



Latest Cretaceous–earliest Paleogene vegetation and climate change at the high southern latitudes: palynological evidence from Seymour Island, Antarctic Peninsula



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ABSTRACT

Fluctuations in Late Cretaceous climate were already influencing biotic change prior to the environmental upheaval at the Cretaceous–Paleogene (K–Pg) boundary, but their general nature, magnitude and timing remain controversial. A high-resolution dataset on terrestrially-derived palynomorphs is presented from the high southern palaeolatitudes that unlocks details of small-scale climate variability throughout this period of significant global change. Specifically, this is a quantitative spore and pollen analysis of an expanded uppermost Cretaceous to lowermost Paleogene (Maastrichtian–earliest Danian) shallow marine sedimentary succession from Seymour Island, off the northeastern tip of the Antarctic Peninsula, then (as now) located at ~65°S. Using nearest living relatives the first detailed vegetation, habitat and climate reconstruction is presented for the emergent volcanic arc at this time. On the coastal lowlands, a cool to warm temperate rainforest is envisaged growing in a riverine landscape, with both wet (river margin, pond) and relatively dry (interfluvium, canopy gap) habitats. Diverse podocarps and southern beech trees grew alongside angiosperm herbs and shrubs in mean annual temperatures of ~10–15 °C. Higher altitude araucarian forests gave way to open ericaceous heathland, beyond the tree line, in subalpine to alpine conditions with mean annual temperatures of a cold ~5–8 °C. There is no exact modern botanical equivalent, but the closest modern flora is that of the Andes of southern Chile and Argentina. Maastrichtian climate is shown to have fluctuated from cool, humid conditions, through a rapid warming ~2 million years prior to the K–Pg transition, followed by cooling during the earliest Danian, a trend supported by previous work on this interval.

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1. Introduction

Major climatic fluctuations during the latest Cretaceous were already influencing global biotic change immediately prior to the Cretaceous–Paleogene (K–Pg) boundary at 66 million years ago (Ma) (Keller, 2001; O’Dea et al., 2011). However, details of small-scale climate variability, particularly from the climatically-sensitive high palaeolatitudes, have been lacking due to a paucity of suitable Upper Cretaceous sedimentary successions. This paper presents a detailed quantitative analysis of terrestrially-derived palynomorphs (spores and pollen) from a continuous and superbly-exposed succession on Seymour Island, off the northeast tip of the Antarctic Peninsula (Fig. 1). Seymour Island represents the most expanded and best exposed uppermost Cretaceous to lowermost Paleogene succession from the high southern latitudes.

Furthermore, it has remained at approximately its present latitude (65°S) since the Cretaceous (Hathway, 2000).

It is well established that climates were cool and dynamic during the Late Cretaceous and there is indirect evidence for ephemeral ice sheets on Antarctica (Barrera, 1994; Barrera and Savin, 1999; Li et al., 2000; Miller et al., 2005; Davies et al., 2009; Thibault et al., 2010; Bowman et al., 2013a). Global climate change at this time has been associated with episodes of outgassing from major volcanic events (Courtillot et al., 1986; Hansen et al., 1996; Chenet et al., 2009), orbital cyclicity (Miller et al., 2003; Stüben et al., 2003; Gallagher et al., 2008) and tectonism (Frank and Arthur, 1999), before culminating at 66 Ma in the cataclysmic upheaval caused by a large bolide impact at Chicxulub, on the Yucatán Peninsula, Mexico (Schulte et al., 2010).

In the mid to high southern latitudes, records of latest Cretaceous terrestrial fossils are sparse; these include wood (Francis and Poole, 2002; Poole et al., 2005), leaves (Kennedy et al., 2002) and spores and pollen (Askin, 1989, 1990a, 1990b; Dettmann, 1994; Askin and Spicer,

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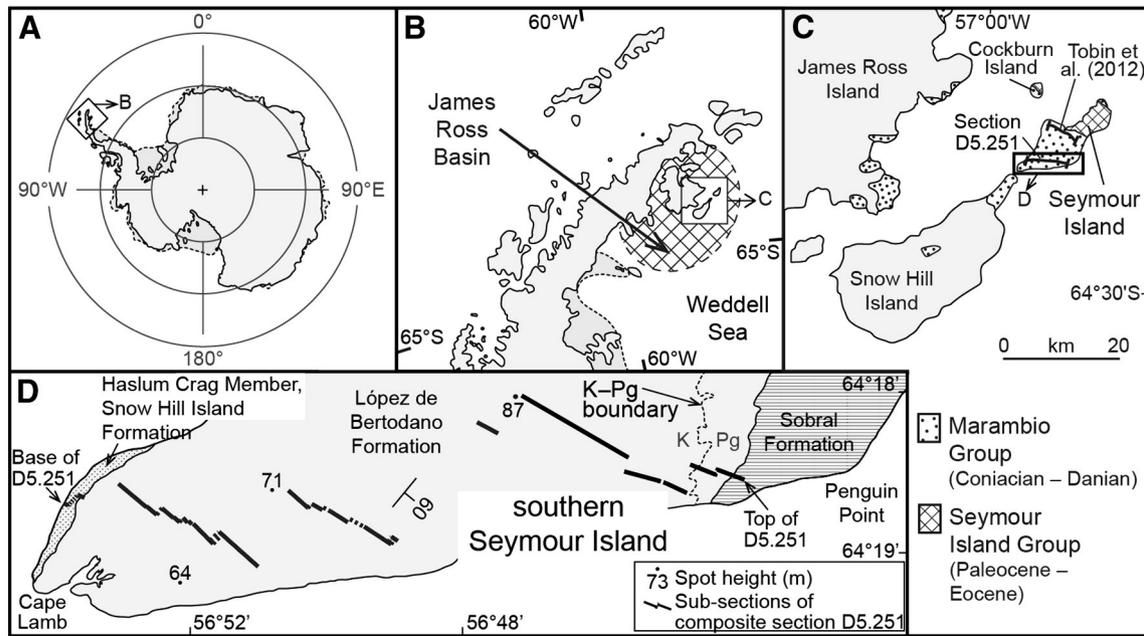


Fig. 1. Location maps showing the measured section D5.251 across southern Seymour Island, Antarctic Peninsula. A–C, The maps show modern geography with outcrop of the Marambio and Seymour Island groups on islands in the James Ross Basin. Refer to Bowman et al. (2012) for palaeogeographic maps of this region during the Maastrichtian. D, Measured section D5.251, across the southern part of Seymour Island is a composite of sub-sections (correlated along strike in the field) and includes the oldest strata on the island north of Cape Lamb. The sedimentary sequence on southern Seymour Island dips at a shallow angle to the southeast. K, Cretaceous; Pg, Paleogene. The location of the K–Pg boundary is shown within the uppermost López de Bertodano Formation.

1995). Quantitative biostratigraphical analyses of terrestrially-derived palynomorphs have concentrated on the K–Pg transition, rather than the immediately underlying successions (Askin and Jacobson, 1996; Vajda et al., 2001; Vajda and Raine, 2003; Vajda and MacLoughlin, 2004; Barreda et al., 2012; Vajda and Bercovici, 2012). The role of vegetation in latest Cretaceous climates has also been explored in modelling studies (Upchurch et al., 1998, 1999; Hunter et al., 2008), however the effectiveness of global climate models in deriving Cretaceous conditions in the high latitudes is somewhat contentious (Craggs et al., 2012).

This study aims at providing the first high-resolution vegetation and palaeoclimatic reconstruction for the latest Cretaceous and earliest Danian of the high southern palaeolatitudes. Well-preserved spore, pollen and other terrestrial palynomorphs (e.g. algal spores and fungal remains) are documented from the López de Bertodano Formation of Seymour Island, and assessments made on their likely analogues by comparison with modern palynomorphs. The observed fossil ranges and quantitative abundance data are then used to reconstruct vegetation types within various habitats on the eastern flank of the Antarctic Peninsula. Palaeoclimatic trends inferred from changes in these plant associations through time are consistent with cool to warm temperate climates and humid to super-humid conditions on Seymour Island and the surrounding areas during the Maastrichtian, across the K–Pg boundary and into the earliest Danian.

2. Geological setting

The shallow marine López de Bertodano Formation of the Marambio Group crops out on southern Seymour Island in the James Ross Basin, Antarctic Peninsula, unconformably intercalated between the Snow Hill Island Formation beneath and the Sobral Formation above (Fig. 1; Rinaldi et al., 1978, revised by Crame et al., 2004; Olivero et al., 2008). The first comprehensive studies of the geological setting, palaeontology and age of the López de Bertodano Formation were carried out by authors in Feldmann and Woodburne (1988), and are summarised by Bowman et al. (2012).

During the Maastrichtian to earliest Danian, southern Seymour Island was submerged in an inner to mid shelf setting within a back-

arc basin (the Larsen Basin). The Antarctic Peninsula may have been joined to southern South America by a narrow land bridge to the distant north (Hathway, 2000; Leppe et al., 2012), and the Larsen Basin opened into the Weddell Sea to the east. There, huge volumes of fine-grained sediment accumulated, having been eroded from the Antarctic Peninsula volcanic arc immediately to the west (Hathway, 2000; Crame et al., 2004; Olivero et al., 2008). Partial inversion of the northern Larsen Basin during the Late Cretaceous led to shallow tilting to the southeast, and the basinward progradation of shallow marine facies (Hathway, 2000). Sediment provenance studies suggest significant volcanic input from the emergent arc, but the intensity of volcanic activity apparently decreased during the deposition of the Marambio Group (Pirrie, 1991). No evidence for any discrete ash deposits within the López de Bertodano Formation was found during sedimentary logging. It seems therefore unlikely that significant tectonic upheavals or volcanic events occurred in this region during the Maastrichtian and earliest Danian that could have affected the near-offshore palynomorph record. The palaeogeography of the Antarctic Peninsula region at this time suggests that the eastern flank of the emergent arc, perhaps tens of kilometres to the west of what is now Seymour Island, was the only potential source area for the terrestrially-derived palynomorphs recovered in this study.

The López de Bertodano Formation comprises ~1000 m of unconsolidated silty-clays and clayey-silts and contains no sedimentological evidence of significant hiatuses (Fig. 2). Dinoflagellate cyst biostratigraphy, macropalaeontology, magnetostratigraphy, strontium isotope stratigraphy and a minor iridium anomaly at the K–Pg boundary confidently date this major unit as Maastrichtian to Danian (Fig. 2; Elliot et al., 1994; McArthur et al., 1998; Bowman et al., 2012; Tobin et al., 2012). The López de Bertodano Formation of southern Seymour Island is hence one of the most expanded successions of this age in the world.

3. Materials and methods

A composite section (D5.251) 1100 m thick was measured perpendicular to strike across southern Seymour Island from the coast immediately north of Cape Lamb, to the southeast coast near Penguin Point

counts, but for some that were consistently fragmented (e.g. *Azolla* spp., *Grapnelispora* sp. 1, and fungal spores and hyphae) only presence/absence data were recorded.

Reconstructing past vegetation from dispersed spore and pollen records is essential for understanding past climates. The identification of a modern spore or pollen grain that is comparable with a fossil morphotype, assuming little evolutionary change in morphology or habitat preference during the intervening period, forms the basis of the “nearest living relative” technique (e.g. Wolfe, 1995), which is used herein. Nearest living relatives (NLRs) of the spore and pollen taxa recorded here are based primarily on Askin (1990a), MacPhail et al. (1994), Gallagher et al. (2008), Truswell and MacPhail (2009) and Raine et al. (2011), and references therein (Table 1). Preferred temperature and precipitation ranges of the NLRs based on their modern geographic distributions have been derived from the Atlas of Living Australia (ALA, <http://www.ala.org.au/>) and specifically for *Araucaria araucana* (monkey puzzle tree) from Sanguinetti and Kitzberger (2008) (Table 2). The climatic data downloaded from the ALA, from the WorldClim database (<http://www.worldclim.org>, after Hijmans et al., 2005) is averaged for each taxon and includes worldwide (though primarily Australasian and Papua New Guinean) and spatially valid records. Climate parameters are used only for NLRs at species and/or genus level for taxa naturally distributed in Australasia to keep the climate reconstruction Southern Hemisphere-focused and as realistic as possible. Preferred climate types are then defined for each NLR based on mean annual temperature (MAT) ranges within the Holdridge Life-Zone Classification System (Emanuel et al., 1985) (Table 2).

The validity of these interpretations, based on the NLR technique, depends on the recognition of inherent uncertainties particularly relevant to deep time records. For example, difficulties may arise because a particular fossil spore or pollen type may be affiliated with a modern family, genus or species group with non-uniform ecological tolerances (Martin, 1997). It is also possible that a single fossil taxon may have a conservative morphology and actually represent more than one modern taxon (e.g. Hill, 1990). Similarly, potential extinctions of ecotypes can render interpretations on pre-Quaternary palynofloras somewhat tenuous (Jordan, 1997). Although not directly resolvable from the fossil palynomorph record, there may also have been a variety of extraneous factors influencing vegetation composition on the Antarctic Peninsula during the Maastrichtian and Danian. For example, the dynamics of modern *Nothofagus* forests in New Zealand have been found to be not only a result of climate-induced change, but may also reflect internal stand processes (Stewart and Rose, 1990). Furthermore, the palynomorph record is of terrestrial material washed or blown into marine sediments and as such, taphonomic processes prior to fossilisation must also be considered. These may include the potential for reworked material, the size and location of the source area, ocean circulation, physical barriers, geochemical conditions and the resistance of sporomorphs (spores and pollen) to degradation through long transport paths. For example, in temperate latitudes wind-pollinated plants producing bisaccate pollen (e.g. *Pinus*) are over-represented in marine pollen spectra in part due to their resistance to oxidation (e.g. Rossignol-Strick and Paterne, 1999). In addition, interpretations based on abundance patterns of quantitative terrestrial palynomorph counts must consider factors including the relative pollen production of the nearest living relative plants. In the Seymour Island sequence, this may influence the representation of *Nothofagidites* pollen, which due to high levels of production is known to be transported over long distances, particularly when pollen grains reach higher levels of the atmosphere, also true for bisaccate pollen (e.g. Close et al., 1978; Kappen and Straka, 1988; Gassmann and Pérez, 2006). *Nothofagus fusca*-type pollen has a particularly high power of pollen dispersal (McQueen and MacPhail, 1983). Askin and Jacobson (1996) discussed further specific factors affecting the marine and terrestrial palynomorph record in the López de Bertodano Formation on Seymour Island. The interpretations herein take all of these factors into account, and provide as realistic a

reconstruction of Maastrichtian to earliest Danian vegetation and palaeoclimate as possible from the material available.

To explore the palynological dataset further, a ‘Humidity Index’ has been generated based on a weighted averaging function using spore and pollen taxa with affinities to known hydrological groups (Table 1). Plants are grouped in order of moisture level preference from Thermo-/Xerophytic (prefer warm and dry, or well-drained conditions) to Hygrophytic (preferring very humid conditions). The resulting Humidity Index is a one-dimensional summary of wetness based on the same principle as the hydroclimatic index used in Holocene plant macrofossil research (e.g. Daley et al., 2012). Thermo-/Xerophytic, Mesophytic, Hygro-mesophytic and Hygrophytic taxa in a sample were given arbitrary scores of 1, 2, 3 and 4 respectively. A weighted average (WA) score was then calculated from the relative percentages of classified taxa within a sample.

The WA score was calculated as follows:

$$(x_1 + w_1 + x_2 + w_2 \dots x_n + w_n) / (w_1 + w_2 \dots w_n) = \sum_{i=1 \dots n} (x_i w_i) / \sum_{i=1 \dots n} w_i$$

where

<i>x</i>	taxon percentage abundance
<i>w</i>	taxon weight
<i>i</i>	a given stratigraphic height in the section.

Climatic and ecological interpretations based on NLR analysis of the palynological dataset are necessarily cautious within the constraints already discussed. However, the high stratigraphic resolution of the samples, excellent preservation of the fossils and quantitative laboratory analyses also allow an exploration of the results using multivariate numerical methods, although this is not the focus of this study. To assess potential ecological gradients, and provide support to our qualitative ecological interpretations based on NLR techniques, Non-metric Multi-dimensional Scaling (NMDS) using the Bray–Curtis dissimilarity distance analysis was employed (Supplementary Dataset 2).

4. Results

Samples throughout the López de Bertodano Formation yielded well-preserved terrestrial plant-derived and freshwater palynomorphs (Figs. 3 and 4). Marine palynomorphs from the same sequence have been described in Askin (1988), Thorn et al. (2009) and Bowman et al. (2012, 2013a,b). Forty-four spore and pollen species from thirty-two genera were recorded throughout the section, in addition to further specimens identified to generic level, rare freshwater algal spores and fungal remains (Appendix 1, Supplementary Dataset). A single testate amoeba specimen was tentatively identified from 567 m (Fig. 4-29), although this may also represent a fungal spore. Most taxa are present throughout hundreds of metres of the section with a slight increase in the frequency of appearance of new taxa in the latest Maastrichtian (Fig. 5A). There appears to be no evidence from this section of significant extirpation of land plant taxa across the K–Pg transition in this region (Fig. 5B, Supplementary Dataset). Rare adherent clusters of same-taxon pollen grains were recorded (Fig. 3-35, -41) implying that transport to the depositional site (and subsequent laboratory processing) involved little energy and confirms close proximity to the source vegetation. Fragments of cuticle, conifer tracheid and abundant inertinite are also present. Spore and pollen recovery was variable but largely good with between 1142 and 15,281 palynomorphs, including significantly reworked grains, per gramme of sediment recorded (Fig. 6).

It is considered that only minor proportions of the terrestrial palynoflora are obviously reworked (average 1.4%, Supplementary Dataset), either from the Permian–Triassic or from earlier in the Cretaceous (Fig. 4-21 to -27). Askin and Elliot (1982) also noted

Permian–Triassic and Early Cretaceous reworking within Seymour Island sediment.

The relative abundances of the most common palynomorphs are presented in Fig. 6, plotted against stratigraphical depth and grouped by NLR. To facilitate discussion, this terrestrial palynomorph record is divided into six phases delimited by notable changes in spore and pollen abundance (Figs. 5 and 6). The palynoflora is dominated throughout by the bisaccate pollen grains *Phyllocladidites mawsonii* and *Podocarpidites* spp., comprising up to 34% and 40% of the palynoflora respectively (Fig. 6). *Nothofagidites* spp. are also abundant throughout, reaching their highest levels in the lowermost and uppermost parts of the section.

Phyllocladidites mawsonii varies in abundance up-section; it exhibits the most striking pattern of all the pollen taxa. This species increases in abundance gradually from the base to 746 m, through phases 1 and 2, from 3% to 17% of the terrestrial palynoflora (Fig. 6). Above 746 m, it rises rapidly to a peak of 33% at 816 m during phase 3 (Fig. 6). An abrupt drop in abundance to a low of 4% at 833 m, perhaps exaggerated by the lower spore and pollen recovery at this horizon, is followed by a further gradual increase during phase 4 (Fig. 6). *Phyllocladidites mawsonii* then suddenly decreases in abundance over the K–Pg transition, followed by a rapid rise and fall during phase 5. Here it attains its highest level in the section at 1024 m (34%), before decreasing to 2% at the top of the section (phase 6, Fig. 6).

Podocarpidites spp. comprises a larger component of the palynoflora than *Phyllocladidites mawsonii*. Although variable, it exhibits a subtle increase in abundance throughout phase 1 and stays at high levels for

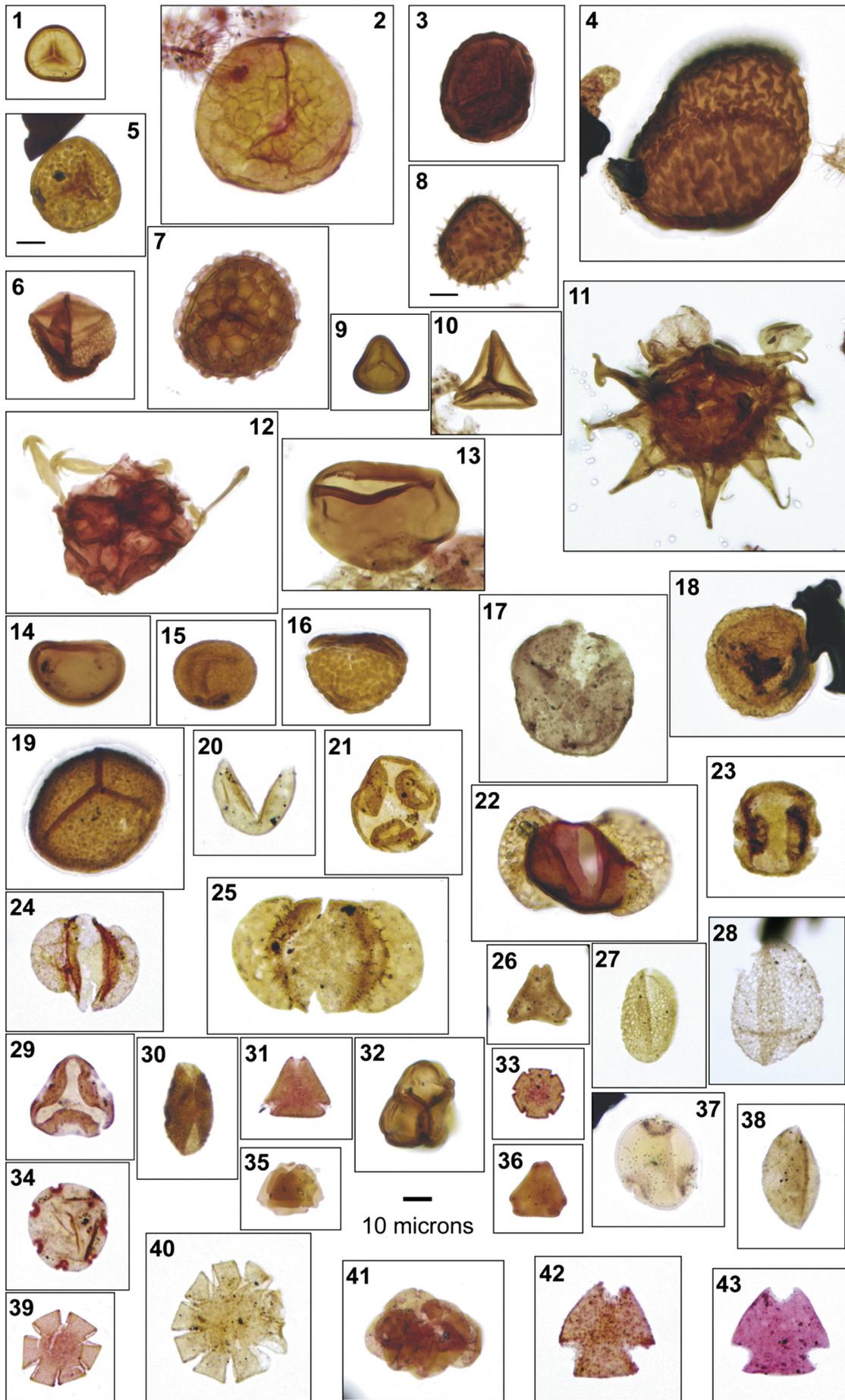
most of phase 2 (Fig. 6). During phase 3, the abundance of *Podocarpidites* spp. varies in inverse proportions to that of *Phyllocladidites mawsonii* with a peak up to 38% at the base, dropping to 16% by the top, followed by a rapid increase to 36% at the start of phase 4 (Fig. 6). *Podocarpidites* spp. are relatively common throughout phase 4, decreasing briefly to 9% across the K–Pg boundary (Fig. 6). *Podocarpidites* spp. increase rapidly again thereafter to a peak of 31% at 1014 m, immediately prior to that of the post K–Pg *Phyllocladidites mawsonii* peak at 1024 m. *Podocarpidites* spp. then remain relatively abundant to the top of the section.

Nothofagidites spp. represent the third major component of the terrestrial palynoflora, and appear to subtly vary in inverse proportions to the abundance of *Phyllocladidites mawsonii* (Fig. 6). Although variable in abundance in the lowermost part of the section, *Nothofagidites* spp. decrease in abundance throughout phase 2 from 32% to 11% and increases to approximately 20% during phase 3 (Fig. 6). During phase 3, slight changes in abundance indicate a decrease throughout down to 12%, followed by a rapid increase to a minor peak of 22% within phase 4 (Fig. 6). Thereafter a variable but gradual decrease in abundance occurs throughout phase 4, followed by a rapid increase in abundance (despite relatively low recovery) across the K–Pg boundary, peaking at 29% in the lowermost Danian sample at 1008 m.

Additional taxa that comprise a significant proportion of the terrestrial palynoflora include *Laevigatosporites ovatus*, *Peninsulapollis gillii* and *Stereisporites antiquasporites* (Fig. 6). *Laevigatosporites ovatus* occurs consistently throughout, and exhibits no particular abundance trend. The broad peak in abundance of this species across the K–Pg transition

Fig. 3. Transmitted light images of terrestrial palynomorph specimens from section D5.251, Seymour Island, Antarctic Peninsula. Slide number and England Finder coordinates are quoted for each specimen. For taxon authors see the Taxonomic Notes.

1. *Stereisporites antiquasporites*, D5.1192.1A, F49-2.
2. *Triporoletes reticulatus*, D5.1121.1A, L53-2.
3. *Camarozonosporites ambigens*, D5.1289.1A, Q43-0.
4. *Camarozonosporites ohioensis*, D5.1160.1A, L62-4.
5. *Stereisporites regium*, D5.621.1A, R54-4.
6. *Lycopodiadites bullerensis*, D5.1132.1A, U48-3. Equatorial compression.
7. *Retitriletes austroclavatidites*, D5.1279.1A, O58-4.
8. *Ceratosporites equalis*, D5.1268.1A, U57-3.
9. *Cyathidites minor*, D5.1248.1A, D43-0.
10. *Gleicheniidites senonicus*, D5.1268.1A, T53-0.
11. *Grapnelispora* sp. 1, D5.1001.1A, U51-4.
12. *Azolla* sp., D5.1215.1A, B47-0. Note three-barbed glochidia.
13. *Laevigatosporites major*, D5.1147.1A, K55-0.
14. *Laevigatosporites ovatus*, D5.1215.1A, N42-0.
15. *Peromonolites bowenii*, D5.1230.1A, K63-2.
16. *Polypodiisporites speciosus*, D5.1210.1A, W40-2.
17. *Araucariacites australis*, D5.1343.1A, G40-0.
18. *Dacrydiomites praecupressinoides*, D5.1343.1A, M41-2.
19. *Osmundacidites wellmanii*, D5.1248.1A, W63-0.
20. *Taxodiaceapollenites hiatus*, D5.1174.1A, N51-1.
21. *Microcachryidites antarcticus*, D5.1106.1A, C47-0.
22. *Podocarpidites* sp., D5.1155.1A, U46-0.
23. *Phyllocladidites mawsonii*, D5.1106.1A, Q66-1.
24. *Podocarpidites* sp., D5.1205.1A, B47-2.
25. *Podocarpidites* sp., D5.866.1A, F64-1.
26. *Gambierina rudata*, D5.1179.1A, V65-3.
27. *Liliacidites* sp. cf. *L. kaitangataensis*, D5.1106.1A, K63-3.
28. *Liliacidites* sp. cf. *L. variegatus*, D5.1155.1A, F56-2.
29. *Trichotomosulcites subgranulatus*, D5.1205.1A, F46-0.
30. *Clavamonocolpites polygonalis*, D5.1165.1A, R47-0.
31. *Cranwellia striata*, D5.1268.1A, J45-1.
32. *Ericipites scabratus*, D5.1192.1A, J68-0.
33. *Nothofagidites senectus*, D5.1132.1A, N61-4.
34. *Nothofagidites flemingii*, D5.1215.1A, N40-0.
35. *Propylipollis subscabratus*, D5.1179.1A, H48-0. Adherent cluster.
36. *Propylipollis subscabratus*, D5.1121.1A, L58-2.
37. *Myricipites* sp. cf. *M. cavilloratus*, D5.1363.1A, R49-2.
38. *Liliacidites* sp. 1 of Askin (1994), D5.1237.1A, E62-4.
39. *Nothofagidites dorotensis*, D5.1132.1A, N60-1.
40. *Nothofagidites asperus*, D5.1363.1A, F41-2.
41. *Nothofagidites* sp., D5.827.1A, N50-1. Adherent cluster.
42. *Peninsulapollis askinia*, D5.1258.1A, W57-1.
43. *Peninsulapollis gillii*, D5.1151.1A, H41-2.



is unremarkable, and well within the range of variability observed throughout. The abundance pattern of *P. gillii* is similarly unremarkable throughout most of the section, except for a peak of 11% (its highest level in the section) post K–Pg at 1014 m, coincident with a post K–Pg peak in *Podocarpidites* spp. (Fig. 6). *S. antiquasporites* occurs in low numbers ($\leq 3\%$) throughout phases 1 and 2, after which it begins to increase in abundance, reaching a peak of 16% at 1054 m. There is a slight drop in the abundance of *S. antiquasporites* at the K–Pg boundary, but this appears to be within the variation for that part of the section.

Other spore and pollen taxa that occur in minor proportions and consistently throughout are *Cyathidites minor*, *Osmundacidites wellmanii*, *Proteacidites* spp. and *Retitriletes austroclavatidites* (Fig. 6, Supplementary Dataset). These forms all show subtle variability in abundance throughout, however are slightly more abundant during phase 4. *Araucariacites australis* exhibits an interesting abundance pattern. It occurs rarely ($\leq 3\%$) below the K–Pg boundary, then peaks abruptly up to 6% in the lowestmost Danian sample at 1008 m, coincident with an isolated peak in *Nothofagidites* spp. Thereafter it returns to low levels during the remainder of phase 5, increases again within phase 6, and peaks at its highest level in the section at 15% in the uppermost sample at 1084 m (Fig. 6).

5. Discussion

5.1. Terrestrial palynomorph biostratigraphy

All, except *Tricolpites lilliei*, of the spore and pollen species from the López de Bertodano Formation have long stratigraphical ranges that include the Late Cretaceous and Danian of the Southern Hemisphere (e.g. Harris, 1965, 1972; Stover and Partridge, 1973; Raine et al., 2011), thereby confirming the age of this succession. However, due to these long stratigraphical ranges of the cosmopolitan forms, and the high proportion of endemic angiosperms (Askin, 1989) within this section, further refinement of the terrestrial palynobiostratigraphy within this

interval is limited. The shorter stratigraphical ranges of the marine palynomorphs from the same section have, however, been useful for establishing a regional dinoflagellate cyst biozonation scheme (Bowman et al., 2012).

The only biostratigraphically significant terrestrial palynomorph species from the López de Bertodano Formation is *Tricolpites lilliei*, which is known to have its range top at the K–Pg boundary in Australia and New Zealand (Vajda et al., 2001; Ocampo et al., 2006; Ferrow et al., 2011). This species is restricted to preliminary biozone PM2 in New Zealand (upper Lower Haumurian to Upper Haumurian = middle Campanian to Maastrichtian) (Raine, 1984; Crampton et al., 2004; Hollis et al., 2010). In Australia, it is restricted to the *Tricolporites* (al. *Tricolpites*) *lilliei* and *Tricolpites longus* Zones of the *Proteacidites* Superzone, correlated with the lower to middle part of New Zealand zone PM2 (Helby et al., 1987). The ages of the bases of these two zones are considered to be 77 and 73 Ma respectively using Schiøler et al. (2002). In the López de Bertodano Formation on southern Seymour Island, *Tricolpites lilliei* is present close to the base, ranging up to 984 m (Taxon 48 in Fig. 5, Supplementary Dataset), ~24 m below the K–Pg boundary (Bowman et al., 2012).

The base of zone PM2 in New Zealand is marked by the first occurrence of *Tricolpites lilliei*, which occurs in older strata on Vega Island in the James Ross Basin (Dettmann and Thomson, 1987), suggesting that (based solely on the terrestrial palynomorph record) the lowermost strata exposed on southern Seymour Island can be no older than middle Campanian. The dinoflagellate cyst record implies that the base of the section is within the Maastrichtian (Bowman et al., 2012). The top of zone PM2 is marked by the first occurrence of *Tricolpites secarius* in New Zealand, which overlaps slightly with the range of *T. lilliei*, and is considered to correlate approximately with the K–Pg boundary (Raine, 1984). *Tricolpites secarius* was not recorded from the López de Bertodano Formation on Seymour Island. The New Zealand biozone PM3 extends into the Waipawan (Early Ypresian) (Raine, 1984), beyond the top of section D5.251.

Fig. 4. Transmitted light images of terrestrial palynomorph specimens from section D5.251, Seymour Island, Antarctic Peninsula. Slide number and England Finder coordinates are quoted for each specimen. For taxon authors see the Taxonomic Notes. *, reworked.

1. *Polycolpites* sp. cf. *P. langstonii*, D5.1121.1A, O44-0. Equatorial compression.
2. *Proteacidites adenanthoides*, D5.1184.1A, U47-1.
3. *Proteacidites angulatus*, D5.1198.1A, F48-0. Note that the central hole is a tear, not a pore.
4. *Proteacidites* sp. cf. *P. crassus*, D5.1198.1A, L44-3.
5. *Proteacidites parvus*, D5.1320.1A, G68-0.
6. *Proteacidites* sp. 1, D5.1106.1A, L50-3.
7. *Stellidiopollis annulatus*, D5.1279.1A, O33-2 [slide at 90°].
8. *Proteacidites* sp. cf. *P. scabroratus*, D5.1205.1A, V63-2.
9. *Proteacidites pseudomoides*, D5.1198.1A, F39-0.
10. *Proteacidites subpalisadus*, D5.1121.1A, J41-1.
11. *Tetracolpites* sp. 1 (aberrant tricolpate pollen), D5.1242.1A, W63-4.
12. ?*Nothofagidites* sp. 1 (tetra-aperturate pollen), D5.1220.1A, N49-0.
13. *Tricolpites confessus*, D5.1215.1A, B40-1.
14. *Tricolpites lilliei*, D5.807.1A, F51-2.
15. *Tricolpites* sp. cf. *T. phillipsii*, D5.1387.1A, R64-4.
16. *Tricolpites reticulatus*, D5.886.1A, J42-0.
17. *Tricolporites* sp., D5.1184.1A, O57-2.
18. *Tripopollenites* sp., D5.1174.1A, H39-4.
19. ?Zygnemataceae spore A, D5.1142.1A, U46-0.
20. ?Zygnemataceae spore B, D5.1205.1A, N45-0.
21. **Perotriletes majus*, D5.1106.1A, M62-3.
22. **Verrucosporites* sp. 1, D5.587.1A, F53-4.
23. **Cyathidites* sp. cf. *C. australis*, D5.672.1A, F58-1.
24. **Matonisporites* sp. cf. *M. cooksoniae*, D5.1106.1A, U60-1.
25. **Plicatipollenites gondwanensis*, D5.990.1A, O65-3.
26. *?*Potonieisporites* sp., D5.886.1A, P64-1.
27. **Protohaploxypinus ?amplius*, D5.807.1A, N72-2.
28. *Botryococcus braunii*, D5.1155.1A, N46-2.
29. ?Testate amoeba indeterminate (or possibly fungal spore), D5.388.1A, E32-0 [slide at 90°].
30. *Pluricellaesporites* sp., fungal spore, D5.1187.1A, U60-4.
31. *Pediastrum* sp., D5.401.1A, Q43-0. Phase contrast.
32. *Tetraporina* sp. 1, D5.641.1A, N56-2. Phase contrast.

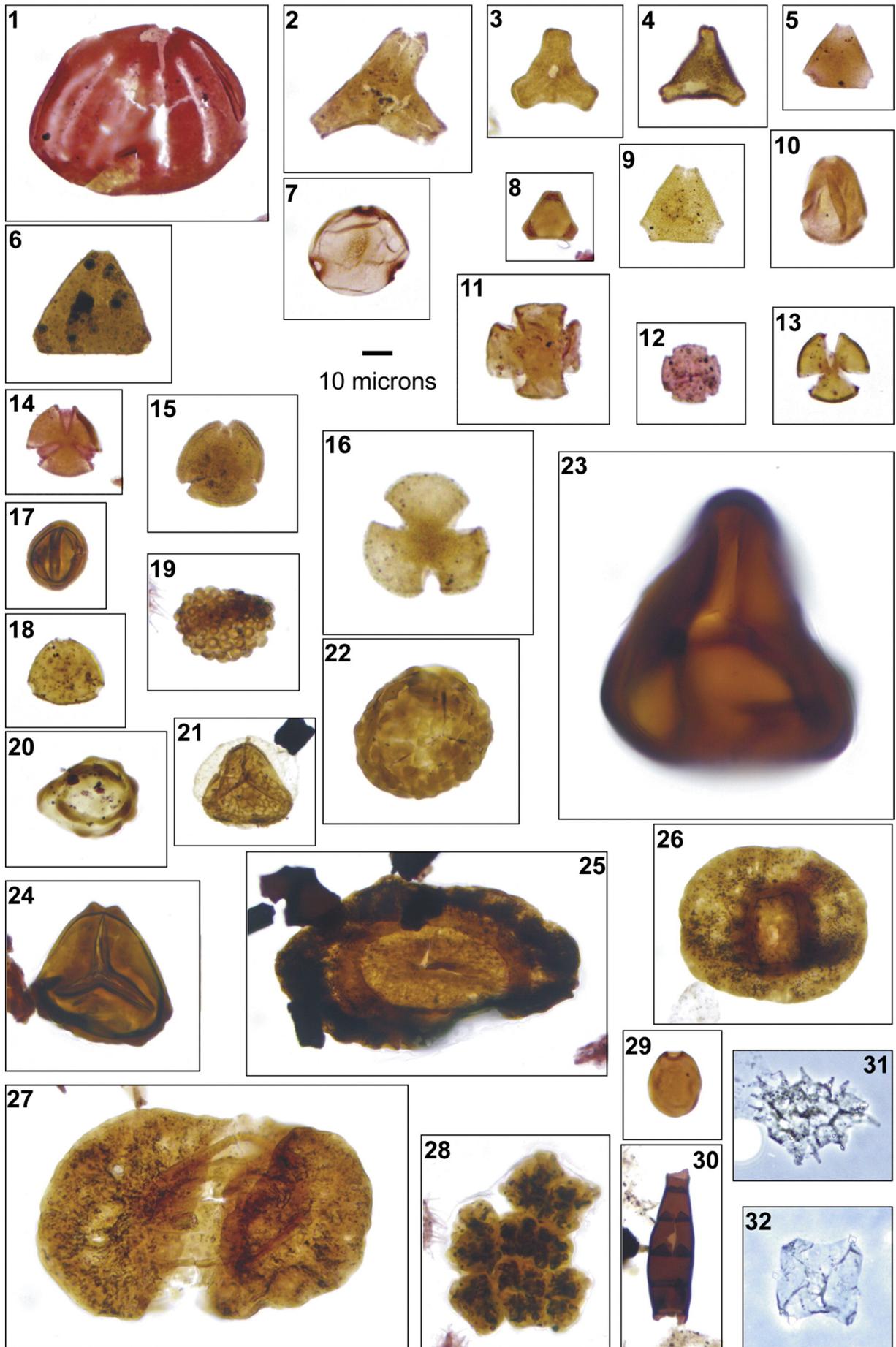


Table 1
Botanical affinities, and their ecological types, of terrestrial palynomorph taxa recorded from the Maastrichtian to lowermost Danian López de Bertodano Formation, Seymour Island. Botanical affinities and nearest living relatives after Askin (1990a), MacPhail et al. (1994), Gallagher et al. (2008), Truswell and MacPhail (2009) and Raine et al. (2011), and references therein. Additional references are noted with the relevant taxon. Ecological type after Wang et al. (2005): H, Hygrophytic; H-M, Hygro-Mesophytic; M, Mesophytic; T/X, Thermo-/Xerophytic; U, Unknown.

Fossil taxon	Botanical affinity	Ecological type
Bryophyta		
<i>Stereisporites antiquasporites</i>	Sphagnaceae (<i>Sphagnum</i>)	H
<i>Stereisporites regium</i>	Sphagnaceae	H
<i>Triporetetes reticulatus</i>	Hepaticae (cf. <i>Riccia beyrichiana</i> [Purple crystalwort])	H
Lycopodiophyta		
<i>Camarozonosporites ambigens</i>	Lycopodiaceae/Selaginellaceae; Volkheimer et al., 2007 (source of natural affinity interpretation uncited)	H
<i>Camarozonosporites ohioensis</i>	Lycopodiaceae	H
<i>Ceratosporites equalis</i>	Selaginellaceae (<i>Selaginella</i>)	H
<i>Lycopodiacidites bullerensis</i> / <i>Retitriletes austroclavatidites</i>	Lycopodiaceae (<i>Lycopodium</i>)	H
Pteridophyta		
<i>Azolla</i> spp.	Salvinales, Salviniaceae (<i>Azolla</i>); Collinson, 2002; Nagalingum et al., 2008	H
<i>Cyathidites minor</i>	Filicopsida, Cyatheaceae	H-M
<i>Echinosporis</i> sp. 1 of Askin 1990	Filicopsida, Marattiaceae/Polypodiaceae	H
<i>Gleicheniidites senonicus</i>	Filicopsida, Gleicheniaceae (<i>Gleichenia circinata</i> * group/ <i>Dicranopteris</i>)	H
<i>Grappnelispora</i> sp. 1	Salvinales, ?Salviniaceae; Askin, 1990b	H
<i>Laevigatosporites major</i>	Filicopsida, ?Blechnaceae	H
<i>Laevigatosporites ovatus</i>	Filicopsida, ?Blechnaceae	H
<i>Osmundacidites wellmanii</i>	Filicopsida, Osmundaceae	H
<i>Peromonolites bowenii</i>	Filicopsida	H
<i>Polypodiisporites speciosus</i>	Polypodiaceae, <i>Microsorium</i> ; Harris, 1965	H
Gymnospermae		
<i>Araucariacites australis</i>	Araucariaceae (<i>Araucaria</i> [?Araucaria <i>arucana</i> , Monkey puzzle]/ <i>Agathis</i> [Kauri]); Heusser, 1971	T/X
<i>Dacrydioidites praecupressinoides</i>	Podocarpaceae, <i>Dacrydium</i> group B/ <i>Dacrydium cupressinum</i> [Rimu]	M
<i>Microcachryidites antarcticus</i> / <i>Trichotomosulcites subgranulatus</i>	Podocarpaceae (<i>Microcachrys</i> [e.g. Creeping pine]/ <i>Microstrobus</i>)	M
<i>Phyllocladidites mawsonii</i>	Podocarpaceae (<i>Lagarostrobos franklinii</i> [Huon pine]); Playford and Dettmann, 1978	H
<i>Podocarpidites</i> spp.	Podocarpaceae (<i>Podocarpus</i> / <i>Dacrydium</i>)	M
<i>Taxodiaceapollenites hiatus</i>	?Cupressaceae/?Taxodiaceae	M
<i>Trichotomosulcites subgranulatus</i>	Podocarpaceae, <i>Phyllocladus</i> /extinct <i>Microcachrys</i>	M
Angiospermae		
<i>Clavamonocolpites polygonalis</i>	Dicotyledonae, ?Chloranthaceae; Askin, 1994	M
<i>Cranwellia striata</i>	Dicotyledonae, Loranthaceae (? <i>Elytranthe</i> [Mistletoe]); Srivastava, 1966	M
<i>Ericipites scabratus</i>	Dicotyledonae, Ericaceae; Harris, 1965; Dettmann, 1994; Jordan and Hill, 1996; Kron et al., 2002	T/X
<i>Gambierina rudata</i>	Dicotyledonae, extinct clade	U
<i>Liliacidites</i> sp. cf. <i>L. kaitangataensis</i>	Monocotyledonae, Liliaceae (? <i>Lilium</i> [Lily])	T/X
<i>Liliacidites</i> sp. cf. <i>L. variegatus</i>	Monocotyledonae, Liliaceae/Amariyllidaceae, Bromeliaceae, Iridaceae, etc., Askin, 1994; Dicotyledonae, Monimiaceae (cf. <i>Laurelia novaezelandiae</i> [Pukatea]), Raine et al., 2011 (refer also to Sampson, 1996)	T/X
<i>Liliacidites</i> sp. 1 of Askin, 1994	Monocotyledonae, ?Liliaceae; Askin, 1994	T/X
<i>Liliacidites</i> spp.	Monocotyledonae, ?Liliaceae	T/X
<i>Myricipites</i> sp. cf. <i>M. cavilloratus</i>	Dicotyledonae, ?Juglandaceae [Walnut family]; Drugg, 1967	M
<i>Nothofagidites asperus</i>	Dicotyledonae, Nothofagaceae [Southern beech], <i>Nothofagus</i> , subgenus <i>Lophozonia</i>	M
<i>Nothofagidites dorotensis</i>	Dicotyledonae, Nothofagaceae, <i>Nothofagus</i> , subgenus ? <i>Brassospora</i>	M
<i>Nothofagidites flemingii</i>	Dicotyledonae, Nothofagaceae, <i>Nothofagus</i> , subgenus <i>Fuscospora</i> / <i>Nothofagus</i>	M
<i>Nothofagidites senectus</i>	Dicotyledonae, Nothofagaceae, <i>Nothofagus</i> ancestral, subgenus ? <i>Fuscospora</i> / <i>Nothofagus</i>	M
? <i>Nothofagidites</i> sp. 1 (tetra-aperturate pollen)	?Dicotyledonae, unknown natural affinity	U
<i>Nothofagidites</i> spp.	Dicotyledonae, Nothofagaceae (<i>Nothofagus</i>)	M
<i>Peninsulapollis askiniae</i>	Dicotyledonae, Proteaceae	T/X
<i>Peninsulapollis gillii</i>	Dicotyledonae, Proteaceae (? <i>Beauprea</i> -type); Dettmann and Jarzen, 1988; extinct clade?	T/X
<i>Polycolpites</i> sp. cf. <i>P. langstonii</i>	Dicotyledonae, Pedaliaceae [Sesame family] (?cf. <i>Josephinia</i>); Askin, 1989; Cranwell, 1969	T/X
<i>Propylipollis subscabratus</i>	Dicotyledonae, Proteaceae	T/X
<i>Proteacidites adenanthoides</i> / <i>Proteacidites</i> sp. cf. <i>P. crassus</i>	Dicotyledonae, Proteaceae (<i>Adenanthos</i>)	T/X
<i>Proteacidites angulatus</i>	Dicotyledonae, Proteaceae	T/X
<i>Proteacidites parvus</i>	Dicotyledonae, Proteaceae (<i>Bellenden montana</i> [Mountain rocket] type)	T/X
<i>Proteacidites pseudomoides</i>	Dicotyledonae, Proteaceae (<i>Carnarvon</i> [Red oak] type/cf. <i>Lomatia</i>)	T/X
<i>Proteacidites</i> sp. cf. <i>P. scabratus</i>	Dicotyledonae, Proteaceae	T/X
<i>Proteacidites subpalisadus</i>	Dicotyledonae, Proteaceae	T/X
<i>Proteacidites</i> sp. 1	Dicotyledonae, ?Proteaceae	T/X
<i>Proteacidites</i> spp.	Dicotyledonae, Proteaceae	T/X
<i>Stellidiopollis amulatus</i>	?Dicotyledonae, unknown natural affinity	U
<i>Tetracolpites</i> sp. 1 (aberrant tricolpate pollen)	?Dicotyledonae, unknown natural affinity	U
<i>Tricolpites confusus</i>	Dicotyledonae	U
<i>Tricolpites lilliei</i>	Dicotyledonae, Ranunculaceae (cf. <i>Clematis</i>); Specht et al., 1992	M
<i>Tricolpites</i> sp. cf. <i>T. phillipsii</i>	Dicotyledonae	U
<i>Tricolpites reticulatus</i>	Dicotyledonae, Gunneraceae, <i>Gunnera macrophylla</i> ; Jarzen, 1980; Wanntorp et al., 2004	H
<i>Tricolpites</i> spp.	Dicotyledonae	U
<i>Tricolporites</i> spp.	Dicotyledonae	U
<i>Triporopollenites</i> spp.	Dicotyledonae, ?Proteaceae	T/X
Freshwater green algae		
<i>Botryococcus braunii</i>	Chlorophyta, Botryococcaceae; e.g. Aaronson et al., 1983	H
<i>Pediastrum</i> spp.	Chlorophyta, Hydrodictyaceae; Eviitt, 1963	H
<i>Tetraporina</i> sp. 1	?Chlorophyta, Lindgren, 1980; Zygnemataceae, <i>Mougeotia</i> , Jarzen, 1979; Grenfell, 1995	H
?Zygnemataceae spore A	Charophyta, ?Zygnemataceae	H
?Zygnemataceae spore B	Charophyta, ?Zygnemataceae	H

Table 2

Temperature data, and derived climate type, of nearest living relatives (NLRs) of the terrestrial palynomorph taxa, Maastrichtian to lowermost Danian López de Bertodano Formation, Seymour Island. Cross-reference to Table 1 and see Section 5.3 for discussion. Averaged temperature parameters for each taxon (except *Araucaria araucana*), WorldClim data (after Hijmans et al., 2005) from the Atlas of Living Australia (ALA, <http://www.ala.org.au/>), mostly records from Australasia and Papua New Guinea: MAT, mean annual temperature; CQMT, coldest quarter mean temperature; WQMT, warmest quarter mean temperature. *Araucaria araucana* climatic data after Sanguinetti and Kitzberger (2008): MJanT, mean January temperature; MJulT, mean July temperature. Climate type after Emanuel et al. (1985): STr, Subtropical MAT 17–24 °C; WT, warm temperate MAT 12–17 °C; CT, cool temperate MAT 6–12 °C; Sn, Snow (Boreal) MAT 3–6 °C. Table is sorted by climate type. All of the fossil taxa associated with the NLRs in this table occur rarely throughout section D5.251, except for *Podocarpidites* spp. (*Podocarpus*), *Phyllocladidites mawsonii* (*Lagarostrobos franklinii*) and *Nothofagidites* spp. (*Nothofagus*).

Nearest living relative	MAT (°C)	CQMT (°C)	WQMT (°C)	Climate type
<i>Carnarvonia</i>	21.2	17.5	24.1	STr
<i>Adenanthos</i>	16.2	11.7	21.0	WT
<i>Podocarpus</i>	15.2	10.7	19.0	WT
<i>Gleichenia</i>	13.4	8.9	17.5	WT
<i>Lomatia</i>	12.5	7.5	17.1	WT
<i>Araucaria araucana</i>	–	MJulT 7–8	MJanT 17–19	CT
<i>Lagarostrobos franklinii</i>	10.5	7.0	14.0	CT
<i>Nothofagus</i>	10.1	6.4	13.8	CT
<i>Bellenden montana</i>	6.0	2.1	10.0	CT
<i>Microcachrys</i>	5.5/8.0 ^a	1.6	9.5	Sn

^a Second MAT figure from Biffin et al. (2011).

5.2. Vegetational composition and 'nearest living relatives'

The overall composition of the terrestrial palynomorph assemblage is relatively stable throughout the entire López de Bertodano Formation, with the only significant perturbation in the proportions of the major groups being evident near the K–Pg boundary (summary plot, Fig. 6; Supplementary Dataset 2). Abundant *Podocarpidites* spp., *Nothofagidites* spp. and *Phyllocladidites mawsonii*, despite some likely over-representation in the palynoflora (Section 3) suggest a lowland to mid altitude vegetation of mixed podocarp-southern beech temperate rainforest, with abundant available moisture, growing on the eastern flank of the Antarctic Peninsula arc throughout the Maastrichtian and earliest Danian (Table 1, Fig. 7). The presence of *Araucariacites australis*, *Ericipites scabratus*, *Microcachrydites antarcticus* and *Proteacidites parvus* implies a component of the palynoflora that also reflects a higher altitude, more open, heath-like vegetation at the margin of montane araucarian forests (Table 1, Fig. 8).

5.2.1. Lowland to mid altitude mixed temperate forests

The arborescent canopy was comprised primarily of diverse podocarps (e.g. *Podocarpus*, *Dacrydium*) and southern beech with rare ?Cupressaceae/?Taxodiaceae trees and possibly mistletoe (*Elytranthe*). *Elytranthe* is locally common in New Zealand today, especially on *Nothofagus* (McQueen and MacPhail, 1983). It was a relatively open canopy, at least locally, to allow the growth of a diverse understory.

Mixed beech forests in New Zealand today are distributed between podocarp-broadleaf lowland forests and pure beech forests of montane and subalpine zones (Ogden et al., 1996). In Australia, *Podocarpus* grow where MATs are ~15 °C in mainly southern temperate climates (Table 2). The ecology and climate of *Nothofagus*, the southern beech, is described in detail by Veblen et al. (1996), and grows in cool temperate environments (Table 2). The co-occurrence of southern beech and podocarps occur today in New Zealand and Tasmania where there is high moisture availability, although natural differences in shade tolerance means that these taxa may have been in forest stands dominated by one or the other on the Antarctic Peninsula lowlands (Poole, 1987; Veblen et al., 1996; Gallagher et al., 2008).

The nearest living relative of *Phyllocladidites mawsonii* is *Lagarostrobos franklinii* (the Tasmanian Huon Pine), and is of particular

interest due to the distinctive abundance pattern of this pollen type throughout the López de Bertodano Formation (Fig. 6). *Lagarostrobos franklinii* trees are evergreen, large (up to 30 m tall), long-lived (>220 years), slow-growing and are closely related to *Dacrydium* (Quinn, 1982; Mabberley, 1997). *Lagarostrobos franklinii* seeds are buoyant, and they remain viable after floating for one to two months (Shapcott, 1991). This helps their dispersal in freshwater, and their entrainment into the fossil record (Hill, 1990; Molloy, 1995). Their terrestrial dispersal rate is otherwise slow, commonly via bird transport and gravity (Molloy, 1995; Gibson et al., 2006). However, they are capable of vegetative regrowth, dominating canopy gaps even before fast-growing species (Gibson and Brown, 2006). Their modern habitat is closely linked with flowing water, and today they are indigenous to riverine margins in wet, southwest Tasmania, occasionally reaching up wet hillsides to 750 m altitude (Molloy, 1995; Farjon, 2010). Rainfall in this region is >1200 mm/year (Colhoun et al., 1988). Rarely they reach subalpine habitats near the tree line up to 1040 m, tolerating low temperatures down to –12.6 °C (Anker et al., 2001; Bannister and Neuner, 2001), but generally live in cool temperate conditions with a MAT of 10.5 °C (Table 2). Pollen attributed to *Lagarostrobos franklinii* is common (often dominant) in the Paleogene/Neogene sediments of Australia, but may have been produced by a much larger group of species in the past, with most becoming extinct (Hill, 1990). With this caveat, *L. franklinii* has retained ecological stability over a long period of geological time, always requiring high humidity levels (Martin, 1997), which makes it a useful modern analogue for palaeoenvironmental reconstructions.

Non-vascular plants (bryophytes, e.g. *Sphagnum* moss and the liverwort *Riccia*) and lycophytes (*Lycopodium*, *Selaginella*) grew on the damp rainforest floor associated with an understory of shade-tolerant ferns (Cyathaceae/Dicksoniaceae/Schizaeaceae and other *Cyathidites* analogues) (Tripathi and Srivastava, 2012). The ferns may have included climbers, epiphytes and tree ferns (Aspleniaceae/Blechnaceae/Osmundaceae/Polypodiaceae; *Laevigatosporites*, *Osmundacidites* and *Polypodiisporites* analogues).

Warmth-loving ferns (*Dicranopteris/Gleichenia*, Schizaeaceae) and angiosperms (?Chloranthaceae, ?Juglandaceae, *Gunnera macrophylla* and proteas) may have occupied north-facing, sheltered niches, probably associated with gaps in the canopy (Tables 1 and 2). Modern *Gleichenia* prefers lowland to subalpine heaths and boggy ground in warm temperate climates (Allan, 1961; Mabberley, 1997; Table 2). *Gleicheniidites senonicus*, affiliated with *Gleichenia*, occurs rarely throughout the section on Seymour Island, but implies a generally humid climate with sheltered habitat niches throughout the Maastrichtian (Supplementary Dataset). *Clavamonocolpites polygonalis* (possibly affiliated with the Chloranthaceae) occurs in the latest Maastrichtian, interpreted by Bowman et al. (2013a) as a warm climatic phase. Modern Chloranthaceae are distributed in tropical and warm temperate latitudes (Askin, 1994; Mabberley, 1997). Further, *Tricolpites reticulatus* is a rare, but distinctive, pollen grain that also occurs during warm phases of the Maastrichtian (Bowman et al., 2013a), and has been compared with the pollen of *G. macrophylla*, a modern *Gunnera* that occupies tropical and south temperate super-humid environments (Jarzen, 1980; Wanntorp et al., 2004).

In slightly more elevated, open and well-drained habitats, perhaps on interfluvies, monocotyledonous plants (probable Liliaceae) and dicotyledonous herbs (*Josephinia* – sesame family), proteaceous shrubs or small trees (*Adenanthos*) may have been growing. *Proteacidites adenanthoides* and *Proteacidites* sp. cf. *Proteacidites crassus* may have a natural affinity with the protea *Adenanthos*, native to warm temperate climates of south and west Australia (Tables 1 and 2; Mabberley, 1997). Although rare in the section, these distinctive proteaceous pollen grains also provide an indication of warm, sheltered habitats in the Antarctic Peninsula forest at this time. In addition, *Proteacidites pseudomoides* has two possible living relatives within the proteas: *Carnarvonia* and *Lomatia*. *Carnarvonia* is a modern genus of a single

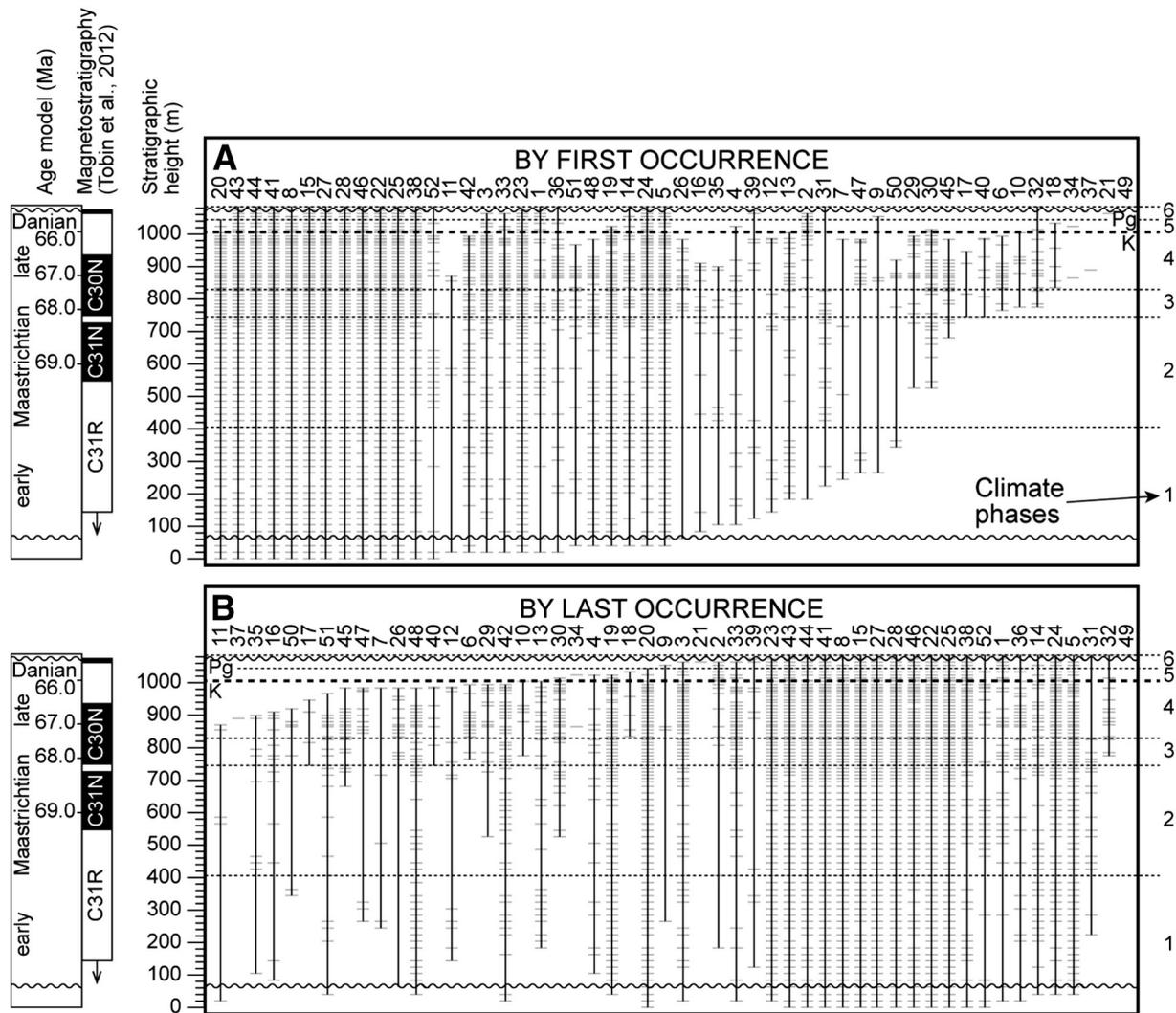


Fig. 5. Observed stratigraphical ranges of terrestrial palynomorph taxa from section D5.251, Seymour Island, Antarctic Peninsula. Important note: Observed stratigraphical range bases and tops from this section are not intended to imply speciations and extinctions, respectively. Data presented in this figure is only from section D5.251 of this study. However, data from other parallel sections suggest 10 of the 14 taxa here with apparent range tops during the latest Maastrichtian actually extend to the top of the López de Bertodano Formation (Askin, 1990a,b, 1994 and unpublished data). Taxa considered to be entirely reworked are not included. A, Plotted in stratigraphical order of their first appearance datums. B, Plotted in stratigraphical order of their last appearance datums. Horizontal tick marks indicate observed occurrence of each taxon throughout their range. K, Cretaceous. Pg, Paleogene. Climate phases are discussed in Section 5.3 and also shown in Fig. 6. 1, *Araucariacites australis*; 2, *Azolla* spp.; 3, *Camarozonosporites ambigens*; 4, *Camarozonosporites ohaiensis*; 5, *Ceratosporites equalis*; 6, *Clavamonocolpites polygonalis*; 7, *Cranwellia striata*; 8, *Cyathidites minor*; 9, *Dacrydiomites praecupressinoides*; 10, *Ericipites scabratus*; 11, *Gambierina rudata*; 12, *Gleichenioides senonicus*; 13, *Grapnelispora* sp. 1; 14, *Laevigatosporites major*; 15, *Laevigatosporites ovatus*; 16, *Liliacidites* sp. cf. *L. kaitangataensis*; 17, *Liliacidites* sp. cf. *L. variegatus*; 18, *Liliacidites* sp. 1; 19, *Lycopodiadites bullerensis*; 20, *Microcachrydites antarcticus*; 21, *Myricipites* sp. cf. *M. cavilloratus*; 22, *Nothofagidites* spp.; 23, *Osmundacidites wellmanii*; 24, *Peninsulapollis askiniae*; 25, *Peninsulapollis gillii*; 26, *Peromonolites bowenii*; 27, *Phyllocladites mawsonii*; 28, *Podocarpidites* spp.; 29, ?Zygnemataceae spore A; 30, ?Zygnemataceae spore B; 31, *Polycopites* sp. cf. *P. langstonii*; 32, *Polypodiisporites speciosus*; 33, *Propylipollis subscabratus*; 34, *Proteacidites adenanthoides*; 35, *Proteacidites angulatus*; 36, *Proteacidites* sp. cf. *P. scaboratus*; 37, *Proteacidites* sp. cf. *P. crassus*; 38, *Proteacidites parvus*; 39, *Proteacidites pseudomoides*; 40, *Proteacidites subpalisadus*; 41, *Retitriletes austroclavatidites*; 42, *Stellidiopollis annulatus*; 43, *Stereisporites antiquasporites*; 44, *Stereisporites regium*; 45, *Taxodiaceapollenites hiatus*; 46, *Trichotomosulcites subgranulatus*; 47, *Tricolpites confessus*; 48, *Tricolpites lillieii*; 49, *Tricolpites* sp. cf. *T. phillipsii*; 50, *Tricolpites reticulatus*; 51, *Triporoletes reticulatus*; 52, *Triporopollenites* spp.

species (*Camarvonía araliifolia*) growing into large trees (Hyland, 1995). It is endemic to the wet northeastern corner of Australia (Mabberley, 1997) where the MAT is 21.2 °C (Table 2). *Lomatia* grows in cooler, but still warm temperate climates (MAT 12.5 °C, Table 2) as prostrate shrubs and small trees. It is known from the marine palynological record that both cold and warm phases occur in the Antarctic Peninsula region during the latest Maastrichtian (Bowman et al., 2013a) and *P. pseudomoides* is recorded throughout the López de Bertodano Formation. This suggests that it is likely that this fossil taxon does represent more than one living relative with differing habitat preferences.

Proteaceae were a diverse and important part of the Antarctic Peninsula flora, in both rainforest understorey to more open areas, although, as discussed by Askin and Baldoni (1998), they are likely under-represented in the spore and pollen counts. They are not prodigious producers of pollen like the wind-pollinated *Nothofagus* and

conifers, due to their different pollination mechanisms. Thus they do not appear in the graphs of more commonly occurring species (Fig. 6), with the exception of *Peninsulapollis gillii*, which is of uncertain ancestral proteaceous affiliation. Throughout the López de Bertodano Formation, the varied species typically occur as single to rare specimens in any one sample, and the family as a whole (excluding *P. gillii* in this study) rarely reaches 2% of the terrestrial count (Askin, unpublished data).

In low-lying areas, freshwater ponds were present with aquatic ferns (Salviniaceae), algae and perhaps testate amoebae on the boggy margins. Possible zygospores of the Zygnemataceae (green filamentous algae) indicate that the ponds were clean, oxygen-rich, probably still, shallow and warm for at least part of the year. Furthermore, the presence of these spores indicates seasonality in order to stimulate zygospore formation (Jarzen, 1979). Fungal palynomorphs were

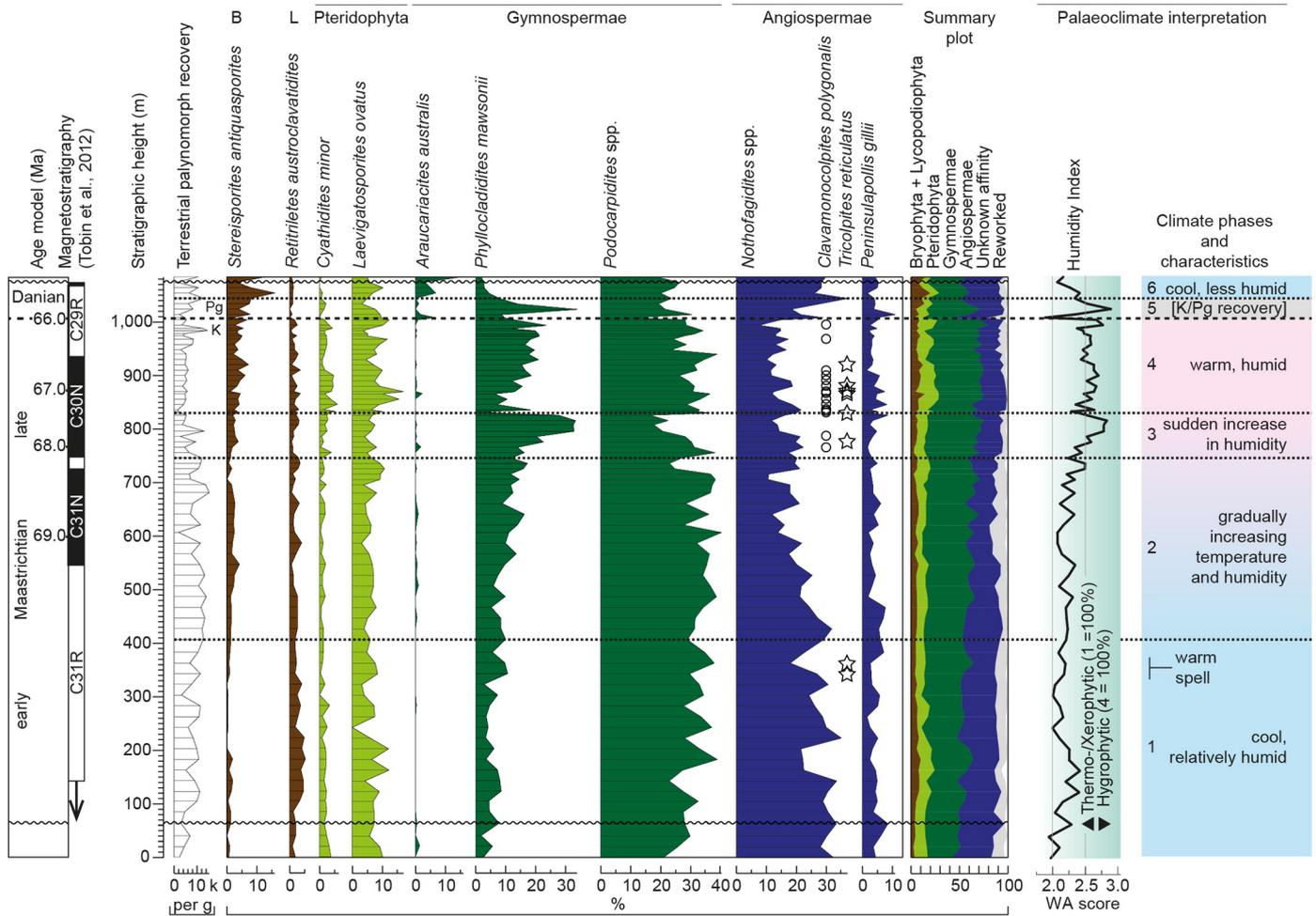


Fig. 6. Terrestrial palynomorph abundance for selected taxa and palaeoclimate interpretation, section D5.251, Seymour Island, Antarctic Peninsula. Note x-axis units: k, thousand; g, gramme. K, Cretaceous. Pg, Paleogene. Terrestrial palynomorph recovery includes all counted spores and pollen, including freshwater green algae and reworked material. Each taxon plotted is a prominent component of the palynoflora (Supplementary Dataset). The stratigraphic occurrence of *Clavamonocolpites polygonalis* (circles) and *Tricolpites reticulatus* (stars) are also plotted (although too rare to plot as abundance curves) because of their thermophilic nearest living relatives (?Chloranthaceae and *Gunnera macrophylla* respectively, Section 5.3). The summary abundance plot shows how the proportions of each plant type vary throughout the section (spores and pollen grouped by modern botanical affinity, see Table 1). The Humidity Index is a one-dimensional summary of ecological groupings using a weighted average (WA) model based on habitat moisture level preference (Table 1). It is an expression of how wet the palaeoclimate was through the Maastrichtian to earliest Danian at this locality. The palynofloral trends are divided into six climatic phases for ease of discussion, which record both temperature and humidity fluctuations throughout this time period.

recorded throughout the section and reflect the saprophytic degradation of terrestrial biomass in a humid palaeoenvironment.

5.2.2. High altitude *Araucaria* forest and heathland

Some elements of the terrestrial palynomorph assemblages suggest a well-drained, higher altitude habitat for part of this flora, with marginal forest environments typified by *Araucaria* trees (see Kershaw and Wagstaff, 2001) and open heath-like vegetation with Ericaceae (*Ericipites scabratus*) and *Microcachrys* (*Microcachrydites antarcticus*) on infertile soils (MacPhail et al., 1999) (Fig. 8). Alete pollen grains comparable with *Araucariacites australis* are produced today by *Araucaria araucana* (the monkey puzzle tree), a distinctive araucarian tree (Heusser, 1971) that extends to the tree line in modern southern Chile and Argentina. Today, the monkey puzzle tree grows in cool temperate conditions where mean July temperatures (coldest month) are 7–8 °C, and mean January temperatures are 17–19 °C (Table 2; Sanguinetti and Kitzberger, 2008). High abundances of araucarian pollen, as recorded above 1044 m in the Seymour Island section, are indicative of dense, emergent cover of *Araucaria* in relatively dry conditions (Kershaw and Wagstaff, 2001).

The trisaccate pollen *Microcachrydites antarcticus* is affiliated to the modern creeping shrub *Microcachrys tetragona* (the sole species of that genus), which is endemic to western Tasmania and grows at high

altitude in a boreal-type (snow) climate, where MATs are ~5–8 °C (Table 2; Silba, 1984; Biffin et al., 2011). *Microcachrydites antarcticus* occurs consistently throughout the Maastrichtian part of section D5.251 implying that the subalpine/alpine zones of the Antarctic Peninsula arc retained some vegetation throughout this period. It is possible that at these altitudes *Microcachrys* grew alongside other low-growing shrubs such as the protea *Bellendena montana* (the NLR of *Proteacidites parvus*, Table 1), which today also occupies high altitudes in Tasmania with similar climatic tolerances (Table 2).

5.2.3. Late Cretaceous south polar forests and climate

Mixed forests of similar composition to those observed herein, with both closed and more open canopies, were growing across the high southern latitude landmasses during the Late Cretaceous (Specht et al., 1992). Dettmann and Jarzen (1990) discussed a similar co-occurrence of rainforest and sclerophyllous Proteaceae in southern Australia during the Late Cretaceous and invoked the lack of a nearest living relative, which is certainly the case for complex forests in a polar light regime (Hill and Dettmann, 1996). However, these Late Cretaceous lowland to mid latitude rainforests of the eastern Antarctic Peninsula do have similarities with the modern Valdivian rainforests of Chile, which have an angiosperm-dominated canopy with subordinate gymnosperms, and an

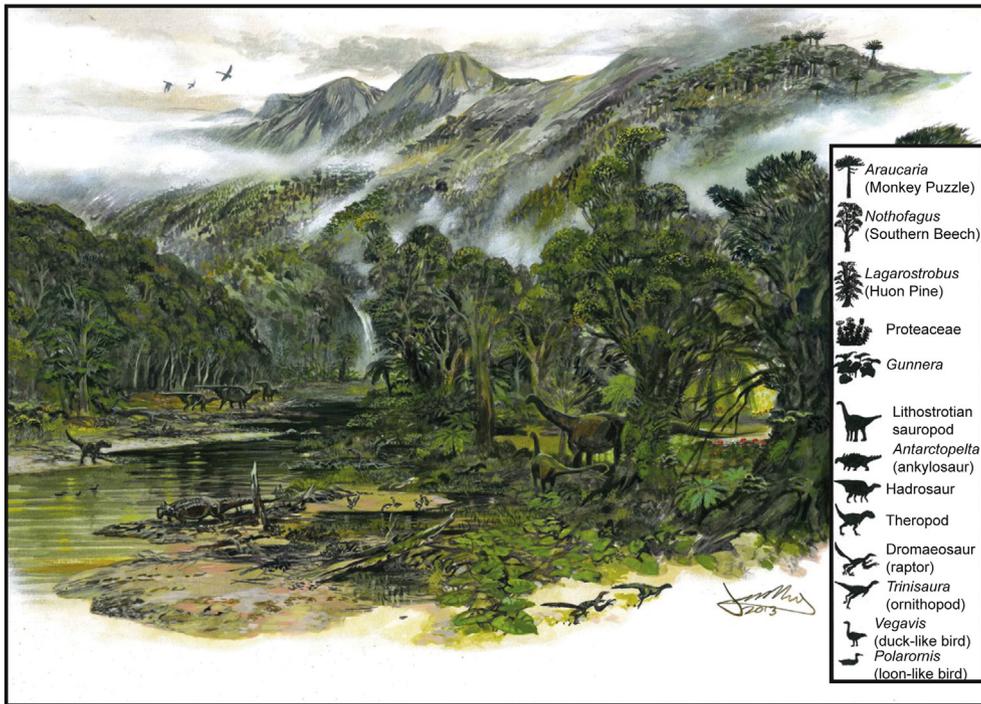


Fig. 7. Artist's impression of the eastern flank of the Antarctic Peninsula during the Maastrichtian. The vegetation composition and habitat types are based on the nearest living relatives of the terrestrial palynoflora from Seymour Island discussed in this paper. Mixed temperate rainforest grew in the lowlands to mid altitudes composed mainly of a *Nothofagus*–podocarp–Proteaceae canopy with *Lagarostrobos* (Tasmanian Huon Pine) occupying the super-wet habitats along riverine margins. Freshwater pools hosted aquatic ferns and green algae with bordering wetlands filled with diverse mosses and ferns. At higher altitudes, open heath-like vegetation may have grown beyond the tree line of montane araucarian forests (detailed in Fig. 8). All fauna are known from the Cretaceous fossil record of the James Ross Basin (Chatterjee, 1989, 2002; Case et al., 2000, 2003, 2007; Clarke et al., 2005; Salgado and Gasparini, 2006; Cerda et al., 2012; Coria et al., 2013).

Artist: James McKay, University of Leeds.

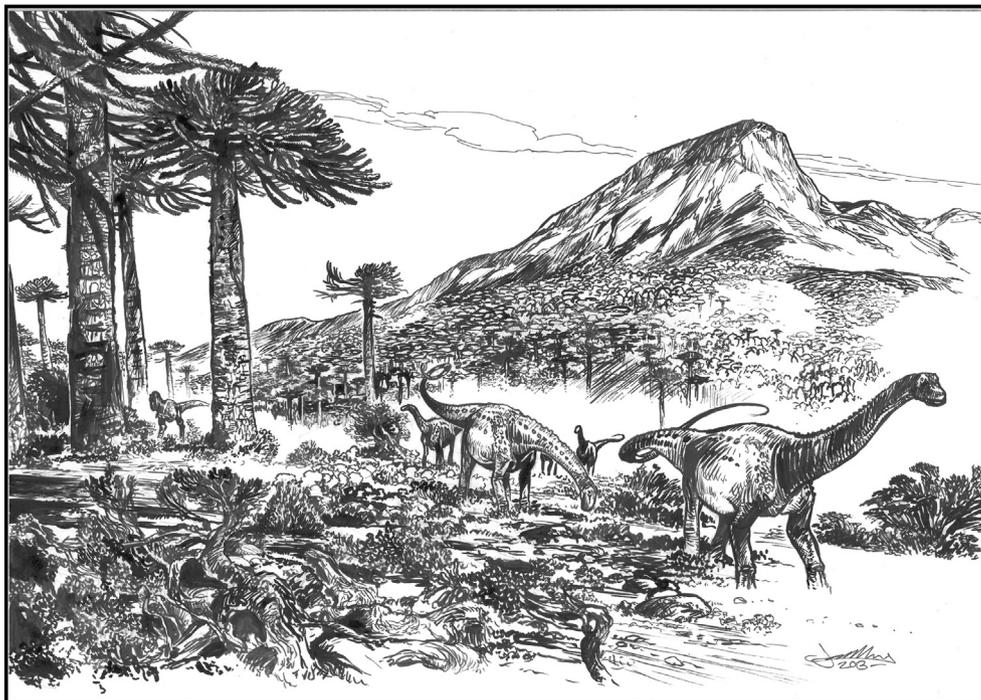


Fig. 8. Artist's impression of high-altitude vegetation on the Antarctic Peninsula, Maastrichtian. At the tree line, araucarian-dominated forest stands may have bordered subalpine to alpine, well-drained montane heaths. The distinctive monkey puzzle trees (*Araucaria araucana*) in the mountains of southern Chile and Argentina are considered to be a likely analogue for *Araucariacites australis* pollen (see Section 5.3). The theropod and sauropods are known from small bone fragments in the Cretaceous fossil record of the James Ross Basin (Case et al., 2003; Cerda et al., 2012).

Artist: James McKay, University of Leeds.

understory of other angiospermous plants (e.g. Liliaceae) and ferns (Leppe et al., 2012).

The mixture of terrestrial taxa from many plant groups, as seen in the López de Bertodano Formation palynoflora, most likely represents a mosaic of habitats and vegetation types from different altitudes growing on the eastern flank of the Antarctic Peninsula during the Maastrichtian and earliest Danian. These habitats include open and closed canopy forest, river margins, freshwater ponds, well-drained interfluvies, montane araucarian-dominated forests and high altitude, infertile heath. Based on the climatic preferences of the NLRs, the lowland to mid altitude eastern flanks of the Antarctic Peninsula mountains probably existed in a very humid, generally cool to warm temperate climate during the Maastrichtian with MAT ~10–15 °C (Table 2). Such average temperatures would not have precluded freezing conditions in the winter, particularly at the cooler end of this range. In sheltered, perhaps north-facing niches, temperatures may have risen higher supporting diverse proteas in particular (Table 2). At high altitude, the montane forests grew at the cooler end of this range, and subalpine/alpine heathlands grew in cold, boreal-type conditions of ~5–8 °C MAT (Table 2). This diverse mixture of vegetation types was also clearly capable of surviving the extreme polar light regime together with a fauna that included dinosaurs (in the Maastrichtian) and birds (e.g. Clarke et al., 2005; Cerda et al., 2012) (Figs. 7 and 8).

5.3. Vegetational change and climate history throughout the deposition of the López de Bertodano Formation

The terrestrial palynomorph record throughout section D5.251 is divided into six phases (Figs. 5 and 6). Throughout phase 1 there is a gradual, but consistent incoming of new species with *Nothofagidites* spp. and *Podocarpidites* spp. dominating the assemblage (Figs. 5 and 6). Abundant *Nothofagidites* spp., consistent moss and terrestrial fern spores, the presence of aquatic fern spores (*Azolla* spp., *Granelispora* sp. 1) and rare freshwater algal spores suggest this was a cool and relatively humid period (Read et al., 2010). The Humidity Index suggests moisture levels remained relatively stable throughout this phase with WA scores mainly between 2.0 and 2.5 (Fig. 6). All the extant subgenera of *Nothofagus* grow within high rainfall regions in the high southern latitudes (Hill and Dettmann, 1996), with subgenus *Brassospora* (fossil pollen “*brassii* group”) limited today to warmer though upland areas of New Caledonia and New Guinea. In this study, differentiation of the different pollen types of *Nothofagidites* has not been done, though it should be noted that *Nothofagidites* “*menziesii* group” (subgenus *Lophozonia*) is always very rare and often absent, and that the pollen “*fusca*” (subgenera *Fuscospora* and *Nothofagus*) and “*brassii*” groups vary in relative abundance though typically occur in similar frequencies, including near the K–Pg boundary (Askin, unpublished data). Further work on these pollen types may provide additional insights on the Maastrichtian vegetation and climate dynamics.

Phase 1 could be interpreted as the final stage in the development of the lowland forests of the eastern Antarctic Peninsula towards a compositional state in equilibrium with the “new” cool and humid climate, following the mid Cretaceous greenhouse. Minor climatic fluctuations are apparent from variations in the terrestrial palynomorph abundances during this phase (Fig. 6). The best example of this is at ~350 m where rare *Tricolpites reticulatus* (Gunneraceae) occur together with a fall in the abundance of *Nothofagidites* spp. and a rise in *Podocarpidites* spp., suggestive of a brief warm spell (Fig. 6).

At 407 m, a period of relative stasis in vegetation composition began with only one pollen taxon (*Taxodiaceapollenites hiatus*) appearing for the first time within ~340 m of sediment (phase 2, Fig. 5). Within this phase, the only significant change in vegetation composition is that *Nothofagidites* spp. decreased in abundance, suggesting that the southern beech became increasingly limited by gradually warming temperatures. Rare, possible Palmae pollen appeared near the base of phase 2 in a parallel section (Askin, 1994), consistent with a warming trend. In

addition, *Phyllocladidites mawsonii* increased in abundance implying a gradual increase in humidity (Fig. 6). The Humidity Index expresses this gradual change in moisture levels with WA score values reaching 2.5 by the top of this phase (Fig. 6).

During the relatively short phase 3, rapid environmental changes occurred with synchronous falls in abundance of both *Podocarpidites* spp. and *Nothofagidites* spp., coincident with a steep rise in abundance of *Phyllocladidites mawsonii* to its highest level prior to the K–Pg boundary (phase 3, Fig. 6). These abundance trends suggest that southern beech is again limited by warming temperatures, while *Lagarostrobos* became highly successful in a wet palaeoclimate. The Humidity Index expresses a sudden shift from relatively low to high moisture levels during this phase, followed by a sharp decrease again into phase 4 (Fig. 6). Modern *Nothofagus* tend to outcompete podocarps only where the climate or soil is suboptimal (McGlone et al., 1984; Case, 1988). However, with both of these in decline towards the top of this phase, one explanation could be that podocarps were limited not by temperature or soil conditions, but by the super-humid climate favoured by *Lagarostrobos*.

Bryophytes began to increase slightly in abundance during phase 3, a trend that continued upwards. Also at the beginning of this phase (between 746 and 776 m), there was an increase in the number of presumed thermophilic species (including *Clavamonocolpites polygonalis*, ? Chloranthaceae and *Tricolpites reticulatus*, Gunneraceae), with five new taxa appearing over 30 m in this section (Fig. 5). Note, however, that three of those five taxa (*C. polygonalis*, *Liliacidites* sp. cf. *Liliacidites variegatus* and *Proteacidites subpalisadus*) occur lower in the López de Bertodano Formation in other parallel sections on Seymour Island (Askin, 1990a,b, 1994). The presence of *Ericipites scabratus* pollen at 776 m may represent ericaceous plants from the higher and drier hinterland of the arc, but still within a climate of potentially warm summers (e.g. Bowman et al., 2013a). The terrestrial palynomorph record during phase 3, in only 84 m of the section, suggests there may have been a sudden period of increasing humidity possibly associated with a culmination of the warming trend that began at the start of phase 2.

At 830 m the abundance of *Phyllocladidites mawsonii* pollen decreases dramatically, together with a significant increase in other podocarp pollen and a minor increase in *Nothofagidites* spp., suggestive of slight but abrupt warming and drying, corroborated by a significant decrease in the Humidity Index (Fig. 6). Phase 4 is characterised throughout by relatively high abundances of *Podocarpidites* spp. and relatively low levels of *Nothofagidites* spp., with many of the taxa present affiliated with modern thermophilic plants (e.g. *Clavamonocolpites polygonalis*–?Chloranthaceae, and *Tricolpites reticulatus*–Gunneraceae; Bowman et al., 2013a). In this part of other parallel sections, Askin (1989) records the distinctive pollen *Anacolisidites sectus* (Olacaceae), about 28 m below the K–Pg boundary and Bombacaceae about 44 m below the boundary. Other thermophilic types were reported sporadically throughout the López de Bertodano Formation, such as Sapindaceae (Cupanieae tribe; Askin, 1989, 1990a), with increased occurrences of these and possible Palmae pollen (Askin, 1994), near the K–Pg boundary, and appearances of two species of *Beauprea*-type Proteaceae (Askin, 1989) through phase 4.

Bryophyte abundances are relatively high, and the fern spore *Laevigatosporites ovatus* reached its highest level in the section. Within phase 4, *Phyllocladidites mawsonii* recovers almost immediately (by 836 m), only to drop again followed by a gradual recovery almost to the K–Pg boundary, which is also reflected in the fossil wood record of *Phyllocladoxylon* (Cantrill and Poole, 2005). Gallagher et al. (2008) also noted an increase in abundance of *P. mawsonii* towards the K–Pg boundary in southeast Australia. Relative abundance of *P. mawsonii* can also be high (up to 22%) in the latest Cretaceous (Haumurian) of New Zealand (Pole and Vajda, 2009). The spore and pollen assemblage and abundance trends in this part of the section are corroborated by relatively high Humidity Index values suggesting that this phase was warm and very humid (Fig. 6). The marine palynomorph record from the same samples supports this interpretation (Bowman et al., 2013a). The

recovery of the other podocarps during phase 4 implies their growth may no longer have been limited by the super-humid conditions favoured by *Lagarstrobus* and they grew well in this warmer climate immediately prior to the K–Pg transition. The coincident increase in bryophyte abundance supports a humid climate at this time suggesting one possible scenario of *Sphagnum* segregation in wetland habitats between more well-drained areas supporting podocarp-dominated forest. However, interpretation of such fine-scale climate fluctuations and habitat mapping must necessarily remain speculative considering the many controlling factors on the palynomorph assemblage recorded. These factors, for example potential changes in the source sediments with climate change and disturbance, will have shifted through time and are considered further in the Methods and materials section above.

Phase 5 (the K–Pg boundary to 1044 m) is characterised by a rapidly changing sequence of abundance peaks of different taxa, which may indicate a successional turnover in forest composition as the landscape and vegetation adjusted to the post-boundary conditions. Detailed analysis of this interval across the K–Pg boundary is being undertaken at much higher resolution to resolve the specifics of the vegetational change both prior to and following the K–Pg impact. By 1044 m, the composition of the lowland vegetation (i.e. mixed temperate rainforest) appears to have largely returned to its state during phase 1 (presumed early Maastrichtian), with low abundances of *Phyllocladidites mawsonii* and relatively high abundances of *Podocarpidites* spp. and *Nothofagidites* spp. The duration of phase 5 is approximately 190 kyr using the present age model for the López de Bertodano Formation.

Throughout phase 6 at the top of the section, across the unconformity into the Sobral Formation, the apparent recovery of the palynoflora suggests a return to cool climatic conditions. High abundances of *Araucariacites australis* and *Nothofagidites* at the top of the section are coincident with low *Phyllocladidites mawsonii* abundances, and a brief spike in *Sphagnum* spores.

The abundance pattern of *Araucariacites australis* is of particular interest. This species is rare throughout most of the section, but increased significantly above 1044 m in the Danian (Fig. 6). This pattern suggests that araucarian trees grew in low numbers on the Antarctic Peninsula throughout both the cool and warm phases of the Maastrichtian. Araucariaceae were capable of surviving long periods of adverse climatic conditions during the Early Pleistocene, but most modern araucarians have subtropical to mesothermal climatic preferences (Kershaw and Wagstaff, 2001; Wagstaff et al., 2001). The exception is the Chilean monkey puzzle tree (*Araucaria araucana*), which prefers cooler conditions (Kershaw and Wagstaff, 2001). The ability to grow in cool conditions supports the suggested affinity of *A. australis* with a montane taxon such as the monkey puzzle tree that could retreat higher up into the hinterland during the warmer interval of the latest Maastrichtian (phases 3 and 4). Above 1044 m (phase 6, Fig. 6), the sudden increase in abundance of *A. australis* may reflect cooling, which caused an expansion in the range of montane araucarians in the hinterland with a lowering of the tree line. This apparent expansion of araucarian forest at this time was also noted in the fossil wood flora from Antarctica, which shows an increase in abundance of araucarian wood across the K–Pg boundary into the Early Paleocene (Cantrill and Poole, 2005). The lack of these montane araucarians during the cool climate phases 1 and 2 is enigmatic. One explanation for increased abundance of araucarians at the top of the section may be that the upland terrestrial palynomorph signature became more prominent in the offshore record following the disruption to lowland vegetation communities after the K–Pg event. This event may have effectively cleared the pollen transport path resulting in rapid outwashing from more open and well-drained upland habitats in the Antarctic Peninsula hinterland. This may explain the significant decrease in the Humidity Index into this uppermost phase (Fig. 6). Interestingly, numbers of *Sphagnum* also increase, perhaps reflecting additional transport factors that concentrated some of the lowland wetland spores.

5.4. The broader context

This reconstruction of Antarctic Peninsula palaeoclimates in the lead-up to, and immediately beyond, the K–Pg catastrophe provides a general picture of a relatively cool early Maastrichtian and a warm, humid late Maastrichtian, possibly cooling again following the K–Pg event. This is consistent with interpretations of the marine palynomorph record from the same section (Bowman et al., 2013a). Other fossil plant and palynomorph records from the Upper Cretaceous of the Antarctic Peninsula region support this interpretation, although such records are sparse and qualitative. These include terrestrial deposits from the fore-arc (Birkenmajer and Zastawniak, 1989; Cao, 1992; Shen, 1994) and back-arc (Dettmann and Thomson, 1987; Dettmann and Jarzen, 1988; Askin, 1990a,b; Dutra and Batten, 2000; Césari et al., 2001; Salzmann et al., 2011) regions of the Antarctic Peninsula. Preliminary analysis of dispersed plant cuticles from the López de Bertodano Formation, Seymour Island, suggest MATs of 8 to 15 °C for the latest Maastrichtian, which corroborate the MAT estimates from the terrestrial palynology (Upchurch and Askin, 1989; Upchurch, personal communication (1990) cited in Askin, 1992). All of the palynomorph assemblages known from the region, including those from the López de Bertodano Formation in this study, have similar components but differ in their constituent proportions, which are likely to be related to differences in source habitat. They are all interpreted as representing rainforest vegetation growing on both sides of the Antarctic Peninsula arc during this time within a cool to warm temperate and humid palaeoclimate (Askin, 1992), consistent with the results of this study.

In addition to leaves and palynomorphs, fossil wood has also been analysed from Upper Cretaceous sediments in the Antarctic Peninsula region (Francis and Poole, 2002; Cantrill and Poole, 2005). Tree ring analysis on fossil wood from the López de Bertodano Formation on Seymour Island (although sample resolution is low compared with the current study) suggests a cool mean annual temperature (MAT) of ~7 °C for the Maastrichtian samples (Francis and Poole, 2002), close to the lowest estimate of 10 °C for lowland to mid altitude forests suggested herein. A cooling into the Paleocene, as seen in this study, is supported by a decrease in MAT to 4–8 °C across the K–Pg boundary interpreted from fossil wood tree ring analysis from Seymour Island (Francis and Poole, 2002).

Global benthic foraminifera carbon and oxygen isotope data suggest cool ocean temperatures during the early Maastrichtian (Friedrich et al., 2012). This was followed by a further decline in ocean temperatures throughout the Maastrichtian in the James Ross Basin and at Maud Rise (Barrera et al., 1987; Barrera and Huber, 1990; Pirrie and Marshall, 1990; Ditchfield et al., 1994). Terrestrial palynofloras from the Gippsland Basin in southeastern Australia confirm cool Maastrichtian temperatures (Gallagher et al., 2008). Evidence from this study from Seymour Island of a warm interval during the latest Maastrichtian, and increasingly wet conditions at this time, supports previous interpretations from the Antarctic fossil plant and palynomorph record (Askin, 1989, 1990a; Dettmann, 1989; Francis, 1991; Bowman et al., 2013a), $\delta^{18}\text{O}$ interpretations from planktonic foraminifera (Abramovich and Keller, 2003) and modelled Maastrichtian climates (Parrish et al., 1982; Hunter et al., 2008). Similarly, consistent with the data presented herein, Stott and Kennett (1990) and Barrera and Savin (1999) also suggested a cooling into the Paleocene based on oxygen isotope records.

Global sea level compilations for the Maastrichtian indicate a fall, followed by a rise within the final ~2 million years of the Cretaceous, exemplified by estimates based on the sequence stratigraphy of the New Jersey passive margin (Haq et al., 1987; Hallam and Wignall, 1999; Miller et al., 2005; Cramer et al., 2011). Palaeoclimate interpretations from this study support the concept of a cool early Maastrichtian, possibly cool enough for limited ice on continental Antarctica, which would contribute to a lowering of global sea level (see also Bowman et al., 2013a). Despite the lack of a direct modern analogue, it is considered possible for a complex vegetation to have existed at these latitudes

during the partial glaciation of Antarctica because even the most sensitive of plants, the Salviniaceae (e.g. *Azolla*), could have survived sub-zero temperatures (Janes, 1998). The latest Maastrichtian rise in sea level, and the main eruption of Deccan Traps volcanism (Chenet et al., 2009), coincided with the warm interval interpreted from this study immediately prior to the K–Pg boundary. However, there is no sedimentological evidence for major sea level change throughout the Seymour Island section.

6. Summary

This paper presents the first quantitative terrestrially-derived palynological record from the high southern palaeolatitudes throughout the Maastrichtian and earliest Danian. The data offers an unprecedented high-resolution record of polar palaeoclimate through this interval of dramatic global change, comparable in detail to oceanic oxygen isotope analyses, but providing a direct record of atmospheric conditions from the terrestrial realm.

Using a nearest living relative approach, a diverse mixed rainforest has been reconstructed that grew on riverine lowlands on the eastern flank of the Antarctic Peninsula. The canopy would have been relatively open in places supporting flowering (and perhaps aromatic) herbs and shrubs. This lowland to mid altitude forest comprised tall trees of diverse podocarps and southern beech trees, which hosted mistletoe and epiphytic ferns. Huon Pine lined the riverbanks and duckweed ferns covered freshwater ponds. Diverse mosses, shade-tolerant ground and tree ferns, together with proteaceous shrubs grew on the forest floor and saprophytic fungi degraded the leaf litter. Associated with canopy gaps, particularly during warmer time intervals, thermophilic ferns and angiosperms colonised these sheltered habitats. Higher ground, between catchments, supported a relatively open shrubland with lilies, members of the sesame family and proteaceous shrubs or small trees. Mean annual temperatures in these lowland to mid altitude forests may have been ~10–15 °C, with the higher end of the range reflecting the sheltered habitat niches, and perhaps the warmer climatic phase prior to the K–Pg boundary. The cooler end of the range would not have precluded freezing temperatures during the winters. At higher altitudes, near the tree line, monkey puzzle trees dominated the forest margins opening on to well-drained, ericaceous heathland. In this subalpine to alpine zone, mean annual temperatures may have been a cold ~5–8 °C. Moisture availability seems to be the most important ecological factor affecting the vegetation throughout this landscape. The closest modern analogue of the Antarctic Peninsula rainforests would be the Valdivian forests of the southern Andes in Chile, although the Antarctic rainforests were apparently more protea-rich. The upland araucarian forest was similar to modern high-altitude monkey puzzle forests from southern Chile and Argentina.

Changing vegetation patterns at the margin of Antarctica suggest that, following mid Cretaceous greenhouse temperatures, the early Maastrichtian climate was relatively cool and humid, gradually warming and increasing in humidity during the mid Maastrichtian. A rapid warming ~2 million years prior to the K–Pg boundary, consistent with evidence from the marine palynomorph record, coincided with a super-humid interval, before a return to cool conditions in the earliest Danian. These results do not preclude small ice caps on the Antarctic continent at this time because even the most sensitive of plants, the Salviniaceae, could have survived sub-zero temperatures at the margins. Causative mechanisms for this palaeoclimatic trend prior to the K–Pg impact remain speculative, but could have been related to changing orbital parameters and the sudden influx of greenhouse gases associated with the main eruption of the Deccan Traps. The nature of vegetational change in the south polar region suggests that terrestrial

ecosystems were already responding to relatively rapid climate change prior to the K–Pg catastrophe.

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Appendix 1. Taxonomic notes

This section comprises an alphabetical list of terrestrial palynomorph taxa recorded in this study with taxonomic and biostratigraphical notes where relevant. Most author references linked to the taxa listed below can be found in Raine et al. (2011); additional citations that are not included in Raine et al. (2011) can be found in the reference list herein. Nearest living relatives of the contemporaneous sporomorphs are listed in Table 1. * Reworked.

Bryophyta

Streisporites antiquasporites (Wilson and Webster 1946) Dettmann, 1963 [Fig. 3-1]

Streisporites regium (Drozastichich in Samoilovitch and Mtchedlishvili 1961) Drugg 1967 [Fig. 3-5]

Triporoletes reticulatus (Pocock 1962) Playford 1971 [Fig. 3-2]

Lycopodiophyta

Camarozonosporites ambigens (Fradkina, 1967) Playford 1971 [Fig. 3-3]

Camarozonosporites ohaiensis (Couper, 1953) Dettmann and Playford 1968 [Fig. 3-4]

Ceratosporites equalis Cookson and Dettmann, 1958 [Fig. 3-8]

Lycopodiacidites bullerensis Couper, 1953 [Fig. 3-6]

Taxonomic note – As noted by Askin (1990b, as *Retitriletes* sp. cf. *R. eminulus*), the specimens observed in this study are comparable to the type material of *Lycopodiacidites bullerensis* except the former have a more triangular amb and more irregular distal reticulum. They are also slightly smaller than the type material. Raine et al. (2011) considered the *Retitriletes* sp. cf. *R. eminulus* specimen

illustrated by Askin (1990b) from Seymour Island to be within the species concept of the senior synonym *Lycopodiacidites bullerensis*, which is used herein.

**Perotriletes majus* (Cookson and Dettmann, 1958) Evans 1970 [Fig. 4-21]

Taxonomic note – The distinctive zonate spore *Perotriletes majus* is the only consistently occurring taxon recorded throughout the section that is considered reworked (Supplementary Dataset). The specimens recorded include some that are slightly smaller than the type material (for example, Fig. 4-21). The specimen illustrated also does not have the serrated edge or conical spines described in Cookson and Dettmann (1958), but this may be within intra-specific variation. This species had a wide geographical distribution during the mid to Late Cretaceous, with the latest published being from the Maastrichtian of Seymour Island (Askin, 1990a; Raine, 2005). It has since been recorded from the Paleocene Sobral and Cross Valley formations from Seymour Island (unpublished data). It remains uncertain as to whether this species is contemporaneous or reworked in the current section as its exine colour and preservation are variable. Here it is considered questionably to be reworked due to its rare occurrence within any one sample, its dark coloured exine compared with definitely contemporaneous terrestrial palynomorphs and its frequently folded and fragmented preservation.

Retitriletes austroclavatidites (Cookson 1953) Doring et al. in Krutzsch 1963 [Fig. 3-7]

Pteridophyta

Azolla Lamarck, 1783 spp. [Fig. 3-12]

Taxonomic note – *Azolla* spp. occurred as fragments of massula, often with glochidia attached, and as isolated glochidia. Askin (1990b) recorded three morphotypes of *Azolla* glochidia from earlier studies on the López de Bertodano Formation on Seymour Island, but stated that the different sizes of two of these forms may relate to maturity. Occasional specimens of yet another type encountered in this study exhibited multi-barbed glochidia (for example, Fig. 3-12), but can still be attributed to *Azolla* sp. (Margaret Collinson, personal communication, 2013). No attempt has been made here to systematically differentiate the fragments of *Azolla* recorded, which require further detailed taxonomic analysis.

**Cyathidites* sp. cf. *C. australis* Couper, 1953 [Fig. 4-23]

Taxonomic note – This specimen is compared with *Cyathidites australis* Couper, 1953 due to its large size (110 µm diameter). The type material is 54–77 µm diameter (Couper, 1953) and those illustrated by Dettmann (1963) are 50–73 µm diameter.

Cyathidites minor Couper, 1953 [Fig. 3-9]

Echinosporis sp. 1 of Askin 1990b

Gleicheniidites senonicus Ross 1949 [Fig. 3-10]

Grapnelispora Stover and Partridge 1984 sp. 1 [Fig. 3-11]

Taxonomic note – Fragments identified herein as *Grapnelispora* sp. 1 are likely to be the same taxon that Askin (1990b) recorded from the López de Bertodano Formation as *Grapnelispora* sp. cf. *Grapnelispora evansii*. However, again, its differentiation from *Grapnelispora evansii*

sensu stricto is based on its smaller size (Askin, 1990b), which may also be related to maturity, or possibly depositional setting, and requires additional taxonomic analysis.

Laevigatosporites major (Cookson 1947) Krutzsch 1959 [Fig. 3-13]

Laevigatosporites ovatus Wilson and Webster 1946 [Fig. 3-14]

**Matonisporites* sp. cf. *M. cooksoniae* Dettmann, 1963 [Fig. 4-24]

Taxonomic note – This specimen is slightly smaller than the type material, which ranges from 59 to 78 µm diameter (Dettmann, 1963), and the exinal thickenings at the apices are not smoothly rounded, although this is within intraspecific variation.

Osmundacidites wellmanii Couper, 1953 [Fig. 3-19]

Peromonolites bowenii Couper, 1953 [Fig. 3-15]

Polypodiisporites speciosus (Harris 1965) Khan and Martin 1971 [Fig. 3-16]

**Verrucosisporites* Potonié and Kremp 1955 sp. 1 [Fig. 4-22]

Taxonomic note – Although the colour of the illustrated specimen (Fig. 4-22) is close to that of the definitely contemporaneous palynomorphs, its rarity suggests that it is reworked.

Gymnospermae

Araucariacites australis Cookson 1947 [Fig. 3-17]

Taxonomic note – In this study, pollen grains that match the description of *Araucariacites australis* include those with a slightly coarser sculpture that is comparable with the description of *Dilwynites granulatus* Harris 1965. Here these grains are treated as end members of the same species in the absence of more detailed taxonomic analysis.

Dacrydiiumites praecupressinoides (Couper, 1953) Truswell, 1983 [Fig. 3-18]

Taxonomic note – The specimens recorded are slightly larger than the type material, but within the size range recorded by Truswell (1983).

Microcachrydites antarcticus Cookson 1947 [Fig. 3-21]

Phyllocladidites mawsonii Cookson 1947 ex Couper, 1953 [Fig. 3-23]

**Plicatipollenites gondwanensis* (Balme and Hennelly 1955) Lele 1964 [Fig. 4-25]

Podocarpidites Cookson 1947 ex Couper, 1953 spp. [Fig. 3-22, -24, -25]

Taxonomic note – Some bisaccate pollen grains from this sedimentary sequence on Seymour Island may be better included in *Alisporites*, though we consider that these are probably reworked based on our broader knowledge of Cretaceous terrestrial palynology in Antarctica. *Alisporites* is a genus used for specimens up into the Cretaceous, but it is not typically a Maastrichtian form in Antarctica. Although the specimens illustrated in Fig. 3-24 and -25 appear to have sacci that are no wider than the central body we have retained them within *Podocarpidites* as some well-accepted species of this genus have small sacs (e.g. *Podocarpidites otagoensis* Couper, 1953 and *Podocarpidites rugulatus* Pocknall and Mildenhall, 1984). Further, we consider that Fig. 3-24 is similar to, but not directly

attributable to, *Podocarpidites ellipticus*, and Fig. 3-25 appears to have pleats at the sacci bases, which is a *Podocarpidites* character not generally seen in *Alisporites*. Therefore, we refer the many bisaccate pollen grains of overall *Podocarpidites* character that are unidentifiable beyond generic level (through grain morphology, and also their commonly folded nature in these slides) to this genus.

*?*Potonieisporites* (Bhardwaj, 1954) Bharadwaj, 1964 sp. [Fig. 4-26]

Taxonomic note — Although torn, the specimen illustrated (Fig. 4-26) has a remnant, vertically-aligned, monolete scar.

**Protohaploxylinus ?amplus* (Balme and Hennelly 1955) Hart 1964 [Fig. 4-27]

Taxodiaceapollenites hiatus (Potonié 1931) Kremp 1949 [Fig. 3-20]

Trichotomosulcites subgranulatus Couper, 1953 [Fig. 3-29]

Angiospermae

Clavamonocolpites polygonalis Askin 1994 [Fig. 3-30]

Cranwellia striata (Couper, 1953) Srivastava, 1966 [Fig. 3-31]

Ericipites scabratus Harris, 1965 [Fig. 3-32]

Gambierina rudata Stover in Stover and Partridge, 1973 [Fig. 3-26]

Liliacidites sp. cf. *L. kaitangataensis* Couper, 1953 [Fig. 3-27]

Taxonomic note — As recorded by Askin (1994), the specimens observed in this study compare well to the description of *Liliacidites kaitangataensis*, but are much smaller than the type material.

Liliacidites sp. cf. *L. variegatus* Couper, 1953 [Fig. 3-28]

Taxonomic note — The specimens observed in this study have similar variability to those recorded by Askin (1994). They compare closely to the description of *Liliacidites variegatus*, but vary in their form (elliptical to subspherical), commonly with a finer mesh than the type material.

Liliacidites Couper, 1953 sp. 1 of Askin (1994)

Liliacidites Couper, 1953 spp.

Myricipites sp. cf. *M. cavilloratus* Drugg 1967 [Fig. 3-37]

Taxonomic note — This single specimen is comparable to the type material of *Myricipites cavilloratus*, except for the presence of two pore plugs. Drugg (1967) observed similar specimens with plugged pores referring them only questionably to *Myricipites*, but stated they were probably “aberrant examples of *M. cavilloratus*”.

Nothofagidites asperus (Cookson 1959) Romero 1973 [Fig. 3-40]

Nothofagidites dorotensis Romero 1973 [Fig. 3-39]

Nothofagidites flemingii (Couper, 1953) Potonié 1960 [Fig. 3-34]

Nothofagidites senectus Dettmann and Playford 1968 [Fig. 3-33]

Nothofagidites Erdtman 1947 ex Potonié 1960 spp. [Cluster of adherent grains, Fig. 3-41]

Taxonomic note — The morphological variety and commonly folded nature of *Nothofagidites* spp. grains restricted identification of most specimens to generic level within the scope of this study. *Nothofagidites* spp. grains were all consequently counted to generic rather than species level.

Peninsulapollis askinia Dettmann and Jarzen, 1988 [Fig. 3-42]

Peninsulapollis gillii (Cookson 1957) Dettmann and Jarzen, 1988 [Fig. 3-43]

Taxonomic note — *Peninsulapollis gillii* is only questionably proteaceous and has some, but not all, features of extant *Beauprea* type pollen, which is today endemic to New Caledonia (Pocknall and Crosbie, 1988; Askin and Baldoni, 1998).

Polycopites sp. cf. *P. langstonii* Stover in Stover and Partridge, 1973 [Fig. 4-1]

Taxonomic note — The specimens recorded compare well to the description of the type material, but are larger than the type material at up to 78 µm diameter (for example, Fig. 4-1).

Propylipollis subscabratus (Couper, 1960) Askin 2000 [Fig. 3-35 (adherent cluster), -36]

Proteacidites adenanthoides Cookson 1950 [Fig. 4-2]

Taxonomic note — The two specimens recorded in this study (and that of *Proteacidites* sp. cf. *P. crassus*) in the López de Bertodano Formation extends the known palaeobiogeographical distribution of this type of *Proteacidites* spp. pollen onto the Antarctic Peninsula where it was previously thought to be absent (Askin and Baldoni, 1998).

Proteacidites angulatus Stover in Stover and Partridge, 1973 [Fig. 4-3]

Biostratigraphical note — Known from Australia only from the Paleogene (e.g. Stover and Partridge, 1973; Hill, 1994), the rare occurrence of this taxon below the K–Pg boundary in this study extends its known stratigraphical range back into the Maastrichtian.

Proteacidites sp. cf. *P. crassus* Cookson 1950 [Fig. 4-4]

Taxonomic note — This single specimen is closely comparable with the type description of *Proteacidites crassus* (but it is smaller) and is similar to *Proteacidites adenanthoides* except possessing a coarser reticulum.

Proteacidites parvus Cookson 1950 [Fig. 4-5]

Taxonomic note — These specimens compare well to the description of the type material, but include smaller specimens down to 25 µm diameter (for example, Fig. 4-5).

Proteacidites pseudomoides Stover in Stover and Partridge, 1973 [Fig. 4-9]

Proteacidites sp. cf. *P. scabroratus* Couper, 1960 [Fig. 4-8]

Taxonomic note — The specimens recorded compare well to the description of the type material, but are smaller in size. The illustrated specimen (Fig. 4-8) is 18 µm diameter and the type material ranges between 33 and 46 µm diameter (Couper, 1960).

Proteacidites subpalisadus Couper, 1953 [Fig. 4-10]

Proteacidites Cookson 1950 ex Couper, 1953 sp. 1 [Fig. 4-6]

Taxonomic note — These specimens are similar to specimens classified as *Proteacidites* sp. 3 by Truswell (1983), except for possessing a less prominent ornamentation. *Tripoporollenites ambiguous* Stover in Stover and Partridge, 1973 has a similar ornamentation, but has a slightly more angular amb. Further detailed taxonomic work is required to definitively classify this morphotaxon as either *Proteacidites* Cookson 1950 ex Couper, 1953 or *Tripoporollenites* Pflug & Thomson in Thomson & Pflug 1953. The similarity of the specimens from this study to Truswell's (1983) *Proteacidites* sp. 3, and the placement of *Propylipollis ambiguus* (Stover in Stover and Partridge, 1973) Dettmann & Jarzen 1996 in the Proteaceae allow that, for the present, the designation *Proteacidites* sp. 1 is retained.

Proteacidites Cookson 1950 ex Couper, 1953 spp.

Stellidiopollis annulatus Dettmann and Hedlund 1988 [Fig. 4-7]

Tetracolpites Vimal 1952 ex Srivastava 1967 sp. 1 (aberrant tricolpate pollen) [Fig. 4-11]

Taxonomic note — A single scabrate tetracolpate pollen grain was recorded. It has a quadrangular amb, is symmetrical and angulaperaturate. It has equatorial colpi (but the margins are not thickened), which are incised up to 40% of the grain diameter. *Tetracolpites* sp. of Mildenhall (1994), from the Cretaceous of the Chatham Islands, is similar, but the specimen from this study has a more orthogonal amb and straighter sides. It is also possible that, as only one specimen of this morphotype was recorded, that this is an aberrant tricolpate pollen grain.

?*Nothofagidites* sp. 1 (tetra-aperturate pollen) [Fig. 4-12]

Taxonomic note — Several echinate tetra-aperturate pollen grains were recorded. They have a quadrangular amb, are symmetrical and angulaperaturate. They have equatorial apertures, which have slightly thickened margins and incised up to ~15% of the grain diameter. This morphotype is distinguished from *Tetracolpites* sp. 1 by its smaller size and echinate sculpture. These may be aberrant grains of *Nothofagidites* spp. and further detailed taxonomic analysis is required.

Tricolpites confessus Stover in Stover and Partridge, 1973 [Fig. 4-13]

Tricolpites lilliei Couper, 1953 [Fig. 4-14]

Tricolpites sp. cf. *T. phillipsii* Stover in Stover and Partridge, 1973 [Fig. 4-15]

Taxonomic note — This single specimen recorded compares well to the type material, except for a thicker exine and somewhat longer colpi.

Tricolpites reticulatus Cookson 1947 ex Couper, 1953 [Fig. 4-16]

Tricolpites Cookson 1947 ex Couper, 1953 spp.

Tricolporites Cookson 1947 spp. [Fig. 4-17]

Tripoporollenites Pflug and Thomson in Thomson and Pflug 1953 spp. [Fig. 4-18]

Indeterminate sporomorphs

Taxonomic note — Contemporaneous palynomorphs that appeared to be of terrestrial origin, but were too folded or obscured to identify further.

Fungi

Pluricellaesporites Van der Hammen 1954 sp. [Fig. 4-30]

Indeterminate fungal spores and hyphal fragments.

Freshwater green algae

Botryococcus braunii Kützing, 1849 [Fig. 4-28]

Pediastrum Meyen, 1829 spp. [Fig. 4-31]

Tetraporina Naumova 1939 ex Lindgren 1980 sp. 1 [Fig. 4-32]

?Zygnemataceae spore A [Fig. 4-19]

Taxonomic note: These resemble spores of the freshwater alga, Zygnemataceae (*Zygnema* type), Van Geel and Grenfell, 2002. Supporting this interpretation is their similar range in section D5.251 to *Azolla* spp., suggesting a preference for humid conditions.

?Zygnemataceae spore B [Fig. 4-20]

Taxonomic note: These specimens have a subspherical form with regular, low rounded verrucae and no visible laesurae or other apertures. They occur throughout a similar range in section D5.251 to ?Zygnemataceae spore A and *Azolla* spp. These specimens may be related to the Zygnemataceae.

?Testate amoeba

?Testate amoeba indeterminate (or possibly fungal spore) [Fig. 4-29]

Taxonomic/ecologic note: Very similar to contemporary amoeba species *Cryptodiffugia oviformis* Penard, 1902. Fresh water environments, usually on aquatic vegetation and in *Sphagnum*.

Dinoflagellate cysts

Senegalinium obscurum (Drugg 1967) Stover and Evitt, 1978

Appendix 2. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2014.04.018>.

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