# Early Oligocene *Nothofagus* from CRP-3, Antarctica: Implications for the Vegetation History

D.J. CANTRILL

Geological Sciences, British Antarctic Survey, Natural Environment Research Council, Madingley Road, High Cross Cambridge CB3 0ET -United Kingdom (djca@pcmail.nerc-bas.ac.uk)

Received 27 September 2000; accepted in revised form 3 July 2001

**Abstract** - A single fossil leaf of *Nothofagus* from CRP-3 drillhole in the Victoria Land Basin provides further evidence for woody vegetation in the Tertiary of East Antarctica. The plicate vernation of this small leaf indicates a deciduous habit and suggests a cold climate. Located in the interval between 44.12 to 44.18 mbsf this extends the range of these small-leaved deciduous taxa to the Early Oligocene, and adds to the sparse macrofossil record of the East Antarctic vegetation of this period. This further reinforces the suggestion that the transition from a diverse and mesic vegetation in the Eocene to a depauperate flora in the Early Oligocene was a relatively rapid event in East Antarctica. Despite limited Tertiary plant material



from East Antarctica, an emerging picture is one of substantially cooler climates than that seen in West Antarctica at the same time.

## INTRODUCTION

Antarctica fossil floras provide unique insights into the vegetation history of this now glaciated landscape. The Tertiary record of Antarctica is particularly interesting as it records biotic changes associated with the final stages of separation of Gondwana fragments. The isolation of Antarctica in a polar position, and subsequent reorganization of oceanic circulation patterns, led to climatic cooling and the development of a large ice sheet. This resulted in widespread extinction of most of the terrestrial biota from Antarctica, and created disjunct distributions that characterize many Southern Hemisphere groups today. For example, New Zealand/Australian genera and species in a number of families (e.g. Nothofagaceae, Stylidiaceae, Proteaceae) often have their nearest relatives in South America (e.g. Manos, 1987; Weston & Crisp, 1987). Antarctic Tertiary floras are critical for understanding the history of these Southern Hemisphere groups. However, although the climatic cooling through the Tertiary was one of the major mechanisms for creating such striking biogeographic patterns, it is still unclear how rapidly climate change affected the biota. Was it one of rapid decline in diversity, or did floral elements progressively drop out over millions of years?

The record of Antarctic Tertiary floras is largely confined to the Antarctic Peninsula region. On the west side of the Antarctic Peninsula, floras in the South Shetland Islands (King George Island) range from Palaeocene to earliest Oligocene in age (Zastawniak et al., 1985, and references therein). Rare occurrences of fossil wood are also reported from latest Oligocene marine strata (Destruction Bay Formation, Birkenmajer, 1984; Dingle & Lavelle, 1998). To the east of the Antarctic Peninsula, in the James Ross Island region, Tertiary floras of Palaeocene to ?earliest Oligocene are known from Seymour Island and include leaf (Dusen, 1908; Case, 1988; Gandolfo et al., 1998a, 1998b), wood (Gothan, 1908) and spore/pollen (Askin, 1988) assemblages. Sparse occurrences of Tertiary plant fossils are also present elsewhere throughout the Antarctic Peninsula (e.g. Elgar Uplands, Alexander Island; Thomson & Burn, 1977), but generally these macrofloras are poorly age-constrained and have not been fully described.

Despite the relatively greater land area of East Antarctica, there are noticeably fewer Tertiary floras than seen in the Antarctic Peninsula. Erratics of fluvial to shallow marine sandstones from the McMurdo sound (Minna Bluff) region have yielded Eocene to Oligocene plant fossils (Francis, 2000; Pole et al., 2000; Askin, 2000). The flora comprises wood of araucarian and podocarp conifers, and *Nothofagus* angiosperms (Francis, 2000). Leaf assemblages are numerically dominated by flowering plants, with *Nothofagus* as the main component; minor araucarian conifers are also present (Pole et al., 2000). Palynological assemblages from the erratics indicate a greater diversity than that seen in the wood and leaf assemblages, but still support macrofossil evidence for

a vegetation dominated by podocarps and Nothofagus (Askin, 2000). Post-Eocene macrofloral records from East Antarctica consist of Nothofagus from the Late Oligocene of the CIROS-1 hole (Hill, 1989) and Pliocene Sirius Group deposits (Francis & Hill, 1996; Carlquist, 1987; Hill et al., 1996). However, undescribed isolated seeds and in- growth-position cushion plants and mosses occur in Sirius Group deposits (Ashworth et al., 1997). These point to greater diversity than currently recognized. At present, there is a temporal break between the Pliocene/late Oligocene floras and the more diverse Eocene assemblages. Identifying floras from within this time gap is critical to understanding the rate of floristic changes associated with the onset of glacial conditions. This report adds a further record of Nothofagus from the Early Oligocene of East Antarctica.

## MATERIALS AND METHODS

Cape Roberts Project drillhole CRP-3, sited 11.76 km offshore from Cape Roberts, Antarctica at 77.0106° S and 163.6404° E (see location map) provided the material for this study. Preserved as a compression, the leaf occurs in a muddy medium to fine-grained sandstone at 44.12 to 44.18 mbsf. The fossil leaf was revealed by degaugement of the surrounding matrix, and photographed immersed in alcohol. A camera lucida drawing made with an Olympus stereo dissecting microscope SZH0-10 was used to help interpretation of venation patterns (Fig. 1C). The leaf is largely skeletonized, with compressed organic material lying over the main secondary and tertiary veins. Attempts were made to prepare cuticular material by dilute chromic acid, Schulze's reagent, and gentle maceration in hydrogen peroxide. However, the leaves were extremely fragile and yielded very small and poorly preserved fragments. Descriptive terminology follows that recommended in the manual for leaf architecture (1999), and Hickey (1988). The material is lodged at the Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand with accession number B1347.

#### DESCRIPTION

Leaf with plicate vernation, 18 mm long by 10 mm wide, apex acute, rounded, margin lobed to serrate. Venation pinnate, primary vein straight, persisting to the apex with a slight taper. Secondary veins craspedodromus, straight or slightly curved apically, opposite, terminating at the margin approximately in the centre of each marginal serration. Tertiary veins percurrent, alternate or opposite, obtuse. Quaternary veins alternate

percurrent. Higher order veins present but arrangement unclear, aerolation well developed. No marginal fimbrial vein observed. Leaf margin lobed to serrated, teeth apparently compound with the major tooth being supplied by a secondary vein, and lower order teeth being supplied by branches from the secondaries. Cuticle thin, poorly preserved, no cellular detail observed.

## DISCUSSION

Based on leaf form, shape and venation pattern, this small craspedodromus leaf is best placed in the Southern Hemisphere genus Nothofagus. Although the lack of cuticular details precludes firm identification, further support for the affinity of the leaf comes from palynological evidence that points to Nothofagus being one of the main elements of the vegetation (Cape Roberts Science Team, 2000; Askin & Raine, 2000; Raine & Askin, this volume). The distinctive pattern of raised ridges between the secondary veins indicates that the leaf was folded in the bud prior to leaf expansion (plicate vernation) (Fig. 1A). This type of leaf development in Nothofagus is found exclusively in the deciduous species (Philipson & Philipson, 1988) and indicates the fossil material was also deciduous. This perhaps explains the delicate nature of the leaf cuticle, which is generally thinner in deciduous species. However, deciduousness is not a phylogenetically informative character, and so the leaf cannot be placed with any confidence within one of the four extant subgenera of the genus. Placement of fossil Nothofagus leaves into an extant subgenus relies on good preservation of leaf architectural and cuticular characters (Jordan & Hill, 1999), and the latter is lacking for this material. However, it should be noted that most of the Nothofagus pollen diversity at this time in the Antarctic is made up of Nothofagus subgenus Fuscospora (Raine & Askin, this volume).

A large number of fossil species have been ascribed to *Nothofagus* in the Southern Hemisphere (Romero & Dibbern, 1985; Tanai, 1986; Hill, 1989; Scriven et al., 1995; Hill et al. 1996), but few have features diagnostic of deciduous taxa (*i.e.* plicate vernation). Amongst the deciduous taxa, those from East Antarctica include *Nothofagus beardmorensis* from the Pliocene Sirius Group (Hill et al., 1996). Although *N. beardmorensis* can be more than twice as long as the leaf described here, it shares a number of important similarities. For example, in both the secondary veins are straight and they also terminate the marginal lobes/serrations. In this respect, the leaf described here is also like the extant *N. alessandri* (*Fuscospora*) and *N. obliqua* (*Lophozonia*).

Other deciduous taxa include a single leaf from the Late Oligocene of the CIROS-1 hole (Hill, 1989). This leaf differs, as the secondary veins terminate in the sinus of the lobes where they branch to form a



*Fig. 1 - Nothofagus* leaf. A, whole specimen illustrating the plicate morphology and crenate margin terminated by straight secondary veins. B, leaf immersed in ethyl alcohol to enhance venation detail. C, interpretive drawing of leaf venation pattern. D, details of the higher-order venation revealed by immersion in ethyl alcohol. A-C, scale bar = 5 mm, D, scale bar = 1 mm.

marginal vein, much like the extant *N. gunnii* (Hill, 1989, fig. 3). Elsewhere in East Antarctica poorly preserved Eocene *Nothofagus* leaves occur in the McMurdo Sound region (Pole et al., 2000). These leaves are small (10-20 mm long), plicate, and have a crenate leaf margin, but details of the vein architecture are not well preserved. Pole et al. (2000) compared this material to *N. gunnii*, *N. pumilio* and the Oligocene fossil from CIROS-1 mentioned above. The lack of details of higher order venation patterns precludes meaningful comparison with the material described here.

In the Antarctic Peninsula region, leaves referred to *Nothofagus* occur in Palaeocene to ?Oligocene strata on Seymour Island (Dusen, 1908; Case, 1988; Gandolfo et al., 1998a) and in the South Shetland Islands (Zastawniak et al., 1985). Amongst these leaves considerable diversity exists in leaf size class, margin type, and venation architecture. Those few with plicate vernation are largely confined to the latest Eocene to earliest Oligocene (R. Hunt, pers. comm.). All these leaves are still poorly circumscribed, making comparison with the material described above difficult.

## AGE

Biostratigraphy of the upper 200 m of the CRP-3 core is based on diatoms (*Cavitatus jouseanus*) and calcareous nannofossils (*Transversopontis pulcheroides*) and is supported by magnetostratigraphy (Cape Roberts Science Team, 2000). The combined data indicate deposition in the mid-part of magnetochron C12r of Early Oligocene age.

#### VEGETATION

Terrestrial palynofloras in CRP-3 are of a low diversity, and largely dominated by Nothofagidites and Podocarpidites. These anemophilous (wind-pollinated) taxa produce a large amount of pollen, and so it is perhaps not surprising that they are most frequently encountered in residues. However, palynomorph yield in CRP-3 is low: this could be due to either a high flux of sediment, or sparseness of vegetation in the source area (Cape Roberts Science Team, 2000). The palynoflora includes rare grains of bryophytes (Coptospora), lycophytes (Lycopodiumsporites), pteridophytes (Cyathidites, Laevigatosporites and Rugulatisporites), conifers (Podocarpidites sp) and angiosperms (?Cyperaceaepollis, Tricolpites, Triporopollenites, ?Proteacidites, Myricipites harrisii, Stellaria-type, Chenopodipollis) (Cape Roberts Science Team, 2000). These all point to a low diversity vegetation with broad similarities to present day magellanic or alpine vegetation (Askin & Raine, 2000).

The relatively depauperate Early Oligocene palynoflora (*e.g.* Cape Roberts Science Team, 2000; Mohr, 1990), when compared to older Eocene assemblages (e.g. Askin, 2000; Mohr, 1990), suggests a major change in the vegetation. This interpretation is supported by the macrofossil record: Eocene floras in East Antarctica include Araucaria, Nothofagus (both deciduous and evergreen), and at least three other angiosperm types (Pole et al., 2000). These Eocene leaves range from notophyllous to microphyllous in size, a contrast from the microphyllous foliage of the Oligocene. Such a shift in leaf size class is to be expected as climatic conditions cooled. The pattern seen in the fossil leaf material is also supported by palynology. Eocene strata contain considerable more diversity, particularly in podocarp conifers and angiosperms (Proteaceae and others), than seen in Early Oligocene strata (Askin, 2000; Askin & Raine, 2000; Raine & Askin, this volume).

## CLIMATE

The marked change in composition and abundance of palynofloral residues between the Eocene and the Early Oligocene (Askin, 2000; Askin & Raine, 2000; Raine & Askin, this volume) suggests a major change in vegetation. This has potentially important implications, as a change from forest to tundra vegetation would result in increased albedo, and lead to positive feedback loop that reinforces the climatic cooling seen in this part of the stratigraphic column. Indeed recent modeling experiments suggest that high latitude vegetation played an important role in mediating the climate of these regions (Otto-Bliesner & Upchurch, 1997). Although a single leaf is not representative of the vegetation as a whole, the affinity of the leaf can be used to infer past climate conditions. This is largely due to more wide-ranging studies on extant (e.g. Hill & Truswell, 1993; Hill & Jordan, 1996) and fossil (Francis & Hill, 1996) Nothofagus assemblages that provide physiological limits to growth in this taxon. Hill & Truswell (1993) estimated frost tolerance limit of deciduous Nothofagus species at -22°C but this may be conservative, particularly for ground hugging forms (Hill & Jordan, 1996). As plant growth relies on liquid water at least part of the year must have been above freezing. Hill & Jordan (1996) suggested that in summer months "temperature must have been at least 5°C for several weeks" for Nothofagus beardmorensis to survive. The highly seasonal nature of polar environments is often not considered when using nearest living relative approaches to estimate climatic conditions from fossil Nothofagus (e.g. Mercer, 1986, 1987). However, Francis & Hill (1996) based their estimates of mean annual temperature for Nothofagus beardmorensis on comparisons to Northern Hemisphere angiosperms (Salix) growing in a similar environment and with a similar habit. This suggests that the growing season was short and warm (up to 5 °C) but the winter season down to -15 to -22 °C, possibly with a mean annual temperature of -12 °C (Francis & Hill 1996). These estimates are probably equally applicable to the leaf described in this study.

#### CONCLUSIONS

The Tertiary history of Antarctic vegetation is still relatively poorly known and much work remains to be done, both in terms of fully describing known deposits, and discovering new deposits from critical time periods. Despite this, an emerging pattern suggests that climatic cooling profoundly influenced the vegetation history. The presence of small deciduous Nothofagus leaves in the Early Oligocene substantially narrows the time gap between depauperate "glacial" floras and the more diverse mesic floras of the Eocene. It appears that the transition from cool temperate and relatively diverse vegetation in the mid- to Late Eocene to tundra-type vegetation seen in the Pliocene may have occurred relatively rapidly (i.e. between the Latest Eocene and the earliest Oligocene). Establishing the exact nature and timing of vegetational changes will be important when examining potential positive feedbacks to climatic cooling.

Comparison of the Antarctic Peninsula floras (i.e. Palaeocene to Oligocene) with those of the Ross Sea region suggests that Antarctic vegetation was regionally heterogeneous. Although Eocene floras from the Ross Sea region are poorly preserved, and limited material is available, the flora is relatively smaller-leaved compared to coeval floras in the Antarctic Peninsula. Furthermore, East Antarctic floras are of lower diversity (this may be a reflection of the limited sample size) and contain more deciduous taxa than Eocene floras in the Antarctic Peninsula. This points to a cooler East Antarctica compared to the more maritime Antarctic Peninsula. However, importantly the Antarctic Peninsula floras show an increase in diversity of deciduous taxa towards the Eocene-Oligocene boundary, supporting a cooling trend in this region also.

## REFERENCES

- Ashworth A.C, Harwood D.M., Webb P.-N. & Mabin M.C.G., 1997. A weevil from the heart of Antarctica. In: Studies in Quaternary Entomology – an inordinate fondness for insects. *Quaternary Proceedings*, 5, 15-22.
- Askin R.A., 1988. Campanian to Palaeocene palynological succession of Seymour and adjacent islands, northeastern Antarctic Peninsula. *Geological Society of America Memoir*, 169, 131-153.
- Askin R.A., 2000. Spores and pollen from the McMurdo Sound erratics, Antarctica. In: Stilwell J.D. & Feldmann R.M. (eds), Palaeobiology and Palaeoenvironments of Eocene fossiliferous erratics. McMurdo Sound, East Antarctica. *Antarctic Research Series*, **76**, 161-181.
- Askin R.A. & Raine J.J., 2000. Oligocene and Early Miocene terrestrial palynology of the Cape Roberts Drillhole CRP-2/2A, Victoria Land Basin, Antartica. *Terra Antartica*, 7, 493-501.

- Birkenmajer K., 1984. Geology of the Cape Melville Area, King George Island (south Shetland Islands, Antarctica): pre-Pliocene glaciomarine deposits and their substratum. *Studia Geologica Polonica*, **79**, 7-35.
- Carlquist S., 1987. Pliocene Nothofagus wood from the Transantarctic Mountains. Alsio, 11, 571-581.
- Cape Roberts Science Team, 2000. 5 Palaeontology. Terra Antartica, 7, 133-170.
- Case J.A., 1988. Palaeogene floras from Seymour Island, Antarctic Peninsula. *Geological Society of America Memoir*, 169, 523-530.
- Dingle R.V. & Lavelle M., 1998. Antarctic Peninsula cryosphere: Early Oligocene (c. 30 Ma) initiation and a revised glacial chronology. *Journal of the Geological Society, London*, 155, 433-437.
- Dusen P., 1908. Über die Tertiäre flora der Seymour Insel. Wissenschaftliche Ergbnisse der Schwedischen Stidpolar-Expedition 1901-1903, 3, 1-127.
- Francis J.E., 2000. Fossil wood from Eocene high latitude forests McMurdo Sound, Antarctica. In: Stilwell J.D. & Feldmann R.M. (eds), Palaeobiology and Palaeoenvironments of Eocene fossiliferous erratics, McMurdo Sound, East Antarctica. *Antarctic Research Series*, **76**, 253-260.
- Francis J.E. & Hill R.S., 1996. Fossil plants from the Pliocene Sirius Group, Transantarctic Mountains: evidence for climate from growth rings and fossil leaves. *Palaios*, 11, 389-396.
- Gandolfo M.A., Marenssi S.A. & Santillana S.N., 1998a. Flora y palaeoelima de la Formación La Meseta (Eoceno Medio), Isla Marambio (Seymour), Antártida. Asociación Palaeontológica Argentina Publicación Especial, 5, 155-162.
- Gandolfo M.A., Hoc P., Santillana S.N. & Marenssi S.A., 1998b. Una flor fósil morphológicamente afín a las Grossulariaceae (orden Rosales) de la Formación La Meseta (Eoceno Medio) Isla Marambio, Antárctida. Asociación Palaeontológica Argentina Publicación Especial, 5, 147-153.
- Gothan W., 1908. Die fossilen Hölzer von der Seymour und Snow Hill-Insel. Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901-1903, 3(8), 1-33.
- Hickey L.J., 1988. Revised classification of the architecture of dicotyledonous leaves. In: Metcalfe C.R. & Chalk L. (eds), Anatomy of the Dicotyledons, Volume 1, Systematic anatomy of the leaf and stem. 2nd Edition. Clarendon Press, Oxford, 25-39.
- Hill R.S., 1989. Fossil leaf, Antarctic Cenozoic history from the CIROS-1 Drillhole, McMurdo Sound. New Zealand Department of Scientific and Industrial Research Bulletin, 245, 143-144.
- Hill R.S., Harwood D.M. & Webb, P-N., 1996. Nothofagus beardmorensis (Nothofagaceae), a new species based on leaves from the Pliocene Sirius Group, Transantarctic Mountains, Antarctica. Review of Palaeobotany and Palynology, 94, 11-24.
- Hill R.S. & Truswell E.M., 1993. Nothofagus leaves in the Sirius Group, Transantarctic Mountains: leaves and pollen and their climatic implications. Antarctic Research Series, 60, 67-73.
- Hill R.S. & Jordan G.J., 1996. Macrofossils as indicators of Plio-Pleistocene climates in Tasmania and Antarctica. *Papers and Proceedings of the Royal Society of Tasmania*, 130, 9-15.
- Jordan G.J. & Hill R.S., 1999. The phylogenetic affinities of Nothofagus (Nothofagaceae) leaf fossils based on combined molecular and morphological data. International Journal of Plant Sciences, 160, 1177-1188.
- Manual of leaf architecture 1999. Morphological description and categorization of dicotyledonous and net veined monocotyledonous angiosperms by Leaf Architecture Working Group. Smithsonian Institution, Washington, 1-65.
- Manos P.S., 1997. Systematics of *Nothofagus* (Nothofagaceae) based on rDNA spacer sequences (ITS): taxonomic congruence with morphology and plastid sequences. American Journal of Botany, 84, 1137-1155.
- Mercer J.H., 1986. Southern Chile: a modern analog of the southern shores of the Ross Embayment during Pliocene warm intervals. Antarctic Journal of the United States, 21, 103-105.
- Mercer J.H., 1987. The Antarctic ice sheet during the Late Neogene. In: Coetzee J.T. (ed.), Palaeoecology of Africa and the surrounding islands, A.A. Balkema, Rotterdam, 21-23.

- Mohr B.A.R., 1990. Eocene and Oligocene sporomorphs and dinoflagellate cycsts from leg 113 drillsites, Weddell Sea, Antarctica. *Proceedings of the Ocean Drilling Project*, *Scientific Results*, **113**, 595-612.
- Otto-Bliesner B.L. & Upchurch G.R., 1997. Vegetation-induced warming of high-latitude regions during the Late Cretaceous period. *Nature*, **385**, 804-807.
- Philipson W.R. & Philipson M.N., 1988. A classification of the genus Nothofagus (Fagaceae). Botanical Journal of the Linnean Society, 98, 27-36.
- Pole M., Hill R.S. & Harwood D., 2000. Eocene plant macrofossils from erratics, McMurdo Sound, Antarctica. In: Stilwell J.D. & Feldmann R.M. (eds), Palaeobiology and Palaeoenvironments of Eocene fossiliferous erratics, McMurdo Sound, East Antarctica. Antarctic Research Series, 76, 243-251.
- Raine J.I. & Askin R.A., 2001. Terrestrial palynology of Cape Roberts Drillhole CRP-3, Victoria Land Basin, Antarctica. This volume.
- Romero E.J. & Dibbern M.C., 1985. A review of the species described as *Fagus* and *Nothofagus* by Dusen.

Palaeontographica Abt. B, 197, 123-137.

- Scriven L.J., McLoughlin S. & Hill R.S., 1995. Nothofagus plicata (Nothofagaceae), a new deciduous Eocene macrofossil species, from southern continental Australia. Review of Palacobotany and Palynology, 86, 199-206.
- Tanai T., 1986. Phytogeographic and phylogenetic history of the genus Nothofagus Bl. (Fagaceae) in the southern hemisphere. Journal of the Faculty of Science Hokkaido University Series IV, 21, 505-582.
- Thomson M.R.A. & Burn R.W., 1977. Angiosperm fossils from latitude 70°S. *Nature*, **269**, 139-141.
- Weston P.H. & Crisp M.D., 1987. Evolution and biogeography of the waratahs. In: Armstrong J.A. (ed.), Waratahs, their biology cultivation and conservation, Occasional Publication No. 9 Australian National Botanic Gardens, Canberra, 17-34.
- Zastawniak E., Wrona R., Gazdzick A. & Birkenmajer K., 1985. Plant remains from the top of the Point Hennequin Group (Upper Oligocene) King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica*, **81**, 143-164.