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Neogene vegetation of the Meyer Desert Formation (Sirius Group) Transantarctic Mountains, Antarctica

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Abstract

A tundra vegetation consisting of at least 18 plant species is described from the Meyer Desert Formation which outcrops along the Beardmore Glacier in the Transantarctic Mountains, about 500 km from the South Pole. The fossils include pollen, seeds, fruits, flowers, leaves, wood, and in situ plants, of which wood and leaves of *Nothofagus* and a pollen assemblage had been previously reported. The plants include a cryptogamic flora of mosses and liverworts, conifers, and angiosperms in the families Gramineae, Cyperaceae, Nothofagaceae, Ranunculaceae, Hippuridaceae, ?Caryophyllaceae, and ?Chenopodiaceae or ?Myrtaceae. The plants grew in a weakly-developed soil formed within a complex periglacial environment that included moraines, glacial outwash streams, well-drained gravel ridges, and poorly drained depressions in which peat and marl were being deposited.

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1. Introduction

The Antarctic flora today is dominated by cryptogams, most of which only grow in the most sheltered coastal locations north of 65°S. Only two species of vascular plants are known, a grass *Deschampsia antarctica* Desv. (Poaceae) and a herbaceous carophyllid, *Colobanthus quitensis* (Kunth.) Bartl (Car-

yophyllaceae). Both species occur in the area from the islands of the Scotia Ridge, along the west coast of the Antarctic Peninsula south to the current southernmost site on Alamo Island, Terra Firma Islands at 68°42' S. On the eastern side of the Antarctic Peninsula, adjoining the frozen Weddell Sea, vascular plants extend only as far south as 65° (Kappen and Schroeter, 2002). Both *D. antarctica* and *C. quitensis* are considered to have colonized the Antarctic Peninsula during the Holocene. Convey (1996) felt that the main reason why only two species had successfully invaded was because of the geographic isolation of Antarctica. The asymmetry in the geo-

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graphic ranges of the species on the Antarctic Peninsula, however, suggests that climatic factors play an important role in their distribution. Support for the importance of climate in limiting distribution comes from the failure of experiments to transplant the species further south (Lewis Smith, 1994).

The simple vegetational communities and the low plant diversity seen today contrast with the rich fossil record. Diverse forests of conifers (podocarps and araucarians) and angiosperms (Cunoniaceae, Nothofagaceae, Proteaceae, Lauraceae) inhabited the continent during the Late Cretaceous and Paleogene Periods (Dettmann and Thomson, 1987; Askin, 1992; Cantrill and Poole, 2002). The geographic isolation associated with the breakup of Gondwana, and the development of the Antarctic ice sheets, resulted in radical changes to the vegetation. However, the nature and the timing of extinctions caused by climatic cooling is still being debated largely due to the paucity of Neogene fossil sites (Cantrill, 2001).

Mercer (1972, p. 432) was the first to suggest that an examination of the contact between the Sirius Formation, a formation he named, and the underlying bedrock in the Oliver Bluffs, Dominion Range, might result in the discovery of ‘... a palaeosol, or traces of vegetation.’ His intuition proved to be correct. *Nothofagus* wood was described by Carlquist (1987) and Webb et al. (1987) and pollen by Askin and Markgraf (1986). Further descriptions of the wood, pollen, and well-preserved leaves of a new species of *Nothofagus*, *Nothofagus beardmorensis*, were made by Hill and Truswell (1993), Webb and Harwood (1993), Hill et al. (1996), and Francis and Hill (1996). Today, the climate of the Oliver Bluffs is too cold and dry to support vascular plant or cryptogram growth. The reports of Neogene fossil wood, leaves, and pollen of *Nothofagus* from a site so far south are one of the most important palaeobotanical discoveries to have been made in Antarctica. The discoveries provided the basis for palaeoclimatic interpretations that became significant in an ongoing debate about the relative stability of the Antarctic ice sheets.

An expedition to the Oliver Bluffs during the 1995 austral summer resulted in the discovery of new fossil materials. These included two species of curculionid beetles (Ashworth et al., 1997; Ashworth and Kuschel, 2003), one species of a cycloraphid fly (Ashworth and Thompson, 2003), and one species

each of a freshwater bivalve and a lymnaeid gastropod (Ashworth and Preece, 2003). The new fossil plant materials reported here include moss stems and leaves, in situ cushion plants, and fruits, stems and flowers of several species of vascular plants. The discoveries indicate a more diverse Neogene flora than was previously known and, together with the previously discovered fossils, enable a more complete interpretation of the Neogene vegetation and landscape in the Transantarctic Mountains.

2. Stratigraphy and age

The Meyer Desert Formation (MDF) is the name given to the mostly nonmarine glacial deposits forming the upper part of the Sirius Group, formerly the Sirius Formation, in the Meyer Desert and Dominion Range region of the Transantarctic Mountains (Mercer, 1972; McKelvey et al., 1991; Webb et al., 1996). The deposits are gently inclined to the north and are fractured by numerous normal faults with throws of up to 300 m (McKelvey et al., 1991). The MDF occurs in discrete, terraced sedimentary packages, with a combined thickness of about 185 m. Each of the packages is unconformable on the bedrock of a multi-tiered, glacially-scoured erosion surface, representing several distinct episodes of uplift and erosion followed by deposition.

The fossils are from beds within the topographically lowest and stratigraphically younger part of the formation exposed in the Oliver Bluffs, on the eastern flank of the upper valley of the Beardmore Glacier at latitude 85°07' S, longitude 166°35' E. The Oliver Bluffs, at an elevation of 1760 m above sea level, are located about 170 km south of the confluence of the Beardmore Glacier with the Ross Ice Shelf and about 500 km north of the South Pole (Fig. 1). The new fossils are from a horizon about 20 m above the base of an erosional spur located near the northern end of the bluffs (Fig. 2A). The section is about 900 m north of the one from which leaves of *Nothofagus beardmorensis* were described (Hill et al., 1996). The section consists of 85.5 m of interbedded diamictites, coarse cross-bedded sandstones, and wood-bearing siltstones and sandstones. On the scree slope immediately north of the spur, we discovered a thin lithified peat interbedded between thin marlstone deposits (Fig. 2F), at a similar

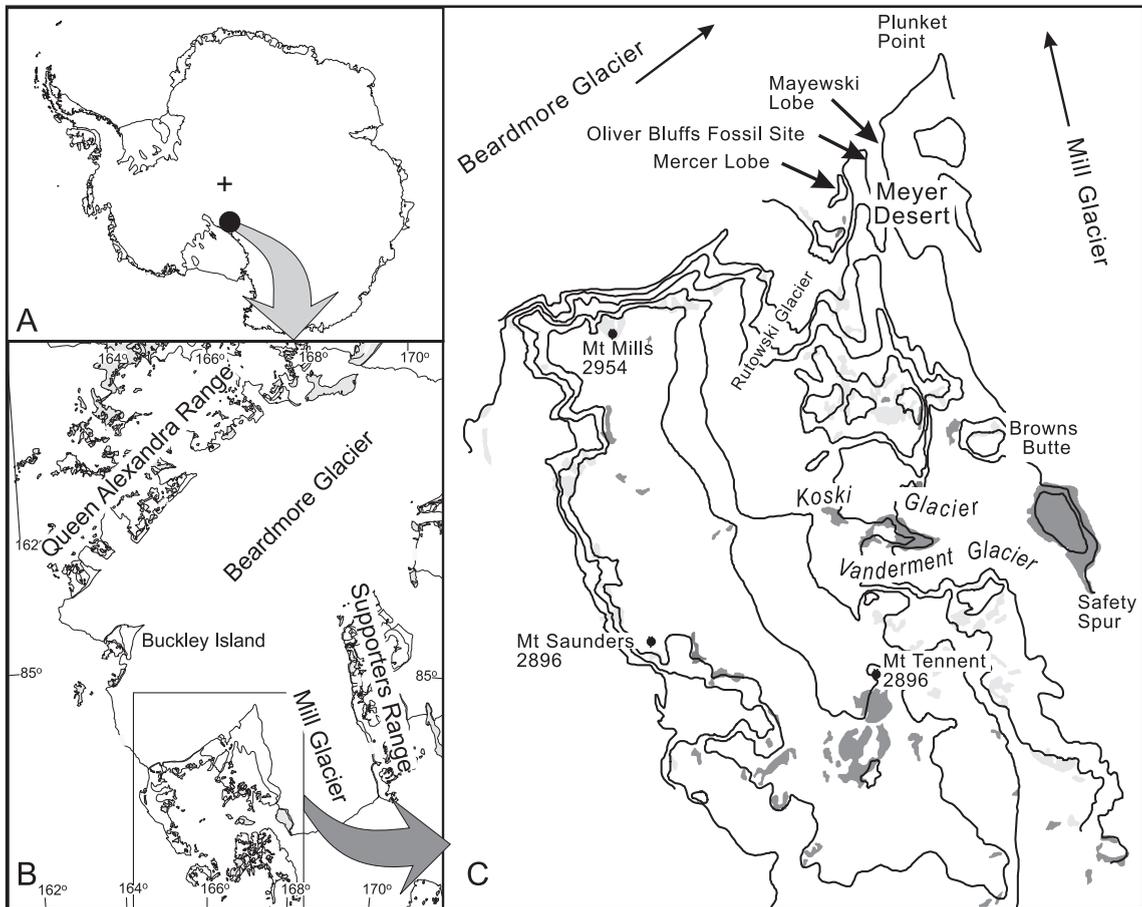


Fig. 1. Locality map of the fossil site at the Oliver Bluffs on the Beardmore Glacier in the Meyer Desert region of the Dominion Range, Transantarctic Mountains.

stratigraphic level to the wood-bearing siltstones and sandstones. The horizon is also at about the same level as a palaeosol identified as the lower of two Viento types by Retallack et al. (2001, Fig. 5). McKelvey et al. (1991) interpreted the diamictites as lodgement tills deposited by the ancestral Beardmore Glacier during a series of advances and retreats; they interpreted the fossiliferous deposits to have accumulated during an interglaciation.

Agglutinated foraminifera and other marine microfossils occur in the tillites at the southern end of the bluffs below the horizon containing leaves of *Nothofagus beardmorensis*. Webb et al. (1996) correlated the foraminifera assemblage with a similar assemblage from the upper part of the Cloudmaker Formation. The Cloudmaker Formation, the lower part of the Sirius

Group in the Beardmore region, outcrops about 90 km down-glacier from the Oliver Bluffs. Webb et al. (1996) interpreted the non-stratified and stratified drift with dropstones as glaciomarine sediments deposited by grounded and floating ice in a wide fjord. The Cloudmaker Formation is overlain by the MDF implying that the fjord infilled with sediment either by subsidence and progradation or by changes in base level. Webb et al. (1996) also proposed that subsequent to deposition, the Sirius Group deposits were uplifted by about 1300 m.

A biostratigraphic age of less than 3.8 Ma has been assigned to the MDF based on the occurrence in the Oliver Bluffs glacial sediments of reworked marine diatoms (Harwood, 1986; Webb et al., 1996). The same diatom taxa occur in situ with tephra in the

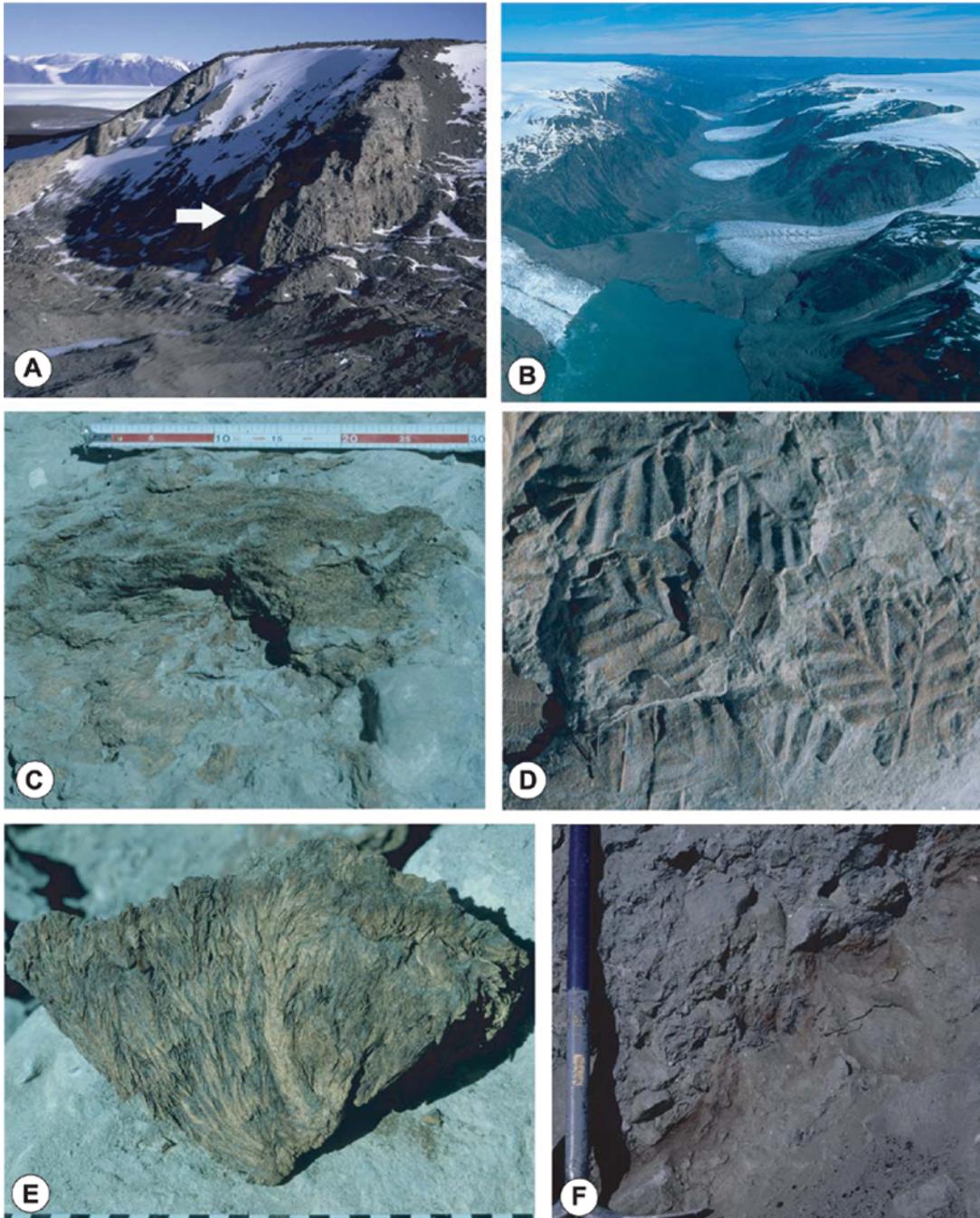


Fig. 2. Outcrop photos of the Oliver Bluffs and analogous present-day environments in Greenland. (A) Oliver Bluffs with the plant fossil locality marked (arrow). The Mill Glacier and Supporters Range are in the background. (B) Analogue for the fossil site. Fjord and deglaciated valley in southwestern Greenland. Patches of shrub tundra vegetation occur on the feldmark of the valley floor. Photo courtesy of Gary Comer. (C) In situ cushion plant, scale is a dm rule. (D) *Nothofagus beardmorensis* leaf mat; leaves are approximately 4.5 cm in length. (E) Portion of a fossil cushion plant in which the robust plant axes are clearly visible. The scale bar at bottom of the photograph is in 1-cm divisions. (F) Contact between overlying diamictite and underlying, deformed, thin peat bed. Handle of hammer 65 cm long.

CIROS-2 core from the Ross Sea with $^{40}\text{Ar}/^{39}\text{Ar}$ ages of 2.77 Ma (Barrett et al., 1992). *Nothofagus* pollen of the same type that occurs in the MDF has also been reported from DSDP Site 274 in the Ross Sea with a biostratigraphic age of about 3 Ma (Fleming and Barron, 1996). The pollen showed no signs of having been reworked and Fleming and Barron considered the most likely source would have been from *Nothofagus* growing on the Ross Sea coast. A Pliocene age is also supported by the degree of weathering and development of palaeosols in the MDF (Retallack et al., 2001). The palaeosol closest to the fossil horizon was assigned an age of between 1.3 and 4.1 Ma (Retallack et al., 2001).

The biostratigraphic age assignment depends on the diatoms being incorporated in the glacial deposits directly from the reworking of older marine sediments. That interpretation has been challenged in several studies in which it is considered more probable that the diatoms were wind-deposited (Burckle and Potter, 1996; Burckle et al., 1996; Kellogg and Kellogg, 1996; Stroeven et al., 1996; Barrett et al., 1997) or from the fall-out of sediments blasted from the deep ocean floor by the Eltanin asteroid (Gersonde et al., 1997). In either case, the MDF is considered to be older than the diatoms.

3. Field and laboratory methods

Approximately 400 kg of samples were collected from the different lithologies and shipped to the laboratory for preparation. All samples were disaggregated first by soaking in water to soften the calcite cement and then by wet sieving through a 300- μm sieve. The fossils were then picked from the grain residue under a binocular microscope. The samples that preserved the best cellular detail were obtained from about 50-cm depth, indicating that oxidation of organic material is occurring at the surface of the outcrop. Lithologies varied with respect to the yield and the composition of fossils. The marl contained fragments of mosses along with freshwater molluscs (shells of the bivalve *Pisidium* and a species of lymnaeid gastropod; Ashworth and Preece, 2003), a single fish tooth, "and rare achenes (*Ranunculus* type). The peat yielded moss and shell fragments and some achenes (*Ranunculus* type), while the siltstones yielded cushion plants,

abundant achenes (all types), along with fragments of mosses, wood, insects, and ostracods.

All fossils were mounted on micropalaeontological slides for preservation and are part of the collection of the Quaternary Entomology Laboratory at North Dakota State University. Statistical analysis of the achenes involved accurately drawing outlines of every specimen at a magnification of about $25\times$ using a camera lucida attached to a binocular microscope. The images were then scanned and the area and lengths of major and minor axes were determined (in pixels) using a Fourier-based method described by Cheng (2003). The measurements were then converted from pixels to millimeters to plot the graphs (Fig. 7).

4. Biodiversity

4.1. *Cryptogams*

Fossil moss cushions were reported to occur in the MDF at the Oliver Bluffs (Hill et al., 1996), but no descriptions of them were made. In our samples, vegetative axes that lack vascular tissue are common and these are interpreted as the remains of mosses. In all, more than 500 fragments were recovered. The majority, however, are small (less than a few millimeters long), unbranched, and often leafless, although the leaf bases may be present. The fragmentary nature of the axes mostly precludes identification to the generic or family level. Where whole leaves were preserved, leaf arrangement, morphology, and cell structure were used for identification. We identified at least five different types of mosses but we believe that represents a minimum number of species.

Moss type 1 comprises axes with distinctly distichously arranged leaves and is represented by 15 specimens (Fig. 3A). Leaves are strongly recurved and a central nerve extends from base to apex (not excurrent). Leaf cells of the lamina are small and rectangular, ranging from 10 to 16 μm long by 10 to 16 μm wide (Fig. 3B). The upper leaf surface is smooth and the lower surface is strongly papillate (Fig. 3D), but less so over the midregion of the leaf. Cells over the central nerve are c. 25–45 μm long by 9–11 μm wide. The strongly papillate leaves suggest affinities with the Pottiaceae.

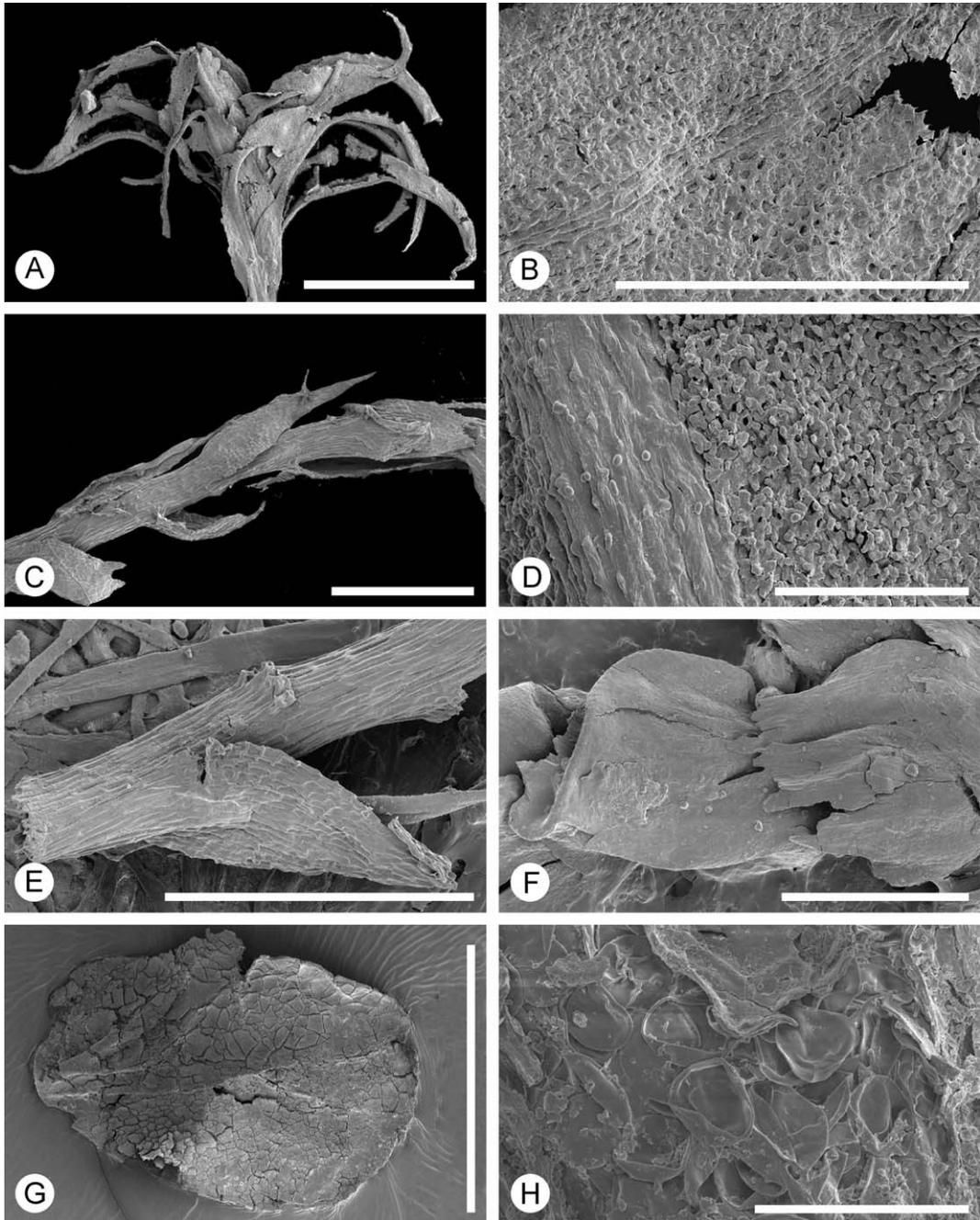


Fig. 3. Scanning electron micrographs of cryptogamic fossils. A, B, and D: Moss type 1. (A) Overview of habit with strongly recurved leaves. (B) Cell arrangement on upper leaf surface. (D) Lower leaf surface adjacent to midrib. Note the prominent papillae. C and E: Moss type 2. (C) Habit of axes with small widely spaced appressed leaves. (E) Close up of individual appressed leaf. F: Moss type 3. G and H: Spore bearing body. (G) Small ovate body with medial ridge that apparently bifurcates. (H) Small smooth walled 20–30 μm spores with trilete marks. Scale bars A and G represent 1 mm; B, C, E, and F represent 200 μm ; D and H represent 50 μm .

Moss type 2 is represented by two strands, the longest c. 5 mm long (Fig. 3C). This axis is covered by widely spaced and appressed linear lanceolate leaves, up to 0.4 mm long. The leaf margin is entire, and the leaf apex is narrowly acute and tapered (Fig. 3E). Cells of the lamina are composed of small rectangular cells 10–18 μm long by 8–10 μm wide.

Moss type 3 appears to have four ranks of leaves that are strongly imbricate. The leaves are ovate to lanceolate, 0.3–0.6 mm long by 0.2–0.4 mm wide; leaf surfaces are smooth, margins entire, apex rounded (Fig. 3F).

Moss type 4 is by far the most common component of the moss flora represented by at least 150 specimens. The majority of the axes are missing leaves but leaf bases are intact. The axes are generally unbranched, but occasionally, there are rare lateral branches. Leaves are arranged in three or four ranks, lanceolate, and lacking a central nerve (Fig. 4A). Leaf margins are entire and leaf apices are acute (Fig. 4A). Leaves are inserted at greater than 45° . Leaf cells are uniformly elongate with length–width ratios between 8 and 10. Cells range from 60 to 100 μm long by 7 to 10 μm wide. No specialized cells around the leaf bases were observed.

Moss type 5 is represented by four isolated leaves. However, the distinctive nature of the leaf material indicates that this is a different species. The leaves are small (0.65–0.8 mm long by 0.4 mm wide), ovate with a contracted base, and a prominent nerve that extends to the leaf apex (Fig. 4B). The nerve is compound comprising three to four rows of cells. Cells of the nerve are elongate, 80–100 μm long by 10–12 μm wide. Cells of the leaf lamina are rectangular, rarely polygonal, and 18–32 μm in diameter (Fig. 4B).

No reproductive mesofossils of cryptogams were identified, but spores have been reported from the deposits. Smooth, thick-walled bodies, or resting spores, point to the presence of algal and fungal groups (Askin and Markgraf, 1986; Hill and Truswell, 1993). A low diversity assemblage of bryophytes is also indicated by three *Coptospora* species and Marchantiaceae spores (Askin and Raine, 2000). Palynological examination of the marls and peat (Askin and Ashworth, 1998) yielded similar low diversity assemblages.

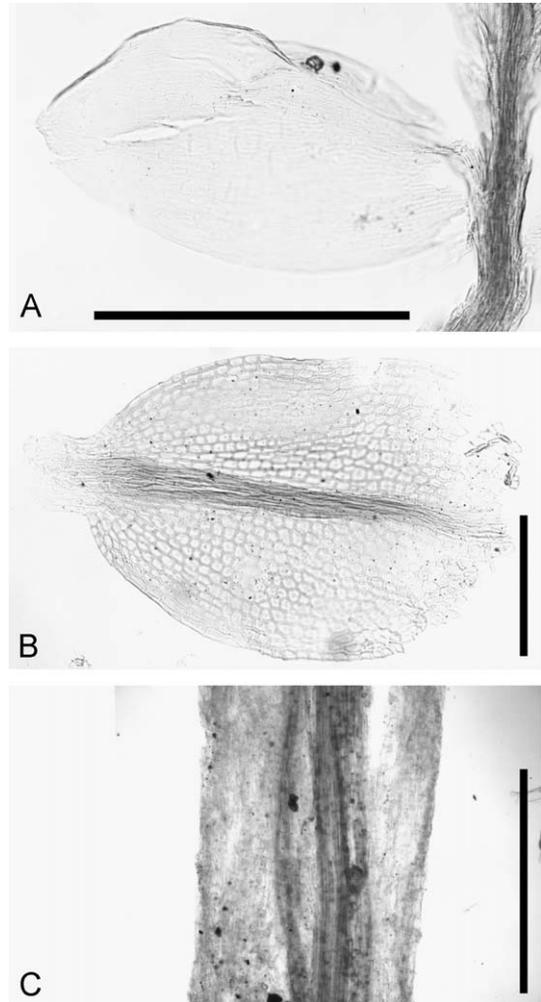


Fig. 4. Light micrographs of plant fossils. (A) Moss type 4 with simple lanceolate leaves. (B) Moss type 5 with small ovate leaf that have a prominent central midrib and isodiametric cells. (C) Portion of ?grass blade with a central vascular strand surrounded by cells filled with brownish material. Scale bars A–C represent 0.5 mm.

A single fossil, 1.5 mm long by 1.0 mm wide, obovate in shape, may represent a part of a lower plant (Fig. 3G). The base is tapered and terminated in a semicircular structure that superficially resembles a leaf attachment point. A single vein-like ridge arises at the base and branches once. The surface is smooth, but cell structure is visible in some places and comprises small rectangular cells. The ridge-like vein is fractured, and the interior is packed with small, triangular, smooth-walled trilete spores (Fig. 3H), ranging from 15 to 20 μm in diameter.

4.2. Conifers

Conifers have been recorded in the pollen assemblages by the presence of rare bisaccate pollen grains initially identified as ?*Dacrydium* (Askin and Markgraf, 1986), but more recently referred to *Podocarpidites* sp. b (Askin and Raine, 2000). The only other reference to conifers is that of fossil wood (Carlquist, personal communication, in Askin and Markgraf, 1986), but a later study (Carlquist, 1987) stated all of the wood collected belonged to *Nothofagus*. Francis and Hill (1996) reported only *Nothofagus* wood, and all of the wood from our samples is angiospermous.

4.3. Angiosperms

Flowering plants are represented by vegetative material including leaves and wood and reproductive structures including pollen, seeds and fruits, and flower parts. Much has been written about the spectacularly preserved *Nothofagus* leaves (Hill and Truswell, 1993; Hill et al., 1996) and wood (Webb and Harwood, 1987; Carlquist, 1987; Francis and Hill, 1996) from the MDF and is not repeated here. The pollen record is dominated by single type of *Nothofagidites* that was compared to *Nothofagidites lachmaniae* (Askin and Markgraf, 1986; Hill and Truswell, 1993) and placed in the subgenus *Fusco-spora* (Hill and Truswell, 1993). It should be noted that *N. lachmaniae* is placed in the subgenus *Nothofagus* by Dettmann et al. (1990).

Although *Nothofagus* pollen dominates the assemblages, other angiosperm diversity is recognized by the presence of rare tricolpate grains (*Tricolpites* sp. 2 of Truswell, 1983; *Tricolpites* sp. a of Raine, 1998; Askin and Raine, 2000) that is thought to be related to Polygonaceae or Laminaceae (Askin and Markgraf, 1986; Hill and Truswell, 1993; Raine, 1998).

Vegetative remains indicate further diversity to this sparse pollen record. Within the fossiliferous horizon at the Oliver Bluffs, mounds up to 30 cm in basal diameter and 16 cm in height are encountered (Fig. 2C and E). Although moss cushions have been recorded (Hill et al., 1996), this material differs substantially. Internally, the mounds are fibrous in appearance and composed of robust woody axes radiating with a

bifurcating branching habit towards the outside of the mound (Fig. 2E). The axes range from 2 to 8 mm in diameter. The density of the outer surface and the packing of the axes indicate a compact habit rather than an open shrubby habit. The axes are covered basally in leaves. The leaves, however, are not well-preserved except for the outer ones which are linear to linear lanceolate (Fig. 5A). The woody texture suggests that the mounds were formed by vascular plants with a cushion-like habit. This is confirmed by vascular tissue seen in the leaf and the recognition of stomata on the leaf surface (Fig. 5B). A cushion-like habit is found in many southern hemisphere angiosperm families such as Caryophyllaceae (e.g. *Colobanthus*), Apiaceae (e.g. *Azorella*), Umbelliferae (e.g. *Bolax*), Donatiaceae (e.g. *Donatia*), and Asteraceae (e.g. *Haastia*, *Raoulia*). Other vegetative material includes a long, linear leaf fragment that is 16.5 mm long by 0.5 mm wide that may be part of a grass blade. Internally, the leaf has a central vascular strand surrounded by distinctive brown-coloured cells (Fig. 4C). The brown colouration is confined to small regions within the cells, and these are interpreted to be the remains of chloroplasts. The position of the cells is similar to bundle sheath cells observed in grasses.

Reproductive materials support the presence of more vascular plant diversity. A single flower was recovered from the organic residues. The flower is not well-preserved but terminates a robust pedicel (Fig. 4E–G). Unfortunately, the abrasion of the material has resulted in the loss of the outer whorls of the calyx, but scars show the position of parts. The outer whorl of parts surrounds a central cup that appears to be five partite (Fig. 5G). Details of the anthers and ovary are not preserved, but the flower appears to have a superior ovary. The present lack of detail of floral number and arrangement precludes systematic placement.

A poorly preserved structure thought to represent another flower type was also identified (Fig. 5C and D). This structure appears to have two outer bracts subtending a complex of perianth parts. By far, the most interesting reproductive organs recovered from the MDF deposits are 366 specimens of small seeds and fruits ranging from 0.4 to 2.0 mm long (Fig. 6). There are five distinctive morphologies, but the majority (98.7%) probably represent one genus and possibly one species.

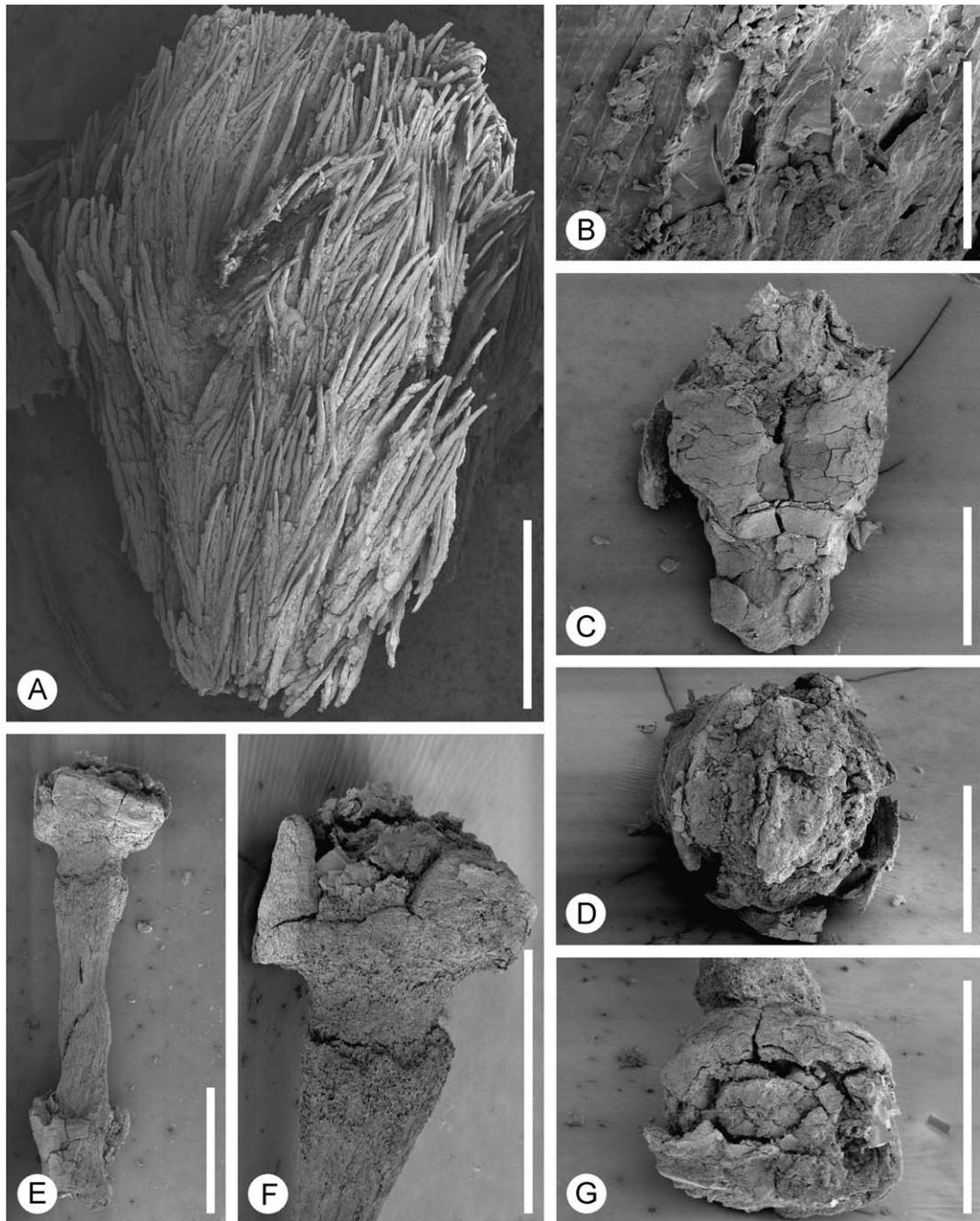


Fig. 5. Mesofossils of cushion plants and flowers. A and B: Cushion Plant. (A) Portion of axis with imbricate linear leaves. (B) Fractured surface of the leaf revealing poorly preserved stomata. C and D: Small inflorescence. (C) Lateral view of possible bipartite inflorescence. (D) Apical view of same structure. E–G: Flower. (E) Overview of whole axes terminating in flower. (F) Lateral view showing perianth parts. (G) Apical view illustrating five partite arrangement of perianth. Scale bar A represents 5 mm; B represents 50 μ m; C–G represents 1 mm.

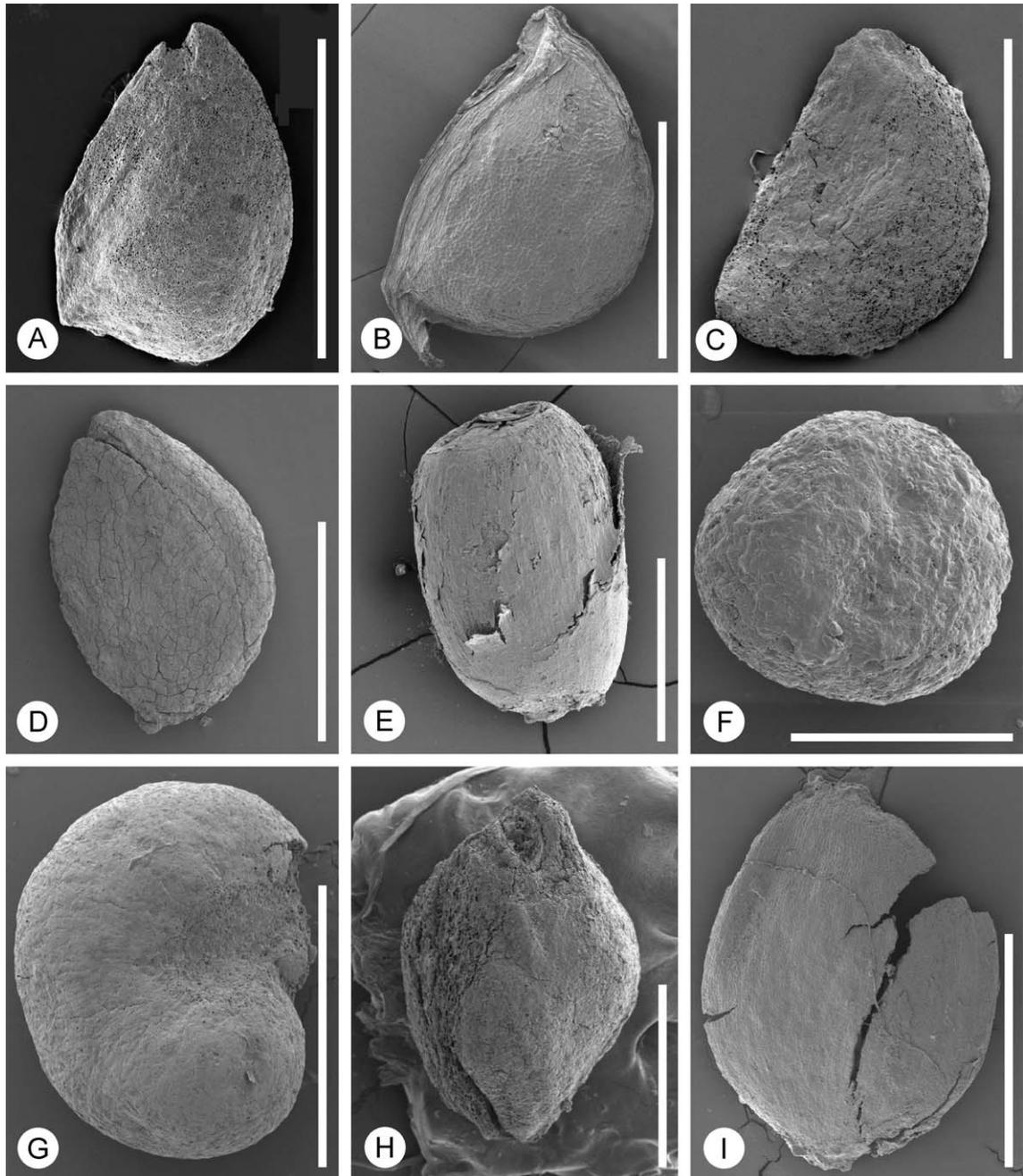


Fig. 6. Dispersed seed and fruit flora. A, C, and D: Type 1 fossil achenes. (A) More complete specimen. (C) Eroded specimens. (D) Laterally compressed specimen revealing ventral suture. (B), Modern achene of *Ramunculus peduncularis* Sm. from Tierra del Fuego for comparison with the fossils. E: Type 2 fruit, a barrel-shaped seed identified as *Hippuris*. F: Type 6—?seed. G: Type 5, small reniform seed. H: Type 3 fruit identified as Cyperaceae. I: Type 4 fruit identified as Cyperaceae. Scale bars A–C represent 2 mm; D–F and I represent 1 mm; G and H represent 0.5 mm.

Type 1 are achenes that are broadly elliptical to obovate, with a more or less straight to slightly convex ventral side, and a distinctly convex dorsal side (Fig. 6A, C, and D). The specimens, which are laterally compressed, range in size from 1.1 to 1.7 long by 0.6 to 1.3 wide. The bases are narrow, often with distinct oblique attachment points (Fig. 6A). On a few specimens, the apex is prolonged into a short beak, but this feature has been abraded in the majority of specimens. Where the outer wall has not been abraded, the achenes appear to be smooth. The cells exposed in the abraded walls are equidimensional, randomly oriented, and $20 \times 20 \mu\text{m}$ in size. Occasionally, two distinct veins are present that are characterized by longitudinally orientated cells. These arise in the attachment point and extend for up to three quarters of the achene length.

The distinctive shape of the better-preserved achenes is most similar to that seen in extant *Ranunculus* species (buttercups) (Fig. 6B) with which we compare it here. The lengths of major and minor axes were plotted against area for 328 of the better preserved specimens. Significant regression analyses r^2 and p values indicate that the morphological variation is continuous (Fig. 7). The most parsimonious interpretation of the data is that they represent a single species, with the variation attributable to a combination of natural and taphonomic causes. Some variation in morphology results from the position in which the achenes developed on the inflorescence head. Other variation resulted from abrasion of the achenes before burial and later crushing and distortion in the sediment.

Four additional types of seeds or fruits are also present but are represented by one or a few specimens. Type 2 is a fruit represented by a single distinctive specimen that is 1.74 mm long by 0.98 mm wide, oblong, spherical, with a distinct small basal stalk and a round opening in the apex (Fig. 6E). The lack of material makes comparisons difficult, but similarities with extant *Hippuris* (mare's tails) are remarkable. *Hippuris* is a widespread, perennial herb of shallow water and mud flats, occurring from high arctic to temperate latitudes in North America and Eurasia, but also occurring in Australia and southern South America where it is native (Cronquist, 1981; Moore, 1983). The bipolar distribution is believed to result from dispersal of fruits or rhizomes by migratory birds (e.g. Arctic terns).

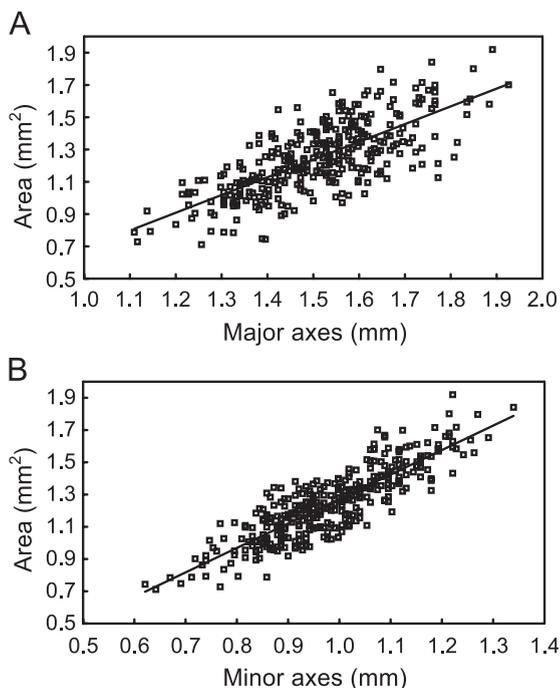


Fig. 7. Regression analyses of area in relation to (A) minor axes ($r^2=0.745$, $p \leq 0.001$) and to (B) major axes ($r^2=0.537$, $p \leq 0.001$) for 328 fossil achenes of *Ranunculus*.

Type 3 is a fruit represented by a single distinctive specimen that is 1 mm long by 0.7 mm in diameter, broadly fusiform, with a distinct small basal stalk, and a tapering apex (Fig. 6H). The specimen has the morphology of a Cyperaceae fruit (sedges).

Type 4 is a flattened fruit that is elliptical to ovate in outline, 1.75 mm long by 1.25 mm wide (Fig. 6I). It has a distinct contracted basal attachment and apically appears to terminate in a contracted and possible mucronate style. The outer surface has a faint ornament of raised cell walls. The specimen has the morphology of a Cyperaceae fruit but of a different species than represented by Type 3.

Type 5 is a small reniform seed, campylotropous, 0.75 mm long by 0.5 mm in diameter, and slightly asymmetrical (Fig. 6G). Cells on the outer surface are transversely orientated and the anticlinal walls are smooth. The placentation seen in this type is rare in angiosperms but is widespread in the caryophyllids including families such as Chenopodiaceae and also in families such as the Myrtaceae.

It is interesting to note that Wilson et al. (1998) recorded a Chenopodiaceae pollen grain from Sirius Group strata in the Reedy Valley.

In addition to the five types of achenes and fruits, there are two additional specimens that may represent a sixth type. The specimens are spherical and broadly ovate in shape, 0.3–0.5 mm in diameter (Fig. 6F).

5. Sedimentary environments, the physical landscape, and the extent of the East Antarctic Ice Sheet

The Sirius Group, formerly the Sirius Formation, is patchily distributed throughout the Transantarctic Mountains (TAM) at elevations ranging from 1750 to 3000 m (Mayewski and Goldthwaite, 1985). Deposition of the tillites, fluvio-glacial, glaciolacustrine, and glaciomarine deposits clearly reflect a warmer and wetter climatic regime than exists in Antarctica today. The relationship of the deposits, however, to the extent and the dynamics of the East Antarctic Ice Sheet (EAIS) is contentious. Passchier (2001) summarized various hypotheses that have been proposed. The first is that deposition was from glaciers that flowed from ice caps developed on plateaus in the TAM during the early stages of uplift and prior to the formation of the EAIS (Mercer, 1972). The second is that the high elevation Sirius deposits in the Dry Valleys were deposited by alpine glaciers and not by outlet glaciers of the EAIS, although it was in existence (Stroeven and Prentice, 1997). The third is that the deposits represent the overriding of a preexisting TAM by a greatly expanded EAIS during an episode of major continental glaciation (Mayewski, 1975; Webb et al., 1984; Denton et al., 1984). The fourth is that the higher elevation Sirius deposits are associated with an EAIS that overrode the TAM and that the younger deposits are those associated with valley glaciers that incised the TAM as a result of uplift (Brady and McKelvey, 1979, 1983; Barrett and Powell, 1982; Webb et al., 1996; Van der Wateren et al., 1999; Passchier, 2001; Hambrey et al., 2003).

For the deposition of the MDF, we prefer the last mentioned interpretation. We believe that the EAIS was already in existence, and the ancestral Beardmore Glacier was already within a valley incised into the TAM. The occurrence of agglutinated foraminifera in

the beds immediately below the fossiliferous beds is a strong indication that deposition occurred close to sea level. Furthermore, the occurrence of glaciomarine deposits of the Cloudmaker Formation down valley indicates marine inundation and the existence at times of a fjord as far inland as the Oliver Bluffs. Postdepositional uplift suggests that landscape relief at the time of deposition of the MDF was more than a thousand meters lower than today. The stratigraphy at the Oliver Bluffs of multiple lodgement tillites, interbedded with wood-bearing sandstones and siltstones, is evidence of a dynamic ice margin during which the glacier advanced and retreated on several occasions. The occurrence of palaeosols at several horizons indicates episodes of relative stability during which soils formed (Retallack et al., 2001). The lithofacies variations over short distances within the fossiliferous bed suggest a generally unstable sedimentary environment. We envisage a landscape of low-relief moraines and a wide, braided outwash plain that existed between the East Antarctic Ice Sheet, the glacier margin, and the fjord. The moraines provided more stable surfaces for plant colonization, but plants would also have been able to have colonized the gravel bars and ridges between the channels of the braided meltwater streams. Abandoned channels on the margins of the active system would have provided locations in which thin peats and marls accumulated. In many respects, the appearance of the landscape would have been similar to that of the fjords of western Greenland today (Fig. 2B).

6. Diversity and plant palaeoecology

Antarctica has been essentially in a polar position since the Early Cretaceous (Lawver et al., 1992) and at 85°S receives no sunlight from the middle of March until the end of September. The total amount of solar radiation received today is about 2250 W/m² and the number varies by a small amount because of changes in the eccentricity of the earth's orbit. The amount of radiation received is about 42% of that received over Tierra del Fuego at 55°S. The absence of solar heating for about 5.5 months, even though there would have been additional heat from the ocean, would have resulted in a low mean annual temperature. We expect that the indirect effects would have been low

atmospheric moisture content, low annual precipitation, a short growing season, slow rates of chemical weathering and low nutrient availability, especially nitrogen and phosphorus, and permafrost with restricted drainage and poor aeration. Furthermore, strong adiabatic winds from the glacier, winter snow cover, summer snow and ice storms, and frosts throughout the growing season would have contributed to a severe environment for plant growth.

The growing season, sandwiched between early summer snow melt and killing autumnal frosts, would be expected to be between about 6 and 12 weeks long. Above-ground vegetative growth would occur mostly immediately after snow melt. Root growth would be delayed by the frozen soil but would continue after killing frosts. Photosynthesis would continue throughout the 24-h photoperiod enabling plants to grow rapidly. Flowering, reproduction, and seed production would probably only occur in the summers with the most favourable climatic conditions.

Plant species in the High Arctic are so well-adapted to low temperature that they have evolved physiologies and morphologies that enable them to survive winter desiccation and where special adaptations for photosynthesis, respiration, and absorption of nutrients enable them to grow at similar rates to those in more temperate latitudes (Chapin and Shaver, 1985). The MDF plants also had to be highly-adapted to exist in the reduced photoperiod and low temperatures at lat. 85°S.

The plants of the MDF flora, based on compiling various lines of fossil evidence, include at least three types of liverworts, five species of mosses, a species of conifer (Podocarpaceae), and at least seven species of vascular plants, including representatives from the grasses (Gramineae), sedges (Cyperaceae), southern beeches (Nothofagaceae), buttercups (Ranunculaceae), mare's tails (Hippuridaceae), and ?Caryophyllaceae, and ?Chenopodiaceae or Myrtaceae. The number of taxa is higher than has been reported previously from the MDF but still at the low level of diversity that would be expected for a tundra flora growing at lat. 85°S.

We surmise that the first colonizers on the landscape at the head of the Beardmore fjord would have been cushion-forming species of mosses that trap organic matter and contribute to soil formation (Lewis Smith, 1994). The fossils occur in association with a

palaeosol (Viento-type) exhibiting weakly-developed structures characteristic of a permafrost landscape (Retallack et al., 2001). The asymmetric growth rings of fossil *Nothofagus* wood indicate a low sprawling habit for these shrubs with some evidence for wind abrasion (Francis and Hill, 1996). The exceedingly narrow growth rings (Francis and Hill, 1996) further indicate an environment in which soil-forming and biotic processes were slow.

Within the fossil horizon are in situ cushions of vascular plants and mosses. The woody tissue of the vascular plants forms cushions that are 30 cm in diameter at the base and 16 cm high. Cushion plants in tundra habitats are characteristic of wind-exposed sites with well-drained soils (Bliss, 1997). The specimens evidently were sufficiently well-rooted to be buried in their growth positions by outwash deposits.

Leaves from *Nothofagus beardmorensis* form a dense leaf mat that probably represent a deciduous leaf fall and accumulation in a shallow pool of water (Webb and Harwood, 1993). In polar latitudes, shrubby deciduous taxa are restricted to the warmest and most protected habitats (Bliss, 1997). Evidence from growth ring anatomy of the fossil wood indicates that the shrubs had a low prostrate growth form (Francis and Hill, 1996). We consider this a more realistic interpretation than the patch of upright shrubs illustrated by Webb and Harwood (1993).

Peat lenses, between 1 and 10 cm in thickness, occur within the fossiliferous horizon. At one locality, a thin peat about 5 cm in thickness is underlain and overlain by marl deposits about 2 cm in thickness; the marls contain abundant broken shells of a species of lymnaeid gastropod and a species of *Pisidium*, a fingernail clam (Ashworth and Preece, 2003). The peat and marl beds were deformed during a glacial advance and were squeezed up between the boulders of a lodgement till. The peats contain only occasionally recognizable moss stems suggesting that they are either strongly humified moss bank or mire deposits, or that they are microbial mats formed by cyanobacteria and algae.

The variety of growth forms in the MDF fossil assemblage represents a typical tundra assemblage in which there is selection in the harsh environment for phenological plasticity. The growth forms of dwarf and prostrate shrubs, cushion, and graminoid would be adaptive to the different microtopographic sites.

The cushion forms would mostly be morphological adaptations to the most exposed windswept locations. We envisage a tundra environment in which there was a mosaic of well-drained and poorly-drained microsites in which nutrient availability would have been patchily distributed. Mean summer temperatures, based on the minimal thermal requirements for *Nothofagus*, listroderine weevils, and freshwater molluscs, are estimated to have been about 4 to 5 °C for at least two summer months (Francis and Hill, 1996; Hill and Jordan, 1996; Ashworth and Kuschel, 2003; Ashworth and Preece, 2003).

The fossils we have identified are from deposits that are interbedded between lodgement tills. The organisms colonized the head of the Beardmore fjord as the glacier retreated. Those communities were later destroyed by glacial advance. The palaeosol associated with the horizon is just one of several that have been identified in the Meyer Desert Formation (Retallack et al., 2001). Palaeosols with abundant root casts and fossil wood higher in the Oliver Bluffs stratigraphic section indicate multiple phases of recolonization of the landscape associated with glacial retreat. Fossil wood, presumably *Nothofagus*, and moss stems reported from near the base of the MDF on the Cloudmaker about 90 km north of the Oliver Bluffs, suggests that a tundra vegetation had a much wider distribution in the Beardmore region (Webb et al., 1996). Reports of wood, woody tissue, or moss stems from Sirius Group strata, or their stratigraphic equivalents, at localities separated by hundreds of kilometers in the TAM suggest that tundra may have occurred in coastal locations in East Antarctica extending inland up fjords during warmer intervals, possibly from the Oligocene to the Pliocene (Wilson et al., 2002; Hambrey et al., 2003; Marchant, personal communication, Marchant et al., 2002).

7. Biogeography

Ever since J.D. Hooker (1853), biogeographers have debated the relationships between organisms on the widely separated continents of the southern hemisphere. Similarities are explained either by reference to ancient Gondwana relationships or by more recent dispersal. With the development of the plate tectonics hypothesis, the vicariance biogeogra-

phers gained the upper hand, although it has always been understood that the natural terrestrial biota of remote, geologically young, volcanic subantarctic islands must have reached their destinations either by transport on ocean currents or by birds. Molecular genetic studies of plants, including species of Ranunculaceae, suggest that many plant relationships, formerly considered to be ancient, may be considerably younger, and that their current distributions result from dispersal and not vicariance (Lockhart et al., 2001; Winkworth et al., 2002). To the vicariance biogeographers, Antarctica is viewed as an evolutionary centre and, to the dispersalists, as a possible stepping stone between South America and Australia and New Zealand.

Potentially, the MDF fossil assemblage could represent either a relictual Antarctic biota or one that dispersed to Antarctica during warm intervals during the Neogene. Francis and Hill (1996) discussed this question with respect to *Nothofagus beardmorensis*. They concluded that because of the dispersal mechanisms available to *Nothofagus*, it was much more probable that *N. beardmorensis* was a descendant from a long lineage of Antarctic species. We cannot really be sure, however, that all the plants in the MDF are relictual (e.g. Ranunculaceae, Hippuridaceae). Molecular genetic studies of a subset of alpine New Zealand *Ranunculus* species indicate a Pliocene radiation and subsequent dispersal to Australia and the New Zealand subantarctic islands (Lockhart et al., 2001; Winkworth et al., 2002). This indicates the possibility of long distance dispersal to Antarctica during the Neogene. However, it does not preclude the chance that these plants may also be a relictual component of the Cretaceous and early Tertiary Antarctic biota.

The identification of a *Hippuris*-like fruit in the MDF is biogeographically fascinating; the implication is that the existing bipolar distribution of *Hippuris vulgaris* L (Water Mare's Tail) between the northern and southern hemispheres is ancient. We imagine that melting of the EAIS during the Neogene permitted the ancestors of existing bird species to extend their long-distance migrations into the fjords deep in the interior of Antarctica carrying with them plants and invertebrate animals.

The isolation of Antarctica as a result of plate tectonic processes undoubtedly played an important

role in the evolution of the earth's climate system. A general decline in global temperatures through the Tertiary is overprinted by rapid cooling events (e.g. 33.5 Ma) as indicated by shifts in oxygen isotopes (e.g. Zachos et al., 2001; DeConto and Pollard, 2003), and these signal the initial formation of Antarctic ice and a subsequent rapid expansion of Antarctic ice sheets. The cooling of Antarctica and the associated reorganization in oceanic and atmospheric circulation had a profound effect on the vegetation of the continent. Prior to the Oligocene, the floras of Antarctica were relatively diverse, although it is clear that cool temperate elements such as *Nothofagus* become increasingly important during the Eocene in regions such as the Ross Sea (Pole et al., 2000) and the Antarctic Peninsula (Poole, 2002; Poole and Cantrill, submitted for publication). Following a major cooling event around the Eocene/Oligocene boundary, there is a marked increase in glacially-derived sediments, and the record of fossil vegetation is sparse, confined to a few records of *Nothofagus* leaves in boreholes (Hill, 1989; Cantrill, 2001). The lack of outcrop has hindered our understanding of the patterns of changing diversity and the nature of the vegetation. This raises important questions as to whether the cool temperate flora was rapidly replaced at this time or declined gradually throughout the Neogene.

For many years, it was believed that the Antarctic flora became extinct when the first ice sheets formed in the Oligocene. The huge volume of glacially-derived shelf sediments made it difficult to envisage that a vegetation could have existed anywhere on the continent. This notion conflicted with evidence from palynology that suggested the presence of temperate forest well into the Oligocene in the Antarctic Peninsula region (Stuchlik, 1981) and East Antarctica (Kemp, 1975; Kemp and Barrett, 1975). However, radiometric dating of sequences in the Antarctic Peninsula has proved problematic and pollen assemblages indicate substantially older ages (Truswell, 1990). These assemblages are now known to be Eocene age. Similar problems existed with the interpretation of palynological assemblages from East Antarctica where low yields and reworking made it difficult to determine what part of the assemblage was in situ (Truswell, 1990). Consequently, the nature of

Oligocene vegetation was uncertain due to poor age control and difficulty in interpretation.

The drilling of the CIROS-1 borehole, with better age correlations, provided solid evidence for the presence of a depauperate Oligocene vegetation represented by a *Nothofagus* leaf (Hill, 1989) and a sparse pollen record (Mildenhall, 1989). A decrease in species richness is noted higher in the stratigraphic section in both the CIROS-1 and MSSTS-1 boreholes (Truswell, 1990), pointing to a progressive decline in diversity and vegetation. Similar patterns have recently been confirmed by the Cape Roberts Drilling Program where a single *Nothofagus* leaf occurs in the Oligocene (Cantrill, 2001), and the palynological assemblages show a species-poor flora that decreases in abundance and diversity from the Oligocene through the early Miocene (Raine, 1998; Raine and Askin, 2001). The palynological record clearly indicates that a tundra vegetation, containing vascular plant species, existed in the Ross Sea region until the early Miocene.

The question is when did the Neogene vegetation become extinct. Was it following the mid-Miocene warm interval at c. 17 Ma when deglaciation might have resulted in fjords extending from the Ross Sea to the heads of the valleys in the Transantarctic Mountains, or was it following a mid-Pliocene warm interval at about 3 Ma? A coupled GCM BIOME 4 model experiment using the USGS PRISM2 global data showed that the simulated Pliocene vegetation of the deglaciated coastal areas of Antarctica and over the Antarctic Peninsula would be cushion-forb-lichen-moss tundra, prostrate shrub tundra, and dwarf shrub or shrub tundra (Haywood et al., 2002).

8. Conclusions

Based on numerous lines of evidence, we interpret the fossil plants of the MDF to represent a complex mosaic of periglacial environments in which there was abundant water from melting snow and glacier ice. The diversity and dynamic nature of the environment resulted in a mosaic of tundra plant communities that included feldmark, cushion plant heath, prostrate shrubland, localized turfs and mosses, and possibly microbial mats. Ultimately, this vegetation became extinct and was replaced by a polar desert as the ice

sheets expanded and the climate of the interior became ultracold and ultraxeric. Future work to resolve the spatial and temporal aspects of this ecosystem, together with improved identification of the plants, will be important for developing a better understanding of the palaeoecology and biogeography of Neogene polar plant communities.

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