



Southern high-latitude terrestrial climate change during the Palaeocene–Eocene derived from a marine pollen record (ODP Site 1172, East Tasman Plateau)

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Abstract. Reconstructing the early Palaeogene climate dynamics of terrestrial settings in the high southern latitudes is important to assess the role of high-latitude physical and biogeochemical processes in the global climate system. However, whereas a number of high-quality Palaeogene climate records has become available for the marine realm of the high southern latitudes over the recent past, the long-term evolution of coeval terrestrial climates and ecosystems is yet poorly known. We here explore the climate and vegetation dynamics on Tasmania from the middle Palaeocene to the early Eocene (60.7–54.2 Ma) based on a sporomorph record from Ocean Drilling Program (ODP) Site 1172 on the East Tasman Plateau. Our results show that three distinctly different vegetation types thrived on Tasmania under a high-precipitation regime during the middle Palaeocene to early Eocene, with each type representing different temperature conditions: (i) warm-temperate forests dominated by gymnosperms that were dominant during the middle and late Palaeocene (excluding the middle/late Palaeocene transition); (ii) cool-temperate forests dominated by southern beech (*Nothofagus*) and araucarians that transiently prevailed across the middle/late Palaeocene transition interval (~59.5 to ~59.0 Ma); and (iii) paratropical forests rich in ferns that were established during and in the wake of the

Palaeocene–Eocene Thermal Maximum (PETM). The transient establishment of cool-temperate forests lacking any frost-sensitive elements (i.e. palms and cycads) across the middle/late Palaeocene transition interval indicates markedly cooler conditions, with the occurrence of frosts in winter, on Tasmania during that time. The integration of our sporomorph data with previously published TEX₈₆-based sea-surface temperatures from ODP Site 1172 documents that the vegetation dynamics on Tasmania were closely linked with the temperature evolution in the Tasman sector of the Southwest Pacific region. Moreover, the comparison of our season-specific climate estimates for the sporomorph assemblages from ODP Site 1172 with the TEX₈₆^L- and TEX₈₆^H-based temperature data suggests a warm bias of both calibrations for the early Palaeogene of the high southern latitudes.

1 Introduction

The Southern Ocean is an important region for early Cenozoic (65–34 Ma) climates, being the dominant region for deep-water formation during that time (Thomas et al., 2003; Sijp et al., 2011; Hollis et al., 2012). South Pacific

sea-surface and global intermediate water temperatures increased from the late Palaeocene to the early Eocene, with maximum warmth during the Early Eocene Climatic Optimum (EECO; 53–51 Ma), followed by a cooling trend during the middle and late Eocene (Zachos et al., 2001, 2008; Bijl et al., 2009; Hollis et al., 2012). This cooling trend ultimately culminated in the establishment of a continental-scale ice shield on Antarctica during the earliest Oligocene (e.g. Zachos et al., 1994, 2008; Barrett, 1996), which represented a decisive step in the earth's transition from a “greenhouse” into an “icehouse” world.

Organic geochemical surface-water temperature proxy records from the high-latitude Southwest Pacific Ocean (notably TEX₈₆; Bijl et al., 2009) closely mirror trends in the benthic foraminiferal oxygen isotope data from the late Palaeocene to the early Oligocene (Zachos et al., 2001, 2008), which lends further support to the suggestions that the southern ocean was the main region for deep-water formation (Thomas et al., 2003). Irrespective of the calibration used, Southwest Pacific TEX₈₆-derived sea-surface temperatures (SSTs) were relatively cool during the early and middle Palaeocene. During the late Palaeocene and early Eocene, SSTs gradually rose to tropical values (> 26 °C), with maxima being reached during the Palaeocene–Eocene Thermal Maximum (PETM; Sluijs et al., 2011) and the EECO (Bijl et al., 2009; Hollis et al., 2009, 2012). Towards the end of the early Eocene (49–50 Ma), a pronounced SST cooling of ~4 °C occurred on the Australo-Antarctic margin; this cooling has been attributed to the onset of westbound surface-water throughflow across the Tasmanian Gateway (Bijl et al., 2013a). A similar cooling trend is registered for surface waters off New Zealand (Hollis et al., 2009, 2012) and in the Tasman sector of the Southwest Pacific Ocean (Bijl et al., 2009; Hollis et al., 2012). Strikingly low SSTs are recorded for the high-latitude Southwest Pacific Ocean during the interval spanning the middle/late Palaeocene transition (59.5–59.0 Ma); TEX₈₆-derived SST decreased by ~3 °C during that time (Bijl et al., 2009; Hollis et al., 2012, 2014). Along with this SST drop, lowered sea level and marked bathyal erosion suggest that a transient growth of an Antarctic ice sheet may have occurred (Hollis et al., 2014).

While an increasing amount of data has become available on the marine climate evolution in the southern high latitudes during the early Palaeogene, the coeval terrestrial climate dynamics of that region are yet poorly documented (e.g. Passchier et al., 2013). For the Palaeocene, palaeobotanical records reflect the thriving of temperate, gymnosperm-rich forests dominated by podocarps in Southeast Australia (e.g. Macphail et al., 1994; Greenwood et al., 2003; Greenwood and Christophel, 2005), on Seymour Island (Antarctica; Askin, 1990), and in New Zealand (Mildenhall, 1980; Raine et al., 2009).

In contrast, highly diverse angiosperm forests containing taxa that today are restricted to tropical environments characterize the early Eocene vegetation in the higher-latitude

Southwest Pacific region. This vegetation is widely known from Southeast Australia (Macphail et al., 1994; Greenwood et al., 2003; Greenwood and Christophel, 2005), Tasmania (Truswell, 1997; Carpenter et al., 2012) and New Zealand (Raine et al., 2009; Handley et al., 2011); notably, it also thrived on the Wilkes Land margin of the Antarctic continent, i.e. at palaeo-latitudes of ~70° South (Pross et al., 2012; Contreras et al., 2013).

The pronounced vegetation turnover from temperate forests during the Palaeocene to near-tropical forests during the early Eocene suggests a marked, climatically driven change in terrestrial environments in the high southern latitudes. However, the transitional process between these two vegetation types and the underlying change in terrestrial climate conditions of the Southwest Pacific region have remained poorly understood. The gaps in the documentation of terrestrial climate dynamics during the early Palaeogene appear particularly pronounced considering the coeval data sets for the marine realm from the same region (Bijl et al., 2009, 2013a; Hollis et al., 2009; 2012, 2014). This is due to the fact that prior palaeobotanical studies are mainly based on stratigraphically discontinuous outcrops that provided only limited insights into the Palaeocene and early Eocene vegetation of the region (Greenwood et al., 2003). In addition, available studies on sporomorphs from the early Palaeogene of the Southwest Pacific region have predominantly focused on the taxonomical characterization of the assemblages and the generation of biostratigraphic schemes (e.g. Stover and Evans, 1973; Stover and Partridge, 1973; Truswell, 1997; Macphail, 1999). In any case, estimates of terrestrial temperatures in the high southern latitudes and a comparison with the currently available SST estimates from the marine realm can strongly enhance the understanding of the climate evolution in the high southern latitudes during the early Palaeogene.

In light of the above, we here explore the vegetation response to high-southern-latitude climate forcing from the Palaeocene to the “hothouse” conditions of the early Eocene based on a new, chronostratigraphically well-calibrated (Bijl et al., 2013b) sporomorph record from Ocean Drilling Program (ODP) Site 1172 off eastern Tasmania. We quantitatively evaluate the compositional variations of the sporomorph assemblages and carry out quantitative sporomorph-based palaeoclimatic reconstructions. For a further assessment of the terrestrial climatic conditions in the Southwest Pacific region, we apply the same palaeoclimate reconstruction approach to previously published sporomorph records from Southeast Australia (Bass Basin, Gippsland Basin, Southeast Highlands) and New Zealand. Finally, we compare our terrestrial palaeoclimate estimates with previously published TEX₈₆-based (i.e. TEX₈₆^L and TEX₈₆^H calibrations; Kim et al., 2010) SST reconstructions from the same site (Bijl et al., 2009, 2013b; Hollis et al., 2014) in order to contribute to a better understanding of the early Palaeogene climate dynamics in the high southern latitudes.

1.1 Regional setting and palaeoceanography

During the early Palaeogene, Tasmania and the East Tasman Plateau (ETP) were located at $\sim 65^\circ$ S, much closer to Antarctica than today (Exon et al., 2004b). Palaeoceanographic patterns as determined by winds and gateway configuration were likely vital for regional climates on land (Sijp et al., 2011). The study site was located close to the Tasmanian promontory, which hampered deep ocean exchange between the Southwest Pacific and the Australo-Antarctic Gulf for most of the early Palaeogene (Shipboard Scientific Party, 2001b; Stickley et al., 2004; Fig. 1). During the Palaeocene and early Eocene, the Tasman region was under the persistent influence of the Antarctic-derived Tasman Current; in contrast, the Australo-Antarctic Gulf (west of Tasmania) was bathed by the low-latitude-derived proto-Leeuwin Current (Huber et al., 2004; Sijp et al., 2011; see Fig. 1). This palaeoceanographic configuration determined marine biogeographical patterns in the region (Huber et al., 2004; Bijl et al., 2011, 2013a). The onset of the deepening of the Tasmanian Gateway at ~ 49 – 50 Ma initiated a westbound Antarctic Counter Current flowing along the Antarctic margin from the Pacific into the Australo-Antarctic Gulf (Bijl et al., 2013a). Continued rifting through the Eocene and accelerated deepening of the Tasmanian Gateway (~ 35.5 Ma) led to the inflow of Australo-Antarctic Gulf waters through the Tasmanian Gateway into the southern Pacific during the early Oligocene (Stickley et al., 2004; Sijp et al., 2011). These palaeoceanographic reorganizations had important effects on terrestrial climates in the Australo-Antarctic region (Bijl et al., 2013a).

2 Material and methods

The middle Palaeocene to early Eocene strata studied here were recovered at ODP Site 1172, which is located ~ 100 km east of Tasmania on the western side of the East Tasman Plateau (ETP; $43^\circ 57.6' \text{ S}$, $149^\circ 55.7' \text{ E}$; Fig. 1) (Shipboard Scientific Party, 2001b).

2.1 Age model, lithology and depositional environment

We here follow the corrected sample depths for ODP Hole 1172D as published in Sluijs et al. (2011) based on detailed correlation of the X-ray fractionation core scanning to the γ -ray downhole log. The age model of the studied sequence is based on the magnetostratigraphy, chemostratigraphy and dinoflagellate cyst (dinocyst) biostratigraphy as presented in Bijl et al. (2013b). For the interval studied (60.7–54.2 Ma), the age model is based on three magnetic reversals confidently correlated to the Geomagnetic Polarity Time Scale (GPTS) of Vandenberghe et al. (2012), the PETM (~ 56 Ma), which exhibits a negative carbon isotope excursion of $\sim 3\%$ between 611.89 and 611.86 rmbfsf (revised metres below sea floor) (Sluijs et al., 2011), and several dinocyst first and last occurrence data that have been calibrated regionally fol-

lowing Crouch et al. (2014). The magnetostratigraphic age model for the Palaeocene section (Röhl et al., 2004) was adjusted by Bijl et al. (2010) on the basis of the recognition of the PETM in Core 1172D-15R (611.8 rmbfsf; Sluijs et al., 2011). The missing interval between Cores 16R and 17R (~ 620 rmbfsf) represents a ~ 1.3 Ma-long hiatus that spans the time interval correlative to between infra-subchrons C26n and C25n (57.7–59 Ma; Bijl et al., 2010, 2013b).

The upper 60 cm of section in Core 17R (i.e. below the hiatus) are heavily disturbed and have many sediment characteristics more consistent with Core 16R than with the underlying sediment (Röhl et al., 2004). We therefore follow Röhl et al. (2004) in their suggestion that this interval represents caved material of late Palaeocene age.

The middle Palaeocene to Lower Eocene succession of ODP Site 1172 consists mainly of grey to greyish brown clay- and siltstones with low abundances of calcareous and siliceous microfossils (Shipboard Scientific Party, 2001a; Röhl et al., 2004). Environmentally, the succession is interpreted to reflect very shallow to restricted marine conditions, with marked runoff from the nearby shores (Röhl et al., 2004).

Any study on sporomorphs from marine sediments critically relies on the identification of the source region in order to provide meaningful palaeoclimatic information. An in-depth discussion of this issue is provided in Sect. 4.1.

2.2 Sample processing and data analysis

Eighty-nine samples from the Palaeocene and Eocene of ODP Site 1172, originally processed at the Laboratory of Palaeobotany and Palynology, Utrecht University (Bijl et al., 2011), were here reanalysed for terrestrial palynomorphs. Sample processing followed standard palynological techniques, including treatment with HCl (10 %) and HF (38 %) and sieving through a $15 \mu\text{m}$ nylon mesh (e.g. Pross, 2001). The microscope slides were prepared using glycerine jelly as a mounting medium. The residues and slide preparations are stored in the collection of the Laboratory of Palaeobotany and Palynology at Utrecht University. Whenever possible, 300 sporomorphs (excluding reworked specimens) were analysed per sample and determined to the species level; this required the analysis of up to six slides per sample. The analyses were performed using a light microscope at 200x magnification; morphological details were studied with a magnification of 1000x. Sporomorph identifications are mainly based on Couper (1960), Harris (1965), Stover and Partridge (1973), Truswell (1983), Raine et al. (2008) and Truswell and Macphail (2009). The botanical affinities are given following Macphail et al. (1994), Raine (1998) and Truswell and Macphail (2009). All sporomorph data (including photomicrographs of key taxa) are provided in the Supplementary Information.

Rarefaction was applied to evaluate sporomorph diversity; this allows us to estimate the number of sporomorph species

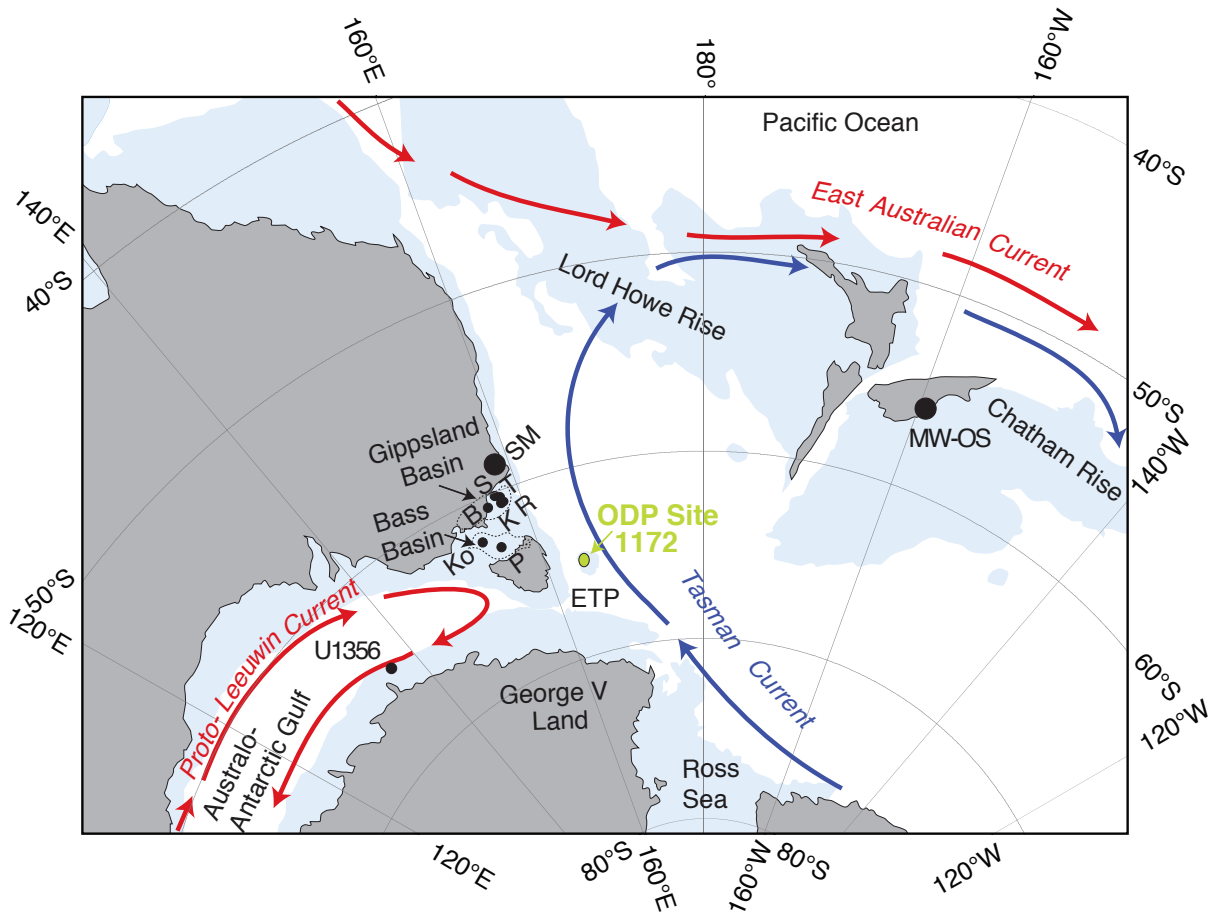


Figure 1. Map of the Southwest Pacific Ocean showing the early Eocene (~53 Ma) continental configuration, illustrating modern continents (grey), areas shallower than 300 m (blue) and locations of ODP Site 1172 and localities listed in Table 1. SM = Southern Monaro Sections (Southeast Highlands), B = Burong-1, K = Kingfish-8, Ko = Konkon-1, MW-OS = Middle Waipara and Otaio River sections, P = Poonboon-1, R = Roundhead-1, S = Sweetlips-1, T = Turrum-4, ETP = East Tasman Plateau. Modified after Cande and Stock (2004) and Sluijs et al. (2011).

at a constant sample size (Raup, 1975). Detrended correspondence analysis (DCA) is an ordination technique that was used to analyse floral composition change through time.

To constrain the source region of the sporomorphs from ODP Site 1172, we compared the floristic composition of our record with coeval sporomorph records from Southeast Australia (Bass Basin – data from Blevin, 2003; Gippsland Basin – Department of Primary Industries, 1999; Southeast Highland sections – Taylor et al., 1990) and New Zealand (Middle Waipara and Otaio River sections – Pancost et al., 2013) using DCA (see Fig. 1 for locations and Table 1 for further details and references). From all records derived from drill holes, only data from core or sidewall core samples were evaluated to avoid potential contamination by caving. To exclude a bias as it could have been introduced into our comparison through different taxonomic criteria, we have standardized all data sets using broader groups of taxa (e.g. *Gleicheniidites* spp./*Clavifera* spp., *Phyllocladites* spp., *Nothofagidites* spp. [*fusca* group]) when neces-

sary. Due to the differences in sample sizes, sporomorph percentages were used as input for the DCA, and only samples with counts ≥ 100 individuals were evaluated.

2.3 Sporomorph-based climate reconstructions

Quantitative sporomorph-based climate estimates were carried out following the bioclimatic analysis approach of Greenwood et al. (2005). For each taxon with a known nearest living relative (NLR; Table 2), climatic profiles were generated with regard to mean annual temperature (MAT), coldest month mean temperature (CMMT), warmest month mean temperature (WMMT), and mean annual precipitation (MAP). The climate profiles are derived from (i) the data set of Pross et al. (2012), which is mainly based on distribution data from the Australian National Herbarium online database (Australian National Herbarium, 2011) and the mathematical climate surface software ANUCLIM 5.156 (Houlder et al., 1999), and (ii) the PALAEOFLORA database, which contains climatic information for a plant taxon based on its

Table 1. Sporomorph data sets evaluated in this study from the Southeast Australia (Bass Basin, Gippsland Basin, Southeast Highlands) and New Zealand (Middle Waipara and Otaio River sections). Asterisks indicate data derived from palynological reports in Department of Primary Industries (1999). Plus signs denote data derived from Appendix C of Blevin (2003). Biozones and ages are based on Stover and Evans (1973), Stover and Partridge (1973) and Partridge (2006).

Section	Region	Age	Pollen biozone	Authors
Southern Monaro sections	highlands of southeastern Australia	60–58 Ma	Lygistepollenites balmei	Taylor et al. (1990)
Burong-1	onshore Gippsland Basin	late Palaeocene	Upper L. balmei	* Partridge and Macphail (1997)
Kingfish-8	offshore Gippsland Basin	early Eocene	Lower Malvacipollis diversus	* Partridge (1992)
Konkon-1	Bass Basin	middle to late Palaeocene, early Eocene	L. balmei and Lower M. diversus	+ Partridge (2003)
Otaio and Middle Waipara sections	New Zealand	58–56 Ma		Pancost et al. (2013).
Poonboon-1	Bass Basin	late Palaeocene, early Eocene	Upper L. balmei, Lower M. diversus	+ Partridge (2003)
Roundhead-1	offshore Gippsland Basin	middle to late Palaeocene, early Eocene	L. balmei, Lower M. diversus	* Partridge (1989)
Sweetlips-1	offshore Gippsland Basin	middle to late Palaeocene	L. balmei	* Partridge (1989)
Turrum-4	offshore Gippsland Basin	middle to late Palaeocene	L. balmei	* Partridge (1993)
Turrum-4	offshore Gippsland Basin	middle to late Palaeocene	L. balmei	* Partridge (1993)

global distribution (Utescher and Mosbrugger, 2013). Following Greenwood et al. (2005), the climatic values for each assemblage were calculated based on the zone of overlap of the majority of taxa from that assemblage with respect to a given climate parameter. This overlap interval was calculated using the 10th percentile (as lower limit) and 90th percentile (as upper limit) of the total range of the NLRs recorded in that assemblage. The climate estimate is given as the midpoint between the lower and upper limits, with the error spanning from the lower to the upper limit. Only samples with counts ≥ 100 individuals were used in the climate reconstructions.

Palaeoclimate estimates based on the NLR concept may be influenced by a number of factors that need to be considered prior to the application of NLR-based reconstruction methods (e.g. Mosbrugger and Utescher, 1997; Mosbrugger, 1999; Pross et al., 2000; Utescher et al., 2000). These factors include (i) the potential misidentification of the fossil taxa and/or NLRs; (ii) the potentially incomplete coverage of the climatic tolerances of the NLRs; (iii) potentially unidentified differences between the climatic tolerances of fossil taxa and their NLRs; and (iv) a weakening of the connection between fossil taxa and NLRs the further one goes back in time. Generally, these issues become increasingly important with the age of the floras analysed and may diminish the significance of the results (e.g. Poole et al., 2005). They can, however, be identified and corrected via the application of multi-proxy approaches. In particular, the NLR concept has been successfully applied to both macrofloral and sporo-

morph assemblages from the early Palaeogene of the higher southern latitudes (Greenwood et al., 2003; Carpenter et al., 2012; Pross et al., 2012; Contreras et al., 2013); the validity of the NLR-based results has been demonstrated through the comparison with data from other, independent proxies.

2.4 Statistical examination of the connection between floristic composition and temperature

To examine the correlation between the floristic composition of our sporomorph record from ODP Site 1172 (as represented by DCA Axis 1 sample scores; Figs. 2 and 4) and $\text{TEX}_{86}^{\text{L}}$ - and $\text{TEX}_{86}^{\text{H}}$ -derived SST values from the same site (Bijl et al., 2013b; Hollis et al., 2014), we applied a state space model. State space models or dynamic linear models allow data distributed along time to be interpreted as the combination of several components, such as trends, or seasonal or regressive components (Petris et al., 2009; see West and Harrison, 1997, for further details on the advantages and development of the method). In essence, we modelled the dynamics of the “true” (but unknown) SST and DCA Axis 1 sample scores in time, and modelled the observed values as deviations from these true values.

The model was fitted with a Bayesian approach. The likelihood is defined by Eqs. (1) and (2), with both SST and DCA for each time point where either one or both was measured. We compared 60 SST data points with our 40 values of the DCA Axis 1 scores. Because only six of the SST data points and DCA Axis 1 sample scores are from the exact

Table 2. List of fossil sporomorph taxa from the middle Palaeocene to Lower Eocene of ODP Site 1172 with known botanical affinities and literature source, the nearest living relative (NLR) used in the climate reconstruction, and database where climate profiles of the NLRs are derived from. Database (1)=PALAEOFLORA (Utescher and Mosbrugger, 2013), Database (2)=Pross et al. (2012). Taxa used in the climatic evaluation are printed in boldface.

Fossil taxon	Botanical affinity	Source	NLR used for climate analysis	Database
Araucariacites spp.	Araucariaceae	Raine et al. (2008)	Araucariaceae	1, 2
Arecipites spp.	Arecaceae	Nichols et al. (1973)	Arecaceae	1
Baculatisporites spp.	Osmundaceae	Raine et al. (2008)	Osmundaceae	1
<i>Banksiaeaidites arcuatus</i>	Proteaceae (<i>Banksia</i> , <i>Dryandra</i> , <i>Musgravea</i>)	Raine et al. (2008)		
<i>Beaupreaaidites</i> cf. <i>diversiformis</i>	Proteaceae (<i>Beuprea</i>)	Raine et al. (2008)		
<i>Caryophyllidites</i> sp.	Caryophyllaceae	Raine et al. (2008)		
<i>Ceratosporites</i> spp.	<i>Lycopodiaceae</i> , <i>Selaginellaceae</i>	Raine et al. (2008)		
Crassoretitrites cf. <i>vanraadshooveni</i>	<i>Lygodium</i>	Germeraad et al. (1968)	<i>Lygodium</i>	1
Cyathidites spp.	Probably Cyatheaceae	Mohr (2001)	Cyatheaceae	1
Cycadopites spp.	Cycadales	Raine et al. (2008)	Cycadales: <i>Bowenia</i> , <i>Lepidozamia</i> , <i>Macrozamia</i>	1
Dacrycarpites australiensis	Podocarpaceae (<i>Dacrycarpus dacrydioides</i>)	Raine et al. (2008)	<i>Dacrycarpus</i>	1
Dacrydimites florinii	Podocarpaceae (<i>Dacrydium</i>)	Raine et al., 2008	<i>Dacrydium</i>	1
Dacrydimites spp.	Podocarpaceae (<i>Dacrydium</i>)	Raine et al. (2008)	<i>Dacrydium</i>	1
<i>Dilwynites granulatus</i>	Araucariaceae (<i>Wollemia/Agathis</i>)	Macphail et al. (2013)		
<i>Dilwynites tuberculatus</i>	Araucariaceae (<i>Wollemia/Agathis</i>)	Macphail et al. (2013)		
<i>Ephedripites</i> sp.	<i>Ephedra</i>			
Gleicheniuidites senonicus	Gleicheniaceae	Raine et al. (2008)	<i>Dicranopteris</i> , <i>Diplopterygium</i> , <i>Gleichenia</i> , <i>Sticherus</i>	1
Gleicheniuidites spp.	Gleicheniaceae	Raine et al. (2008)	<i>Dicranopteris</i> , <i>Diplopterygium</i> , <i>Gleichenia</i> , <i>Sticherus</i>	1
<i>Intratripopollenites</i> cf. <i>notabilis</i>	Sterculioideae?, Bombacoideae?, Tilioidae?	Raine et al. (2008)		
Malvacipollis diversus	Euphorbiaceae (<i>Austroboxus</i> , <i>Dissiliaria</i> , <i>Petalostigma</i>); Eumalvoideae?	Raine et al. (2008)	Euphorbiaceae	1
Microalatidites spp.	Podocarpaceae (cf. <i>Phyllocladus</i>)	Raine et al. (2008)	<i>Phyllocladus</i>	1
Microcachrydites antarcticus	Podocarpaceae (<i>Microstrobus</i> , <i>Microcachrys tetragona</i>)	Raine et al. (2008)		
Myricipites harrisii	Casuarinaceae, possibly also Myricaceae	Raine et al. (2008)	Casuarinaceae (all Australian species)	1
Myrtacidites spp.	Myrtaceae	Raine et al. (2008)	Myrtaceae	1
Nothofagidites asperus complex	Nothofagaceae (<i>Nothofagus</i> subg. <i>Lophozonia</i>)	Truswell and Macphail (2009)	<i>N. cunninghamii</i> , <i>N. moorei</i>	1
Nothofagidites brachyspinulosus complex	Nothofagaceae (<i>Nothofagus</i> subg. <i>Fuscospora</i>)	Truswell and Macphail (2009)	Nothofagaceae (<i>Nothofagus</i> subg. <i>Fuscospora</i>)	2
Nothofagidites emarcidus complex (including <i>N. endurus</i>)	Nothofagaceae (<i>Nothofagus</i>)	Truswell and Macphail (2009)	all subgenera (including <i>Brassospora</i>)	2
Nothofagidites flemingii complex	Nothofagaceae (<i>Nothofagus</i> subg. <i>Nothofagus</i>)	Raine et al. (2008)	Nothofagaceae (<i>Nothofagus</i> subg. <i>Fuscospora</i>)	2
Nothofagidites lachlaniae complex	Nothofagaceae (<i>Nothofagus</i> subg. <i>Fuscospora</i>)	Raine et al. (2008)	Nothofagaceae (<i>Nothofagus</i> subg. <i>Fuscospora</i>)	2
Nothofagidites sp.1	Nothofagaceae (<i>Nothofagus</i>)		all subgenera (including <i>Brassospora</i>)	2
Nothofagidites spp. undifferentiated	Nothofagaceae (<i>Nothofagus</i>)		all subgenera (including <i>Brassospora</i>)	2
Osmundacidites spp.	Osmundaceae	Raine et al. (2008)	Osmundaceae	1
<i>Parvisaccites catastus</i>	Podocarpaceae (<i>Halocarpus</i>)	Raine et al. (2008)		
Phyllocladidites mawsonii	<i>Lagarostrobos</i>	Raine et al. (2008)	<i>Lagarostrobos</i>	2
Podocarpidites ellipticus	Podocarpaceae (<i>Podocarpus</i>)	Raine et al. (2008)	<i>Podocarpus</i>	1
<i>Podocarpidites exiguus</i>	Podocarpaceae	Raine et al. (2008)		
Proteacidites adenanthoides	Proteaceae (<i>Adenanthos</i>)	Raine et al. (2008)	<i>Adenanthos</i>	2
Proteacidites annularis	Proteaceae (<i>Xylomelum occidentale</i> or <i>Lambertia</i>)	Raine et al. (2008)	<i>Xylomelum</i> (all Australian species)	2

Table 2. Continued.

Fossil taxon	Botanical affinity	Source	NLR used for climate analysis	database
<i>Proteacidites</i> cf. <i>amolosexinus</i>	Proteaceae (<i>Knightia excelsa</i> type)	Raine et al. (2008)		
<i>Proteacidites</i> cf. <i>adenanthoides</i>	Proteaceae (<i>Adenanthos</i>)	Raine et al. (2008)	<i>Adenanthos</i>	2
<i>Proteacidites parvus</i>	Proteaceae (<i>Bellendena montana</i> type)	Raine et al. (2008)	<i>Bellendena montana</i>	2
<i>Proteacidites reticulosabratus</i>	Proteaceae (<i>Gevuina/Hicksbeachia</i> type)	Raine et al. (2008)	<i>Gevuina, Hicksbeachia</i>	2
<i>Proteacidites symphyonemoides/P. pseudomoides</i>	Proteaceae (<i>Symphyonema, Carnarvonia</i>)	Raine et al. (2008)	<i>Symphyonema, Petrophile</i>	2
<i>Pseudowinterapollis</i> sp.	Winteraceae	Raine et al. (2008)		
<i>Retitriletes</i> cf. <i>rosewoodensis</i>	Lycopodiaceae (<i>Lycopodium</i>)	Raine et al. (2008)		
<i>Retitriletes facetus</i>	Lycopodiaceae (<i>Lycopodium</i>)	Raine et al. (2008)		
<i>Rubinella</i> cf. <i>major</i>	<i>Leptolepis?</i>	Raine et al. (2008)		
<i>Spinizonocolpites prominatus</i>	<i>Nypa</i> (Arecaceae)	Muller (1968)	<i>Nypa</i>	1
<i>Stereisporites</i> sp.	Sphagnaceae	Truswell and Macphail (2009)		
<i>Triporoletes</i> cf. <i>reticulatus</i>	cf. <i>Riccia beyrichiana</i>	Raine et al. (2008)		
<i>Troporopollenites ambiguus</i>	Proteaceae (<i>Telopea truncata, Oreocallis pinnata</i>)	Raine et al. (2008)		
<i>Tripunctisporites maastrichtiensis</i>	Sphagnaceae?			

same depths, we treated the missing data with multiple imputation; in essence, we estimated them as extra parameters to be estimated (e.g. Gelman et al., 2003). The cross-covariance between two points was calculated following Eq. (3) and the final correlation using Eq. (4):

$$SST_i \sim N(x_{SST}(t(i)), \tau_{SST}^2) \quad (1)$$

$$DCA_i \sim N(x_{DCA}(d(i)), \tau_{DCA}^2) \quad (2)$$

$$\Delta d \begin{pmatrix} \sigma_{11}^2 & \rho\sigma_{11}\sigma_{22} \\ \rho\sigma_{11} & \sigma_{22} \end{pmatrix} + \begin{pmatrix} \sigma_{SST}^2 & 0 \\ 0 & \sigma_{DCA}^2 \end{pmatrix} \quad (3)$$

$$\text{corr}(SST, DCA) = \frac{\Delta t \rho \sigma_{DCA} \sigma_{SST}}{\sqrt{(\Delta t + \tau_{DCA}^2)(\Delta t \sigma_{SST}^2 + \tau_{SST}^2)}} \quad (4)$$

The model was fitted using OpenBUGS run through the BRugs package (Thomas et al., 2006) of the R software for statistical computing (R Development Core Team, 2011) fitted in a Bayesian framework using the BRugs package. The R script and further explanation of the analysis is given in the Supplementary Information.

3 Results

3.1 Sporomorph results from ODP Site 1172

Of the 89 palynological samples processed from the middle Palaeocene to Lower Eocene of ODP Site 1172, 40 samples yielded sporomorph counts ≥ 100 individuals and were further used in our analyses. The preservation of sporomorphs is generally good. A total of 197 sporomorph types were identified. A range chart with the relative abundances of key taxa is presented in Fig. 2; a full account of the identified taxa and

their abundance data along with photomicrographs of key taxa is provided in the Supplementary Information. Based on rarefied values, the entire study interval is characterized by rich sporomorph assemblages (mean \pm s.d. = 29.2 ± 3.4 taxa/sample at 100 individuals, $n = 40$). Remarkably low sporomorph species numbers are recorded for the samples corresponding to the PETM (22.8 and 24.5 species/sample at 100 individuals; Fig. 2). The DCA results of our sporomorph record yield distinctly different values for the Axis 1 and Axis 2 sample scores (Fig. 3a). They allow us to define three sample groups, with each sample group being characteristic for specific time intervals of our record (Fig. 3a). These intervals are: (i) the middle (60.7–59.5 Ma) and late Palaeocene (59.0–55.6 Ma); (ii) the middle/late Palaeocene transition (~ 59.5 to ~ 59.0 Ma); and (iii) the early Eocene including the PETM (55.6–54.2 Ma). All three sample groups comprise characteristic sporomorph assemblages that are portrayed in the following.

3.1.1 Middle Palaeocene (60.7–59.5 Ma) and late Palaeocene (59.0–55.6 Ma) intervals

The sporomorph assemblages from the middle and late Palaeocene intervals (excluding the middle/late Palaeocene transition, see below) are represented by 20 samples. They are dominated by gymnosperm pollen, which on average accounts for 45 % of all sporomorphs. The gymnosperm pollen is represented mainly, in the order of decreasing abundances, by *Podocarpidites* spp. (botanical affinity: Podocarpaceae; podocarps), *Dilwynites granulatus* (*Wollemia* [Wollemi pine]/*Agathis* [Kauri]; Macphail et al., 2013), *Phyllocladites mawsonii* (*Lagarostrobos franklinii*; Huon pine), and

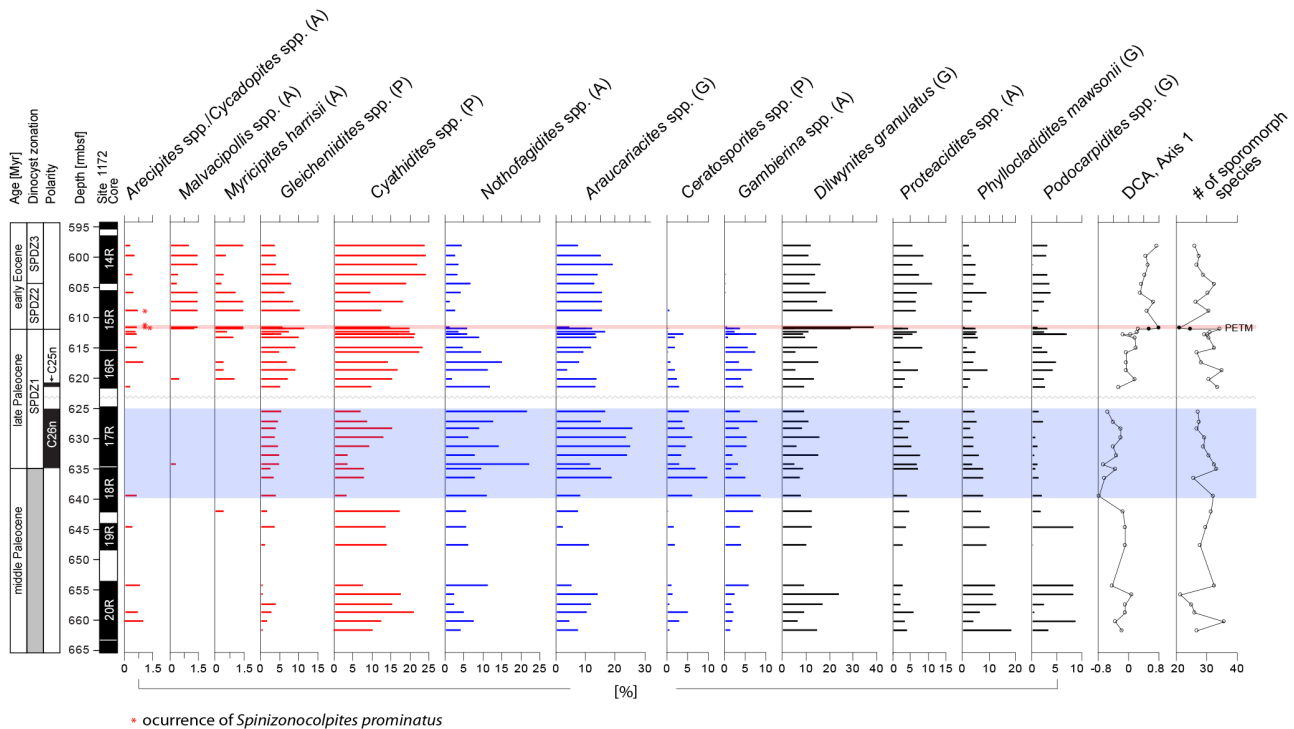


Figure 2. Relative abundances of selected sporomorph taxa ((A) angiosperms, (G) gymnosperms, (P) pteridophytes) representative of the middle Palaeocene to early Eocene assemblages from ODP Site 1172. DCA Axis 1 scores represent the fluctuations in floristic composition between samples. Relative abundances and DCA results are based on samples with counts ≥ 100 individuals only. Numbers of sporomorph species are rarefied at 100 individuals. The intervals corresponding to the middle/late Palaeocene transition and PETM are marked by horizontal blue and red bars, respectively. Age model and dinocyst zonation after Bijl et al. (2013b).

Araucariacites spp. (Araucariaceae; *Agathis* [Kauri] and *Araucaria*) (Fig. 2). Other abundant sporomorphs are, in the order of decreasing abundances, *Cyathidites* spp. (probably Cyatheaceae), *Nothofagidites* spp. (*Nothofagus*; southern beech), *Gambierina* spp., *Gleichenioidites* spp. (Gleicheniaceae) and *Ceratosporites* spp. (Lycopodiaceae, Selaginellaceae).

Although the sporomorph assemblages from the middle to late Palaeocene have very similar floristic compositions, differences exist with regard to the percentages of some taxa (Fig. 2). For instance, the early part of the middle Palaeocene exhibits relatively high ($\sim 30\%$) percentage of podocarpaceous pollen – mainly *Podocarpidites* spp. (Podocarpaceae; podocarps) and *Phyllocladites mawsonii* (*Lagarostrobos franklinii*; Huon pine). In contrast, the latest Palaeocene is characterized by lower abundances of these taxa ($\sim 14\%$), but exhibits higher percentages of *Cyathidites* spp. ($\sim 18\%$) and the constant presence of *Myricipites harrisii* (probably Casuarinaceae; sheoak). Remarkably, both the middle and late Palaeocene are characterized by the presence of *Arecipites* spp. (Arecaceae; palms) and *Cycadopites* spp. (Cycadales).

3.1.2 Middle/late Palaeocene transition interval (59.5–59.0 Ma)

The sporomorph assemblages of the middle/late Palaeocene transition interval are represented by 10 samples. They exhibit higher percentages of *Araucariacites* spp. (Araucariaceae; $\sim 19\%$), *Nothofagidites* spp. (*Nothofagus*; $\sim 13\%$) and *Ceratosporites* spp. (Lycopodiaceae, Selaginellaceae; $\sim 6\%$) than the assemblages from the under- and overlying Palaeocene strata described in Sect. 3.1.1 (Fig. 2). Other abundant taxa are, in the order of decreasing abundances, *Cyathidites* spp. (Cyatheaceae), *Dilwynites granulatus* (*Wollemia/Agathis*) and *Gleichenioidites* spp. (Gleicheniaceae). The percentages of podocarpaceous types (*Podocarpidites* spp. (Podocarpaceae) and *Phyllocladites mawsonii* (*Lagarostrobos franklinii*)) are lower ($\sim 10\%$) than in assemblages from the under- and overlying middle and late Palaeocene. Notably, the assemblages from the middle/late Palaeocene transition interval are devoid of *Arecipites* spp. (Arecaceae; palms) and *Cycadopites* spp. (Cycadales) pollen.

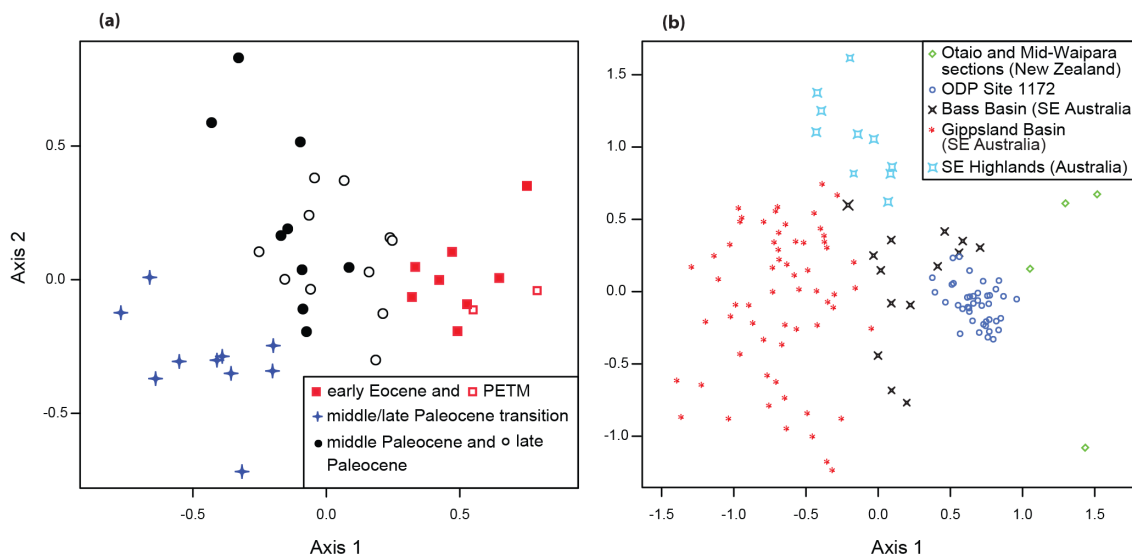


Figure 3. Comparison of the floristic composition based on the DCA sample scores for (a) middle Palaeocene to early Eocene sporomorph assemblages from ODP Site 1172 (Axis 1: 14.6 % of variance; Axis 2: 9.6 % of variance); (b) Palaeocene/early Eocene sporomorph assemblages from Southeast Australia (Bass Basin, Gippsland Basin, Southeast Highlands), New Zealand (Middle Waipara and Otaio River sections) and ODP Site 1172 (Axis 1: 38.9 % of variance; Axis 2: 23 % of variance). Results are based on samples with counts ≥ 100 individuals only.

3.1.3 PETM and early Eocene interval (55.6–54.2 Ma)

Assemblages from the PETM are documented in two samples with counts ≥ 100 individuals. They are characterized by high percentages (up to 39 %) of *Dilwynites granulatus* (*Wollemia/Agathis*). Other abundant taxa are, in the order of decreasing abundances, *Cyathidites* spp. (Cyatheaceae), *Araucariacites* spp. (Araucariaceae), and *Gleicheniidites* spp. (Gleicheniaceae). The assemblages of the PETM interval are further characterized by the presence of *Malvacipollis* spp. (Euphorbiaceae, probably Eumalvoideae) and *Myricipites harrisii* (probably Casuarinaceae). Findings of *Spinizonocolpites prominatus* (*Nypa* palm) are restricted to the PETM and the earliest Eocene (Fig. 2).

Sporomorph assemblages of the early Eocene interval are documented in 8 samples. They show in general very high percentages (mean: 20 %) of *Cyathidites* spp. (probably Cyatheaceae; Fig. 2). Other abundant taxa are, in the order of decreasing abundances, *Dilwynites granulatus* (*Wollemia/Agathis*), *Araucariacites* spp. (Araucariaceae), *Podocarpidites* spp. (Podocarpaceae), and *Phyllocladidites mawsonii* (*Lagarostrobos franklinii*). The early Eocene interval is also characterized by relatively high percentages of *Proteacidites* spp. (~ 7 %) and the constant presence of *Malvacipollis* spp. (Euphorbiaceae, probably Eumalvoideae), *Myricipites harrisii* (probably Casuarinaceae), *Arecipites* spp. (Arecaceae; palms), and *Cycadopites* spp. (Cycadales).

3.2 Sporomorph-based palaeoclimate estimates

The palaeoclimate estimates derived from the sporomorph assemblages from ODP Site 1172 are presented in Fig. 4. Weighted averages with their respective propagated errors are given in Table 3. For the middle Palaeocene (60.7–59.5 Ma), all reconstructed temperature parameters yield relatively cool values (MAT = 9–16 °C; CMMT = 5–9 °C; WMMT = 15–22 °C). A pronounced further cooling is documented in all temperature parameters for the middle/late Palaeocene transition interval (59.5–59.0 Ma). The reconstructed values represent the lowest temperatures of the entire record; values are 8–14 °C for MAT, 4–7 °C for CMMT and 15–20 °C for WMMT (see Fig. 4). Markedly higher temperatures prevailed during the late Palaeocene (59.0–55.6 Ma) and early Eocene (55.6–54.2 Ma), with estimates for that interval being on the order of 11–22 °C for MAT, 6–18 °C for CMMT and 17–26 °C for WMMT. The highest temperatures of the entire study interval are recorded for the Palaeocene/Eocene transition interval (including the PETM); MAT, CMMT and WMMT reached values of ~ 22 °C, ~ 18 °C and ~ 26 °C, respectively, during that time (Fig. 4). The sporomorph-based MAP estimates yield high (138–208 cm/yr $^{-1}$; see Fig. 4 and Table 3), near-constant values throughout the sequence studied.

Table 3. Sporomorph-based climate estimates for Palaeocene to early Eocene records from Southeast Australia (Bass Basin, Gippsland Basin, Southeast Highlands), New Zealand (Middle Waipara and Otaio River sections) and ODP Site 1172. SST values given for each stratigraphic interval represent average values of the data of Bijl et al. (2013b) and Hollis et al. (2014), with (H) and (L) denoting $\text{TEX}_{86}^{\text{H}}$ (calibration error ± 2.5 °C) respectively $\text{TEX}_{86}^{\text{L}}$ (calibration error ± 4.0 °C). Sporomorph-derived climate estimates are based on the methodology of Greenwood et al. (2005) and are presented with the weighted averages and their respective propagated errors (see Supplementary Information for further details). MAT = Mean Annual Temperature, CMMT = Coldest Month Mean Temperature, WMMT = Warmest Month Mean Temperature, MAP = Mean Annual Precipitation.

Age	Location	SST (°C)	MAT (°C)	CMMT (°C)	WMMT (°C)	MAP (cm yr ⁻¹)
Early Eocene	ODP Site 1172	23.4 ± 1.7 (L) 27.8 ± 2.5 (H)	12.5 ± 3.8	6.9 ± 3.8	19.3 ± 3.7	180 ± 86
	Bass Basin		20.2 ± 4.8	12.3 ± 3.4	24.8 ± 2.4	198 ± 114
	Gippsland Basin		17.2 ± 6.4	9.1 ± 6	21.3 ± 3	201 ± 119
	Otaio section		18.9 ± 3.4	11.8 ± 1.1	24.1 ± 0.4	125 ± 24
Late Palaeocene	ODP Site 1172	22 ± 1.2 (L) 25.5 ± 1.1 (H)	12.7 ± 5.2	7.4 ± 3.3	20.9 ± 2.9	172 ± 98
	Bass Basin		15.8 ± 5.8	9.3 ± 4	21.5 ± 2.9	195 ± 112
	Gippsland Basin		15.8 ± 5.9	8.6 ± 4.1	20.4 ± 3.6	200 ± 108
	Southern Morano sections		15.3 ± 6.4	8.5 ± 3.8	20.7 ± 4.1	194 ± 105
	Middle Waipara section	14 ± 1.6 (L) 19.3 ± 1.7 (H)	15.2 ± 2.8	6.9 ± 2.4	15.1 ± 2.9	179 ± 98
Middle/late Palaeocene transition	ODP Site 1172	16.5 ± 1.5 (L) 21.2 ± 1.1 (H)	10.6 ± 3.9	5.9 ± 2.8	15 ± 2.4	177 ± 86
Middle Palaeocene	ODP Site 1172	18.1 ± 1.9 (L) 23.5 ± 1 (H)	11.2 ± 4.6	6.4 ± 3.5	15.2 ± 3.1	181 ± 89
	Bass Basin		14.8 ± 8.7	7.5 ± 5.1	19.9 ± 4.5	205 ± 121
	Gippsland Basin		14.1 ± 5.8	7.5 ± 4.4	19.3 ± 3.6	198 ± 99

4 Interpretation

4.1 Constraints on sporomorph source region

Several lines of evidence suggest that eastern Tasmania was the main source of the sporomorphs encountered in the middle Palaeocene to Lower Eocene of ODP Site 1172. The distance of this site to the palaeo-shoreline of eastern Tasmania during the Palaeocene–early Eocene was of the order of ~ 100 km, whereas the minimum distance to George V Land (Antarctica) amounted to ~ 500 km (Fig. 1). A Tasmanian source is further suggested based on the distribution pattern of reworked Permian and Triassic sporomorphs. The assemblages from ODP Site 1172 are characterized by the constant presence of elements reworked from Permian and Triassic strata (e.g. *Cannanoropollis* spp., *Protohaploxypinus* spp., *Alisporites* spp.; see Supplementary Information, Plate II); the percentages of reworked sporomorphs reach up to 16% of the total assemblages. A similar input of reworked Permian and Triassic material is known for sporomorph assemblages from Palaeocene–Eocene strata along the Australo-Antarctic Gulf (Otway Basin; Harris, 1965) and from the Eocene of the Wilkes Land margin (Contreras et al., 2013). In the Tasmania region, reworked Permian and Trias-

sic sporomorphs are recorded in the Palaeocene–Eocene of the Bass Basin (Partridge et al., 2003) as well as in Eocene strata off western Tasmania and on the South Tasman Rise (Truswell, 1997). This pattern is consistent with the fact that sporomorph-bearing sediments of Permian and Triassic age occur in several regions of Tasmania (e.g. Playford, 1965; Truswell, 1978; Calver et al., 1984). In contrast, reworked sporomorphs on the continental shelf off George V Land (Antarctica; Fig. 1) comprise only taxa with Cretaceous and Cenozoic ages (Truswell, 1983). A similar picture emerges for the Cenozoic of the Gippsland Basin where Permian and Triassic sporomorphs occur only sporadically and in low numbers (see reports in Department of Primary Industries, 1999).

A further constraint on the source of the sporomorphs at ODP Site 1172 comes from the DCA-based comparison of the floristic composition of the Site 1172 record with other coeval Palaeocene–Eocene sporomorph records from Southeast Australia (Bass and Gippsland Basins, Southeast Highlands) and New Zealand (Middle Waipara and Otaio River sections) (Fig. 3b; see Fig. 1 and Table 1 for site locations and details on records). It suggests marked differences in floristic compositions between most records, a result that can be further corroborated for the Bass and Gippsland Basins based

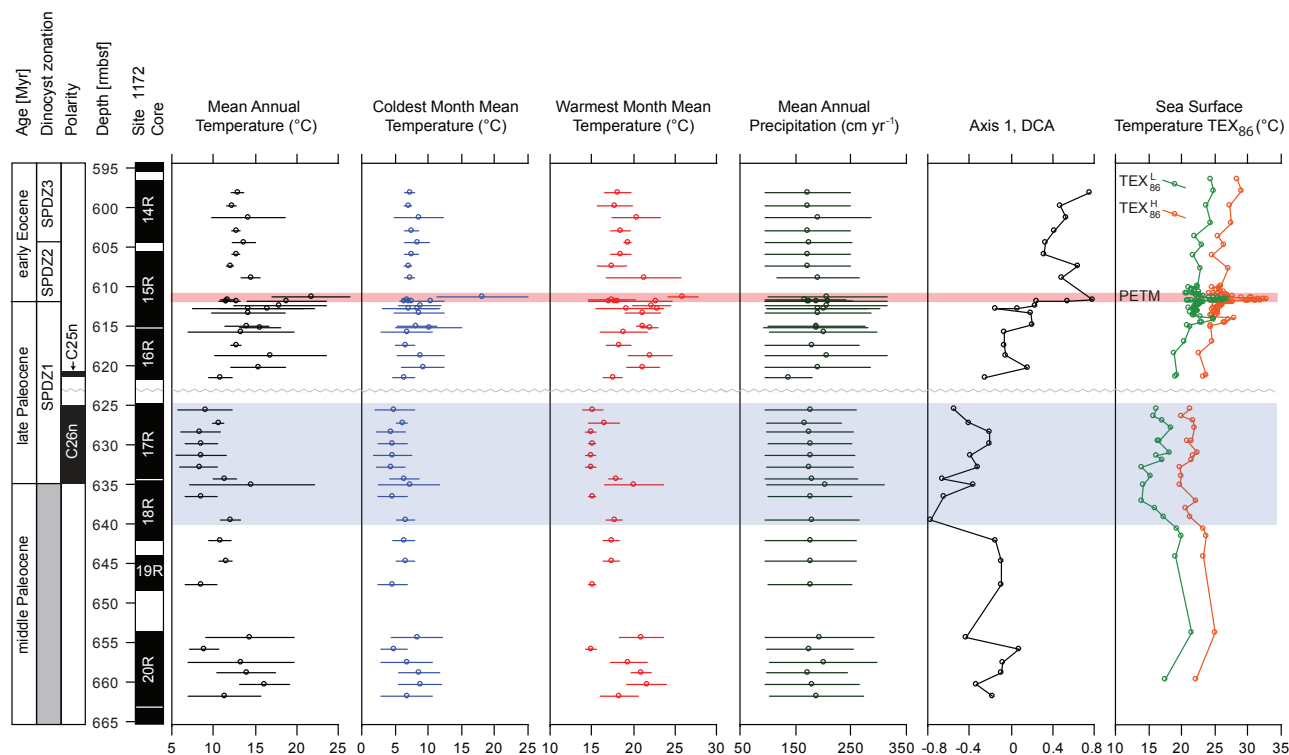


Figure 4. Comparison of the sporomorph-derived climate estimates, SST values based on $\text{TEX}_{86}^{\text{L}}$ and $\text{TEX}_{86}^{\text{H}}$, and DCA Axis 1 sample scores from the middle Palaeocene to Lower Eocene of ODP Site 1172. Sporomorph-derived climate estimates are based on the methodology of Greenwood et al. (2005). Error bars represent the minimum and maximum estimates determined using that method. SST data are from Bijl et al. (2009, 2013b) and Hollis et al. (2014). Sporomorph-derived climate estimates and DCA results are based on samples with counts ≥ 100 individuals only. The intervals corresponding to the middle/late Palaeocene transition and the PETM are marked by horizontal blue and red bars, respectively. Age model and dinocyst zonation after Bijl et al. (2013b).

on carbon-isotope data from both basins. The Palaeocene–Eocene successions of these basins exhibit distinctly different bulk carbon isotope values, which is interpreted to reflect the signal from different plant communities contributing to the organic carbon input into the basins during that time (Boreham et al., 2003). However, despite the floristic differences between the records analysed, there is a remarkable similarity in DCA scores between the records from ODP Site 1172 and the Bass Basin (Fig. 3b), which is located mainly on the shelf off northern Tasmania, but also extends into Northeast Tasmania (Moore et al., 1984). This similarity further corroborates the scenario of a Tasmanian source for the ODP Site 1172 sporomorph assemblages.

4.2 Floristic and climatic evolution

Based on our qualitative and quantitative results from the sporomorph record from ODP Site 1172, three main vegetation types prevailed on Tasmania from the middle Palaeocene to early Eocene. These vegetation types (i) exhibit different floristic compositions based on the DCA results (Figs. 2 and 3a), (ii) show similar diversities based on the rarefaction results (Fig. 2), and (iii) represent specific climatic conditions

based on our sporomorph-derived palaeoclimatic reconstructions (Fig. 4). The floristic characteristics and climatic requirements of all three vegetation groups are discussed in the following sections.

4.2.1 Middle Palaeocene (60.7–59.5 Ma) and late Palaeocene (59.0–55.6 Ma) intervals

During both time intervals, the flora of Tasmania was characterized by gymnosperm-rich forests dominated by podocarps; Araucariaceae, ferns, Proteaceae and *Nothofagus* were further important components of the vegetation. Arecaceae (palms) and Cycadales were present during both time intervals. Although the middle Palaeocene and late Palaeocene forests exhibited a strongly similar composition, important differences existed. Podocarps reached a markedly stronger dominance during the middle Palaeocene than during the late Palaeocene, whereas the late Palaeocene was characterized by higher abundances of ferns (mainly Cyatheaceae) and the presence of Casuarinaceae (Fig. 2).

With regard to modern analogues, these forests bear resemblance to the extant warm-temperate, Podocarpaceae-dominated forests of Southeast Australia and New Zealand

(e.g. Kershaw, 1988). Based on the structure of extant temperate forests from the southern latitudes (Kershaw, 1988; Enright and Hill, 1995; Veblen et al., 1996; Reid et al., 1999), the overstorey of Tasmanian forests during the middle and late Palaeocene was dominated by Podocarpaceae and, to a somewhat lesser extent, Araucariaceae and *Nothofagus*. The understorey, in turn, was likely dominated by ferns, with Cyatheaceae being particularly abundant during the late Palaeocene. Considering the habitats of their extant representatives, Arecaceae (palms), Cycadales, Proteaceae and Casuarinaceae formed parts of both the over- and understorey (compare Johnson and Wilson, 1993; Hill, 1994; Morley, 2000; Jones, 2002).

Climatically, the presence of tree ferns (i.e. Cyatheaceae), Arecaceae and Cycadales implies mild climates with no or merely rare frost events. Owing to physiological constraints (including manoxylic wood, large, unprotected buds, soft, water-rich tissues, and a near-absence of frost-“hardening” mechanisms), all these plants are unable to cope with sustained freezing (Sakai and Larcher, 1987; Wing and Greenwood, 1993); today, they only occur in settings with CMMT ≥ 5.5 °C (Greenwood and Wing, 1995; Utescher and Mosbrugger, 2013).

4.2.2 Middle/late Palaeocene transition interval (59.5–59.0 Ma)

Across the middle/late Palaeocene boundary, the warm-temperate forests characterizing the vegetation on Tasmania during most of the middle and late Palaeocene as described above were transiently replaced by cool-temperate forests dominated by *Nothofagus* (mainly *N. fusca* type) and Araucariaceae. Ferns, podocarps and Proteaceae were further prominent components of this vegetation. Palms (Arecaceae) and Cycadales, as they occurred both during the preceding part of the middle (60.7–59.5 Ma) and the subsequent part of the late Palaeocene (59.0–55.6 Ma; see above), were absent (Fig. 2). In light of the age control and the temporal resolution of our record, these cool-temperate forests prevailed on Tasmania for ~ 0.5 Ma (based on the duration of elevated *Nothofagus* percentages) respectively ~ 0.3 Ma (based on the absence of tropical to subtropical indicators such as palms and Cycadales). The 1.3-Myr-long hiatus precludes us from firmly determining the complete duration of the cold interval in the mid-Palaeocene (Fig. 2). However, from marine records from New Zealand we deduce a duration of 0.5 Ma (Waipara section and ODP Site 1121; Hollis et al., 2014).

Today, vegetation dominated by *Nothofagus* (*N. fusca* type) is typical of cool-temperate forests from southern Australia and New Zealand (Kershaw, 1988). Considering the structure of such forests (e.g. McGlone et al., 1996; Reid et al., 1999), the vegetation thriving during the middle/late Palaeocene transition interval was characterized by a canopy dominated by *Nothofagus* and open understories dominated by ferns (mainly Cyatheaceae and the parent plants of *Cer-*

atosporites spp. [Lycopodiaceae, Selaginellaceae]). Araucariaceae were also present. Because extant members of Araucariaceae are tall trees generally confined to the lower mid-latitudes (Kershaw and Wagstaff, 2001), their presence appears at first sight incompatible with an occurrence of cool-temperate forests. However, members of the genus *Araucaria* also thrive in cold temperate forests in mountainous areas of Chile (Veblen, 1982) and can withstand frost events as cold as -15 °C (Prentice et al., 1992), which supports our observation that Araucariaceae were a component of the cool-temperate forests of Tasmania across the middle/late Palaeocene transition.

Based on the overall floristic evidence, Tasmania witnessed a transient period of cooler conditions lasting from ~ 59.5 to ~ 59.0 Ma. In light of the frost sensitivity of Arecaceae, Cycadales and Cyatheaceae (compare Sect. 4.2.1), the decline or total absence of these taxa across the middle/late Palaeocene transition (Fig. 2) suggests harsher winters (with particularly frequent and/or cold frost events) during that time. Such lower temperatures are corroborated by the comparison with coeval TEX₈₆^L- and TEX₈₆^H-based SST data from ODP Site 1172 (Bijl et al., 2009; 2013b; Hollis et al., 2014). For the interval from ~ 59.4 to ~ 59.0 Ma, they show the lowest values of the entire Palaeocene–Eocene SST record (Fig. 4, Table 3).

4.2.3 PETM and early Eocene interval (55.6–54.2 Ma)

During the early Eocene, the composition of the forests on Tasmania was distinctly different from that of the temperate forests thriving during the Palaeocene (Figs. 2 and 3a); the underlying floristic turnover coincides with the onset of the PETM (see DCA Axis 1 sample scores in Fig. 2). Based on our sporomorph data, the early Eocene vegetation was dominated by ferns and different angiosperms (mainly Proteaceae, Casuarinaceae and Euphorbiaceae/Eumalvoideae). Remarkably, taxa that were common during the Palaeocene – e.g. *Ceratosporites* spp. (Lycopodiaceae, Selaginellaceae) and *Gambierina* spp. (extinct clade) – declined dramatically in abundance or disappeared completely during that time (Fig. 2). Because extant Selaginellaceae and Lycopodiaceae are cosmopolitan families (Jermy, 1990; Øllgaard, 1990), it is difficult to connect the disappearance of these taxa on Tasmania during the earliest Eocene with specific ecological and climatic conditions.

The coexistence of frost-tolerant (e.g. Araucariaceae, Podocarpaceae) and thermophilous taxa (e.g. Casuarinaceae, Arecaceae [palms]) suggests the presence of paratropical forests sensu Morley (2000). In particular, the occurrence of *Nypa* from the PETM onward into the early Eocene suggests the presence of tropical mangrove vegetation along the coast of Tasmania. A similar vegetation, also containing thermophilous taxa such as *Nypa* and *Gymnostoma* (Casuarinaceae), is documented in early Eocene macrofloras from western Tasmania (Pole, 2007; Carpenter et al.,

2012). Hence, forests on Tasmania during the early Eocene consisted temporarily of at least two vegetation associations: (i) a mangrove association characterized by *Nypa*, which is only recognized during the PETM and the earliest Eocene, and (ii) a paratropical association characterized by the coexistence of frost-tolerant taxa (i.e. Araucariaceae, Podocarpaceae and *Nothofagus*) and thermophilous elements such as palms and Casuarinaceae.

Considering the ecology of the nearest living relatives of the plants represented by the encountered sporomorphs, the overstorey vegetation during the early Eocene comprised taxa such as Araucariaceae, Podocarpaceae and *Nothofagus*, whereas the understorey was probably dominated by ferns (mainly Cyatheaceae). Members of the Proteaceae, Casuarinaceae, Cycadales, Arecaceae (palms) and Euphorbiaceae/Eumalvoideae may have been both components of the over- and the understorey (Johnson and Wilson, 1993; Hill, 1994; Morley, 2000; Jones, 2002).

The number of sporomorph species registered at ODP Site 1172 remained relatively constant from the middle Palaeocene to the early Eocene (Fig. 2). This observation is in contrast to Southeast Australia, where sporomorph assemblages from non-marine and marginal marine settings (Partridge, 1976) exhibit a considerably higher diversity during the early Eocene than during the Palaeocene (Macphail et al., 1994; see Sect. 4.3.2). The reasons behind this discrepancy may be sought in the particularly high sea level during the early Eocene as it is recorded regionally based on sedimentological and palaeontological data from ODP Site 1172 (Exon et al., 2004a) and globally (Miller et al., 2005; Cramer et al., 2011). Owing to the selective nature of marine sporomorph transport as a function of transport distance (e.g. Moss et al., 2005), the higher sea level during the early Eocene than during the Palaeocene potentially caused a diversity decrease of the sporomorph assemblages at ODP Site 1172 (see also below).

Our data suggest that the floristic change connected to the PETM is similar to that registered for the early Eocene. However, unravelling the exact anatomy of vegetation change across the PETM at ODP Site 1172 is difficult due to the low sporomorph yields in the respective sediments at that site. In addition, the interpretation of the available data is hampered by the sea-level rise during the PETM (Sluijs et al., 2011); the transgression-induced change in depositional setting towards more distal conditions may have caused a bias in the composition and diversity patterns of sporomorph assemblages, with the resulting assemblages being skewed towards a dominance of easily transported sporomorphs (compare Traverse, 1994, 2008). In light of this bias, the high abundances (up to 39 %; Fig. 2) of *Dilwynites granulatus* (*Wollemia/Agathis*) and the remarkably low diversities (Fig. 2) in the PETM samples from ODP Site 1172 likely represent a change in depositional setting rather than a true palaeoecological signal. This interpretation is supported by the higher abundances of the same species (~ 35 %) in early Palaeocene sediments de-

posited in distal environments of the Bass Basin when compared to the markedly lower abundances (~ 10 %) in coeval sediments from nearshore settings in the same basin (see reports in Partridge et al., 2003). Nevertheless, our data show that the environmental perturbations connected to the PETM had a profound impact on the vegetation on Tasmania. They lead to the extirpation of various ferns (e.g. *Perinomonoletes* spp., *Ceratosporites* spp. [Lycopodiaceae, Selaginellaceae]) and angiosperms (e.g. *Gambierina rudata*, *Nothofagidites* sp. 1 [Nothofagus]), and the appearance of new angiosperms mainly within the Proteaceae family (e.g. *Proteacidites grandis*).

4.3 Integration with other terrestrial vegetation records and temperature estimates from the southern high latitudes

Our results from ODP Site 1172 yield a ~ 6.5 Ma-long vegetation record for the Tasman sector of the SW Pacific region spanning from the middle Palaeocene to the early Eocene. To obtain insights into the potential regional differentiation of terrestrial ecosystems and climates in the high southern latitudes during that time, we have integrated our data from ODP Site 1172 with the available information on terrestrial ecosystems and temperatures from other parts of the SW Pacific domain. Our integration is augmented by newly generated temperature estimates for previously published sporomorph records from Southeast Australia and New Zealand (see Tables 1 and 3 for further information on records evaluated and results). Because other continuous, stratigraphically well-calibrated vegetation records across the middle/late Palaeocene transition interval are not yet available for the SW Pacific region, we focus our comparison on the middle Palaeocene, late Palaeocene and early Eocene.

4.3.1 Middle and late Palaeocene

Palaeobotanical records for the middle and late Palaeocene are well known from Southeast Australia (e.g. Bass Basin – Macphail et al., 1994; Blevin, 2003; Gippsland Basin – Stover and Partridge, 1973; Macphail et al., 1994; Department of Primary Industries, 1999). In summary, the middle and late Palaeocene vegetation in this region consisted predominantly of warm-temperate forests characterized by podocarps, Araucariaceae and ferns; angiosperms were represented mainly by Proteaceae (e.g. Taylor et al., 1990; Macphail et al., 1994; Greenwood et al., 2003; Greenwood and Christophel, 2005). Similar warm temperate forests dominated by podocarps and Araucariaceae, and with a strong contribution of Proteaceae, thrived on New Zealand (Mildenhall, 1980; Raine et al., 2009).

Based on our results, Podocarpaceae together with Araucariaceae, Cyatheaceae and Proteaceae were also the prevailing group of plants during the middle and late Palaeocene on Tasmania (Fig. 2; compare also Sect. 4.2.1). However,

important floristic differences existed between Southeast Australia, New Zealand and Tasmania (Fig. 3b); they are mainly based on the restriction of certain sporomorph taxa to specific regions (e.g. *Liliacidites* spp., *Cibotiidites tuberculiformis* – New Zealand; *Ilexpollenites* spp. – Southeast Australia [Bass and Gippsland Basins, Southeast Highlands]; *Tripunctisporis maastrichtiensis* – New Zealand, Bass Basin and Tasmania). Despite the differences in floristic composition, the remarkable dominance of Podocarpaceae and Araucariaceae in Southeast Australia, Tasmania and New Zealand suggests that warm-temperate forests dominated by gymnosperms were the prevalent vegetation type in the Southwest Pacific region during the middle and late Palaeocene. Moreover, thermophilous taxa such as palms, Olacaceae (*Anacolosa*) and Cupanieae first appeared and/or increased significantly in abundance and diversity during the latest Palaeocene in Southeast Australia (Kemp, 1978; Macphail et al., 1994). On New Zealand, typical tropical taxa (e.g. Cupanieae, *Austrobuxus* [Euphorbiaceae], *Nypa*) also begin to appear during the latest Palaeocene prior to the PETM (Crouch and Brinkhuis, 2005; Raine et al., 2009). Hence, the arrival of thermophilous elements indicates the onset of warmer conditions in the Southwest Pacific region during the latest Palaeocene. A scenario of warm conditions is further corroborated by MAT estimates reaching $\sim 18^\circ\text{C}$ as derived from latest Palaeocene macrofloras in Southeast Australia (Greenwood et al., 2003).

Considering our sporomorph-based climate estimates for Southeast Australia and Tasmania (Table 3), temperatures were higher during the late Palaeocene than during the middle Palaeocene. Hence, the overall climatic and vegetation signal suggests that terrestrial settings across the Southwest Pacific region consistently experienced a pronounced warming during the late Palaeocene.

4.3.2 PETM and early Eocene

The effects of the PETM on terrestrial ecosystems in the high southern latitudes are yet poorly constrained. Available records from Southeast Australia (Bass and Gippsland Basins) covering the PETM and the earliest Eocene suggest the widespread presence of *Nypa* during that time (Partridge, 1976). Climatically, this indicates a MAT $> 21.7^\circ\text{C}$ (Utescher and Mosbrugger, 2013). For the South Island of New Zealand, sporomorph data from nearshore marine sediments document the development of *Nypa* mangrove swamps and the appearance of pollen from the thermophilous subfamily Cupanieae connected to the PETM interval (Handley et al., 2011); moreover, the PETM is characterized by a percentage increase of fern spores as well as of Euphorbiaceae/Eumalvoideae and Myrtaceae pollen at the expense of gymnosperm pollen percentages (Handley et al., 2011). Similarly, sporomorph data for the North Island of New Zealand as available from the Tawanui section show the presence of *Nypa* pollen connected to the PETM (Crouch and

Visscher, 2003). However, besides a marked increase of *Dilwynites granulatus* (*Wollemia/Agathis*) pollen, no other significant changes in floristic composition occur (Crouch and Visscher, 2003). Considering that the PETM sediments of the Tawanui section are part of a transgressive systems tract (Crouch and Brinkhuis, 2005; Sluijs et al., 2008), the high abundances of *Dilwynites granulatus* (*Wollemia/Agathis*) may represent a taphonomic rather than a palaeoecological signal as suggested for the sporomorph record of the PETM from ODP Site 1172 (see Sect. 4.2.3).

With regard to the early Eocene, the majority of vegetation records in the Southwest Pacific region come from Southeast Australia; they suggest that by early Eocene times the warm temperate, conifer-dominated forests of the late Palaeocene had been replaced by more diverse, meso- to megathermal angiosperm forests (Macphail et al., 1994; Greenwood et al., 2003; Greenwood and Christophel, 2005). Although sporomorph percentages are extremely variable within the available records from Southeast Australia, Araucariaceae, Casuarinaceae, Euphorbiaceae/Eumalvoideae, Proteaceae, and ferns are generally the dominant taxa; typical tropical elements such as *Nypa*, *Anacolosa* and Cupanieae are also recorded (Kemp, 1978; Macphail et al., 1994). This trend in vegetation development during the early Eocene is also documented for Tasmania.

On New Zealand, early Eocene sporomorph assemblages exhibit a mixed Palaeocene–Eocene character, with a continued high abundance of conifer pollen (Crouch and Visscher, 2003; Raine et al., 2009). However, thermophilous taxa such as Cupanieae, Casuarinaceae and Euphorbiaceae (*Austrobuxus*) are constantly present in these records (Pocknall, 1990; Raine et al., 2009), and Casuarinaceae pollen abruptly started to dominate the sporomorph assemblages from ~ 54.5 Ma onwards (Raine et al., 2009). On the Wilkes Land margin (Antarctica), paratropical vegetation has been recorded during the early Eocene (53.9–51.9 Ma) with the notable presence of thermophilous taxa such as Arecaceae (palms) and Bombacoideae (Pross et al., 2012; Contreras et al., 2013),

With regard to temperature conditions, early Eocene macrofloras from Southeast Australia suggest a MAT of $\sim 19^\circ\text{C}$ from ~ 56 to ~ 53 Ma (Greenwood et al., 2003), which is very similar to our MAT estimates for coeval sporomorph records (55.8–54.3 Ma; lower Malvacipollis diversus zone of Partridge, 2006; Table 1) from the Bass and Gippsland Basins ($\sim 18^\circ\text{C}$; Table 3). On the Wilkes Land margin, climatic estimates for the early Eocene (53.9–51.9 Ma) suggest a MAT of $\sim 16^\circ\text{C}$ for the lowland regions (Pross et al., 2012). Although occasionally MAT values as high as $\sim 23^\circ\text{C}$ are recorded during the earliest Eocene at ODP Site 1172, the MATs for this time interval are of the order of 12 – 14°C (Fig. 4). This is markedly lower than those from Southeast Australia, and even lower than those from the Wilkes Land margin. Considering that our sporomorph-derived climate data from ODP Site 1172 mainly reflect

climate conditions along the coast of eastern Tasmania (compare discussion on sporomorph source region in Section 4.1), these relatively low values may suggest that the eastern part of Tasmania was influenced by the relatively cool Tasman Current (Fig. 1). However, this argument is not supported by the TEX_{86} -derived SSTs from ODP Site 1172 for the early Eocene, which are much higher (mean: $23^\circ\text{C} - \text{TEX}_{86}^{\text{L}}$, $28^\circ\text{C} - \text{TEX}_{86}^{\text{H}}$; Bijl et al., 2013b). Terrestrial, macroflorally derived temperatures on the order of 24°C from western Tasmania (Carpenter et al., 2012) suggest that this region was significantly warmer than the eastern part of Tasmania. Alternatively, another potential explanation for this discrepancy is that the sea-level rise during the early Eocene biased the composition of the sporomorph assemblages at ODP Site 1172 (compare Sect. 4.2.3) towards a dominance of easily transported and/or particularly abundant sporomorphs indicative of cool conditions at the expense of rarer sporomorphs indicative of warmer conditions. This scenario is supported by the fact that many thermophilous plants from the Lower Eocene of the Southwest Pacific region (e.g. *Areaceae* [palms], *Cupanieae*, *Ilex*, *Nypa*) are mainly insect-pollinated (Bush and Rivera, 1998; Barfod et al., 2011). Hence, these taxa reach only low abundances in pollen spectra when compared to wind-pollinated taxa, and they are not likely to be transported over larger distances before they settle (Jackson, 1994).

Despite the potential bias on the early Eocene sporomorph assemblages at Site 1172, the supraregional replacement of temperate forests by paratropical forests during the early Eocene in Southeast Australia, New Zealand and Tasmania and the widespread occurrence of *Nypa* palms during the PETM in the same regions consistently indicate a pronounced reorganization of the vegetation during the early Eocene in the high southern latitudes connected to the PETM.

4.4 Integration with other precipitation records from the southern high latitudes

Based on our palaeoclimatic results from the sporomorph record of ODP Site 1172, MAP on Tasmania was relatively constant ($\sim 180\text{ cm yr}^{-1}$) from the middle Palaeocene to the early Eocene (Fig. 4; Table 3). These values are comparable to the present-day precipitation received by rainforests in western Tasmania at $\sim 42^\circ\text{S}$ (185 cm yr^{-1} , Corinna; Bureau of Meteorology, 2012), along the west coast of the South Island of New Zealand (212 cm yr^{-1} ; Westport; NIWA, 2012), northern Australia (180 cm yr^{-1} , Darwin Botanic Gardens; Bureau of Meteorology, 2012) and on the east coast of New Caledonia (197 cm yr^{-1} , Puoébo; Pesin et al., 1995). The high-precipitation regime on Tasmania during the early Palaeogene as deduced from the sporomorphs is further corroborated by the dominance of the dinocyst genus *Senegalinium* at ODP Site 1172 during this time interval (Sluijs et al., 2011); this genus is characterized by many freshwater-

tolerant species (Sluijs et al., 2005; Brinkhuis et al., 2006). Hence, the observed *Senegalinium* dominance, which is best explained by substantial freshwater input, is well compatible with high precipitation on Tasmania and a resulting strong freshwater influx on the Tasmanian continental shelf during the early Palaeogene.

Because of the general lack of precipitation data from other sites at high southern latitudes we can mainly compare our estimates from Tasmania with values deduced from other coeval palaeobotanical records. Based on our results from sporomorph assemblages from Southeast Australia (Table 3), this region experienced similarly high precipitation (MAP: $\sim 200\text{ cm yr}^{-1}$) during the early Palaeogene; this is consistent with MAP mean estimates ($186\text{--}240\text{ cm yr}^{-1}$) as derived from macrofloral records from the Upper Palaeocene to Lower Eocene of the same region (Greenwood et al., 2003). On the Wilkes Land margin (Antarctica), high precipitation values (MAP mean: $\sim 132\text{ cm yr}^{-1}$) are also suggested for the early Eocene (Pross et al., 2012). These high precipitation values ($> 100\text{ cm yr}^{-1}$) have been corroborated recently by alkaline major element geochemistry for Eocene sediments from Antarctica (Passchier et al., 2013).

Based on the overall precipitation data, Tasmania and the Australia-Antarctic region experienced high rainfall conditions during the early Palaeogene, comparable with present-day rainforests from southern latitudes. This lends support to modelling studies that include high atmospheric humidity as an important warming mechanism for the higher latitudes (e.g. Abbot et al., 2009).

4.5 Comparison with marine temperature evolution

Based on our sporomorph data (as evidenced in the Axis 1 sample scores of the DCA results, which represent the variation in floristic composition along the studied interval; Fig. 4) and the $\text{TEX}_{86}^{\text{L}}$ and $\text{TEX}_{86}^{\text{H}}$ data of Bijl et al. (2009, 2013b) and Hollis et al. (2014), there is a strong correlation between the vegetation composition on eastern Tasmania and SST at ODP Site 1172 (Fig. 4). This connection is clearly borne out by our results from the state space model, where there is a very strong correlation of 0.997 when DCA Axis 1 sample scores are compared with $\text{TEX}_{86}^{\text{L}}$ (95 % highest posterior density: 0.633–0.999 based on Eq. 4; compare Section 2.4) and 0.978 when DCA Axis 1 sample scores are compared with $\text{TEX}_{86}^{\text{H}}$ (95 % highest posterior density: 0.879–0.997 based on Eq. 4; compare Sect. 2.4). Hence, the strong correlation between the temperature variability derived from TEX_{86} and the floristic composition recorded at ODP Site 1172 demonstrates the impact of temperature on the vegetation dynamics in the Southwest Pacific region during the early Palaeogene.

A close coupling between the temperature evolution in the marine and the terrestrial realms is also evident through the comparison of our sporomorph-based temperature estimates (notably WMMTs) with the TEX_{86} -derived SSTs (Fig. 4 and

Table 3); it is only during the early Eocene that the pronounced warming trend recorded by $\text{TEX}_{86}^{\text{L}}$ and $\text{TEX}_{86}^{\text{H}}$ is not clearly reflected in the sporomorph-based temperature estimates, likely due to the sea-level increase during the early Eocene (compare Sects. 4.2.3 and 4.3.2).

The terrestrial, sporomorph-derived MATs are markedly cooler than the SSTs derived from $\text{TEX}_{86}^{\text{L}}$ and $\text{TEX}_{86}^{\text{H}}$ (Fig. 4), which, based on the traditional perception of the TEX_{86} proxy, are supposed to represent surface-water MAT (e.g. Schouten et al., 2002). At the same time, the TEX_{86} -derived SSTs are closely related to the sporomorph-derived WMMTs (Fig. 4, Table 3). These observations suggest that TEX_{86} -based temperatures may be biased towards warm conditions when applied to early Palaeogene records from the high southern latitudes. Such a warm (summer) bias has also been suggested for other early Palaeogene records from the high southern latitudes based on different multiproxy approaches (Bijl et al., 2009, 2013a; Sluijs et al., 2011; Hollis et al., 2012; Pancost et al., 2013).

5 Conclusions

The middle Palaeocene to early Eocene vegetation on Tasmania as reconstructed from the sporomorph record of ODP Site 1172 was characterized by three different forest types that thrived in high-precipitation regimes under different temperature conditions. These forest types were: (i) warm-temperate rainforests dominated by Podocarpaceae during the middle and late Palaeocene; (ii) cool-temperate rainforests dominated by *Nothofagus* and Araucariaceae that transiently prevailed across the middle/late Palaeocene transition interval (iii) paratropical rainforests dominated by Cyatheaceae during the early Eocene with the remarkable presence of the mangrove palm *Nypa* during the PETM and the earliest Eocene. The comparison with other, previously published floral records from the Southwest Pacific region (including Southeast Australia and New Zealand) supports the validity of our data for Tasmania. It shows that temperate forests were replaced by paratropical forests during the early Eocene throughout the Southwest Pacific region. This reorganization in vegetation composition included an increase in fern (mainly Cyatheaceae) and angiosperm abundances (e.g. Proteaceae, Euphorbiaceae/Eumalvoideae, Casuarinaceae) at the expense of gymnosperms (mainly podocarps).

The integration of terrestrial (i.e. floristic) and previously published marine (i.e. TEX_{86} -based SST) climate information from ODP Site 1172 shows that the surface-water cooling of $\sim 3^\circ\text{C}$ across the middle/late Palaeocene transition interval (~ 59.5 to ~ 59.0 Ma) was paralleled by a transient demise of frost-sensitive plants (i.e. palms and cycads) and the establishment of cool-temperate forests dominated by *Nothofagus* and Araucariaceae on Tasmania. This suggests that cooler conditions (and notably harsher winters with

strong and/or frequent frosts) prevailed on Tasmania during that time.

In light of the statistically robust connection between the floristic composition of the sporomorph record from ODP Site 1172 and the previously published TEX_{86} -based SST record from the same site, the vegetation dynamics on Tasmania during the middle Palaeocene to early Eocene were mainly driven by temperature; precipitation remained high (with a MAP mean of $\sim 180\text{ cm yr}^{-1}$) throughout that time. Based on the comparison of our sporomorph-derived temperatures with the TEX_{86} -based SSTs, we conclude that $\text{TEX}_{86}^{\text{L}}$ - and $\text{TEX}_{86}^{\text{H}}$ -derived temperatures for the high southern latitudes of the early Palaeogene are likely biased towards summer conditions.

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