Exceptionally preserved lacustrine ostracods from the Middle Miocene of Antarctica: implications for high latitude palaeoenvironment at 77° south

Mark Williams[1,*], David J. Siveter[1], Allan C. Ashworth[2], Philip R. Wilby[3], David J. Horne[4], Adam R. Lewis[2] and David R. Marchant[5]

[1]*Department of Geology, University of Leicester, Leicester LE1 7RH, UK*

[2]*Department of Geosciences, North Dakota State University, Stevens Hall, Fargo, ND 58105-5517, USA*

[3]*British Geological Survey, Keyworth, Nottingham, NG12 5GG, UK*

[4]*Department of Geography, Queen Mary, University of London, Mile End Road, London E1 4NS, UK*

[5]*Department of Earth Sciences, Boston University, Boston, MA 02215, USA*

*Author for correspondence (mri@le.ac.uk)

A newly discovered Konservat-Lagerstätte from the Middle Miocene of the western Olympus Range, Dry Valleys, Antarctica, yields cypridoidean ostracods complete with preserved body and appendages. This is the first record of 3-dimensionally fossilized animal soft tissues from the continent. The ostracods are preserved in goethite, secondary after pyrite, representing a novel mode of exceptional preservation. They signal a high latitude (>77°S) lake setting (Palaeolake Boreas) viable for benthic animal colonisation prior to 14 Ma. Their presence supports the notion of warmer, tundra-like environmental conditions persisting in the Dry Valleys until the Middle Miocene.

Keywords: ostracods; Konservat Lagerstätte; Dry Valleys; Miocene palaeoclimate; palaeolake; pyritization; soft-tissues.

1. INTRODUCTION

There are an estimated 60,000 described species of living and fossil ostracods (Ikeya *et al*. 2005), a group of small crustaceans that have colonized marine, non-marine and even semi-terrestrial habitats. The taxonomy of ostracods is based on their shell morphology and especially details of their appendages and other soft anatomy. However, although the most abundant arthropods in the fossil record (ca. 30,000 described species), the soft-anatomy of ostracods is rarely preserved (see Smith 2000).

Fossil ostracods are documented from marine Cenozoic strata of the Antarctic region (e.g. Dingle 2000; Szczechura 2001). However, apart from a putative record of non-marine ostracods from the Neogene (Ashworth *et al*. 2002) there is no record of fossilized ostracods from freshwater (lacustrine) continental interior sites of Cenozoic age. Ostracods occur in northern high latitude lakes today, as in the Faroe Islands (Jeppesen *et al*. 2002), Greenland (Anderson & Bennike 1997), Svalbard (Svenning *et al*. 2006) and Lena River delta of the Siberian Arctic (Wetterich *et al*. 2007), but are scant in southern high latitude lakes. Cypridid and candonid ostracods have been reported from freshwater lakes and ponds in sub-Antarctic South Georgia and Signy Island (Pugh *et al*. 2002; Dartnell 2005; Peck *et al*. 2005), but are unknown from the continental (interior) zone of Antarctica, including the Dry Valleys region.

Here, we describe a new and exceptionally well-preserved monospecific Middle Miocene ostracod fauna from the western Olympus Range in the Dry Valleys Region of the Transantarctic Mountains. The ostracods form part of an ancient lake biota, Palaeolake Boreas, preserved between Mount Boreas (which is situated at 161° 5'E, 77° 47'S) and Mount Aeolus at an elevation of 600 m above the floor of

McKelvey Valley (at altitude 1425 m; for locality details see Lewis *et al*. 2008, figs 1, 2). Although ostracod carapaces have been reported in association with an exceptionally well-preserved Jurassic fossil assemblage in the Transantarctic Mountains (Babcock *et al.* 2006), none retain details of their soft anatomy. The material documented here represents the first record of 3-dimensionally preserved fossilized animal soft-tissues from the continent. Additionally, it represents the only confirmed record of lacustrine ostracods from the continental interior of Antarctica for the entire Neogene. This has important implications for climatic conditions in the Dry Valleys region during the Middle Miocene, prior to the establishment of much colder conditions after 14 Ma (Lewis *et al*. 2007, 2008).

2. PALAEOLAKE BOREAS ENVIRONMENT

Palaeolake Boreas developed in a small basin (1.4×10^4 m^2) behind a glacial moraine (Ashworth *et al*. 2007). Its sediments have a total thickness of about 0.75 m and are dominated in the lower part of the succession by interlaminated moss peat and diatomaceous silts, and in the upper part by diatomaceous silts. The former record repeated fluctuations in water level during a low-stand phase, and the latter reflect a prolonged high-stand phase (Ashworth *et al*. 2007). They are conformably overlain by sands and gravels with a coarsening-upwards motif, indicating final infill and burial of the basin by a prograding alluvial fan complex. The lacustrine sediments have been correlated with a comparable moraine-damned lake sequence 3 km to the east which has yielded an $^{40}Ar/^{39}Ar$ age of 14.11±0.11 Ma (Lewis *et al*. 2007), later recalculated to 14.07±0.05 Ma (Lewis *et al*. 2008).

Palaeolake Boreas had an indigenous freshwater biota which included mosses, diatoms and ostracods; beetles inhabited the hinterland (Ashworth *et al*. 2007).

Geomorphic, stratigraphic and chronological evidence indicates that a climate supporting cold-based glaciation has persisted in the region from 14 Ma to the present. The lake therefore preserves the last vestige of a warmer, tundra fauna and flora (Lewis *et al*. 2007).

The mosses correspond to shallowing events and include the semi-aquatic *Drepanocladus*, some modern species of which thrive in mineral- and nutrient-rich mires and extend southward to Tierra del Fuego, the Falkland Islands and Kerguelen Island (Ashworth *et al*. 2007). In addition to semi-aquatic forms, two species of terrestrial haplolepidous mosses have been identified and were presumably washed or blown in from the margins. The diatoms are abundant and well-preserved. Those in the moss-rich lower part of the sequence comprise colonial benthonic alkaliphilous species. They are replaced higher in the sequence by a different assemblage of benthonic taxa, and finally by a suite of acidophilous planktonic forms indicating deepening and increasing acidification of the lake (Lewis *et al*. 2008). The presence of a diversified diatom flora implies that the water-body was both permanent and seasonally ice-free, and that the lake derived considerable nutrients from the catchment (Ashworth *et al*. 2007).

Ostracods occur at a single level in a 4 cm thick bed of interlaminated moss peat and diatom-bearing silt (see Lewis *et al*. 2008). They are abundant and indicate a temporarily favourable environment for colonisation by benthic crustaceans.

3. SYSTEMATIC PALAEONTOLOGY

Phylum: Arthropoda, Subphylum: Crustacea, Class: Ostracoda.

Order: Podocopida Sars, 1866

Suborder: Cypridocopina Jones, 1901

Superfamily: Cypridoidea Baird, 1845

?Family: Candonidae Kaufmann, 1900

Genus: *Lacalgida* gen. nov.

Derivation of name: Latin *Lacus*, lake, + *algidus*, cold. Gender: feminine.

Diagnosis: Carapace elongate sub-reniform in lateral view, ca. twice as long as high. First antenna elongate, distally tapering; comprises five podomeres, the proximal two being relatively large. Labrum broadly triangular, convex and with rounded corners. Labium elongate, narrowly triangular. First maxilla with basipod and short endopod; basipod has three endites, at least one of which has a minimum of two terminal setae. Second maxilla endopod unsegmented. Large, elongate genital lobes in female. Stout furcal rami.

Species: *Lacalgida avia* sp. nov.

Derivation of name: Latin *avius*, remote or solitary.

Diagnosis: As for genus, which is monotypic.

Holotype: A carapace, about 0.6 mm long, with soft anatomy (Figure 1b, d, e, g-i). The specimen, the best preserved in our material, appears to show adult characteristics and has a full complement of limbs and well-developed genital lobes, but is smaller than our largest specimen and therefore possibly represents the penultimate (A-1) instar. Oxford University Museum of Natural History, Oxford, England, OUMNH NS.1.

Material: 38 valves and carapaces including the holotype (OUMNH NS.1-NS.38), of which two preserve recognisable soft parts and several appear to show degraded soft tissues.

Locality and stratigraphy: Middle Miocene (Langhian Stage), Palaeolake Boreas, western Olympus Range, between Mount Boreas and Mount Aeolus (see Lewis *et al.*

2007, fig. 1), 600 m above the floor of the McKelvey Valley (at 1425 m altitude), Antarctica.

The carapace is elongate sub-reniform in lateral view and about twice as long as high (length ranges 0.46 to 0.82 mm, height ranges 0.26 to 0.50 mm), with maximum height at or a little behind mid-length (Fig. 1a). In dorsal view the carapace is moderately inflated, with rounded anterior and posterior extremities and with maximum width at about mid-length. The left valve is slightly larger than the right valve. The calcified inner lamella is narrow, and broadest posteriorly (Fig. 1c). Muscle scars are not visible.

The first antenna (preserved only on the right side) is elongate, distally tapering, and comprises five visible podomeres, of which the proximal two are relatively large (Fig. 1b, 1d). A pair of small setae just posterior to the first antenna may belong to that limb. The second antenna is represented on each side by a large, tubular structure that may be the basis; the endopod is missing on both sides (Fig. 1b, 1d). The labrum is convex, broadly triangular-shaped, with rounded corners; behind it the labium is elongate, narrowly triangular, with its short (anterior) side a little behind the posterior edge of the labrum; the atrium oris occupies a narrow, sediment-filled area between labium and labrum (Fig. 1g, 1h). Only the distal parts of the mandibular endopods are preserved, the left one with two small terminal setae projecting towards the atrium oris, the right one apparently with its distal end broken (Fig. 1b). The first maxillae, positioned either side of the atrium oris, each have three endites on the basipod and a short endopod (dislodged on left side), with at least two terminal setae evident on the third endite on the left side (Fig. 1b, 1e). The second maxilla is represented only by a tapering, posteriorly-projecting, endopod on each side (Fig. 1b, 1e). The sixth limbs are stout, with the distal parts broken away; on the left side only the basipod is visible, whilst on the right side the basipod and the proximal podomere of the endopod are preserved (Fig. 1b, 1e). Small lobes just behind and exsagittal to the sixth limbs are taken to represent the proximal parts of the seventh limbs (Fig. 1b) which would normally be positioned well within the carapace, alongside the posterior part of the body of the animal. Posterior to these is a pair of large, elongate genital lobes (Fig. 1i), which together with the form of the fifth limbs indicate that the animal is female. Posteriorly there is a pair of stout furcal rami with their distal ends broken off (Fig. 1i).

Remarks: *L. avia* can be assigned to the Cypridoidea based on the morphology of the fifth limb endopod (unsegmented), the single pair of walking legs (sixth limb) and the stout furcal rami. Of the four cypridoidean families (Horne *et al*. 2002), an assignment to the notodromadids is unlikely because they invariably have relatively high, not elongate, carapaces, often with flattened ventral margins. Affinity to the ilyocyprids is similarly ruled out because they have characteristically sub-rectangular carapaces and a fifth limb endopod with two or three segments. Assignment to the Candonidae is slightly more likely based on overall carapace shape, the relatively large fifth limb palps and the elongate genital lobes; indeed the Antarctic species is quite similar in general appearance to smaller members of the candonid genus *Fabaeformiscandona* Krstić, 1972 (see Meisch 2000). However, because of a lack of the adductor muscle scars or knowledge of the distal parts of the limbs, the possibility that the species belongs to the Cyprididae cannot be ruled out. Both the Candonidae and Cyprididae include swimming (nektobenthonic) and non-swimming (benthonic) taxa. The quality of preservation of the first and second antenna of our specimens is not good enough to determine whether or not the species had swimming setae, but on the basis of the relatively elongate carapace morphology, it is more likely that it was benthonic and a non-swimmer. The living Candonidae include some terrestrial and semi-terrestrial representatives, found in such habitats as damp leaf-litter and mosses (Pinto *et al.* 2005); by its small size and carapace shape *L. avia* quite strongly resembles the modern Brazilian terrestrial candonine *Caaporacandona* Pinto, Rocha & Martens, 2005. In this context the association of *L. avia* with mosses is intriguing, but without full knowledge of its appendage morphology it is impossible to determine the precise habitat and mode of life.

4. OSTRACOD TAPHONOMY

The body and appendages of ostracods are highly susceptible to post-mortem decay. Examples of fossil ostracods preserving soft anatomy are scarce, but are known from the Silurian through to the Quaternary (see Smith 2000). They are preserved in a variety of ways including as void fills in calcite (e.g. Siveter *et al.* 2003, 2007) and as replacements and coatings in silica (Leggitt 2006) and apatite (e.g. Bate 1972). The only previously reported high latitude example (from Alaska) differs markedly from that described here in that the soft anatomy is mummified (Schmidt & Sellman 1966).

The ostracods from Palaeolake Boreas are preserved in iron oxide (presumed to be goethite), frequently with detrital minerals adhering to their surfaces. They include isolated valves, empty carapaces and carapaces enclosing soft anatomy. One specimen preserves a near full complement of soft-parts (see Fig. 1): several others preserve partial details, and many contain structures interpreted to be remnants of degraded soft-tissue (*cf.* Smith 2000). The style of preservation is broadly comparable to that of silicified (Leggitt 2006) and phosphatised ostracod faunas (Smith 2000). It consists of a combination of fine-scale replacement and crude coatings (overgrowths), both styles typically occurring within individual specimens and in close proximity. Void fills are also important and result in excessive apparent cuticle thicknesses, particularly for appendages and setae. Locally, a thin gap (<1 μm) occurs between replaced tissues and any external coating, suggesting the epicuticle to have remained un-mineralized. Similarly, the carapace exhibits evidence of differential mineralization, with certain layers (see Yamada *et al*. 2004) not being subject to mineralization.

The fidelity of preservation of the Palaeolake Boreas ostracods varies considerably between specimens and is interpreted to be dependant on the timing of mineralization relative to decay, the extent of replacements relative to coatings, the coarseness of the mineral microfabrics, and the quantity of obscuring detrital materials. Exceptionally, sub-micron scale details such as setae and wrinkles are preserved as external moulds by coarse-grained coatings, but such resolution is typically associated with replacements by microcrystalline fabrics.

The goethite exhibits a variety of crystal habits, including tabular, crudely prismatic and globular aggregates, as well as skeletal crystals and moulds of cubo-octahedra. The latter two suggest the goethite to be secondary after another, presumably ferroan, phase. Locally, the goethite occurs in association with synchronous accessory gypsum rosettes. Goethite and gypsum are common products of pyrite oxidation (weathering) in the presence of calcium carbonate, here present as remnants of biogenic calcite in the ostracod carapaces having survived pyritization.

Broadly analogous mineralization of arthropods occurs in the Lower Cambrian Chengjiang Lagerstätte (Gabbott *et al.* 2004), though there the original pyrite microfabrics are more faithfully pseudomorphed by the iron oxides. Pyritization requires animals to be buried in sediment with a low concentration of organic carbon and a high concentration of reactive iron (Briggs *et al.* 1991, 1996). This ensures that bacterial sulphate reduction, and hence pyrite precipitation, is localised at the decaying carcass rather than being dispersed throughout the sediment. Floral evidence indicates that the shallow waters of Palaeolake Boreas may have had elevated concentrations of dissolved minerals, particularly during low-stands; modern aquatic environments occupied by Cypridoidea include those with high sulphate concentrations (Marmonier *et al.* 2005). It is postulated that partial dissolution of the ostracod carapaces in the increasingly acidic waters created a favourable microenvironment for the pyritization of soft-parts by locally increasing the pH (*cf.* Raiswell 1997).

5. PALAEOENVIRONMENTAL SIGNATURE OF THE OSTRACOD FAUNA

The modern Dry Valleys form the largest relatively ice-free area (ca. 4800 km^2) in the Antarctic. They are characterised by perennially ice-covered lakes, ephemeral streams, wide areas of exposed soil, low temperatures (Mean Annual Temperatures are in the range -14.8ºC to -30.0ºC; see Doran *et al.* 2002), limited precipitation, and salt accumulation. The lakes generally lack outlets and their levels are controlled by melt water influx. Typically, they are ice covered to a depth of 3-6 m (sometimes greater; see Doran *et al.* 2003), thin enough to allow photosynthesis to occur. They support ecological communities dominated by micro-organisms (Doran *et al.* 2004), especially diatoms, small invertebrates including nematodes and tardigrades, and mat-forming cyanobacteria. Copepod crustaceans have been observed in Lake Joyce (Roberts *et al.* 2004).

The exceptionally well preserved ostracods from Palaeolake Boreas include a range of carapace sizes (lengths ca. 0.4-0.8 mm). This indicates that several instars were living in the lake at a single time (‘horizon’), and were not transported in from elsewhere, for example by winds or streams, or reworked from older deposits. Living ostracods have not been recorded from modern lakes of the Dry Valleys. The most southerly modern lacustrine ostracod communities are those of the South Orkney Islands (Pugh *et al*. 2002; Dartnell 2005), at latitude 60°35'S, where, the annual mean temperature is around 0°C, with summer maxima reaching 12°C. Lake temperatures are typically above freezing throughout the year (see Quayle *et al*. 2002). Though lacustrine ostracods can survive for short periods below temporary ice cover, their initial colonisation requires that the lake, or an adjacent hydrologically-linked water body such as a river, be open to the atmosphere. Thus, those from Palaeolake Boreas unequivocally demonstrate the water-body to have been exposed for colonisation by benthic ostracods. They signal a Middle Miocene environment considerably warmer than the modern Dry Valleys (cf. Doran *et al*. 2002), and one which is consistent with a decrease in annual mean temperature, between the Middle Miocene and present, of some 30°C (Lewis *et al*. 2007).

The diatom record indicates that Palaeolake Boreas was long-lived (Ashworth *et al*. 2007). Restriction of the ostracods to a single horizon implies that their colonisation was serendipitous, and that the lake was only temporarily viable. This is consistent with the ostracod morphology, which suggests a benthonic mode of life. The monospecific assemblage may signal geographical isolation and difficulty of colonisation, a situation noted for other isolated lakes (e.g., see Holmes *et al*. 1998). There is little evidence for the occurrence of a continental Antarctic ostracod fauna during the Neogene: the only other known occurrence of putatively non-marine ostracods of this age is in the Meyer Desert Formation (Ashworth *et al*. 2002). Thus, rather than the ostracods representing the vestige of a once widespread Antarctic lake ostracod fauna, it is most likely that their introduction was by chance, perhaps via a biological vector such as birds (e.g., Pugh *et al*. 2002). Dispersal of ostracod eggs attached to the feathers or feet of migratory birds is an important influence on modern ostracod distribution (e.g., Purasjoki 1948; Sandberg & Plusquellec 1974; De Deckker 1977; Grigg & Siddiqui 1993; Horne & Smith 2004). Other passive dispersal media include the transport of desiccation- and freeze-resistant eggs by high-altitude winds (Sohn & Kornicker 1979), and adult ostracods clinging to the legs of aquatic beetles (Kaufmann 1900; Wohlgemut 1914).

The ostracods were discovered by Richard Thomasson, an undergraduate student, during screening of the sediments in Ashworth's laboratory at North Dakota State University. We thank David Riley, Alex Page and Rob Wilson (Leicester) for help with scanning electron microscopy, Lloyd Peck and Pete Convey (BAS) for information about ostracod distribution in Antarctica, Ian Wilkinson (BGS) for literature on freshwater ostracods, and Robin Smith (Lake Biwa Museum, Japan) for images of comparative ostracods. Allan Ashworth and David Marchant acknowledge National Science Foundation grants OPP- 0230696, ANT -0440761 and ANT-0440711. Mark Williams thanks the University of Leicester for study leave. Philip Wilby publishes with the permission of the Executive Director, BGS.

REFERENCES

Anderson, N.J., Bennike, O. 1997. Holocene lake sediments in West Greenland and their palaeoclimatic implications. *Geology of Greenland Survey Bulletin*, **176**, 89-94.

Ashworth, A.C., Cantrill, D.J., Kuschel, G., Preece, R.C. & Thompson, F. 2002. Extinction of the Antarctic terrestrial biota. *Geological Society of America, Annual Meeting*, Paper No. **104-15**.

Ashworth, A.C., Lewis, A.R., Marchant, D.R., Cantrill, J.D., Francis, J.E., Leng, M.J., Raine, J.I., Newton, A.E., Williams, M. & Wolfe, A.P. 2007. The Neogene biota of the Transantarctic Mountains. In *Antarctica; A Keystone in a Changing World-Online Proceedings for the 10th International Symposium on Antarctic Earth Sciences* (ed. Cooper, A., Raymond, C., & the 10th ISAES Editorial Team): U.S. Geological Survey and The National Academies; USGS OF-2007-1047, Extended Abstract. 071 [*http://pubs.usgs.gov/of/2007/1047/*]

Babcock, L.E., Leslie, S.A., Elliot, D.H., Stigall, A.L., Ford, L.A. & Briggs, D.E.G. 2006. The “Preservation Paradox”: microbes as a key to exceptional fossil preservation in the Kirkpatrick Basalt (Jurassic), Antarctica. *The Sedimentary Record*, **4** (4), 4-8.

Baird, W. 1845. Arrangement of the British Entomostraca, with a list of species, particularly noticing those which have as yet been discovered within the bounds of the club. *Transactions of the Berwickshire Naturalists’ Club*, **2** (13), 145-158.

Bate, R.H. 1972. Phosphatized ostracods with appendages from the Lower Cretaceous of Brazil. *Palaeontology*, **15**, 379–393.

Briggs, D.E.G., Bottrell, S.H. & Raiswell, R. 1991. Pyritization of soft-bodied fossils: Beecher’s Trilobite Bed, Upper Ordovician, New York State. *Geology*, **19**, 1221-1224.

Briggs, D.E.G., Raiswell, R., Bottrell, S.H., Hatfield, D. & Bartels, C. 1996. Controls on the pyritization of exceptionally preserved fossils: An analysis of the Lower

Devonian Hunsrück Slate of Germany. *American Journal of Science*, **296**, 633-663.

Dartnell, H.J.G. 2005. Freshwater invertebrates of subantarctic South Georgia. *Journal of Natural History*, **39**, 3321-3342.

De Deckker, P. 1977. The distribution of the "giant" ostracods (Family: Cyprididae, Baird, 1845) endemic to Australia. In *Aspects of ecology and zoogeography of recent and fossil Ostracoda* (ed. Löffler, H. & Danielopol, D.L.), pp. 285-294. Junk, The Hague.

Dingle, R.V. 2000. Ostracoda from CRP-1 and CRO-2/”A, Victoria Land Basin, Antarctica. *Terra Antarctica*, **7**, 479-492.

Doran, P.T. McKay, C.P. Clow, G.D., Dana, G.L., Fountain, A.G., Nylen, T. & Lyons, W.B. 2002. Valley floor climate observations from the McMurdo dry valleys, Antarctica, 1986–2000. *Journal of Geophysical Research*, **107**(D24), 4772, doi:10.1029/2001JD002045.

Doran, P.T., Fritsen, C.H., McKay, C.P., Priscu, J.C. & Adams, E.E. 2003. Formation and character of an ancient 19-m ice cover and underlying trapped brine in an “ice-sealed” east Antarctic lake. *PNAS*, **100**, 26-31.

Doran, P.T., Wharton, R.A. & Lyons, W.B. 2004. Paleolimnology of the McMurdo Dry Valleys, Antarctica. *Journal of Paleolimnology*, **10**, 85-114.

Gabbott, S.E., Hou, X.-G., Norry, M.J. & Siveter, D.J. 2004. Preservation of Early Cambrian animals of the Chengjiang biota. *Geology*, **32**, 901-904.

Grigg, U.M. & Siddiqui, Q.A. 1993. Observations on distribution and probable vectors of five cytheracean ostracod species from estuaries and mudflats near Dartmouth, Nova Scotia, Canada. In *Ostracoda in the Earth and life sciences* (ed. Jones, P. & McKenzie, K.G.), pp. 503-514. Balkema, Rotterdam.

Holmes, J., Fothergill, P.A., Street-Perrott, F.A. & Perrott, R.A. 1998. A high-resolution Holocene ostracod record from the Sahel zone of Northeastern Nigeria. *Journal of Paleolimnology*, **20**, 369-380.

Horne, D.J., Cohen, A. & Martens, K. 2002. Taxonomy, morphology and biology of Quaternary and living Ostracoda. In *The Ostracoda: applications in Quaternary research* (ed. Holmes, J.A. & Chivas, A.). *Geophysical Monograph*, **131**, 5-36.

Horne, D.J. & Smith, R.J. 2004. First British record of *Potamocypris humilis* (Sars, 1924), a freshwater ostracod with a disjunct distribution in Europe and southern Africa. *Bolletino della Societa Paleontologica Italiana,* **43** (1-2), 297-306.

Ikeya, N., Tsukagoshi, A. & Horne, D.J. 2005. Preface: the phylogeny, fossil record and ecological diversity of ostracod crustaceans. In: Ikeya, N., Tsukagoshi, A. & Horne, D.J. (eds.), Special Issue: Evolution and diversity of Ostracoda. *Hydrobiologia*, **538**, vii-xiii.

Jeppesen, E., Christofferson, K., Malmquist, H.J., Faafeng, B. & Hansson, L.-A. 2002. Ecology of five Faroese lakes: summary and synthesis. *Annales Societatis Scientificarum Færoensis Supplementum*, **36**, 2002, 126-139.

Jones, T.R. *in* Chapman, F. 1901. On some Fossils of Wenlock Age from Mulde, near Klinteberg, Gotland. *Annals and Magazine of Natural History* (7)**7**, 141–160 [pp. 146–147: a table by T. R. Jones].

Kaufmann, A. 1900. Cypriden und darwinuliden der Schweiz. *Revue Suisse de Zoologie*, **8**, 209-423.

Krstić, N. 1972. Neue Ostracoden aus dem Obermiozän von Donja mutnica (Paracin, Serbien). *Bulletin Scientifique*, **A17**, 5-6, 153-155.

Leggitt, L.V. 2006. Lacustrine ostracods and other microcrustaceans with preserved appendages from the Miocene Barstow Formation. *Geological Society of America Abstracts with Programs*, **38** (7), 64

Lewis, A.R., Marchant, D.R., Ashworth, A.C., Hemming, S.R. & Machlus, M.L. 2007. Major middle Miocene climate change and the extinction of tundra communities: Evidence from the Transantarctic Mountains. In *Antarctica; A Keystone in a Changing World-Online Proceedings for the 10th International Symposium on Antarctic Earth Sciences* (ed. Cooper, A., Raymond, C., & the 10th ISAES Editorial Team): U.S. Geological Survey and The National Academies; USGS OF-2007-1047, Extended Abstract. 135 [*http://pubs.usgs.gov/of/2007/1047/*]

Lewis, A.R., Marchant, D.R., Ashworth, A.C., Hedenäs, L., Hemming, S.R., Johnson, J.V., Leng, M.J., Machlus, M.L., Newton, A.E., Raine, J.I., Willenbring, J.K., Williams, M. & Wolfe, A.P. 2008. Major mid-Miocene cooling and extinction of tundra in continental Antarctica. *PNAS*, **105**, in press.

Marmonier, P., Boulal, M. & Idbennacer, B. 2005. *Marococandona*, a new genus of Candonidae (Crustacea, Ostracoda) from southern Morocco: morphological characteristics and ecological requirements. *Annals of Limnology – International Journal of Limnology*, **41**, 57-71.

Meisch, C. 2000. Freshwater Ostracoda of western and central Europe. Süsswasserfauna von Mitteleuropa 8/3. Spektrum Akademischer Verlag. Heidleberg; Berlin. 522 pp.

Okubo, I. 1990. Seven new species of freshwater Ostracoda from Japan. *Researches on Crustacea (Carcinological Society of Japan)*, **19**, 1-12.

Peck, L.S., Convey, P. & Barnes, K.A. 2005. Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. *Biological Reviews*, **81**, 75-109.

Pinto, R.L., Rocha, C.E.F. & Martens, K. 2005. On new terrestrial ostracods (Crustacea: Ostracoda) from Brazil, primarily from São Paulo State. *Zoological Journal of the Linnean Society*, **145**, 145-173.

Pugh, P.J.A., Dartnall, H.J.G. & McInnes, S.J. 2002. The non-marine Crustacea of Antarctica and the islands of the Southern Ocean: biodiversity and biogeography. *Journal of Natural History*, **36**, 1047-1103.

Purasjoki, K.J., 1948. *Cyprilla humilis* G.O. Sars, an interesting ostracod discovery from Finland. *Societas Scientiarum Fennica, Commentationes Biologicae*, **10** (3), 1-7.

Quayle, W.C., Peck, L.S., Peat, H., Ellis-Evans, J.C. & Harrigan, P.R. 2002. Extreme responses to climate change in Antarctic lakes. *Science*, **295**, 645.

Raiswell, R. 1997. A geochemical framework for the application of stable sulphur isotopes to fossil pyritization. *Journal of the Geological Society, London*, **154**, 343-356.

Roberts, E.C., Priscu, J.C., Wolf, C., Lyons, W.B. & Laybourn-Parry, J. 2004. The distribution of microplankton in the McMurdo Dry Valley Lakes, Antarctica: response to ecosystem legacy or present day climatic controls? *Polar Biology*, **27**, 238-249.

Sandberg, P.A. & Plusquellec, P.L. 1974. Notes on the anatomy and passive dispersal of *Cyprideis* (Cytheracea, Ostracoda). *Geoscience and Man*, **6**, 1-26.

Sars, G.O. 1866. Oversigt af Norges marine ostracodes. *Norske Videnskaps-Akademiens Forhandlinger,* **1865**, 1-130.

Schmidt, R.A.M. & Sellman, P.V. 1966. Mummified Pleistocene ostracods in Alaska. *Science*, **153**, 167-168.

Siveter, D.J., Sutton, M.D., Briggs, D.E.G., Siveter, D.J. 2003. An ostracode crustacean with soft parts from the Lower Silurian. *Science*, **302**, 1749-1751.

Siveter, D.J., Siveter, D.J., Sutton, M.D., Briggs, D.E.G. 2007. Brood care in a Silurian ostracod. *Proceedings of the Royal Society*, **B274**, 465-469.

Smith, R.J. 2000. Morphology and ontogeny of Cretaceous ostracods with preserved appendages from Brazil. *Palaeontology*, **43**, 63-98.

Sohn, I.G. & Kornicker, L.S. 1979. Viability of freeze-dried eggs of the freshwater *Heterocypris incongruens*. In *Proceedings of the 7th International Symposium on Ostracodes, Belgrade* (ed Krstić, N.), pp. 1-4.

Svenning, M.-A., Klemetsen, A. & Olsen, T. 2006. Habitat and food choice of Arctic charr in Linnevatn on Spitsbergen, Svalbard: the first year-round investigation in a High Arctic lake. *Ecology of Freshwater Fish*, **16**, 70-77.

Szczechura, J. 2001. Ostracods from the Eocene of Seymour Island, Antarctic Peninsula. *Palaeontologica Polonica,* **60**, 157-181.

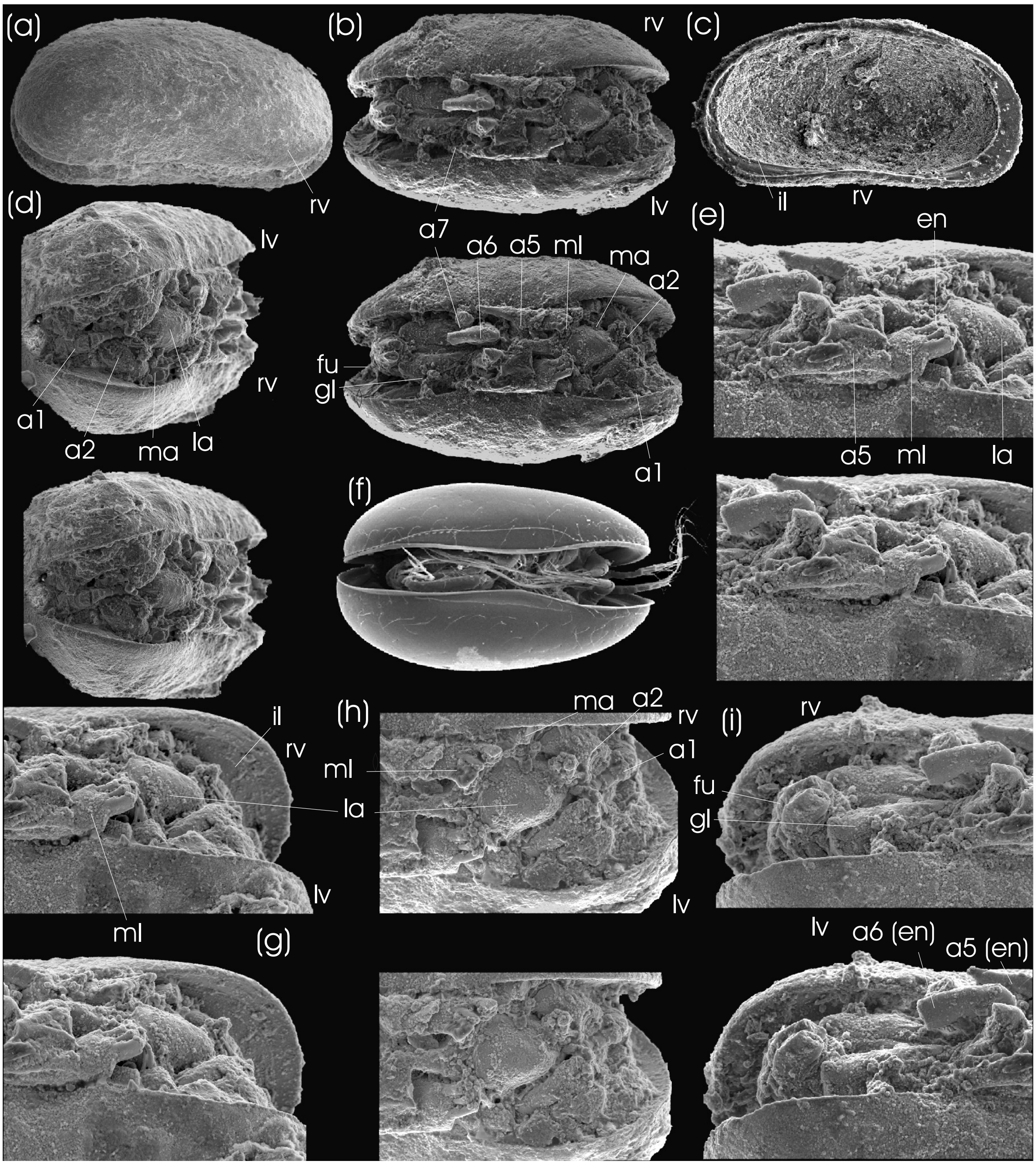
Wetterich, S., Schirrmeister, L., Meyer, H., Viehberg, F.A. & Mackensen, A. 2007. Arctic freshwater ostracods from the modern periglacial environments in the Lena River delta (Siberian Arctic, Russia): geochemical applications for palaeoenvironmental reconstructions. *Journal of Paleolimnology*, **39**, 427-449.

Wohlgemut, R. 1914. Beobachtungen und Untersuchungen über die Bilogie der Süßwasser-Ostracoden, ihr Vorkommen in sachsen und Böhmen, ihre Lebensweise und ihr Fortpflanzung. *Internationale Revue der gesamten Hydrobiologie und Hydrographie (Biologisches Supplement 2)*, 1-100.

Yamada, S., Tsukagoshi, T. & Ikeya, N. 2004. Ultrastructure of the carapace in some *Semicytherura* species (Ostracoda: Crustacea). *Micropaleontology*, **50**, 381-389.

Figure 1. *(a-e, g-i)* Scanning electron micrographs of *Lacalgida avia*: *(a)* right lateral view of carapace, OUMNH NS.2, x82.5; *(b, d, e, g-i)*, holotype with near complete complement of appendages and soft anatomy, OUMNH NS.1; *(b)* ventral view (stereo-pair), x84; *(d)* anterior view (stereo-pair) showing first and second antenna (visible on the right side), mandible and labrum, x100; *(e)* oblique ventral view of labrum, mandible and second maxilla (stereo-pair), the basipod of the latter with three terminal endites, x160; *(g)* oblique ventral view of anterior (stereo-pair), x160; *(h)* ventral view of anterior (stereo-pair) with first and second antennae visible on the right side, x160; *(i)* oblique ventral view of posterior (stereo-pair) with endopods of sixth and seventh walking appendages, genital lobes and furcal rami, x160. *(c)* right valve, internal lateral view, OUMNH NS.3, x94; (f) Modern female specimen of the candonid ostracod *Physocypria nipponica* Okubo, 1990, ventral view, x81. This specimen, from the southern basin of Lake Biwa, Shiga Prefecture, Japan, is used for a simple comparison of soft anatomy and no close relationship to *L. avia* is inferred.

Abbreviations: a1, first antenna; a2 second antenna; a5-a7, fifth to seventh appendages, a5en, a6en, endopods; ma, mandible; ml, first maxilla; la, labrum; fu, furcal ramus; rv, right valve; lv, left valve; il, inner lamella; gl, genital lobe; en, endite.


(a)
rv
(b)
rv
lv
(c)
il
rv
(d)
lv
rv
a1
a2
ma
la
a7
a6
a5
ml
ma
a2
fu
gl
a1
(e)
en
a5
ml
la
(f)
il
rv
la
lv
ml
(g)
(h)
ma
a2
rv
ml
a1
lv
(i)
rv
fu
gl
lv
a6 (en)
a5 (en)