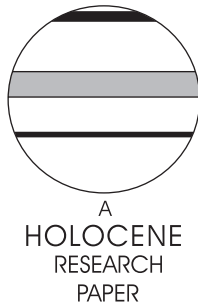


# Holocene development of the fauna of Lake Boeckella, northern Antarctic Peninsula

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**Abstract:** The origins of the freshwater fauna that inhabits Antarctic lakes are poorly known. The species present today could be relict species that have survived Quaternary glaciations on the continent, or Holocene migrants from more temperate regions. One approach to investigating these questions is to study faunal microfossils in lake sediment. This approach was applied to a 293 cm sediment core from Lake Boeckella, located at the northern tip of the Antarctic Peninsula. The microfossils indicated that most of the metazoan species that occur in the lake today have been present since soon after the lake's formation c. 5.5 ka ago. In particular, the centropagid copepod *Boeckella poppei* (Mrázek) has been present throughout the lake's history, suggesting a local source for this species. The development of biodiversity in the lake with time was in general more consistent with local (Antarctic) rather than distant (South American) sources, though an alternative explanation is that dispersal to Antarctica was more efficient in the mid-Holocene. Evidence of dispersal from extra-continental sites comes from the scattered occurrence throughout the core of *Eubosmina chilensis* (Daday), a South American species that does not reach the Antarctic or the sub-Antarctic islands at present, and which failed to establish a permanent population in the lake.

**Key words:** Antarctica, Lake Boeckella, fauna, copepods, colonization, vicariance, dispersal, *Boeckella poppei*, climate change, Holocene.

## Introduction

The origin and history of the metazoan fauna of freshwater Antarctic lakes are poorly known. It is uncertain whether the animals present in the lakes today, which include arthropods, tardigrades, nematodes and rotifers, survived Quaternary glaciations in refugia on the continent or have invaded from more temperate regions during the Holocene. A recent review of the crustacea of Antarctic freshwater lakes concluded that all species are Holocene migrants (Pugh *et al.*, 2002). There is little direct evidence to support this conclusion, but there is also limited evidence to suggest the presence of continental refugia. Only very few Antarctic lakes are known to predate the last glacial maximum (Doran *et al.*, 1994; Hodgson *et al.*, 2005), but a study of the sediments of one of these, Lake Reid in the Larsemann Hills (69°23.13'S, 76°22.72'E), has shown that at least two species – the cladoceran *Daphniopsis studeri* Rühle and the rotifer *Notholca* sp. – have been present in the

lake throughout its lifetime (Cromer *et al.*, 2006). Bayly *et al.* (2003) used morphological and biogeographical arguments to conclude that two copepod species found in East Antarctic freshwater lakes – *Boeckella poppei* (Daday) and *Gladioferens antarcticus* Bayly – have had long associations with the Antarctic continent and probably survived in local refugia. There is also evidence from the terrestrial fauna for the presence of endemic nematodes, tardigrades, springtails and mites that must have survived glaciation on the continent (Andrássy, 1998; McInnes and Pugh, 1998; Marshall and Coetzee, 2000; Stevens and Hogg, 2003; Convey and McInnes, 2005).

Understanding the origins of the Antarctic limnetic fauna is important if the biogeography of the continent is to be placed in a global context. If all the species present are Holocene migrants, then the lakes of the continent are merely biogeographical extensions of more northerly regions. If, in contrast, the lakes contain an endemic fauna, they can provide fascinating insights into the biodiversity and ecology of these habitats in earlier, possibly preglacial, times. Furthermore, the species present will provide important information about the

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characteristics required and strategies used to survive glaciation on the continent.

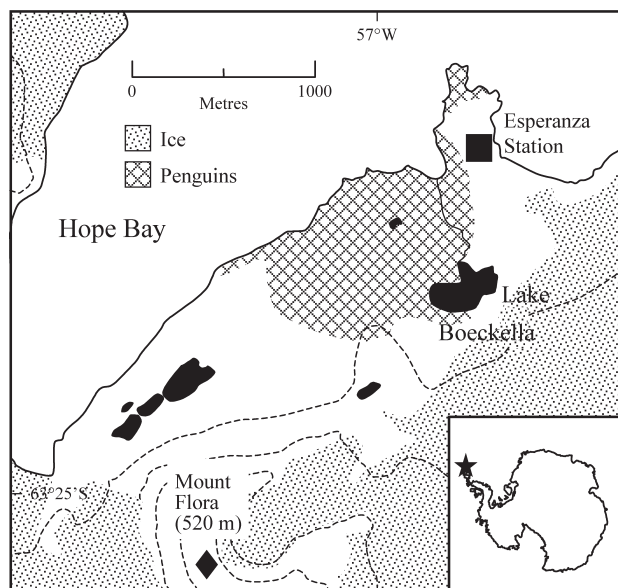
In this paper we discuss the distribution of animal microfossils in the sediment of Lake Boeckella, which is located at Hope Bay, c. 20 km from the northern extremity of the Antarctic Peninsula. If the colonization of lakes of the Antarctic Peninsula was from further north, this lake may have been one of the first continental sites reached by invading species (Ellis-Evans and Walton, 1990; Marshall, 1996). The record of such arrivals will be preserved in the sediment: colonizing species will first appear in a particular sediment horizon (though if the species has no body part or egg that is preserved there will be no evidence of its arrival). If colonization of the lake was from local sources, species are more likely to first occur soon after the onset of biological sedimentation, with later arrivals probably from more distant sources. A similar diversity–time relationship would be expected if long-distance colonization was a common occurrence. Clearly the ability of the organism to survive in the lake once it has arrived is also of prime importance (Ellis-Evans and Walton, 1990; Clarke, 2003). Conversely, if colonization from South America has been limited to occasional extraordinary events, a gradual increase in biodiversity with time in the lake might be expected.

This sediment-based approach has been previously used to identify a period in which the anostracan *Branchinecta gaini* Daday was present in lakes on James Ross Island, c. 60 km to the south of Lake Boeckella on the eastern side of the Antarctic Peninsula (Björck *et al.*, 1996). Jones *et al.* (2000) showed that *Branchinecta gaini*, *Boeckella poppei* and two species of mite, *Alaskozetes antarcticus* (Michael) and *Halozetes belgicae* (Michael), have been associated with Sombre and Heywood Lakes on Signy Island (South Orkney Islands, c. 660 km to the northeast of Lake Boeckella), for much of the lakes' existence. The Holocene colonization of lakes on Greenland has also been studied by this method (Bennike, 2000). Here we provide the first information on the colonization of a lake on the Antarctic Peninsula by animals, with the aim of identifying when the colonizations occurred and the implications for the sources of the fauna. The species dynamics also provide insights into the ecological history of the lake and its surrounds.

## Study site

Lake Boeckella is located in a small (< 5 km<sup>2</sup>) ice-free area at Hope Bay, near the northern extremity of the Antarctic Peninsula (Figure 1). It lies in a glacially gouged depression and is dammed by a moraine. The lake is located at 49 m above sea level approximately 500 m from the ocean. The maximum depth recorded in a bathymetric survey was 4 m (Izaguirre *et al.*, 1993), though Zale and Karlén (1989) report collecting the core used in this study from 6.9 m. The lake receives meltwater from glaciers on nearby Mount Flora, and therefore has low conductivity. An outlet stream runs from the lake to Hope Bay. Further details of the lake can be obtained from Izaguirre *et al.* (1993, 2003), Vinocur and Pizarro (1995) and Almada *et al.* (2004).

The biology of Lake Boeckella has been the topic of numerous studies. The phytoplankton community was described by Izaguirre *et al.* (1993), and consists of *inter alia* cyanophytes, chlorophytes and diatoms. Further cyanobacterial and algal species form the periphyton (Vinocur and Pizarro, 1995). The only crustacean recorded is the copepod *Boeckella poppei*, which has a nekto-benthic habit in the lake (Almada *et al.*, 2004). Other members of the zooplankton include the



**Figure 1** Map showing Lake Boeckella and the surrounding area. The inset shows the location of Hope Bay on a map of Antarctica (star)

scarce rotifers *Notholca walterkosteii* de Paggi and *Philodina gregaria* Murray (Izaguirre *et al.*, 2003). Tardigrades are also present in the lake at low abundance, but the species present have not been determined.

Hope Bay is the site of a major Adélie penguin rookery that extends up from the coast and into the drainage basin of Lake Boeckella (Figure 1). The total number of breeding pairs in this rookery in 1986 was approximately 120 000 (Myrcha *et al.*, 1988), and there is evidence that the colony has increased dramatically in size since 1945 (Zale, 1994a). The number of penguins that actually nest in the drainage basin of the lake has not been recorded. Tatur (1989) reported abandoned rookeries in the area, suggesting either that the breeding sites have moved periodically, or that penguin abundance may have been higher in the past. Both the inhabited and the abandoned rookeries are major sources of nutrients to the lake (Tatur and Myrcha, 1983). As a result of this input, Lake Boeckella lies mid-way along a lake series in the Hope Bay area that ranges from oligotrophic (no penguin influence) to hypereutrophic (extreme penguin influence) (Izaguirre *et al.*, 2003).

## Methods

The collection in late 1987 of the sediment core used in this study was described by Zale and Karlén (1989). Further details of this core have been discussed by Zale (1994a,b) and Björck *et al.* (1991). The 293 cm long core was collected from the centre of the lake and sectioned at 5 cm intervals (except for a 3 cm section from 0 to 3 cm). After the initial subsampling the remaining core was preserved with polyethyleneglycol (PEG) using the method of Tippet (1964), and stored at 4°C until further analysis.

A 0.5–1.0 g subsample of each preserved section was placed in ~ 10 mL distilled water in a glass vial to dissolve the PEG. A few drops of Rose Bengal stain were added, and the sample allowed to stand overnight to disperse the sediment. In some cases short bursts of ultrasonication aided dispersal. The sediment was then rinsed through a stack of 200 µm, 100 µm and 44 µm sieves with thorough washing with distilled water. The contents of the sieves were backwashed into vials for storage in distilled water. The samples were viewed through a

dissecting microscope, and all animal-derived microfossils, including eggs, body parts, spermatophores and loricae, were counted and where possible identified. Larger subsamples (typically 5 g) were treated similarly (without the addition of Rose Bengal and passage through the 100  $\mu\text{m}$  sieve only) for the isolation of mite carapaces. Further subsamples for the textural characterization of the sediment were ultrasonicated for  $\sim 5$  min after standing in distilled water overnight. For each sample an estimate was made of the relative abundance of volcanic tephra and moss stems. Loss on ignition (LOI) was determined prior to preservation of the core at 1 cm resolution as described previously (Zale and Karlén, 1989).

Because of the unknown percentage of PEG in each sample it was impossible to determine the actual dry mass of sediment examined. Therefore the abundances of microfossils presented here will be underestimates (perhaps by up to 50%) of the true value on a per dry mass basis. However, the occurrence or absence of a microfossil type could still be monitored, and the percentages of the different microfossils within a segment would not have been affected. A further concern was that the available subsamples from the 5 cm segments did not necessarily represent the complete segment when the core was originally sectioned, and it was also not possible to homogenize all the sediment available prior to removal of the subsample for isolation of microfossils. As discussed further below, there was evidence of significant within-segment variation in the microfossils present in some cases.

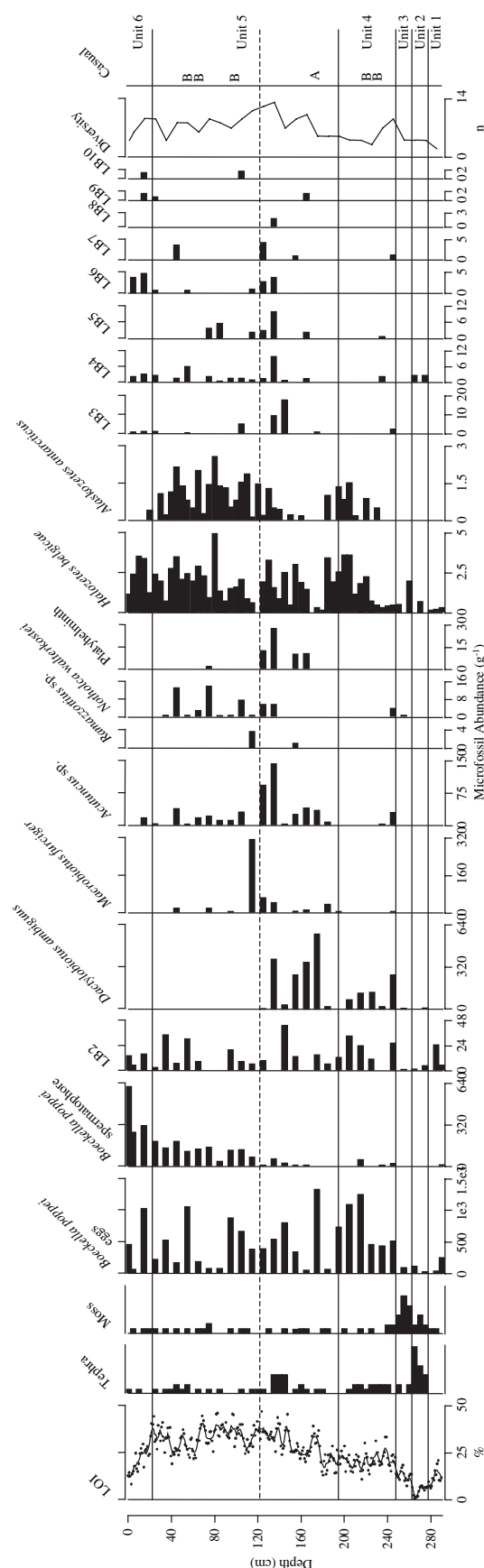
## Results

### Sediment characteristics

The core could be separated into six major units based on distinct changes in sediment characteristics (Figure 2). The sediment at the base of the core (Unit 1) contained fine grey silts and clays interspersed with narrow bands of orange sediment, possibly indicating subaerial oxidation. Organic content was near 20%, and laminations occurred only at the top of the unit. There was no direct evidence that coring had penetrated into sediment formed prior to the onset of biogenic activity (glacial till), but the colour and texture of the sediment suggested that the base of the core was laid down soon after exposure of the lake basin.

Tephra was absent from the deepest sediment, but was particularly plentiful in 15-cm thick Unit 2 (Figure 2) that began at 278 cm. Tephra shards were present throughout the remainder of the core but at much lower abundance. There was a negative relationship between LOI and tephra abundance in Unit 2, as well as higher than usual non-volcanic clastic material. The observations of tephra were consistent with those made at the time of recovery of the core: using magnetic techniques, Zale (1994b) recorded the strong peak at 268 cm, as well as further bands at 230, 205, 177, 161 and 107 cm. The relatively coarse sampling interval (5 cm) used in the current study precluded identification of these apparently less intense horizons. The occurrence of tephra in other segments of the core is due to waterborne transport of tephra from the lake's drainage basin. Moss stems and leaves were also present throughout the core (Figure 2), but were particularly abundant in Unit 3, immediately above the tephra layer (263–248 cm). The stems showed moderate etiolation, indicating that the moss had grown *in situ* under water in the lake (Seppelt and Kanda, 1986).

Unit 4 consisted of finely laminated sediment that continued to 195 cm. Under the microscope the laminations appeared as well-defined dark green layers a few tens of microns thick interspersed with less strongly coloured material. These may



**Figure 2** A plot of the abundance per gram of microfossils in the sediment of Lake Boeckella. Also shown are the percentage loss on ignition (LOI) (individual data points and a five-point running mean); the occurrence of tephra and moss on arbitrary scales; the diversity (number of microfossil types recorded in each segment); and the occurrence of other species observed by casual observation (A, the thecate amoeba *Diffugia* sp.; B, the cladoceran *Eubosmina chilensis*). The six units defined in the text are indicated, along with the subdivision of Unit 5

have been annual varves. The LOI in this unit averaged near 25%. In the 193–198 cm segment there was a sudden change from fine laminations to yellower, often coarser sediment that contained only occasional and less well-defined laminations. This change defined the beginning of Unit 5. At *c.* 180 cm the LOI increased to above 30% and, after an initial decrease to near 20%, this level or higher was maintained with a few local minima (near 110 cm and more recently between 40 and 64 cm) to 30 cm. The most recent sediments in Unit 6 (0–25 cm) were characterized by higher sand content (also see X-radiographs of this section of the core in Zale and Karlén, 1989) and markedly lower LOI than sediments from Unit 5.

### Dating the core

Radiocarbon dates for six segments of the core were obtained soon after collection (Zale and Karlén, 1989; Björck *et al.*, 1991; Zale, 1994b). The dates, given in Table 1, are difficult to interpret because of the presence of 'old' marine-derived carbon through the input of faecal material from penguins that nest in the drainage basin of the lake. Zale (1994b) developed a geochemical model that took into account the input of this old carbon to calculate 'true' ages (Table 1). From this work it was estimated that deglaciation of the area occurred approximately 6.3 ka BP.

An alternative dating approach is tephrochronology. Björck *et al.* (1991) allocated the tephra of Unit 2 to AP14, a tephra band recognized across the northern Antarctic Peninsula and nearby offshore islands that was derived from an eruption of Deception Island (62°57'S, 60°38'W), which is 190 km to the west of the lake (Björck *et al.*, 1991). AP14 has been dated at *c.* 4.7 ka BP (Björck *et al.*, 1991), and it is now generally accepted that deglaciation at the northern end of the Antarctic Peninsula and on nearby islands occurred at about 5.5–5.0 ka BP (Hjort *et al.*, 2003).

Because of the preservation of the core with PEG, it was not possible to use more modern techniques to obtain new dates on the core.

### Animal microfossils

#### Copepods

Only fragmentary copepod exoskeletal material was found in the near-surface sediment, which was not surprising as copepod bodies are in general poorly preserved in sediments (Warner, 1989). In contrast, copepod eggs were the most abundant microfossil in the core (Figure 2). These eggs had the same characteristics as those of gravid females of *Boeckella poppei* collected from Lake Terrasovoje, Prince Charles Mountains, Antarctica. As this species occurs in Lake Boeckella today, it was concluded that the eggs were from this species. The majority of the eggs were empty, and many were represented by a single hemisphere. The occurrence in fresh-water sediments of similar empty, presumably hatched copepod

eggs of this and other species has been recorded previously (Bennike, 1998; Jones *et al.*, 2000; Knapp *et al.*, 2001). Copepod eggs were present in all segments including the oldest sediment from Unit 1, though large shifts in abundance occurred (Figure 2).

Copepod spermatophores that were identical in shape to those of modern *Boeckella poppei* were also abundant in recent sediments, with numbers decreasing roughly exponentially with depth. Two sizes of spermatophore were observed that were similar in shape, but which had different dimensions (Figure 3). The longer spermatophores were abundant at the top of the core, but disappeared more rapidly with depth than the smaller ones. The distribution of spermatophores in the sediment suggests that they are broken down *in situ*, and therefore changes in their abundance cannot be used to infer changes in lake conditions or animal populations.

The occurrence of the two spermatophore types might suggest the presence of more than one copepod species in the lake. However, *Boeckella poppei* occurs in two size morphs on South Georgia (Hessen *et al.*, 1989), and it is possible a similar situation occurs in Lake Boeckella. Hessen *et al.* (1989) recorded that the eggs of both morphs were the same size. Alternatively, the different spermatophores may be associated with the formation of diapause eggs, noted previously in copepods from Lake Boeckella (Izaguirre *et al.*, 2003). Further study of the reproduction of the extant population is required to confirm the origins of the two spermatophore sizes in Lake Boeckella. The absence of a second species of copepod was supported by molecular genetic analysis of the sediment, which indicated that *Boeckella poppei* was the only copepod present in the lake both early in the lake's history as well as in the most recent sediments (Bissett *et al.*, 2005).

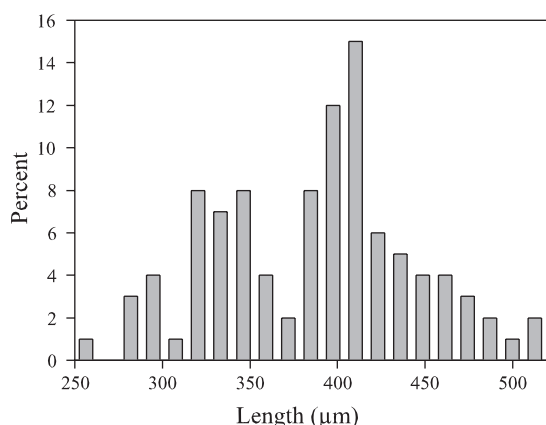
#### Cladocera

Cladoceran remains are generally well preserved in lake sediments (Korhola and Rautio, 2001). Occasional cladoceran exoskeletal fragments were observed casually at some depths in the core, including near 225 and 100 cm, but they were more common over a short interval from 53 to 68 cm. Within this narrow depth range there were clearly periods when the cladocera were abundant and others when they were absent: exoskeletal remains were not recovered from all subsamples of the segments studied. No estimates of abundance were made. The species present was identified as *Eubosmina chilensis* (Daday) (M.C. Marinone, personal communication, 2005) (Figure 4), which is widely distributed in southern South America. The only previous records of bosminids from the Antarctic region are of *Bosmina obtusirostris* Sars (though this identification has been questioned (Pugh *et al.*, 2002)), *Eubosmina longispina* (Leydig) and *Bosmina cf. kessleri* (Brooks *et al.*, 2005), all from the Falkland Islands.

**Table 1** Radiocarbon ages of sediment from Lake Boeckella

Depth (cm)	Sample number	Uncalibrated radiocarbon age ( $^{14}\text{C}$ yr BP)	Modelled age (yr BP)
0–2	ST11990	2275 ± 70	0
0–23	ST11746	2585 ± 70	
83–113	ST11747	2140 ± 70	470
143–173	ST11620	3720 ± 70	
203–233	ST11748	4085 ± 120	2620
263–293	ST11619	8615 ± 170	5360

Uncalibrated ages are from Björck *et al.* (1991) and modelled ages from Zale (1994b).



**Figure 3** Distribution of spermatophore length in sediment from 3 to 8 cm showing the occurrence of two size classes

### Tardigrades

Remains of tardigrades have rarely been reported from lake sediments (Frey, 1964). Tardigrade bodies and exuviae decompose rapidly after sedimentation, and there are only a few records of the recovery of tardigrade eggs from sediment cores (Frey, 1964; Jankovska, 1991).

Tardigrade eggs were surprisingly abundant in the Lake Boeckella core. Four types of egg were observed, of which three were common. The spherical surface of the most abundant egg type was covered with tapered conical projections (Figure 5); these eggs were attributable to the lacustrine species *Dactylobiotus ambiguus* (Murray) or a closely related species (Binda and Pilato, 1999; McInnes and Pugh, 1999). *Dactylobiotus* cf. *ambiguus* eggs were present at low abundance from Unit 2, and were common in most segments in Unit 4 and the first half of Unit 5, above which they were strictly absent (Figure 2).

The second egg type was slightly elliptical, with the projections on the surface of the eggs ending in complex bifurcations (Figure 5). These eggs are attributable to *Macrobrotus furciger* Murray, a terrestrial species that is often associated with the nitrophilous alga *Prasiola crista* (Lightfoot) Kützing but which may be present in the littoral zone at the lake margin (McInnes and Pugh, 1999; S.J. McInnes,

personal communication, 2005). This egg type was observed intermittently throughout the core at low abundance, though a sharp peak occurred in Unit 5 after the disappearance of *Dactylobiotus* cf. *ambiguus* (Figure 2).

The third egg type was smaller (diameter *c.* 70 µm), with short rods between inner and outer surface layers, giving it a speckled look. These were similar to eggs of *Acutuncus antarcticus* (Richters), a typically terrestrial species that also lives in lakes (Pilato and Binda, 1997; McInnes and Pugh, 1999), but could also have been from a related species. We refer to this egg type as *Acutuncus* sp. These small eggs were present throughout much of Unit 5 (Figure 2), though there was an isolated occurrence early in Unit 4 that was associated with high relative abundances of other microfossil types (eg. copepod spermatophores and rotifers).

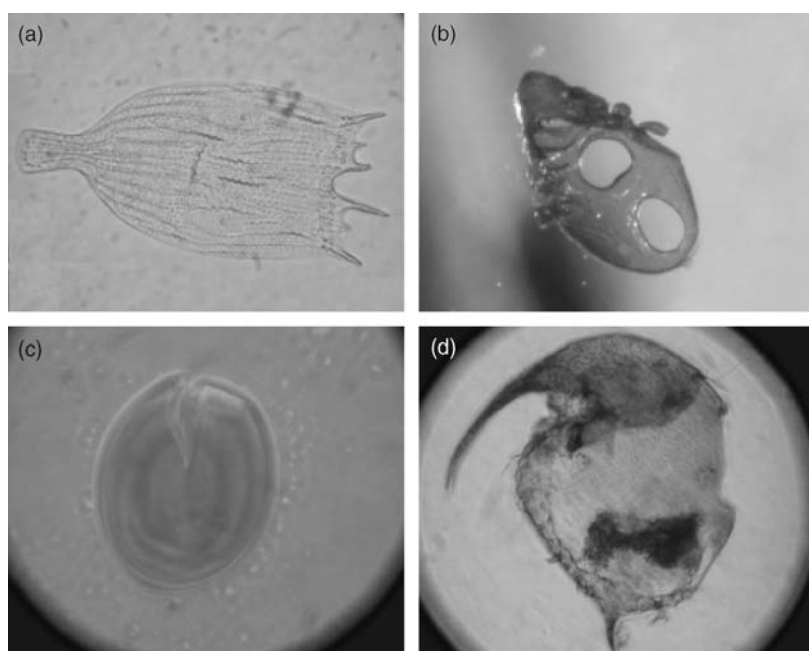
Occasional examples of a fourth egg type, attributable to a member of the genus *Ramazzottius*, which has distinctive eggs, were observed in a few samples in Unit 5. Members of this genus are terrestrial in habit.

### Rotifers

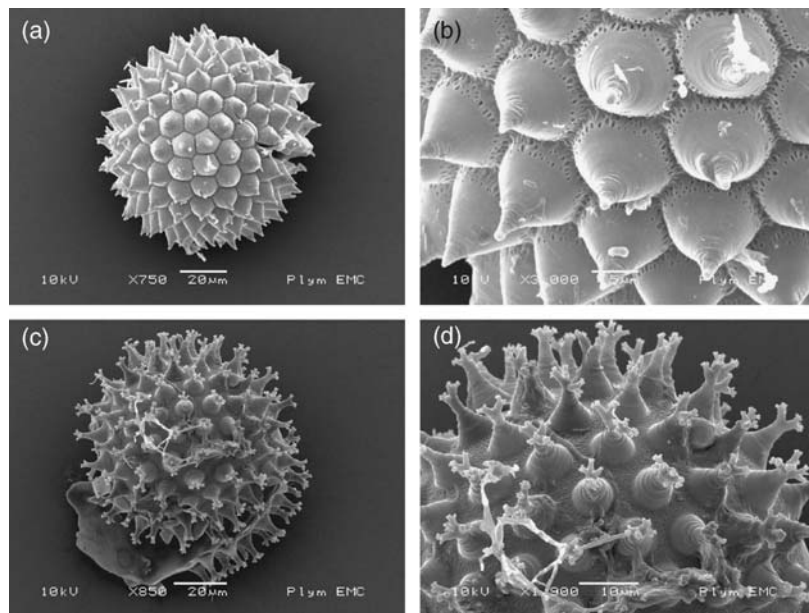
Rotifer remains have rarely been recorded from lake sediments, though they are sometimes abundant in peat bogs (Frey, 1964). One exception to this rule is members of the genus *Notholca*, loricae of which have been reported from sediments of fresh-water and saline lakes in the Vestfold and Larsemann Hills, Antarctica (Swadling *et al.*, 2001; Cromer *et al.*, 2005, 2006).

Loricae of the rotifer *Notholca walterkosteii* (Figure 4) were present in Lake Boeckella sediments throughout the second half of Unit 5, with scattered occurrences in Units 3 and 4. The appearance of *Notholca walterkosteii* in Unit 5 coincided with the disappearance of the eggs of *Dactylobiotus* cf. *ambiguus*. *Notholca walterkosteii* has been recorded in the zooplankton of Lake Boeckella in a recent study (Izaguirre *et al.*, 2003), and occurs elsewhere in maritime Antarctica and South America (Dartnall and Hollowday, 1985; Battistoni, 1992).

Other rotifer species have been recorded from Lake Boeckella (Izaguirre *et al.*, 2003) that have undoubtedly been present for an extended period. Most of these species are bdelloids that do not produce a lorica, and are therefore not preserved in the sediment.



**Figure 4** Examples of microfossils found in the sediment of Lake Boeckella. (a) Lorica of *Notholca walterkosteii* (length: 200 µm); (b) *Halozetes belgicae* cuticle (length: 600 µm); (c) platyhelminth egg (length: 70 µm); and (d) *Eubosmina chilensis* exoskeleton (length: 400 µm)



**Figure 5** Tardigrade eggs from the sediment of Lake Boeckella. (a) Egg of *Dactylobiotus* cf. *ambiguus*; (b) detail of processes on the surface of the egg of *Dactylobiotus* cf. *ambiguus*; (c) egg of *Macrobiotus furciger*; and (d) detail of processes on the surface of the egg of *Macrobiotus furciger*. Note the scale bars at bottom of each figure

#### Oribatid mites

Remains of two different species of oribatid mite were recorded in the sediment: *Alaskozetes antarcticus* and *Halozetes belgicae* (Figure 4). Both these species have been recorded in the Hope Bay region in recent times (Wallwork, 1967), and are typically inhabitants of terrestrial habitats, with *Alaskozetes antarcticus* often associated with areas rich in organic debris and *Halozetes belgicae* more specifically crustose lichens. However, both species can survive for extended periods in aquatic habitats (Goddard, 1979) and the supralittoral zone (Pugh and MacAlister, 1994). Both the ventral plates of immature stages and adult cuticles were observed in the sediment; the number of mite remains recorded in Figure 2 is the total of all complete or near complete adult cuticles and late stage nymphal plates recorded for each species. Numerous other fragments of cuticles, legs and other body parts were observed, but were not counted.

*Halozetes belgicae* was present in all units, though *Alaskozetes antarcticus* was not observed at the base of the core, appearing first in Unit 4. Maximum abundance of both species occurred during Unit 5, though both were (nearly) absent early in this unit. *Alaskozetes antarcticus* was not recorded in the most recent sediments.

#### Thecate amoebae

Tests of thecate amoebae are commonly observed in lake sediments and have been used extensively in palaeolimnological reconstructions (Beyens and Meisterfeld, 2001). Tests of a single species, *Diffugia* sp., were common in one subsample taken from 173–178 cm, but were not observed in any other subsample from this depth or elsewhere in the core. This microfossil was not one that would have been overlooked during the systematic counts.

#### Platyhelminth

Eggs of a rhabdocoel platyhelminth (Figure 4) were observed in Unit 5, with only a single occurrence in the latter part of the unit.

#### Unidentified eggs

At least nine other, unidentified egg types were observed in the core. The most abundant, LB2, was observed in all units

at moderate abundance. This egg was the same size as those of *Boeckella poppei*, but had a thicker external membrane that was a different colour (yellow brown, as opposed to colourless). There was a reasonable correlation between the abundances of *Boeckella poppei* eggs and this type ( $R^2 = 0.375$ ,  $n = 31$ ,  $p < 0.05$ ); if it is accepted that only one copepod species occurs in the lake, it is possible that this egg is a diapause egg of *Boeckella poppei*. It is plotted in Figure 2 with the other copepod remains for easier comparison.

The other egg types are described in more detail in Appendix 1. Most of these eggs were present at highest abundance in Unit 5, though some were observed in earlier units and/or were present in the latest sediments (Figure 2).

#### Diversity

Diversity, defined as the number of different microfossils recorded in a particular sample, was greatest in Unit 5, with the peak occurring just prior to the disappearance of eggs of *Dactylobiotus* cf. *ambiguus*. An earlier peak in diversity occurred at the base of Unit 4 associated with an increase in LOI and reduction in the importance of moss in the lake. It should be noted, however, that the plot in Figure 2 does not reflect total metazoan diversity, rather the diversity of the species that left microfossils.

## Discussion

### Regional climate setting and its effect on the biota

Palaeolimnological data from Antarctic lakes has been used widely to develop models of local and regional climate change (Hodgson *et al.*, 2004). Previous analyses of the characteristics of the Lake Boeckella core used in this study led to the conclusions that the area had been deglaciated 5.5–6.3 ka BP (Zale, 1994b; Hjort *et al.*, 2003); that a major climate downturn occurred that ended at *c.* 4.7 ka BP (as indicated by the sharp drop in LOI: Zale, 1994a); that the climate recovered after this downturn (mid-Holocene warm period); and that penguins had been present in the area throughout the lake's history except for a short period during the climate downturn (Zale, 1994a). Our re-interpretation based on analysis of faunal

microfossil distribution and other characteristics of the core questions some of these conclusions, and is summarized below.

Lake Boeckella was a shallow, oligotrophic pond in the period when the deepest sediment recovered (Unit 1) was formed, as reflected by the low LOI and occasional subaerial oxidation of the surface sediment. It is probable that there were few penguins in the drainage basin of the lake at this time (see below). A large eruption of Deception Island (or another nearby volcano) that resulted in a major input of tephra into the lake defined the boundary between Units 1 and 2. Approximately 15 cm of tephra was deposited, though this would have included in-wash from the drainage basin. A similar tephra layer over 1 m thick attributable to the same eruption has been reported from a lake on King George Island (Tatur *et al.*, 1999). Zale and Karlén (1989) suggested that the concomitant decrease in LOI that occurred with this tephra input was an indicator of deterioration in climate. However, the low LOI is attributable to dilution by clastic material and a reduction in productivity resulting from the deposition of fine ash into the lake that would have reduced light penetration (Figure 2). After the end of the input of the volcanic material, extensive growth of aquatic moss occurred in the lake, which is indicative of low nutrient, low productivity conditions (Heywood *et al.*, 1980). This implies a lack of significant nutrient input from penguins, and therefore the probable absence of breeding birds from the drainage basin of the lake at this time (Zale, 1994a).

The boundary between Units 3 and 4 occurred when moss became less important and water column and benthic productivity by algae and cyanobacteria increased, possibly as a result of the slow release of nutrients from the drainage basin. A peak in diversity early in the unit suggests that many species were present in the lake that could take advantage of the changed conditions or alternatively colonized the lake over a relatively short period of time. The finely laminated sediments of Unit 4 indicate seasonal peaks in productivity or possibly grazing. The organic sediment in this zone (and throughout most of the core) consisted largely of very finely divided material that probably had been ingested and excreted by *Boeckella poppei* or other grazers. The fine laminations suggested that there was close coupling between primary productivity and grazing.

The shift to the poorly laminated, yellower sediment of Unit 5 was abrupt, indicating a rapid change in the lake conditions. This is consistent with an increase in nutrient input into the lake with the arrival of significant numbers of penguins in the area. Zale (1994a) developed a proxy for penguin numbers based on geochemical parameters in the sediment. This proxy showed a marked increase at this time from near background levels, also indicating an increase in penguin abundance. Productivity in the lake was no longer limited by nutrient availability, and is likely to have occurred less in short blooms, but more generally throughout the year when light was available. Grazing became uncoupled from productivity because of the abundance of food. The increase in LOI early in Unit 5 was consistent with an increase in both productivity and nutrient content of the lake.

The two mite species, *Alaskozetes antarcticus* and *Halozetes belgicae*, were nearly absent for a period early in Unit 5, which implies harsher conditions in the moss-beds and lichen that they inhabit (Hodgson and Convey, 2005). Paradoxically, the absence of the mites coincided with an increase in LOI, suggesting increased productivity in the lake. An explanation is that an increase in penguin numbers occurred during a period of climate deterioration, and possibly reflects an increase in range of Adélie penguins as conditions at the northern end of the Antarctic Peninsula, particularly the disposition of sea ice

(Fraser and Trivelpiece, 1996), became more suitable for them. Other studies have shown that a period of neoglaciation occurred about the same time (*c.* 2.5 ka BP), consistent with our interpretation (Hjort *et al.*, 2003; Mosley-Thompson and Thompson, 2003). The return of the mites later in Unit 5 can be interpreted as an increase in terrestrial organic productivity as a result of nutrient input from penguins or an amelioration of the climate that did not result in disappearance of the penguins.

Unit 5 can be split into two sections, with the break coinciding with the disappearance of eggs of *Dactylobiotus cf. ambiguus* from the sediments. There was no other clear change in sediment characteristic that occurred at the same time, except that this period was one of high LOI. It may have been that the tardigrade species was not adapted to eutrophic lake conditions, possibly because of the effects of anoxia in the surface sediments on egg viability (S.J. McInnes, personal communication, 2005). Other species were apparently better adapted to the highly productive conditions, notably *Notholca walterkosteii*, which increased in abundance after the disappearance of the tardigrade, and *Boeckella poppei*.

The final unit of the lake (25 cm and above) was characterized by falling LOI, increased clastic material and decreased mite numbers (with the disappearance *Alaskozetes antarcticus* early in the unit). Zale (1994a) recorded a drop in his penguin proxy in the same interval. It therefore appears that penguin numbers declined, reducing nutrient availability both in the lacustrine and terrestrial habitats. The steady rather than abrupt decline in LOI may reflect continued mobilization of nutrients from abandoned rookeries (Tatur, 1989), rather than a slow decrease in penguin abundance.

### Colonization of Antarctic lakes by invertebrates

The distribution of faunal microfossils in the sediment of Lake Boeckella suggests that three different behaviours occurred amongst colonizers of the lake. These can be characterized as early colonizers, later colonizers and unsuccessful colonizers.

The oldest sediments studied contained microfossils of only two species, *Boeckella poppei* and *Halozetes belgicae*, along with unidentified egg type LB2. These species clearly reached the lake soon after its formation, though the core used here did not penetrate into sediments formed prior to the onset of biological sedimentation. *Boeckella poppei* occurs in Patagonia, the islands of Drake Passage (where it has been present on Signy Island for at least 5500 years (Jones *et al.*, 2000)) and along the western side of the Antarctic Peninsula as far south as Alexander Island (Heywood, 1977; Bayly, 1992), suggesting that it could be a Holocene immigrant from South America that then dispersed quite widely on the continent. In some ways this is surprising, as centropagid copepods are poor colonizers. Bayly and Morton (1978) emphasized the apparent paradox that these copepods, which produce desiccation-resistant eggs and might therefore be expected to disperse readily, usually have more restricted distributions than cyclopoid copepods that lack resistant eggs.

An alternative explanation for the occurrence of *Boeckella poppei* in this region is that it survived the last glacial maximum in epishelf lakes or other lakes along the western side of the Antarctic Peninsula. Epishelf lakes, which contain a layer of freshwater dammed by an ice-shelf that 'floats' on seawater (Gibson and Andersen, 2002), could have been present through the glacial period, and therefore provided refuge for freshwater species. Two epishelf lakes on Alexander Island (71°S, 70°W), Ablation and Moutonnée Lakes, contain *Boeckella poppei*, as do many ponds near the lakes (Heywood, 1977). These lakes, as well as other epishelf lakes that have disappeared after failure of the ice dam (Mueller *et al.*, 2003;

Bentley *et al.*, 2005) and the numerous proglacial and moraine ponds that occur along the margins of the Antarctic Peninsula ice shelves, may have provided further refuges for this species. Local dispersal of the copepods could then have occurred, which would obviate the necessity for over-ocean migration from Patagonia.

A further consideration is that *Boeckella poppei* seems to be quite an adaptable species. It occurs in large, deep ultraoligotrophic lakes (Bayly *et al.*, 2003) and small ponds (Heywood, 1977). It is able to alter its reproductive cycle to suit food availability (Izaguirre *et al.*, 2003), and is found in two size morphs, the occurrence of which is possibly related to the presence of predators (Hessen *et al.*, 1989). If the source of this species were colonization from South America, its flexibility may have meant that it could colonize newly formed ponds and lakes more efficiently than other potential colonizers that arrived at the same time.

The other early colonizer evident in the sediment, the mite *Halozetes belgicae*, is endemic to the western margin of the Antarctic Peninsula and nearby sub-Antarctic islands (Wallwork, 1967; Pugh and Convey, 2000). As this is a largely terrestrial species that can survive in the supralittoral zone (Pugh and MacAlister, 1994), it does not have the same need for a lacustrine glacial refugium; any ice-free land with sufficient build up of organic material in the supralittoral zone would suffice. If no ice-free land remained in the Hope Bay region during the last glacial maximum, *Halozetes* could have been transported by currents from other, nearby areas. It then colonized newly exposed land from the littoral zone reaching the Lake Boeckella basin soon after its formation. As pointed out by Pugh (2003), aerial dispersal of mites is highly unlikely.

The second group of colonizers, which included *Notholca walterkosteii*, *Dactylobiotus cf. ambiguus*, *Macrobiotus furciger*, *Acutuncus* sp. and the species that produced many of the unknown egg types appeared in the core in Units 2 or 3, or at the start of Unit 4, resulting in a peak in diversity early in Unit 4. *Alaskozetes antarcticus* first appeared in the middle of Unit 4. None of these species appeared to become regular inhabitants of the lake after this initial colonization, with the exception *Dactylobiotus cf. ambiguus* and the mite. The other species all disappeared from the sediment record, but may have continued to occur in the lake at low densities until the lake environment became more productive, allowing greater abundance, or the disappearance of a competing species. If the species did become extinct in the lake, they may have reinvaded from local (perhaps other lakes in the Hope Bay area) or more distant sources. Similarly, the absence of these species from the earliest sediments in the lake does not necessarily preclude their colonization soon after the lake's formation as they might not have become sufficiently numerous to be recorded in the sediment until the increase in nutrients at the start of Unit 4 resulted in the production of a more abundant food supply. This conclusion is indicated by the presence of *Notholca walterkosteii* in modern Lake Boeckella, albeit at low abundance (Izaguirre *et al.*, 2003), but its absence from recent sediments. It may be that the species has been present throughout Unit 6 even though the sediment record would suggest otherwise.

The final group of colonizers are those that appeared in the lake for a short period but then disappeared. The cladoceran *Eubosmina chilensis* apparently reached the lake on a number of occasions, but was unable to develop sustainable populations. *Diffflugia* sp. reached the lake on at least one occasion, but prospered in the lake for a very short period. Other species undoubtedly reached the lake, but did not develop long-term populations. It is surprising that the anostracan *Branchinecta*

*gairi* colonized a lake only 60 km to the south of Lake Boeckella (Björck *et al.*, 1996), but either did not reach Lake Boeckella or did not prosper there.

These observations indicate that there has been a continual arrival of new propagules to the lake, including, presumably, of the species that successfully colonized the lake early in its existence. It is surprising, then, that no new species that leaves microfossils appears to have successfully colonized the lake since the middle of Unit 4, perhaps 3.5 ka BP (with the exception of a few rare, unidentifiable species). Furthermore, *Dactylobiotus cf. ambiguus* appears to have been unable to recolonize the lake in Unit 6 when lake conditions were similar to those of Unit 4 when this species was abundant. It may be that colonization processes were more efficient during the mid-Holocene warm period, when Units 2–4 were deposited, than in later, cooler times. This suggests that all species adapted to colonization of this region did so quite early in the lake's existence and that there has not been sequential colonization due to rare colonization events from the north.

The data presented here provide the earliest dates for the occurrence of *Boeckella poppei*, *Notholca walterkosteii*, *Dactylobiotus cf. ambiguus*, *Macrobiotus furciger*, *Acutuncus* sp., *Ramazzottius* sp., *Halozetes belgicae* and *Alaskozetes antarcticus* on the Antarctic Peninsula and in most cases the Antarctic continent. Little can be concluded definitely from this single study about the routes and methods of colonization: a comparative study of a series of lakes in the area is needed to tease out the processes occurring. However, the study does show that many of the species arrived quite early in the lake's history, and hint that the efficiency of colonization has varied with time.

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## Appendix 1

This data file lists characteristics of unidentified microfossils recorded in the sediments of Lake Boeckella (Figure A1).

### LB3

This microfossil had a clear, often deformed outer membrane with a strongly stained centre. The whole microfossil was typically 130 µm in diameter, with the strongly stained central portion 30 µm.

### LB4

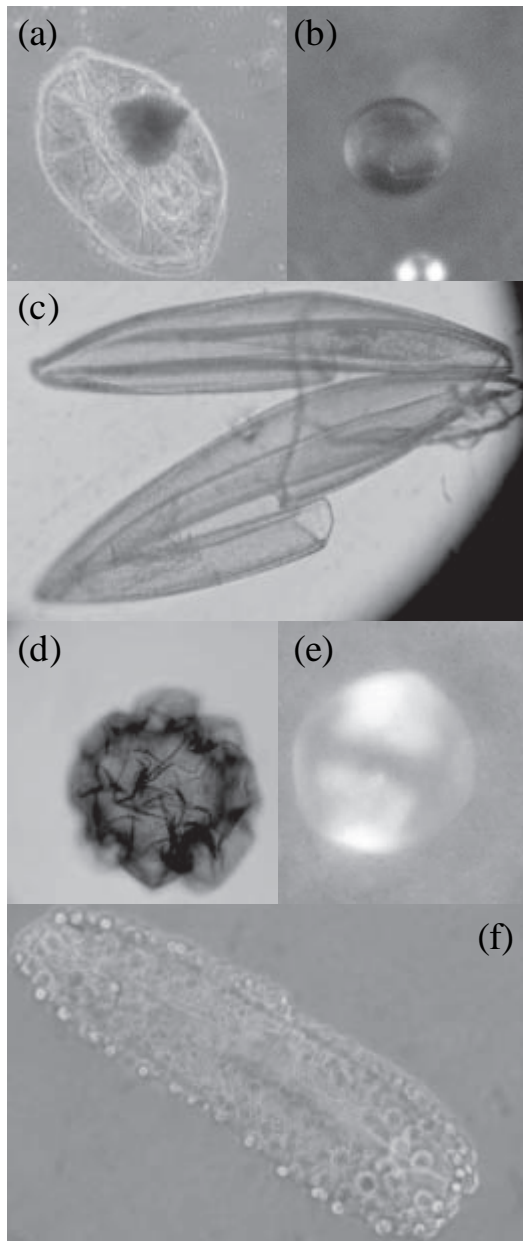
This spherical egg was 120 µm in diameter, and was uniformly and darkly stained.

### LB5

This lozenge-shaped microfossil which was up to 300 µm long was the outer membrane of an unidentifiable, hatched egg.

### LB6

This microfossil was light amber coloured when not stained. It was 160 µm in diameter, and was characterized by extensive flanges giving it a crumpled look. Similar microfossils have



**Figure A1** Light micrographs of (a) LB3; (b) LB4; (c) LB5; (d) LB6; (e) LB10; and (f) LB7

been found in sediments from elsewhere on the continent (L. Cromer, personal communication, 2005).

#### **LB7**

This microfossil appeared as a cylinder *c.* 320  $\mu\text{m}$  long and 70  $\mu\text{m}$  in diameter covered with scattered raised hemispheres 5  $\mu\text{m}$  in diameter. It appears that this microfossil was originally a spherical egg that deformed into a cylinder on hatching.

#### **LB8**

Egg type LB8 was spherical, 150  $\mu\text{m}$  in diameter, opaque, and did not stain.

#### **LB9**

This microfossil was similar to LB3, but had an amber outer area surrounding the stained centre. It was *c.* 120  $\mu\text{m}$  in diameter.

#### **LB10**

This spherical microfossil was *c.* 160  $\mu\text{m}$  in diameter, and was characterized by a distinctive H-shape to the area stained by Rose Bengal.

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