

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

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ABSTRACT

Reconstructing the early Paleogene 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 Paleogene 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 Paleocene 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 Paleocene 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 Paleocene (excluding the middle/late Paleocene transition); (ii) cool-temperate forests dominated by southern beech (*Nothofagus*) and araucarians that transiently prevailed across the middle/late Paleocene 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 Paleocene–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 Paleocene 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 $\text{TEX}_{86}^{\text{L}}$ - and $\text{TEX}_{86}^{\text{H}}$ -based temperature data suggests a warm bias of both calibrations for the early Paleogene 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 Paleocene 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 TEX_{86} ; Bijl et al., 2009) closely mirror trends in the benthic foraminiferal oxygen isotope data from the late Paleocene 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 TEX_{86} -derived sea-surface temperatures (SSTs) were relatively cool during the early and middle Paleocene. During the late Paleocene and early Eocene, SSTs gradually rose to tropical values ($>26^{\circ}\text{C}$), with maxima being reached during the Paleocene-Eocene

76 Thermal Maximum (PETM; Sluijs et al., 2011) and the EECO (Bijl et al., 2009;
77 Hollis et al., 2009; 2012). Towards the end of the early Eocene (49–50 Ma), a
78 pronounced SST cooling of $\sim 4^{\circ}\text{C}$ occurred on the Australo-Antarctic margin; this
79 cooling has been attributed to the onset of westbound surface-water throughflow
80 across the Tasmanian Gateway (Bijl et al., 2013a). A similar cooling trend is
81 registered for surface waters off New Zealand (Hollis et al., 2009; 2012) and in the
82 Tasman sector of the Southwest Pacific Ocean (Bijl et al., 2009; Hollis et al., 2012).
83 Strikingly low SSTs are recorded for the high-latitude Southwest Pacific Ocean
84 during the interval spanning the middle/late Paleocene transition (59.5–59.0 Ma);
85 TEX₈₆-derived SST decreased by $\sim 3^{\circ}\text{C}$ during that time (Bijl et al., 2009; Hollis et al.,
86 2012; 2014). Along with this SST drop, lowered sea level and marked bathyal erosion
87 suggest that a transient growth of an Antarctic ice sheet may have occurred (Hollis et
88 al., 2014).

89 While an increasing amount of data has become available on the marine climate
90 evolution in the southern high latitudes during the early Paleogene, the coeval
91 terrestrial climate dynamics of that region are yet poorly documented (e.g., Passchier
92 et al., 2013). For the Paleocene, paleobotanical records reflect the thriving of
93 temperate, gymnosperm-rich forests dominated by podocarps in Southeast Australia
94 (e.g., Macphail et al., 1994; Greenwood et al., 2003; Greenwood and Christophel,
95 2005), on Seymour Island (Antarctica; Askin, 1990), and in New Zealand
96 (Mildenhall, 1980; Raine et al., 2009).

97 In contrast, highly diverse angiosperm forests containing taxa that today are restricted
98 to tropical environments characterize the early Eocene vegetation in the higher-
99 latitude Southwest Pacific region. This vegetation is widely known from Southeast
100 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 paleo-latitudes of $\sim 70^\circ$ South (Pross et al., 2012; Contreras et al., 2013).

The pronounced vegetation turnover from temperate forests during the Paleocene 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 Paleogene appear particularly pronounced considering the coeval datasets 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 paleobotanical studies are mainly based on stratigraphically discontinuous outcrops that provided only limited insights into the Paleocene and early Eocene vegetation of the region (Greenwood et al., 2003). In addition, available studies on sporomorphs from the early Paleogene of the Southwest Pacific region have predominantly focussed 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 Paleogene.

In light of the above, we here explore the vegetation response to high-southern-latitude climate forcing from the Paleocene 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 paleoclimatic reconstructions. For a further assessment of the terrestrial climatic conditions in the Southwest Pacific region, we apply the same paleoclimate reconstruction approach to previously published sporomorph records from Southeast Australia (Bass Basin, Gippsland Basin, Southeast Highlands) and New Zealand. Finally, we compare our terrestrial paleoclimate estimates with previously published TEX₈₆- (i.e., TEX₈₆^L and TEX₈₆^H calibrations; Kim et al., 2010) based 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 Paleogene climate dynamics in the high southern latitudes.

1.2 Regional setting and paleoceanography

During the early Paleogene, Tasmania and the ETP were located at ~65°S, much closer to Antarctica than today (Exon et al., 2004b). Paleoceanographic 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 Paleogene (Shipboard Scientific Party, 2001b; Stickley et al., 2004; Fig. 1). During the Paleocene 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 paleoceanographic 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 paleoceanographic reorganizations had important effects on terrestrial climates in the Australo-Antarctic region (Bijl et al., 2013a).

2 Material and methods

The middle Paleocene 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°57.6' S, 149°55.7' 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 ~3‰ between

611.89 and 611.86 rmbsf (revised meters below sea floor) (Sluijs et al., 2011), and several dinocyst first and last occurrence data that have been calibrated regionally following Crouch et al. (2014). The magnetostratigraphic age model for the Paleocene 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 rmbsf; Sluijs et al., 2011). The missing interval between Cores 16R and 17R (~620 rmbsf) 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 Paleocene age.

The Middle Paleocene to lower Eocene succession of ODP Site 1172 consists mainly of gray to grayish 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 paleoclimatic information. An in-depth discussion of this issue is provided in Section 4.1 (“Constraints on sporomorph source region”).

2.2 Sample processing and data analysis

Eighty-nine samples from the Paleocene 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 µm 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 to estimate the number of sporomorph species 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 **drillholes**, 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 datasets using broader groups of taxa (e.g., *Gleicheniidites* spp./*Clavifera* spp., *Phyllocladidites* spp., *Nothofagidites* spp. [*fusca* group]) when necessary. 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 (NRL; 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 dataset 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 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.

Paleoclimate 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 analyzed 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 sporomorph assemblages from the early Paleogene 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, 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 (Petrís 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 Equations (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 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 Equation (3) and the final correlation using Equation (4).

$$SST_i \sim N(x_{\text{SST}}(t(i)), t_{\text{SST}}^2) \quad \text{Eq. (1)}$$

$$DCA_i \sim N(x_{\text{DCA}}(d(i)), t_{\text{DCA}}^2) \quad \text{Eq. (2)}$$

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

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

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 Paleocene 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 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 Paleocene (59.0 – 55.6 Ma); (ii) the middle/late Paleocene 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 Paleocene (60.7 – 59.5 Ma) and late Paleocene (59.0 –

55.6 Ma) intervals

The sporomorph assemblages from the middle and late Paleocene intervals (excluding the middle/late Paleocene 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), *Phyllocladidites mawsonii* (*Lagarostrobos franklinii*; Huon pine), and *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., *Gleicheniidites* spp. (Gleicheniaceae), and *Ceratosporites* spp. (Lycopodiaceae, Selaginellaceae).

Although the sporomorph assemblages from the middle to late Paleocene 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 Paleocene exhibits relatively high (~30%) percentage of podocarpaceous pollen (mainly *Podocarpidites* spp. [Podocarpaceae; podocarps] and *Phyllocladidites mawsonii* [*Lagarostrobos franklinii*; Huon pine]). In contrast, the latest Paleocene is characterized by lower abundances of these taxa (~14%), but exhibits higher percentages of *Cyathidites* spp. (~18%) and the constant presence of *Myricipites harrisii* (probably Casuarinaceae; sheoak). Remarkably, both the middle and late Paleocene are characterized by the presence of *Arecipites* spp. (Arecaceae; palms) and *Cycadopites* spp. (Cycadales).

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

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

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 paleoclimate estimates

The paleoclimate 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 Paleocene (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 Paleocene 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 Paleocene (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 Paleocene/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; see Fig. 4 and Table 3), near-constant values throughout the sequence studied.

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 Paleocene to Lower Eocene of ODP Site 1172. The distance of this site to the paleo-shoreline of eastern Tasmania during the Paleocene–early Eocene was on 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 Paleocene–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 Triassic sporomorphs are recorded in the Paleocene–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 Paleocene–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 on carbon-isotope data from both basins. The Paleocene–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

Paleocene 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 paleoclimatic reconstructions (Fig. 4). The floristic characteristics and climatic requirements of all three vegetation groups are discussed in the following sections.

4.2.1 Middle Paleocene (60.7 – 59.5 Ma) and late Paleocene (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, protealeans and *Nothofagus* were further important components of the vegetation. Arecaceae (palms) and Cycadales were present during both time intervals. Although the middle Paleocene and late Paleocene forests exhibited a strongly similar composition, important differences existed. Podocarps reached a markedly stronger dominance during the middle Paleocene than during the late Paleocene, whereas the late Paleocene 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 Paleocene 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 Paleocene. 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 $\geq 5.5^{\circ}\text{C}$ (Greenwood and Wing, 1995; Utescher and Mosbrugger, 2013).

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

Across the middle/late Paleocene boundary, the warm-temperate forests characterizing the vegetation on Tasmania during most of the middle and late Paleocene as described above were transiently replaced by cool-temperate forests dominated by *Nothofagus* (mainly *N. fusca* type) and Araucariaceae. Ferns, podocarps and protealeans 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 Paleocene (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

500 Cycadales). The 1.3-Myr-long hiatus precludes us from firmly determining the
 501 complete duration of the cold interval in the mid-Paleocene (Fig. 2), however from
 502 marine records from New Zealand we deduce a duration of 0.5 Ma (Waipara section
 503 and ODP Site 1121; Hollis et al., 2014).
 504 Today, vegetation dominated by *Nothofagus* (*N. fusca* type) is typical of cool-
 505 temperate forests from southern Australia and New Zealand (Kershaw, 1988).
 506 Considering the structure of such forests (e.g., McGlone et al., 1996; Reid et al.,
 507 1999), the vegetation thriving during the middle/late Paleocene transition interval was
 508 characterized by a canopy dominated by *Nothofagus* and open understories dominated
 509 by ferns (mainly Cyatheaceae and the parent plants of *Ceratosporites* spp.
 510 [Selaginellaceae, Lycopodiaceae]). Araucariaceae were also present. Because extant
 511 members of Araucariaceae are tall trees generally confined to the lower mid-latitudes
 512 (Kershaw and Wagstaff, 2001), their presence appears at first sight incompatible with
 513 an occurrence of cool-temperate forests. However, members of the genus *Araucaria*
 514 also thrive in cold temperate forests in mountainous areas of Chile (Veblen, 1982) and
 515 can withstand frost events as cold as -15°C (Prentice et al., 1992), which supports our
 516 observation that Araucariaceae were a component of the cool-temperate forests of
 517 Tasmania across the middle/late Paleocene transition.
 518 Based on the overall floristic evidence, Tasmania witnessed a transient period of
 519 cooler conditions lasting from ~59.5 to ~59.0 Ma. In light of the frost sensitivity of
 520 Arecaceae, Cycadales and Cyatheaceae (compare Section 4.2.1), the decline or total
 521 absence of these taxa across the middle/late Paleocene transition (Fig. 2) suggests
 522 harsher winters (with particularly frequent and/or cold frost events) during that time.
 523 Such lower temperatures are corroborated by the comparison with coeval TEX₈₆^L-
 524 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 Paleocene–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 Paleocene (Figs. 2, 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 Paleocene (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 Paleocene 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 Paleocene (Macphail et al., 1994; see Section 4.3.2. below). 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 paleontological 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 Paleocene 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 paleoecological signal. This interpretation is supported by the higher abundances of the same species (~35%) in early Paleogene sediments deposited 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 Paleocene 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 Paleocene transition interval are not yet available for the SW Pacific region, we focus our comparison on the middle Paleocene, late Paleocene and early Eocene.

4.3.1 Middle and late Paleocene

Paleobotanical records for the middle and late Paleocene 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 Paleocene 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

625 Proteaceae were also the prevailing group of plants during the middle and late
626 Paleocene on Tasmania (Fig. 2; compare also Section 4.2.1). However, important
627 floristic differences existed between Southeast Australia, New Zealand and Tasmania
628 (Fig. 3b); they are mainly based on the restriction of certain sporomorph taxa to
629 specific regions (e.g., *Liliacidites* spp., *Cibotioidites tuberculiformis* – New Zealand;
630 *Ilexpollenites* spp. – Southeast Australia [Bass and Gippsland Basins, Southeast
631 Highlands]; *Tripunctisporis maastrichtiensis* – New Zealand, Bass Basin and
632 Tasmania). Despite the differences in floristic composition, the remarkable
633 dominance of Podocarpaceae and Araucariaceae in Southeast Australia, Tasmania and
634 New Zealand suggests that warm-temperate forests dominated by gymnosperms were
635 the prevalent vegetation type in the Southwest Pacific region during the middle and
636 late Paleocene. Moreover, thermophilous taxa such as palms, Olacaceae (*Anacolosa*)
637 and Cupanieae first appeared and/or increased significantly in abundance and
638 diversity during the latest Paleocene in Southeast Australia (Kemp, 1978; Macphail et
639 al., 1994). On New Zealand, typical tropical taxa (e.g., Cupanieae, *Austrobuxus*
640 [Euphorbiaceae], *Nypa*) also begin to appear during the latest Paleocene prior to the
641 PETM (Crouch and Brinkhuis, 2005; Raine et al., 2009). Hence, the arrival of
642 thermophilous elements indicates the onset of warmer conditions in the Southwest
643 Pacific region during the latest Paleocene. A scenario of warm conditions is further
644 corroborated by MAT estimates reaching ~18°C as derived from latest Paleocene
645 macrofloras in Southeast Australia (Greenwood et al., 2003).

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

pronounced warming during the late Paleocene.

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°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 paleoecological signal as suggested for the sporomorph record of the PETM from ODP Site 1172 (see Section 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

675 times the warm temperate, conifer-dominated forests of the late Paleocene had been
 676 replaced by more diverse, meso- to megathermal angiosperm forests (Macphail et al.,
 677 1994; Greenwood et al., 2003; Greenwood and Christophel, 2005). Although
 678 sporomorph percentages are extremely variable within the available records from
 679 Southeast Australia, Araucariaceae, Casuarinaceae, Euphorbiaceae/Eumalvoideae,
 680 Proteaceae, and ferns are generally the dominant taxa; typical tropical elements such
 681 as *Nypa*, *Anacolosa* and Cupanieae are also recorded (Kemp, 1978; Macphail et al.,
 682 1994). This trend in vegetation development during the early Eocene is also
 683 documented for Tasmania.

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

694 With regard to temperature conditions, early Eocene macrofloras from Southeast
 695 Australia suggest a MAT of ~19°C from ~56 to ~53 Ma (Greenwood et al., 2003),
 696 which is very similar to our MAT estimates for coeval sporomorph records (~55.8–
 697 54.3 Ma; lower Malvacipollis diversus zone of Partridge (2006; Table 1) from the
 698 Bass and Gippsland Basins (~18°C; Table 3). On the Wilkes Land margin, climatic
 699 estimates for the early Eocene (53.9–51.9 Ma) suggest a MAT of ~16°C for the

lowland regions (Pross et al., 2012). Although occasionally MAT values as high as ~23°C are recorded during the earliest Eocene at ODP Site 1172, the MATs for this time interval are on 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 TEX₈₆-derived SSTs from ODP Site 1172 for the early Eocene, which are much higher (mean: 23°C - TEX₈₆^L, 28°C - TEX₈₆^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 Section 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., Arecaceae [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 of 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 on 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 paleoclimatic results from the sporomorph record of ODP Site 1172, MAP on Tasmania was relatively constant (~180 cm/yr) from the middle Paleocene to the early Eocene (Fig. 4; Table 3). These values are comparable to the present-day precipitation received by rainforests in western Tasmania at ~42 °S (185 cm/yr, Corinna; Bureau of Metereology, 2012), along the west coast of the South Island of New Zealand (212 cm/yr; Westport; NIWA, 2012), northern Australia (180 cm/year, Darwin Botanic Gardens; Bureau of Metereology, 2012) and on the east coast of New Caledonia (197 cm/year, Puoébo; Pesin et al., 1995). The high-precipitation regime on Tasmania during the early Paleogene 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 Paleogene. 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 paleobotanical records. Based on our results from sporomorph assemblages from Southeast Australia (Table 3), this region experienced similarly high precipitation (MAP: ~200 cm/yr) during the early Paleogene; this is consistent with MAP mean estimates (186–240 cm/yr) as derived from macrofloral records from the Upper Paleocene to Lower Eocene of the same region (Greenwood et al., 2003). On the Wilkes Land margin (Antarctica), high precipitation values (MAP mean: ~132 cm/yr) are also suggested for the early Eocene (Pross et al., 2012). These high precipitation values (>100 cm/yr) 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 Paleogene, comparable with present-day rainforests from southern latitudes. This lends support to modeling 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 Equation [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 Equation [4]; compare Section 2.4). Hence, the strong correlation between the temperature variability derived from TEX₈₆ 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 Paleogene.

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 TEX₈₆-derived SSTs (Fig. 4 and Table 3); it is only during the early Eocene that the pronounced warming trend recorded by TEX₈₆^L and TEX₈₆^H is not clearly reflected in the sporomorph-based temperature estimates, likely due to the sea-level increase during the early Eocene (compare Sections 4.2.3 and 4.3.2).

The terrestrial, sporomorph-derived MATs are markedly cooler than the SSTs derived from TEX₈₆^L and TEX₈₆^H (Fig. 4), which based on the traditional perception of the TEX₈₆ proxy are supposed to represent surface-water MAT (e.g., Schouten et al., 2002). At the same time, the TEX₈₆-derived SSTs are closely related to the sporomorph-derived WMMTs (Fig. 4, Table 3). These observations suggest that TEX₈₆-based temperatures may be biased towards warm conditions when applied to early Paleogene records from the high southern latitudes. Such a warm (summer) bias has also been suggested for other early Paleogene 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 Paleocene 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 Paleocene; (ii) cool-temperate rainforests dominated by *Nothofagus* and Araucariaceae that transiently prevailed across the middle/late Paleocene 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 reorganisation 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., TEX₈₆-based SST) climate information from ODP Site 1172 shows that the surface-water cooling of ~3°C across the middle/late Paleocene 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 TEX₈₆- based

SST record from the same site, the vegetation dynamics on Tasmania during the middle Paleocene to early Eocene were mainly driven by temperature; precipitation remained high (with a MAP mean of ~180 cm/yr) throughout that time. Based on the comparison of our sporomorph-derived temperatures with the TEX₈₆-based SSTs, we conclude that TEX₈₆^L- and TEX₈₆^H-derived temperatures for the high southern latitudes of the early Paleogene are likely biased towards summer conditions.

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TABLE AND FIGURE LEGENDS

Table 1. Sporomorph datasets 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 the Appendix C of Blevin (2003). Biozones and ages are based on Stover and Evans (1973), Stover and Partridge (1973) and Partridge (2006).

Table 2. List of fossil sporomorph taxa from the Middle Paleocene 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.

Table 3. Sporomorph-based climate estimates for Paleocene 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 TEX_{86}^H (calibration error $\pm 2.5^{\circ}C$) respectively TEX_{86}^L (calibration error $\pm 4.0^{\circ}C$). 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.

Figure 1. Map of the Southwest Pacific Ocean showing the early Eocene (~53 Ma) continental configuration, illustrating modern continents (gray), 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).

Figure 2. Relative abundances of selected sporomorph taxa ([A] angiosperms, [G] gymnosperms, [P] pteridophytes) representative of the middle Paleocene 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 Paleocene transition and PETM are marked by horizontal blue and red bars, respectively. Age model and dinocyst zonation after Bijl et al. (2013b).

Figure 3. Comparison of the floristic composition based on the DCA sample scores for (a) middle Paleocene to early Eocene sporomorph assemblages from ODP Site 1172 (Axis 1: 14.6 % of variance; Axis 2: 9.6 % of variance); (b) Paleocene/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.

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 Paleocene 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 Paleocene transition and the PETM are marked by horizontal blue and red bars, respectively. Age model and dinocyst zonation after Bijl et al. (2013b).

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Table 1

Section	Region	Age	Pollen Biozone	Authors
Southern Monaro sections	highlands of southeastern Australia	60 – 58 Ma	Lygiestepollenites balmei	Taylor et al., 1990
* Burong-1	onshore Gippsland Basin	late Paleocene	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 Paleocene, early Eocene	L. balmei and Lower M. diversus	Partridge, 2003
Otaio and Middle Waipara sections	New Zealand	58 – 56 Ma		Pancost et al., subm.
+ Poonboon-1	Bass Basin	late Paleocene, early Eocene	Upper L. balmei, Lower M. diversus	Partridge, 2003
* Roundhead-1	offshore Gippsland Basin	middle to late Paleocene, early Eocene	L. balmei, Lower M. diversus	Partridge, 1989
* Sweetlips-1	offshore Gippsland Basin	middle to late Paleocene	L. balmei	Partridge, 1989
* Turrum-4	offshore Gippsland Basin	middle to late Paleocene	L. balmei	Partridge, 1993
* Turrum-4	offshore Gippsland Basin	middle to late Paleocene	L. balmei	Partridge, 1993

Table 2

Fossil taxon	Botanical affinity	Source	NLR used for climate analysis	database
<i>Araucariacites</i> spp.	Araucariaceae	Raine et al., 2008	Araucariaceae	1, 2
<i>Arecipites</i> spp.	Arecaceae	Nichols et al., 1973	Arecaceae	1
<i>Baculatisporites</i> spp.	Osmundaceae	Raine et al., 2008	Osmundaceae	1
<i>Banksiaeidites arcuatus</i>	Proteaceae (<i>Banksia</i> , <i>Dryandra</i> , <i>Musgravea</i>)	Raine et al., 2008		
<i>Beaupreaidites</i> cf. <i>diversiformis</i>	Proteaceae (<i>Beauprea</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		
<i>Crassoretitriletes</i> cf. <i>vanraadshooveni</i>	<i>Lygodium</i>	Germeraad et al., 1968	<i>Lygodium</i>	1
<i>Cyathidites</i> spp.	Probably Cyatheaceae	Mohr, 2001	Cyatheaceae	1
<i>Cycadopites</i> spp.	Cycadales	Raine et al., 2008	Cycadales: <i>Bowenia</i> , <i>Lepidozamia</i> , <i>Macrozamia</i>	1
<i>Dacrycarpites australiensis</i>	Podocarpaceae (<i>Dacrycarpus dactyloides</i>)	Raine et al., 2008	<i>Dacrycarpus</i>	1
<i>Dacrydiumites florinii</i>	Podocarpaceae (<i>Dacrydium</i>)	Raine et al., 2008	<i>Dacrydium</i>	1
<i>Dacrydiumites</i> 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>			
<i>Gleicheniidites senonicus</i>	Gleicheniaceae	Raine et al., 2008	<i>Dicranopteris</i> , <i>Diplopterygium</i> , <i>Gleichenia</i> , <i>Sticherus</i>	1
<i>Gleicheniidites</i> spp.	Gleicheniaceae	Raine et al., 2008	<i>Dicranopteris</i> , <i>Diplopterygium</i> , <i>Gleichenia</i> , <i>Sticherus</i>	1
<i>Intratropopollenites</i> cf. <i>notabilis</i>	Sterculioideae?, Bombacoideae?, Tilioidae?	Raine et al., 2008		

<i>Malvacipollis diversus</i>	Euphorbiaceae (<i>Austrobuxus</i> , <i>Dissiliaria</i> , <i>Petalostigma</i>); Eumalvoideae?	Raine et al., 2008	Euphorbiaceae	1
<i>Microalatidites</i> spp.	Podocarpaceae (cf. <i>Phyllocladus</i>)	Raine et al., 2008	<i>Phyllocladus</i>	1
<i>Microcachrydites antarcticus</i>	Podocarpaceae (<i>Microstrobos</i> , <i>Microcachrys tetragona</i>)	Raine et al., 2008		
<i>Myricipites harrisii</i>	Casuarinaceae, possibly also Myricaceae	Raine et al., 2008	Casuarinaceae (all Australian species)	1
<i>Myrtaceidites</i> spp.	Myrtaceae	Raine et al., 2008	Myrtaceae	1
<i>Nothofagidites asperus</i> complex	Nothofagaceae (<i>Nothofagus</i> subg. <i>Lophozonia</i>)	Truswell and Macphail, 2009	<i>N. cunninghamii</i> , <i>N. moorei</i>	1
<i>Nothofagidites brachyspinulosus</i> complex	Nothofagaceae (<i>Nothofagus</i> subg. <i>Fuscospora</i>)	Truswell and Macphail, 2009	Nothofagaceae (<i>Nothofagus</i> subg. <i>Fuscospora</i>)	2
<i>Nothofagidites emarcidus</i> complex (including <i>N. endurus</i>)	Nothofagaceae (<i>Nothofagus</i>)	Truswell and Macphail, 2009	all subgenera (including <i>Brassospora</i>)	2
<i>Nothofagidites flemingii</i> complex	Nothofagaceae (<i>Nothofagus</i> subg. <i>Nothofagus</i>)	Raine et al., 2008	Nothofagaceae (<i>Nothofagus</i> subg. <i>Fuscospora</i>)	2
<i>Nothofagidites lachlaniae</i> complex	Nothofagaceae (<i>Nothofagus</i> subg. <i>Fuscospora</i>)	Raine et al., 2008	Nothofagaceae (<i>Nothofagus</i> subg. <i>Fuscospora</i>)	2
<i>Nothofagidites</i> sp.1	Nothofagaceae (<i>Nothofagus</i>)		all subgenera (including <i>Brassospora</i>)	2
<i>Nothofagidites</i> spp. undifferentiated	Nothofagaceae (<i>Nothofagus</i>)		all subgenera (including <i>Brassospora</i>)	2
<i>Osmundacidites</i> spp.	Osmundaceae	Raine et al., 2008	Osmundaceae	1
<i>Parvisaccites catastus</i>	Podocarpaceae (<i>Halocarpus</i>)	Raine et al., 2008		
<i>Phyllocladidites mawsonii</i>	<i>Lagarostrobos</i>	Raine et al., 2008	<i>Lagarostrobos</i>	2
<i>Podocarpidites ellipticus</i>	Podocarpaceae (<i>Podocarpus</i>)	Raine et al., 2008	<i>Podocarpus</i>	1
<i>Podocarpidites exiguus</i>	Podocarpaceae	Raine et al., 2008		
<i>Proteacidites adenanthoides</i>	Proteaceae (<i>Adenanthos</i>)	Raine et al., 2008	<i>Adenanthos</i>	2
<i>Proteacidites annularis</i>	Proteaceae (<i>Xylomelum occidentale</i> or <i>Lambertia</i>)	Raine et al., 2008	<i>Xylomelum</i> (all Australian species)	2

<i>Proteacididites</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, Carnarvon</i>)	Raine et al., 2008	<i>Symphyonema, Petrophile</i>	2
<i>Pseudowinterapollis</i> sp.	Winteraceae	Raine et al., 2008		
<i>Retitriteles</i> cf. <i>rosewoodensis</i>	Lycopodiaceae (<i>Lycopodium</i>)	Raine et al., 2008		
<i>Retitriteles 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 maastrichtensis</i>	Sphagnaceae?			

Table 3

Age	Location	SST (°C)	MAT (°C)	CMMT (°C)	WMMT (°C)	MAP (cm/year)
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 Paleocene	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 Paleocene 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 Paleocene	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