

***Diacyclops* (Copepoda: Cyclopoida) in Continental Antarctica, including three new species**

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Abstract: Contrary to earlier beliefs, crustaceans are present in ice-covered lakes of Antarctica. Interpretation of the significance of this has been hampered by the absence of robust identification of taxa present. We examine cyclopoid copepods from three widely separated lakes. All belong to the *michaelseni* group of the genus *Diacyclops*, which is widespread across Continental Antarctica, but do not fit into any existing species. Two new species were identified from eastern Antarctica, *D. walkeri* from Pineapple Lake (Vestfold Hills) and *D. kaupi* from Transkriptsii Gulf (Bunger Hills). Most significant was a dense population of a new epibenthic species (*D. joycei*) associated with microbial mats in Lake Joyce, one of the smaller McMurdo Dry Valleys lakes. This represents the first record of adult cyclopoid copepods from the ice-covered lakes of the Transantarctic Mountains. Continental Antarctica is the centre of diversity for this group of crustaceans and we argue that this is better explained by persistence through past glacial advances rather than by recent post-glacial colonization. The existence of a species endemic to Lake Joyce but apparently absent from other Dry Valleys lakes is discussed in relation to our understanding of the history of the McMurdo Dry Valleys lakes and their faunas.

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Introduction

The factors controlling the distribution of crustaceans in freshwater Antarctic lakes are thought to involve both environmental and biogeographical components. The lakes are often considered harsh environments, where water temperatures are persistently close to zero, whilst long periods of perennial ice-cover and strong seasonality in light availability for primary productivity places severe constraints on the ability of these environments to support complex Metazoa (Magalhães *et al.* 2012). The geographical isolation of many of the lakes is another barrier to colonization, either from elsewhere on the continent or from extra-continental sources. Many of the crustaceans that might inhabit freshwater lakes, such as calanoid and harpacticoid copepods, are known to be poor colonizers that would not be expected to be able to cross the long distances involved (Karanovic & Cooper 2012, Karanovic & Krajčec 2012). The net result of these factors is that there is only a limited suite of species known to occur on the Antarctic continent (Gibson & Bayly 2007). Nearly all of the records of crustaceans are for lakes in

coastal ice-free areas (also termed ‘oases’; see Parker *et al.* 1982), such as the Vestfold and Larsemann hills and along the Antarctic Peninsula (see Fig. 1). In two cases, the Bunger Hills and the northern Prince Charles Mountains, the lakes are in nominally coastal oases that are separated from the open ocean by extensive floating ice shelves.

In recent years, discussion of the origins of modern crustacean communities has begun to address the extent to which the extant fauna is a consequence of colonization from outside the Antarctic since the Last Glacial Maximum (LGM, c. 19–22 Kyr BP) or contains elements that survived the LGM in continental refugia and have subsequently expanded (Bayly *et al.* 2003, Gibson & Bayly 2007, Convey *et al.* 2008). Many of the current freshwater lakes of the Antarctic Peninsula, for example, show strong links to those of South America and nearby sub-Antarctic islands, with no endemic species, and are consistent with relatively recent colonization (Gibson & Bayly 2007). In contrast, the current fauna of coastal oases of Continental Antarctica appear more likely to have resulted from the long-term survival of lacustrine crustaceans on the continent, possibly since prior to the LGM (Convey *et al.* 2008).

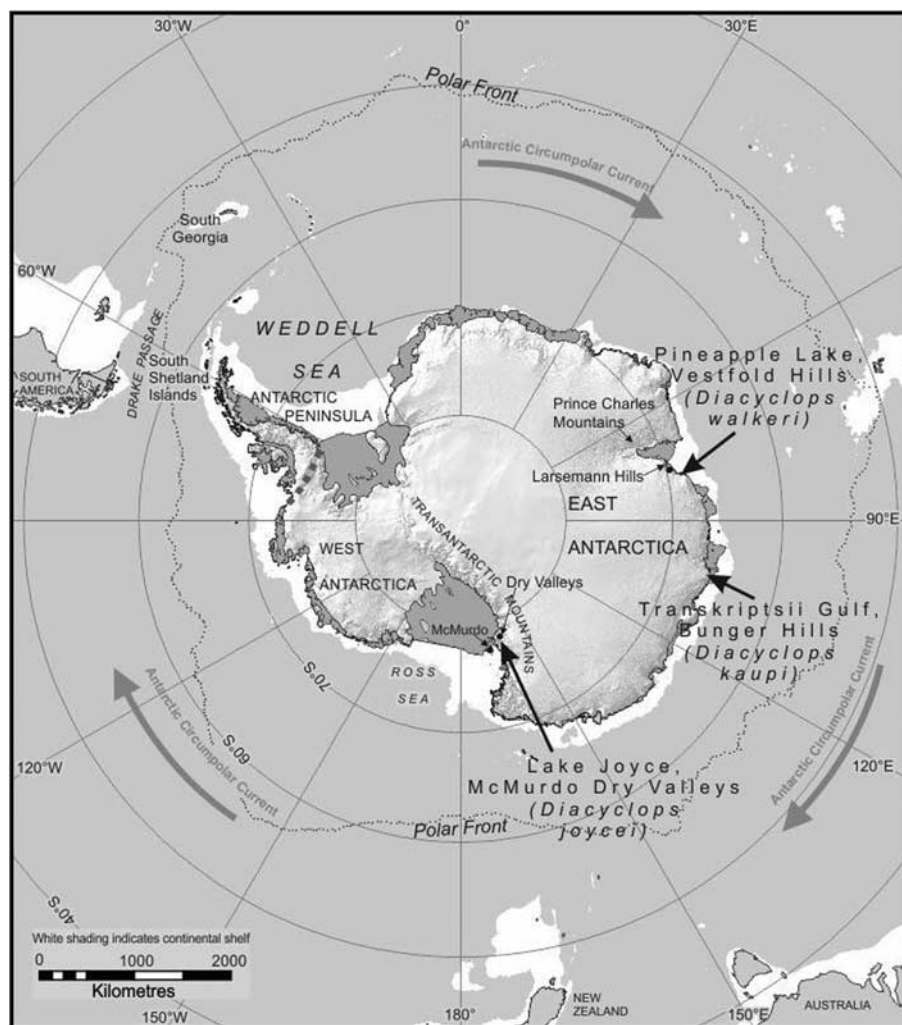


Fig. 1. Map of the Antarctic continent showing sample collection sites and other locations referred to in the text.

In particular, the calanoid copepod *Gladioferens antarcticus* Bayly 1994, which has been recorded in only a few lakes of the Bunger Hills (see Fig. 1 for location) (Bayly *et al.* 2003), is morphologically primitive compared to Australian congeners, and it has been concluded that this species has persisted on the continent since the separation of Australia and Antarctica approximately 65 million years ago (Gibson & Bayly 2007). Similarly, it has been shown that the isolated populations of *Boeckella poppei* (Mrázek, 1901) in three lakes in the northern Prince Charles Mountains are not a recent anthropogenic introduction as once suggested (Pugh *et al.* 2002), but probably pre-date the LGM (Cromer *et al.* 2006, Gibson & Bayly 2007). Such conclusions are supported by the increasing awareness that many of the currently ice-free areas on the Antarctic continent remained, at least in part, ice-free at the LGM (e.g. Gore *et al.* 2001, Stevens *et al.* 2006), and therefore may have provided refugia for survival through the last glacial cycle and possibly over much longer periods (Convey *et al.* 2008).

Some of the most intensively studied Antarctic lakes are in the McMurdo Dry Valleys, the largest ice-free area on the Antarctic continent (Burnett *et al.* 2006, Bockheim *et al.* 2008). Repeated sampling for over 40 years had failed to find a single crustacean, and the lakes were widely believed to be free of copepods, cladocera or other crustaceans (Cathey *et al.* 1981). This absence from the lakes of the McMurdo Dry Valleys was often interpreted in terms of the considerations discussed above. The lakes in this area are also thought to be variable features, with a series of high and low stands resulting from shifts in hydrological conditions since the LGM. The most recent high stands are dated at 2000–3000 ^{14}C yr BP (Hall *et al.* 2010), while low stands, which tend to be associated with either complete drainage or evaporation of lakes to small, hypersaline ponds, generally occurring 1000–2500 cal yr BP. Since then the lakes have re-established relatively fresh upper layers, and this short period for colonization combined with geographic isolation of the Dry Valleys and the perennial ice cover on most of the lakes of the area

were given as reasons for the absence of crustaceans. It was, therefore, a surprise when Roberts *et al.* (2004) reported the occurrence of juvenile copepods in one of the least studied lakes of the area, Lake Joyce. No adults were collected in that study, which also sampled other McMurdo Dry Valleys lakes intensively without locating any copepods, and no conclusions could be drawn about the species present. However, the observation implied a breeding population of copepods in the lake, which indicated that a reconsideration of the ability of crustaceans to colonize and survive in lakes of the area was necessary. Later, Hansson *et al.* (2011) reported collecting a single sub-adult calanoid copepod (as *Boeckella* sp.) from the nearby Lake Hoare, suggesting that crustaceans may be more widely distributed and diverse in this region than previously thought.

During the Antarctic summer of 2010–11, adult copepods were collected from Lake Joyce. These were initially identified to belong to the genus *Diacyclops* Kiefer, 1927. This genus was already known to occur on the Antarctic continent: *Diacyclops mirnyi* (Borutzky & Vinogradov, 1957) was described (as *Acanthocyclops mirnyi*) from samples collected from a freshwater lake in the Bunger Hills (Borutzky & Vinogradov 1957), and this species was subsequently reported to occur in the Vestfold Hills (Borutzky 1962) and Larsemann Hills (Dartnall 1995). In the current paper, we report a morphological study of animals collected from Lake Joyce, Transkriptsii Gulf in the Bunger Hills, and Pineapple Lake in the Vestfold Hills. No samples were available from the Larsemann Hills and, unfortunately, the type material of *D. mirnyi* appears to have been lost (Alexey Kotov, personal communication 2012). Here we describe three new species of *Diacyclops* from Antarctica, for which we provide detailed descriptions. An analysis of the morphological similarities and differences between these and other species of *Diacyclops* is given, along with comments on the biogeography of the group to which these new species belong.

Study locations

Samples of copepods were obtained from Lake Joyce in the McMurdo Dry Valleys (77.720°S 161.624°E); Transkriptsii Gulf, Bunger Hills (66.237°S 100.593°E); and Pineapple Lake, Vestfold Hills (68.655°S 78.222°E) (Fig. 1).

Lake Joyce is a pro-glacial, perennially ice-covered, meromictic lake with a maximum depth of *c.* 40 m. Lake chemistry is characterized by fresh, hyperoxic waters overlying an anoxic sodium chloride (NaCl) brine (Shacat *et al.* 2004). The ice ranges from 5–6 m thick and immediately below this the upper waters have an unusually high pH, sometimes exceeding 10, that declines to around neutral in the anoxic water. Spigel & Priscu (1998) provided high resolution density profiles for Lake Joyce that, in December 1993, showed a complex salinity-based structure to the water column. When we visited the lake in November 2010 it

comprised an upper mixed layer from below the ice to 10 m depth, conductivity 0.4 mS cm⁻¹, separated by a 2 m density gradient from a second mixed layer from 12 to 14 m (0.8 mS cm⁻¹), below which the water was amictic and conductivity gradually increased to 7.3 mS cm⁻¹. Hendy & Hall (2006) provide ¹⁴C dates for dissolved inorganic carbon that constrain its deepest water age to within the last few thousand years, with surface waters emerging as modern. The biota of Lake Joyce includes a sparse phytoplankton, dominated by flagellates, that is dispersed within the upper part of the water column (Roberts *et al.* 2004). The lake also has a significant benthic biota with abundant oscillatorian cyanobacteria and pennate diatoms (Wharton 1994), sometimes forming complex calcified structures. Microbial mats in the shallower parts of Lake Joyce are dominated by *Leptolyngbya* cf. *antarctica*, *Oscillatoria* cf. *sancta* and *Phormidium* cf. *autumnale* in declining order of abundance.

Transkriptsii Gulf is a large epishelf lake located on the western edge of the southern Bunger Hills. An epishelf lake is a body of freshwater that maintains a hydraulic connection with the ocean under an ice shelf or floating glacier, and is thus tidal (Gibson & Andersen 2002). The western margin of Transkriptsii Gulf is ice of the Edisto Glacier, a component of the Shackleton Ice Shelf. Transkriptsii Gulf is over 120 m deep, and has a permanent ice cover that was 2.6 m thick in 1992, increasing to 3.9 m by January 2000. Physical profiles recorded in January 2000 indicated that the water temperature was less than 0.4°C throughout, and that 83 m of water of salinity 1.0 g l⁻¹ overlaid more saline water (Gibson & Andersen 2002). The maximum measured salinity at the base of the water column approached 30 g l⁻¹. Little is known about the biology of the lake, though chlorophyll *a* levels of less than 0.3 µg l⁻¹ were reported by Klokov *et al.* (1990).

Pineapple Lake is a poorly known epishelf lake on the southern margin of the Vestfold Hills, with tidal activity evidenced by tide cracks clearly observable in Google Earth images. The southern margin of the lake is ice of the Sørsdal Glacier. The lake has a maximum recorded depth of 29 m, a salinity of less than 0.1 g l⁻¹, and when sampled in December 2010 had an ice cover 2.8 m thick.

Diacyclops specimens occur in many other lakes of the Vestfold and Bunger hills, but are yet to be examined by expert taxonomists.

Material and methods

Sampling

Sampling of Lake Joyce was undertaken in November 2010. Initially, samples of microbial (cyanobacterial) mat from 6–8 m depth were collected by SCUBA divers operating through a hole made through the 5 m thick ice cover, and returned to the lake surface in sealed plastic boxes. In a laboratory tent on the lake ice, these samples

were searched using a binocular microscope; individual copepods were removed using a pipette, rinsed in lake water and preserved in 70% ethanol. To obtain some information on the distribution of copepods, we made repeated vertical hauls with a 50 µm mesh plankton net and deployed simple traps made from weighted, opaque 250 ml Nalgene bottles. Six replicate traps were laid on their sides on the microbial mat covering the lake floor at each of 6, 11, 17 and 21 m depth by SCUBA divers and left in place with their tops off for 24–48 hours. After this time the divers carefully closed the bottles, then returned them to the lake surface where the copepods were counted. No traps were set in open water.

At the outset of sampling on 10 November 2010, adult males and females were observed, and at that time several females were noted to bear eggs. Ovigerous females were not taken in late November. No copepods were taken in the vertical plankton net hauls, rather all seemed to be epibenthic in habit and consistently associated with the cyanobacteria-dominated microbial mats. Depth profiles were consistent with this, of a total catch of 64 animals taken in traps in late November, 51 were taken at 6 m (8.5 ± 3.2 per trap; mean \pm standard deviation), ten at 11 m (1.7 ± 1.9), two at 17 m, and one at 21 m. Active cyanobacterial biomass is largely restricted to depths shallower than 16 m, while the 5 m ice cover precludes organisms from shallower depths.

Samples were collected from Transkriptsii Gulf, Bunger Hills, on 19 March 1992 using a zooplankton net deployed through a hole drilled in the ice cover, and were preserved in 4% aqueous formaldehyde. Between sampling each lake the net was rinsed in boiling water followed by an ethanol rinse and drying/freezing.

Samples were collected from Pineapple Lake, Vestfold Hills, on 24 December 2010 using a 100 µm mesh conical zooplankton net deployed through a hole drilled in the ice cover. The net was hauled from 23 m to the surface and nine individuals were collected.

Taxonomy

Specimens were dissected and mounted on microscope slides in Faure's medium. For the urosome or the entire animal, two human hairs were mounted between the slide and coverslip, so the parts would not be compressed. By manipulating the coverslip carefully by hand, the whole animal or a particular appendage could be positioned in different aspects, making the observation of morphological details possible. During the examination the water slowly evaporates and the appendages eventually remain in a completely dry Faure's medium, ready for long-term storage. All line drawings were prepared using a drawing tube attached to a Leica MB2500 phase-interference compound microscope, equipped with N-PLAN (5x, 10x, 20x, 40x and 63x dry) or PL FLUOTAR (100x oil) objectives. Specimens that were not drawn were examined in propylene glycol and, after examination, were preserved in 99.9% ethanol. Specimens for scanning electron microscopy (SEM)

were dehydrated through an ethanol series, transferred to pure isoamyl-acetate, critical-point dried, mounted on stubs, and coated in gold using a sputter coater Cressington 108auto. Most specimens were observed under a Hitachi S-2380N SEM microscope on the in-lens detector, with an accelerating voltage of 8 kV; black and white photographs were taken on film (Kodak Tri-X 400 pro) and subsequently scanned. Some specimens were observed under Jeol JSM-6330F field emission SEM microscope, with accelerating voltage of 5 kV; micrographs were captured via the built-in digital camera. All examined specimens are deposited in the Western Australian Museum (WAM) in Perth, Australia.

Morphological terminology follows Karanovic (2006). Sensilla and pores on all somites (body segments) were numbered consecutively from the anterior to posterior part of the body and from the dorsal to ventral side, to aid in the recognition of serially homologous structures and future comparisons with other species; they are not intended as a novel terminology (see Karanovic *et al.* 2013). Only the first presented species is described in full, while two subsequent descriptions are shortened by making them comparative (Appendix S1 which can be found at <http://dx.doi.org/10.1017/S0954102013000643>).

Systematics

Diacyclops kaupi n. sp. (Figs S2–S12, Appendix S1)

Type locality: Antarctica, Bunger Hills, Transkriptsii Gulf, 66.237°S 100.593°E; freshwater epishelf lake.

Type material: Holotype female dissected on one slide (WAM C47229). Allotype male also dissected on one slide (WAM C47230). Other paratypes are five males, two females and 64 copepodids in alcohol (WAM C47231), one male dissected on one slide (WAM C47232), one female dissected on one slide (WAM C47233), one male on one slide *in toto* (WAM C47234), and two males and two females on one SEM stub (WAM C47235), together with specimens of *D. walkeri* n. sp. and *D. joycei* n. sp. (see below); all collected at type locality; leg. D. Andersen, 19 March 1992.

Diagnosis: Surface ornamentation of somites consisting of 80 pairs and eight unpaired (mid-dorsal) pores and sensilla. Habitus relatively slender, not dorso-ventrally compressed, with prosome/urosome ratio 1.2 and greatest width in dorsal view at mid-length of cephalothorax. Genital double-somite with deep lateral recesses at level of sixth legs and without dorsal sclerotized flange; seminal receptacle with rounded anterior expansion. Anal operculum small, short, slightly convex, representing from 45–50% of anal somite width. Caudal rami cylindrical, parallel, very close, *c.* 4.7 times as long as wide and 2.4 times as long as anal somite, ornamented with several rows of slender spinules along inner margin and on ventral surface; dorsal seta about 0.85 times as long as ramus; outermost terminal seta 0.7 times as long as

ramus; innermost terminal seta 1.2 times as long as outermost terminal seta; principal terminal setae without breaking planes, inner one about 1.7 times as long as outer one and 4.4 times as long as caudal rami. Female antennula 11-segmented, with armature formula 8.4.8.4.2.2.3.2 + ae.2.3.7 + ae (ae = aethetasc). All swimming legs with three segmented endopods and exopods, third exopodal segment spine formula 2.3.3.3 and setal formula 4.4.4.4. First swimming leg with one seta on second endopodal segment. Fourth swimming leg with inner seta on first exopodal segment; third endopodal segment *c.* 2.3 times as long as wide and 1.4 times as long as second endopodal segment, with parallel apical spines, inner apical spine 1.24 times as long as outer, almost as long as segment, and less than 0.4 times as long as distal inner seta. Fifth leg inserted ventro-laterally, relatively small, two-segmented; first segment much narrower at base than at distal part, almost trapezoidal in shape, as long as greatest width, ornamented with single pore on anterior surface close to proximal margin, armed with single outer slender seta, inserted on substantial outer protopodal protrusion; second segment cylindrical, 1.2 times as long as first segment and 2.4 times as long as wide, unornamented, armed with apical long seta and subapical inner spine; apical seta 1.3 times as long as protopodal seta, 3.6 times as long as second segment, and more than 10 times as long as subapical spine; subapical spine strong and bipinnate, 0.7 times as long as second segment. Full species description in Appendix S1.

Etymology: The species is named in honour of Dr Enn Kaup, Estonian limnologist, who has studied Antarctic lakes, including those of the Bunger Hills, over many years. The name is a noun in the genitive singular.

Diacyclops walkeri n. sp. (Figs S13–S18, Appendix S1)

Type locality: Antarctica, Vestfold Hills, Pineapple Lake, 68.655°S 78.222°E; freshwater epishelf lake.

Type material: Holotype female dissected on two slides (WAM C47236). Allotype male also dissected on two slides (WAM C47237). Other paratypes are three copepodids in alcohol (WAM C47238), one male dissected on one slide (WAM C47239), and one male on one SEM stub (WAM C47235), together with specimens of *D. kaupi n. sp.* and *D. joycei n. sp.*; all collected at type locality; leg. J. van den Hoff, 24 December 2010.

Diagnosis: Surface ornamentation of somites consisting of 62 pairs and three unpaired (mid-dorsal) pores and sensilla. Habitus robust, not dorso-ventrally compressed, with prosome/urosome ratio 1.5 and greatest width in dorsal view at first third of cephalothorax. Genital double-somite with deep lateral recesses and without dorsal sclerotized flange; seminal receptacle with rounded anterior expansion. Anal operculum small, short, slightly convex, representing *c.* 50% of anal somite width. Caudal rami cylindrical, parallel,

very close, 4.8 times as long as wide and 2.5 times as long as anal somite, ornamented with several rows of slender spinules along inner margin and on ventral surface; dorsal seta 1.2 times as long as ramus; outermost terminal seta 0.6 times as long as ramus; innermost terminal seta 1.2 times as long as outermost terminal seta; principal terminal setae without breaking planes but outer principal terminal seta with small outer nob; inner principal terminal seta almost 3.5 times as long as outer one and 4.8 times as long as caudal rami. Female antennula 11-segmented, with armature formula 8.4.8.4.2.2.3.2 + ae.2.3.7 + ae. All swimming legs with three segmented endopods and exopods, third exopodal segment spine formula 2.3.3.3 and setal formula 4.4.4.4. First swimming leg with one seta on second endopodal segment. Fourth swimming leg with inner seta on first exopodal segment; third endopodal segment 2.5 times as long as wide and 1.35 times as long as second endopodal segment, with parallel apical spines, inner apical spine 1.23 times as long as outer, slightly longer than segment, and 0.45 times as long as distal inner seta. Fifth leg inserted ventro-laterally, relatively small, two-segmented; first segment much narrower at base than at distal part, almost trapezoidal in shape, as long as greatest width, ornamented with single pore on anterior surface close to proximal margin, armed with single outer slender seta, inserted on substantial outer protopodal protrusion; second segment cylindrical, 1.1 times as long as first segment and 2.5 times as long as wide, unornamented, armed with apical long seta and subapical inner spine; apical seta 1.2 times as long as protopodal seta, almost 4 times as long as second segment or subapical spine; subapical spine strong and bipinnate, almost as long as second segment. Full species description in Appendix S1.

Etymology: This species is named in honour of Dr Terry Walker, Australian scientist, who was the first to recognize that the species of *Diacyclops* present in the lakes of the Vestfold Hills differed from *D. mirnyi*. The name is a noun in the genitive singular.

Diacyclops joycei n. sp. (Figs S19–27, Appendix S1)

Type locality: Antarctica, McMurdo Dry Valleys, Lake Joyce, 77.720°S 161.624°E; freshwater proglacial lake.

Type material: Holotype female dissected on two slides (WAM C47240). Allotype male also dissected on two slides (WAM C47241). Other paratypes are four males, seven females and 18 copepodids in alcohol (WAM C47242), one male dissected on one slide (WAM C47242), one male on one slide *in toto* (WAM C47243), and two males and four females on one SEM stub (WAM C47235), together with specimens of *D. kaupi n. sp.* and *D. walkeri n. sp.*; all collected at type locality; leg. I. Hawes, 3 November 2010.

Diagnosis: Surface ornamentation of somites consisting of 53 pairs of pores and sensilla. Habitus dorso-ventrally compressed, with cephalothoracic shield and pleurons of

free prosomites flared laterally; prosome/urosoma ratio 1.5 and greatest width in dorsal view at posterior end of cephalothorax. Genital double-somite with prominent central dorsal fringe; seminal receptacle butterfly-shaped, with relatively short but wide anterior expansion and slightly longer but medially more constricted posterior expansion. Anal operculum strongly convex, almost reaching posterior margin of anal somite, representing 50% of anal somite width. Caudal rami cylindrical, parallel, relatively close, *c.* 4 times as long as wide, with inner margin and ventral surface completely smooth; dorsal seta 0.85 times as long as ramus; outermost terminal seta 0.7 times as long as ramus; principal terminal setae with breaking planes, inner principal terminal seta almost 1.9 times as long as outer one and 4.1 times as long as caudal rami. Female antennula 11-segmented, with armature formula 8.4.8.4.2.2.3.2 + ae.2.3.7 + ae. All swimming legs with three segmented endopods and exopods, third exopodal segment spine formula 2.3.3.3 and setal formula 4.4.4.4. First swimming leg with one seta on second endopodal segment. Fourth swimming leg without inner seta on first exopodal segment; third endopodal segment much wider proximally, *c.* 1.7 times as long as wide and 1.5 times as long as second endopodal segment, its setae only slightly reaching beyond distal tips of apical spines; apical spines slightly divergent; inner apical spine 1.24 times as long as outer apical spine, about as long as segment, and nearly 0.7 times as long as distal inner seta. Fifth leg inserted ventro-laterally, relatively small, two-segmented; first segment narrower at base than at distal part, almost trapezoidal in shape, as long as greatest width, ornamented with row of spinules at base of second segment and single pore on anterior surface, armed with single outer slender seta, inserted on short outer protopodal protrusion; second segment almost cylindrical, about as long as first segment and twice as long as wide, unornamented, armed with apical long seta and subapical inner spine; apical seta 1.2 times as long as protopodal seta, 3.6 times as long as second segment or subapical spine; subapical spine strong and bipinnate, almost as long as second segment. Full species description in Appendix S1.

Etymology: The species is named after Ernest Joyce, Antarctic explorer with Scott and Shackleton, who was a great Antarctic survivor. Lake Joyce is also named after Ernest Joyce. The name is a noun in the genitive singular.

Species affinities

Similarities of and differences between the three new species

There is no doubt that *D. kaupi* and *D. walkeri* are much more closely related to each other than either of them is to *D. joycei*. As most of the morphological differences were mentioned in their comparative descriptions and are pointed to with arrows in the line drawings (Figs S2–27, Appendix S1), only some of the more important differences are highlighted here.

Diacyclops joycei is characterized by a dorso-ventrally compressed habitus, which is markedly different to those of the other two species. *Diacyclops kaupi* and *D. walkeri* share the same non-flattened habitus, elongated caudal rami ornamented with long spinules on inner margin and ventrally rounded anterior part of the receptacle seminis, extremely long setae on the third endopodal segment of the fourth leg, inner seta present on the first exopodal segment of the fourth leg, smooth basal segment of the fifth leg, and very similar pore and sensilla pattern on most somites. They differ mostly in the proportions of the caudal rami armature, with the outer principal terminal setae being very short in *D. walkeri* and the dorsal setae very long.

Affinities of the new species to other members of Diacyclops

Diacyclops kaupi, *D. walkeri* and *D. joycei* all belong to the *D. michaelsoni* group of species as defined by Borutzky & Vinogradov (1957) and later amended by Morton (1985). *Diacyclops* is the largest cyclopoid genus in freshwater habitats (100+ species), cosmopolitan in distribution, with a centre of diversity in the temperate Palaearctic region (Karanovic 2006). The genus is most probably polyphyletic (Karanovic *et al.* 2013). The *michaelsoni* group (Morton 1985) is a circum-Antarctic assemblage, characterized by 11-segmented female antennulae, all swimming legs three-segmented and slender fourth swimming legs. The following taxa have previously been included in the group:

Diacyclops michaelsoni (Mrázek, 1901)

Diacyclops skottsbergi (Lindberg, 1949)

Diacyclops mirnyi (Borutzky & Vinogradov, 1957)

Diacyclops cryonastes Morton, 1985.

Mrázek (1901) described *D. michaelsoni* (as *Cyclops michaelsoni*) from small freshwater ponds in Tierra del Fuego and the Falkland Islands, without defining the type locality. It has been regularly recorded from the Falkland Islands (Dartnall & Hollwedel 2007), and may also occur on Iles Kerguelen in the southern Indian Ocean (Pugh *et al.* 2002). Today there are two accepted synonyms of this species: *Cyclops lobulosus* Ekman, 1905, described also from Tierra del Fuego and the Falkland Islands (Ekman 1905), and *Cyclops michaelsoni* var. *falklandi* T. Scott, 1914, described from the Falkland Islands (Scott 1914). Lindberg (1949) described *D. skottsbergi* (as *A. skottsbergi*) from a single damaged male from the Pera River estuary in Patagonia and considered it closely related to *D. michaelsoni*. Without females we cannot be sure that this species belongs to the *michaelsoni* group, but there is no doubt that this is a valid species in the genus *Diacyclops*. Borutzky & Vinogradov (1957) described *D. mirnyi* (as *A. mirnyi*) from a freshwater lake in the Bunge Hills in Antarctica (Fig. 1). The species was later recorded from Crooked Lake in the Vestfold Hills (Borutzky 1962), other lakes in the Vestfold Hills and from lakes in the Larsemann

Hills (Dartnall 1995). There is also a possible record from the Falkland Islands (Dartnall & Hollwedel 2007). Finally, Morton (1985) described *D. cryonastes* from several localities in Tasmania and high alpine areas in Victoria and southern New South Wales, Australia. There are also records of *D. cryonastes* at lower latitude and altitude from subterranean waters in Tamworth and Hunter Valley in New South Wales (T. Karanovic, unpublished data).

Diacyclops kaupi differs from *D. michaelsoni* by the following characteristics: longer caudal rami with inner spinules, much longer setae on the third endopodal segment of fourth leg, parallel apical spines on the third endopodal segment of fourth leg and different shape of the inner process on basis of fourth leg. It differs from *D. skottsbergi* by longer caudal rami and shorter innermost apical setae on them. From *D. mirnyi* it differs by the following characteristics: longer caudal rami with inner spinules, longer setae on the third endopodal segment of fourth leg, parallel apical spines on the third endopodal segment of fourth leg and different shape of the receptaculum seminis. Finally, *D. kaupi* differs from *D. cryonastes* by longer caudal rami with inner spinules, proportionately shorter innermost terminal setae on the caudal rami, much longer setae on the third endopodal segment of fourth leg, parallel apical spines on the third endopodal segment of fourth leg, different shape of the inner process on basis of fourth leg and smooth basal segment of the fifth leg.

Diacyclops walkeri differs from all previously described species in all the same characteristics as *D. kaupi*, plus it has a much shorter outer principal terminal setae on the caudal rami, as well as longer dorsal setae on the caudal rami.

Diacyclops joycei differs from all previously described species by its dorso-ventrally compressed habitus and the flared-out pleurons of its prosomites, as well as by a dorsal sclerotized flange on the genital double-somite. Additionally, it differs from *D. michaelsoni* by the shape of the seminal receptacle, larger anal operculum, spinules on the basal segment of fifth leg, and very short distal part of the male antennulae. From *D. skottsbergi* it differs by longer and smooth caudal rami, as well as proportionately shorter innermost terminal seta on the caudal rami and shorter setae on the third endopodal segment of fourth leg. From *D. mirnyi* it differs by shorter setae on the third endopodal segment of fourth leg and spinules on the basal segment of fifth leg. Finally, *D. joycei* differs from *D. cryonastes* by longer caudal rami and proportionately shorter dorsal setae on the caudal rami, shorter and less robust apical spines on the endopod of fourth leg, absence of inner seta on the first exopodal segment of fourth leg and the presence of only one row of spinules on the basal segment of the fifth leg.

Two *Diacyclops* species were described from subterranean waters of the Yucatan Peninsula, Mexico, by Fiers *et al.* (1996) that also have 11-segmented antennulae (at least in some specimens) and all swimming legs were three-segmented: *D. chakan* Fiers & Reid in Fiers *et al.* 1996

and *D. puuc* Fiers in Fiers *et al.* 1996. Both, however, have an additional seta on the second endopodal segment of the first leg, different shape of the fifth leg (with small basal segment and much longer subapical spine on the distal segment), short and widely spaced caudal rami, as well as the outer apical spine on the third endopodal segment of the fourth leg longer than the inner apical spine. All this shows that they are only remotely related to the *michaelsoni* group, and that the 11-segmented antennulae originated convergently more than once in this genus.

There are also three species described from Lake Baikal, Russia, that share some of the characteristics of the *michaelsoni* group, although their descriptions are incomplete: *A. notabilis* Mazepova, 1950, *A. profundus* Mazepova, 1950, and *A. similis* Flössner, 1984 (see Mazepova 1950a, 1950b, Flössner 1984). They all have 11-segmented antennulae, three-segmented swimming legs and the fifth leg of the *Acanthocyclops/Diacyclops* general type. *Acanthocyclops notabilis* has the outer apical spine on the third endopodal segment of the fourth leg longer than the inner spine (like the two abovementioned Mexican species), as well as a shorter subapical spine on the fifth leg, and could indeed be a member of the genus *Acanthocyclops* Kiefer, 1927. *Acanthocyclops profundus* has very short antennulae and caudal rami, as well as a somewhat shorter subapical spine on the fifth leg. *Acanthocyclops similis*, as far as one can judge from the very schematic drawings of Flössner (1984), should be transferred to the genus *Diacyclops* on the account of its long subapical spine on the fifth leg. It differs from the species of the *michaelsoni* group by an additional seta on the second endopodal segment of the first leg (like the Mexican species). It is quite probable that the 11-segmented antennulae originated convergently in this group of Baikal species as well, as they seem to be only remotely related to the *michaelsoni* group.

Discussion

Biogeography

As mentioned above, *D. kaupi*, *D. walkeri* and *D. joycei* all belong to the *michaelsoni* group of species of the genus *Diacyclops*, which includes a further four valid species: *D. michaelsoni*, *D. skottsbergi*, *D. mirnyi* and *D. cryonastes*. Unfortunately, the descriptions of the four known species are all lacking in detail, and they would have to be re-described if we are to properly assess their phylogenetic relationships. Without a proper phylogenetic framework, it is difficult to assess their detailed biogeographical connections.

Diacyclops kaupi was collected from Bunge Hills (Fig. 1), close to the type locality of *D. mirnyi*. However, when compared to the available limited set of drawings of *D. mirnyi*, this species differs by a number of important morphological taxonomic characteristics. In fact, without any locality data, one would be led to assume that *D. mirnyi*

shares most morphological characteristics with *D. joycei*. It is possible that Borutzky and Vinogradov (1957) described *D. mirnyi* based on specimens that belong to two different species. Unfortunately, the type material is lost (Alex Kotov, personal communication 2012), so we are unable to comment further until specimens are obtained with exactly the same morphological characteristics as those illustrated by Borutzky & Vinogradov (1957) from Lake Algae, its type locality. Lake Algae differs from Transkriptsii Gulf in being a freshwater lake that is only seasonally covered by ice, and it has a well-developed periphyton which may provide a food source. In contrast, Transkriptsii Gulf is tidal, permanently ice-covered and *D. kaupi* was collected from the water column at a deep site.

For the time being, we have to accept the possibility of the existence of four different species of *Diacyclops* in Antarctica, which makes this continent the centre of diversity of the *michaelseni* group. Two other members of the group live in southern South America (*D. michaelseni* and *D. skottsbergi*) and one in south-eastern Australia (*D. cryonastes*). The group is most definitely cryophilic and probably evolved in Antarctica.

Although superficial examination may leave the impression that all species in the *michaelseni* group are closely related, detailed examination of the three new species revealed that *D. kaupi* and *D. walkeri* are much more closely related than either of them is to *D. joycei* and potentially *D. mirnyi*. *Diacyclops joycei* shares the same shape and ornamentation of the fifth leg with the Australian *D. cryonastes*, and they may form a separate clade within the *michaelseni* group. These relationships, however, are not supported by the ecology of the species. *Diacyclops walkeri* and *D. joycei* are characterized by a close association with the periphyton, with only one or more naupliar stages entering the water column (Roberts *et al.* 2004). Furthermore, both species are colourless. In contrast, adult *D. kaupi* were collected from the water column and the animals are bright orange-red. The three new species from Antarctica may be just the 'tip of the iceberg' of Antarctic diversity once more freshwater lakes are investigated. The population reported as *A. mirnyi* by Dartnall (1995) in lakes in the Larsemann Hills, c. 100 km from the Vestfold Hills, has yet to be studied in detail.

Borutzky & Vinogradov (1957) assumed that *D. mirnyi* evolved in South America and was carried to Antarctica by the constant westerly winds. This was in line with the long established paradigms that: 1) cold places cannot harbour great diversity, and especially cannot be considered as centres of origin, and 2) Antarctica was swept clean of terrestrial organisms by glacial advances during the LGM and that the continent has only been recolonized recently. Current research on deep-sea diversity, particularly in the Southern Ocean (Brandt *et al.* 2007), serves best to dispel the first of these, and the significance of ice-free terrestrial refugia during glacial maxima is now widely recognized (Convey *et al.* 2009).

Our current view is that the *michaelseni* group of species originated in freshwater lakes of Antarctica prior to the onset of glaciation (late Pliocene) or during one of the interglacial periods in the Quaternary, possibly from an ancestor that looked like the present day Australian *D. humphreysi* Pesce & De Laurentiis, 1996 (see Karanovic 2006). In this scenario, one branch of the *michaelseni* group invaded southern South America from Antarctica giving rise to *D. michaelseni* and *D. skottsbergi*, while another one (closely related to *D. joycei*) invaded Tasmania and south-eastern Australia giving rise to *D. cryonastes*. These northward invasions possibly happened during glacial periods, when ice sheets extended much more towards lower latitudes. All South American and Australian species are cryophilic, i.e. they are not able to extend their ranges into more temperate (northern) regions. This indicates that the invasions could be fairly recent, which lends support for the hypothesis of Quaternary origin. Further support comes from the current distribution of *D. cryonastes* in Australia. This species lives in surface water habitats at all altitudes in Tasmania, but only at high altitudes in Victoria and New South Wales (Morton 1985). However, newly discovered populations in the Hunter Valley and Tamworth regions in New South Wales (Karanovic, unpublished data), which extend its known distribution northward significantly, are both subterranean. This probably indicates that *D. cryonastes* invaded these regions during periods of colder climate and is now a glacial relict there.

Implications for the shifting paradigm on inhospitable Antarctica

The discovery of *D. joycei*, and the realization that the species in the Bunker and Vestfold hills are not the same, provides further insight into the biology of crustaceans in Antarctic lakes and tests a number of widely held beliefs. Firstly, the occurrence of a self-maintaining breeding population of copepods in the permanently ice-covered, cold Lake Joyce indicates that these conditions, shared with other high latitude Antarctic lakes, are not inimical to zooplankton survival. This conclusion is further supported by the collection of a single sub-adult calanoid copepod from another of the McMurdo Dry Valleys lakes (Hansson *et al.* 2011). Copepods thrive in permanently ice-covered lakes at lower Antarctic latitudes, for example they have been previously recorded in epishelf lakes of the Bunker Hills and Beaver Lake in the northern Prince Charles Mountains, as well as lakes on the Antarctic Peninsula, and at high latitudes in the Canadian Arctic (van Hove *et al.* 2001). Furthermore, water temperatures in the ocean offshore from the Antarctic continent rarely rise above 0°C, and crustaceans certainly survive well in these conditions. Low measured chlorophyll *a* is not in itself a limiting factor for crustacean survival, as the observed concentrations are the balance between production and consumption.

Furthermore, in most Antarctic lakes there is a thick microbial mat covering the sediment that provides a continual food source, and in Lake Joyce it is clear that the adult copepods are making use of this food source. Therefore, it can be concluded that environmental conditions as such do not limit the distribution of copepods in Antarctic lakes.

Secondly, our observations offer further insight into the sources of Antarctic crustacean and, in particular, a re-evaluation of doctrines that propose recent colonization from the north. The discovery of three new species, none of which has been recorded outside the continent, does not preclude recent colonization from extra-continental sources, but the likelihood of the existence of three species unrecorded elsewhere invading the continent is minute. Rather, continental speciation and limited inter- and intra-continental dispersal better explains our observations. Indeed, the presence of *D. joycei* in Lake Joyce, but apparently not in other nearby lakes of the McMurdo Dry Valleys, suggests that dispersal over even short distances is rare. Lakes Fryxell and Hoare, in particular, offer suitable habitat, with near-freshwater and abundant microbial mats below ice cover (Wharton 1994), and both have been searched by us in detail since finding *D. joycei*. All of the Taylor Valley lakes have also been examined for microzooplankton using techniques that identified nauplii in Lake Joyce (Roberts *et al.* 2004). A more pragmatic conclusion is that these species are long-term inhabitants of the Antarctic continent, and have survived past glaciations in local refugia. All of the Antarctic locations from which *Diacyclops* have been recorded (the three described here and the Larsemann Hills) are known to have been partially ice-free at the LGM, supporting the possibility of long-term survival in local refugia. Another copepod species, *Gladioferens antarcticus*, is suggested to have survived on the Antarctic continent since the separation of Australia and Antarctica (Gibson & Bayly 2007); *D. kaupi* shares its habitat and may have a similar lineage. Similar suggestions can be made for the other species. We are lucky, however, to have sampled Lake Joyce. While *D. joycei* does not appear to be a recent colonist, it now appears to be restricted to a single lake.

Could the Lake Joyce population be a relic of times when freshwater crustaceans were widespread? Palaeo-studies have shown that the nearby Palaeolake Boreas (McKelvey Valley) supported a diverse set of metazoans, including ostracods, until *c.* 14 million years ago when the McMurdo Dry Valleys became much colder and dryer (Williams *et al.* 2008). Could the Lake Joyce population be a relic? At the peak of LGM, 20 K yr BP, the whole of Taylor Valley to *c.* 350 m above sea level is thought to have been filled by Lake Washburn (Hall *et al.* 2010), trapped behind a thicker Ross Ice Shelf. Lake Joyce is situated at close to 350 m in the Lake Washburn basin and could have been part of this water body – it would have been a marginal region and potentially ideal habitat for *D. joycei*; similar conclusions

have been proposed for springtails (see Nolan *et al.* 2006). However, after the LGM, Lake Washburn gradually declined in volume, and a minimum stand of Taylor Valley lakes are thought to have occurred *c.* 1000 yr BP. That draw-down resulted in complete drainage of some lakes, with others evaporating to hypersaline pools (Lyons *et al.* 2005), a phase in which these habitats would be unsuited to copepod survival. The recent (< 1000 years) ¹⁴C age of dissolved inorganic carbon in basal waters of Lake Joyce and the absence of a hypersaline ‘sump’ led Hendy & Hall (2006) to conclude that Lake Joyce drained at that time and has since refilled. If this was the case *D. joycei* would have had to colonize Lake Joyce from another McMurdo Dry Valleys lake within the last 1000 years. Understanding the history of Lake Joyce over recent millennia, perhaps by sediment coring, is necessary to determine whether *D. joycei* could be a relic of Lake Washburn or whether recent colonization has occurred.

Conservation issues

At present, Lake Joyce is acting as a refugium essential for the long-term persistence of *D. joycei*. Such tenuous survival raises considerations for the conservation of Antarctic inland ecosystems. It demonstrates the low probability that some aquatic taxa may naturally disperse and hence the importance of minimizing anthropogenic species transfers over both local and longer distances (see Karanovic & Krajicek 2012). It also provides a salutary lesson that refugia are not simply features of the LGM but exist currently and, since the presence of copepods in Lake Joyce was unexpected, are difficult to identify *a priori*. Therefore, great care is indicated if rare elements of Antarctic ecosystems are not to be compromised.

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Supplemental material

An Appendix and 26 figures can be found at <http://dx.doi.org/10.1017/S0954102013000643>

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