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# Colonization of maritime glacier ice by bdelloid Rotifera ☆

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ABSTRACT

Very few animal taxa are known to reside permanently in glacier ice/snow. Here we report the widespread colonization of Icelandic glaciers and ice fields by species of bdelloid Rotifera. Specimens were collected within the accumulation zones of Langjökull and Vatnajökull ice caps, among the largest European ice masses. Rotifers reached densities up to ~100 individuals per liter-equivalent of glacier ice/snow, and were freeze-tolerant. Phylogenetic analyses indicate that glacier rotifers are polyphyletic, with independent ancestries occurring within the Pleistocene. Collectively, these data identify a previously undescribed environmental niche for bdelloid rotifers and suggest their presence in comparable habitats worldwide.



## 1. Introduction

The permanently cold and harsh conditions of glacial environments present formidable challenges for animal life, requiring enzymatic (Marshall, 1997; Smalas et al., 2000; D'Amico et al., 2002; Siddiqui and Cavicchioli, 2006; Struvay and Feller, 2012), metabolic (Pörtner et al., 1998; Johnston et al., 1998; Peck, 2002; White et al., 2012), bioenergetic (Luyet and Gehenio, 1940; Napolitano and Shain, 2004) and membrane compositional (Russell, 1997; Kahlke and Thorvaldsen, 2012) adaptations across multiple cell types. Consequently, few animal taxa have taken the evolutionary step to reside permanently in glacier ice/snow, or firn (i.e., snow transitioning into ice), a habitat fundamentally different from more commonly studied cryoconite holes (i.e., aquatic microenvironments formed by substrate-induced melting on glacier surfaces) (Zawierucha et al., 2015). These include glacier ice worms (Annelida: Enchytraeidae) of North America and Tibet (Emery, 1898; Tynen, 1970; Liang et al., 1979) and a few arthropod taxa [e.g., Collembola (Fjellberg, 2010) and a Himalayan Chironomidae (Kohshima, 1984)]. Of these, only ice worms reside "in" glacier ice/firn (i.e., the thin water layer occurring between ice crystal boundaries on maritime glaciers, which maintain core ice temperatures of 0 °C over geological time), as opposed to residing "on" the glacial surface (e.g., arthropod taxa). Note that water-filled "vein" networks occurring in polar and continental glaciers (i.e., where ice temperatures fall well below 0 °C and display ice densities up to 900 kg/m$^3$) comprise a different habitat wherein vein widths of only a few microns permit prokaryotic life but exclude larger eukaryotes (Price, 2000; Mader et al., 2006); by contrast, spaces between ice granules are >10 μm within the upper few meters of maritime glacier ice/firn, where ice densities reach up to 500 kg/m$^3$ (Patterson, 1994; Nye, 1999). And while all known glacier invertebrates are comparatively small (i.e., less than a few milligrams), they maintain sophisticated animal behaviors and processes (e.g., muscle-based movement, neuronal communication, etc.) in this extreme environment.

Within the animal phylum Rotifera, the class Bdelloidae is known for its unusual biological properties. For example, this animal group is thought to have persisted as an asexual lineage for at least 40 million years with no male representatives (Poinar and Ricci, 1992; Waggoner and Poinar, 1993; Judson and Normark, 1996; Fontaneto et al., 2007; Tang et al., 2014), though recent evidence suggests some atypical allele sharing (Signorovitch et al., 2015). Some species are known to acquire genetic diversity by horizontal gene transfer across domains of life (Gladyshev et al., 2008; Boschetti et al., 2012; Flot et al., 2013), others undergo

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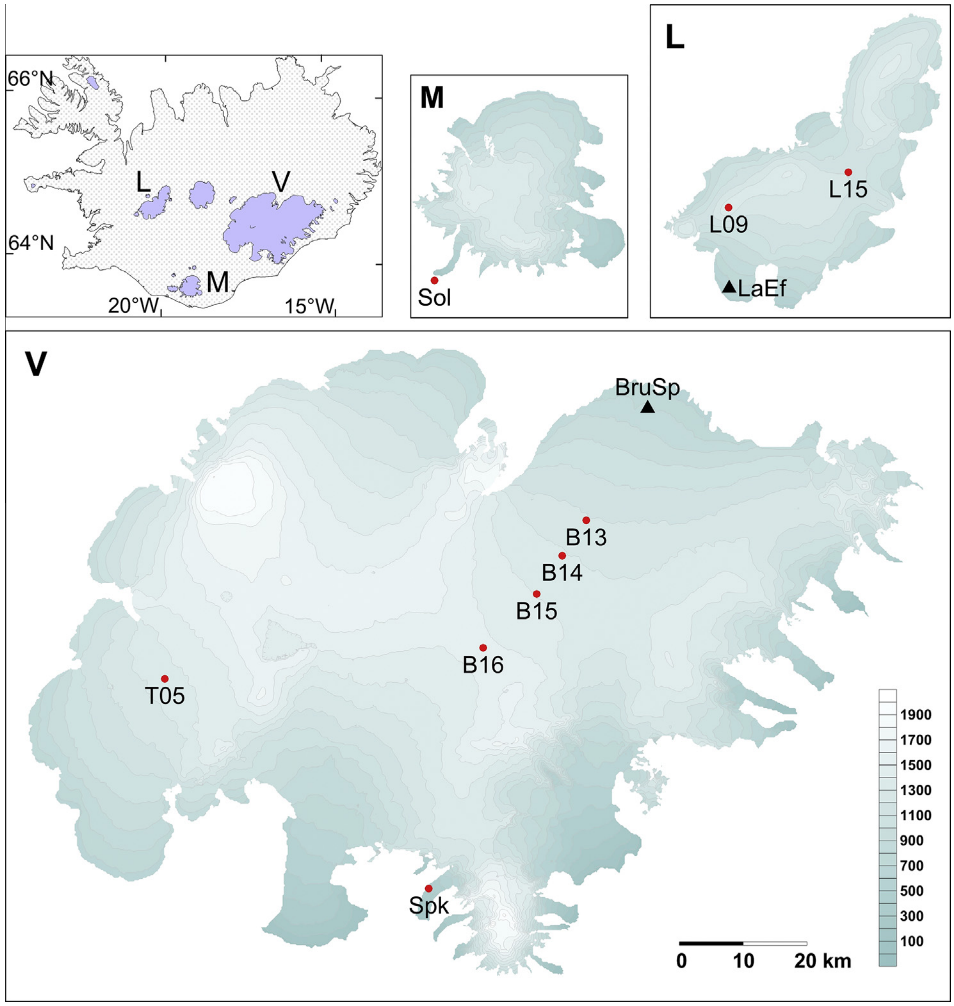


**Fig. 1.** Geographic locations of Icelandic glaciers and field sites. The upper left panel identifies major ice fields in Iceland: L – Langjökull; M – Mýrdalsjökull; V – Vatnajökull. Remaining panels are scaled representations of each ice field with indicated field sites (*cf* Table 1). Solid triangles identify LaEf (585 m) and BruSp (805 m) weather stations. Elevation is in meters above sea level.

**Table 1**
Glacier field sites and corresponding data for collected rotifer specimens.

| Field site | Glacier/ice field | Geographic coordinates | Elevation (m) | Collection date/2014 | Specimens (per liter) | Individuals processed | Species/haplotypes |
|---|---|---|---|---|---|---|---|
| B13 | Vatnajökull | N64° 34.518 W16° 19.732 | 1216 | 10/12/14 | ~10 | 2 | 1/1 |
| B14 | Vatnajökull | N64° 31.639 W16° 24.705 | 1315 | 10/12/14 | <5 | 3 | 2/3 |
| B15 | Vatnajökull | N64° 28.487 W16° 30.016 | 1399 | 10/12/14 | <5 | 2 | 1/1 |
| B16 | Vatnajökull | N64° 21.125 W16° 40.853 | 1526 | 10/16/14 | <5 | 0 | –/– |
| L09 | Langjökull | N64° 37.647 W20° 27.477 | 1371 | 10/23/14 | ~50 | 3 | 2/3 |
| L15 | Langjökull | N64° 40.819 W20° 4.093 | 1175 | 10/23/14 | ~100 | 6 | 1/6 |
| Sol | Solheimajökull | N63° 31.611 W19° 22.032 | 110 | 8/24/14 | 0 | 0 | –/– |
| Spk | Skaftafellsjökull | N64° 03.000 W16° 53.000 | 400 | 8/23/14 | 0 | 0 | –/– |
| T05 | Tungnaarjökull | N64° 22.287 W17° 43.012 | 1344 | 10/11/14 | ~10 | 2 | 2/2 |

anhydrobiosis to survive desiccation or to escape fungal parasites (Ricci and Covino, 2005; Wilson and Sherman, 2010), and others resist extreme levels of ionizing radiation (Gladyshev and Meselson, 2008). Collectively, more than 400 species of bdelloid rotifers have been described, and are known worldwide as a major component of zooplankton in freshwater and terrestrial (moist soil, moss) habitats, with a few described marine species (Fontaneto et al., 2006; Segers, 2007; Velasco-Castrillón et al., 2014).

We report here that two distinct bdelloid rotifer species have independently colonized the two largest ice caps in Iceland, the