MACROFOSSILS AS INDICATORS OF PLIO–PLEISTOCENE CLIMATES IN TASMANIA AND ANTARCTICA

by R.S. Hill and G.J. Jordan

(introduction)

One approach to the assessment of palaeoclimates from plant fossils is to identify the fossils as accurately as possible, and then to use the distribution and ecology of the nearest living relatives (NLRs) to assess the climate. NLR estimates of Tasmanian palaeoclimates have been both qualitative (e.g. Macphail 1979 for microfossil data; Jordan et al. 1995 for the use of combined macro- and microfossil data) and semi-quantitative (e.g. Markgraf et al. 1986), particularly using palynological data. Macrofossils in Late Pleistocene deposits can usually be ascribed to species which still live in the region under consideration. The pollen and spores can usually be ascribed to extant genera, and sometimes to species. However, the specific identity of older fossils is less certain. Thus, most Early Tertiary species are extinct (e.g. Jordan 1992, 1995a, Jordan & Hill 1994), and also, by averaging over all the taxa or all the species, the models predicting climates averaging over all taxa or all leaves are quite coarse in their resolution and of little use with Plio-Pleistocene floras (G.J. Jordan, pers. obs.). The use of the variation within species may provide some refinement of NLR climatic estimates (e.g. Jordan & Hill 1994). Similarly, wood anatomy (dendrochronological methods) can only provide coarse climate estimates when applied independent of the taxonomy, but can provide higher resolution when applied within species (Schweingruber 1988).

Well-preserved leaves and fruit of a wide range of extant and extinct species occur in a number of Pleistocene (ages follow Harland et al. 1990) sites in western Tasmania, and leaves and wood of a single species of *Nothofagus* occur in the probable Pliocene Sirius Group sediments in Antarctica. The present paper uses both NLR and morphological/ anatomical data to assess Pleistocene climates from Tasmania and Pliocene climates from Antarctica.

SITES

Antarctica

The fossil material occurs in the Meyer Desert Formation of the Sirius Group at Oliver Bluffs, in the Dominion Range, Transantarctic Mountains, approximately 500 km from the south pole and 200 km inland from the junction of the Beardmore Glacier and the Ross Ice Shelf. The present elevation is approximately 1760 m above sea level (a.s.l.), but the mountains may have been uplifted to this altitude during the past two million years (Webb & Harwood 1993). This site is currently at 85°S and was at a similar latitude during the Pliocene. Plant macrofossils are preserved within several levels of the sediments, which consist of diamictics, sandstones and mudstones, interpreted to be the products of glacial, fluvial and lacustrine environments (Webb & Harwood 1993). This glacial material was carried by ice sheets from East Antarctica and deposited along the walls of a pre-Pleistocene valley system which bisected the Transantarctic Mountains.
The age of the sediments at Oliver Bluffs has been constrained by the presence of recycled marine diatoms in the glacial diamictites of the lower marine part of the formation. The youngest stratigraphic age of these diatoms suggests that the Sirius Group is younger than Late Pliocene in age (3.1–2.5 Ma) (Harwood 1983, 1986a, b, Webb & Harwood 1991). Radiogenic dating of volcanic ash in equivalent marine sediments in the CIROS-2 borehole in McMurdo Sound supports these dates (Barrett et al. 1992).

However, the dating of the sediments at Oliver Bluffs is still not clearly resolved. There have been claims that the diatoms may have been wind-blown in origin and trapped in fractures in the sediments, thus invalidating the diatom dates (e.g. Burckle & Pokras 1991). However, Nothofagidites pollen of the same species that is known from the Sirius Group has been reported in marine sediments from Cape Adare (DSDP Site 274, Ross Sea) of mid Pliocene age, supporting the view that Nothofagus trees were present on Antarctica at this time (Fleming & Barron, in press).

Tasmania

The Marionoak Formation at the Huskisson/Marionoak divide (41°44'S, 145°31'E, 430 m a.s.l.) contains glacial sediments overlain by fine-grained lacustrine sediments, including microfossils and some macrofossils. Palynostratigraphy implies that these sediments are likely to be Pleistocene and are no younger than the early part of the Middle Pleistocene (Macphail et al. 1993). However, these sediments are magnetically normal and underlie magnetically reversed sediments, implying that they are at least as old as the Jaramillo event in the Early Pleistocene; they are considered to be Early Pleistocene (Augustinus et al., in press).

Clasts containing well-preserved macro- and microfossils occur in Middle–Late Pleistocene gravels at Regatta Point, western Tasmania (42°10'S, 145°20'E, 10 m a.s.l.) (Hill & Macphail 1985). Macphail et al. (1993) assigned an Early–Middle Pleistocene age to a number of these clasts based on palynostratigraphy. One clast (referred to as RP2U) is palynostratigraphically at least as old as the Huskisson/Marionoak sediments and probably older. This clast is, therefore, of Early Pleistocene age. This RP2U clast contains three thin, intensely fossiliferous layers. The composition of each layer differs little from the others. Other clasts (collectively referred to as RP1U and including the clast described by Hill & Macphail 1985) are palynostratigraphically of same age as the Huskisson/Marionoak sediments (Macphail et al. 1993) and are likely to be Early Pleistocene age. One clast (RPA) is palynostratigraphically younger than the Huskisson/Marionoak site and is considered to be of Early–Middle Pleistocene age (Jordan et al. 1995).

The Regency Formation in western Tasmania (42°10'S, 145°38'E, 180 m a.s.l.) consists of a 0.8 m thick layer of highly organic sediments, much of which is almost entirely composed of fossil leaves, fruit and twigs, and overlies an Early Pleistocene till. The formation was considered by Fitzsimons et al. (1990) to be of Early–Middle Pleistocene age, but is more likely to be of Middle Pleistocene age (E.A. Colhoun, pers. comm., Jordan & Hill 1994). The parts of the Langdon River sediments (41°58'S, 145°32'E, 520 m a.s.l.) discussed here are highly organic sediments made up of compressed beds of leaves and twigs (Colhoun et al. 1989). These represent some Middle Pleistocene interglacial, although a Last Interglacial age cannot be excluded at present (Colhoun et al. 1989).

METHODS

Climatic estimates were made from Tasmanian Pleistocene leaf macrofossil data, using the ranges in climatic parameters of the nearest living relatives of macrofossils. For Australian taxa, climatic parameters were estimated using ESOClim (H. A. Nix, J. P. Busby, M. F. Hutchinson & J. P. McMahon pers. comm.; Hutchinson 1991) analysis of a large data set of compiled point distributions (Floyd 1990; Environmental Resources Information Network; Department of Environment and Land Management, Tasmania; Tasmanian Herbarium; Australian National Herbarium; Australian National Botanic Gardens Herbarium). Distributions for New Zealand taxa were derived from Poole & Adams (1986), M. S. McGlone (pers. comm.) and G. J. Jordan (pers. obs.). Approximate climatic ranges for the New Zealand taxa were then derived from local climatic averages (New Zealand Meteorological Service 1981), allowing for an altitudinal lapse rate of 0.65°C/100 m. Unfortunately, more detailed climatic or distributional data was not available for New Zealand, but this does not affect the results of this work. The climatic ranges of the NLRs within sites were then compared graphically by simultaneously plotting ranges of climatic parameters of NLRs for all fossil taxa, and looking for overlaps. The region of overlap is assumed to be the best range of climatic estimates. Extreme outlier taxa were obvious and were excluded from the estimates. This method is similar to that of Kershaw & Nix (1988) and is reasonably robust, since random subsets of the data provide essentially the same estimates (i.e. supporting the method), and the method allows for taxa to be present near the ends of their ecological range. It also allows for the identification of outlying taxa, which may represent extinct species, extinct ecoregions or taxa whose modern ranges underestimate their potential climatic ranges.

Climatic estimates for the Sirius Group were prepared using qualitative methods, which will be explained in detail in the text below.

PALAEOCLIMATES

Sirius Group

The most controversial feature of the palaeoclimate of the Sirius Group is temperature, and the macrofossils present can be used to place clear constraints on this. Three aspects of temperature will be discussed: mean annual temperature, minimum winter temperatures, and mean summer maximum temperature. In order to demonstrate how these temperatures were estimated, some features of the macrofossils must be summarised.

1) The leaves, wood and pollen in the Sirius Group sediments all belong to a single species of Nothofagus (Nothofagaceae), the southern beech. It is reasonable to presume that it was the same species, that is, that one biological species contributed all three organs to the sediments. The leaves have been formally described as N. beardmoreensis (Hill et al., in press), and that name will be used for the species forthwith.
(2) *Nothofagus beardmorensis* was a winter deciduous species (Hill & Truswell 1993, Hill et al., in press). This is usually difficult to prove for a fossil, but in this case the evidence is very convincing.

(3) *Nothofagus beardmorensis* was a ground-hugging shrub, with no main axis, but many small, twisted branches with distinct, but very small growth rings (Francis & Hill in press). There is abundant evidence for abrasion on the wood, indicative of the effect of wind-borne ice and sand particles (Francis & Hill, in press).

(4) The macrofossils have not been transported more than a few metres from the growth position of the parent plant, and they have not been reworked. This is clear because of the thousands of delicately preserved leaves in a dense mat which could not have been reworked, and which certainly did not travel a long distance to be deposited in such dense numbers. It is also highly unlikely that leaves, wood and pollen, which have such different dispersal properties, could occur in the same sediments in such numbers if they had been transported long distances or, indeed, if they had been reworked. This is an important point because, although there is still doubt about the age of the fossils, there can be no doubt that the plants were growing on the site when the sediments were forming, and thus are a reliable guide to the prevailing climate, whenever it was.

From a combination of these features, estimates of temperature were made.

Minimum winter temperature
There are more than 30 living species of *Nothofagus*, but only seven are winter deciduous, six in South America and one in Tasmania. Some research has been done to estimate the frost tolerance of these species, and this has been summarised by Hill & Truswell (1993). Frost tolerance is likely to be a major factor limiting the distribution of a species as far as minimum winter temperatures are concerned.

Direct frost damage occurs when ice crystals form within cells and lacerate the cell membranes. The damage this causes is irreversible, and the cell dies. Clearly, if this is widespread through the plant tissues, the plant will not survive. Frost damage does not necessarily occur at the same temperature in all organs and, for example, is unlikely to be relevant in the leaves of a winter deciduous species, since leaves are absent during the coldest part of the year. According to the data summarised by Hill & Truswell (1993), the lowest frost survival temperature yet recorded for *Nothofagus* is $-22\, ^\circ C$, and this occurred in a winter deciduous species (*N. antarctica*). This is likely to be a conservative estimate, since relatively few data have been collected for extant species, and *N. beardmorensis* is likely to have had a frost resistance at the low end of the extant range and possibly well beyond it. It should also be recognised that the temperature at which frost death occurs is not necessarily a good estimate of minimum winter temperature, since many plant species are known to be insulated against extreme cold in winter by a thick covering of snow. That is, if *N. beardmorensis* was covered in snow during winter, then temperatures could have fallen well below its frost death temperature without the plants being subjected to them. For these reasons, the estimate of $-22\, ^\circ C$ for minimum winter temperature should be considered as a very conservative estimate.

Mean summer maximum temperature
A crude but very effective limit can be applied to summer temperatures—in order for a vascular plant to grow it must have continued access to liquid water. If air temperatures rise above freezing, but the ground stays frozen, it is possible for a plant to transpire itself to death, as it loses what liquid water it has in its tissues but cannot replace it from the frozen ground. Clearly, at the time that *N. beardmorensis* was growing, summer temperatures were sufficient to thaw soil water to some reasonable depth to allow steady transpiration. This requires temperatures well above 0°C. Furthermore, in order to produce a crop of leaves and the reproductive structures required to produce the pollen present in the sediments, it is reasonable to assume that the daily maximum temperature must have been at least 5°C for several weeks. This is a conservative estimate based on woody plant growth requirements at high northern and southern latitudes today. It is probable that there were no particularly low minimum summer temperatures, since there is no evidence of frost damage on any of the leaf fossils.

Mean annual temperature
Francis & Hill (in press) argued that the wood macrofossils in the Sirius Group were very similar in form and function to the wood of the extant Arctic willow (*Salix arctica*), although there is no close taxonomic relationship between them. In fact, this model seems very precise, and since *S. arctica* grows further north than any other woody plant today, the lowest mean annual temperature at which it can grow provides a good physiological constraint on the peculiarities of wood structure observed in the fossil *Nothofagus*. Francis & Hill (in press) note that this mean annual temperature is approximately $-15\, ^\circ C$.

Comparison with the Sirius Group today
In order to understand the significance of these temperature estimates, it is useful to have some indication of comparable temperatures at the fossil locality today. No direct measurements exist, but approximations can be made by applying a lapse rate ($-0.65\, ^\circ C$ per 100 m) to data from the nearest climate station. This has been done (D.M. Harwood, pers. comm.), but these estimates may contain considerable error. Nevertheless, the difference between these estimates and those from the fossils (table 1) are so great that any errors of calculation of extant temperatures must be small by

<table>
<thead>
<tr>
<th>Temperature data for Vanda Station* and estimates for the fossil location today†</th>
<th>Vanda Station</th>
<th>Fossil location (extant)</th>
<th>Fossil location (extant)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean summer maximum temperature</td>
<td>$+2, ^\circ C$</td>
<td>$-10, ^\circ C$</td>
<td>$+5, ^\circ C$</td>
</tr>
<tr>
<td>Minimum winter temperature</td>
<td>$-36, ^\circ C$</td>
<td>$-48, ^\circ C$</td>
<td>$-22, ^\circ C$</td>
</tr>
<tr>
<td>Mean annual temperature</td>
<td>$-18, ^\circ C$</td>
<td>$-28, ^\circ C$</td>
<td>$-15, ^\circ C$</td>
</tr>
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* 77°32'S 161°33'E near L. Vanda.
† Based on a lapse rate of 0.65°C/100m altitude (data provided by D.M. Harwood). Estimates for the fossil location at the time when *Nothofagus beardmorensis* was growing are discussed in the text.
comparison. The differences between mean summer maximum temperature and mean annual temperature are 15°C and 13°C respectively, with the site being warmer in the past, but the close correspondence between these two figures is probably fortuitous, given the inherent errors in the method. The difference between minimum winter temperature now and in the past at the fossil site is higher (26°C), but it was stressed earlier that the estimate for the fossils was likely to be conservative, thus infusing the difference.

Therefore, as a first approximation, a temperature difference in the order of 13–15°C occurred between the present day and the time at which the fossil plants were growing. Other factors may enter into this; for example, the possibility of post-depositional uplift of the fossil locality (Webb & Harwood 1993), which would artificially increase the temperature differential, although such uplift seems unlikely.

The other feature of interest in table 1 is that the difference in temperature between Vanda Station today (77°32'S 161°33'E, near Lake Vanda and about 800 km from the fossil site on about the same longitude) and the requirements for the fossil species is not very great at all, being, with the exception of the conservative minimum winter temperature, only 3°C. This is important, since it is usually considered that Antarctica is far too cold to support woody plant growth; that is not the case, and this may explain one of the dilemmas those arguing for the continual habitation of Antarctica by Nothofagus until the Pliocene. In fact, there is no reason for Nothofagus, in the time leading up to a Pliocene warming, not to have survived periods almost as cold as those that occur today, without recourse to unlikely long-distance dispersal of seed across prevailing winds.

**Tasmania**

Early Pleistocene

The macrofossil-bearing sediments at the Huskisson/Marionoak Divide, the overlying tills and the intervening slope deposits form a sequence representing the onset of a major Early Pleistocene glacial. Microfossils suggest that the vegetation was similar to subalpine woodland which now grows on the eastern Central Plateau of Tasmania. If correct, this indicates a rainfall in the order of 17–18 cm although it is only about 5–6 mm thick, since this undoubtedly represents a short depositional period (a few years or less) and the composition is similar to that of the other layers.

The RP1 and RP2 floras which now occur at low altitudes in the region, but also contains a group of taxa which no longer occur in lowland western Tasmania, including apparent warm climate indicators such as macrofossils of *Quintinia* and *Decarycarpus* (Hill & Maephil 1985, Jordan & Hill 1991, 1994, Jordan 1992, 1995, Jordan & Dalton, 1995). The temperature range of the macrofossils do not all overlap (fig. 2). However, all but four NLRs occur in sites with mean annual temperatures between 11°C and 12°C, although this is at the extreme end of the range of several taxa. Any temperature estimate outside this range involves more discrepancies. The current mean annual temperature at Regatta Point is about 12°C. The four taxa which do not occur at mean annual temperatures of 11°C–12°C are *Microcachrys tetragona*, *Richea milliganii/acerosa*, Rubus nebulosus and *Callistis macleayanus*. Both the *Rubus* and *Callistis* fossils are globally extinct species, and the discrepancies in temperatures are small. It is likely that these species tolerated cooler climates than their NLRs. The fossil *M. tetragona* has foliage indistinguishable from the extant species, but the distinctive pollen type is common in Tertiary deposits containing a wide range of floras, including many from...
undoubtedly much warmer climates than the modern range of this species. It is unlikely that the macrofossils of *M. tetragona* were derived from uplands areas (Jordan & Hill 1994; Jordan 1995b). The identification of the *Richera*- type fossil is relatively broad, and this may also represent an extinct species. A possible scenario to explain the apparent anomalies is that the Regatta Point sediments were deposited early in an early interglacial, with the warm climate indicators occurring in more fertile wet forest and cool climate taxa persisting in oligotrophic areas. It is common now for subalpine type vegetation to occur in oligotrophic sites at moderate altitude alongside more typical lowland vegetation on less oligotrophic areas, particularly in areas of abundant rainfall.

There is little local topography in the Regatta Point area, and the fossiliferous clasts are highly unlikely to have been transported far, so their original site of deposition was not significantly higher than their present location. There are no micro- or macrofossils in the flora which indicate an estuarine environment. The sediments are at low altitude (10 m a.s.l.) beside an estuary, so sea level at the time of deposition was not more than about 10 m above present sea level. This also argues against the climate being significantly warmer than it is today. Thus, it is highly likely that the mean annual temperature at Regatta Point at the time of deposition of the RPU2 sediments was similar to the modern mean annual temperature and precipitation.

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Current ranges in mean annual temperature and mean annual precipitation for the nearest living relatives (NLRs) of macrofossil seed plant taxa (A–J) found in the Early–Middle Pleistocene RPA sediments at Regatta Point. A = Athrotaxis cupressoides, B = Athrotaxis selaginoides, C = Eucryphia lucida/milliganii, D = Diselma archeri, E = Nothofagus gunnii, F = Nothofagus cunninghamii, G = Telopea truncata, H = Orites milliganii, J = Orites revoluta, K = Phyllocadus asplenifolius. The asterisk indicates the current climate at the site.

Discussion of Tasmanian Pleistocene data

There is no convincing macrofossil or microfossil evidence of climates warmer than now in the Pleistocene in Tasmania. The best estimates of temperature for all sites are the same as, or lower than present climates. The fossils at the Early Pleistocene RPU2 sediments and the Middle Pleistocene Regency Formation are consistent with climates as warm as those which now prevail. There are other Middle and Late Pleistocene sites containing macrofossils, including the Langdon River site (Colhoun et al. 1989) and Melaleuca Inlet (Jordan et al. 1991), which, based on similar arguments, are consistent with temperatures similar to modern temperatures. There are constraints on the upper estimates of climates for lowland sites younger than the Early Pleistocene, since virtually all the taxa involved are still extant in Tasmania and, hence, their climatic ranges include Tasmanian climates. However, it is also clear that many taxa previously used as warm climate indicators probably occurred in cooler climates than their NLRs, and their presence cannot be used as good evidence of warm climates. There is convincing evidence of colder climates than at present at times in the Early–Middle Pleistocene (4–7°C colder at the Huskisson/Marionoak Divide site and 1–4°C colder in the RPA sediments).

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REFERENCES

Macrofossil indicators of Plio-Pleistocene climates, Tasmania and Antarctica


