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ORIGINAL PAPER

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The freshwater fauna of Macquarie Island, including a redescription of the endemic water-flea *Daphnia gelida* (Brady) (Anomopoda: Crustacea)

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Abstract The freshwater invertebrate fauna (excluding the Protozoa) of Macquarie Island is collated. This includes two Platyhelminthes, two Gastrotricha, three Tardigrada, 41 rotifera, at least eight Nematoda, nine Annelida, and 21 Arthropoda. The latter comprises six species of Anomopoda, two Copepoda, two Ostracoda, an Isopoda, five Acarina, and at least five species of Insecta with aquatic or semi-aquatic larvae. The freshwater Anomopoda (Cladocera) of Macquarie Island are re-evaluated, six species are now recognized and the largest, identified as *Daphnia gelida* (Brady), is redescribed. The records of both *Alona weinecki* Studer and *Pleuroxus macquariensis* Frey are confirmed, while that of *Macrothrix hirsuticornis* Norman and Brady is accepted with some reservations. *Alona quadrangularis* (O.F. Müller) is re-instated and records of *Chydorus sphaericus* O.F. Müller ascribed to *C. patagonicus* Ekman.

Introduction

Macquarie Island is a small sub-Antarctic Island approximately 1,500 km southeast of Tasmania, and 1,100 km southwest of New Zealand. The island, formed from ocean floor sediments pushed above sea level by tectonic activity, has never been attached to any other land mass. This implies that all of the flora and fauna are trans-ocean colonists. The objective of this paper is to compile a list of all freshwater invertebrates for comparison with the other sub-Antarctic Islands and to highlight areas for further study, based on a number of new records and a review of previous studies updating the taxonomy and correcting identifications where appropriate. The new material was collected by one of us (HJGD) during the 1989/90 summer at the time of the rotifer survey and sorted at Macquarie Island, prior to specialist identification. For details of the sampling methods employed see Dartnall (1993).

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Macquarie Island

Macquarie Island (158°53′E:54°38′S) is candle-shaped, 34-km long and up to 5.5-km wide, and inclined just 11° east of north. The ‘wick’ is a narrow low-lying isthmus that links Wireless Hill to the main body of the island—a central elevated, undulating plateau (220–300 m above sea level) surrounded by a narrow discontinuous coastal terrace (Fig. 1). Situated in the Southern Ocean, the island has a wet windy and foggy climate typical of mid-latitude oceanic islands. It experiences a northwest to westerly airflow, a cool and narrow temperature range [from −9.4°C (July 2003) to 13.6°C], and a moderate but regular amount of precipitation (913 mm on 303 days in 1989). As a consequence the island, particularly the northern half, is dotted with hundreds of bodies of water ranging from mires—small flooded depressions only a few centimeters deep with soft silty bottoms often surrounded by encroaching aquatic and semi-aquatic vegetation—to medium sized lakes. (see Selkirk et al. 1990 for a detailed description of Macquarie Island).

None of the water bodies have been studied in detail and morphometric and chemical data are patchy. The largest is Major Lake covering 0.5 km^2, while Prion Lake is, at 32.3 m, the deepest. All lakes are oligotrophic and receive most of their ionic input from atmospheric

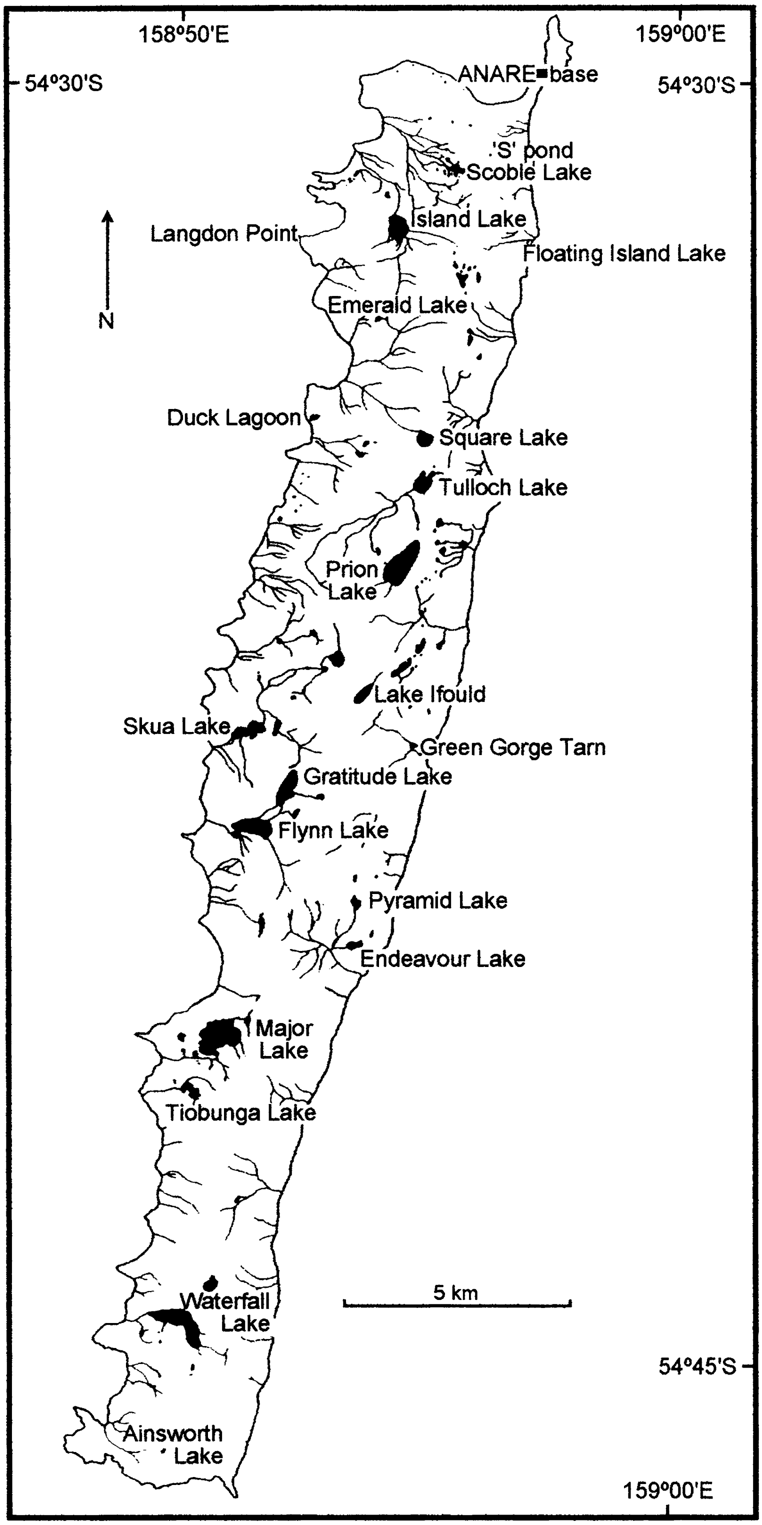


Fig. 1 Map of Macquarie Island showing location of the major lakes

precipitation (Tyler 1972). Since the prevailing wind is from the northwest and west, the salt concentration is greatest in the lakes closest to the west coast (Tyler 1972; Buckney and Tyler 1974). There are some 20 'named' lakes of medium size on the plateau, six smaller 'named' lakes, tarns or lagoons, seven 'named' creeks or streams, and numerous waterlogged peat bogs and mires (Fig. 1).

Results

As well as reviewing previous limnological studies (including Evans 1970; Dartnall 1993; Marchant and Lillywhite 1994) a number of new records, from specimens collected by the senior author during his rotifer

Table 1 The sub-Antarctic and maritime Antarctic distributions of the lower invertebrates found in freshwater on Macquarie Island (for key see Table 4)

	Macquarie Island	Heard Island	Kerguelen	South Georgia	South Orkney Islands	South Shetland Islands
Platyhelminthes	*Minona amnica* Ball and Hay					
	Unknown plathyhelminth					
Gastrotricha	*Chaetonotus disjunctus* Greuter					
	Leptodermella squamatum (Dujardin)					
Tardigrada	*Dactylobiotus* sp					
	Hypsibius dujardin (Doyere)					
	Macrobiotus hastatus/pullari					
Nematoda	*Cerviodellus* spp.					
	Dorylamis spp.					
	Enoploides stewarti Nicholas					
	Eudorylamus spp.					
	Mesodorylamus spp.					
	Mononchus spp.					
	Plectus spp.					
	Prismatolaimus spp.					
Rotifera Monogononta	*Cephalodella catellina* (O F Müller)		+	+	+	+
	Cephalodella delicata (O F Müller)		+	+	+	
	Cephalodella evabroedi de Smet					
	Cephalodella forficula (Ehrenberg)		+			
	Cephalodella gibba (Ehrenberg)		+	+	+	+
	Cephalodella megalocephala (Glascott)			+	+	
	Cephalodella sp.					
	Collotheca ornata cornuta (Dobie)	+		+	+	
	Colurella colurus compressa Lucks	+		+	+	
	Dicranophorus permollis giganthea Dartnall and Hollowday				+	
	Encentrum salinum Dartnall			+		
	Epiphanes senta (O F Müller)	+		+	+	+
	Filinia terminalis (Plate)		+			
	Keratella sancta Russell		+			
	Lecane flexilis (Gosse)		+	+		
	Lepadella acuminata (Ehrenberg)		+	+		
	Lepadella minuta Montet					
	Lepadella patella (O F Müller)	+	+	+		+
	Lepadella triptera Ehrenberg	+	+	+	+	
	Lindia torulosa Dujardin	+	+	+		
	Monommata sp.			+		
	Notholca jugosa Gosse		+			
	Notommata glyphura (Wulfert)		+			
	Polyarthra sp.					
	Ptygura crystalina (Ehrenberg)			+	+	
	Resticula nyassa (Harring and Myres)			+		+
	Rhinoglena frontalis Ehrenberg	+	+			
	Trichocerca bidens (Lucks)		+			
	Trichocerca brachyura (Gosse)	+		+	+	
	Trichocerca rattus (O F Müller)		+			
	Trichocerca tigris (O F Müller)			+		
	Wierzejskiella sp.					
Rotifera Bdelloidea	*Adineta vaga* Davis					
	Adineta sp.					
	Habrotrocha sp					
	Macrotrachela concinna Bryce			+	+	
	Macrotrachela sp. 1					
	Macrotrachela sp. 2					
	Philodina sp. 1					
	Philodina sp. 2					
	Rotaria rotatoria Pallas	+		+		

survey, are presented and some earlier identifications, notably amongst the Anomopoda, are corrected.

Protozoa No dedicated aquatic protozoan studies have been undertaken; however, amoebae including testate amoebae, radiolarians, and a variety of small ciliates were routinely observed and several species of vorticellid were found decorating anomopodan shells and copepod carapaces.

Turbellaria Evans (1970) mentions en passant the presence of several species of turbellarians. Ball and Hay

Table 2 The sub-Antarctic and maritime Antarctic distributions of freshwater Annelida and Arthropods found on Macquarie Island. (For key see Table 4)

	Macquarie Island	Heard Island	Kerguelen	South Georgia	South Orkney Islands	South Shetland Islands
Annelida	*Astacopsidrilus campbellianus* (Benham)					
	Lumbricillus antarcticus Stephenson	+	+	+	+	
	Lumbricillus lineatus (O F Müller)					
	Lumbricillus macquariensis (Benham)	+		+		
	Lumbricillus werthi (Michaelsen)		+			
	Macquaridrilus bennettae Jamieson					
	Marionina antipodum (Benham)					
	Microscolex macquariensis Beddard					
	Nais elinguis O F Müller		+	+		
Arthropoda	*Alona quadrangularis* (O F Müller)					
Anomopoda	*Alona weinecki* Studer	+	+	+	+	+
	Chydorus patagonicus Ekman					
	Daphnia gelida (Brady)					
	Macrothrix hirsuticornis Norman and Brady	+	+	+	+	
	Pleuroxus maquariensis Frey					
Copepoda	*Boeckella brevicaudata* (Brady)	+	+			
	Marionobiotus sp.		+			
Ostracoda	*Cypretta cf seurati*					
	Eucypris virens (Jurine)		+			
Isopoda	*Iais* sp.					
Acarina	*Alaskozetes antarcticus granjeani* Dalenius					
	Halozetes belgica (Michael)			+	+	
	Halazetes marinus minor? Wallwork					
	Acaridae larvae					
	Rhidocaridae larvae					
Insecta	*Ephydrella macquariensis* (Womersley)					
	Erioptera pilipes macquariensis Alexander					
	Schoenophilus pedestris Lamb					
	Smittia sp.					
	Telmatogeton macquariensis (Brundin)					

(1977) recorded just one species, *Minona amnica* in their survey of the Macquarie Island lakes and streams. During the rotifer survey, this eyeless vermiform flatworm was regularly encountered while a large unidentified species with an arrow-shaped head, two conspicuous eyespots and a broad diamond-shaped tail, only found in the 'S' pond, which was one of Evans' sampling sites (Table 1).

Gastrotricha At least two species—'scaly' and 'hairy' forms—were observed during the rotifer survey. Those with scales are provisionally identified as *Leptodermella squamatum*, those with spines and a forked posterior belong to the genera *Chaetonotus* and are tentatively identified as *C. disjunctus* (L. V. Martin, personal communication) (Table 1).

Rotifera Forty-one species of rotifer, including ten not identified to species level, have been recorded for Macquarie Island (Dartnall 1993). Most have been reported from the Antarctic region before. The *Cephalodella* sp. 1 of Dartnall (1993) is now ascribed to *C. evabroedi*, a recently described species from the high Arctic and high altitudes (De Smet 1988), and the tentative identification of *Encentrum mustela* (Milne) has been corrected to *Encentrum salinum* (Dartnall 1997). Of particular interest is the record of *Keratella sancta*, which was previously known only from South Island, New Zealand (Russell 1944) and from Kerguelen (Russell 1959; Lair and Koste 1984; De Smet 2001).

Nematoda Evans (1970) mentions the presence of several unidentified species of Nematoda; while Marchant and Lillywhite (1994) report at least two species in their survey of stream invertebrates though their identifications are limited to 'large' or 'small' taxa. Nicholas and Marples (1995) have identified one of these as *Enoploides stewarti* Nicholas. While *Enoploides* is a marine genus, two species *E. fluviatilis* Micoletzky from the Volga River and *E. stewarti* from Macquarie Island, and Lake Alexandrina, South Australia are both freshwater species. Nematodes were observed in every sample taken during the rotifer survey and these represent at least seven genera (Dr. N. R. Maslen, personal communication) (Table 1). Nematode distributions on Macquarie Island are uncertain but probably ubiquitous.

Tardigrada Evans (1970) mentions the presence of tardigrades. They were observed in every sample taken

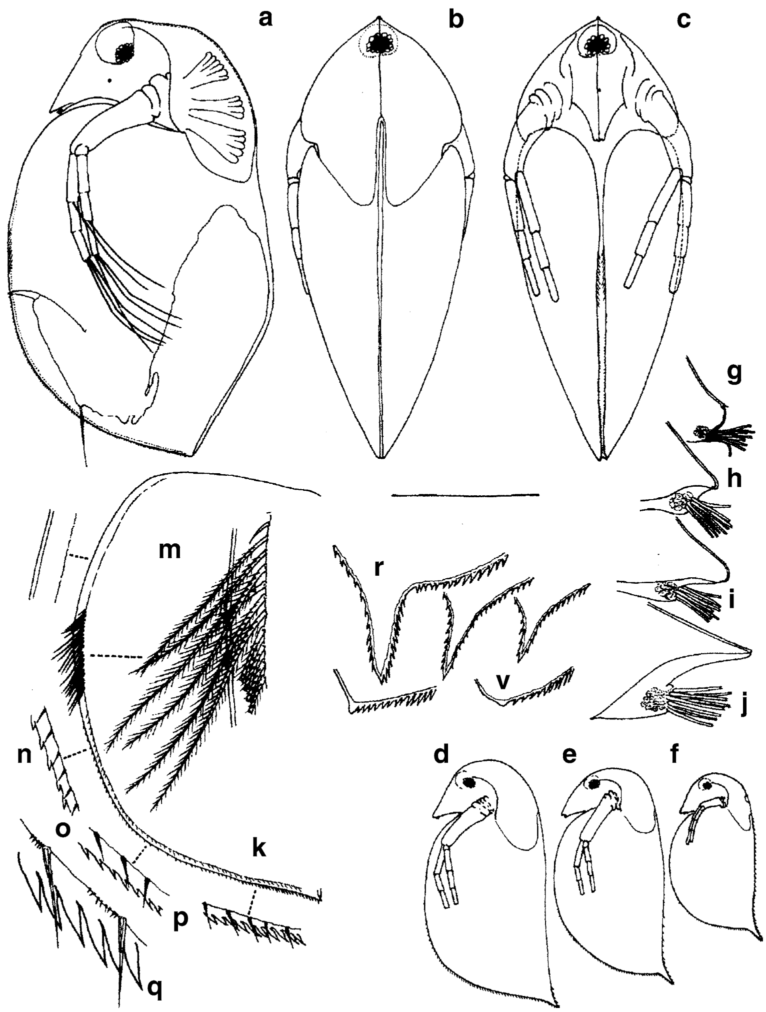


Fig. 2 *Daphnia gelida*, **a** mature parthenogenetical female, lateral view, **b** dorsal view, **c** ventral view, **d–f** unmature females, **g–j** rostrum, from young to adult specimen, **k** shell, inner view, **l–p** details of armature, **q** details of figure **p** at higher magnification, **r–v** distal end of shell, from young to adult specimens. *Scale bar*: 900 μm (**a–f**), 150 μm (**g–j**), 580 μm (**k**), 200 μm (**l–p**, **r–v**), 60 μm (**q**)

during the rotifer survey and three aquatic species have subsequently been identified (Sandra McInnes, personal communication) (Table 1).

Annelida Although oligochaete worms have been regularly reported from freshwater bodies the sub-Antarctic Islands their distribution is complicated by both systematic confusion and the ability of many inshore marine and terrestrial species to survive in freshwater. At least nine species have been reported from freshwater habitats on Macquarie Island (Table 2). Marchant and Lillywhite (1994) recorded six in a kick-sample survey of the streams: including an unidentified species of *Astacopsidrilus*, (subsequently ascribed to *A. campbellianus* (Pinder and Brinkhurst 1997)), the tubificid *Macquaridrilus bennettae*, *Nais elinguis* and three species of unidentified enchytraeids, likely to comprise *Lumbricillus lineatus, L. macquariensis, L. werthi* and *Marionina antipodum* all of which have been reported from Macquarie Island (Benham 1915, 1922), and *Lumbricillus antarcticus*, which has recently been identified from a number of lakes (Dr. K Dozsa-Farkas, personal communication). The ninth freshwater annelid *Microscolex macquariensis*, occurs under stones, among decaying vegetation near penguin rookeries, and has been reported from Scoble Lake (Evans 1970).

Arthropoda Arthropods are the most conspicuous freshwater invertebrates on Macquarie Island. Insects and arachnids including both terrestrial and brackish water species stray into freshwater, and include rafts of springtails (Collembola), which were observed on the surfaces of lakes and wallows, usually round the edge and among encroaching vegetation. These are neither nekton nor plankton, but epineuston terrestrial interlopers that are excluded from this survey.

Most kelp flies (Coelopidae: Diptera: Hexapoda) have also been excluded as these occur among beached rotting kelp. Some species do have aquatic or semi-aquatic larvae, indeed Marchant and Lillywhite (1994) recorded both *Schoenophilus pedestris* and *Ephydrella macquariensis* in a number stream samples along with the crane fly *Erioptera pililes* (Tipulidae) (presumably the subspecies

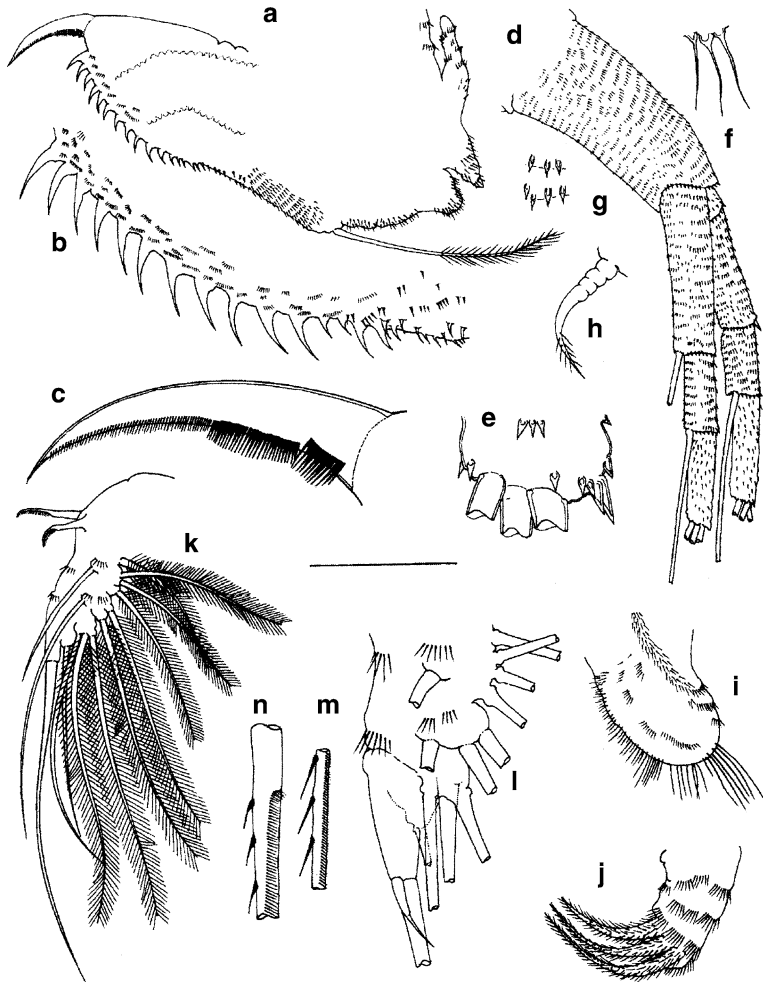


Fig. 3 *Daphnia gelida*, **a** postabdomen, **b** dorsal margin, anal spines, **c** claw, **d** antenna, **e** tip of third segment of exopodite, **f** ventral armature of basipodite, **g** dorsal armature of basipodite, **h** distal seta of basipodite, **i** labrum, **j** maxillule, **k** first trunk limb, **l** detail of first trunk limb, **m** armature of hard seta, **n** armature of longer seta of exopodite. *Scale bar*: 140 µm (**a**–**i**), 120 µm (**b**, **j**), 65 µm (**c**, **e**–**h**), 850 µm (**d**), 580 µm (**k**), 20 µm (**l**), 35 µm (**m**–**n**)

macquariensis recorded by Alexander (1962). Chironomid midges (Chironomidae) also have aquatic or semi-aquatic larvae and two species, *Smittia* sp. and *Telmatogeton macquariensis*, are known from Macquarie Island Chironomid larval cases were recovered from 'the soak' at the northern end of Macquarie Island during the rotifer survey, but it was not possible to identify the species from the ecdysial cases. Finally, moth flies (Psychodidae) should be considered as their immature stages are found in mud and wet earth along the margins of ponds and streams. Three species *Psychoda alternata* Say, *P. parthenogenetica* Tonnoir and *P. surcoufi* Tonnoir, are known from Macquarie Island though none of these have been recorded in any freshwater survey.

Acarina Five terrestrial edaphic/hemi-edaphic mite species have survived inundation after being washed into Macquarie Island lakes (Pugh and Dartnall 1994) (Table 2).

Crustacea The only truly freshwater inhabitants on Macquarie Island are represented by six species of Anomopoda, which are redescribed here, two copepods, two ostracods and an isopod.

Redescription of *Daphnia gelida* (Brady 1918)

Specimens deposited at Tasmanian Museum and Art Gallery, Hobart Reg. No G5473.

Originally described as a new species *Simocephalus gelidus* (Brady 1918), the largest anomopodan on Macquarie Island has been given various names being subsequently labeled as *Daphnia carinata* King by Evans (1970), a species widely distributed through Australia (Hebert 1977), which Frey (1993) noted as being most unlikely to inhabit the sub-Antarctic Islands. Without examining any specimens Frey (1993) mistakenly inferred that Evans had found *Daphniopsis studeri* Rühe, which occurs on a number of other sub-Antarctic Islands (Frey 1993) as well as from the Larsemann, and Vestfold Hills on the Antarctic mainland (Dartnall 1995b; 2000). The Macquarie Island specimens are identified as *Daphnia gelida* following the relocation of

Simocephalus gelidus to *Daphnia gelida* (Orlova-Bienkowskaya 1998). Brady's original (1918) description is very brief requiring a redescription that includes several morphological peculiarities.

Daphnia gelida occurred in all the lakes sampled on Macquarie Island, the specimens illustrated in the following figures are from Floating Island Lake, Duck Lagoon and Langdon Point Lake (Fig. 1).

Body length: 2.4–3.3 mm. General lateral aspect: body subovoid, elongate, narrowing gradually towards posterior end (Fig. 2a–c). The integument is delicately hyaline. Head large and wide (ca. 80% of the greatest body width), ventral margin straight or somewhat convex; anterior margin broadly rounded or with a slight supra-ocular depression, with a weakly developed carina along anterior and dorsal margins. Head not separated from the body by a cervical indentation, though in some older specimens there is a slight depression level with the mandibular articulation. The general shape of head of juveniles is similar that of adults (Fig. 2d–f). Rostrum is tapered and relatively long, with apex directed posteroventrally (Fig. 2i–j), sometimes with a short apical spine in young specimens (Fig. 2g), becoming progressively longer and narrower in older and adult specimens(Fig. 2h–j). Fornix well developed and laterally expanded, gently curved at posterior, produced into a low rounded lobe; anterior end terminates dorsal of the eye (Fig. 2a–c). Secondary fornix absent. Head shield with a dorsal suture typical of subgenus *Ctenodaphnia*, with a narrow and deep incision along mid-dorsal line of posterior part extending up to level of basal articulation of antenna (Fig. 2b). Nuchal organ conspicuous, but only present in smallest specimens (Fig. 2f). Compound eye moderately small (diameter about 5% of total animal length). Optic vesicle large and forms a slight bulge on anterior-ventral angle of head. Ocellus present, but relatively inconspicuous, halfway between eye and ventral margin of head.

Valves subovoid, asymmetrical with ventral margin broadly curved, dorsal margin straight or slightly convex in young specimens but somewhat angled in adults (Fig. 2k). Ventral border with proximal half smooth, without marginal or submarginal spines (Fig. 2l); middle part with a submarginal row of 13–24 soft setae (Fig. 2m), distal part, to dorsal junction of valves, with a row of 111–136 marginal denticles (Fig. 2n–p); the first 7–8 denticles short and widely spaced (Fig. 2n). Parallel to the denticulate marginal is a submarginal row of 40–60 spines that become progressively longer and closer to marginal row so that at the near end of the free margin the tips of the spines extend beyond those of marginal teeth (Fig. 2p–q). Near to the base of the distal members of this row are short rows of tiny spinules (Fig. 2q).

Shell spine in younger specimens is short at 12–15% of body length in youngest (Fig. 2d–f, r–t), but practically absent in adults that have a posterio-dorsal "obtuse angle" (Brady 1918) (Fig. 2a, u–v). Shell spine not extended along longitudinal axis, but oblique to dorsal margin of valves (Fig. 2d–f). Dorsal margin of shell has

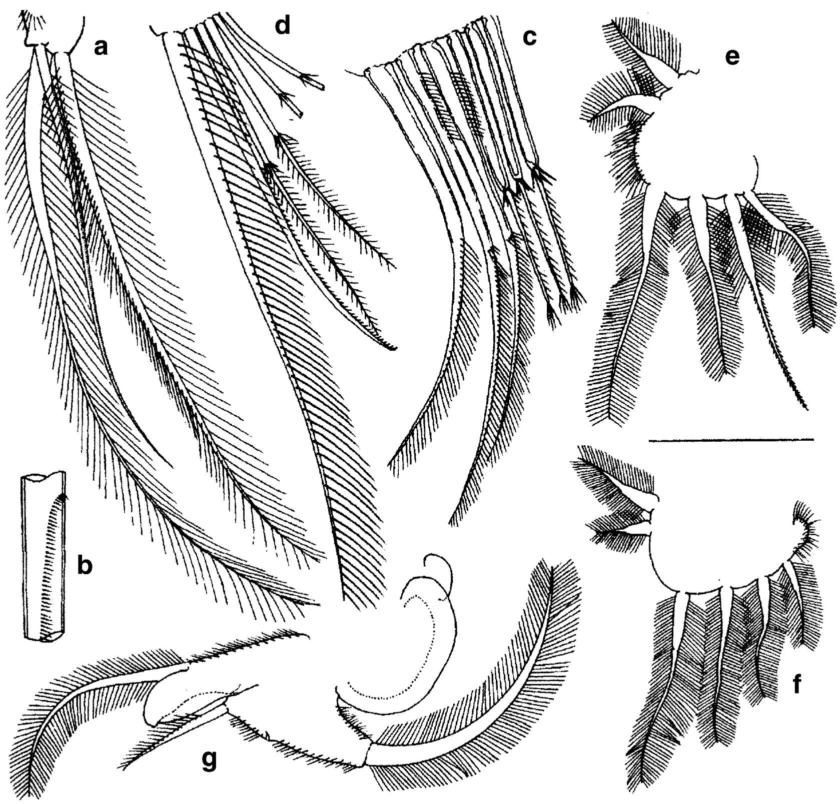


Fig. 4 *Daphnia gelida*, **a** second trunk limb, third endite, **b** armature of hard seta, **c** distal part of gnatobase, **d** denticulate seta of endite, **e** third trunk limb, exopodite, **f** fourth trunk limb, exopodite, **g** fifth trunk limb. *Scale bar*: 20 µm (**a**, **d**), 35 µm (**b**), 70 µm (**c**), 285 µm (**e–f**), 170 µm (**g**)

a double row of spines that extends along whole margin in youngest specimens (Fig. 2f), and is progressively reduced in older individuals, becoming restricted to the distal part: at first there are few spines (3–5) widely separated at proximal extreme and a row of closely arranged spines (11–14) near to and on shell spine (Fig. 2d–e); these proximal spines disappear in older animals, while in adult specimens the distal group along shell spine also disappear (Fig. 2u–v). Postabdomen long and broad, proximal half of dorsal margin concave and anal-postanal dorsal margin broadly convex. Anal margin with 11–15 subequal denticles on each side, separated by distances less than their length (Fig. 3a–b), of which the distal denticle is longer than the rest. Proximal denticles continue on preanal part with a row of shorter but stout denticles (Fig. 3b). Along anal-postanal portion, there is a submarginal row of spinule groups. Ventral and lateral surface of anal and postanal parts smooth, or with barely visible spinules (Fig. 3a), dorsal margin of preanal portion densely covered with clusters of spinules. Postabdominal setae (Fig. 3a) two-jointed with distal joint plumose and 56–96% length of postabdomen. These setae are relatively longer in young specimens than in adults. First abdominal process bent anteriorly and double the length of second, which is bent posteriorly bearing fine distal setules. Third and fourth abdominal processes small, mammiliform and densely covered with setules (Fig. 3a). Postabdominal claw slightly more than three times longer than postabdomen; with two proximal pectens including a basal pecten with 12–8 stout and relatively long spines and a distal pecten of 23–29 spines, which are longest in centre, followed by a row of fine setae along the concave margin of the distal half of the claw (Fig. 3c).

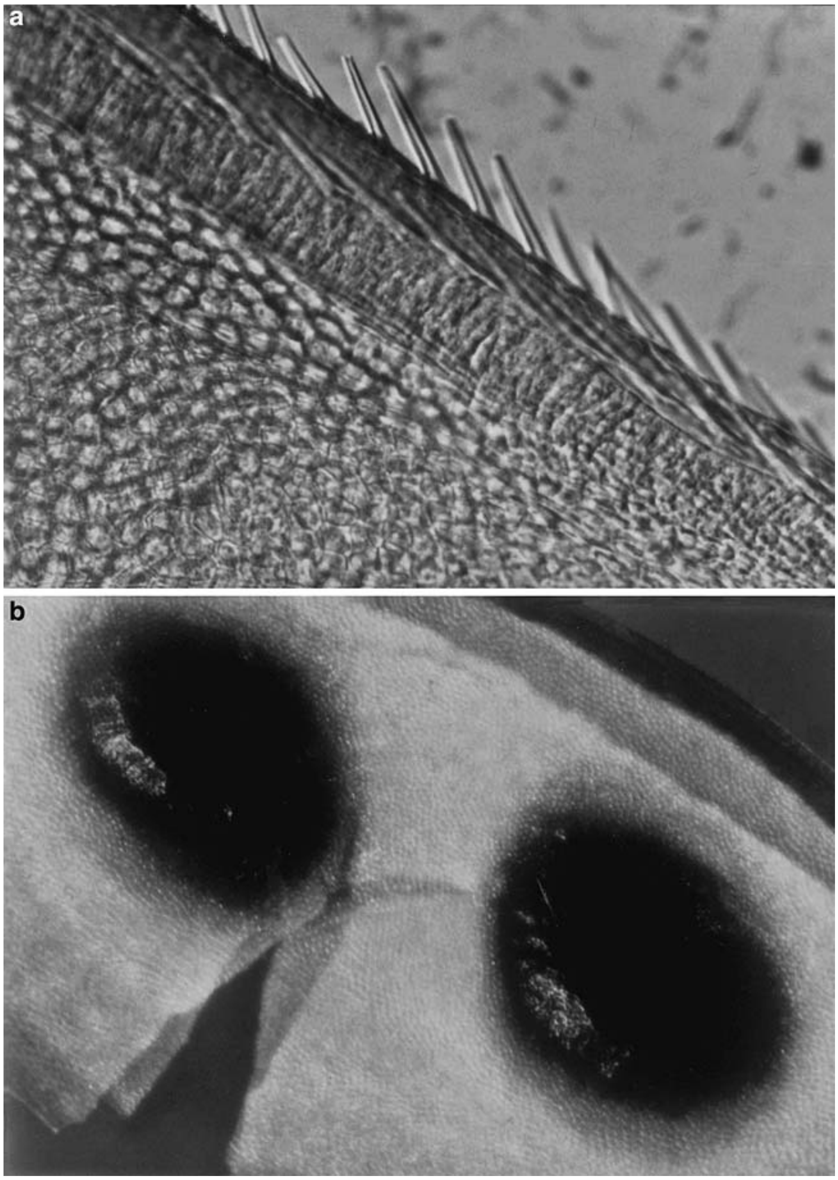


Fig. 5 *Daphnia gelida*, (**a**—upper photograph) Ephippium, dorsal margin, (**b**—middle photograph) Ephippium, photograph taken using reflected light, (**c**—lower photograph) Head of male

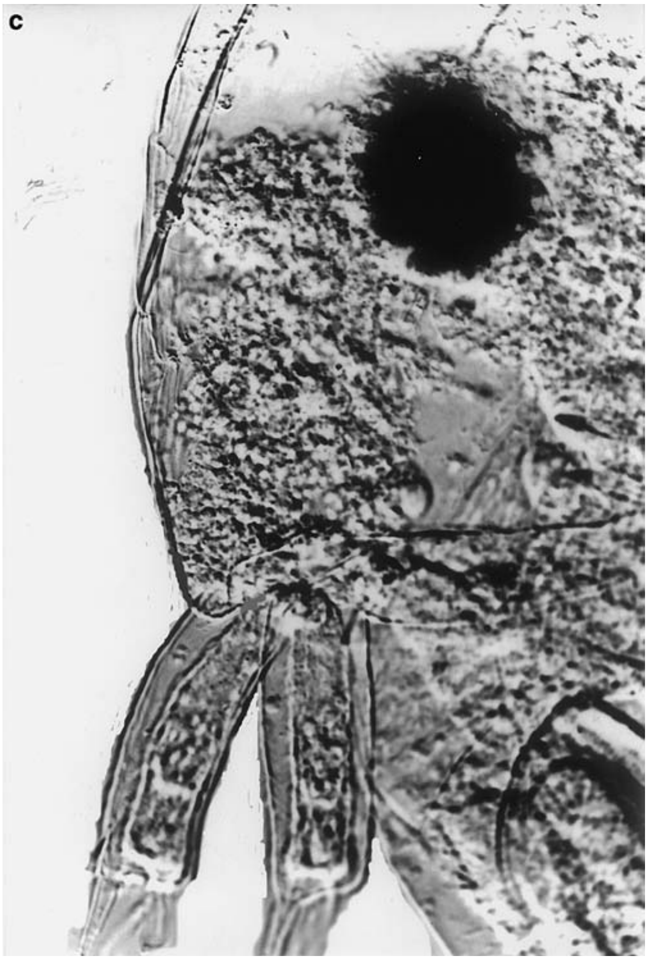


Fig. 5 (Contd.)

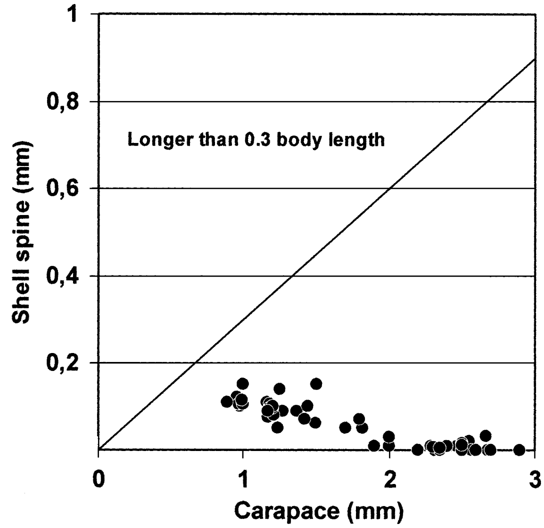


Fig. 6 Relationship between length of carapace and shell spine in *Daphnia gelida*, population from Duck Lagoon, Macquarie Island

Antennules with small but distinct basal mound. Nine aesthetascs reach tip of rostrum. In young specimens apex of rostrum shorter than aesthetascs but this is reversed in adults, where aesthetascs are shorter than rostrum. A short but barely visible sensory lateral seta is present (Fig. 2g–j). Antennae, as common for the genus, length of the segments relative to length of rami as follows: endopodite = 2–4.3–3.7; exopodite = 11.6–7–4.8–3 (Fig. 3d).

Swimming setae plumose and articulate, approximately equal in length and as long as or a little longer than rami, not reaching posterior margin of valves. Terminal setae somewhat shorter than lateral setae. Antennal formula: 0-0-1-3/1-1-3. A short spine is present at tip of second and third segments of exopodite, the last one accompanied by other three smaller spines (Fig. 3d–e). Surface of dorsal part of basipodite and proximal segment of rami covered with rows of setulae (Fig. 3f); on the contrary ventral part of basipodite and distal segment of the rami is covered with short spines (Fig. 3g). Tip of basipodite, and each segment of rami, with a row of stout denticles. Large but inconspicuous seta at distal part of basipodite between bases of rami (Fig. 3h).

Labrum lobular and fringed with numerous setae, the longest being located at distal part (Fig. 3i). Maxillule with three stout curved setae, and a short pilose lobe. Stem and curved setae densely setose (Fig. 3j) Mandible: elongate and smooth as common in Daphniidae, with 41–50 ridges on the grinding surface.

First trunk limb with two long ejector hooks on proximal part of comb and several rows of setules on anterior surface (Fig. 3k–l). Endopodite with eight plumose soft setae and four asymmetrically setulate stiff setae (Fig. 3m). Stiff seta on first endopodial segment long with tip extending beyond base of exopodial seta. Armature of stiff setae barely visible though they are asymmetrically setulated (Fig. 3m). Exopodite with two unequal setae (Fig. 3l), the longest one with distal half asymmetrically setulate (Fig. 3n).

Second trunk limb with five setae on endopodite and two plumose setae on exopodite. Third endite with two subequal soft plumose setae and one stiff seta about 30% shorter than plumose setae (Fig. 4a). Stiff seta with distal part fringed with a row of short and fine setulae (Fig. 4b). Gnatobase with a comb of 18–19 setae; three proximal setae with distal half backwardly curved (Fig. 4c). Denticulate seta on inner margin a little longer than longest rake setae (Fig. 4d).

Third trunk limb with 91–102 filtering setae, exopodite subrectangular with six plumose setae. Distal half of fifth seta fringed with short setulae, length of setae relative to exopodite width: 126–179–140–189–56–73% (Fig. 4e).

Fourth trunk limb with 69–80 filtering setae similar to those of third trunk limbs with exception of the fifth seta. Subovoid exopodite with six similar plumose setae that are shorter than those of third trunk limb, length of setae relative to exopodite width: 49–76–93–115 –31–50% (Fig. 4f).

Table 3 Comparison of the morphological features of *Daphnia gelida*, *D. carinata* and *D. nivalis*

	gelida	*carinata*	*nivalis*
Colouration	Translucent light-brown	Transparent pale-green	Red
Head, anterior margin	Convex or flat	Convex or flat	Deeply concave
Body widest	Close to mid-line	Close to mid-line	Posteriorly
Spines on dorsal margin of carapace	Absent	Present	Present
Trunk limb 3, length of exopod setae 1:5	1 > 5	1 < 5	1 < 5
Trunk limb 4, length of exopod setae 1:4	1 < 4	1 > 4	1 < 4
Length of exopod setae 3:4	3 < 4	3 > 4	3 < 4
Ephippium	White with black egg chambers	White with black egg chambers	completely black
Tail	Short or absent	Long, usually at least 0.3 body length	Short or absent

Fifth trunk limb with two unequal setae on ventral margin of exopodite, distal one about a third the length of proximal one. Endopodite with a lobe fringed with setulae and a plumose seta about twice longer than distal seta of exopodite (Fig. 4g).

Ephippial female

Body length: 2.6–3.1 mm. Ephippium extended along three quarters the length of dorsal margin of valves, "D"-shaped, surface reticulated with small cells

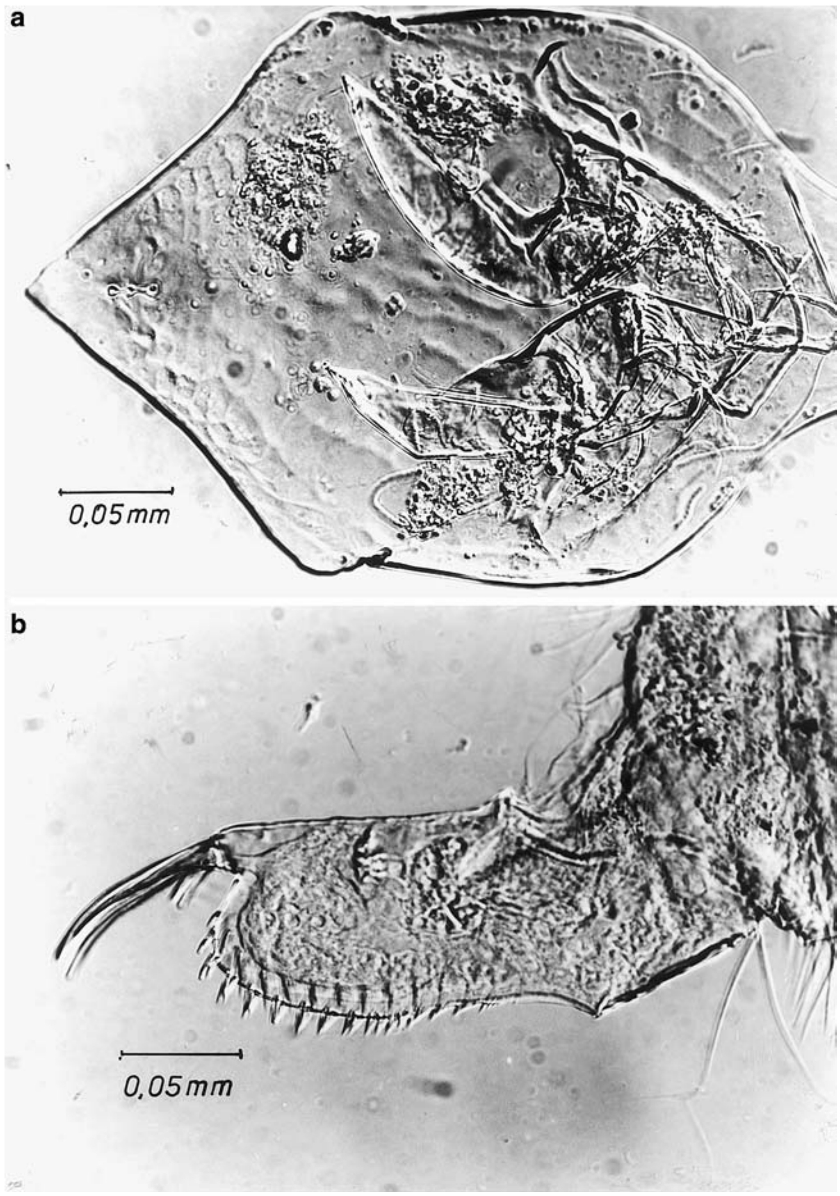


Fig. 7 *Alona quadrangularis* (**a**—upper photograph) female, head shield with three median pores, (**b**—middle photograph) female, postabdomen, (**c**—lower photograph) female

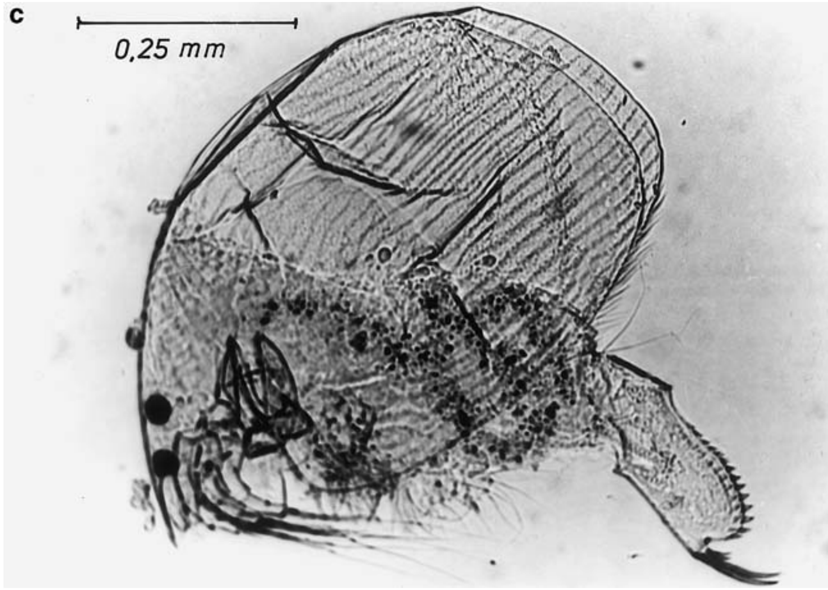


Fig. 7 (Contd.)

(Fig. 5a). Dorsal margin with a double row of strong spines, with elongate anterior and posterior processes (Fig. 5a). White with black egg chambers (Fig. 5b).

Male

Body length: 1.0–1.4 mm. The four males in our material are smaller than the females and are possibly immature, dorsal margin of shell nearly straight or slightly curved, ventral margin arched with 16 long setae, shell spine less than one third of body length, ventral and dorsal margin more densely spinulated than those of the female; no depression between head and dorsal margin. The frontal part of the head does not protrude anteriorly (Fig. 5c). The compound eye is large and the ocellus small. The rostrum is rounded, antennules slightly curved, 3.5-times as long as broad, and the flagellum is longer than the width of the antennule (Fig. 5c). Postabdominal processes are reduced.

This species, originally described as a member of the genus *Simocephalus* (Brady 1918) was recently assigned to the genus *Daphnia* without any discussion about this decision (Orlova-Bienkowskaya 1998). Our observations show that *D. gelida* can be assigned to the subgenus *Ctenodaphnia* and that it shares many features with *D. nivalis* Hebert and the closely related *carinata* complex. At first glance *Daphnia gelida* resembles members of the "*carinata* group" without a shell spine. It shares the most important diagnostic features of *D. carinata* King, but cannot be assigned to any of the species described by Hebert (1977). It also resembles *D. nivalis* in that it has a short carapace tail in young specimens, but no tail in adults. The two taxa differ in that the body of *D. gelida* is broadest close to midline, and the anterior margin of the head at eye is convex (not deeply concave). The shape of the head is similar to that of *D. carinata* complex, but the tail is very short or absent and < 0.3 of the body length (Fig. 6). This last feature is considered a characteristic of the *D. carinata* complex by Benzie (1988). According to Hebert (1977) one of the most important diagnostic characters that differentiate *D. nivalis* from the *D. carinata* complex is the complete pigmentation of the ephippium of *D. nivalis*. In the *D. carinata* complex and *D. gelida*, the pigment is limited to the egg chambers. Except for the relative length of the setae on the exopodites of the third and fourth trunk limbs, there are no significant differences in the morphology of the trunk limbs between the Macquarie specimens of *D. gelida* and *D. nivalis* and *D. carinata*. However, the taxonomic value of these features is currently not well known. A summary of the main features separating *D. gelida* from its close relatives *D. carinata* and *D. nivalis* are given in Table 3.

Because of its general aspect *D. gelida* resembles *D. dadayana* from Patagonia, which was recently redescribed and reassessed (Paggi 1999); however, we do not believe that this indicates a true phylogenetic affinity. The material from Macquarie Island belong to a "true *Ctenodaphnia*" species, whereas, judging by the morphological features, *D. dadayana* has an intermediate taxonomical position between *Ctenodaphnia* and *Daphnia sensu-stricto*. The *D. gelida* specimens lack at least two of the main *D. dadayana* diagnostic characters principally (1) no ontogenetic shift of the shape of the dorsal suture from *Ctenodaphnia*-like to *Daphnia*-like. while the inner, sub-marginal row of setae on ventral margin of carapace is short, as in most species of *Ctenodaphnia*. (2) The proximal and middle pectens of claw are not well developed (as in *D. dadayana*), while young specimens of *D. gelida* lack the characteristic horn-like head protuberance.

Finally, we should consider whether this taxon should be a member of the genus *Daphniopsis* Sars (Hrbáček 1987 and Fryer 1991). Hann (1986) compared 21 morphological characters for *Daphnia*, *Daphniopsis*

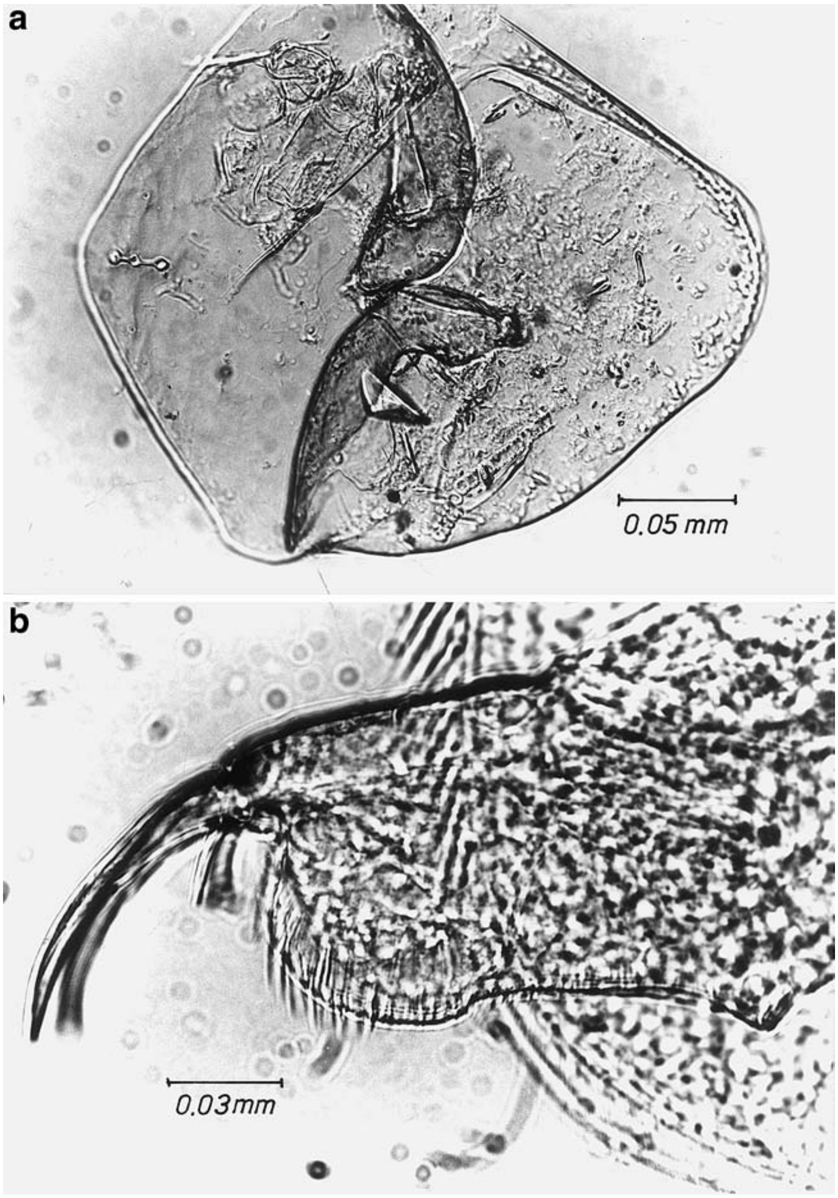


Fig. 8 *Alona weinecki* (**a**—upper photograph) female, head shield with median and lateral pores, (**b**—lower photograph) female, postabdomen

and *Simocephalus* (Table 1, pp 256–257) but found no unequivocal features separating these genera. One feature that clearly separates some species of *Daphniopsis* from *Daphnia* is an ephippium with only one egg chamber, yet this also occurs in *Daphnia truncata* Hebert and Wilson. Hann (1986) also considered the absence of spines on both ventral and dorsal margins of carapace to be diagnostic of *Daphniopsis*. In *Daphnia truncata*, the external spinescence on the dorsal and ventral margins though present is weak and similar to that in *Daphniopsis wardi* Hebert and Wilson (Hebert and Wilson 2000). To conclude we consider, if we were to include, the Macquarie Island taxon in the genus *Daphniopsis*, which then would be included in the group with two egg chambers in the ephippium, close to *Daphniopsis queenslandensis* Sergeev and *Daphniopsis studeri* Rühe. The Macquarie Island taxon is distinguished from these two *Daphniopsis* species because of the differences in the shape of the rostrum, the distribution and number of spines and setae on the margins of the carapace and the cervical indentation. To conclude, we consider *Daphnia gelida* to be an intermediate between *Daphnia* and *Daphniopsis* even though the dorsal spiniscence of the carapace is absent in adult specimens, the ventral margin is fringed with a well-developed row of spines similar to that found in *Daphnia carinata*. Until the taxonomic status of *Daphniopsis* is clarified, we assign the Macquarie Island taxon, originally described by Brady (1918) as *Simocephalus gelidus*, to the genus *Daphnia*.

Alona quadrangularis (O.F. Müller 1785)

While Evans (1970) includes this species in his faunal list for Macquarie Island, Frey (1993) doubts this record on account of his theory of non-cosmopolitism (Frey 1987).

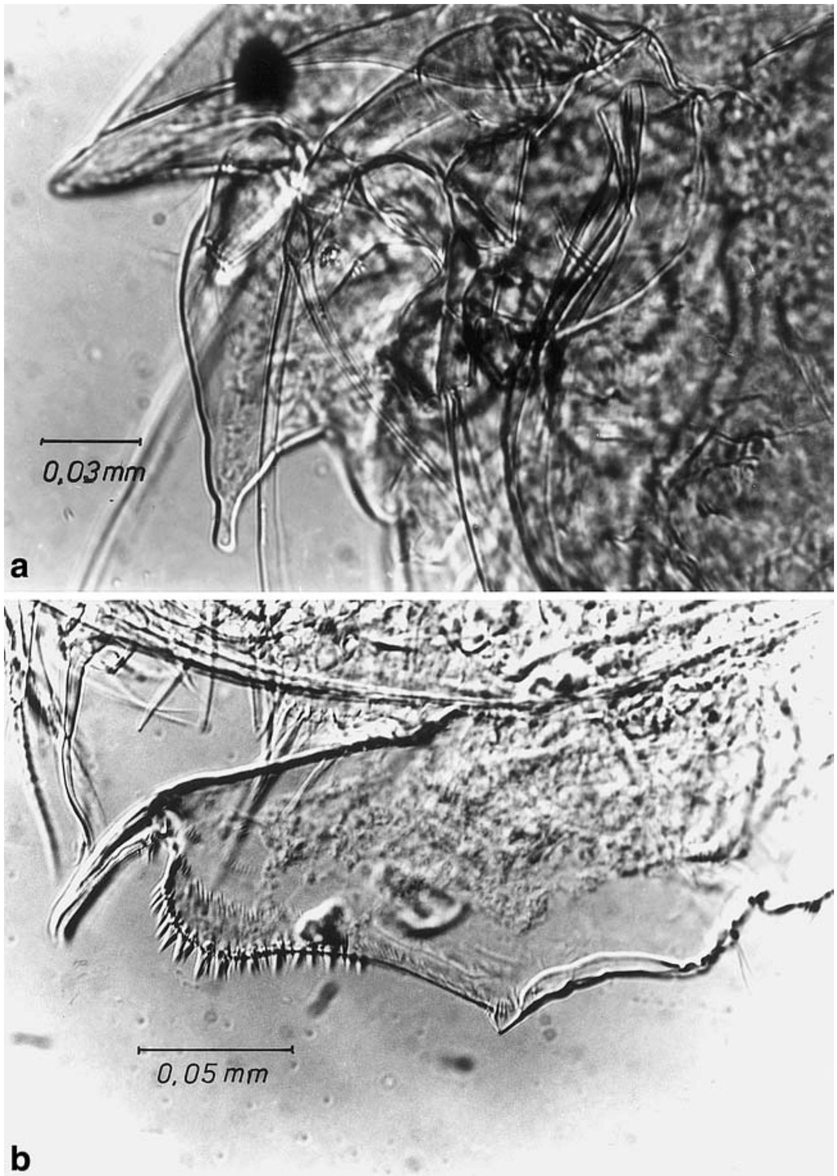


Fig. 9 *Chydorus patagonicus* (**a**—upper photograph) female, elongated apex of labrum plate, (**b**—lower photograph) female, postabdomen

The specimens we examined have several diagnostic features in agreement with the sensu-stricto type specimen including a head shield with three pores (Fig. 7a), wide labral plate, narrow elongated antennules, distally rounded shape of the postabdomen (Fig. 7b) and the absence of setules at the base of the claw. The Macquarie specimens differ from the sensu-stricto specimen in that the maximum height of the valve occurs in the middle rather than in the dorsal third (Fig. 7c), and the presence of distinct stripes on the valve. It is interesting to note that Macquarie Island is the only sub-Antarctic Island, where this species has been found.

Alona weinecki (Studer 1878)

This species has been previously recorded from Macquarie Island (Lofthouse 1967; Smith and Sayers 1971 and Frey 1988), and Evans (1970) who mistakenly identified his specimens as *A. diaphana* King. Our specimens conform to the published descriptions. Distinguishing characters include the ocellus, which is the same size as the eye, and the fact that there are no setae on the postabdominal claw. Also, there is no notch in posterior margin of shell, but there are pores between middle and anterior median pores (Fig. 8a), and the preanal angle of postabdomen is rounded (Fig. 8b). *Alona weinecki* is found on most of the sub-Antarctic Islands as well as South Island, New Zealand (Frey personal communication) and Easter Island (Dumont and Martens 1996).

Chydorus patagonicus (Ekman 1900)

There has been considerable confusion concerning this Macquarie Island chydorid. Thomson (1895) identified his specimens as *Chydorus minutus*, which he had previ-

Fig. 10 *Pleuroxus macquariensis* (**a**—upper photograph) female, rostrum, (**b**—middle photograph) female, postabdomen, (**c**—lower photograph) female, deformed postabdomen

ously described from Australia (Thomson 1879), while Brady (1918) established a new species *C. maquariensis*, which he emphasized (without explanation) as being similarity to *C. piger*. Smirnov (1996) lists both *C. minutus* and *C. macquariensis* as incertae sedis. In 1967, Lofthouse recorded *C. sphaericus* (O.F. Müller) without description, as being a cosmopolitan species present on a number of sub-Antarctic Islands. The faunal list of Evans (1970) alludes to a '*Chydorus poppei-barroisi* group'. Frey (1982) relocated both *C. barroisi* (Richard) and *C. poppei* (Richard) to the new genus *Ephemeroporus* in which nearly all species have teeth at the posterior–ventral angle of the valve, distinct teeth on the labral plate, and 2–4 longer postanal denticles. Our specimens do not possess these characteristics. After due consideration, we consider the Macquarie Island specimens to be *C. patagonicus* rather than *C. sphaericus*, as they are in close agreement with the original description (Ekman 1900). The labral plate is cuneiform, the tip of the elongated apex is not pointed (Fig. 9a), the subquadrangular postabdomen possesses 11–15 anal teeth (Fig. 9b), the postabdominal claw has two basal spines, though the proximal one is tiny. We did not find any males, or ephippial females, with which to confirm our identification.

Pleuroxus macquariensis (Frey 1993)

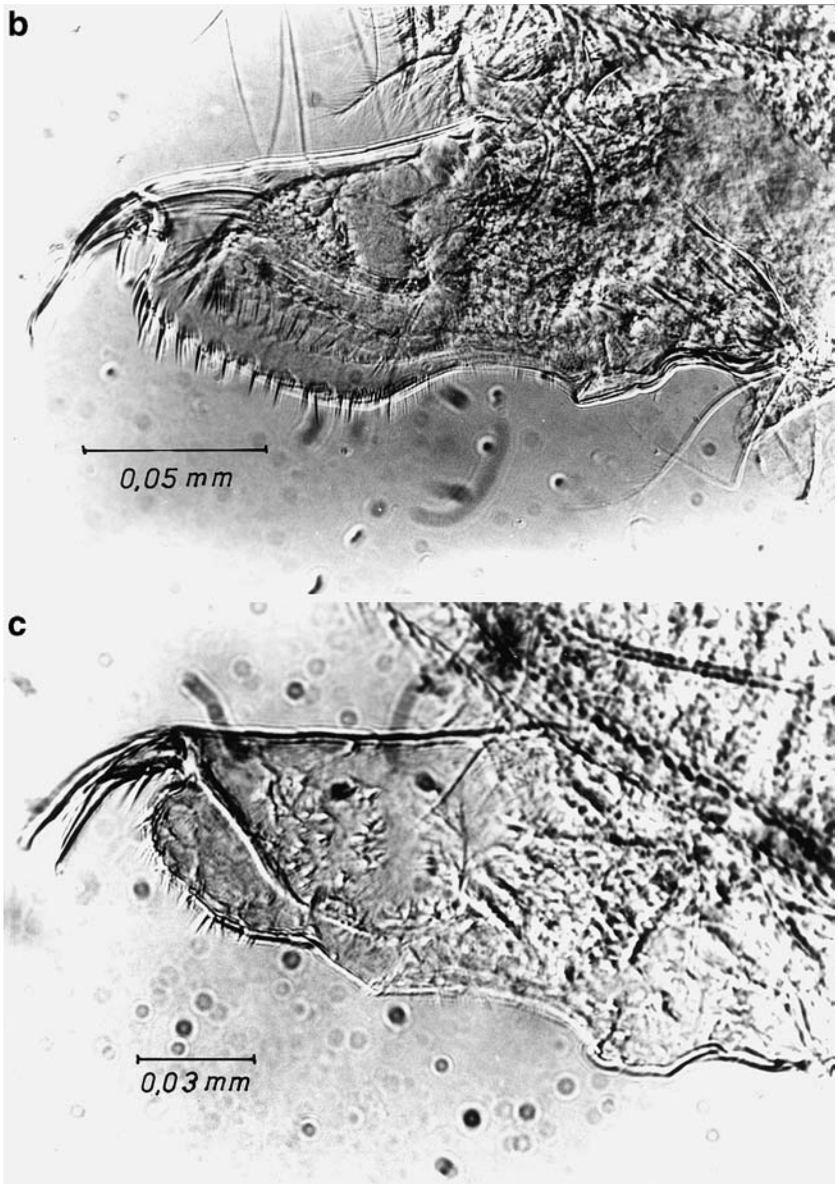
Frey (1993) described this species from a small number of specimens collected in 1963 and 1986 that were previously identified as *P. aduncus wittsteini* Studer and *P. scopuliferus* Ekman (Lofthouse 1967; Evans 1970 and Smith and Sayers 1971). We examined more than 250 specimens but did not find males, which are still unknown. The females agree with Frey's original description in that the shell is smooth and not chocolate coloured, the dorsal margin is evenly curved from tip of rostrum to posterior-dorsal angle, and bears a single small tooth at posterior-ventral angle (Frey 1993). The rostrum is shorter than the labrum (Fig. 10a), which is triangular, with a rounded tip, convex anterior margin, and concave posterior margin. The aesthetascs of the antennules do not reach the tip of rostrum. The postabdomen (Fig. 10b) is short and broad, the proximal preanal section strongly concave, and the anal margin is shorter than the postanal margin. The postanal portion bears 10–12 teeth accompanied by clusters of setae. The postabdominal claw is large and stout, has a concave margin with a row of setules, and two basal spines. One of the specimens has a deformed postabdomen (Fig. 10c), is smaller and not as broad. The denticles standing in groups are smaller and differently directed. The postabdominal claw looks crippled though the spine is well developed. Such deformities, especially in this genus, have been reported by several authors (Anders 1992; Hollwedel 1970) and probably occur at moulting.

Macrothrix hirsuticornis (Norman and Brady 1867)

This species was collcted in most of the lakes. While it has been reported by most of the earlier surveys (Lofthouse 1967; Evans 1970; Smith and Sayers 1971; and Croome, 1984) it should be remembered that the late David Frey considered all Antarctic identifications of *Macrothrix hirsuticornis* to be dubious as this is a Boreal Northern Hemisphere species. We concur with Smirnov (1992) in calling for a review of this taxon and cannot comment further on its identification and distribution.

Two species of Copepod have been reported from Macquarie Island—the calanoid *Boeckella brevicaudata* Brady, which was the subject of Evans' (1970) ecological study, and a harpacticoid, a species of *Marionobiotus* (Richard Hamond, personal communication). The calanoid is particularly common in the lakes. Marchant and Lillywhite (1994) also recorded a harpacticoid, presumably *Marionobiotus*, in most of the streams they sampled. According to Evans (1970), ostracods of the genus *Cypretta* are present in some lakes and pools. Marchant and Lillywhite (1994) recorded an unidentified ostracod in their survey of the streams on Macquarie Island. Two species collected during the rotifer survey were *Cypretta* cf *seurati*, which presumably equates to that found by Evans, and a new record for the island—*Eucypris virens* (Prof. Koen Martens, personal

Fig. 10 (Contd.)



communication). Evans (1970) also found an isopod, of the family Janiridae, in streams. According to Marchant and Lillywhite (1994), this is a species of *Iais*, which appears to be restricted to the streams as none were found lakes. According to Wilson and Wägele (1994) three *Iais* species occur at Macquarie Island, but only one in freshwater.

Discussion

A list of the freshwater invertebrate species so far recorded from Macquarie Island (Table. 1 and 2) includes two species of platyhelminth, two gastrotrichs, three tardigrades, 41 rotifers, at least eight nematodes, nine annelids and 21 arthropods. This list is thought to be both accurate and complete for the arthropods, annelids and to a lesser extent for the rotifers though all taxa require further elucidation. Gastrotrichs and tardigrades are probably not very important in the lake ecosystems but platyhelminths are important crustacean predators and scavengers. Nematodes have been similarly overlooked, and the need for a specialized survey is obvious.

All of the rotifers recorded at Macquarie Island were collected during a 15-week survey in 1989/90. Then new records were acquired regularly throughout the sampling period that led to the suggestion that many more species remain undetected (Dartnall 1993). Most of the rotifers are common cosmopolitan species and nearly three-quarters (29 of 41) have been reported from other Antarctic and sub-Antarctic locations (Table 1). Overall the total of 41 species is generally comparable with the 55 species known for

Table 4 The freshwater invertebrate fauna of Macquarie Island, and other sub-Antarctic and Maritime Antarctic locations

		Macquarie Island	Heard Island	Kerguelen	South Georgia	South Orkney Islands	South Shetlands
Platyhelminthes		2+	1+	?	4+	2	?
Gastrotricha		2+	1	?	2+	3	?
Tardigrada		3+	2	?	6	8	6
Nematoda		7	2+	?	5	2+	6
Rotifera	Monogononta	32	21	45	43	29	19
	Bdelloidea	9	5	3	12	9	?
Annelida[a]		9	6	4	4	1	4
Arthropoda	Anostraca	0	0	0	1	1	1
	Anomopoda	6	4	5	6	4	1
	Copepoda	2	2	6	5	3	2
	Ostracoda	2	0	3	3	2	0
	Isopoda	1	0	0	0	0	0
	Acarina[b]	5+	8	?	10	5	3
	Coleoptera	0	0	0	1	0	0
	Diptera	5+	0	?	2	2	1

Key ? = not yet investigated.
[a]Michaelsen 1902, 1905a, b; Stephenson 1932; Cernosvitov 1935; Tétry 1947; Jamieson 1968; Lee 1968
[b]Review article Pugh and Dartnall 1994
Macquarie Island: Evans 1970; Ball and Hay 1977; Frey 1993; Dartnall 1993; Marchant and Lillywhite 1994; current study
Heard Island: Frey 1993; Dartnall 1995a,2003, 2005; Hollwedel and Dartnall 1998.
Kerguelen Cernosvitov 1935; Beauchamp 1940; Russell 1959; Duchene 1989; Frey 1993; De Smet 2001
S. Georgia: Dartnall and Heywood 1980; Frey 1993; Hansson et al. 1996
S. Orkney Is: Heywood 1967, 1970; Priddle and Dartnall 1978; Heywood et al. 1979, 1980; Dartnall and Hollowday 1985; Frey 1993
S. Shetland Is: Beauchamp 1913; De Paggi 1982; Paggi 1987; Kuczynski 1987; Janiec 1993; Janiec and Salwicka 1996; Downie et al. 2000

South Georgia (Dartnall unpublished), the 38 from Signy Island, South Orkney Islands (Dartnall and Hollowday 1985), 48 from Kerguelen (Beauchamp 1940; Russell 1959; Lair and Koste 1984; De Smet 2001) and 26 from Heard Island (Dartnall 1995a, 2003, 2005) (Table 4).

The kick-sampling method of Marchant and Lillywhite (1994) yielded a number of annelids, and insects with aquatic and semi-aquatic larvae that had not been found using more conventional plankton nets (Evans 1970); Dartnall 1993). Since kick-sampling has not been tried elsewhere in the Antarctic region there is an expectation of a similar increase in such species for other sub-Antarctic locations, but not on the Antarctic Continent. While crustaceans are the most familiar freshwater invertebrates, there has been a steady increase in the number of species recognized at Macquarie Island. This is exemplified by the Anomopoda where numbers have risen from one in 1879 in the six of the present survey; however, this steady increase may be simply explained in terms of improved sampling procedures and more thorough surveys.

While the number of freshwater species known from Macquarie Island compares very favourably with those known from other sub-Antarctic and Maritime Antarctic locations (Table 4), the lists are incomplete and much work remains to be done. More specialist surveys of certain groups, such as the tardigrades, at specific locations, such as Kerguelen, and general investigations of some groups, such as nematodes, throughout the region are clearly needed.

Our knowledge of the fauna of Macquarie Island is as well documented as that of any other Antarctic or sub-Antarctic location. The high incidence of endemic species, across a wide range of invertebrate groups including the free-living flatworm *Minona amnica*, the worms *Macquaridrilus bennettae* and *Microscolex macquariensis*, the two waterfleas *Daphnia gelida* and *Pleuroxus macquariensis*, and three insects *Erioptera pilipes macquariensis*, *Ephydrella macquariensis* and *Telmatogeton macquariensis* is of particular interest (Table. 1 and 2). The island's youthful history, mild climate, isolation and lack of contact with other land masses all contribute to this and make Macquarie Island the most fascinating of the sub-Antarctic Islands.

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