Age and implications of the Forest Bed, Falkland Islands, southwest Atlantic Ocean: Evidence from fossil pollen and spores

Mike Macphail, David J. Cantrill

Abstract

Diverse pollen and spore assemblages (microfloras) are preserved in organic clays and lignites associated with fossil tree remains in the Forest Bed. At present, these microfloras provide the only reliable basis for determining the age, composition, structure and affinity of the Forest Bed community. The Bed is suggested to be Middle Miocene to Early Pliocene (age range Oligocene – Early Pliocene) based on the time distribution of a number of rare pollen types and the present-day ecology of their nearest living relatives in central–southern America and the southwest Pacific. The wet forest community whose remains form the Forest Bed was a form of broadleaf-gymnosperm temperate rainforest in which Dacrydium, Lagarostrobos and Podocarpus are likely to have formed the overstorey above a closed canopy dominated by Nothofagus (Nothofagus) spp. The latter subgenus is now endemic to uniformly wet regions in southern South America whilst two of the tall gymnosperms (Dacrydium, Lagarostrobos) are now endemic to the southwest Pacific region. An extinct, probable shrub-sized, conifer (Podosporites microsaccatus) appears to have formed the ground cover. Ferns and fern allies were very rare, in contrast to most living Nothofagus-gymnosperm communities. Fossil pollen and spore types produced by uncommon subcanopy tree, shrub and fern species potentially provide a means for more accurately dating the deposit once their time of first occurrence and extinction at subantarctic latitudes in the southwest Atlantic region is established (nearest living equivalents given in parentheses) — Clavatipollenites cf glarius (Hedyosmum), Thymelaepollis sp. (Ovidia-type) and Cyatheacidites annulatus (Lophosoria). This will require palynostratigraphic analysis of Late Palaeogene–Neogene sediments recovered from basins surrounding the Falkland Islands, for example from DSDP Site 329 drilled on the Maurice Ewing Bank at the eastern margin of the Falkland Plateau.

Keywords: Southwest Atlantic; Falkland Islands; Forest Bed; Miocene; Pliocene subantarctic flora; Vegetation; Palaeoclimate

1. Introduction

The discovery of fossil forests in regions that are now too cold to support timber-sized trees is compelling evidence that Cenozoic climates at high latitudes were warmer in the past than now. Examples are the Middle Eocene ‘polar forests’ preserved on Axel Heiberg and Ellesmere Islands (Francis, 1990) and the Pliocene Dawson Cut forest bed in the Fairbanks area, Alaska (Westgate et al., 2003). All fossil sites are now located in or just outside of the Arctic Circle. One of the few comparable sites in the Southern Hemisphere is the Forest Bed preserved on West Point Island, one of approximately 230 naturally treeless islands that make...
up the Falklands Archipelago at $\sim 51^\circ$S in the subantarctic Atlantic Ocean (Fig. 1).

This deposit, which incorporates tree trunks over 1.5 m in diameter in a lignitic matrix, was found outcropping on the foreshore of West Point Harbour in 1899. The sequence was measured and sampled by the eminent Swedish geologist Thoré Halle in 1907 and gained international prominence some twelve years after its discovery due to his identification in the Forest Bed of two southern South American gymnosperms, which do not now grow south of latitude of $44^\circ$S in Chile (Halle, 1911; Veblen et al., 1996) — *Austrocedrus chilensis* (D.Don) Florin and *Boutelje* (Cupressaceae) and *Podocarpus salignus* D.Don (Podocarpaceae). Samples of the lignitic matrix collected in 1907 were archived in the Swedish Museum of Natural History (S. 3559-01 and S. 3599-02). In 1996, yellow clays with organic lenses (stringers) that overlie the lignitic horizon were sampled by Ms. E. Edwards (Department of Oil, Falkland Islands Government) at two localities close to Halle’s measured sections (Fig. 2).

### 1.1. Previous hypotheses

The Forest Bed was, and remains, difficult to study due to its remote location and burial under Quaternary boulder beach and stony periglacial solifluction deposits, and its age and phytogeographic implications remain equivocal for several reasons. Firstly, Halle (1911) assumed that the fossil wood came from extant South American species and did not compare the samples with gymnosperms growing on other landmasses. Secondly, none of the fossil trunks were found in growth position, leading H.A. Baker to propose in 1924 that the deposit was an ancient accumulation of driftwood and other plant debris carried by sea-currents from further north (Clark et al., 1995). Circumstantial support for this hypothesis is provided by the common occurrence on the Falkland Islands of driftwood which has become buried under blanket peat: examples occur in Bull Cove (Halle, 1911), in Driftwood Creek on Weddell Island (E. Edwards, personal observations) and, more widely, on other now-treeless sub-Antarctic islands (Barber et al., 1959; Lewis-Smith, 1985). Thirdly, the Forest Bed has
Fig. 2. Locality map.
proved very difficult to date, either by isotopic methods, stratigraphic position or plant fossil content. For example, wood of an unidentified *Nothofagus* Bl. species in the deposit gave an effectively infinite radiocarbon date of 35,960 BP (D.D. Harkness, quoted in Birnie and Roberts, 1986). Other age estimates range from Quaternary, based on the excellent preservation (Halle, 1911), to pre-Miocene (possibly Early Oligocene) based on plant microfossil content and palaeogeographic constraints (Birnie and Roberts, 1986). For example the nearest living relatives (NLRs) of miospores included two gymnosperms that are now endemic to the southwest Pacific (*Dacrydium, Lagarostrobos*). More recently, Macphail and Edwards (1999) have proposed that the age of the Forest Bed is early Late Neogene (possibly Early Pliocene) age, based on the absence of fossil miospores that are diagnostic of Oligocene to Middle Miocene sequences in central and southern Argentina, for example the fossil fern spore *Cyaetheacidites annulatus* whose NLR *Lophosoria quadrapinnata* is now endemic to South America (see Dettmann, 1986; Hill et al., 2001).

1.2. Regional significance

If the proposed Late Tertiary age is broadly correct, then the Forest Bed is of considerable importance, not only because it is the only formation of Tertiary age identified onshore in the Falklands Archipelago, but also because of the paucity of information on Late Tertiary floras, vegetation and terrestrial climates in the southwest Atlantic region as a whole (see Markgraf et al., 1996). For example, Cenozoic sediments on the Falkland Plateau have been cored as part of the Deep Sea Drilling Project (Bratzeva, 1983) but the youngest sediments preserving plant microfossils are Early Oligocene due to marine erosion associated with opening of Drakes Passage to deep-water circulation (see Lawver and Gahagan, 2003). This paper uses fossil pollen and spores (miospores) preserved in Halle’s (1907) and Edward’s (1996) samples to refine the age of the Forest Bed, reconstruct the palaeovegetation, assess its relationship to modern temperate rainforests growing at high latitudes or elevations in South America, New Zealand, southern Australia and montane New Guinea, and infer climatic conditions which allowed a forest community to thrive on the now-treeless Falklands archipelago.

2. Geological setting

The majority of surface rocks outcropping in the Falkland Islands are of Devonian, Carboniferous or Permian age, chiefly well-cemented sandstones with smaller exposures of siltstone and mudstone, unconformably overlying Precambrian granites, gneisses and schists (Greenway, 1972). The succession closely resembles the geology of the Cape Fold Belt of South Africa, leading to broad acceptance of the view that the Falkland Plateau upon which the archipelago sits is a microplate rifted off southern South Africa during the Mesozoic (see Marshall, 1994; Clark et al., 1995; Curtis and Hyam, 1998; Macdonald et al., 2003).

Folding, faulting and subsequent erosion of the Upper Palaeozoic rocks has produced a subdued topography with broad shallow valleys, separated by ridges and hills, which rise inland to a maximum elevation of about 500 m. Drowning of river valleys that have been graded to an elevation about 50 m below present-day sea-level (Clapperton and Roberts, 1986) has created a deeply indented coastline with numerous small to large bays and lagoons. Among the more important features of the Islands’ geological history are (a) the location of the Falklands Plateau contiguous with the South American continental shelf since the mid-Cretaceous (Marshall, 1994); (b) erosion or non-deposition of sediments during the Mesozoic and Tertiary and (c) limited development of glaciers but very widespread periglacial mass-wasting during the Quaternary (Clark et al., 1995; Rosenbaum, 1996). Interfluve areas are covered by thin soils and Holocene blanket peat whilst thicker sequences of Quaternary sediments such as solifluxion deposits, stone rivers (“runs”), blockfields, block-slopes and colluvial scree, alluvium and wind-blown sand, have accumulated along drainage lines and at the rear of sheltered embayments.

3. West Point Forest Bed

West Point Island (51°21′10″S 60°41′30″W), West Falklands, is located on the northwest fringe of the Falklands Archipelago and ca. 520 km due east of the Straits of Magellan (Fig. 1). The youngest lithified rocks are Devonian. Valleys sloping down from high western spine of the island are choked with Quaternary solifluxion deposits. Climates are cold temperate with a relatively low mean annual rainfall of about 600 mm and mean temperatures which rarely rise above 10 °C during summer months (Moore, 1968; Buxtehude, 1981). Although the island is windswept, West Point Harbour in general and the site in particular (Fig. 1) are relatively protected from the prevailing westerly winds that reach their maximum strength in the southwest Atlantic at about 50°S.
The Forest Bed is sandwiched between Quaternary clays and the Palaeozoic bedrock at the rear of West Point Harbour. No equivalent deposit of densely packed tree remains in an organic mud matrix has been found anywhere else in the Falklands, suggesting that accumulation and long-term preservation of the deposit are the result of highly unusual circumstances. These almost certainly include topographic factors, for example the bay is encircled by steep hills, and the protection afforded to the wood-rich stratum by the overlying stony solifluction clays (Fig. 3). More speculatively, West Point Harbour may have been infilled during the Pleistocene by solifluction deposits or barrier sands, which have been removed during the Holocene when relative sea-level are believed to have reached up to 6–8 m above present (Clapperton and Roberts, 1986).

3.1. Stratigraphy

Halle (1911: 210–211) subdivided the Forest Bed into two units (layers) based on texture and organic content: Layer c, comprising a stone-free massive yellow clay with thin organic laminae (stringers); and Layer d, which comprises tree trunks and abundant smaller fragments of wood in a sandy organic mud matrix. When examined in 1907, sufficient evidence was found to show that the formation extends for at least 550 m around the foreshore, and from below present-day low water mark to at least 30 m inland where the top of the stratum was found at a depth of 2.75 m below ground level, equivalent to 5.75 m above high water mark. If these measurements apply to the Forest Bed as a whole, then the formation dips at approximately 11° towards the centre of the bay and the wood-rich stratum (Layer d) may extend under Holocene marine sediments flooring West Point Harbour (A.E. Felton, quoted in Halle, 1911).

3.2. Depositional environment

Since none of the fossil tree trunks are in growth position, Halle (1911) argued that the Forest Bed is the remains of a forest buried by a landslide. More recently, Birnie and Roberts (1986) concluded that the organic-rich clay matrix in the Forest Bed is typical of an organic slope deposit accumulating under highly oceanic conditions. The latter interpretation is supported by the fossil pollen data (this study). For example, pollen of aquatic taxa are absent except for trace numbers of *Sparganiaceae* pollenites (*Sparganiaceae*). Nonetheless many but not all of the fossil gymnosperm and *Nothofagus* spp. have NLRs that are tolerant of water-saturated soils, for example *Lagarospatha* and *Dacrydium*. Quantitative analyses of lignites from the Bass and Gippsland Basins and Southeastern Highlands in southeast Australia indicate that another commonly occurring gymnosperm in the Forest Bed (*Podosporites microsaccatus*) was common in heath and some coastal freshwater swamps, and in analogous upland environments during the Tertiary (Tulip et al., 1982; Macphail et al., 1994, M.K. Macphail and A.D. Partridge unpubl. data).

3.3. Working hypothesis

Our working hypothesis is that the Forest Bed represents the redeposited remains of a forest growing on a thick organic soil, possibly the O/A horizons of a groundwater podzol developed on poorly draining slopes close to the palaeocoastline. The closest modern analogue on the Falkland Islands is the “black plastic humus” (Moore, 1968) accumulating under *Chiliotrichum* (*Asteraceae*) heath. Because of tectonic uplift (Clark et al., 1995), it is not possible to assume that the
inferred seaward dip of the Forest Bed (see above) accurately reflects the palaeotopography at the time of accumulation. Nevertheless trace numbers of a poorly preserved marine dinoflagellate (Operculodinium sp.) in upper organic clay facies (Layer c) are circumstantial evidence that the Forest Bed accumulated at a time when sea-levels were close to their present-day position (compare to Clapperton and Roberts, 1986).

4. Biostratigraphy

4.1. Material and methods

Samples collected in 1996 and 1907 represent Halle’s Layers c and d, respectively. The two sample sets were processed by Konrad Weiss, Laola Pty. Ltd., Perth, in 1996 and 2004, respectively. This involved standard physical and oxidative chemical techniques designed to eliminate clays (Hydrofluoric Acid) and the more labile organic compounds (Schultze Solution) followed by filtration through sieve-cloth to eliminate 5 μm or smaller particles. It is possible that small pollen types with this minimum diameter will have been lost by sieving, for example fossil equivalents of types produced by broadleaf rainforest trees belonging to the Cunoniaceae and Eucryphiaceae. Four microscope slides (strew mounts), each containing upward of 5000 fossil pollen, spores and other plant microfossils, were obtained from each sample. One strew mount from each sample was counted at high (788×) magnification using a Zeiss Photomicroscope II fitted with top-of-the-range (10–1000×) Planapo oil objectives until a minimum count of 440 identifiable fossil pollen and spores was reached. The remainder of these strew mounts and an additional two to three strew mounts for each sample were then scanned at lower magnifications (120–600×) to locate rare taxa: identification were verified at 788–1250× magnification. Slides from Halle’s original collection are housed at the Swedish Museum of Natural History (Stockholm).

4.2. Presentation of microfossil data

Fossil pollen and spore types able to be identified to family, genus or species level are listed in Table 1. The relative abundances of commonly occurring (>1%) taxa are given in Table 2. A comprehensive selection of age-diagnostic and other fossil pollen and spore morphotypes are illustrated in Appendix A. NLR(s) are given in parentheses after the fossil taxon in the text. Plant thermal response classes (Nix, 1991) are defined by mean air temperature and assume that precipitation was not limiting in any season: megatherm (>24 °C), mesotherm (>12 to <24 °C) and microtherm (<12 °C). It is emphasised that microfossil data can be difficult to reconcile with plant macrofossils preserved in the same deposit. Reasons include: (1) the two lines of evidence often represent different areas of vegetation; (2) the taxa represented by wood, foliage or fruit may produce/disperse very low numbers of miospores; and (3) many fossil miospores lack distinctive morphological features that enable their botanical affinity to be reliably identified.

4.3. Taxonomic considerations

Many of the pollen and spore morphotypes recovered from the Forest Bed are geographic variants of fossil (form) species first described from the southwest Pacific region (see Cookson and Pike, 1954; Couper, 1960; Stover and Partridge, 1973). These include some fossil species whose NLRs are now endemic to South America. Examples are Nothofagidites flemingii (Nothofagus subgenus Nothofagus) and Granodiporites nebulosus (Embothrium coccineum). One consequence of the pan-Pacific distribution of many Tertiary fossil species has been a de facto broadening of taxonomic concepts to include morphotypes that bear limited resemblance to the designated holotype. Examples are spores referred to Matonisporites ornamentalis and Rugulatisporites mallatus, and pollen referred to Glencopollis ornatus (Barreda and Palamarczuk, 2000b). In other instances, morphotypes separated out into distinct species in one region are considered to fall within the morphological spectrum of a separate fossil species elsewhere. Examples are the South American fossil species Nothofagidites saraensis, and N. americanus and N. tehuelchesii, which would be accommodated within N. flemingii and N. asperus, respectively, if found in Tertiary deposits in Australia or New Zealand. Conversely, apparently identical morphotypes have been described as different form genera or species in different regions of the Southern Hemisphere. Examples include Muricingulisporis (≈ Polypodiaceoispores), Baumannipollis (≈ Malvacipollis) and Striatocolporites gamмерои (≈ Alanthipites paenestriatus). Other complications are: (1) immature pollen grains may have been described as separate species. For example, grains assigned to Nothofagidites acromega-canthea in this study could include immature N. saraensis (compare to Dettmann et al., 1990). (2) Plants of widely differing stature and ecological preferences may be represented by the same fossil species. For example, pollen closely resembling N.
saraensis are produced by all five living species within the subgenus Notofagus (Hill and Read, 1991) in South America (see Heusser, 1971). Life-forms in this subgenus include deciduous (N. antarctica, N. pumilo) and evergreen (N. betuloides, N. dombeyi, N. nitida) species, range in size from low shrubs to tall trees, and occupy ±warm/wet to cold/xeric habitats (see Veblen et al., 1996). Similarly, the sole living representative of Tertiary Phyllocladidites mawsonii (Lagarostrobos franklinii) typically is an emergent tree in lowland cool temperate rainforest but can occur as a krumholtz shrub in the upper subalpine zone (Read, 1999).

Because the parent plants of pollen and spores found on the Falkland Islands are likely to be only distantly related to their counterparts in the southwest Pacific region, pollen and spore taxa ±identical to fossil species that have been formally described or illustrated in the South American literature are referred to these species. NLRs are based on descriptions and illustrations of the modern Chilean pollen flora published by Heusser (1971). Fossil species with no close analogue in South America are referred to the nearest formally described equivalent in the southwest Pacific literature; several of the more distinctive but undescribed species have been given the manuscript suffixes, for example sp. A., sp. B, etc., and illustrated in Plates I–V.

5. Age of the Forest Bed

Two related lines of evidence allow the Forest Bed to be dated to within a Geologic Period (Middle? Miocene to Early Pliocene), and potentially to be dated to within a Geologic Stage level once a detailed palynostratigraphy is developed for the Late Palaeogene–Neogene of the southwest Atlantic region. These are (a) the presence or absence of widely dispersed miospores whose time-distributions have been established in southern Argentina, Tierra del Fuego and Falkland Plateau, and (b) a comparison of the inferred local conditions under which the Forest Bed vegetation was growing, against known trends in Late Palaeogene–Neogene climates in the subantarctic Atlantic region. The latter (ecostratigraphic) age limits are based on two empirically defensible assumptions: (a) The relative abundance of plant macro- and microfossils in the Forest Bed is reliable proxy evidence of community dominance and structure. (b) Even if the composition of the Forest Bed community reflects a strong edaphic control (see Section 3.3), climatic change remains the primary determinant of plant community dominance and structure on the Falkland Islands during the Tertiary (see comments in Birks and Birks, 1980; Hill, 1994; Macphail et al., 1994; Chaloner and McElwain, 1997; Jordan, 1997).


5.1. Constraints

No formal palynostratigraphic zonation exists for Cenozoic terrestrial palynosequences in the southwest Atlantic region, including the Falkland Islands, and the nearest reference sequences come from the Falkland Plateau, Tierra del Fuego and the Catamarca, Chubut, Santa Cruz and San Juan Provinces of central–southern Argentina (Fig. 1). Time distribution data from these regions are difficult to apply directly to the Falklands Islands for four reasons. (1) Rapid uplift of the southern Andes since the Eocene has resulted in increasingly dry climates in central Argentina whereas cold, maritime climates have persisted in Tierra del Fuego and the Falkland Islands, due to opening of Drakes Passage to deep-water circulation during the Oligocene (Flynn et al., 2003; Lawver and Gahagan, 2003), compounded by formation of the West Antarctic Ice Sheet during the Late Miocene (Ciesielski et al., 1982). General consensus exists that the Early Pliocene was the most recent interval of sustained global warmth, with sea surface temperatures at high latitudes in the south Atlantic estimated to have been up to 2–3 °C higher than today (see King, 1996; Billups et al., 1998). (2) Times of first appearance of shared species are likely to vary between South America and the
### Table 1
Species list, West Point Forest Bed

<table>
<thead>
<tr>
<th>Fossil taxon</th>
<th>Family</th>
<th>Nearest living relative(s)</th>
<th>Samples</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Chile</td>
<td>Southwest Pacific</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(From Heusser, 1971)</td>
<td>(From Large and Braggins, 1991; Macphail et al., 1994; Moar, 1993)</td>
</tr>
<tr>
<td>Cryptogams</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Botryococcus braunii</td>
<td>Botryococcaceae</td>
<td>Botryococcus</td>
<td>• • •</td>
</tr>
<tr>
<td>Baculatisporites cf comaumensis</td>
<td>Hymenophyllaceae?</td>
<td>Hymenophyllum cruentum</td>
<td>Botryococcus flexuosum (NZ)</td>
</tr>
<tr>
<td>Baculatisporites disconformis</td>
<td>Hymenophyllaceae</td>
<td>–</td>
<td>Hymenophyllum sanguinolentum (NZ)</td>
</tr>
<tr>
<td>Baculatisporites turboensis</td>
<td>(Philesiaceae?)</td>
<td>(cf Lapageria, Philesia)</td>
<td>(Philesiaceae?)</td>
</tr>
<tr>
<td>Cyathidites australis</td>
<td>Cyatheaceae</td>
<td>Cyatheae</td>
<td>•</td>
</tr>
<tr>
<td>Dictyophyllidites cf arcuatus</td>
<td>Gleicheniaceae</td>
<td>cf Dicranopteris</td>
<td>cf Dicranopteris</td>
</tr>
<tr>
<td>Foveotriletes palaequetrus</td>
<td>Lycopondiaceae</td>
<td>Huperzia fuegianum</td>
<td>Incl. Lycopodium australianum (Aust., NZ)</td>
</tr>
<tr>
<td>Ischyosporites cf areapunctatis</td>
<td>Dicksoniaceae</td>
<td>Dicksonia berteroa</td>
<td>cf Dicksonia fibrosa (NZ)</td>
</tr>
<tr>
<td>Laevigatosporites ovatus</td>
<td>incl. Blechnaceae</td>
<td>numerous genera</td>
<td>numerous genera</td>
</tr>
<tr>
<td>Matonisporites ornamentalis</td>
<td>Dicksoniaceae</td>
<td>extinct? Dicksonia</td>
<td>Dicksonia antarctica (Australia)</td>
</tr>
<tr>
<td>Monolites alveolatus</td>
<td>Polypodiaceae</td>
<td>Belvisia</td>
<td>–</td>
</tr>
<tr>
<td>Perononolites vellosus</td>
<td>Blechnaceae</td>
<td>–</td>
<td>Unidentified species</td>
</tr>
<tr>
<td>Polypodispores inangahuiensis</td>
<td>Polypodiaceae</td>
<td>Polyponium flexilliferi</td>
<td>Davalliaeeae, Polypodiaceae</td>
</tr>
<tr>
<td>Polypodispores radiatus</td>
<td>Polypodiaceae</td>
<td>extinct?</td>
<td>Davalliaeeae, Polypodiaceae</td>
</tr>
<tr>
<td>Triletes tuberculiformis</td>
<td>Dicksoniaceae</td>
<td>–</td>
<td>Extinct (Dicksonia dissecta)</td>
</tr>
<tr>
<td>Triletes cf tuberculiformis</td>
<td>Dicksoniaceae?</td>
<td>–</td>
<td>Extinct (cf Dicksonia dissecta)</td>
</tr>
<tr>
<td>Diversity</td>
<td>8 9 14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gymnosperms</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Araucariacites australis</td>
<td>Araucariaceae</td>
<td>Araucaria</td>
<td>Araucaria</td>
</tr>
<tr>
<td>Cupressacites</td>
<td>Cupressaceae</td>
<td>Austrocedrus, Fitzroya</td>
<td>Numerous genera</td>
</tr>
<tr>
<td>Equisetosporites claricristatus</td>
<td>Ephredraeeae</td>
<td>Ephredra americana</td>
<td>–</td>
</tr>
<tr>
<td>Inaperturopollenites sp.</td>
<td>Podocarpaceae</td>
<td>cf Saxegothea conspicua</td>
<td>–</td>
</tr>
<tr>
<td>Lygistepollenites florinii</td>
<td>Podocarpaceae</td>
<td>–</td>
<td>Incl. Dacrydium cupressinum (NZ)</td>
</tr>
<tr>
<td>Microalatidites palaeogenicus</td>
<td>Podocarpaceae</td>
<td>–</td>
<td>Phyllocladus</td>
</tr>
<tr>
<td>Phyllocladidites mawsonii</td>
<td>Podocarpaceae</td>
<td>–</td>
<td>Lagarostrobos franklinii (Tasmania)</td>
</tr>
<tr>
<td>Podocarpites cf rugulosus</td>
<td>Podocarpaceae</td>
<td>Podocarpus rubiginis</td>
<td>Podocarpus, Prumnopitys, Retrophyllum</td>
</tr>
<tr>
<td>Podocarpites spp. (&gt;3 types)</td>
<td>Podocarpaceae</td>
<td>cf Dacrydium fonkii</td>
<td>Podocarpus, Prumnopitys, Retrophyllum</td>
</tr>
<tr>
<td>Podosporites microsaccatus</td>
<td>Podocarpaceae</td>
<td>–</td>
<td>Extinct trisaccate (cf Microcachrys)</td>
</tr>
<tr>
<td>Trisaccites sp.</td>
<td>Podocarpaceae</td>
<td>–</td>
<td>Extinct trisaccate (aff Microcachrys)</td>
</tr>
<tr>
<td>Diversity</td>
<td>12 11 9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Angiosperms (monocotyledons)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arecipites sp.</td>
<td>Liliales</td>
<td>Iridaceae, Liliaeeae</td>
<td>Incl. Areaceae, Liliaeeae</td>
</tr>
<tr>
<td>Lateropora glabra</td>
<td>Pandanaeeae</td>
<td>–</td>
<td>Freycinetia</td>
</tr>
<tr>
<td>Liliaceae cf lanceolatus</td>
<td>Liliaeeae, Bromeliaceae</td>
<td>Herreria, Puya</td>
<td>Areaceae, Liliaeeae sensu lato</td>
</tr>
<tr>
<td>Liliacees sp. aff bainii</td>
<td>Liliaeeae, Bromeliaceae</td>
<td>Alophia, Deuterochonia</td>
<td>Areaceae, Liliaeeae sensu lato</td>
</tr>
<tr>
<td>Luminidites cf phormoides</td>
<td>Agavaceae, Liliaeeae</td>
<td>Pasithea coerula</td>
<td>Dianella (Australia)</td>
</tr>
<tr>
<td>Monosulcites sp. A</td>
<td>Liliales</td>
<td>cf Trichopetalum</td>
<td>Areaceae? Liliaeeae cf Astelia</td>
</tr>
<tr>
<td>Sparganiaceae pollenites sphericus</td>
<td>Sparganiaceae</td>
<td>–</td>
<td>Sparganium</td>
</tr>
<tr>
<td>Inaperturate echinate type</td>
<td>Philesiaceae</td>
<td>cf Lapangiera rosea</td>
<td>Philesiaceae?</td>
</tr>
</tbody>
</table>

(continued on next page)
The time of extinction of many species in the Late Neogene flora of southern South America remains unknown. A related complication is that a number of the gymnosperms represented in the Forest Bed palynoflora now survive on isolated landmasses in the southwest Pacific, for example *Dacrydium* [fossil equivalent *Lygistepollenites* (al. *Dacrydiumites*) *florinii*] in New Zealand and parts of Southeast Asia, and *Lagarostrobos* (fossil equivalent *P. mawsonii*) in Tasmania. (4) Constraints imposed by the unusual depositional environment of the Forest Bed are

<table>
<thead>
<tr>
<th>Fossil taxon</th>
<th>Family</th>
<th>Nearest living relative(s)</th>
<th>Samples</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Chile (From Heusser, 1971)</td>
<td>Southwest Pacific (From Large and Braggins, 1991; Macphail et al., 1994; Moar, 1993)</td>
</tr>
<tr>
<td>Diversity Angiosperms (dicotyledons)</td>
<td></td>
<td></td>
<td>Layer 6</td>
</tr>
<tr>
<td><em>Canthiumidites cf bellus</em></td>
<td>Rubiaceae?</td>
<td>–</td>
<td>Randia?</td>
</tr>
<tr>
<td><em>Chenodopollis chenopodiaceoides</em></td>
<td>Chenopodiaceae</td>
<td>Numerous genera</td>
<td>Numerous genera</td>
</tr>
<tr>
<td><em>Clavatisporites cf glarius</em></td>
<td>Chloranthaceae</td>
<td><em>Hedyosmum</em></td>
<td><em>Ascarina lucida</em> (New Zealand)</td>
</tr>
<tr>
<td><em>Compositoipollenites cf tarragoensis</em></td>
<td>Myzodendronaceae</td>
<td><em>Myzodendron</em></td>
<td>–</td>
</tr>
<tr>
<td><em>Ericipites sp.</em></td>
<td>Ericales</td>
<td><em>cf Gaultheria myrtilloides</em></td>
<td>Ericaceae, Epacridaceae</td>
</tr>
<tr>
<td><em>Gothenipollis cf bassensis</em></td>
<td>Loranthaceae</td>
<td><em>Loranthaceae</em> (extinct genus)</td>
<td>Loranthaceae (extinct genus?)</td>
</tr>
<tr>
<td><em>Graumaripollis sp.</em></td>
<td>Poaceae</td>
<td>Numerous genera</td>
<td>Numerous genera</td>
</tr>
<tr>
<td><em>Granodiporites diporites</em></td>
<td>Proteaceae</td>
<td><em>Embothrium coccineum</em></td>
<td><em>(Contaminant)</em></td>
</tr>
<tr>
<td><em>Myrtaceidites eucalyptoides</em></td>
<td>Myrtaceae</td>
<td><em>(Incl. Austromyrtus, Myrcuegenia)</em></td>
<td>Eucalyptus gunnifera-type (Australia)</td>
</tr>
<tr>
<td><em>Myrtaceidites parvus-mesomensus</em></td>
<td>Myrtaceae</td>
<td>–</td>
<td>Incl. <em>Eugenia, Metrosiders, Syzygium</em></td>
</tr>
<tr>
<td><em>Myrtaceidites verrucosus</em></td>
<td>Myrtaceae</td>
<td><em>Incl. Austromyrtus, Myrcuegenia</em></td>
<td><em>Austromyrtus</em>-type</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Myrtaecidites</em> (dicotylspore) sp.</td>
<td>Myrtaecidites</td>
<td><em>Tepaulia stipularis</em></td>
<td>–</td>
</tr>
<tr>
<td><em>Nothofagidites americus</em></td>
<td>Nothofagidites</td>
<td><em>Nothofagus obliqua</em></td>
<td><em>Nothofagus</em> (Lophozonia) spp.</td>
</tr>
<tr>
<td><em>Nothofagidites cf acromegacanthus</em></td>
<td>Nothofagidites</td>
<td><em>(Extinct? Nothofagus)</em></td>
<td>–</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nothofagidites cf brachyspinulosus</em></td>
<td>Nothofagidites</td>
<td><em>(Extinct? Nothofagus)</em></td>
<td><em>Nothofagus</em> (Fuscospora) spp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nothofagidites flemingii</em></td>
<td>Nothofagidites</td>
<td><em>Nothofagus</em>(Nothofagus)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nothofagidites saraensis</em></td>
<td>Nothofagidites</td>
<td><em>Nothofagus</em>(Nothofagus)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Polycolporopollenites esosalteus</em></td>
<td>Polygalaceae</td>
<td><em>Polygala stricta</em></td>
<td><em>Comesperma, Polygala</em> (Australia)</td>
</tr>
<tr>
<td><em>Proteacidites</em> (Propylipollis)</td>
<td>Proteaceae</td>
<td><em>Genus avellana</em></td>
<td><em>Genus, Hicksbeachea</em> (Australia)</td>
</tr>
<tr>
<td>reticulascabratra*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Proteacidites sp. A</em></td>
<td>Proteaceae</td>
<td><em>Orites myrtoidea</em></td>
<td></td>
</tr>
<tr>
<td><em>Protocladopollis sp. B</em></td>
<td>Proteaceae</td>
<td><em>cf Lomatia dentata</em></td>
<td><em>Lomatia</em> (Australia)</td>
</tr>
<tr>
<td><em>Pseudowinterapollis couperi</em></td>
<td>Winteraceae</td>
<td><em>Drimys winteri</em></td>
<td><em>Tasmanina lanceolata</em> (Australia)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Quintiniapollis sp.</em></td>
<td>Grossulariaceae</td>
<td>–</td>
<td><em>Quintina</em></td>
</tr>
<tr>
<td><em>Rhapisites</em> sp. A*</td>
<td>Celastraceae</td>
<td><em>cf Maytenus disticha</em></td>
<td></td>
</tr>
<tr>
<td><em>Striatocolporites (Allanthipites) cf</em></td>
<td>Anacardiaceae</td>
<td><em>cf Lithraea caustica</em></td>
<td></td>
</tr>
<tr>
<td><em>Thymelaeopollis sp.</em></td>
<td>Thymelaeaceae</td>
<td><em>Ovidia</em></td>
<td><em>Incl. Kelleria (NZ), Pimelea</em> (Australia)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tricolpites reticulatus</em></td>
<td>Gunneraceae</td>
<td><em>Gunnera</em></td>
<td><em>Gunnera</em> (New Zealand, Tasmania)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tricolpores cf trioblatus</em></td>
<td>Convolvulaceae?</td>
<td>–</td>
<td><em>cf Wilsonia</em> (Australia)</td>
</tr>
</tbody>
</table>

Falkland Islands, due to the apparently fortuitous nature of plant dispersal across the ~500 km ocean gap and low vagility of many rainforest species. (3) The time of extinction of many species in the Late Neogene flora of southern South America remains unknown. A related complication is that a number of the gymnosperms represented in the Forest Bed palynoflora now survive on isolated landmasses in the southwest Pacific, for example *Dacrydium* [fossil equivalent *Lygistepollenites* (al. *Dacrydiumites*) *florinii*] in New Zealand and parts of Southeast Asia, and *Lagarostrobos* (fossil equivalent *P. mawsonii*) in Tasmania. (4) Constraints imposed by the unusual depositional environment of the Forest Bed are...
compounded by cryoturbation of the upper organic clay unit (Layer c) during the Pleistocene.

5.2. Age limits

For the reasons outlined above, it is possible to infer several (conflicting) age limits for the Forest Beds. These range from Oligocene to Early Pliocene depending on the relative ‘weight’ given to the various indicator taxa, although a Middle? Miocene to Early Pliocene age is considered to provide the ‘best fit’ for the combined evidence:

1. The ‘oldest’ maximum age for the Forest Bed is Oligocene, based on *Sparganiaceaepollenites sphericus* (Sparganiaceae), a wetland herb that first appears in southern South America during the Oligocene. This age limit is strongly supported by

---

Table 2
Relative abundance of commonly occurring taxa, Forest Bed

<table>
<thead>
<tr>
<th>Fossil Taxon</th>
<th>Nearest living relative (NLR) [family/genus]</th>
<th>Distribution (after Mabberley, 1997)</th>
<th>Sample</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Layer c</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Σ %</td>
</tr>
</tbody>
</table>

Cryptogams

- *Monolites alveolatus* Poly podiaceae: *Belvisia* Old World tropics
- *Laevigatosporites ovatus* Incl. Blechnaceae Cosmopolitan

Undescribed trilete spores Numerous families Cosmopolitan

Total cryptogams

Gymnosperms

- *Araucariacites australis* Araucariaceae: *Araucaria* SW Pacific–Chile
- *Araucariacites sp.* Podocarpaceae cf *Sixegothea* Chilean Andes
- *Cupressacites* Cupressaceae Cosmopolitan
- *Lygistepollenites florinii* Podocarpaceae: *Dacrydium* SE Asia–NZ
- *Phylocladidites mawsonii* Podocarpaceae: *Lagarostrobus* SW Tasmania
- *Podocarpidites spp.* Podocarpaceae: *Podocarpus s.l.* America
- *Podosporites microsaccatus* Podocarpaceae Extinct–NZ–South America

Total gymnosperms

Angiosperms

- *Clavatisporites cf glarius* Chloranthaceae: *Hedyosmum* SE Asia–tropical America
- *Compositoipollenites sp.* Myzdendoronaeae: *Myzdendron* 1 + 1 +
- *Liliacidites cf phormioides* Liliaceae cf *Dianella* Africa–Western Pacific
- *Liliacidites spp.* Areaceae, Liliaceae Cosmopolitan
- *Myrtaceidites parvus* Myrtaceae (non-eucalyptoid) S. Hemisphere
- *Nothofagiidites cf acromegacanthus* Nothofagaceae (Nothofagus) Extinct? (immature)
- *Nothofagiidites americanus* Nothofagaceae (Nothofagus) SE Aust., NZ, South America
- *Notofagus cf brachyspinulosus* Nothofagaceae (Nothofagus) SE Aust., NZ
- *Nothofagiidites saraensis* Nothofagaceae (Nothofagus) South America
- *Proteacidites spp.* Proteaceae Subcosmopolitan
- *Sparganiaceaepollenites sphericus* Sparganiaceae Subcosmopolitan
- *Rhoipites spp.* Numerous families –
- *Tricolpites spp.* Numerous families –
- *Tricolporites spp.* Numerous families –

Total angiosperms

Unassigned taxa Numerous families

Pollen sum

Fungal spores No data

Charcoal particles No data

Raw spore–pollen data listed under Σ: percentages are based on the total spore–pollen count (+ = values <1%).
the absence of subtropical–tropical taxa which last occur in the Eocene in central–southern Argentina, for example Anacolosidites (Anacolosa), Longasperites (Arecaceae?) and Proxasperites (Arecaceae?), but is inconsistent with the absence of C. annulatus (Lophosoria), which is present in Oligocene marine facies on the Falkland Plateau (Bratzeva, 1983).

2. The ‘youngest’ maximum age for the Forest Bed is Late Miocene to Early Pliocene, based on Thymlaeapolpis. This distinctive crotonoid pollen type produced by the Thymlaeaceae does not appear to have been found in any Tertiary pollen sequence in southern South America but is present in trace numbers in Last Interglacial deposits between two glacial diamicts exposed on the Pan American Highway, Chilean Lake District (Heusser, 1974). The most likely source is the Ovidia, a genus of small trees? and shrubs found in temperate vegetation types in South America (Mabberley, 1997). Other genera of Thymlaeaceae found in South America are mostly restricted to the tropics except for Daphanopsis, which extends into Eastern Argentina and is found associated with deciduous Nothofagus spp. (N. obliqua, N. alpina) in the middle latitude Valdivian province of Chile (Veblen et al., 1996; Marchant et al., 2002). Identical morphotypes, cited as Thymlaeopolpis sp. or Pimelea-type, first appear in southeast Australia in the Late Pliocene (Macphail, 1997) and in New Zealand during the Pliocene (Mildenhall, 1980; Mildenhall and Pocknall, 1989), respectively. Comparable microfossils (Thymelipollis reticulatipus, Phaleria-type) first appear in the Early Miocene in Cameroon, Africa, and in the Late Miocene in Mexico (see Muller, 1981). Today Phaleria is restricted to Indomalesia and the Western Pacific (Macphail, 1997).

3. The preferred Middle? Miocene to Early Pliocene age limits are based on presence of the (now) mesothermal genera Araucaria, Hedyosmum and Ovidia in a type of evergreen rainforest (podocarp-Nothofagus) tall closed forest sensu Specht, 1970) that is now confined to relatively cool and uniformly wet climates in southern South America, New Zealand and Tasmania (see Sections 6 and 7). Because of the oceanic location, such a ‘mixed climate’ palaeoflora potentially could have developed on the Falklands during the Oligocene and survived into the Early Pliocene ‘warm period’ (see Mercer, 1976; Mercer and Sutter, 1981; Hodell and Warnke, 1991; King, 1996; Billups et al., 1998; Lawver and Gahagan, 2003). However, at present there is no evidence that Thymlaeaceae were established in South America before the Early Miocene first appearance of Thymlaeapolpis in Africa: The long distance dispersal of Thymlaeapolpis (Ovidia-type) onto West Point Island from southern South America, or? Africa, almost certainly will have been curtailed by intensifying cooling events related to waxing and waning of the East Antarctic ice-sheet since the Late Miocene (see references in Rabassa et al., 2005).

6. Palaeovegetation

Reconstruction of the Forest Bed vegetation assumes that (a) the pollen production and dispersal abilities (representivity) of the component species were qualitatively similar to those of their NLRs and (b) community structure can be deduced by analogy with floristically similar temperate communities in South America, New Zealand, Tasmania and montane New Guinea. Key observations are: (1) unlike the Northern Hemisphere, the overwhelming majority of trees, shrubs, herbs and ferns species growing at middle to high latitudes in the Southern Hemisphere are severely under-represented by their pollen or spores unless the parent plants grew on (or upstream from) the site (see Macphail and McQueen, 1983; Macphail et al., 1994). Tertiary taxa likely to be in this category include cryptogams such as Foveotiretes palaquetrus (Huperzia fujigianum), wind-pollinated gymnosperms such as Podosporites microsaccatus (Podocarpaceae comparable to Microcachrys), and insect-pollinated angiosperms such as Compositopollinites (Myzodendron), Ericitipes (Ericales), Gothanipollis (Loranthaceae), Granodiporites nebulosus (Embothrium coccineum), Myrtaceidites (Myrtaceae), Polycolporpollinites esobaleus (Polygalaceae), Proteacidites (Proteaceae), Rhoipites sp. A (Maytenus), Straticolporpollinites cf gammeroi (Anacardiaceae), Thymlaeapolpis (Ovidia-type) and Tricolpites reticulatus (Gunnera). (2) A comparison of Late Quaternary and modern pollen rain data from South America, New Zealand and Tasmania confirm that a small number of tree and herb species are well- to over-presented in that their pollen or spores are present whether or not the parent plants were present in the local vegetation, e.g. Clark et al. (1998): Tertiary genera in this category (Macphail et al., 1994) include cryptogams such as Cyathidites (Cyatheaa) and Matonisporites (Dicksonia), gymnosperms such as Araucariacites (Araucaria), Dacrycarypites (Dacrycarpus), Lygistempollinites (Dacrydium), Microalatidites (Phyllocladus) and Podocarpidites (Podocarpus–Prumnopitys), and angiosperms such as Clavatipollenites (Ascarina, Hedyosmum), Nothofagidites (Nothofagus) and Pseudowinterapolpis (Winteraceae). Most but not all
<table>
<thead>
<tr>
<th>Fossil taxa</th>
<th>Central Argentina</th>
<th>Southern Argentina and Tierra del Fuego</th>
<th>Falkland Plateau</th>
<th>West Point Forest Bed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>45–50°S</td>
<td>50–55°S</td>
<td>50–55°S</td>
<td>51°30′S</td>
</tr>
<tr>
<td>Paleoeocene</td>
<td>~ Late Eocene</td>
<td>~ Early Oligocene</td>
<td>~ Middle Miocene</td>
<td>~ Late Miocene</td>
</tr>
<tr>
<td></td>
<td>~ Late Oligocene</td>
<td>~ Early Miocene</td>
<td>~ Middle Miocene</td>
<td>~ Late Miocene</td>
</tr>
<tr>
<td>References</td>
<td>1–4</td>
<td>5–6</td>
<td>7–8</td>
<td>7, 9</td>
</tr>
<tr>
<td></td>
<td>10–11</td>
<td>12–13</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>This study</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Ferns and fern allies**
- Baculatisporites cf comaumensis
- Baculatisporites turboensis
- Clavifera triplex
- Cyathaeacidites annulatus
- Cyathidites spp.
- Foveotrilites palaquestrus
- Ischysporites areaquunctatis
- Matonisporites ornamentalis
- Muriculingulospores
- Permononilites velosus
- Polydisisporites spp.
- Trilites tuberculiformis

**Gymnosperms**
- Araucariacites australis
- Cupressacites
- Dacrycarpites australiensis
- Equisitosporites claricristatus
- Equisitosporites notensis
- Inaperturopollenites (Saxegothea)
- Lygisteospores florinii
- Microalatidites palaeogenicus
- Microcachrydites antarcticus
- Phyllocladidites mawsonii
- Podocarpidites spp.
- Podosporites microsaccatus

**Angiosperms**
- Anacolosidites spp.
- Acaciapollenites myriosporites
- Arecitites spp.
- Baumannipollis (Malvicipollis)
- Canthiumidites sp. cf C. bellus
- Compositopollenites cf tarragoensis
- Chenopodium pollis
- Clavatipollenites cf gladius
- Concolpites leptos
- Corsinipollenites antarctica
- Cupanisopites reticularis
- Cyperaceaeipollis

*(continued on next page)*
<table>
<thead>
<tr>
<th>Fossil taxa</th>
<th>Central Argentina</th>
<th>Southern Argentina and Tierra del Fuego</th>
<th>Falkland Plateau</th>
<th>West Point Forest Bed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>45–50°S</td>
<td>50–55°S</td>
<td>50–55°S</td>
<td>51°30′S</td>
</tr>
<tr>
<td></td>
<td>Pale–Eocene</td>
<td>~ Late?</td>
<td>~ Early</td>
<td>~ Late</td>
</tr>
<tr>
<td></td>
<td>Oligocene</td>
<td>Miocene</td>
<td>Miocene</td>
<td>Miocene</td>
</tr>
<tr>
<td></td>
<td>~ Middle</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>References</td>
<td>References</td>
<td>References</td>
<td>References</td>
<td>References</td>
</tr>
<tr>
<td></td>
<td>1–4</td>
<td>5–6</td>
<td>7–8, 7, 9</td>
<td>10–11</td>
</tr>
<tr>
<td></td>
<td>12–13, 14</td>
<td>14</td>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>This study</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>neogenicus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diporites aspis</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ericipites spp.</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glencopolis ornatus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gothamopolis spp.</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Graminidites spp.</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Granodiporites nebulusus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haloragacidia harrisi</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ilexpollenites</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Luminidites cf phormoides</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Longapertites spp.</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Margocolporites vanwijhi</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Matsiapollis viteauensis</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Myrtaceidites verrucosus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>[Nothofagus (Brassospora) spp.]</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>[Nothofagus (Fuscospora) spp.]</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nothofagidites acromeganthus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nothofagidites americana/</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>tehuelchensis</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nothofagidites saraensis/</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>flemingii</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parsonsidites spp.</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peninsulapolis (al. Tricolpites) gillii</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Periporopollenites demarcatus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polapissutes sp.</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polyadopollenites cf</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>miocenicus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polycolporopollenites esohaleus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proteacidites reticuloscabratus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proteacidites sp. 1</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proxapertites spp.</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudowinterapollis couperi</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quintiniapollis</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sparganiaceaepollenites sphericus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Striayncolpites laxus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Striatricolporites gamerroi</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thymelaepollis sp.</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tricolpites reticulatus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tricolpites trioblatus</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tubulifloridites spp.</td>
<td>•</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

of these taxa are wind-pollinated and typically are most abundant in, or on the margins of, wet forest types. Unlike under-represented taxa, low relative abundance values of pollen are not unequivocal evidence for a local source since similar (<5%) values occur when the parent plants are abundant in distant vegetation, or when the local pollen influx is very low. In such instances, pollen of some under-represented associates can be useful as proxy evidence for the local presence of well-represented species. An example is *Myzodendron*, which is parasitic on *Nothofagus* (Heusser, 1966).

### 6.1. Diversity

The combined microfossil data (Table 1) indicate a minimum of 60 distinctive fossil pollen and spore types are preserved in the Forest Bed. The majority of these miospores represent angiosperms (>35 genera) whose NLRs are dominants in the canopy stratum of cool–cold (microtherm) rainforest and rainforest scrub, especially *Nothofagidites* spp., or which include species that grow in wet vegetation types, for example *Eriepites* (Ericales), *Myrtaceidites verrucosus* (Austromyrtus-type) and *Proteacidites reticuloscabratus* (Gevuina). Most of these represent trees and/or shrubs, with at least two being parasitic epiphytes (Loranthaceae, *Myzodendron*). Other potential epiphytes are *Myrtacidites parvus* (Metrosideros-type) and *Laevigatosporites* (Blechnaceae?). Herbs appear to be very rare (5 genera including? Phileiaceae) although one species, *Luminidites cf phormoides* (Pasithea coerula?) comprises 2% of the pollen count.

The number of identifiable fossil gymnosperm taxa are much lower (12) but in terms of relative pollen abundance are more prominent than angiosperms (65–66% versus 32–34%, respectively). These genera encompass almost all of the distinctive morphotypes produced by the Southern Hemisphere conifers. For example, at least four distinctive morphotypes have been lumped under *Podocarpidites* spp. The two notable absences are the gymnosperms *Dilwynites* and *Microcachrydites australis* whose NLRs (Agathis/Wollemia, Microcachrydites) are now endemic to southeast Australia and Tasmania, respectively. Ferns and fern allies are rare in terms of their diversity (10 fossil genera) and also in relative abundance (<1%) in the lignite samples but become more common (9%) in the organic clays. *Baculatisporites cf comamenis* could represent either a filmy fern (Hymenophyllaceae) or a liverwort (see Large and Braggins, 1991); it is also possible that a second species of *Baculatisporites* found in the Forest Bed (*B. turboensis*) represents the herbaceous angiosperm genera *Lapageria* or *Philesia* (Phileiaceae) rather than a cryptogam (compare Fig. 116 in Appendix 1 with Figs. 159–160 in Heusser, 1971).

### 6.2. Dominance

Modern height:stem relationships for conifers found in southern South America confirm that tree trunks over 1.5 m diameter will represent tall trees up to 20–50 m in height at the time of death (Veblen et al., 1995). Although the affinity of the stems found in the Forest Bed are equivocal, their presence, combined with the significant representation of *N. saraensis* (*Nothofagus* subgenus *Nothofagus*) and *Lygistepollenites florinii* (*Dacrydium*) pollen, indicates these taxa formed the canopy and/or (*Dacrydium*) overstorey in a form of cool temperate rainforest (tall closed forest sensu Specht, 1970). Other potential canopy taxa are *Araucariacites australis* (*Araucaria*), *Phyllocladidites mawsonii* (*Lagarostrobus*), *Podocarpidites* (*Podocarpus–Prumnopitys*) and *Nothofagidites cf acromegacanthus* (*Nothofagus* subgenus *Nothofagus*).

On the evidence available, the subcanopy was dominated by small trees, shrubs and woody epiphytes rather than herbs or ferns. Genera present in this stratum are likely to include *Hedysossum*, Loranthaceae, *Myzodendron* (=*Compositoipollenites*), Myrtaceae (*Myrtacidites*), Proteaceae such as *Embothrium* (*Granodiportis nebulosus*), Gevuina (*P. reticuloscabratus*), *Lomatia* (*Proteacidites sp. B*) and *Orites* (*Proteacidites sp. A*), *Luminidites cf phormoides* (Pasithea?;), and the parent plants of most pollen types assigned to *Rhoipites*, *Tricolpites* and *Tricolporites*. The relative abundance and probable life-form of *P. microsaccatus* are sufficiently high to indicate that a now extinct shrub podocarp related to *Microcachrydites* formed the ground cover within or around the margins of the forest.

Other microfossils are a less reliable guide to community structure given the range of life-forms that potentially are encompassed by these pollen or spore types. For example, NLRs of *Tricolpites reticulatus* include both the giant rainforest herb *Gunniera chilensis* whose leaves measure up to 2 m in diameter and small herb species such as *Gunniera magellanica*. It is also possible that some of the less common pollen and spore species were derived from distant, mainly temperate, vegetation types by wind (see Clark et al., 1998). Examples are *Ischyosporites areapunctatis* (*Dicksoniae*), *Polypodiisporites* (*Polypodiaceae*), *Microalatidites* (*Phyllocladus*), *Equisetisporites cf clariciristatus* (*Ephedra americana*), *Chenopodipollis chenopodiaceoides* (*Chenopodiaceae–Amaranthaceae*), *Nothofagidites americanus*...
7. Palaeoenvironment

West Point Harbour is encircled by steep hills, and mild conditions inferred from the composition and structure of the Forest Bed vegetation may not apply to more exposed areas on West Point Island or elsewhere in the Falkland archipelago. Nevertheless, the small size of the island makes it probable that the inferred mean annual and seasonal distribution of rainfall is broadly representative of the archipelago as a whole.

7.1. Precipitation

The high relative abundance of Podosporites microsaccatus (Section 3.3) makes it likely that the composition and structure of the Forest Bed vegetation has been influenced by water-logging and the low mineral nutrient status and pH of soils developed on Palaeozoic sandstones surrounding West Point Harbour. Analogous effects are observed for Araucaria araucana and Nothofagus (Nothofagus) communities in southern South America, for example N. betuloides—N. pumilo rainforest scrub in gullies and other sheltered areas in Magellanic moorland developed on saturated soils or nutrient-poor Andean diorite (Veblen et al., 1983, 1996).

The prominence of shrub taxa with mesophytic NLRs, and the dominant role of Nothofagus and Podocarpaceae in the Forest Bed, make it almost certain that local to regional climates were uniformly wet (aseasonal perhumid) with mean annual receipts exceeding 1200 mm (Read, 1999). Nevertheless, it is noted that at least one extant species within the subgenus Nothofagus now extends into xeric habitats (N. antarctica) whilst two gymnosperms species (Araucaria araucana, Prumnopitys andina) are also tolerant of dry summers in central southern South America (Veblen et al., 1995). Wet summers and/or saturated soils may explain the paucity of Araucaria if the parent plant(s) had similar ecological tolerances to living A. araucana (see Veblen et al., 1995: 131).

7.2. Temperature

Palaeotemperatures are more difficult to estimate because of the wide latitudinal range and microtherm to mesotherm tolerance of NLRs in southern South America (see Fig. 3 in Heusser, 1966), for example Austromyrtus-type, Drimys, Embothrium, Ericales, Gevuina, Gunnera, Lomatia, Maytenus, Nothofagus (Nothofagus) spp. and Tepualia. An added complication is the conflicting conditions implied by the few taxa whose NLRs have relatively narrow ecological amplitudes (see Marticorena and Rodriguez, 1995).

At present the most reliable indications that temperatures were at the lower end of the mesotherm range rather than within the microtherm or upper mesotherm–megatherm range are the present-day latitudinal limits of the gymnosperms inferred to have formed the canopy and any overstorey strata, and presence of Hedyosmum and Ovidia in the understory. (1) Dacrydium cupressinum, now one of the tallest emergent gymnosperm in New Zealand lowland rainforest, is most common south of ~38°S (see Ogden and Stewart, 1995) whilst Dacrydium spp. in New Guinea and New Caledonia also are primarily found in relatively cool montane rainforest communities (see Jaffre, 1995, Enright, 1995). Similarly Araucaria in South America includes one species (A. araucana) which is common in montane–subalpine forests between 37°20′–40°20′S (see Fig. 6.4 in Veblen et al., 1995). Mean summer temperatures at the southern limits of the two other conifer families represented by fossil pollen in the Forest Bed straddle the mesotherm/microtherm boundary (Buxtehude, 1981): These are ~13 °C for Austrocedrus chilensis (Cupressaceae) and Podocarpus salignus (Podocarpaceae), which reach latitude 43°S, and ~11 °C for Saxegothea (Podocarpaceae) which reaches latitude 46°S. One species of Cupressaceae (Pilgerodendron uviferum), which can reach a height similar to Araucaria araucana, is found as far south as 54°S in Tierra del Fuego (see Fig. 154 in Marticorena and Rodriguez, 1995). (2) Hedyosmum is a small understory tree restricted to rainforests in the American tropics and Southeast Asia. Although its pollen is widely dispersed by wind (see Salgado-Labouriau, 1979; Behling et al., 1997), Late Quaternary records are confined to sites in northern South America (Heusser, 1974; Salgado-Labouriau, 1979; Grabant, 1980; Haberle, 1997), where it is listed as a cool-adapted taxon, for example by Colinvaux et al. (1996) and Haberle and Maslin (1999). Aescina, which produces pollen identical to those of Hedyosmum (see Moar, 1993), is restricted to cool and wet but frost-free localities in New Zealand and New Guinea.

8. Discussion and conclusions

The combined data (including negative palynostratigraphic evidence and oxygen isotopic data for climatic change in the southwest Atlantic during and since the

(Nothofagus alpina, N. obliqua), Pseudowinterapollis couperi (Drimys/Tasmannia) and Sparganiaceaepolle-nites sphericus (Sparganiaceae).
Late Palaeogene indicate that the maximum age limits of the Forest Bed are Oligocene to Early Pliocene, respectively. The Middle? Miocene to Early Pliocene ‘best fit’ age limit assume that the parent plants of Araucariacites, Clavatipollenites cf glarius and Thymelaepollis had similar preferences to their mesotherm NLRs. However, we recognise that the ‘younger’ maximum age limit of Middle? Miocene also may prove to be too old for two reasons. (a) The age limit presumes that the Thymelaeaceae had dispersed from northern Africa into the southwest Atlantic region during or before the Middle Miocene but did not reached northern South America until the Late Miocene; (b) This dispersal pattern is ecologically improbable since the first known appearance of Thymelaepollis in southeast Australia and New Zealand at comparable (middle–high) latitudes to the Falkland Islands is Late Pliocene. We also accept that similar objections can be raised regarding a Late Miocene age limit presumes that the Thymelaeaceae had dispersed from northern Africa into the southwest Atlantic region at about the same time as in northern South America (Mexico), which in turn is possible only if the Thymelaeaceae had evolved into cool- and warm-adapted ecotypes by this time.

None of these assumptions can be independently tested using palynostratigraphic data currently available for the subtantarctic Atlantic region and we note that many of the uncertainties regarding the age of the Forest Bed also apply to the Argentine palynosequences. One example is the less diverse but otherwise close analogue of the Forest Bed palynoflora preserved on Isla Grande, in Tierra del Fuego. This assemblage, which does include Cytatheacidites annulatus, has been assigned a “probable” Late Eocene age by Olivero et al. (1998), based on the “absence of typical Oligocene–Neogene palynomorphs” (presumably Chenopodipollis, Cyperaceaeopollis, and Tubulifloridites). The assumption, that time distributions of species will be the same under highly oceanic climates in southernmost South America as in rain-shadowed regions of central Argentina some 10° latitude to the north, is suggested to be ecologically improbable, and we propose that the Isla Grande microflora could be a broad-scale (latest Palaeogene–early Late Neogene) correlate of the Forest Bed.

Refining the age limits of the Forest Bed will be helped by determining the First or Last Occurrence of species that are now very rare or extinct at subtantarctic latitudes in South America. Examples highlighted in this study include Cytatheacidites annulatus, Araucariacites australis, P. microsaccatus, Lygistepollenites florinii, Clavatipollenites cf glarius, Polycolporopollenites esobalteus (Polygalaceae) and Thymelaepollis as well as a range of tricolpate, tricolporate and orate taxa whose botanical affinities are unknown (Appendix 1). One potentially useful site for establishing a continuous spore–pollen record for the Late Cenozoic is Deep Sea Drilling Project (DSDP) Site 329 drilled on the Maurice Ewing Bank at the eastern margin of the Falkland Plateau (see Shipboard Party et al., 1976; Ciesielski et al., 1982). Here, Oligocene deposits are unconformably overlain by a ~350 m thick sequence of Middle–Late Miocene calcareous and siliceous ooze sediments, which in turn are disconformably capped by Pliocene and Quaternary facies. Other sampled sections which may preserve Late Tertiary palynosequences occur in the four major sedimentary basins surrounding the Falkland Islands – the North and South Falkland Basins, the Falkland Plateau Basin and Malvinas Basin – and the Argentine Basin between the Falklands and Argentina, where about 60 commercial holes have been drilled so far (see www.falklands.gov.fk/dmr/planification-geology.htm).

No equivalent forest or shrub analogue of the Forest Bed community exists in the Southern Hemisphere since the palaeoflora includes taxa that are wholly extinct, for example Podosporites microsaccatus, taxa whose NLRs are endemic to the southwest Pacific, for example Dacrydium and Lagarostrobus, and taxa whose NLRs are endemic to South America, such as Ephedra americana, Nothofagus (Nothofagus) spp. and Embthrium coccineum. An additional complication is the apparent association of woody taxa that are mostly restricted to mesotherm–megatherm environments, for example Araucaria Hedyosmum and Ovidia, with herbaceous species that are typically associated with microtherm conditions, for example Huperzia fuegianum and Nothofagus (Nothofagus) spp. Depending whether the greater weight is given to the NLR(s) of the gymnosperm or to the NLRs of the Nothofagus component, some modern rainforest communities whose generic composition and physiognomy are not-dissimilar to that inferred for the Forest Bed community are: (1) species-poor Dacrydium cupressinum–Podo-carpus–Nothofagus fusca broadleaf-gymnosperm forests found in the northwest of the South Island, New Zealand (see Ogden and Stewart, 1995; Ogden et al., 1996). One major difference between this wet forest type and the Forest Bed community is the prominence of cryptogams, including tree ferns such as Cyathea, in New Zealand microtherm rainforests. (2) Species-poor Nothofagus pumilo subtantarctic deciduous rainforest in southern South America. However stands of this wet
forest type, which occurs between 900 and 1100 m elevation in the Southern Chilean Lake District (40–42°S), include *Drimys*, Ericales (*Gaultheria*, *Pernettya*), *Gunnera*, *Maytenus*, *Myzodendron* and *Ovidia*, but lack Podocarpaceae (see Heusser, 1974). (3) Species-poor *Nothofagus dombei*–*Podocarpus nubigenus* rainforest in Patagonia (see Heusser, 1974). Stands of this wet forest type occur at middle (600–900 m) elevations in the Southern Chilean Lake District but also include a range of broadleaf, liane and cryptogam taxa that are not recorded in the Forest Bed microfloras, for example *Chusquea* (bamboo), *Griselinia*, *Laurelia*, *Pseudopanax*, and *Weinmannia* (see Heusser, 1974).

As with analogous rainforest/rainforest scrub communities established on other subantarctic islands during the Late Tertiary, for example the Kerguelen Islands (Cookson, 1947), South Tasman Rise (Macphail, 2001) and Heard Island (Truswell et al., 2005), and during the Late Eocene to Early Neogene on the Antarctic continent (Raine, 1998; Macphail and Truswell, 2004a,b; Truswell and Macphail, 2004), we conclude that the community whose remains comprise the Forest Bed was a unique variant in the continuum of *Nothofagus*–Podocarpaceae rainforests developed on middle–high latitude landmasses across the Southern Hemisphere during the Late Tertiary. Recently, wind has been demonstrated to be an effective agent in the long distance dispersal of flora around the Southern Hemisphere (see Munoz et al., 2004). This observation, combined with the broad latitudinal and longitudinal distribution of many temperate rainforest genera prior to the Quaternary, suggests the current challenge for island biogeographers is to explain why some of these taxa survived on one or more landmasses but become extinct on other, apparently environmentally comparable, landmasses elsewhere in the southwest Atlantic and/or southwest Pacific regions.

**Acknowledgements**

This study is built upon the efforts of many, not least Thoré Halle for bringing the Forest Bed to the attention of the global scientific community in 1911. Closer to the present-day, the project has depended on Mr. Roddy Napier, the current owner of West Point Island, for permission to recollect the Forest Bed, Ms. Emma Edwards, formerly of the Dept. of Oil, Falkland Islands Government, for collecting one set of samples in 1996, the Directors of the Swedish Natural History Museum for providing access to Halle’s samples, Mr. Konrad Weiss *Laola* Pty. Ltd., Perth, for his skillful perseverance in processing obdurate clay material, and Drs. Don Aldiss and Phil’ Stone (British Geological Survey) for their sustained interest in the project. Dr. Viviana Barreda (Museo Argentino de Ciencias Naturales, Buenos Aires) kindly provided copies of her ground-breaking research into the Late Tertiary palynofloras of Argentina. Professor Geoff Hope, Australian National University, funded the preparation of the text figures. All are most cordially thanked.

**Appendix A. Photomicrographs of selected fossil pollen spores and related plant microfossils**

All photomicrographs taken at ×788 magnification except for Figs. 32, 98 and 105, taken at ×1250 (Plates I–V).

Nearest living relative (family or genus) given in parentheses.
Plate I. Cryptogams.

1. Spineose spore of an unidentified bryophyte (found only in Unit C1)
2. Baculatisporites cf. comaunensis (Hymenophyllum). Sample 3959-01
3. Baculatisporites disconformis (Hymenophyllum). Unit C1
4. Monolites alveolatus (Belvisia). Sample 3959-01
5. Polypodispores radiatus (Davalliaceae/Polypodiaceae). Unit C1
6. Polypodispores anangahuensis (Davalliaceae/Polypodiaceae). Sample 3959-01
7. Peromonolites alveolatus (Blechnaceae). Unit C1
8–9. Foveotriletes palaequetrus (Huperzia fuegianum). Sample 3959-02
10. Cyathidites cf. palaeospora (Cyathea). Unit C1
11. Cyathidites australis (Cyathea). Unit C1
12–13. Ischyosporites cf. areapunctatis (Dicksonia). Sample 3959-02
14–15. Triletes tuberculiformis var. (Dicksonia). Sample 3959-02
16. Verrucosisporites sp. (unknown affinity). Sample 3959-02

Plate II. Gymnosperms (see page 621).

17. Araucariacites australis (Araucaria). Sample 3959-02
18. Inaperturopollenites sp. (cf Saxegothea). Sample 3959-01
19. Cupressacites sp. (Cupressaceae–Taxodiaceae). Unit C1
20. Microalatidites palaeogenicus (Phyllocladus). Sample 3959-02
21. Phyllocadidites mawsonii (Lagarostrobos). Sample 3959-01
22. Lygistepollenites florinii (Dacrydium). Sample 3959-01
23–24. Podocarpidites sp. (Podocarpus–Prumnopitys). Sample 3959-01
27. Podocarpidites sp. (Podocarpus–Prumnopitys). Sample 3959-02
28. Trichotomosulcites subgranulosus (cf Microcachrys). Sample 3959-01
32. Equisetosporites claricristatus (Ephedra). Sample 3959-02. ×1250

Plate III. Angiosperms (porate grains) (see page 622).

33. Graminidites sp. (Poaceae). Unit C1
34. Sparganiaceepollenites sphericus (Sparganium). Unit C1
35. Lateropora glabra (Freycinetia). Unit C1
36. Granodiporites nebulosus (Embothrium). Sample 3959-02
37–38. Compositopollenites cf. tarragoensis (Myzodendron). Sample 3959-01
39–40. Canthiumidites cf bellus (cf Randia). Unit C1
41–42. Triporopollenites sp. (unknown dicotyledon). Sample 3959-02
43. Proteacidites minutus ms. (Proteaceae). Sample 3959-02
44–46. Proteacidites sp. 1 of Barreda (Proteaceae). Sample 3959-02
49. Proteacidites cf rinthius. Sample 3959-02
50. Triporopollenites sp. (Proteaceae?). Unit C1
51. Thymelaepollis sp. (Ovidia). Sample 3959-02
52–61. Angiosperms (sulcate grains)
52. Echinate monsulcate sp. (Astelia?). Sample 3959-02
53. Baculate monosulcate sp. (unknown monocotyledon). Sample 3959-02
54. Arecites sp. (Arecaceae?). Sample 3959-02
55. Arecites sp. (Arecaceae?). Sample 3959-02
56–58. Clavatipollenites cf glarius (Hedyosmum). Sample 3959-01
59. Liliacidites cf lanceolatus (Liliaceae). Sample 3959-02
60–61. Luminidites cf phormoides (Pasithea). Sample 3959-02
Plate I (caption on page 619).
Plate II (caption on page 619).
Plate III (caption on page 619).
Plate IV. Angiosperms (colpate grains).

62. *Tricolpites* sp. (unknown affinity). Unit C1
63. *Tricolpites* sp. (unknown affinity). Sample 3959-01
64. *Tricolpites cf. incisus* (unknown affinity). Unit C1
65. *Tricolpites reticulatus* (*Gunnera*). Unit C1
66. *Tricolpites* sp. (unknown affinity). Sample 3959-01
67. *Tricolpites* sp. (unknown affinity). Unit C1
68. *Tricolpites* sp. (*Verbenaceae*?). Sample 3959-02
69. *Tricolpites* sp. (unknown affinity). Sample 3959-01

70–71. Gen. et sp. nov. (unknown affinity). Sample Unit C1
72. *Nothofagidites americanus* [*Nothofagus* (*Lophozonia*)]. Sample 3959-02
73. *Nothofagidites americanus* [*Nothofagus* (*Lophozonia*)]. Unit C1
74. *Nothofagidites cf acromegacanthus* (*Nothofagus*). Sample 3959-01
75. *Nothofagidites cf acromegacanthus* (*Nothofagus*). Unit C1
76. *Nothofagidites cf acromegacanthus* (*Nothofagus*). Sample 3959-01
77. *Nothofagidites saraensis* [*Nothofagus* (*Nothofagus*)]. Unit C1
78. *Nothofagidites saraensis* [*Nothofagus* (*Nothofagus*)]. Sample 3959-02
79. *Nothofagidites cf flemingii* [*Nothofagus* (*Nothofagus*)]. Sample 3959-01
80–81. *Nothofagidites brachyspinulosus* [*Nothofagus* (*Fuscospora*)]. Unit C1
82. *cf Lymingtonia* (*Portulaccaceae*). Unit C1
83–84. Angiosperms (colporoidate grain)
85–87. Angiosperms (tricolporate grains)
88. *Rhoipites* sp. (unknown affinity). Sample 3959-02
89–90. *Rhoipites* A (*Maytenus*). Unit C1
91. *Schizocolpus* sp. (unknown affinity). Sample 3959-02
92. *Ailanthipites cf paenestriatus* (*Anacardiaceae*). Unit C1
93. *Striatocolporites cf gamerroi* (*Anacardiaceae*). Sample 3959-02
94. *Rhoipites* sp. (unknown affinity). Unit C1
95–96. *Rhoipites* sp. (unknown affinity). Unit C1
97–104. Angiosperms (parasyncolporate grains)
97. *Gothanipollis cf bassensis* (*Loranthaceae*). Sample 3959-02
98. *Gothanipollis cf bassensis* (*Loranthaceae*). Sample 3959-02. ×1250
99. *Myrtaceidites parvus* (*Metrosideros*). Sample 3959-01
100. *Myrtaceidites eucalyptoides* (*Eucalyptus gummifera*-type). Sample 3959-02
102. *Myrtaceidites verrucosus* (*Myrteola*-type). Sample 3959-02
103–104. *Myrtaceidites verrucosus* (*Myrteola*-type). Unit C1
105–108. Angiosperms (pericolporate grains)
106. *Quintiniapollis sp.*. (*Quintinia*?). Unit C1
107–108. *Polyporopollenites esobalteus* (*Polygala*). Sample 3959-01
109–113. Angiosperms (tetradss)
109. *Eriicipites* sp. (*Ericaceae*). Sample 3959-01
110. *Eriicipites* sp. (*Ericaceae*). Sample 3959-02
111–112. *Pseudowinterapollis couperi* (*Drimys*). Unit C1
113. Stripped *Pseudowinterapollis couperi*. Unit C1
114–116. Unassigned taxa
114. *Coptospora* sp.? (*Bryophyta*?). Unit C1
115. *Retitriletes* sp.? (*Lycopodiaceae*?). Sample 3959-012
116. Echinate inaperturate? sp. (cf *Philesiaceae*). Sample 3959-01

Plate V. Angiosperms (tricolporate grains) (see page 625).

88. *Rhoipites* sp. (unknown affinity). Sample 3959-02
89–90. *Rhoipites* A (*Maytenus*). Unit C1
91. *Schizocolpus* sp. (unknown affinity). Sample 3959-02
92. *Ailanthipites cf paenestriatus* (*Anacardiaceae*). Unit C1
93. *Striatocolporites cf gamerroi* (*Anacardiaceae*). Sample 3959-02
94. *Rhoipites* sp. (unknown affinity). Unit C1
95–96. *Rhoipites* sp. (unknown affinity). Unit C1
97–104. Angiosperms (parasyncolporate grains)
97. *Gothanipollis cf bassensis* (*Loranthaceae*). Sample 3959-02
98. *Gothanipollis cf bassensis* (*Loranthaceae*). Sample 3959-02. ×1250
99. *Myrtaceidites parvus* (*Metrosideros*). Sample 3959-01
100. *Myrtaceidites eucalyptoides* (*Eucalyptus gummifera*-type). Sample 3959-02
102. *Myrtaceidites verrucosus* (*Myrteola*-type). Sample 3959-02
103–104. *Myrtaceidites verrucosus* (*Myrteola*-type). Unit C1
105–108. Angiosperms (pericolporate grains)
106. *Quintiniapollis sp.*. (*Quintinia*?). Unit C1
107–108. *Polyporopollenites esobalteus* (*Polygala*). Sample 3959-01
109–113. Angiosperms (tetradss)
109. *Eriicipites* sp. (*Ericaceae*). Sample 3959-01
110. *Eriicipites* sp. (*Ericaceae*). Sample 3959-02
111–112. *Pseudowinterapollis couperi* (*Drimys*). Unit C1
113. Stripped *Pseudowinterapollis couperi*. Unit C1
114–116. Unassigned taxa
114. *Coptospora* sp.? (*Bryophyta*?). Unit C1
115. *Retitriletes* sp.? (*Lycopodiaceae*?). Sample 3959-012
116. Echinate inaperturate? sp. (cf *Philesiaceae*). Sample 3959-01
Plate IV (caption on page 623).
Plate V (caption on page 623).
References


Barreda, V.D., 1997e. Palinoestratigrafia de la Formacion San Julian en al area de Playa La Mina (Provincia de Santa Cruz), Oligoceno de la Cuenca Austral. Ameghiniana 34, 283–294.


Habberle, S.G., Maslin, M.A., 1999. Late Quaternary vegetation and climate change in the Amazon Basin based on a 50,000 year pollen record from the Amazon Fan, ODP Site 932. Quaternary Research 51, 27–38.


