographic structure across latitudinal and environmental gradients implies that their presence in simple Antarctic soil ecosystems is stable, so long as physical and biological controls on their distributions remain within viable parameters. Recent evidence that *S. lindsayae* populations are in decline suggests that their high dispersal rates are insufficient to buffer current, unfavorable environmental changes and may foreshadow longer-term ecosystem disruption.

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Introduction

Scottnema lindsayae Timm 1971 is the most abundant and often the single metazoan representative in the southern Victoria Land soils (Freckman and Virginia 1998; Powers et al. 1998; Treonis et al. 1999; Virginia and Wall 1999). This endemic species was first described and ranked by Timm (1971) from a location near the La Croix Glacier in Taylor Valley, South Victoria Land and is the sole member of a monotypic genus within the Cephalobidae. It has been found in Northern Victoria Land near Cape Hallett (Barrett et al. 2006) and reported from the opposite side of the continent, in East Antarctica, at the Syowa station on East Ongul Island (Mouratov et al. 2001; Shishida and Ohyama 1986) and near Admiralty Bay on the Antarctic Peninsula (Mouratov et al. 2001) (Fig. 1).
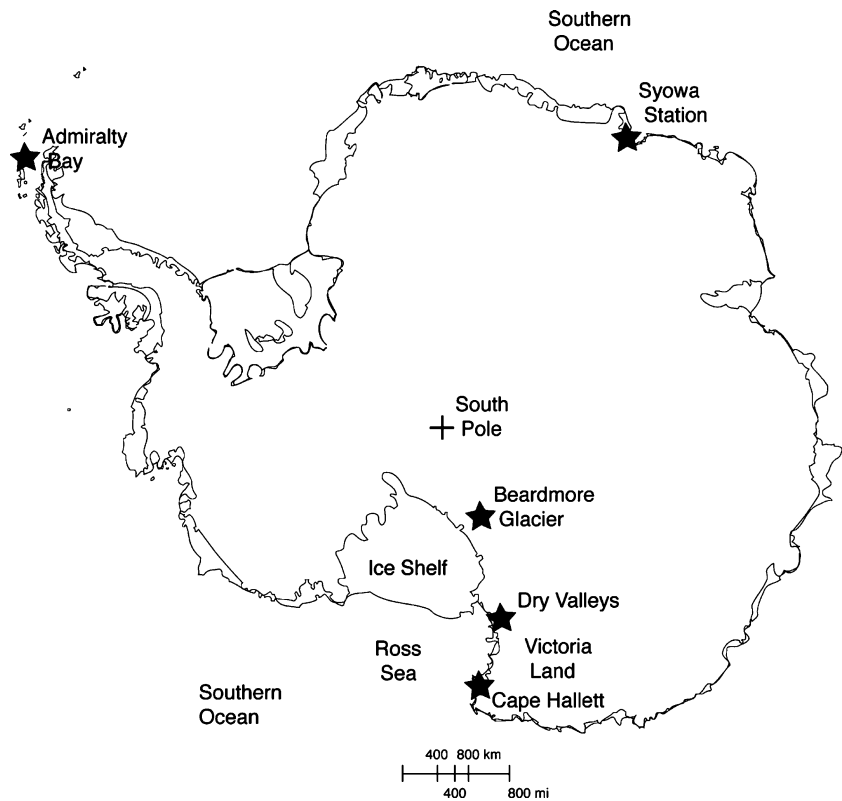
Morphologically *S. lindsayae* is most similar to cephalob species of the genus *Acrobeles*. Distinguishing features of *S. lindsayae* are extended cephalic probolae and five fine, triangular projections from between the cephalic probolae (dorsal and subventral). This microbivore (feeding on yeast and bacteria) has a very long lifecycle (218 days at 10°C), low fecundity and a relatively long embryonic and post-embryonic development time compared to other cephalob genera, such as *Acrobeles* (Barrett et al. 2004; Moorhead et al. 2002; Overhoff et al. 1993; Porazinska et al. 2002; Porazinska and Wall 2002). Thus, its life cycle more closely resembles a "K-selected" reproductive strategy (Johnson et al. 1974). Three other nematode species occur in Southern Victoria Land and are not closely related to *S. lindsayae*—all are members of different families (Monhysteridae, Dorylaimidae, Plectidae).

Much of the work on the distribution of *S. lindsayae* at local scales has been from the McMurdo Dry Valleys, where mean annual air temperatures range from −16 to −21°C, and annual precipitation is less than 10 cm (Clow et al. 1987; Doran et al. 2002a). About 60–70% of the soils across this landscape are devoid of metazoans (Freckman and Virginia 1998).

Scottnema lindsayae dominates the soil invertebrate community in abundance and biomass across the landscape compared to the three other nematode species found in the Dry Valley region. It occurs where average

soil temperatures (0–10 cm depth) range from −22.8 to 23.3°C, with soil surface temperatures about 1°C higher than 5–10 cm below the surface (Moorhead et al. 2002; Treonis et al. 2000). Its distribution is patchy across Taylor Valley and elsewhere, but soil habitats for this species are characterized as having lower moisture (soil moistures from 0.9–2.9%), higher pH, higher EC and higher inorganic C (Freckman and Virginia 1997) compared to habitats of the other three species (Adams et al. 2006; Barrett et al. 2004, 2005; Courtright et al. 2001; Porazinska et al. 2002).

Some 700 km further south from the McMurdo region and 500 km NNE of the South Pole in the vicinities of the Beardmore and Shackleton Glaciers are some of the southernmost exposed soils on earth. Visits to this region by the New Zealand Alpine Club in 1959–1960, and by Wise in 1964–1965, had previously reported the southernmost occurrences for several taxa including mites, springtails (Collembola), rotifers, lichens, moss and algae (Tyndale-Biscoe 1960; Wise and Shoup 1971). The predominant rock type near the Beardmore Glacier are "Ross Supergroup" metasediments originally of the graywacke type with crosscutting by granodiorites and quartz-diorite (Oliver 1972). Smaller rock sediments in the Beardmore area are predominantly gray to dark gray and can retain considerable heat during favorable climatic conditions in the limited summer months with ground surface temperatures

approaching 20°C (I. Hogg, unpublishd data). Fine-grained material (<125 μm) is often found beneath these smaller sediments. As in the Dry Valleys, liquid water occurs from melt streams at the interface between snow packs and rocky outcrops (Gooseff et al. 2003).

A putative adaptive response to survival in a cold, dry climate, *S. lindsayae* are anhydrobiotic, wherein they coil, cease observable metabolic activity (Treonis et al. 2000) and like other nematodes may lose up to 99% of their water content (Crowe and Madin 1975; Demeure et al. 1979). This desiccated condition facilitates wind dispersal (Nkem et al. 2006) within Taylor Valley and suggests wind could be a primary mechanism for long distance dispersal.

Previous work on Antarctic terrestrial invertebrates (e.g., Collembola) has shown that large-scale ice structures such as glaciers as well as the Ross Sea are likely to be appreciable barriers to dispersal/gene flow between the Beardmore Glacier region and Victoria Land (Stevens and Hogg 2003). In contrast, levels of heterozygosity within and among populations of *S. lindsayae* collected from different valleys in Southern Victoria Land show moderately high levels of gene flow and no evidence of historical, long-term barriers to dispersal (Courtright et al. 2000). However, analysis of populations from more distant, isolated regions of Antarctica would allow for a more rigorous examination of the genetic structure of the species across a broader geographic scale, and allow testing of the generality of large-scale ice structures (e.g., glaciers) as barriers to gene flow for terrestrial invertebrates.

Elevated rates of dispersal by eukaryotes smaller than 2 mm have been implicated in ecosystem stability, the idea being that forces that alter species composition are countered by high rates of immigration (Finlay 2002; Finlay and Fenchel 2004). However, high species diversity and functional redundancy complicate the task of identifying changes in ecosystem functioning that are due to the presence or absence of individual species. As the Antarctic Dry Valley soil ecosystem has shown a marked decrease in the abundance of *S. lindsayae* (Doran et al. 2002b), its dominant soil metazoan, the resilience and stability of this ecosystem will be dictated by general patterns of dispersal and immigration. Thus, the Dry Valley soil ecosystem provides an ideal setting to investigate the relationship between dispersal and ecosystem stability because a single metazoan species (*S. lindsayae*) plays a key role in ecosystem functioning (carbon cycling; Barrett et al., unpublished data). As we show, potentially high rates of dispersal are apparently insufficient to buffer population declines of *S. lindsayae* attributed to recent

(decadal) environmental changes (Doran et al. 2002b), implying short-term ecological functional instability in response to environmental change.

Materials and methods

The sampling sites were located on Mt. Harcourt near the base of the Beardmore Glacier (Fig. 1). Soil samples were collected from underneath small flat rocks (<10 cm diameter) on an exposed ridge (S83°48.21′, E172°15.39, 800 m elev.). Two samples to 8 cm were taken within a few meters of each other, one moist due to its proximity to a melting snow patch and one drier sample. Quantitative soil moisture and characterization assays were not conducted in order that all of the sampled soil could be used in the nematode extraction process. Total fresh weight of soil from which nematodes were extracted was 112 and 94 g respectively. Nematodes were extracted from soil using wet sieving methods followed by sugar density gradient centrifugation modified for cold-adapted nematodes, including chilled extraction solutions (Freckman and Virginia 1993, 1997; Powers et al. 1998). Extracted nematodes were visualized in brightfield with an Olympus CK40 inverted compound light microscope. The extraction process was non-concomitant with other soils, and care was taken to prevent the contamination of soils and extraction equipment. All soil processing equipment was cleaned thoroughly prior to extraction, and transfer of soils from field sample bags to extraction containers was carried out under a sterile laminar flow hood. Live nematodes were preserved in either 95% ETOH or 5% hot formalin solution for subsequent DNA and morphological analyses, respectively, and for voucher specimen preparation.

DNA was extracted from individual preserved specimens using DNeasy animal tissue extraction kits (Qiagen Inc., Valencia CA). Ribosomal DNA of the internally transcribed spacer 1 region was PCR amplified using the 18S primer designed by Vrain et al. (1992) which binds in the posterior 3′ portion of the 18s small ribosomal subunit, and the reverse primer of Cherry et al. (1997), which binds in the 5′ end of the 5.8s subunit region. Polymerase chain reactions were carried out in 25 μl volumes. PCR mix was added to each tube: 2.5 μl 10× PCR buffer, 1.5 μl $MgCl_2$, 1 μl dNTP mixture (10 mM each), 1 μl of 10 pM forward primer, 1 μl of 10 pM reverse primer, 0.25 μl of *Taq* polymerase (Continental Laboratory Products, Sand Diego, CA,), 19.55 μl of distilled water and 5 μl of DNA (not quantified, but approximately 10 ng/μl). All PCR reactions were run in a PTC-100 Thermocycler

(MJ Research, Inc., Waltham, MA, USA) with the following cycling profile: 1 cycle of 94°C for 7 min followed by 35 cycles of 94°C for 1 min, 50°C for 1 min, 72°C for 1 min. The last step was 72°C for 10 min. PCR products were purified using QIAquick PCR purification kit (Qiagen Inc.) and sequenced in both directions at the University of Florida ICBR sequencing core facility and the BYU DNA Sequencing Center on Perkin Elmer/Applied Biosystems automated DNA sequencers. DNA sequences of nematodes sampled from the Beardmore glacier were aligned to sequences from other samples of *S. lindsayae* collected from other areas of Antarctica, including multiple individuals from several locations in the McMurdo Dry Valleys: three populations from the Lake Fryxell basin, two populations from Garwood Valley (49 km south of Taylor Valley), one population from Mt. Falconer and three populations from the Lake Hoare basin (Table 1). The ITS rDNA sequence of *S. lindsayae* from 83.48° South was deposited in GenBank (Accession #AY626779). Voucher specimens of representative males, females and juveniles from the same sample have been deposited in the University of California-Davis Nematode Collection (UCDNC #3240).

Results and discussion

The sample taken from the site moistened by glacial meltwater contained *S. lindsayae* individuals as follows: 33 live and 4 dead males, 51 live and 31 dead females and 89 live and 43 dead juveniles. It also contained two individual rotifers. The second sample taken from a drier area was devoid of nematodes but contained 2 individual tardigrades. Identification of the rotifers and tardigrades in the samples is ongoing. Although the Beardmore region and the rest of the continental Antarctic interior has probably been devoid of most metazoan life since the early to mid Neogene, at least 3 Ma; (Ashworth and Kuschel 2003; Askin 1992; Fleming and Barron 1996; Marchant et al. 2002), our findings establish the southernmost indigenous, extant distribution of the Phylum Nematoda.

The 505 bp ITS rDNA sequence of *S. lindsayae* from latitude 83.48°S was identical to all of the sequences of individuals representing populations from the McMurdo Dry Valleys area. Similarly, we detected no conspicuous morphological deviations from the original (Timm 1971) and detailed (Vinciguerra 1994) descriptions of *S. lindsayae*.

The abundance of live nematodes (1.71 g^{-1} fresh soil) representing juvenile through adult life stages suggests that they were extracted from a healthy population and do not represent anhydrobiotic immigrants that were revived upon soil processing. However, the lack of variation at the ITS locus indicates low levels of population structure (Adams 1998; Adams et al. 1998; Cherry et al. 1997; Nguyen et al. 2001; Powers et al. 1997) despite the vast geographic distance between the Beardmore and Southern Victoria Land populations (approximately 713 km). For example, numerous studies have utilized this marker to investigate population structure, and particularly species boundaries, where it typically performs well at revealing meta-population history, presence or absence of gene flow and permanent lineage-splitting events (Adams 2001; Nadler et al. 2000). Our results are consistent with previous surveys of *S. lindsayae* using mtDNA and 28s rDNA loci (Courtright et al. 2000), which also revealed limited genetic variability and structure among McMurdo Dry Valley populations. Larger numbers of individuals from several populations sampled from the Transantarctic Mountains area, and use of more variable genetic loci, will be instrumental in exploring the existence of fine-scale variability and dispersal patterns within and among populations.

Table 1 Location of sampled populations of *Scottnema lindsayae*

Location	Population name	Latitude (south)	Longitude (east)
Beardmore Glacier	K122A	83° 48.210′	172° 15.390′
Lake Brownsworth, Lower Wright Valley	Brownsworth Met Station 4	77° 26.185′	162° 42.301′
Lake Colleen, Garwood Valley	K052 Block 2	78° 01.489′	163° 52.381′
Lake Hoare, Taylor Valley	LH near A2 Eudory 4	77° 37.932′	162° 52.646′
Lake Fryxell, Taylor Valley	F6 CO2 8	77° 36.476′	163° 15.077′
Lake Hoare, Taylor Valley	LH Lake to soil A3	77° 37.940′	162° 53.051′
Lake Hoare, Taylor Valley	LH Lake to soil A4	77° 37.940′	162° 53.051′
Lake Fryxell, Taylor Valley	F6 Bulk 1	77° 36.483′	163° 14.891′
Lake Hoare, Taylor Valley	LH near A2 Eudory 3	77° 37.932′	162° 52.646′
Mt Falconer, Taylor Valley	Mt Faulk A2	77° 34.303′	163° 09.660′
Lake Colleen, Garwood Valley	K052 Block 4	78° 01.505′	163° 52.424′

There have been few comparisons of the species of soil invertebrates found in the McMurdo Dry Valleys to the Beardmore Glacier area. Phylogeographic and gene flow analyses of the springtail *Gomphiocephalus hodgsoni* reveal the McMurdo Sound (which lies between the Beardmore Glacier and Southern Victoria Land) to have been an effective geographic barrier to its dispersal (Stevens and Hogg 2003). However, a similar phylogeographic pattern and population structure does not exist for *S. lindsayae* in the McMurdo Dry Valleys (Courtright et al. 2000). The lack of ITS1 sequence variation among populations of *S. lindsayae* separated by over 700 km and 5° in latitude preclude the notion that the McMurdo Sound effectively retards gene flow or significantly structures disparate populations of *S. lindsayae*, and is consistent with broadcast aeolian transport (Nkem et al. 2006). Katabatics are the predominant surface winds throughout continental Antarctica, which originate high on Antarctic Plateau and move with increasing speed and temperature towards the continental margins (Parish and Bromwich 1987). The warm air then rises and moves toward the pole to replace the colder, vacating surface air (King and Turner 1997). The strength and cyclical direction of Antarctic winds could provide consistent aeolian transport for *S. lindsayae* across virtually all of Antarctica.

Previous work suggests that most organisms smaller than 2 mm have global distributions and persist wherever their required habitats are realized (Finlay 2002; Finlay and Fenchel 2004). Such distributions and persistence are thought to be a consequence of ubiquitous dispersal driven by huge population sizes, and the consequently low probability of local extinction (Finlay 2002; Finlay and Fenchel 2004). *S. lindsayae* is endemic to Antarctica, yet distributed broadly across the continent where viable soil parameters exist and plays a much greater than expected role in ecosystem functioning, particularly carbon efflux; (Barrett et al., forthcoming). However, recent declines in population size attributed to climate change (Doran et al. 2002b) indicate high sensitivity and low stability of the soil ecosystem in response to environmental change, and may portend profound changes in ecosystem functioning. The widespread distribution and potentially high dispersal potential of *S. lindsayae* inferred in the present study indicate that failure to counter the observed decline in population sizes in the Antarctic Dry Valley soil ecosystem is due to an altered physicochemical or biological environment which obviates immigration. Alternatively, life history attributes and physiological constraints may account for the regional decrease in population size in Antarctic Dry Valley soils. In the case of *S. lindsayae*, a K-selective reproductive strategy will result in higher variability of population size, but is also predicted to confer stability across broader (regional) geographic scales (Pribil and Houlahan 2003).

The continuing decline of *S. lindsayae* population sizes (Doran et al. 2002b) in the Antarctic Dry Valleys is linear (Barrett et al., unpublished data), and as yet shows no perceptible response via recruitment or fecundity to the present climate and ecosystem changes (1986 to the present) despite immigration via wind dispersal (Nkem et al. 2006). Thus, the historically high abundances and rates of dispersal of *S. lindsayae* are not sufficient to mount an immediate response to environmental perturbation. Given the prominent role of *S. lindsayae* in mediating Antarctic Dry Valley soil ecosystem functioning, we predict that environmental changes responsible for decreases in population size and distribution will have an immediate and long-term impact on the biodiversity and productivity of these soils.

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