SHORT PAPER

Fossil Rotifers and the Early Colonization of an Antarctic Lake

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Early Holocene sediments from a continental Antarctic lake (Ace Lake, Vestfold Hills, East Antarctica) contained abundant fossil rotifers of the genus *Notholca*. The fossil is similar to specimens of *Notholca* sp. present in modern-day Ace Lake and other fresh and brackish lakes of the Vestfold Hills. Cyanobacteria and protists (chrysophyte cysts, dinoflagellate cysts, and rhizopod tests) were also recovered from the core samples. These sediments were deposited early in the freshwater phase of Ace Lake, soon after deglaciation of the area. The occurrence of this trophically diverse assemblage of organisms at an early stage in the evolution of the lake suggests either that they were part of an endemic Antarctic flora and fauna which pre-dated the last glacial maximum and survived in glacial refugia or that efficient intercontinental dispersal had occurred. © 2001 University of Washington.

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The abundance and diversity of micro-floral and micro-faunal remains in lake sediments provide information about the physical and chemical development of the lakes and changes in the communities inhabiting them. The more commonly studied groups in sediments include diatoms and pollen, as these are well preserved and easily worked with. The abundances of other taxa are generally much lower, but they nevertheless can

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provide useful paleoecological information (e.g., Cwynar and Levesque, 1995; Walker *et al.*, 1997; Hairston *et al.*, 1999) and their importance is being increasingly recognized (Kerfoot *et al.*, 1999). Here we report the occurrence of micro-floral and micro-faunal remains, notably a fossil rotifer, in the basal sediments of an Antarctic lake and infer the occurrence of a well-developed ecosystem in the lake soon after deglaciation. This information has important implications for the postglacial development of Antarctic freshwater ecosystems in the early Holocene and helps to answer the question: Were the initial postglacial Antarctic lake ecosystems composed of species inhabiting local refugia, or were the organisms derived from long-distance transport from more northerly continents or islands?

Saline and freshwater lakes are found at several locations around the margins of the Antarctic continent and are especially numerous in the Vestfold Hills (68°S, 77°E; Fig. 1) of East Antarctica. This 400-km² ice-free region consists of low hills with a maximum relief of 200 m. The ice-free conditions are maintained through low precipitation in combination with the low albedo of the exposed rock (Adamson and Pickard, 1986). More than 300 lakes and ponds, ranging from glacier-fed freshwater lakes (salinity < 0.1‰) to hypersaline waters (salinity > 250‰), are scattered throughout the area. There is increasing interest in the origins and evolutionary history of Antarctic biota (Vincent, 2000a), and the lakes of the Vestfold Hills provide a diverse set of aquatic habitats in which to explore such questions.

We examined the early Holocene sediments of a wellcharacterized lake in the region, Ace Lake, to determine the





FIG. 1. Map of Ace Lake showing the location (star) from which the core was recovered. Also shown is the location (triangle) of the core described by Roberts and McMinn (1999). The insets show the position of Ace Lake in the Vestfold Hills and the locations of the Vestfold and Bunger Hills on the Antarctic continent. The stippled area in the map of the Vestfold Hills denotes polar continental ice or glaciers.

composition of its colonizing biota soon after deglaciation. Ace Lake (68°28'S, 78°10'E) is currently a saline, meromictic (permanently density stratified) lake with a maximum depth of 25 m (Rankin et al., 1999). Its paleolimnological history is complex, and the evidence to date indicates that it has undergone a lacustrine-marine-lacustrine succession since its formation after the retreat of the polar ice cap (Zwartz et al., 1998; Roberts and McMinn, 1999). An analysis of the diatom stratigraphy has resulted in the following chronology (Roberts and McMinn, 1999): Ace Lake basin formed ~12000 cal yr B.P. (all ¹⁴C dates were corrected using an Antarctic reservoir effect of 984 ¹⁴C years) and was initially filled with freshwater, probably from the melting ice cap. These conditions prevailed until \sim 8100 cal yr B.P., when relative sea level rise (Zwartz *et al.*, 1998) created a connection between the lake basin and the ocean. From then until ~1480 cal yr B.P. the basin retained marine characteristics, though it is probable that the marine connection was severed ~6000-5500 yr B.P. (Zwartz et al., 1998). Simplification of the lake's biota has occurred since separation from the ocean and now includes copepods, rotifers, protists, and bacteria (Rankin et al., 1999).

A 185-cm-long sediment core was collected from Ace Lake in November 1994 using an impact corer (3.5 cm diameter). The general characteristics of the core were very similar to those described previously for a core recovered from a nearby location in the lake (Roberts and McMinn, 1999; see Fig. 1 for core locations). Roberts and McMinn (1999) used their core to determine the depositional and diatom history of the lake sediments given above, and from this a history of lake water level was developed (Roberts *et al.*, 1999). From facies comparison with this core we estimated that the basal sediments in our core were deposited \sim 11,000 cal yr B.P. (Fig. 2). It is probable that the sedimentation rate during this period of the lake's development was rapid due to the input of glacially derived clastic material, and the actual age of the sediments at the base of our core could be older than this estimate and closer to the 12,000 cal yr B.P. determined for the basal sediments of the core of Roberts and McMinn (1999).

The core was sectioned into 1-cm segments that were maintained in the dark at 4°C until processed. To study the microfaunal remains the sediments were deflocculated overnight in a 10% solution of sodium hexametaphosphate containing rose bengal stain, rinsed through a 53- μ m sieve, and then examined at 62× magnification. This technique ensured that organic material was not destroyed, in contrast to the methods often used for isolating diatom frustules from sediments, in which strong oxidizing agents are used to remove the organic fraction.

Examination of the basal 1-cm section of our core revealed the presence of subfossil rotifer loricas (outer shells) (Fig. 3) at a density of greater than 300 (g dry sediment)⁻¹. The loricas were elongate, U-shaped, and 180–200 μ m in length, and they clearly belonged to a member of the genus *Notholca*. They were very thin and almost transparent and had conspicuous longitudinal striations on the surface. At the anterior end there were three pairs of short spines. The same species is still present in



FIG. 2. Major facies composition and dating of the Ace Lake core described by Roberts and McMinn (1999), and the facies of the core from which the microfossils described in this paper were recovered. Also shown are the phases of the development of Ace Lake and the nature of the diatoms associated with the sediments (Roberts and McMinn, 1999).



FIG. 3. Lorica (outer shell) of the fossil rotifer, Notholca sp., recovered from early lacustrine sediments of Ace Lake. The length of the lorica is 180 µm.

Ace Lake, where it is found in shallow, less-saline water around the lake's periphery (Dartnall, 2000). The modern specimens are smaller than those of 12,000 years ago, exhibiting a dwarfism similar to that of the inshore marine copepod *Paralabidocera antarctica*, which is also found in Ace Lake (Bayly, 1978). Similar specimens of the rotifer are found in fresh and brackish Vestfold Hills lakes, and in shallow freshwater pools that freeze solid in the winter (Everitt, 1981; Dartnall, 2000).

The species of *Notholca* present in the lakes of the Vestfold Hills is similar to *Notholca verae*, which was originally described from freshwater lakes in the Bunger Hills (Kutikova, 1964), another ice-free Antarctic region approximately 1000 km to the east of the Vestfold Hills (Fig. 1). The species differ slightly, however, in that although they are in general the same size and shape, *Notholca* sp. from the Vestfold Hills has straight rather than serrated striations on the outer surface of the lorica. The fossil and extant rotifers from the Vestfold Hills should therefore be considered an undescribed species within the "squamula" group of this genus.

Following our discovery of *Notholca* sp. fossils in the basal core section, further subsamples were examined at $1000 \times$ magnification with a Zeiss Axioplan fluorescence microscope to

search for the remains of other taxa. Several unicellular organisms were identified, including the filamentous cyanobacterium *Phormidium* spp., a chrysophyte cyst, a dinoflagellate cyst, and a testate amoeba. The chrysophyte cyst and *Phormidium* spp. were particularly abundant. The latter genus and other oscillatorian cyanobacteria are well-known dominants in polar lakes and soils (Vincent, 2000b). No diatom remains were observed in these sediments, consistent with Roberts and McMinn (1999), who reported that diatoms were absent from their Ace Lake core at depths greater than 175 cm (Fig. 2). However, the presence of several protists, cyanobacteria, and the rotifer *Notholca* indicates that a trophically complex food web was established early in the evolution of the lake.

Examination of younger, upper core segments showed that *Notholca* sp. was abundant during both lacustrine phases of Ace Lake but was present in much lower numbers during marine phases. The remains of several other organisms were also observed in the younger sections, including tests of the foraminiferan *Portatrochammina weisneri*, which were common during the marine phase of the lake, and eggs, faecal pellets, and exoskeletal fragments of copepods, which were observed frequently from \sim 8000 cal yr B.P. to the present time. It is likely that the majority

of the copepod remains belong to *Paralabidocera antarctica*. Of particular note was the absence from the pre-marine incursion sediments in Ace Lake of any remains or eggs of two freshwater crustaceans, *Daphniopsis studeri* and *Acanthocyclops mirnyi*, that are abundant and widespread in freshwater lakes of the Vestfold Hills today (Gibson *et al.*, 1998; Dartnall, 2000), suggesting these species may have arrived in the area as later invaders.

The colonization of continental Antarctic lakes at the conclusion of the last glacial maximum continues to be the subject of conjecture (Bayly, 1994; Vincent, 2000a). In the marine-derived saline lakes of the Antarctic, the biota includes a subset of species from the local marine environment (Rankin et al., 1999). The sources of the biota in freshwater lakes, such as the rotifer and other organisms described here, are more difficult to determine. The organisms had to reinvade either from local refugia in which they survived the period of glaciation or from unglaciated regions, such as sub-Antarctic islands and continents to the north. The maritime Antarctic Peninsula shows greater species richness than the rest of the continent, and this has been attributed to the proximity to more temperate regions (southern South America) and frequently favorable notherly winds that could carry propagules to the Antarctic (Ellis-Evans and Walton, 1990). Only those species that are resistant to desiccation and are broadly tolerant of varying thermal conditions, or have highly resistant resting eggs, are likely to be dispersed via wind or animal vectors. Longdistance aerial dispersal to the Vestfold Hills would be more difficult, as it is distant from the nearest nonpolar land mass, and the winds in general spiral out from Antarctica. The subtle differences between the fossil and modern populations of Notholca in the Vestfold and Bunger Hills suggest that they originated from separate sources, and therefore aerial dispersal, which would tend to result in similar and widespread populations around the East Antarctic coastline, is unlikely.

The alternative origin for Antarctic freshwater micro-fauna was proposed by Bayly and Burton (1993), who suggested that refugia in the form of epishelf lakes played a role in the eventual colonization of younger, rock-basin lakes. These epishelf lakes are large, deep bodies of fresh water dammed by floating ice shelves, and are believed to be much older than those lakes associated with ice-free areas. It is also possible that organisms survived in supra-glacial lakes of the type that are currently present on the McMurdo (78°S, 166°E) and Ward Hunt (83°N, 75°W) Ice Shelves. Diverse communities of cyanobacterial mats, unicellular eukaryotes, rotifers, tardigrades, and nematodes occur in these lakes (Vincent et al., 2000) and provide an example of how organisms might have survived periods of extensive glaciation (Vincent and Howard-Williams, 2000). Thus, the populations of Notholca currently present in the Vestfold and Bunger Hills may have survived locally, and the differences in morphology may date from well before the most recent glacial period. This mechanism for survival and recolonization is also consistent with the relatively complex community present in Ace Lake early in its history. The initial colonizing fauna, therefore, could have come from supra-glacial habitats or other local refugia together with other early colonizers of polar continental lakes, such as *Phormidium* spp., which are resistant to desiccation and are easily dispersed (Ellis-Evans and Walton, 1990; Hawes *et al.*, 1992).

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