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New insights into the origins of crustaceans of Antarctic lakes

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Abstract: New evidence regarding the origins of the Crustacea of Antarctic lakes is reviewed. Palaeolimnological data indicates that the cladoceran *Daphniopsis studeri* has been present in Lake Reid, Larsemann Hills, for over 120 000 yr. This is the first direct evidence of a continental lacustrine refugium during the last glacial maximum. There are strong indications that the calanoid copepod *Boeckella poppei* maintained populations over the same period in lakes of the Amery Oasis, and the rapid post-glacial colonization by this species of newly formed lakes on the Antarctic Peninsula and Signy Island argues for a local rather than an extra-continental source. Evidence for the entry of marine-derived species into the longer term fauna of the continent is also presented. It is concluded that many of the Crustacea in Antarctic lakes are likely to have had a long association with the continent.

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Introduction

At least eighteen species of Crustacea, including copepods, cladocerans, ostracods and an anostracan, have been found to inhabit lakes of the Antarctic continent or islands offshore from the Antarctic Peninsula (Table I). Two of these (*Harpacticus furcatus* and an unidentified harpacticoid copepod) recorded in nearshore ponds (Pugh *et al*. 2002) possibly do not reproduce in limnetic environments. A further four species are restricted in the Antarctic region to Signy Island (South Orkney Islands: Fig. 1), and one to Signy Island and the South Shetland Islands. Of the remaining eleven species that occur on the Antarctic continent *sensu stricto*, seven occur in freshwater lakes and four in saline lakes.

The origins of the Crustacea that inhabit Antarctic lakes were discussed in a recent review (Pugh *et al.* 2002), in which it was concluded that 'There are no Antarctic palaeoendemic Crustacea', and that all continental species were Holocene colonizers from either marine or extra-continental sources. Pugh *et al.* (2002) noted, however, that species that inhabited Antarctica prior to the Last Glacial Maximum (LGM) may have reinvaded the continent at the end of the glacial period. This is in contrast to terrestrial animal groups, for which pre-Holocene origins without subsequent recolonization have been deduced. For example, the distribution of the endemic Antarctic mite genus *Maudheimia* suggests an ancient radiation followed by vicariant speciation (Marshall & Coetzee 2000). Similarly, the nematode fauna of the continent is nearly entirely endemic (Andrássy 1998), and there is a strong biogeographic divide between the Antarctic Peninsula and the remainder of the continent within this fauna.

In this paper we reconsider the origins of selected Antarctic lacustrine Crustacea in the light of recent evidence that suggests that at least some may have had much longer associations with the continent. In particular, we make use of palaeolimnological data that has provided new insights into the long-term dynamics of some species.

Evidence

Daphniopsis studeri

With the exception of a single lake in Mac.Robertson Land, the continental populations of *Daphniopsis studeri* are restricted to the Vestfold and Larsemann Hills (Fig. 1). The species also occurs on oceanic sub-Antarctic islands of the Indian Ocean (Gibson *et al.* 1998), and Pugh *et al.* (2002) suggested that these were the probable sources for the continental populations.

The recent discovery that some lakes in the Larsemann Hills have been in continual existence for upwards of 120 000 yr (Hodgson *et al.* 2005) raised the question of whether any of the fauna currently present had survived the LGM *in situ*. Cromer *et al.* (2006) approached this question by searching for preserved microfossils and found ephippia and mandibles of *D. studeri* throughout the glacial and interglacial sediments of one of these lakes, Lake Reid. Therefore this species has been present on the Antarctic continent for at least 120 000 yr, and there is no need to necessarily invoke colonization from sub-Antarctic populations.

Daphniopsis studeri is adapted to survival under often

Table I. Species of crustacea reported to occur in Antarctic lakes. This table is updated from Pugh *et al.* (2002), with unconfirmed records and those from marine lagoons removed. Further references are given where there is relevant, more recent information.

Species	Class	Distribution[1]	Saline or Freshwater	References
Branchinecta gaini Daday de Dées	Anostraca	SOI, SSI, AP	Fresh	Peck 2004
Alona weinecki Studer	Anomopoda	SOI, SSI	Fresh	
Daphniopsis studeri Rühe	Anomopoda	VH, LH, MRL	Fresh	
Ilyocryptus brevidentatus Ekman	Anomopoda	SOI	Fresh	Kotov *et al.* 2002
Macrothrix sp.	Anomopoda	SOI, SSI, AP	Fresh	Toro *et al.* 2007
Boeckella poppei (Mrázek)	Copepoda: Calanoida	SOI, SSI, AP, AO	Fresh	Bayly *et al.* 2003
Gladioferens antarcticus Bayly	Copepoda: Calanoida	BH	Fresh	Bayly *et al.* 2003
Parabroteas sarsi (Daday de Dées)	Copepoda: Calanoida	SOI	Fresh	
Paralabidocera antarctica (I.C. Thompson)	Copepoda: Calanoida	VH	Saline	
Acanthocyclops mirnyi Borutsky & Vinogradov	Copepoda: Cyclopoida	BH, VH, LH	Fresh	
Amphiascoides sp.	Copepoda: Harpacticoida	VH	Saline	
Harpacticus furcatus Lang	Copepoda: Harpacticoida	AP	Saline	
Idomene scotti Lang	Copepoda: Harpacticoida	VH	Saline	
Unknown (Laophontidae)	Copepoda: Harpacticoida	VH	Saline	
Unknown	Copepoda: Harpacticoida	SSI	Saline	
Unknown	Copepoda:?	MDV	Fresh	Roberts *et al.* 2004
Eucypris fontana (Graf)	Ostracoda	SOI	Fresh	
Notiocyridopsis frigogena (Graf)	Ostracoda	SOI	Fresh	

[1] Abbreviations: SOI = South Orkney Islands (in particular Signy Island), SSI = South Shetland Islands, AP = Antarctic Peninsula, MDV = McMurdo Dry Valleys, BH = Bunger Hills, VH = Vestfold Hills, LH = Larsemann Hills, AO = Amery Oasis, MRL = Mac. Robertson Land.

difficult conditions. While it can be abundant in productive lakes of the Vestfold Hills (> 30 000 m^{-3}; T. Walker, personal communication 2005), it occurs in ultra-oligotrophic Crooked and Druzhby lakes at far lower densities (< 35 m^{-3}: Bayliss & Laybourn-Parry 1995). *Daphniopsis studeri* can adapt its life history strategy to suit conditions in particular lakes: it overwinters as developing juveniles in Crooked Lake but as adults in nearby Druzhby Lake (Bayliss & Laybourn-Parry 1995). In Lake Reid, *D. studeri* overwinters as ephippial eggs, as the lake becomes completely anoxic under a thick layer of ice in winter (Kaup & Burgess 2003). After ice break out and re-oxygenation of the water column juveniles rapidly appear (J.C. Ellis-Evans, personal communication 1997).

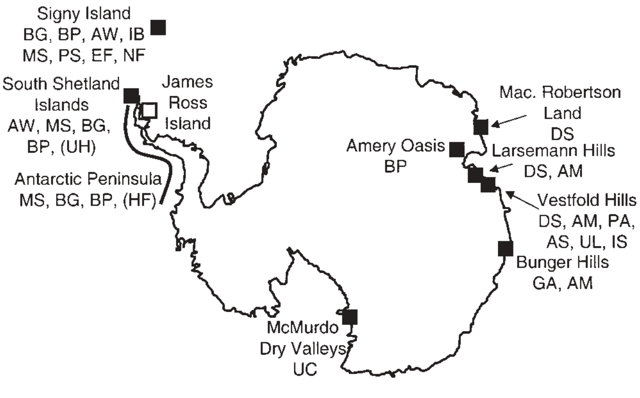

Fig. 1. Map of Antarctica showing the locations mentioned in the text. Filled squares indicate locations with crustacean populations. The species present are indicated by the initials of the generic and specific names (U indicates unknown). The extent of species distributions along the Antarctic Peninsula are indicated by the offshore line. The locations of *Harpacticus furcatus* and the unknown harpacticoid copepod (UH) are shown in brackets to indicate that these species are not widespread and are only found in nearshore ponds. The open square indicates a location mentioned in the text without confirmed crustacean populations.

Daphniopsis studeri is clearly capable of surviving glacial periods in continental refugia. What is not clear from the study of Lake Reid (Cromer *et al.* 2006) is whether the species is a long term (i.e. it has survived multiple glaciations on the continent) or more recent (i.e. it arrived during the previous interglacial) member of the Antarctic fauna. While there is limited evidence that indicates little genetic variation between *D. studeri* on the Antarctic continent and the sub-Antarctic islands (Wilson *et al.* 2002), this study also indicated that *D. studeri* has been isolated from its congeners for *c.* 50 Ma. Clearly *D. studeri* is a true long-term endemic of the broad sub-Antarctic–Antarctic region.

Boeckella poppei

Boeckella poppei is a calanoid copepod that occurs in lakes of South America, the islands of Drake Passage, and the Antarctic Peninsula south to Alexander Island (71°S) (Heywood 1977, Menu-Marque *et al.* 2000). Further, isolated populations, which differ morphologically from South American populations, occur in lakes of the Amery Oasis, East Antarctica (Bayly & Burton 1993, Bayly *et al.* 2003). Pugh *et al.* (2002) concluded that the Antarctic Peninsula populations arose from Holocene colonization, presumably from South America. The Amery Oasis population was adjudged likely to be an anthropogenic introduction.

Recent palaeolimnological evidence has thrown new light on the dynamics of *B. poppei* during the early to mid-Holocene. Jones *et al.* (2000) studied the distribution of microfossils in lakes Heywood and Sombre on Signy Island, and found evidence in the form of empty egg casings for the presence of *B. poppei* in the basal sediments of both lakes. These lakes formed soon after deglaciation of the island, and sedimentation is estimated to have been begun approximately 5500 yr before present (BP). A similar observation was recorded by Gibson & Zale (2006), who found that *B. poppei* has inhabited Lake Boeckella, located at Hope Bay at the northern end of the Antarctic Peninsula, since the formation of this lake, also about 5500 yr ago.

If *B. poppei* were in fact an immigrant from South America, the implication is that dispersal in the early to mid-Holocene was remarkably efficient. However, freshwater calanoid copepods generally have poor dispersal abilities, as indicated, for example, by the distinct faunas of eastern and western Australia (Maly & Bayly 1991). These have been unable to recolonize areas of the continent from which they were separated as long ago as the early Cretaceous (115–110 Ma BP). The disjunct distributional patterns of several South American species (Menu-Marque *et al.* 2000) also indicate poor dispersal. A possible solution to this dilemma is that *B. poppei* reached Antarctica prior to significant deglaciation of the Antarctic Peninsula region and was able to establish populations in proglacial lakes or ponds, a habitat which it rapidly colonizes today (Jones *et al.* 2000). The larger lakes that were formed when more extensive deglaciation commenced were then seeded from these short-lived lakes.

A more parsimonious explanation may be that *B. poppei* survived the last glacial maximum (LGM) in continental refugia. *Boeckella poppei* is an adaptable species, occurring in small, oligotrophic–mesotrophic ponds to large, deep ultra-oligotrophic lakes (Heywood 1977, Bayly *et al.* 2003, Izaguirre *et al.* 2003). It also is known from two epishelf lakes (bodies of fresh water dammed by an ice shelf and floating on denser seawater: Gibson & Andersen 2002, Heywood 1977, Bayly *et al.* 2003). This adaptability means that it may have been able to survive in small, proglacial lakes, and perhaps epishelf lakes dammed by more extensive late Pleistocene ice shelves that have since collapsed. While there is no direct evidence for the survival of *B. poppei* in Antarctic Peninsula refugia, this intriguing possibility is supported by the diverse and unusual nematode fauna of Alexander Island (where *B. poppei* occurs today) (Maslen & Convey 2006). This observation strongly suggests that a long-term ice-free area was present in the area that acted as a refugium at least for nematodes and possibly for other species during the most recent and possibly earlier glaciations.

Further palaeolimnological evidence indicates that *B. poppei* has inhabited Lake Terrasovoje in the Amery Oasis for at least 10 000 yr (recovery of *B. poppei* DNA from lake sediments: Bissett *et al.* 2005), and probably since the onset of biogenic sedimentation over 12 000 yr BP (presence of egg casings and spermatophores: L. Cromer, personal communication 2006). Colonization of this lake therefore pre-dates deglaciation of the Antarctic Peninsula and the earliest records for the occurrence of *B. poppei* there (Jones *et al.* 2000, Gibson & Zale 2006). While colonization of the Amery Oasis from South America or perhaps relict populations on the Antarctic Peninsula is possible, it is more likely that it survived the LGM in a local refugium. Recent cosmogenic isotope data has shown that parts of the oasis have been ice-free for up to 2 Ma (Fink *et al.* 2006), indicating that *B. poppei* could have survived not only the most recent glaciation but also many previous glaciations in the area. While it still cannot be concluded that *B. poppei*, or its ancestors, have been present on the continent since the onset of glaciation, it is likely that the Amery Oasis populations are ancient. Molecular genetic analysis of individuals from the Amery Oasis, Antarctic Peninsula and South America will help to confirm or refute this conclusion.

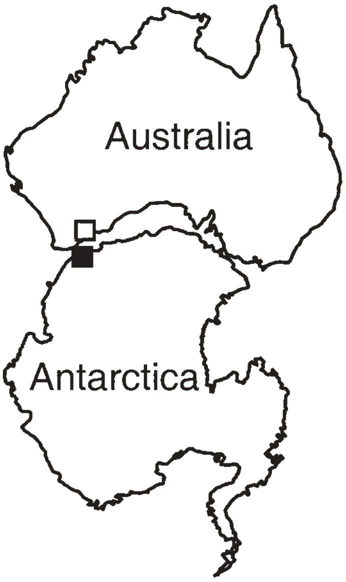

Fig. 2. Partial reconstruction of East Gondwana, showing the close physical relationship between the only known location of *Gladioferens antarcticus* (Bunger Hills: filled square) and the region now inhabited by *Gladioferens imparipes* (open square).

Gladioferens antarcticus

Gladioferens antarcticus is only known from four epishelf lakes in the Bunger Hills (Fig. 1) (Bayly *et al.* 2003), although it may well occur in other, as yet unsampled, epishelf lakes in the area. It appears to be absent from rock-based freshwater lakes of the oasis (Gibson 2000). The genus *Gladioferens* is confined to the Bunger Hills and estuaries along the southern coast of Australia and around

New Zealand, and is apparently absent from the sub-Antarctic islands. None of Australasian species reaches the open ocean, though small numbers of two species occur in neritic waters (Bayly 1994). As noted by Bayly *et al.* (2003), the discovery of *Gladioferens* in Antarctica resulted in a strikingly disjoint distribution for the genus.

Bayly (1994) showed that *G. antarcticus* has significant morphological differences to the other members of the genus, and concluded that it is the most primitive species in its subgenus. Bayly *et al.* (2003) argued that if *G. antarcticus* is a basal species, it could not have colonized Antarctica from an extra-continental site. This is corroborated by the absence of *Gladioferens* from the Southern Ocean, and in particular amongst the inshore marine zooplankton (Razouls *et al.* 2000, K. Swadling, personal communication 2003). Furthermore, the requirement of *G. antarcticus* for fresh or low salinity waters (0.02–4.5‰) (Bayly *et al.* 2003) makes it unlikely that it has recently invaded the freshwater lakes from the marine environment.

Reconstructions of East Gondwana (Fig. 2) indicate that the Bunger Hills lies opposite south-western Western Australia, a region where *G. imparipes* Thomson currently occurs. The most parsimonious conclusion is that *G. antarcticus* (or its forbears) has inhabited the coastline of Antarctica since the separation of Australia and Antarctica *c.* 45 million yr ago. While its ancestors probably inhabited poikilosaline waters, *G. antarcticus* is now adapted to the stable freshwater habitats provided by the epishelf lakes. The continued survival of *G. antarcticus* on the Antarctic continent argues for the existence of epishelf lakes, or similar habitats in which freshwater from summer melt accumulated in lakes, through successive glacial maxima. That part of the Bunger Hills was ice free at the LGM (Gore *et al.* 2001) provides evidence, albeit indirect, for the existence of such habitats (at least for the most recent glacial period) in the immediate area of the modern distribution of *G. antarcticus*.

Paralabidocera antarctica *and other marine-derived copepods*

Colonization of lacustrine environments by marine species involves either physical transport of individuals to supralittoral pools through spray and/or by animal vectors, or through more-or-less passive trapping of animals and subsequent survival in newly-formed lakes resulting from a decrease in local sea level. The records of *Harpacticus furcatus* in Antarctic lakes are thought to be examples of the first mechanism, and probably do not lead to permanent lacustrine populations (Pugh *et al.* 2002). In contrast, the second process has led to reproducing populations in three saline lakes - Ace, Pendant and Abraxas - in the Vestfold Hills that have survived for many thousands of years (Bayly 1978, Swadling *et al.* 2004, Cromer *et al.* 2005). However, there has been little indication that marine species that are trapped in Antarctic lakes could survive glaciations and become part of a longer-term fauna.

The accepted model for the formation of the saline lakes of the Vestfold Hills is that they arose as a result of a drop in sea level after a local mid-Holocene marine highstand (Zwartz *et al.* 1998). Modern Ace and Pendant lakes were isolated 2000–6000 yr BP (Zwartz *et al.* 1998, Coolen *et al.* 2004, Cromer *et al.* 2005). The history of Abraxas Lake is more enigmatic, as the sill between it and the ocean was above the reach of the mid-Holocene marine highstand (Zwartz *et al.* 1998). Pre-LGM sediment has been recovered from this lake (^{14}C dated to > 25 000 cal yr BP; J. Gibson, unpublished data), and the characteristics of the sediment indicate that the lake has existed continuously since that time. It therefore appears that the lake fauna was isolated prior to the LGM. The continued existence of Lake Abraxas through the LGM also implies that at least part of the Vestfold Hills was ice-free throughout this period.

The copepods present in these lakes - *Paralabidocera antarctica*, *Idomene scotti*, *Amphiascoides* sp. and an unidentified member of the Laophontidae (Bayly 1978, Burton & Hamond 1981, Rankin *et al.* 1999) - have undergone some behavioural changes since being trapped, indicating that they are able to adapt to the lacustrine environment. *Paralabidocera antarctica*, for example, has maintained its general life history traits, but has eschewed its typical marine association with ice, in part due to the absence of brine channels in the lake ice (Swadling 2001, Swadling *et al.* 2004). The two harpacticoid copepods in Abraxas Lake provide an interesting contrast. The unidentified Laophontid maintains a benthic habit typical of harpacticoid copepods, whereas *Amphiascoides* sp. thrives in the suboxic zone at the boundary of the oxic and anoxic water of this meromictic lake (Bayly & Eslake 1989). Thus *Amphiascoides* sp. is remarkable in that it is one of very few known planktonic harpacticoid species.

At first glance it would appear that colonization of saline lakes by marine species is unlikely to produce long-term (i.e. surviving through a glacial cycle) members of the continental fauna. Saline lakes are inherently variable environments, and changes in water balance can either lead to hypersaline or hyposaline conditions that may be beyond the tolerance of stenohaline marine species. Euryhaline species are more likely to survive. Cromer *et al.* (2005) showed a general decline in biodiversity in Ace Lake after it was cut off from marine input that was probably in part due to the fluctuating salinity. Other saline lakes in the Vestfold Hills of similar salinities to Ace, Pendant and Abraxas lakes might be expected to contain copepod populations. However, most of these lakes appear to have gone through hypersaline phases (Gibson 1999), and the copepods probably died out. Abraxas Lake is most unusual, in that its salinity has been maintained (at < 45‰) within the tolerance of the marine-derived copepods that have inhabited it since prior to the LGM. Therefore, under these rather unusual conditions, marine-derived copepods have been able to survive glaciation in a lake.

Intriguing evidence for longer term survival of marine-derived species in Antarctic lakes was observed in the study of ancient copepod DNA extracted from the sediment of freshwater Lake Terrasovoje, Amery Oasis (Bissett *et al.* 2005). This study found that an unidentified calanoid copepod with DNA that grouped very closely with that of *P. antarctica* was present from the formation of the lake until *c.* 3000 yr BP. Furthermore, faecal pellets of very similar morphology to those of modern *P. antarctica* from Ace Lake (Cromer *et al.* 2005) were observed through most of the core, but not in sediments formed since 3000 yr BP. While the unknown species was not necessarily *P. antarctica*, it was clearly an acartiid that had adapted to a freshwater environment, contrasting with all other members of the family, which are marine. This enigmatic species is neither present in modern Lake Terrasovoje nor in any other lakes of the area that have been sampled (Bayly *et al.* 2003).

The probable explanation for the occurrence of an acartiid in Lake Terrasovoje is that *P. antarctica*, or a related marine species, colonized a saline lake in the northern Prince Charles Mountains prior to the most recent glacial maximum and possibly much earlier (Fink *et al.* 2006). This euryhaline acartiid adapted to existence at lower salinities, and was eventually able to become a part of the freshwater fauna of the region. It survived glaciations in local refugia (as did *B. poppei*), and was able to colonize Lake Terrasovoje soon after its late Pleistocene formation (Wagner *et al.* 2004). An as yet unknown environmental stress(es) resulted in its extinction (but not that of *B. poppei*) in Lake Terrasovoje.

It is clear that this originally marine species successfully colonized at least one continental lake and was able to survive the LGM in a local refugium. Along with the apparent pre-LGM origin for copepods in Lake Abraxas, this suggests that the other Crustacea found in saline lakes should not be viewed merely as 'marine interlopers' (*sensu* Pugh *et al.* 2002) but rather the possible precursors of similar long-term populations.

Other species

Evidence for the mid- to late Holocene presence of the anostracan *Branchinecta gaini* has been reported for five lakes in the Maritime Antarctic. In addition to *B. poppei* eggs, Jones *et al.* (2000) recorded eggs of *B. gaini* in the basal sediments of Sombre and Heywood Lakes on Signy Island in the South Orkney archipelago, deposited 5500 yr BP. *Branchinecta gaini* has remained a component of the fauna of these lakes throughout their late Holocene histories. *Branchinecta* spp. eggs were also observed in the sediments of Keyhole Lake, Boulder Lake and Hidden Lake on James Ross Island from *c.* 4200 yr BP (Keyhole Lake), though the anostracan does not occur now in these lakes or indeed elsewhere on the eastern side of the Antarctic Peninsula (Björck *et al.* 1996).

These data clearly suggest that, like *B. poppei*, *B. gaini* was able to colonize new lakes on the Antarctic Peninsula and Signy Island that were formed soon after the mid-Holocene deglaciation. While colonization from further north cannot be ruled out, *B. gaini* may have survived on the Antarctic Peninsula through the LGM in a similar manner to that proposed above for *B. poppei*. *Branchinecta gaini* is highly adapted to survival in small and shallow Antarctic ponds (Peck 2004), while its eggs survive freezing, which provides an essential over-wintering strategy. These attributes could well have contributed to survival of glacial periods as clearly these animals should have been able to take advantage of small pools of water that were formed perhaps only in some years. As yet, however, there is no direct evidence for the continued existence of *B. gaini* on the continent through the LGM.

There is also no direct evidence for the origins of the Cladocera that inhabit maritime Antarctic lakes. However, Gibson & Zale (2006) recorded the repeated, though ultimately unsuccessful, colonization of Lake Boeckella by *Eubosmina chilensis* (Daday de Dées), a cladoceran that does not occur in the present day Antarctic or sub-Antarctic. Cladocera produce resting (ephippial) eggs that are resistant to desiccation and other environmental stresses associated with long distance transport clearly evident for *E. chilensis*, and probable for other Cladocera that have colonized lakes of the Antarctic Peninsula.

The known distribution of Crustacea on the Antarctic continent was extended recently when Roberts *et al.* (2004) provided the first positive record of a copepod from the lakes of the McMurdo Dry Valleys. Unidentified nauplii were found in samples from Lake Joyce, but the absence of adults in the collections meant that the species' identity remains unknown. The lack of adults either reflects a typically benthic habit, or a temporal absence resulting from the species' reproductive strategy. This observation, of copepod nauplii in a single, poorly-studied lake, does not preclude the other lakes in the area being crustacean-free. However, identification of this species could well have major biogeographical implications, in particular as the lakes of the McMurdo Dry Valleys have long (300 000 yr) and complex histories (Hendy 2000).

Conclusions

Recent evidence from both continental and peninsular Antarctica strongly suggests that many of the Crustacea that inhabit the lakes of the continent could well been *in situ* prior to the LGM and possibly for much longer. While incontrovertible proof has been shown in only one case (*Daphniopsis studeri* in the Larsemann Hills), the evidence for some other cases, notably *Gladioferens antarcticus* and continental populations of *Boeckella poppei*, is compelling.

Bayly & Burton (1993) concluded, with respect to Antarctic freshwater zoogeography, that "vicariance rather than dispersal may yet prove to be the most parsimonious and reasonable explanation". The evidence in favour of this view is now much stronger. Although dispersal may have played some role, it is unlikely to have been as important as many have hitherto supposed. What is now needed are further palaeolimnological and DNA-based phylogenetic studies.

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