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Fossil weevils (Coleoptera: Curculionidae) from latitude 85°S Antarctica

Allan C. Ashworth^{a,*}, Guillermo Kuschel^b

^a Department of Geosciences, North Dakota State University, Fargo, ND 58105-5517, USA

^b Landcare Research, Private Bag 92 170, Auckland, New Zealand

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Abstract

Two species of fossil listroderine weevils (Coleoptera: Curculionidae: Rhytirhinini: Listroderina) are reported from the Meyer Desert Formation at a locality on the Beardmore Glacier in the Transantarctic Mountains about 500 km from the South Pole. Associated fossils include wood, leaves and pollen of *Nothofagus*, stems and leaves of several species of mosses, achenes of *Ranunculus*, shells of freshwater molluscs and a fish tooth. The age of the fossiliferous strata is contentious but probably within the range of Pliocene to mid-Miocene. The fossils represent organisms that colonised the margins of a glacier at the head of a fjord during an interglaciation. The autecology of the listroderine species indicates that temperatures during summer months averaged 5°C. The mean annual temperature, with winter temperatures constrained by 6 months of darkness, is estimated to have been about –8°C compared to the –26°C estimated for sea level at latitude 85°S today. The closest evolutionary link of the fossil listroderines is with South American rather than Australian or New Zealand taxa. Divergence of the taxa, at least at the level of tribe, had most probably occurred on Gondwana before the continent broke apart. The fossil species are considered to be the descendants of Antarctic lineages which evolved on the continent in the Late Cretaceous or Palaeogene and survived until the Neogene. Extinction of the listroderines and most other Antarctic terrestrial biota occurred with the growth of the polar ice sheets and the change to the polar desert climate.

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1. Introduction

The only higher insects to inhabit Antarctica today are two species of flightless midges (Dip-

tera: Chironomidae). Both of these species occur on the northwest coast of the Antarctic Peninsula, the warmest and wettest part of the continent (Convey and Block, 1996). The only arthropods with adaptations which enable them to survive the low temperatures and desiccation of more southerly latitudes are springtails (Collembola) and oribatid mites (Acari) (Greenslade, 1995; Block, 1996; Convey, 1998). The coastal species are considered to be mostly postglacial immigrants but at

* Corresponding author. Tel.: +1-701-231-7919;

Fax: +1-701-231-7149.

E-mail address: allan.ashworth@ndsu.nodak.edu (A.C. Ashworth).

least four species of mites in the genus *Maudheimia*, which inhabit nunataks on the continental interior, are highly endemic and are considered to be relicts from the Gondwana fauna (Marshall and Pugh, 1996; Starý and Block, 1998). During the Cretaceous and Palaeogene periods, broad-leaved and coniferous forests of *Nothofagus*, Proteaceae and podocarps grew in southern South America, Antarctica and Australia (Askin, 1992). As Gondwana fragmented, Antarctic organisms became isolated from the larger gene pool, first from Australia (~50 Ma) and then South America (~30 Ma) (Lawver et al., 1992). In response to climatic cooling, the forests became less diverse and by the end of the Oligocene (~25 Ma) in the Ross Sea region had been replaced by a shrub *Nothofagus*–herb–moss tundra. A similar biome, depleted in species, persisted into the Neogene before becoming extinct (Fleming and Barron, 1996; Raine, 1998; Askin and Raine, 2000). Until now, knowledge about the insects which inhabited the biome has been based on a single leg segment of a weevil (Ashworth et al., 1997). The discovery of several more fragments of weevils enables us to be more certain about the taxa which inhabited Antarctica, their palaeoecological and palaeoclimatic significance, and their evolutionary relationships with the living members of the southern fauna.

2. Location and stratigraphy

The Meyer Desert Formation (MDF) is the name given to the mostly non-marine, upper part of the Sirius Group, formerly the Sirius Formation (Mercer, 1972; McKelvey et al., 1991; Webb et al., 1996). The formation is well-exposed in the Oliver Bluffs on the western flank of the upper valley of the Beardmore Glacier at 85°07'S, 166°35'E (Figs. 1 and 2). The fossil site is at an elevation of 1760 m above sea level, about 110 km southwest of the confluence of the Beardmore Glacier with the Ross Ice Shelf, and about 500 km from the South Pole.

The stratigraphic section consists of about 85 m of glaciogenic deposits. The fossils come from wood-bearing fine sandstones and siltstones (Section 5 of McKelvey et al., 1991, p. 676, Fig. 2) that are laterally discontinuous, and grade into laminated siltstones, lithified peat and marlstones. These are correlated with Member 2 of McKelvey et al. (1991), a sequence of fluvioglacial beds deposited during an interglacial episode. The fossiliferous deposits are interbedded with thick tillites containing large angular boulders (Fig. 2B–D). In the bluffs immediately north of the fossil site, between the Mayewski Lobe of the Beardmore Glacier and Plunkett Point, the MDF is directly in contact with glacially scoured bedrock of the Ju-

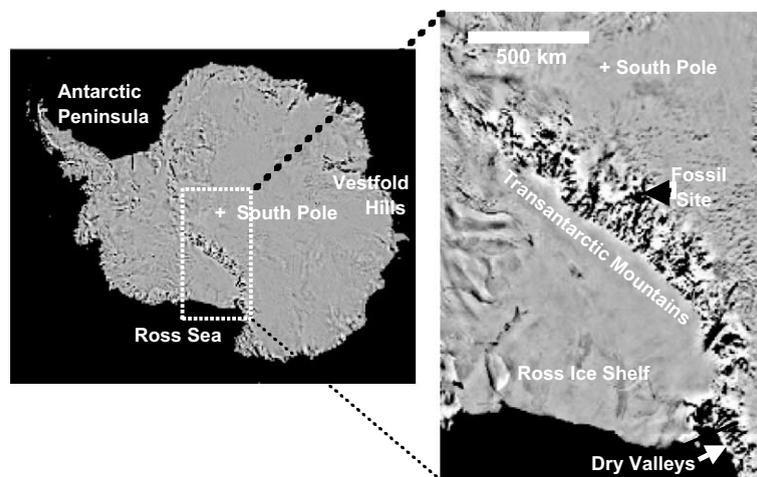


Fig. 1. Location of the fossil site in the Transantarctic Mountains.

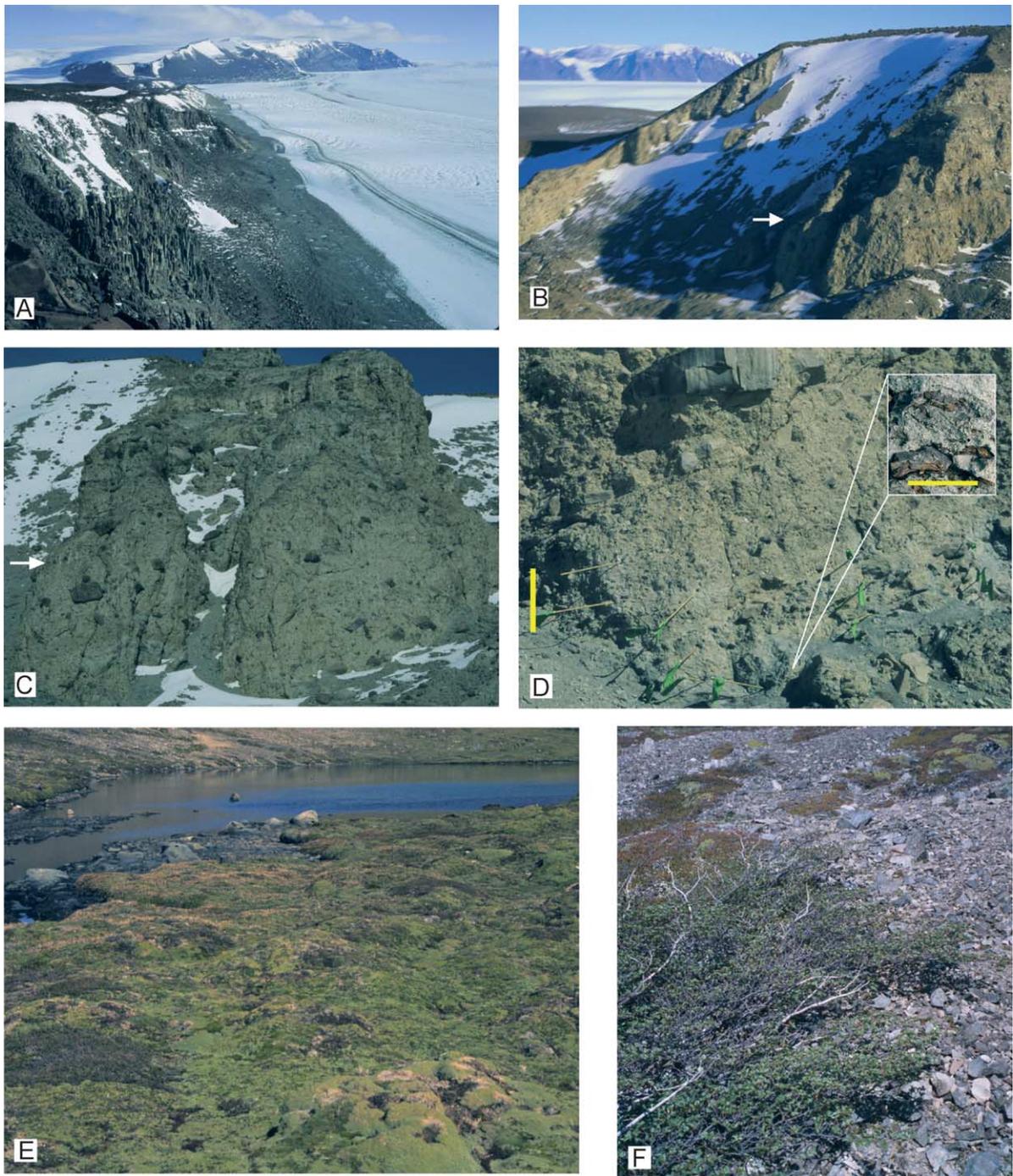
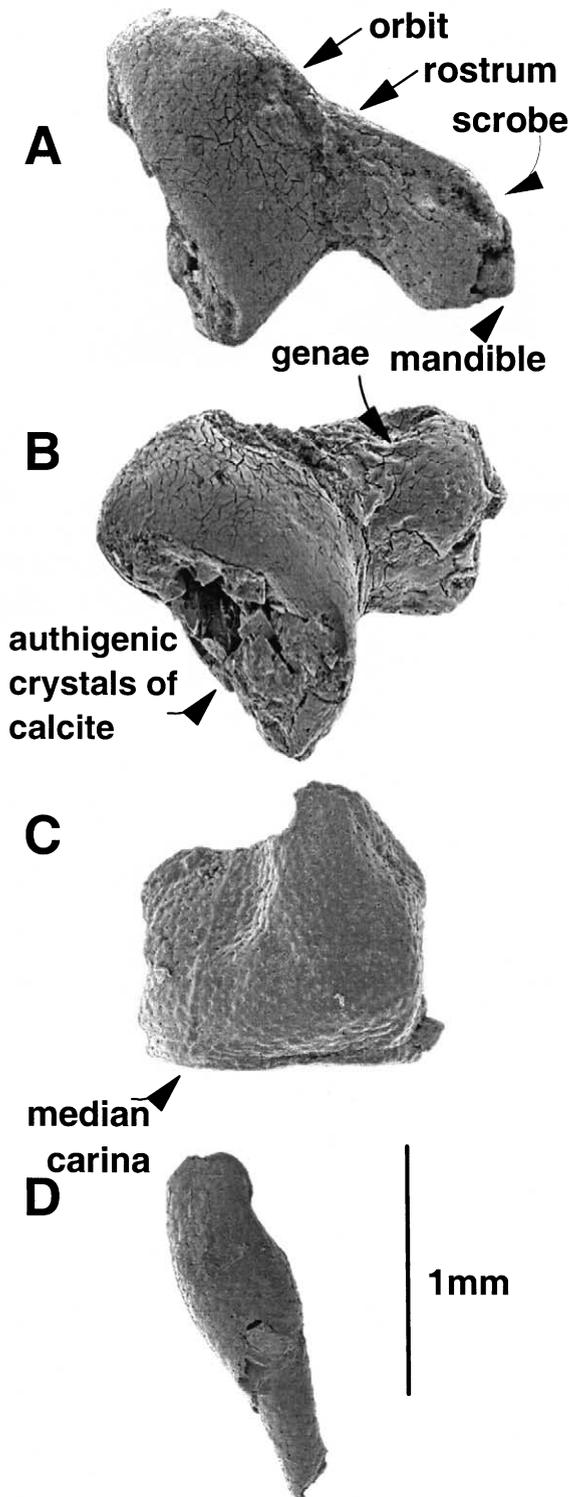


Fig. 2. (A) View looking southward up the Beardmore Glacier from the fossil site. Mount Mills in the Dominion Range and the Polar Plateau are on the horizon. (B) The northern end of the MDF outcrop on the Oliver Bluffs. The fossil horizon is marked by a white arrow. The Mill Glacier and the Supporters Range are in the background. (C) Section 5 of McKelvey et al. (1991) with the fossil horizon marked by a white arrow. (D) The fossil horizon with pieces of *Nothofagus* wood (inset) is located below the green flags. The scale bar in the inset is 2 cm and on the section is 1 m. (E,F) Possible modern analogue for the fossil site between 600 and 650 m elevation above sea level on Cerro Bandera, Puerto Williams, Isla Navarino, Chile, 54°58'S, 067°W. (E) Cushion heath tundra. (F) Prostrate shrub (*Nothofagus*) and cushion forb tundra (photographs by A.C.A.).



rassic Ferrar Dolerite. The striations are oriented northeastward generally paralleling the flow of the Beardmore Glacier (McKelvey et al., 1991, p. 676).

Passchier (2001) proposed that the Sirius Group was deposited during different phases of denudation rather than a single event. She argued for a glacial overriding of the higher ranges of the Transantarctic Mountains during the late Oligocene and/or the early Miocene. This was followed by a shift in the late Miocene or early Pliocene to the development of overdeepened glacial troughs due to uplift and structural segmentation of the Transantarctic Mountains. According to her hypothesis, high-elevation Sirius Group remnants were deposited during overriding of the Transantarctic Mountains, while the MDF and Cloudmaker Formations were deposited in glacial troughs eroded into the older deposits.

Several palaeosols have been described from the MDF in the Oliver Bluffs (Retallack and Krull, 1998; Retallack et al., 2001). The lowermost Viento palaeosol described and illustrated by Retallack et al. (2001, p. 930) is laterally continuous with the fossil horizon. Agglutinated foraminifera, similar to those reported from the stratigraphically lower Cloudmaker Formation, occur in the tillites immediately underlying the fossiliferous horizon (Webb et al., 1996). Because of stratigraphic proximity to glaciomarine deposits, the MDF is interpreted to have been deposited near sea level at the head of a fjord. The amount of postdepositional uplift of the deposits is estimated to have been about 1300 m (Webb et al., 1996).

3. Preparation and treatment of the fossils

The fossiliferous siltstones and fine sandstones are cemented with calcite. They were disaggregated by soaking in water and wet sieving. The fraction greater than 300 μm was examined under a binocular microscope. The fossils are mounted

Fig. 3. Scanning electron micrographs of the exoskeletal parts of two species of listroderine weevils. (A) Head. (B) Head rotated to show the ventral surface of the rostrum. (C) Pronotum. (D) Left femur.

on card slides and are stored in the collections of the Quaternary Entomology Laboratory at North Dakota State University. Other fossils from the deposits, in addition to the beetle exoskeletal parts, include pollen (Ashkin and Markgraf, 1986), wood and leaves of *Nothofagus* (Carlquist, 1987; Francis and Hill, 1996; Hill et al., 1996), the achenes of several species of herbs, including *Ranunculus*, stems, leaves, and spores of several species of mosses, a puparium of a higher fly, shells of a freshwater bivalve and a gastropod species (Ashworth and Preece, 2003), carapaces of an ostracod species, and a single fish tooth (Ashworth et al., 2002). The largest fossil, found at the contact between the basal tillite and the overlying siltstone, is a 45-cm-diameter hemispherical mass of woody tissue representing a cushion plant still in its growth position, and leaving no doubt that the fossil assemblage is in situ. The vegetation represented by the fossils was cushion forb moss and prostrate shrub tundra.

4. Identification and taxonomic relationships of the weevil fossils

The fossils consist of a head, prothorax and a leg of two distinct weevil species (Fig. 3). An illustration of an extant listroderine weevil of similar size to the fossils is provided for comparison (Fig. 4). The head is 1.6 mm in length measured from the posterior dorsal margin to the mandible at the tip of the rostrum (Fig. 3A); it is slightly crushed and cavities, including the orbit, are in-filled with sediment and authigenic calcite crystals. The chitin is brittle, cracked, and bleached indicating that it was weathered before burial. Bleaching is characteristic of chitin weathered under semi-arid or arid conditions. Even so, micro-ornament is preserved in patches, and pits and shallow bifurcating grooves are present on the rostrum near the scrobe. The head is from a beetle that is estimated to have been about 5.5 mm in length.

The pronotum is also slightly crushed but the chitin is better preserved than that of the head and finely punctate (Fig. 3C). The height measured from base to apex along the median line

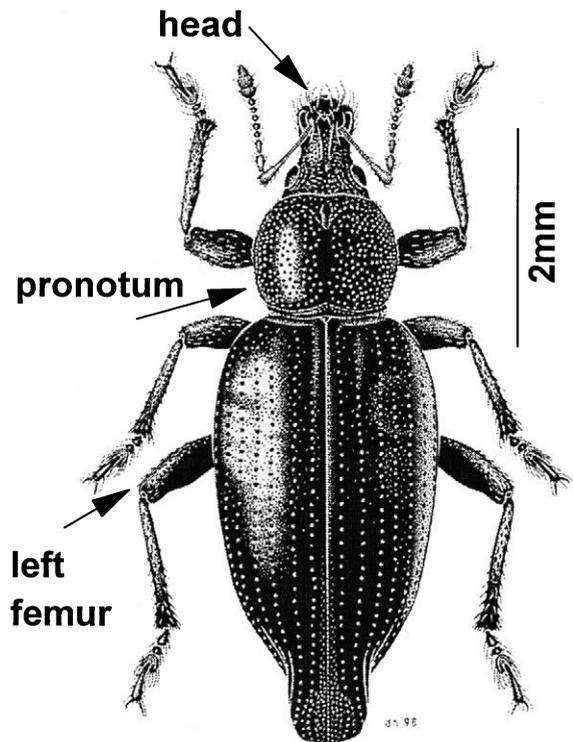


Fig. 4. A typical Magellanic moorland weevil, *Telurus dissimilis* (Fairmaire), in habitus and size probably much like the species represented by the MDF fossils. The specimen was collected by G.K. on January 1959 at an altitude of 300–450 m above Caleta San Martin on Isla L'Hermitte, 55°50'S, 067°43'W, about 30 km WNW of Cape Horn.

is 1.3 mm, which suggests that it came from an individual that was about 5.0 mm in length. The fossil prothorax lacks any ocular lobes and has a similar sculpture to members of the *Falklandius/Telurus* group of the subtribe Listroderina. The leg segment is a well-preserved left femur, 1.6 mm in length, and finely punctate (Fig. 3D). It is similar to one previously described from the MDF by Ashworth et al. (1997).

The relatively short and thick rostrum of the fossil head is characteristic for members of the Entiminae¹, a subfamily of 'broad-nosed weevils'

¹ We follow the higher classification of the 'broad-nosed weevils' by Kuschel (1995). In Marvaldi's (1997) classification there is a proposal to move the Rhytirhinini from the subfamily Entiminae and place them in a new subfamily, the Cyclo-minae.

well represented in high latitudes in both northern and southern hemispheres. In southernmost latitudes, the subfamily is represented by two tribes, the Entimini and Rhytirhinini. Further, the Entimini are subdivided into the subtribes Leptopiina, Otorhynchina and Cylydrorhinina, each characterised by dorsoventrally thickened mandibles and deciduous appendages or cusps attached at their apices in freshly emerged specimens. In older specimens, the cusps are discarded leaving obvious rough surfaces or scars. In the fossil specimen the mandible is dorsoventrally shallow, without any sign of a cusp or scar, and unlike any species of Entimini. After eliminating the Entimini, we have no other choice than to assign the fossil head to the tribe Rhytirhinini and because of the rather bulky rostrum, to the subtribe Listroderina. Skeletal parts with unique characters used to define the Listroderina were not found as fossils but we are confident in our identifications.

The Listroderina are divided into two distinct groups based on the amount of exposure, in dorsal view, of the scrobes at the antennal insertions. Weakly exposed, simple pterygia characterise the *Listroderes* sensu lato complex, and well-exposed, auriculate pterygia define the *Falklandius/Telurus* group of southern South America and the *Gromilus/Nestrius* group of New Zealand and Australia. A dorsal view of the fossil head clearly shows that its pterygia are weakly developed and similar to those of the *Listroderes* complex. The genae at the tip of the ventral surface of the rostrum are considerably broader than in any of the known species of Listroderina, indicating to us that the fossil is extinct and only distantly related to any extant species.

5. Age of the Meyer Desert Formation

A Pliocene age has been assigned to the MDF at the Oliver Bluffs based on the occurrence of recycled marine diatoms of Eocene to Pliocene age in the tillite underlying the fossiliferous horizon. Correlation of the MDF diatoms with the well-defined Southern Ocean biostratigraphy provided an age estimate for the formation of youn-

ger than 3.8 Ma (Webb et al., 1996). The method assumed that the diatoms were from marine sediments that were excavated subglacially and transported northward before being deposited as lodgement tills (Harwood, 1986; McKelvey et al., 1991). Similar diatom taxa, in situ in marine sediments from the CIROS-2 core in the Ross Sea, are interbedded with a volcanic ash with a K–Ar and $^{40}\text{Ar}/^{38}\text{Ar}$ age of ~ 3 Ma (Barrett et al., 1992). A Pliocene age is further supported by the degree of weathering and development of palaeosols in the MDF. The palaeosol stratigraphically closest to the fossiliferous horizon has been assigned an age of between 1.3 and 4.1 Ma (Re-tallack et al., 2001).

The MDF deposits indicate that the interior of Antarctica was substantially deglaciated, and for this to have occurred during the Pliocene is considered to be impossible by several researchers, especially those working in the Dry Valleys. Sea surface temperatures in the Southern Ocean based on stable isotope studies are reported to have been $\sim 3^\circ\text{C}$ warmer during the Pliocene but insufficient to have resulted in any major changes in ice volume (Kennett and Hodell, 1993). A Miocene or older age for the Dry Valleys Sirius Group is supported by $^{40}\text{Ar}/^{39}\text{Ar}$ dating of surfaces and landforms (Marchant et al., 1996), possible preservation of Miocene glacial ice (Sugden et al., 1995a; Schäfer et al., 2000; Marchant et al., 2002), and cosmogenic dating of surfaces developed on the Sirius Group deposits (Brook et al., 1995; Ivy-Ochs et al., 1995; Bruno et al., 1997; Summerfield et al., 1999; Schäfer et al., 1999). The cosmogenic dates, however, may be significantly younger than reported because of problems specific to Antarctica in determining production rates of the cosmogenic isotopes (Stone, 2000). The recycled diatoms, which also occur in the Sirius Group deposits of the Dry Valleys, are considered by several researchers to have infiltrated the tillites long after deposition and consequently cannot be used to assign a Pliocene age (Burckle and Potter, 1996; Kellogg and Kellogg, 1996; Stroeven and Prentice, 1997; Barrett et al., 1997). In the David Glacier valley of the Transantarctic Mountains in southern Victoria Land, the reworked diatoms appear to be restricted in

stratigraphic distribution to Sirius Group tillites implying that whatever their mode of emplacement it was not a process which continued throughout the Pleistocene (Van der Wateren et al., 1999). A general problem for the proponents of the wind-blown hypothesis is that they have not been able to identify a sedimentary source for the reworked diatoms. Gersonde et al. (1997) proposed that the source of the diatoms could have been deep sea sediments ejected by the impact of the Late Pliocene Eltanin asteroid in the Southern Ocean.

6. Discussion

6.1. Palaeoecology

Agglutinated foraminifera in the basal layers of the MDF indicate that the non-marine glaciogenic sediments dominating the Oliver Bluffs were deposited near sea level and have subsequently been uplifted by about 1300 m (Webb et al., 1996). Lithological and sedimentological evidence indicates that the MDF was deposited in an ice-marginal environment, adjacent to the terminus of the glacier, near the head of a wide fjord. The landscape was sufficiently stable for a lake, ice-free for long enough during the summers, to support algae, benthic invertebrates and a species of fish. Based on fossil pollen, spores and plant macrofossils, we interpret that sedges and mosses grew around the margins of the lake, and on the better-drained morainic surfaces, the vegetation was a shrub and herb tundra with cushion plants, *Ranunculus* species (buttercups) and possibly *Empetrum* (crowberry), patches of stunted, dwarf *Nothofagus* (southern beech) and podocarps (conifers). Today, listroderine weevils are associated with similar plant communities in South America. Larvae of broad-nosed weevils (Entiminae), in contrast to most other weevil groups, are free-living (ectophytic) in the soil where they feed almost indiscriminately on any root and plant part that touches the ground. Adults and larvae are well adapted to harsh climates, capable of surviving severe frosts. Adults usually congregate under clusters of dense low vegetation, either mats

or cushions. Listroderines that occur above the treeline are mainly associated with plants in the families Apiaceae and Asteraceae.

6.2. Palaeoclimatology

Today, no arthropods are capable of surviving the extreme climate of the Meyer Desert (Janetschek, 1967). Sublimation and evaporation remove moisture before it can become available for organisms with the possible exception of endolithic bacteria. In the short summers of high latitudes, adequate warmth is especially important for the growth and development of plants and arthropods.

At the treeline in Tierra del Fuego, the coldest habitats in which listroderine weevils live today, the mean summer temperature (MST) is about 5°C. This value was also estimated as the minimum for the growth of *Nothofagus* at the head of the Beardmore fjord (Hill and Truswell, 1993; Webb and Harwood, 1993; Francis and Hill, 1996). At latitude 85°S today, the MST at sea level is estimated to be about -8°C. *Nothofagus* is frost-resistant to -22°C (Hill et al., 1996). Constrained by summer and winter temperatures, and a monthly distribution of temperature in a year with 6 months of darkness, the mean annual temperature (MAT) is estimated to have been about -8°C compared to an estimated MAT at sea level today of -26°C. MATs have also been estimated from the fossil wood and the palaeosols (Francis and Hill, 1996; Retallack et al., 2001). The MAT estimate, based on the comparison of the narrow and deformed growth rings of the fossil *Nothofagus* wood with dwarf arctic willow near the limit of vegetation growth, is -12°C (Francis and Hill, 1996). The Viento palaeosol immediately overlying the fossil horizon is too weakly developed to provide any palaeoclimatic information. However, the Siesta palaeosol, higher in the stratigraphic section, is considered to have characteristics of the soils of Enderby Land. This palaeosol is considered to have formed in the active permafrost layer in a climate with a MAT of between -3 and -11°C and a precipitation of 300–1100 mm/yr (Retallack et al., 2001). The weathered bleached chitin of the fossil listroderine head sup-

ports the interpretation of a climate with a low annual precipitation. The Magellanic Moorland has been suggested as a modern analogue for the site but it is probably too humid (Mercer, 1986). We believe that the treeline environment in Tierra del Fuego and Isla Navarino, in the partial rain shadow of the western mountains bordering the Pacific Ocean, is a better climatic analogue. In this environment, broad-nosed weevils, including listroderines, coexist with prostrate *Nothofagus pumilio* shrubs and cushion plants (Fig. 2E,F).

6.3. Palaeobiogeography

At a distance of about 500 km from the South Pole, the MDF is the most southerly of all Cainozoic fossil deposits. The fossil listroderine weevils are related to extant South American taxa but sufficiently different to indicate that they evolved several million years in isolation before becoming extinct. Hill et al. (1996) discussed the possibility that *Nothofagus beardmorensis*, represented by fossils of leaves, wood and pollen in the MDF, recolonised Antarctica during a late Cainozoic warm interval long after the extinction of the early Cainozoic *Nothofagus* forests. They concluded that it was improbable because *Nothofagus* seeds disperse poorly and do not germinate after prolonged soaking in sea water. We also consider it improbable that listroderine weevils recolonised Antarctica from South America during a Neogene warm interval. All of the existing listroderine genera of cold and cool-temperate climates are flightless. They have vestigial wings, an adaptation which appears to be ancient. The only possible way for listroderines to have been introduced into Antarctica during the late Cainozoic is if pregnant females of two different species were transported more than 1000 km by migrating birds. The probability is low that any of the organisms represented by MDF fossils would have colonised Antarctica from a distant continent; the collective probability is even lower. For this reason, we consider it more probable that the MDF listroderines were the descendants of Gondwana species which had inhabited Antarctica continu-

ously from late Cretaceous or early Palaeogene time.

The modern distribution of listroderine weevils includes South America, the islands of the Tristan da Cunha group, and Australia and New Zealand. In South America, their diversity is greatest in Patagonia, Tierra del Fuego and the Falkland Islands, but species occur in the Andes Mountains at increasingly higher altitudes as far north as Colombia and Venezuela. More than a dozen genera are reported from southern South America whereas only four are known from Australia and New Zealand. The modern distribution of genera supports the hypothesis that listroderine weevils were widely distributed on Gondwana and probably differentiated into different genera. Evidence that the distribution could have included the Antarctic part of Gondwana is provided by a few Jurassic beetle fossils from two widely separated localities, one on the Antarctic Peninsula (Zeuner, 1953) and the other in the Transantarctic Mountains of Victoria Land (Tasch, 1973). The fossils are not curculionoids and probably represent extinct families. The oldest curculionoid fossils, representatives of the primitive family Nemonychidae, are from Jurassic lake beds in Kazakhstan, central Asia (Crowson, 1981). The oldest fossils of the evolutionarily more advanced weevils, the Brentidae and Curculionidae, do not appear until the Cretaceous period where they have been reported from South Africa, Chile and North America (Kuschel et al., 1994). None of the Cretaceous fossils is a rhytirhinine but we assume that they evolved during the late Cretaceous and became widely distributed in Gondwana at the time the continent was starting to fragment. We also assume that some genetic exchange between South American and Antarctic populations was possible during the Palaeogene period, but with the opening of the Drake Passage gene flow would have ceased about 20 Ma.

Pollen analyses of cores from Cape Roberts and DSDP Site 274 in the Ross Sea indicate that an impoverished tundra vegetation existed into the Neogene (Fleming and Barron, 1996; Raine, 1998; Askin and Raine, 2000). Cooling of the climate and the growth of ice sheets asso-

ciated with the opening of the Drake Passage and the formation of the Circumpolar Current between 34 and 22 Ma (Hansom and Gordon, 1998) is the most probable cause for the decline in species diversity of plants and animals. The climate remained relatively warm until 17–15 Ma, the mid-Miocene climatic optimum, after which the climate cooled and by 10 Ma a major ice sheet was established in East Antarctica, and by 6 Ma in West Antarctica (Zachos et al., 2001). Increasingly the climate became more arid, and after 7.5 Ma in the Dry Valleys a shift from wet-based to cold-based glaciations occurred (Armiotti and Baroni, 1999). We speculate that ice-free areas, starved of moisture, became polar deserts resulting in the extinction of vascular plants, most cryptogams, arthropods other than a few species of mites and collembolans, and all aquatic organisms. This extinction occurred after the MDF organisms had colonised the upper reaches of the Beardmore fjord.

The Pliocene was the last time of global warmth and higher sea levels (Crowley, 1996) when fjords in the Transantarctic Mountains might have been ice-free during summers. Various lines of evidence from the Southern Ocean and different parts of Antarctica indicate warmer conditions during the Pliocene. In the Ross Embayment, *Nothofagus* pollen of Pliocene age, and of the same type recorded from the MDF, is considered to be from trees growing nearby and not from a more distant continental source (Fleming and Barron, 1996). From different sides of the continent, an extinct species of scallop from the Antarctic Peninsula (Jonkers and Kelley, 1998) and species of whales and dolphins from the Vestfold Hills confirm that the coastal waters of Antarctica were warmer during the Pliocene (Quilty, 1993; Harwood et al., 2000; Quilty et al., 2000). On land, discontinuities within the glacial sequences of the Miocene and Pliocene-aged Pagodroma Group indicate that during warm episodes the Lambert Glacier retreated 250 km inland from the Amery Ice Shelf where it is positioned today (Hambrey and McKelvey, 2000; Whitehead and McKelvey, 2001). Finally, field-based evidence for Pliocene warmth in Antarctica has been consistently supported by the results of different general

circulation model (GCM) experiments (Chandler et al., 1994; Sloan et al., 1996; Haywood et al., 2000). In the most recent set of Pliocene GCM experiments, the climate model output was converted into biomes using the BIOME 4 model (Haywood et al., 2002). The model predicted a patchy distribution of cushion forb moss and prostrate shrub tundra around the margins of the Antarctic continent.

Evidence for a warmer and wetter climate during the Pliocene is contradicted by evidence from the Dry Valleys, where except for marine inundation of the lower reaches of the fjords, the polar desert landscape appears to have prevailed since ~15 Ma (Denton et al., 1992; Sugden et al., 1995b; Marchant and Denton, 1996). Also, stable isotope evidence from the Southern Ocean, although indicating Pliocene sea surface temperatures ~3°C warmer than today, is not considered to have resulted in significant melting of the East Antarctic ice sheet (Kennett and Hodell, 1993).

We consider the late Pliocene to be the best estimate for the extinction of the MDF organisms but recognise that this age assignment may change depending on how the conflicting evidence for the source and mode of incorporation of the recycled diatoms is finally resolved. If the MDF is demonstrated to be older, then the last time the fjords might have been ice-free during summers was ~16 Ma at the climax of Neogene warmth (Flower and Kennett, 1994), in which case the extinction may have occurred in the middle to late Miocene.

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