Refined Permian–Triassic floristic timeline reveals early collapse and delayed recovery of south polar terrestrial ecosystems

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ABSTRACT

The collapse of late Permian (Lopingian) Gondwanan floras, characterized by the extinction of glossopterid gymnosperms, heralded the end of one of the most enduring and extensive biomes in Earth’s history. The Sydney Basin, Australia, hosts a near-continuous, age-constrained succession of high southern paleolatitude (~65–75°S) terrestrial strata spanning the end-Permian extinction (EPE) interval. Sedimentological, stable carbon isotopic, palynological, and macrofossil data were collected from two cored coal-exploration wells and correlated. Six palynostratigraphic zones, supported by ordination analyses, were identified within the uppermost Permian to Lower Triassic succession, corresponding to discrete vegetation stages before, during, and after the EPE interval. Collapse of the glossopterid biome marked the onset of the terrestrial EPE and may have significantly predated the marine mass extinctions and conodont-defined Permian–Triassic Boundary. Apart from extinction of the dominant Permian plant taxa, the EPE was characterized by a reduction in primary productivity, and the immediate aftermath was marked by high abundances of opportunistic fungi, algae, and ferns. This transition is coeval with the onset of a gradual global decrease in δ¹³Corg and the primary extrusive phase of Siberian Traps Large Igneous Province magmatism. The dominant gymnosperm groups of the Gondwanan Mesozoic (peltasperms, conifers, and corylostperms) all appeared soon after the collapse but remained rare throughout the immediate post-EPE succession. Faltering recovery was due to a succession of rapid and severe climatic stressors until at least the late Early Triassic. Immediately prior to the Smithian–Spathian boundary (ca. 249 Ma), indices of increased weathering, thick red-beds, and abundant pleuromeian lycophytes likely signify marked climate change and intensification of the Gondwanan monsoon climate system. This is the first record of the Smithian–Spathian floral turnover event in high southern latitudes.

INTRODUCTION

Several mass extinction intervals in Earth’s history have been linked to rapid warming driven by elevated levels of greenhouse gases (Bond and Wignall, 2014), e.g., the end-Triassic extinction (McElwain et al., 1999; Steinthorsdottir et al., 2011) and Toarcian oceanic anoxic event (McElwain et al., 2005; Suan et al., 2010). The end-Permian mass extinction (EPE), an episode of Earth history associated with the single greatest loss of biodiversity, is no exception. Extreme warming driven by greenhouse gas emissions from the Siberian Traps Large Igneous Province has been implicated as a proximate cause of this cataclysm (Brand et al., 2012; Payne and Clapham, 2012; Song et al., 2014; Burgess et al., 2017). Approximately 50% of marine invertebrate families were eliminated during this episode of extinctions (Raup and Sepkoski, 1982; Alroy et al., 2008), ~81% of marine fossil species disappeared (Stanley, 2016), and it is the only mass extinction interval with a similar impact on both marine and terrestrial faunas (Benton, 1995; Labandeira, 2005).

The global fossil record of terrestrial floras reveals a greater species turnover between the Permian and Triassic than any other interval in Earth’s history (McElwain and Punnasena, 2007; Cascales-Miñana et al., 2016). Although it has been argued that floral diversity changes across the EPE were modest compared to animals (e.g., Schneebeli-Hermann et al., 2017; Nowak et al., 2019), a major terrestrial ecosystem collapse is represented by the apparently synchronous disappearance of coals across Gondwana (Retallack et al., 1996), the extinction of the primary coal-forming glossopterid gymnosperms (Class Dictyopteridiopsida; McLoughlin, 2011), and the disappearance of key herbaceous to arborescent accessory taxa including a range of sphenophytes, ferns, cordaitaleans, and conifers (Hill et al., 1999). Glossopterids constituted an overwhelming proportion of the Lopingian (late Permian) terrestrial biomass across Gondwana (e.g., Miller et al., 2016) and were the keystones of Lopingian component communities incorporating a broad range of invertebrates, vertebrates, and fungi (Zavada and Mentis, 1992; Prevec et al., 2009; Slater et al., 2012, 2015). Consequently, the loss of these primary producers would have had an unprecedented impact on herbivore populations (van de Schootbrugge and Gollner, 2013) even if gross plant diversity changes were modest.

Systematic analysis of the amplitude and timing of floral productivity changes across the Permian–Triassic will elucidate the progressive patterns of environmental change and the catastrophic diversity losses at higher trophic levels. Moreover, previous reports of a few glossopterids post-dating the initial stages of the EPE interval in Gondwana (see Bomfleur et al., 2018) require testing to assess the timing and significance of relictual communities that might have harbored plant groups that seeded subsequent taxonomic radiations in the Triassic. It is particularly relevant to establish the pace and extent of extinction and recovery in high-latitude biomes, which may have provided the optimal settings for the persistence of thermophilic and hydrophilic plant communities preferring cool and moist environments, while illuminating the adaptations promoting their survival. In this paper, we document the floristic changes from the end-Permian ecological collapse through the stepwise pattern of vegetation recovery in the southern high-latitude Lower Triassic succession of the Sydney Basin, eastern Australia. This floristic succession
provides context for the interpretation of climatic shifts and other global events through the latest Permian and Early Triassic.

**Timing of the End-Permian Extinction and Permian–Triassic Boundary**

In continental settings, the EPE has traditionally been interpreted as a single, rapid destabilization and collapse of the terrestrial biosphere (e.g., Visscher et al., 1996), whereas in the marine realm at least two prominent stages of extinction have been identified, e.g., at the Permian–Triassic boundary (PTB) type section at Meishan, southern China (Jin et al., 2000; Yin et al., 2012; Song et al., 2013). These extinction pulses, and their associated sharp carbon isotope excursions, are separated by ~60 k.y. (Burgess et al., 2014) and have been employed to define an “extinction interval.” Furthermore, the marine record shows a long-term carbon isotope excursion that predates the primary extinction phase and the PTB by more than one million years, which could indicate a prolonged disruption of the global carbon cycle (Korte and Kozur, 2010).

Complex, multi-stage extinctions are consistent with the leading hypothesized cause of the EPE: massive, sustained, or episodic outgassing from Siberian Traps Large Igneous Province magmatism (Benton and Newell, 2014; Cui and Kump, 2015; Burgess et al., 2017). Although the onset of a terrestrial “extinction interval” can be readily identified by the abrupt loss of peat-forming plants (e.g., Retallack et al., 1996), the timing and patterns of terrestrial extinction and recovery are far less well constrained than those of the marine record at present.

The identification of the PTB in continental strata has been confounded because: (1) the system boundary is defined by the first appearance of a marine conodont index taxon, *Hindeodus parvus* (Mei et al., 1998; Metcalfe and Nicoll, 2007), and (2) this bioevent is not coeval with the initial stage of the end-Permian extinction interval (Song et al., 2013; Burgess et al., 2014). Attempts to place the PTB in terrestrial successions have generally employed a combination of palynostratigraphic, lithostratigraphic, and magnetostratigraphic markers (e.g., southern Africa, Smith and Botha-Brink, 2014, Gastaldo et al., 2015; Antarctica, Retallack et al., 2005, Lindström and McLooglin, 2007; China, Bercovici et al., 2015, Bercovici and Vajda, 2016; Russia, Taylor et al., 2009; Svalbard, Housslow and Nawrocki et al., 2008). However, there are no regionally extensive event beds or fossil indices available for consistent, broad geographic correlation of the PTB in terrestrial settings, in contrast to the widely distributed and well-delineated boundary clay of the end-Cretaceous event (Schulte et al., 2010; Esmeray-Senlet et al., 2017). Consequently, terrestrial biostratigraphic studies have proposed widely disparate placements of the system boundary, especially in regions remote from the stratotype section. For example, some have placed the PTB in stratigraphical proximity to the terrestrial EPE (e.g., Laurie et al., 2016), whereas others have favored its placement much higher in the stratigraphic successions (e.g., Looy et al., 2001; Lindström and McLoughlin, 2007; Gastaldo et al., 2015; Zhang et al., 2016). Independent proxies have been increasingly employed to correlate both the PTB and EPE over broad regions, such as U-Pb radiogenic-isotope ages (Burgess et al., 2014; Metcalfe et al., 2015), stable carbon isotope trends (e.g., Morante, 1996; Korte and Kozur, 2010), and/or other geochemical signatures (e.g., Grice et al., 2005; Williams et al., 2012, 2017). The combination of radiogenic isotopic geochronology, lithostratigraphy, and high-resolution biostratigraphy currently provides the most robust method for dating and correlating the key terrestrial bioevents associated with the Permian–Triassic transition and other complex ecological turnovers in Earth’s history.

**Permian–Triassic Palynostratigraphy of Gondwana**

The Permian–Triassic palynostratigraphic schemes most widely employed across Gondwana were established on Australian successions (Foster, 1982; Helby et al., 1987; Price, 1997; Mantle et al., 2010; Fig. 1). Independent correlation proxies in eastern Australia have resulted in arguably the best age-constrained terrestrial Permian to Lower Triassic palynostratigraphic scheme in the world (Stephenson, 2018). These proxies have included stable carbon isotope proxy records (Morante, 1996; Williams et al., 2017), lithostratigraphic markers (Michaelsen, 2002; Wheeler et al., 2019), and recent radiogenic-isotope ages from U-Pb chemical abrasion-isotope dilution-thermal ionization mass spectrometry (CA-ID-TIMS) of zircons (Metcalfe et al., 2015; Ayaz et al., 2016; Phillips et al., 2018; Fielding et al., 2019). These data support approximately synchronous Lopingian (upper Permian) to Lower Triassic palynological zones across eastern Australia (Laurie et al., 2016). Despite this, the precise stratigraphic positions of the PTB and EPE have remained ambiguous owing to a paucity of absolute age constraints for strata overlying the uppermost Permian coals.

The bio- and lithostratigraphic events long-considered concurrent with the PTB boundary (e.g., loss of glossopterid floras: Balme, 1969; Foster et al., 1997; cessation of peat-forming conditions: Retallack et al., 1996) are now considered to be indicators of the terrestrial EPE, which occurred long before the system boundary *sensu stricto* based on correlations with the stratotype section at Meishan, South China. With recent improved chronostratigraphic controls on the Sydney-Gunnedah-Bowen basin succession (Metcalfe et al., 2015; Laurie et al., 2016; Fielding et al., 2019), the Lopingian to Lower Triassic palynozones of eastern Australia have been recalibrated herein (Fig. 1). This refined timeline provides the context for interpreting the stage-by-stage extinctions and recoveries of the latest Permian to Early Triassic southern polar floras.

**Geological Setting**

During the Permian and Triassic, the Sydney Basin was situated at ~65–75°S (Veever, 2006), and it was the southernmost component of the Sydney-Gunnedah-Bowen basin complex. This large foreland basin system and the continental volcanic belt to its east, the New England Orogen, developed in association with active subduction of Panthalassan oceanic crust along the eastern margin of Gondwana (Fig. 2A; Waschbusch et al., 2009). The modern onshore Sydney Basin is in eastern New South Wales, Australia (Fig. 2B) and forms a broad synclinorium with an onshore areal extent of ~60,000 km². It hosts a >5000 m-thick Cisuralian–Middle Triassic succession (Tadros, 1995); the Early–Middle Triassic succession alone comprises 1500 m of strata in the axis of the basin near Sydney (Hertbert, 1997a). The upper Permian succession is especially significant in hosting numerous bituminous coal seams that represent some of the world’s largest steaming- and coking-coal resources (Agnew et al., 1995). Coastal exposures of the Permian–Triassic transition occur in the northern (near Catherine Hill Bay) and southern (near Wollongong) parts of the basin (Fig. 2C).

The Illawarra and Newcastle coal measures constitute the Lopingian successions of the southern and northern Sydney Basin, respectively. These units are characterized by intercalated sandstone, mudstone, and conglomerate facies typical of coastal-plain and deltaic deposits. Fining-upward cycles within these deposits are typically capped by prominent coal seams that represent the development of thick forest mires on floodplains flanking predominantly large, sandy-bed fluvial channels (Brakel, 1986; Bambery et al., 1995; Tadros, 1995; Herbert, 1997b). The overlying Narrabeen Group spans almost the entirety of the Lower Triassic (Metcalfe et al., 2015). This unit is characterized by laterally extensive, sandstone-dominated, fining-upward alluvial plain deposits lacking coals but containing significant packages of gray, green, and red mudrocks (Emerson and Branagan, 2011). A predominantly southward drainage pattern with
(2019). Dashed chronostratigraphic stage/substage boundaries mark those that do not yet have a Global Boundary Stratotype Section and Point and lack well-constrained absolute ages. Dashed biostratigraphic zone boundaries indicate placements with relatively poor age control. “Dead zone” refers to the palynomorph-poor zone identified within the northern Sydney Basin by Vajda et al. (2020). EPE—onset of terrestrially derived sediments in the Sydney Basin: 1—Metcalfe et al. (2015); 2—Fielding et al. (2019). Global chronostratigraphy calibrated using the following sources: Wuchiapingian (Wuch.)—Changhsingian (Co.; Cohen et al., 2013); Permian–Triassic (Burgess et al., 2014); Griesbachian (D.); Ovtcharova et al., 2006; Smithian–Spathamian (this study); Dienerian–Smithian (= Induan [Ind.]; Olenekian; Ovtcharova et al., 2006; Gradstein et al., 2012; Cohen et al., 2013). Arrows indicate radiogenic-isotope (U-Pb zircon) age constraints within the Sydney Basin: 1—Metcalfe et al. (2015); 2—Fielding et al. (2019). Figure 1. Chart of eastern Australian palynostratigraphic schemes showing different correlations to the international timescale and contrasting placements of the Permian–Triassic boundary by various authors. Global chronostratigraphy calibrated using the following sources: Wuchiapingian (Wuch.)—Changhsingian (Co.; Cohen et al., 2013); Permian–Triassic (Burgess et al., 2014); Griesbachian (D.); Otvcharova et al., 2006; Smithian–Spathamian (this study); Dienerian–Smithian (= Induan [Ind.]; Olenekian; Otvcharova et al., 2006; Gradstein et al., 2012; Cohen et al., 2013). Arrows indicate radiogenic-isotope (U-Pb zircon) age constraints within the Sydney Basin: 1—Metcalfe et al. (2015); 2—Fielding et al. (2019).

additional contributions from transverse river systems east- and westward has been determined from paleocurrent indices (Ward, 1972; Cowan, 1993; Tadros, 1995; Herbert, 1997a). Subsidence progressed faster to the northeast, thus accommodating a much thicker and more continuous succession in the region between Sydney and Newcastle (Herbert, 1997a).

Traditionally, a major unconformity has been inferred across much of the Sydney Basin at or near the Permian–Triassic system boundary between the Newcastle Coal Measures and the overlying Narrabeen Group (Helby, 1973; Herbert, 1980; Herbert, 1997a). However, recent radiogenic-isotope ages have demonstrated minimal to no discernible time gap at this contact in sections where the uppermost Permian has not been removed by fluvial downcutting (Metcalfe et al., 2015; Fielding et al., 2019). The well-defined lithostratigraphic contact between these units reflects an abrupt cessation of peat-forming conditions across Gondwana for several million years (Retallack et al., 1996; Retallack, 2011). Above the PTB in eastern Australia, the first occurrence of minor coal laminae is within the Terrigal Formation (Spathamian; ca. 248 Ma), but significant coal deposits are not represented until accumulation of the Nymboida Coal Measures of northern New South Wales in the Middle Triassic (Retallack et al., 1993; Wells, 1995). Some authors have interpreted a prolonged change in the style of terrestrial sedimentation across Australian basins at or near the PTB (Michaelis, 2002), with synchronous changes across other regions of Gondwana (Antarctica, Webb and Fielding, 1993; India, Sarkar et al., 2003; South Africa, Ward et al., 2000, Pace et al., 2009) and beyond (e.g., Arche and Lopez-Gomez, 2005; Sephton et al., 2005; Newell et al., 2010). However, the nature and severity of the depositional transition in Gondwana has been disputed. For example, in Antarctica, forest-derived paleosols are common features of both upper Permian and Lower Triassic strata (Retallack and Krull, 1999), and apart from a clear lack of peat formation in the Early Triassic, the Sydney Basin reveals only limited evidence of change in fluvial sedimentation style (Fielding et al., 2019). The stratigraphic successes in the Sydney Basin examined in this study offer a near-continuous and age-constrained perspective of southern high-latitude continental depositional environments through the Lopingian to late Early Triassic.

MATERIALS AND METHODS

Well Cores and Sedimentology

All data in this study derive from two well cores: (1) Pacific Power Hawkesbury Bunnerong DDH 1 (PHKB-1), central Sydney Basin (lat: 33° 58′ 17.61″S; long: 151° 13′ 43.52″E); and (2) Coalcliff Colliery DDH 27 (CCC-27), southern Sydney Basin (lat: 34° 13′ 25.28″S; long: 150° 56′ 50.67″E). Core samples and plant fossils were collected from the W.B. Clarke Geoscience Centre drillcore library, Londonderry, New South Wales, Australia. Both well cores were logged for sedimentological and macropaleontological features, and these logs are presented graphically (Figs. 3 and 4). PHKB-1 was selected as the primary reference well because of its position near the synclinal axis of the Sydney Basin and its great thickness (>1260 m) of upper Permian–Lower Triassic strata. CCC-27 provides a continuous record of the PTB succession in the southeastern Sydney Basin, which can be related directly to the adjacent and laterally extensive coastal exposures at Coalcliff, New South Wales, sampled for zircon dating (Fielding et al., 2019). For both CCC-27 and PHKB-1, most of the strata from the uppermost coal seam (Bulli Coal) were removed for analysis soon after drilling, so these could not be documented herein.

Sedimentation rates were calculated from the ten U-Pb zircon absolute ages for the Sydney Basin by Metcalfe et al. (2015). These were correlated to PHKB-1 by Fielding et al. (2019), who recorded an additional absolute date from

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Figure 2. (A) Permian–Triassic (ca. 250 Ma) paleogeography of southern Gondwana, oblique south polar perspective; SGB—Sydney-Gunnedah-Bowen, modified from Blakey (2016). (B) Map of modern eastern Australia including the sedimentary basins active during the Permian–Triassic. (C) Generalized geological map of the Sydney Basin with source locations of well cores examined in this study, Pacific Power Hawkesbury Bunnerong DDH 1 (PHKB-1) and Coalcliff Colliery DDH 27 (CCC-27). Geology simplified from New South Wales Geological Survey 1:500,000 Special Sheet Map of the Sydney Basin (1969).
Figure 3. Broad-scale stratigraphy and correlations between the reference well Bunnerong-1 (PHKB-1, central Sydney Basin) and Coalcliff-27 (CCC-27, southern Sydney Basin). Intervals near the terrestrial end-Permian mass extinction (EPE) for both wells are expanded in Figure 4. PTB—probable Permian–Triassic boundary; the position of this horizon for CCC-27 has not been well constrained in this study. Vertical scale of CCC-27 is exaggerated relative to PHKB-1 for clarity. “?” indicates samples for which accurate concentration values could not be displayed because they exceeded the maximum estimates permitted by the method employed herein (see Table A3; see footnote 1). Abundance columns: red—pollen; green—cryptogam spores; blue—non-plant palynomorphs. L. p. — Lunatisporites pellucidus Zone; C—coal; Md—mudrock; Ht—heterolithic facies (interlaminated siltstone and sandstone); Sa/SST—sandstone; Gr—conglomerate; Fm—Formation; Gries.—Griesbachian; D.—Dienerian. PHKB-1 litho-, bio-, and palynofacies and $\delta^{13}$C$_{org}$ data from Fielding et al. (2019). Chronostratigraphy updated from Fielding et al. (2019).

Figure 4. Stratigraphy and correlations of the terrestrial end-Permian mass extinction interval (EPE) between the reference well Bunnerong-1 (PHKB-1, central Sydney Basin) and Coalcliff-27 (CCC-27, southern Sydney Basin). See Figure 3 for the broader stratigraphic contexts of these wells. PTB—probable Permian–Triassic boundary; the position of this horizon for CCC-27 has not been well-constrained in this study. Vertical scale of CCC-27 is relatively exaggerated for clarity; no palynological data were recovered from the coal seam immediately underlying the EPE horizons of both wells because of a lack of available core for analysis. “?” indicates samples for which accurate concentration values could not be displayed because they exceeded the maximum estimates permitted by the method employed herein (see Table A3; see footnote 1). Abundance columns: green—cryptogam spores; blue—non-plant palynomorphs. P. m. — Protohaploxypinus microcorpus. Lithostratigraphy of both wells and biostratigraphic, palynofacies, and $\delta^{13}$C$_{org}$ data of PHKB-1 from Fielding et al. (2019).
We subdivided the strata of PHKB-1 into two distinct successions based on their predominant depositional regimes. The lower stratigraphic succession (>980 m depth in PHKB-1) was deposited primarily under marine conditions (marine shelf) or peat-forming deltaic/coastal-plain settings, whereas the upper portion (>980 m depth in PHKB-1) was deposited primarily in terrestrial settings (coastal and alluvial plain; Fielding et al., 2019). Simple linear functions of sediment accumulation rates for these successions were derived assuming uniform compaction and constant deposition within each portion of the succession. Where indicated, chronostratigraphic placements of zone boundaries were estimated by interpolating these accumulation rates from the probable age of the top of the Bulli Coal (ca. 252.4 Ma), which is the uppermost bed of the Illawarra Coal Measures.

**Palynology**

Seventy-eight well core samples were analyzed in this study; 52 samples from PHKB-1 and 26 from CCC-27. Palynological samples were processed at Global Geolab, Medicine Hat, Canada. Samples were digested using hydrochloric (HCl) and hydrofluoric (HF) acids to remove inorganic mineral content. Kerogen slides were produced for each sample for palynofacies analysis; organic residues were subsequently oxidized with Schulze’s Solution, mounted on glass slides for palynomorph identification and quantitative assessment. Index spore-pollen taxa were counted from both sieved kerogen slides. All palynomorph images were acquired using a Zeiss Axiocam 2 Plus transmitted light microscope equipped with a Zeiss Axiocam MRc camera. All palynological figures are composite images of multiple microphotographs taken at different focal depths (see Bercovici et al., 2009); these were processed digitally with the “Auto-Blend Layers” function in Adobe Photoshop CC 2018. All palynological slides are provided with prefix “S” and housed at the Department of Palaeobiology, Naturhistoriska riksmuseet, Stockholm, Sweden. Detailed palynological count methods and productivity estimates are provided in Appendix 1. Taxonomic categories for palynomorph counts are in Table A2, and palynomorph and palynofacies count data are presented in Table A3 and Table A4, respectively.

Biostratigraphic correlations were based on palynozone definitions by Foster (1982), Helby et al. (1987), and Price (1997). Radiogenic-isotope age controls for the Sydney Basin were provided by Metcalfe et al. (2015) and Fielding et al. (2019); palynozones were calibrated to the global geochronological scheme by Laurie et al. (2016) and further developed herein (see Fig. 1).

Ordination Data Analysis

To gauge whether differences between palynological assemblages represented discrete floristic stages or were better explained by geographic position or local depositional conditions, the quantitative palynofloral data were tested statistically by ordination analyses. The palynomorphs were categorized as outlined in Table A5 (see footnote 1). These categories were tested for (dis)similarities between palynomorph samples as a function of the following three variables: (1) palynostratigraphic zones, as a proxy of the age relative to the terrestrial end-Permian extinction (EPE); (2) sample lithofacies; and (3) geographic position (wells PHKB-1 and CCC-27). It was predicted that all three of these variables would contribute to the differences in palynomorph assemblages but that the pre-EPE and post-EPE zones would be most dissimilar.

Non-metric multidimensional scaling (nMDS) was selected for this analysis because it has long been shown to yield reliable results for ecological data (Minchin, 1987) with promising results in paleopalynological applications (e.g., Bowman et al., 2014; Slater and Wellman, 2015). NMDS ordination is a non-parametric method for discerning similarity between rank-ordered samples and provides a visual representation on a minimal number of axes (Hammer and Harper, 2006). Specifically, samples that are similar in composition plot relatively close in the projected ordination space. All nMDS scaling analyses were plotted in two dimensions (Fig. 5); the resulting stress values of the different data sets (transformed

![Figure 5](https://example.com/figure5.png)

**Figure 5.** Non-metric multidimensional scaling (nMDS) plots of palynomorph group data. (A) Relative abundance (square root transformed); (B) presence/absence (binary). Gray-shaded area—pre-end-Permian mass extinction event (EPE) samples (= *Dulhuntyispora parvithola* Zone); red shaded area—*Playfordiaspora crenulata* Zone; yellow shaded area—other post-EPE samples. SST—sandstone; med.—medium. Note: one outlier sample was excluded from the abundance plot (S014134) for illustration in A.
abundance, untransformed abundance, and binary) were relatively low and similar (\(= 2.1-2.2\)). The replicability of these different tests suggests that the trends in the data were reliable. Ordination analyses were performed using the program Palaeontological Statistics (PAST, v.3.22; Hammer et al., 2001). Additional details of the ordination analyses are provided in Appendix 1.

Stable Carbon Isotopes

Stable carbon isotope data for bulk organic matter (\(\delta^{13}C_{org}\)) were collected from 108 samples of PHKB-1 and 33 samples of CCC-27 (Table A6; see footnote 1). Most of the palynological samples were derived from corresponding \(\delta^{13}C_{org}\) sample levels. In preparation for analysis, samples were powdered, reacted for 24 h with 1N HCl at room temperature to remove inorganic carbon, and rinsed three times in ultra-pure water. Following each rinse, the supernatant was separated by centrifugation and discarded. Samples were then dried in an oven at 40 °C and crushed using an agate mortar and pestle. Carbon isotope compositions were measured using a Costech 4010 Element Analyzer connected to a Thermo Finnigan MAT 253 stable-isotope gas-ratio mass spectrometer in the W.M. Keck Paleoenvironmental and Environmental Stable Isotope Laboratory at the University of Kansas. Carbon isotope compositions of the bulk organic matter fractions are reported in permil (‰) relative to the Vienna PeeDee Belemnite standard (V-PDB). Analyses of powdered dogfish remains (DORM) certified working standards were reproducible to better than ±0.11‰ (1σ SD) for \(\delta^{13}C\).

RESULTS

Sedimentology and Lithostratigraphy

The uppermost succession of the Illawarra Coal Measures in PHKB-1 (Wongawilli Coal, Eckersley Formation, Bulli Coal) consists of an array of erosionally based, single to multi-story sandstone bodies (with minor pebble conglomerate and pebbly sandstone), heterolithic (thinner interbedded to interlaminated) sandstones and siltstones, mudrocks, and coals with common light-colored beds of tuff (Fig. 3). The coals are associated with well-developed hydromorphic palaeosols (Retallack, 1999). Sandstone bodies preserve heterolithic partings, some of which incorporate rhythmic interlaminations of sand and mud, synaeresis cracks, and a sporadically distributed, low-diversity suite of simple trace fossils. These partings and the thicker intervals of heteroliths host various interlamination features (pinstripe, lenticular, wavy, and flaser bedding) with abundant soft-sediment deformation structures. Plant debris is also ubiquitous, ranging from large axes to macerated “coffee grounds,” together with coaly traces and in situ roots. Above the uppermost coal seam (Figs. 3 and 4), facies are broadly similar but lack coal, and initially lack plant debris before it reappears after a few meters of vertical section. The coloration of mudrocks becomes steadily more pronounced above the Bulli Coal, changing from medium gray to initially light gray with increasing blue and yellow hues upward. Tuffs are also almost entirely absent and thinner above the Bulli Coal.

The erosionally based sandstone bodies are interpreted as the deposits of laterally mobile sand bed rivers on a coastal plain. Multi-story sandstone bodies suggest an aggradational pattern of sediment accumulation facilitated by channel filling and lateral migration over time. A location within the coastal backwater zone is indicated for the lower part of the Illawarra Coal Measures by the presence of synaeresis cracks, trace fossils, and rhythmically laminated heterolithic partings, which indicate some tidal modulation of fluvial outflow currents.

Although the uppermost Permian succession (upper Illawarra Coal Measures) contains abundant evidence of terrestrial plant colonization of substrates, the interval immediately above the Bulli Coal seam is devoid of plant fossils, suggesting abrupt biotic change at this level. The Bulli Coal is normally overlain by a regionally extensive package (generally <5 m thick) of gray siltstones. These siltstones are absent in some localities where overlying channel sandstones have been deposited on scour surfaces that extend to the Bulli Coal. Impressions of gymnosperm logs (possibly Voltziopsis) and other woody debris are locally common in lag deposits within these channel sandstones.

The pronounced coloration of mudrocks higher in the Narrabeen Group is interpreted to reflect lowering of the water table soon after deposition, leading to partial or temporary oxidation of iron-bearing minerals in coastal-plain substrates. The continued presence of synaeresis cracks and trace fossils suggests the coastal-plain setting persisted for some time into the Triassic, gradually becoming more continental upward as these features dissipate.

We estimate (compacted) sediment accumulation rates of ~63 m/m.y. for the lower succession (marine shelf/delta/coastal-plain settings) and ~108 m/m.y. for the upper succession (coastal- and alluvial-plain settings) of PHKB-1 (Fig. 6).

![Figure 6. Scatterplot of U-Pb chemical abrasion-isotope dilution-thermal ionization mass spectrometry (CA-ID-TIMS) absolute age estimates from Metcalfe et al. (2015) and Fielding et al. (2019) and their correlative stratigraphic depths in PHKB-1. Age estimate error ranges = 2σ. Filled circles—age estimates from strata formed in predominantly marine depositional settings (marine shelf and deltaic/coastal-plain); hollow circles—age estimates from predominantly terrestrial depositional settings (coastal and alluvial plain). Capit.—Capitanian; D.—Dienerian; G.—Griesbachian; Guad.—Guadalupian; Ind.—Induan; M. Tri.—Middle Triassic; EPE—onset of the terrestrial end-Permian mass extinction interval; SSB—estimated placement of the Smithian–Spathian boundary; chronostatigraphy. For chronostatigraphic boundary calibrations, see Figure 1; additional calibrations from Cohen et al. (2013). Correlative placements of radiochronologic ages to PHKB-1, and paleoenvironmental interpretations from Fielding et al. (2019).](https://pubs.geoscienceworld.org/gsa/gsabulletin/article-pdf/doi/10.1130/B35355.1/4871101/b35355.pdf)
Global chronostrat.

Age (Ma)

259 258 257 256 255 254 253 252 251 249 248 247

Permian
Lopingian
Triassic
Early Triassic
M. Tri
Anisian
Ind.
Olenekian
G.D.
Smithian
Spathian
Aegean

Height from top of Bulli Coal (m)

800 600 400 200 0 200 400 600 800

Depth from top of well (m)

0 200 400 600 800 1000 1200 1400

EPE
SSB

\[ y = 108.33x - 26590 \]

\[ y = 63.342x - 15182 \]
Palynofloras, Macrofloras and Biostratigraphy

Six palynozones were identified in the studied succession. Representative palynofloral and macrofloral taxa for these zones are illustrated (Figs. 7–10) and the key features, stratigraphic distribution, and inferred ages of each zone are outlined below.

Dulhuntyispora parvithola Zone (Mantle et al., 2010) = APP5 Zone (Price, 1997)

Composition. This zone has a distinctive but rather uniform palynological and macrofloral character, which distinguishes it clearly from the overlying zones. The *D. parvithola* Zone is characterized by: (1) a high abundance of laevigate trilete spores (Fig. 7C); (2) abundant *Microbaculatispora* and trilete spores with coarse baculae (*Horriditriletes*, *Neoraistrickia*, *Raistrickia*; Figs. 7A–7B and 7E); (3) diverse *Dulhuntyispora* (Price, 1983; Fig. 7F); (4) abundant pollen typical of glossopterids (*Protohaploxypinus*, *Striatopodocarpites*); and (5) a near total absence of phytoplankton. Relatively high palynomorph concentrations and organic productivity at the time of deposition are indicated by low counts of extrinsic *Lycopodium* spores in both palynomorph and palynofacies data sets (see Appendix 1 for productivity estimation methods). Strata assigned to this zone are also characterized by abundant macrofloral remains of glossopterid gymnosperms (*Glossopteris*, *Brevitriletes bulliensis* *Nu*; (K) Paracalamites *on* 14 November 2019 by Monash University user Downloaded from https://pubs.geoscienceworld.org/gsa/gsabulletin/article-pdf/doi/10.1130/B35355.1/4871101/b35355.pdf); i.e., the zone base was not observed in either studied succession. This zone is equivalent to the upper portion of the inform APP5 Zone (Price, 1997), is equivalent to the upper portion of the inform APP5 Zone (Price, 1997), or Upper Stage 5c (Price, 1983).

Remarks. The examined succession of the *D. parvithola* Zone in the two wells studied is equivalent to the upper portion of the informal APP5 biostratigraphic zone (Price, 1997), the upper Dulhuntyispora Assemblage Zone (Helby, 1973; Foster, 1979), or Upper Stage 5c (Price, 1983).

Stratigraphic depths of zone base. The base of this zone is at >900.22 m depth in PHKB-1 (>95.14 m below the top of the Bulli Coal) and >478.12 m depth in CCC-27 (>2.94 m below the top of the Bulli Coal); i.e., the zone base was not observed in either studied succession. This zone exceeds 95.19 m of strata in PHKB-1 and 2.97 m in CCC-27.

Estimated chronostratigraphic range. Numerous recent zircon U-Pb radiocronologic ages from tuff beds across eastern Australia have provided the *D. parvithola* Zone with the most well-constrained ages of any Permian palynostratigraphic unit in Gondwana (Laurie et al., 2016). These estimates have provided a mid-Wuchiapingian age (ca. 258.0 Ma) for the lower boundary (Metcalfe et al., 2015; Ayaz et al., 2016; Phillips et al., 2018) and a Changhsingian age (ca. 252.3–252.6 Ma) for the upper boundary (Metcalfe et al., 2015; Fielding et al., 2019; Fig. 1). See the Playfordiaspora crenulata Zone section below for further discussion of the upper boundary.

Playfordiaspora crenulata Zone (Foster, 1982)

Composition. The base of this zone is identified by the first appearance data of *Triquitrites*}

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**Figure 7.** Characteristic palynomorphs of the Dulhuntyispora parvithola and Playfordiaspora crenulata zones, Sydney Basin, all scales = 20 µm; C, G, H, J, and M enlarged from Fielding et al. (2019), taxon authorities and specimen details are supplied in Table A7 (see footnote 1). (A–F) Common spores of the *D. parvithola* Zone; (A,B) *Microbaculatispora* sp. cf. *M. nodosa* (A, equatorial view; B, proximal view); (C) *Leiotriletes directus*; (D) *Cyclogranisporites gondwanensis*; (E) *Horriditriletes ramosus*; (F) Dulhuntyispora parvithola. (G–K) Index taxa of the *P. crenulata* Zone; (G) *Triquitrites proratus*; (H) *Reduviasporonites chalastus*; (I) *Brevitriletes bulliensis*; (J) *Playfordiaspora crenulata*; (K) *M. nodosa* (A, equatorial view; B, proximal view); (C) *Leiotriletes directus*; (D) *Cyclogranisporites gondwanensis*; (E) *Horriditriletes ramosus*; (F) Dulhuntyispora parvithola. (G–K) Index taxa of the *P. crenulata* Zone; (G) *Triquitrites proratus*; (H) *Reduviasporonites chalastus*; (I) *Brevitriletes bulliensis*; (J) *Playfordiaspora crenulata*; (K) *M. nodosa* (A, equatorial view; B, proximal view); (C) *Leiotriletes directus*; (D) *Cyclogranisporites gondwanensis*; (E) *Horriditriletes ramosus*; (F) Dulhuntyispora parvithola. (G–K) Index taxa of the *P. crenulata* Zone; (G) *Triquitrites proratus*; (H) *Reduviasporonites chalastus*; (I) *Brevitriletes bulliensis*; (J) *Playfordiaspora crenulata*; (K) *M. nodosa*.
playfordii and Brevitriletes (Apiculatisporis) baliensis in both wells (Figs. 7G and 7I). The palynological record of this boundary is further characterized by: (1) a significant reduction in coarse baculate trilete spores (e.g., Horriditriletes spp., Neoraistrickia spp., Raistrickia spp.); (2) local abundance spikes of the fern spore Thymospora spp. (PHKB-1 only; Fig. 7N) or the alga Quadrisporites horridus (CCC-27 only; Fig. 7L); (3) anomalously high abundances of amorphous organic matter (AOM); and (4) a reduction in plant productivity, as indicated by a relative decrease in palynomorph concentrations in both the strict palynomorph and palynofacies counts. Non-marine algal cysts are abundant in the lower 2 m of this zone in both wells. The last occurrence of D. parvithola is recorded within the P. crenulata Zone, but these specimens are fragmentary and have surface textures indicative of pyrite damage. Within PHKB-1, this degradation style is typical of specimens from the preceding D. parvithola Zone (Fielding et al., 2019). Their occurrence within the P. crenulata Zone may be a consequence of reworking from the underlying D. parvithola Zone. Extrinsic Lycopodium spores added to the samples during processing have a very wide range of abundances within the upper portion of this zone, indicating highly fluctuating plant and phytoplankton productivity.
most part of the Bulli Coal, as has been reported in the Bowen Basin (Foster, 1982). However, the Bulli Coal appears to be of consistent botanical composition throughout, being dominated by glossopterid remains (Diesell, 1992) typical of those occurring throughout the D. parvithola Zone; hence, we consider the D. parvithola—P. crenulata boundary to be best placed at the top of this coal.

In two sections of the Sydney Basin (Frazer Beach, and Snapper Point), the index taxa for the P. crenulata Zone were not observed until ~1.5 m above the uppermost Permian coal (Mishra et al., 2019; Vajda et al., 2020; Fig. 1). This ~1.5 m interval was identified as a post-EPE “dead zone” and is characterized by a high abundance of coalified and charcoalified phytoclasts and a near-total absence of palynomorphs. This “dead zone” is not present across the entire basin, or may be overlooked where sampling is too widely spaced, as no directly correlative interval was identified within CCC-27 or PHKB-1.

Stratigraphic distribution. Assemblages assigned to this zone occur in samples immediately above the Bulli Coal in both wells studied (Vajda et al., 2020; Mishra et al., in press). The depths to the base of this zone (top of the Illawarra Coal Measures) are 805.08 m (in PHKB-1) and 475.18 m (in CCC-27). Despite evidence of erosion at the base of some sandstone bodies within this interval, the P. crenulata Zone has a preserved thickness of 24 m in PHKB-1 and 48 m in CCC-27, consistently thicker than the 7 m type succession of this zone in the Bowen Basin, Queensland (Foster, 1982). Lithostratigraphically, this zone encompasses the Coal Cliff Sandstone in the central part of the basin (PHKB-1) but correlates to both the Coal Cliff Sandstone and the Wombarra Shale southwards (CCC-27), suggesting that these rock units are at least partially time-transgressive.

Estimated chronostratigraphic range. Previously, the age of the Dulhuntyispora parvithola—Playfordiaspora crenulata boundary in eastern Australia was considered within the Wuchiapingian (Mantle et al., 2010) or close to the PTB (Changhsingian–Griesbachian boundary; Laurie et al., 2016; Fig. 1). Recent radiogenic-isotope ages from the Sydney Basin tightly constrain the D. parvithola–P. crenulata zonal boundary to a maximum of 252.6 ± 0.04 Ma (Metcalfe et al., 2015) and a minimum of 252.31 ± 0.07 Ma (Fielding et al., 2019). These new radiochronostratigraphic schemes (Mantle et al., 2010; Laurie et al., 2016) and a minimum of 252.31 ± 0.07 Ma (Fielding et al., 2019). These new radiochronostratigraphic schemes (Mantle et al., 2010; Laurie et al., 2016) and a preliminary U-Pb

The base of this zone is also marked by the last occurrence of fossils with unambiguous glossopterid affinity (e.g., Glossopteris, Verticibraria). Within the broader Sydney Basin, the first occurrences of the peltaspermalean leaf taxon Lepidopteris callipteroides (Fig. 9J) and the conifer Voltziopsis africana, together with persistent examples of Schizoneura gondwanensis (a sphenophyte taxon that survived the EPE), are recorded in this zone (Retallack, 1980, 2002; Vajda et al., 2020). Macrofossils are otherwise scarce in this interval apart from fine woody debris, charcoal fragments, and a few unidentifiable roots.

Remarks. The D. parvithola–P. crenulata zone boundary is equivalent to the APP5–APP6 boundary of Price (1997). In both of the examined successions, large portions of the uppermost coal seam (Bulli Coal) were removed for analysis soon after drilling; consequently, the base of this zone might extend into the upper-
The radiochronologic age indicates an earliest Triassic (Griesbachian) age for the upper *P. crenulata* Zone (Fielding et al., 2019).

Early attempts to tie the spore-pollen biostratigraphy to the global time scale tended to place the PTB above the *Protohaploxypinus microcorpus* Zone, to the radioisotopic geochronology (Metcalfe et al., 2015) interpreted the *P. microcorpus* Zone, and hence the overlying *L. pellucidus* Zone, to be above the PTB (presently dated to 251.902 ± 0.0241; Burgess et al., 2014). The additional age constraints outlined above support a higher position of the PTB relative to the EPE, a pattern also expressed in the PTB-type section in southern China (e.g., Jin et al., 2000). However, the Sydney Basin absolute ages revealed a much longer discrepancy (~400 k.y.) between the terrestrial EPE and PTB than in the marine record, suggesting an early onset of vegetation turnover at high southern latitudes (Fielding et al., 2019). Collectively, these data suggest: (1) the base of this zone correlates to the EPE; and (2) this zone encompasses the PTB (Fig. 1).

In summary, we interpret this zone to range from the upper Changhsingian to lower Induan (?lower Griesbachian) based on lower-boundary U-Pb calibrations (Metcalfe et al., 2015; Fielding et al., 2019) and age estimates of the upper boundary from inferred sediment accumulation rates in the basin (Laurie et al., 2016; this study).

**Protohaploxypinus microcorpus Zone (Foster, 1982)**

**Composition.** We identified the first appearances of index taxa unique to the *P. microcorpus* Zone, specifically *Rewanispora foveolata* and *Lundbladispora springsurensis* (Figs. 10A and 10C–10D), in both wells examined. We also identified the first appearance of *Lundbladispora sp. A* (sensu Foster, 1979), a rare index taxon for this zone (Foster, 1982), but only within the *P. microcorpus* Zone of CCC-27 (Fig. 10B). The first appearances of two additional index species, *Playfordiaspora crenulata* and *Triquitrites pro-ratus* (Figs. 7H and 7J), were identified within this zone; however, these taxa were very rare. Consequently, their stratigraphic ranges possibly extend into the underlying *P. crenulata* Zone within the Sydney Basin, as suggested by other successions in eastern Australia (Helby, 1973; Foster, 1979; Helby et al., 1987) and greater Gondwana (e.g., Pakistan: Balme, 1970; Prince Charles Mountains, Antarctica: Lindström and McLoughlin, 2007). Leiospherid acritarchs and AOM remain abundant throughout this interval, but total palynomorph concentrations were low. The first appearances of *Lepidopteris callipteroi* (peltasperm) fragments (Fig. 9J) and voltzialean conifer remains (Fig. 9O) were identified within PHKB-1 at or near the base of the *P. microcorpus* Zone.

**Remarks.** The *Protohaploxypinus microcorpus* Zone has proven elusive in some studies owing to the probable diachronous distribution of some index taxa (e.g., Price, 1997). As per previous authors (Mantle et al., 2010; Laurie
et al., 2016), we identify the *P. microcorpus* Zone as equivalent to the upper portion of zone APP6 (*sensu* Price, 1997), but the recognition of the above-mentioned, zone-specific index taxa (*Rewaniispora foveolata* and *Lundbladispora springiensis*) has enabled the differentiation of this zone from the preceding *P.crenulata* Zone in both wells studied (cf., Laurie et al., 2016). Further investigation may reveal that this zone, as defined by Foster (1982), has only regional (e.g., basin-wide) utility.

**Stratigraphic distribution.** Lacking any absolute age constraints within the *P. microcorpus* Zone, a short chronostratigraphic range for this zone has been inferred from its relatively small stratigraphic thickness within the wells investigated in our study, in other Sydney Basin wells studied (Helby et al., 1987), and in other eastern Australian Basins (Foster, 1982). This study constrains the base of the *P. microcorpus* Zone to 781.18 m in PHKB-1 (23.9 m above the top of the Bulli Coal) and 427.1 m in CCC-27 (48.08 m above the top of the Bulli Coal), giving zone thicknesses of ~20–25 m in PHKB-1 and 75–80 m in CCC-27. Although this zone is more extensive in the studied wells than in other some successions, this thickness is broadly consistent with previous studies of this zone in the Bowen Basin (Foster, 1982). The lithostratigraphic units encompassing this zone in the southern part of the basin (CCC-27; Scarborough Sandstone and Stanwell Park Claystone) differ from those in the central part of Sydney Basin (PHKB-1; lower Wombarra Shale). This suggests that these rock units are slightly time-transgressive across the basin, consistent with the pattern observed for the rock units correlated with the underlying *P. crenulata* Zone.

**Estimated chronostratigraphic range.** We interpret this zone to be restricted to the ?lower Induan (Griesbachian; Fig. 1) based on previous studies (Laurie et al., 2016) and estimates of depositional rates within the Triassic succession in the Sydney Basin (this study).

**Lunatisporites pellucidus Zone (Foster, 1982)**

**Composition.** The base of this zone is identified by the first occurrence of *Lunatisporites pellucidus* (Fig. 10G) and important accessory taxa: *Limatulasporites* spp. (*e.g.*, *L. limatatus*; Figs. 10E–10F) and *Kraeuselisporites saepatus* (Foster, 1982). The species richness and abundance of zonate trilete spores, which is typical of lycopodytes, increases in this zone, but there is a relative decrease in non-taeniate bisaccate pollen, *e.g.*, *Alisporites* (or *Falcisporites*; Fig. 10I) and *Pteruchipollinites* (Fig. 10H). In other characteristics, this zone is very similar to the preceding *P. microcorpus* Zone.

**Remarks.** The *Lunatisporites pellucidus* Zone corresponds to the lower APII Zone of Price (1997) and, previously, had been considered the lowermost zone of the Triassic (Helby, 1973; Helby et al., 1987; Price, 1997). Helby et al. (1987, p. 8) defined the base of this zone as the “oldest common occurrence of *Lunatisporites pellucidus,*” whereas other palynostratigraphic studies of eastern Australia (Foster, 1982; Price, 1997) employed a more objective criterion: the first appearance datum of *L. pellucidus* as one of the markers for the base of this zone. To avoid ambiguity, the latter, more concrete definition was employed herein. Sparse palynological sampling, rare macrofloral remains, and a lack of absolute age controls preclude detailed interpretations of the duration and temporal patterns of floral change within this zone in the wells studied. A higher resolution study of these successions will likely place the *P. microcorpus- L. pellucidus* Zone boundary stratigraphically lower than indicated herein because it is highly unlikely that any recorded first (or last) appearance datum is genuinely the lowest (or highest) occurrence of a taxon in a given region, an axiom to consider in all biostratigraphic research. This is especially relevant to successions with low sampling densities.

**Stratigraphic distribution.** The base of this zone is registered at 760.09 m in PHKB-1 (44.99 m above the top of the Bulli Coal) and 348.19 m in CCC-27 (126.99 m above the top of the Bulli Coal). The zone is 14.47 m thick in PHKB-1 but of uncertain thickness in CCC-27 as the top was not defined. The *L. pellucidus* Zone is much thicker in the type section in the northern Sydney Basin (152 m; Helby et al., 1987) and has an estimated thickness of >250 m within the lower Rewan Formation of the Bowen Basin, Queensland (de Jersey, 1970; Foster, 1982). This zone correlates to the upper Wombarra Shale in the central portion of the basin (in PHKB-1), but southwards, the lower boundary of this zone commences at or near the base of the Bulgo Sandstone (in CCC-27). This is consistent with the diachronous pattern identified for the underlying lithostratigraphic units.

**Estimated chronostratigraphic range.** The zone is inferred from the ?lower Induan (upper Griesbachian; ?lower Olenekeian (upper Smithian; Fig. 1) based on data from Laurie et al. (2016) and inferences from average sediment accumulation rates in the basin (this study).

**Protopalynopsis samoilovichii Zone (Foster, 1982; Helby et al., 1987)**

**Composition.** This palynzone is identified in our study by the first occurrence of *Aratrisporites* (Figs. 10J–10K; Foster, 1982; Helby et al., 1987). This genus of zonate monocele spores is typically linked to pleuromeian lycopodytes (e.g., *Helby and Martin, 1965; Morbelli and Petriella, 1973*). Fossils of this group become increasingly prevalent in the upper parts of the *P. samoilovichii* Zone, as represented by abundant pleuromeian leaf fragments, megaspores, and cingulate zonate trilete spores (e.g., *Densoisporites*).

The pollen record of this zone is dominated by the taeniate bisaccate pollen *Lunatisporites* and the non-taeniate bisaccate pollen *Alisporites* (or *Falcisporites*) and *Pteruchipollinites*. In the leaf flora, this zone includes the first occurrence of *Dicroidium* (Umkomasiales; Figs. 9A–9B) in PHKB-1 at 587.47 m but cuticular fragments of this and other seed plants are sparse throughout. Charcoalified wood fragments occur consistently through this interval (Fig. 9L), attesting to the persistence of wildfires in the landscape through the Early Triassic. Spinicaudatus were recorded at several levels within the upper part of this zone in PHKB-1 (Fig. 9O), but they have not been identified to genera or species.

This zone is characterized by high-inter-sample variability of AOM and trilete spore morphogroup abundances (particularly cingulate [e.g., *Limatulasporites*; Figs. 10E–10F], granulate [e.g., *Cyclogranisporites*; Fig. 7D], and laevigate [e.g., *Leiotriites*; Fig. 7C forms]). In general, there is a gradual decline in abundance of taxa that flourished in the wake of the EPE, particularly the phytoplankton cyanobacteria *Leiostephearia* (Fig. 7M) and *Quadrisporites* (Fig. 7L) and the fern sporangia *Thymospora* (Marattiales; Balme, 1995; Lesnikowska and Willard, 1997; Fig. 7N). Furthermore, plant sporangia that flourished prior to the EPE (e.g., *Microbaculatispora*, coarse baculate spores; Figs. 7A–B and 7E) decrease to negligible levels upwards through this zone.

**Remarks.** There is some ambiguity in the recognition of this zone in previous studies. The index taxon range chart provided by Helby et al. (1987, Fig. 5) indicates the first sparse occurrences of *Aratrisporites* Zone as low as the *P. microcorpus* Zone, and a consistent distribution of this genus through most of the *L. pellucidus* Zone and the entirety of the *P. samoilovichii* Zone. However, this is inconsistent with their written definition of the *Protopalynopsis samoilovichii* Zone, which stipulates that the base is concurrent with the first appearance of *Aratrisporites* Zone. Herein, we have followed the latter definition of this zonal boundary, which is consistent with that of Foster (1982). Furthermore, Helby et al. (1987) reported a decline of *Alisporites* (or *Falcisporites*) *australis* with a concomitant increase in taeniate bisaccate pollen at the base of this zone. A distinct change from non-taeniate to taeniate-dominated pollen assemblages was identified, but this was observed ~130 m above the base of this zone (614.33 m depth; sample S014124).
**Stratigraphic range.** The depth to the base of this zone is 745.62 m in PHKB-1 (59.46 m above the top of the Bulli Coal). The zone was not detected in the sampled portion of CCCC-27. The *Protohaploxypinus samoilovichii* Zone has the largest observed stratigraphic range of any zone identified in this study. It is estimated to be 360 m thick in PHKB-1, extending from the upper Wombarra Shale to near the top of the Bulgo Sandstone. This is broadly consistent with the reference section for the *P. samoilovichii* Zone in the northern Sydney Basin described by Helby et al. (1987; ≥259 m thick) and the stratotype of the more-or-less coeval *Kraeuselsporites aepatus* Zone of Western Australia (~361 m thick; Dolby and Balme, 1976).

**Estimated chronostratigraphic range.** Dating of the upper boundary is based on U-Pb radiochronologic ages (Metcalfe et al., 2015; Fielding et al., 2019), average sediment accumulation rates in the basin (~108 m/m.y.; Fig. 6), and a distinctive positive δ²⁷⁰CORG excursion (Fig. 3), which marks the Smithian–Spitian boundary (Galfetti et al., 2007; Zhang et al., 2015; Zhang et al., 2019; see Discussion section below). However, owing to the absence of global boundary stratotype sections and points (GSSPs) and precise geochronometric controls for the Lower Triassic substage, and the lack of a refined geochronology for the Dienerian–Smithian interval in eastern Australia, the placement of the upper and lower boundaries of this zone herein must be considered tentative. On the basis of available data, we interpret this zone to range from the lower Olenekian (‘Lower Smithian’) to mid-Olenekian (upper Smithian; Fig. 1).

**Aratrisporites tenuispinosus Zone** (Helby, 1973; Helby et al., 1987)

**Composition.** The base of this unit is identified by a marked increase in the relative abundance of *Aratrisporites* spp., particularly *A. tenuispinosus* and *A. plicatus* (Figs. 10J–10K). This genus constitutes up to 63% of the entire palynomorph count (at 320.1 m depth) but is generally ≤5% in most other samples. Increases in non-taeniate bisaccate pollen, particularly *Alisporites* (Falciisporites) and *Pteruchipollenites* (Figs. 10H–10I), occur near the base of this zone, and their abundances remain relatively high throughout (average abundance per sample ~20%). With these increases, there is a corresponding decrease in *Lunatisporites* (Fig. 10G), the dominant taeniate bisaccate pollen type of the underlying *Protohaploxypinus samoilovichii* Zone. As per the preceding zone, fluctuations in abundance of the primary spore groups (especially granulate and laeavigate acavate trilete spores) continue through the *A. tenuispinosus* Zone. Unexpectedly, the polyplicate pollen *Praecolpatites* spp. has a local first appearance at the base of the *A. tenuispinosus* Zone in PHKB-1, although this taxon has a widely accepted Permian first appearance in eastern Australia (e.g., Foster, 1979) and elsewhere in Gondwana (Antarctica: Balme and Playford, 1967; India: Venkatachala and Kar, 1968; Pakistan: Balme, 1970). These specimens likely indicate local reworking into the Lower Triassic succession. AOM levels decrease to approximately pre-EPE levels. Evidence from macrofossil leaves and cuticle mesofossils indicates the replacement of *Lepidopteris* by *Dicroidium* as the dominant foliage of seed-ferns in this interval. Isoetalean microphylls remain abundant in this zone (Figs. 9G–9I).

**Remarks.** The marked increase in *Aratrisporites*, and the replacement of *Lunatisporites* by *Alisporites* (or *Falciisporites*) as the dominant pollen form, matches previous studies for the base portions of this zone (Helby, 1973; Helby et al., 1987) and the correlative *Triplexisporites playfordii* Zone of Western Australia (Dolby and Balme, 1976; Helby et al., 1987).

**Stratigraphic distribution.** The depth to the base of the *Aratrisporites tenuispinosus* Zone is 383.48 m in PHKB-1 (421.6 m above the top of the Bulli Coal), where it corresponds to the base of the Bald Hill Claystone. The *A. tenuispinosus* Zone also extends to the top of the Garie Formation (Helby, 1973), but the upper boundary of this zone, and that of the Garie Formation, were not observed in this study. The preserved stratigraphic thickness of this zone in PHKB-1 (~145 m) is substantially greater than the Sydney Basin reference section (58 m; Helby et al., 1987). The zone was not detected in the sampled portion of CCCC-27.

**Estimated chronostratigraphic range.** We infer a range of mid-Olenekian (upper Smithian) to lower Anisian for this zone (Fig. 1). The upper boundary was broadly correlated to marine biostratigraphic zones by Helby et al. (1987) and, thence, calibrated to the global geochronological scheme of Gradstein et al. (2012) by Mantle et al. (2010).

The age of the lower boundary of the *Aratrisporites tenuispinosus* Zone (and thus the upper boundary of the *P. samoilovichii* Zone) is partially constrained by U-Pb radiochronologic ages from two tuffs near the base of the Garie Formation in the northern Sydney Basin (248.23 ± 0.13 Ma and 247.87 ± 0.11 Ma; Metcalfe et al., 2015). However, between the base of the *A. tenuispinosus* Zone (upper Bulgo Sandstone within the PHKB-1 reference section) and the Garie Formation is the Bald Hill Claystone, which is dominated by light brown mudrocks of substantial thickness (~90 m) in PHKB-1 and elsewhere in the Sydney Basin (up to 110 m thick; Emerson and Branagan, 2011). Around 100 m of strata separate the base of the *A. tenuispinosus* Zone from the level equivalent to the lowermost dated tuff in the Garie Formation. Based on the overall estimated sedimentation rate of ~108 m/m.y. for the Lower Triassic succession, we infer that this interval corresponds to around 0.9–1 m.y., or perhaps slightly more given the fine-grained nature of these strata. On this basis, we estimate that the base of the *A. tenuispinosus* Zone is close to 249.2 Ma (upper Smithian), thus significantly older than inferred by previous studies (e.g., Mantle et al., 2010).

**Ordination Data Analysis**

Ordination analyses of the palynological data revealed minimal overlap of the pre-EPE (= *Dulhuntyispora parvithola* Zone) and post-EPE (= all other zones) palynoassemblages in the ordination space (Fig. 5). This supports the prediction that there was a major shift in vegetation composition between these intervals. The only exceptions to this distinction between pre- and post-EPE assemblages were assemblages from the *Playfordispora crenulata* Zone, which overlapped to a small degree with those of the preceding *D. parvithola* Zone, but only within the presence-absence ordination. In contrast, the abundance data for these zones separated these assemblages into distinct areas in the ordination space. The post-EPE zones generally show a high degree of overlap, with the oldest of these, the *P. crenulata* Zone, being an exceptional assemblage once again. Specifically, the relative abundance data indicate that this zone is mostly distinct but shares a few palynofloral characters with other post-EPE assemblages, particularly the immediately overlying *Protohaploxypinus microcorpus* Zone. As such, the *P. crenulata* Zone likely represents a succession of distinct transitional assemblages between the classical Permian and Triassic palynofloras (the "ecosystem collapse" stage of Fig. 11).

The relatively small area of the ordination space occupied by the *D. parvithola* Zone assemblages in both analyses reflects a low degree of inter-sample variability, which is typical of a relatively uniform palynoflora (and parent vegetation). In contrast, the zone with the highest inter-sample abundance dissimilarity was the *Aratrisporites tenuispinosus* Zone, which spans a large area in the ordination space. The high inter-sample variability of the *A. tenuispinosus* Zone was largely the result of highly variable abundances of *Aratrisporites* and non-taeniate bisaccate pollen species. Emblematic of this was sample S014134 (PHKB-1, 320.1 m depth), which was an extreme outlier in the relative abundance ordination. Because this sample was...
not an outlier in the binary ordination (Fig. 5B),
the dissimilarity of this sample was due pri-
marily to anomalous abundances rather than
disparate taxa. Specifically, this sample had an
inordinately high abundance of Araritispores,
comprising ~63% of the total, which is nearly
twice as much as the assemblage with the next
highest abundance of this genus (S014131,
PHKB-1, 383.48 m depth). This sample was
not illustrated in Figure 5A because it heavily
compressed the remaining data points, even with
transformed abundance data sets, and made visu-
alization impractical.

Palynostratigraphic zones accounted for most
of the clustering in both ordinations, whereas
sample lithofacies and geographic position
played only minor roles in distinguishing paly-
nomorph content. This suggests that the stage
of floral community evolution played a greater
role in segregating palynomorph assemblage
compositions than local depositional conditions
or regional variations in the flora and supports
the biozones as reflecting discrete palynofloral/
vegetation phases, particularly the well-differen-
tiated D. parvithola and P. crenulata zones.

Carbon Isotope Chemotagratigraphy

The δ13Corg trend from the uppermost Perm-
ian to the upper Lower Triassic reveals a major
negative shift just above the last Permian coal.
Although initially marked by a series of positive
spikes in short succession, the δ13Corg remained
depressed for much of the examined post-EPE
interval. Toward the upper part of the succession,
a gradual positive shift in δ13Corg was observed,
followed by a relatively rapid stepwise increase.
A zone-by-zone description of this broad trend
is outlined below.

The Dulhuntyispora parvithola Zone has a
relatively consistent stable carbon isotope
signature, with high δ13Corg values throughout
(–25 to –23‰), but they decrease notably in the
uppermost strata. Within the Playfordiaspor-
a crenulata Zone, immediately above the
Bulli Coal (which we interpret as the onset of
the EPE herein), we identify overall low δ13Corg
values (generally below –26‰) but also signifi-
cant fluctuations ranging from –28‰ to –22‰.
A similar δ13Corg pattern was not observed in
CCC-27 over the same interval, which is ten-
tatively linked to the lower sampling resolution
in the CCC-27 core. The δ13Corg values reach a
minimum within the Protohaploxypinus micro-
corpus Zone and remain consistently low in this
interval (~30‰ to ~27‰). Within PHKB-1, the
Lunatisporites pellucidus Zone marks the onset
of a second but much longer phase of extreme
δ13Corg variability between samples (~30‰ to
~22‰), a pattern that continues well into the
subsequent Protohaploxypinus samoilovichii
Zone. A shift toward higher δ13Corg, followed by
sustained high values, initiates shortly below the
base of the Araritispores tenuispinus Zone and
is concurrent with an increase in pleuroreme-
lian liycophyte fossils (microphylls, axes, and
zontate trilete and monoolete spores). With one
exception (375.68 m depth), the δ13Corg values
from the A. tenuispinus Zone are all consist-
tently higher than those of the pre-EPE interval
(~26‰ to ~21‰).

DISCUSSION

Vegetation Changes of the Latest Permian
to Early Triassic (Lopingian–Spathian)

Here, we summarize five discrete uppermost
Permian (upper Lopingian) to Lower Triassic
(Spathian) floristic stages within the Sydney Basin that approximately correspond to the palyno-
zones outlined above. Each stage is supported
by a combination of macrofloras, palynofloras,
palynofacies, palynological ordination analyses,
and non-fossil proxy data, such as chemostra-
tigraphic and lithostratigraphic signatures. The
stages have been calibrated to the global time
scale following the chronostratigraphy presented
in the Results (see Fig. 1). These stages are sum-
marized graphically in Figure 11, and the details
of each are presented below.

Stable glossopterid forests (Dulhuntyispor-
a parvithola Zone)

This stage was characterized by a highly
productive glossopterid-dominated, forest-mire
vegetation and dense, broad-leaved deciduous
forests in humid coastal-plain environments.
The macrofloras of both examined wells yield not
only copious Glossopteris leaves but a continu-
ous record of Vertebraria, a distinctive cham-
bered root taxon with clear glossopterid affinities
(Schopf, 1965; Pigg and Taylor, 1993; Decom-
beix et al., 2009), and only minor components of
other groups, such as sphenophytes, ferns, and
lycophytes (Fig. 8). Elsewhere in the Sydney Ba-
sin, strata assigned to this interval also contain
sparse cordaitalean and scale-leaved conifer fo-
liage, rare pteridosperm leaves, and the remains
of various seed-like to scrambling sphenophytes,
ferns, and lycophytes (Townrow, 1968; Holmes,
1995; Shi et al., 2010). A consistent vegetation
type is signified by the relatively small area that
the palynoassemblages of this zone occupy in
the ordination space (Fig. 5). The vegetation
can be equated to a stable arboreal, broad-leaved,
deciduous climax community in the humid high
latitudes. Despite a dominance of hygrophyllous
plants in the assemblages of this zone, macro-
scopic scarpal particles (Fig. 8N) are common
and signify the regular occurrence of wildfires in
the Lopingian wetlands.

The most common pollen groups throughout
this interval are those typical of glossopterids
(taeniate bisaccate forms such as Protohaplox-
ypinus and Striatopodocarpites). However, it is
difficult to use these grains as a measure of floris-
tic diversity because multiple pollen morphogen-
era have been found within individual glosso-
pterid sporangia, demonstrating wide intraspecific
morphological variability of pollen within this
group (Lindström et al., 1997). Furthermore, the
occurrences of these pollen morphotypes extend
well beyond the demonstrable stratigraphic and
geographic ranges of definitive glossopterid
macrofossils, indicating that equivalent pollen
types were produced by several other plant
groups (Balme, 1995). On this latter point, two
of the Lower Triassic palynozones identified in
this study are named for the pollen genus most
commonly associated with glossopterids, Proto-
haploxypinus, but these zones are much younger
(Griesbachian–Smithian) than any reliable re-
cord of Glossopteris. Additionally, the distribu-
tion of glossopterids appears to be restricted to
Gondwana during the Lopingian (McLoughlin,
2011), but Protohaploxypinus has also been
closely associated with peltasperms at vari-
ous locations in Laurasia (e.g., Gomankov and
Meyen, 1986; Balme, 1995).

Similar palyno- and macrofloral assemblages
in Lopingian fluviol-deltaic deposits have been
recorded in continental basins across eastern
Australia (Shi et al., 2010) and other regions
of southern Gondwana (e.g., Antarctica, Taylor
et al., 1992, Gulbranson et al., 2012, Slater et al.,
2015, Miller et al., 2016; southern Africa, Prevec
et al., 2009, 2010). This signifies a very wide dis-
tribution of relatively monotonous glossopterid-
dominated hygrophyllous austral forests. Coals of
this age are common across southern Gondwana,
but their contents are generally homogenized
and obscured by diagenesis (McLoughlin et al.,
1997). The constituents of Gondwanian Perm-
ian coals are best expressed in permineralized
peats distributed across eastern Australia and
Antarctica. These are invariably dominated by
glossopterid remains (Schopf, 1970; Gould
and Delevoryas, 1977; Taylor et al., 1989; Pigg
and McLoughlin, 1997; McManus et al., 2002;
Holdgate et al., 2005; McLoughlin et al., 2019).
Despite the extreme photoperiod regime at polar
palaeolatitudes, late Permian (sub-)polar forests
had a very high, albeit seasonal, rate of pro-
ductivity (e.g., Taylor et al., 1992; Miller et
al., 2016). This high productivity is supported
by the relatively high pollen absolute abundances
in both wells investigated herein. This produc-
tivity appears to have remained high until the end
of this zone, despite independent evidence that

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Figure 11. Timeline of Permian–Triassic floral and palynological bioevents, geochemical and sedimentological features, and stages in terrestrial ecosystem evolution, as recorded from eastern Australian basins. Geochemical, sedimentological, and macrofloral data from Fielding et al. (2019) and this study. FAD—first appearance datum; LAD—last appearance datum; CIA—chemical index of alteration; ?—distribution due to possible reworking; sed.—sedimentary facies; geochem.—geochemical. “Local” refers to an abundance trend evident in only one well herein; “regional” refers to a trend observed in both wells and/or reported from other successions of eastern Australia. Sedimentary facies column characterizes the dominant fine-grained facies at the upper stratum of each fluvial facies succession. For chronostratigraphic boundary calibrations, see Figure 1. For taxon authorities, see Table A3 (see footnote 1).

The biosphere may have been under increasing environmental stress, as outlined below.

Lithologically, the top of the Bulli Coal corresponds to a coal-siltstone interface with no evidence of scouring or sediment remobilization in either of the examined wells. This suggests a widespread and abrupt (e.g., Herbert, 1997a) but conformable transition from the D. parvithola to P. crenulata zones; thus, it provides a continuous record of the initial stages of the terrestrial EPE interval in the wells studied. The Bulli Coal has a relatively high tissue preservation index and moderate to low gelification index characteristic of coals formed in forested mires (Diesel and Smyth, 1995). However, it shows a dulling-up of coals formed in forested mires (Diessel and Smyth, 1995). However, it shows a dulling-up of oxidized macerals (inertinite) toward the top (Shibaoka and Smyth, 1995). Furthermore, chemical analyses of aluminosilicate minerals within the uppermost Lopingian strata reveal a moderate to low gelification index characteristic of coals formed in forested mires (Diesel and Smyth, 1995). However, it shows a dulling-up of oxidized macerals (inertinite) toward the top (Shibaoka and Smyth, 1995). Furthermore, chemical analyses of aluminosilicate minerals within the uppermost Lopingian strata reveal a prominent phase of chemical alteration initiating prior to the EPE (Fielding et al., 2019), as noted for probable coeval deposits in Antarctica (Sheldon, 2006) and China (Cao et al., 2019). Additionally, a reduction in Glossopteris leaf size has been observed in the uppermost Permian strata of southern Africa (Anderson and Anderson, 1985; Zavada and Mentis, 1992). These lines of evidence hint at a shifting climate at high southern latitudes immediately preceding the terrestrial EPE and may indicate destabilization of the glossopterid biome near the end of its temporal range.

**Ecosystem collapse (Playfordiaspora crenulata Zone)**

The synchronous collapse of the glossopterid biome across the continental settings of eastern Australia marks the cessation of Permian peat-forming conditions in the south polar landscape. We interpret the D. parvithola–P. crenulata boundary as concurrent with the onset of the terrestrial end-Permian mass extinction interval (EPE; Figs. 1 and 3–4). The EPE in the Sydney Basin is marked by: (1) the substitution of coals by carbonaceous siltstone capping upward-finishing cyclic fluvial successions; (2) the last occurrence of glossopterids; (3) a significant and prolonged negative δ13Corg excursion; (4) high abundances of amorphous organic matter (AOM); and (5) a massive reduction in plant productivity. High-resolution palynofloral and palynofacies details of the immediate aftermath from additional outcrop sections are outlined elsewhere (Vajda et al., 2020), but a brief summary is included here to indicate the broad-scale changes.

The palynological records of the mudstone/siltstone facies overlying the uppermost Permian coal (“roof shales,” sensu Fielding et al., 2019) are characterized by a series of anomalous, stepwise abundance spikes. These include the fern spore Thymospora (PHKB-1 only), the freshwater alga Quadrisporites (CCC-27 only), and a combination of concurrent leiosphere acritarchs and AOM in both successions. The abundance peak of Thymospora indicates a local proliferation of opportunistic Marattiales, a fern group dominant in many late Paleozoic wet floodplain habitats (Pfefferkorn and Thomson, 1982). Freshwater algal proliferation is indicative of continuing, at least seasonally, wet conditions and a dearth of microfungal consumers in freshwater habitats. Although the palynofloras from this zone have many features in common with younger zones, these abundance spikes result in a high degree of inter-sample variability highlighted by the wide but distinct area of the P. crenulata Zone suites in the abundance ordination plot (Fig. 5A). Although only modest gross palynofloral diversity reduction has been claimed across the EPE (Nowak et al., 2019), the dramatic changes in group representation and loss of the previously dominant taxa indicate a major biotic crisis. The immediately succeeding vegetation appears to have been dominated by opportunistic herbaceous plants and rapidly changing plant communities.

The roof shales above the Bulli Coal are of variable thicknesses (4 m in PHKB-1, 0.4 m in CCC-27) and are truncated above by a thick succession of sandstone commonly incorporating a basal conglomeratic lag of quartz pebbles and intraformational mudstone clasts. The uneven base of the sandstone/conglomerate facies suggests that, although the basal contact of the P. crenulata Zone is likely intact, a portion of the upper part of this short biozone may have been lost to erosion locally. Based on the first appearances of P. crenulata Zone index taxa, and a significant negative δ13Corg excursion, this roof shales likely correlate to the <25-m-thick informally named “marker mudstone” overlying the uppermost Permian coal in the Bowen and Galilee basins, Queensland (Clare, 1985; Michaelsen et al., 2000), although this mudrock unit may be slightly diachronous (Wheeler et al., 2019).
The onset of the terrestrial biotic collapse interval in eastern Australia has been constrained to between 252.60 ± 0.04 Ma (Meta法则 et al., 2015) and 252.31 ± 0.07 Ma (Fielding et al., 2019). In concordance with the marine record (e.g., Jin et al., 2000; Song et al., 2013), the onset of biotic collapse occurred significantly earlier than the PTB. However, these recent age constraints also suggest that the terrestrial EPE in eastern Australia occurred at least 300 k.y. before the marine extinction interval at ca. 251.94 ± 0.037 Ma, as per representation in the Meishan P-T type section (Burgess et al., 2014). The collapse of the Glossopteris flora in the Sydney Basin is concurrent with the initiation of the primary extinction phase of the Siberian Traps Large Igneous Province (STLIP; Burgess and Bowring, 2015), whereas the marine extinction interval has been temporally linked to massive STLIP intrusive magmatism (Burgess and Bowring, 2015; Burgess et al., 2017). Independent support for an earlier terrestrial collapse comes from apparent discrepancies in the marine and terrestrial stable carbon isotope records. Firstly, the marine δ¹³Corg record at Meishan indicates a negative excursion at least 60 k.y. before the marine extinction interval (Burgess et al., 2014). However, diachrony is suggested by the C-isotope signal in Iran, where the δ¹³Corg excursion appears to have initiated during the Clarkina subcarinata conodont biozone (Korte and Kozur, 2010). This would correspond to a level between beds 15 and 20 at Meishan (Cao et al., 2009) and thus be >250 k.y. before the Chinese marine extinction interval (Bowring et al., 1998; Burgess and Bowring, 2015). Secondly, the initial negative excursion of δ¹³Corg from a terrestrial succession at Chahe, southern China (Zhang et al., 2016), has been dated at 252.30 ± 0.07 Ma (Shen et al., 2011; Fig. 12). The onset of this gradual excursion is concurrent with the last occurrences of many plant taxa (Chu et al., 2016; Zhang et al., 2016). The reported age (−360 k.y.) before the marine EPE is concordant with the onset of the terrestrial EPE interval in eastern Australia; however, the zircon data from the ash bed at Chahe should be reanalyzed using the updated age model outlined by Burgess et al. (2014) for more valid comparisons to the Meishan type section. Furthermore, there is an unresolved controversy surrounding the continuity of the Chahe strata across the end-Permian interval (Bourquin et al., 2018a, b; Zhang et al., 2018). Regardless, the strata that include the first signs of the EPE (the uppermost coal bed and onset of δ¹³Corg excursion) appears to be continuous or show only minor disruption (Bourquin et al., 2018a). Thirdly, a major floral overturn has been recorded in northern Norway, which preceded the major δ¹³Corg excursion associated with the onset of marine extinctions by an interval on the order of 100 k.y. (Hochuli et al., 2010). Lastly, the start of the gradual negative δ¹³Corg decline occurs approximately within the uppermost coal laminae and at the base of the P. crenulata Zone in some successions of eastern Australia (e.g., Bowen Basin, Morante, 1996; Sydney Basin, Fielding et al., 2019; Fig. 12). Thus, the estimated age for the start of the terrestrial ecosystem collapse and opportunism stage is approximately concurrent with the initiation of a protracted shift in the global carbon cycle, which may have commenced hundreds of thousands of years prior to the first marine extinction pulse.

There are important limitations of the most recent δ¹³Corg studies in the Sydney Basin that have precluded their direct correlation of this ecosystem collapse interval (−P. crenulata Zone) to other chronostratigraphic signatures of the EPE and PTB. Firstly, high resolution records of δ¹³Corg from the uppermost Permian coals of Sydney Basin are largely lacking (Williams et al., 2012, 2017; Mishra et al., 2019; this study), which would confirm the nature of the carbon isotope signal leading up to the terrestrial EPE. Secondly, in southern China there is a major, rapid carbon isotope excursion with marine δ¹³Corg values of ∼5‰ (at Meishan; Cao et al., 2009) associated with the onset of the marine extinction event, very shortly (−50 k.y.) before the PTB (Burgess et al., 2014) and probable coeval terrestrial δ¹³Corg values of ∼8‰ (at Chahe; Zhang et al., 2016; Fig. 12). In contrast, the δ¹³Corg record of the terrestrial strata directly above the last Permian coals in the Sydney Basin (lower P. crenulata Zone) shows two modest δ¹³Corg excursions of ∼2‰ to ∼3‰ (Williams et al., 2017; Mishra et al., 2019). These values are generally of similar magnitude to the carbon isotope excursions concurrent with the floral ecosystem overturn recorded from the Barents Sea near Norway (Hochuli et al., 2010), which likely occurred long before the marine extinction interval and PTB. However, recent outcrop sampling has revealed a very short but prominent carbon isotope excursion (−5‰) immediately above the uppermost coal in the northern Sydney Basin (Vajda et al., 2020). The differences between the magnitudes of these δ¹³Corg excursions may be due to variations in organic components (e.g., wood fragments, miospores, AOM), which can have a demonstrable and significant impact on the secular δ¹³Corg signal of some Permian–Triassic successions (Foster et al., 1997). Because the correlative PTB horizon is predicted to be on the order of several meters above the uppermost Permian coals (e.g., Chahe, Zhang et al., 2016; within the midst of the P. crenulata Zone in eastern Australia, Morante, 1996, this study; Fig. 12), this short excursion may signal an early disruption to the global carbon cycle, coeval with the collapse of terrestrial ecosystems. At present, however, it is possible that the PTB interval in eastern Australia has either not yet been sampled (e.g., Williams et al., 2012, 2017) or examined at sufficiently high resolution (Morante, 1996; Retallack et al., 2011; this study) to fully characterize the δ¹³Corg signal.

There are some important differences between the Sydney Basin fossil record and other Permian–Triassic successions around the globe. For instance, Reduviasporonites, a microfossil of fungal (Esthet et al., 1995; Visscher et al., 1996; Twitchett et al., 2001) or algal (Afonin et al., 2001; Spina et al., 2015; Hochuli, 2016) origin, is extremely abundant in many localities across Gondwana and Laurasia soon after the initial phase of the EPE (Visscher et al., 1996). It has been considered an opportunistic “disaster taxon” and a key marker for the Permian–Triassic biotic collapse (see Rampono and Esthet, 2018). However, Reduviasporonites occurs in extremely low numbers in the examined successions (Fig. 7K), suggesting either: (1) Reduviasporonites did not have an abundance acme in these parts of the Sydney Basin; or (2) the relevant stratigraphic beds were not sampled in our study. The local increase in Thymospora spores is similar in magnitude and probable duration to the lycophyte spore acme in the Permian–Triassic record of East Greenland (Looy et al., 2001) and Norway (Hochuli et al., 2010), which suggests the temporary emergence of an open herbaceous flora in the aftermath of the EPE. High abundances of spinose acritarchs (e.g., Microstridium and Veryhachium) during the end-Permian extinction interval were found in several marine successions following the end-Permian extinction interval (Sarjeant et al., 1970; Tripathi, 1997; Twitchett et al., 2001; Payne and van de Schootbrugge, 2007), indicating a pulse of primary productivity or dearth of consumers in the oceans. In contrast to the present study in which the acritarch assemblages are dominated by smooth-walled leiospherids, spiny acritarchs are consistently more common in marine successions of the EPE (Lei et al., 2012, 2019; Shen et al., 2013).

There are scattered reports of dominant Lopinigian plant groups surviving beyond the onset of terrestrial ecological collapse. Although the last record of glossopterids in Sydney Basin is more-or-less coincident with the cessation of peat-forming conditions, this group may have persisted in small numbers in disparate Gondwana localities (Antarctica: McManus et al., 2002, Elliot et al., 2017; India: Pant and Pant, 1987; southern Africa: Gastaldo et al., 2015; see Bonmleur et al., 2018), although age controls on these successions are poor. Similarly, scattered
remains of gigantopterids, a major pteridosperm component of the Lopingian Cathaysian (east Asian) floral province, appear to post-date the onset of the terrestrial extinction interval by a brief time interval (Bercovici et al., 2015; Fig. 12). Regardless, these groups never recov-
ered, soon became extinct, and did not produce coal deposits after the onset of the EPE.

Vertebrate remains are very sparse from the *P. crenulata* Zone, but the tracks of small thera-
psids have long been known from terrestrial strata of the Sydney Basin (Harper, 1915). *Lystrosauru*
s has been inferred as the maker of these tracks (Retallack, 1996), a distinctive dicynodontid sur-
vivor of the EPE very commonly found in the relatively low diversity post-EPE strata of the Karoo Basin, southern Africa (King, 1990; Damiani et al., 2004; Viglietti et al., 2013). In that region, herbaceous horsetails (Equisetales) have been inferred as the preferred diet of these small herbivores (Rayner, 1992). The paucity of equisetalean spores (e.g., *Calamospora*, *Lae-vigatosporites*) in the *P. crenulata* Zone sug-
gests that horsetails were not abundant in the

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**Figure 12.** Age correlations of the end-Permian mass extinction intervals and the Permian–Triassic boundary (PTB) between the PTB global stratotype section (Meishan) and three terrestrial stratigraphic successions. All absolute age uncertainties are at 2σ level; 1—Burgess et al., 2014; 2—Bowring et al. (1998); 3—Shen et al. (2011); 4—Metcalfe et al. (2015); 5—Fielding et al. (2019). EPE—onset of terrestrial end-
Permian mass extinction interval; PTB—Permian–Triassic boundary; FAD—first appearance datum; LAD—last appearance datum. Meishan: δ^{13}C_{org} from Cao et al. (2002), δ^{13}C from Cao et al. (2009), and nickel peak placement from Kaiho et al. (2001). Chahe: δ^{13}C_{org} from Zhang et al. (2016), and fossil distributions from Bercovici et al. (2015); PTB is the estimated placement of the Permian–Triassic boundary by Zhang et al. (2016); “damaged area” refers to an interval of apparent structurally deformed strata reported by Bourquin et al. (2018a). Denison NS-20 (Bowen Basin): biostratigraphy from Foster (1982), coal distribution and δ^{13}C_{org} from Morante (1996). Paleolatitudes from Blakey (2008) and Metcalfe (2011). Updated and expanded from Fielding et al. (2019).
The transition to this stage (mid-Permian extinction interval) is characterized by the following features: (1) a large and gradual increase in pleuroeumy lycophyte fossils; (2) common spinicaudataan fossils; (3) a major, step-wise positive δ13Corg excursion; and (4) the prevalence of red beds. The interval immediately preceding this zone, spores of pleuroeumy lycophyte affinity (Densoisporites, e.g., Grauvogel-Stamm and Lugardon, 2004; Aratriporites, e.g., Helby and Martin, 1965; Morbelli and Petriella, 1973) emerge as the dominant palynomorphs, accompanied by abundant lycophyte axes, megaspores, and microfossils.

Ecosystem instability (Aratrisporites tenuispinosus Zone)

Steady recovery (Lunatisporites pellucidus–Protophalloxypinus samoilovichii Zones)

This interval signals the emergence of conifers and pteridosperm seed-ferns as dominant constituents of the Triassic floral biome. Peltaspers (Lepidopteris; Figs. 9E and 9J) persist through this interval, but they are progressively relegated to subsidiary components of the flora. Initially, the dominant pollen types were the bisaccate non-taeniate forms Alisporites (Falcisporites) and Pterichipollenites, indicative of corystospers (and/or conifers; Townrow, 1967b; Clement-Westehof, 1974; Balme, 1995). However, these were soon replaced by the taeniate bisaccate pollen Lunatisporites (Fig. 10G), which likely represents podocarpaceous (Townrow, 1967b) or voltzian (Townrow, 1967a) conifers. The latter group is considered a more likely parent plant group because of the abundant voltzian leaf compressions found in coeval strata (Retallack, 1980). In contrast, taeniate bisaccate pollen of probable peltasper affinity (Protohalloxypinus, Striatopodocarptes; Gomankov and Meyen, 1986; see Balme, 1995) persist in very low abundance. The corystospem Dicroidium (Fig. 9B), a major component of Middle and Late Triassic Gondwanan coal deposits (Balme et al., 2012), appears shortly above the first appearance datum of Lepidopteris in the studied wells (Fig. 11) and becomes progressively more common toward the end of this recovery stage. Over the longer timeframe, there is a protracted reduction of trilete spore groups common during the Permian, such as Microbaculatispora, and the possible osmundalean Horriditribites (Galtier and Taylor, 1994; Figs. 7A–7B and 7E).

The major fluctuations in δ13Corg (~30‰ to ~22‰) through this interval reflect severe changes to the global climate and carbon cycle commonly inferred for the Early Triassic by previous researchers (Payne et al., 2004; Payne and Kump, 2007; Retallack, 2009). Elsewhere throughout the Early Triassic, major changes in palynological suites have been recognized as coinciding with the δ13Corg fluctuations (Herrman et al., 2012). Such δ13Corg oscillations seem to be matched in the palynological record of Sydney Basin by sharp variations in the cingulate, granulate, and laevigate trilete spore morphotypes between samples. A short interval of depressed δ13Corg values was identified in the P. samoilovichii Zone within the Patonga Formation (a correlative of the Bulgo Sandstone) by Morante (1996). This is mirrored herein by a progressive δ13Corg decline in the upper P. samoilovichii Zone, but this part of the zone corresponds to the Bulgo Sandstone, further suggesting time-transgressive lithostratigraphic units within the Sydney Basin.

Strata correlated to the upper P. samoilovichii Zone of the Sydney Basin (Bulgo Sandstone) have yielded body fossils of a range of archo sauriform amniotes (Kea, 2009) and temnospondyl amphibians (Warren, 1991; Damiani, 1999; Greco et al., 2014). However, diverse coprolites suggest an even richer vertebrate fauna than has been recovered to date from these strata (Niedzwiedzki et al., 2016). Similar diverse faunas of aquatic tetrapods and non-marine bony fish have been recovered from Lower Triassic strata of Queensland, Australia; the Rewan Group of the Bowen and Galilee basins (Thulborn, 1986; Warren, 1991; Damiani and Warren, 1996; Northwood, 1999, 2005; Warren et al., 2006). These fossil occurrences correspond to the L. pellucida–P. samoilovichii palynozones (Metcalfe et al., 2015) and are approximately coeval or perhaps slightly older than the Bulgo Sandstone faunas. Although not yet conducive to peat accumulation, the environmental conditions of this time were stable enough to promote a thriving terrestrial ecosystem of diverse terrestrial and marine faunas. The initial interval of the recovery stage shares some important characteristics with the preceding zone, reflecting a gradual transition as indicated by the partial overlap with the P. crenulata Zone in ordination space (Fig. 5). Specifically, primary productivity remained low as shown by low absolute palynomorph abundances and significant abundances of AOM and leiospermoid acritarchs persisting into this zone, which suggest intervals of lacustrine sedimentation and extensive bacterial degradation of organic matter (Payne and van de Schootbrugge, 2007). Relatively open vegetation, dominated by peltasperm seed-ferns, voltzian conifers, and herbaceous sphenophytes and lycophytes, appears to have occupied the landscape throughout this interval (Fig. 9). There are sparse records of Lepidopteris (peltasperm seed-fern) appearing very soon after the terrestrial biotic collapse in various localities around the Sydney Basin (Retallack, 2002; Vajda et al., 2020), in East Antarctica (McLoughlin et al., 1997), and in Madagascar (Carpentier, 1986; see Balme, 1995) persist in the studied Zone. Over the longer timeframe, there is a protracted reduction of trilete spore groups common during the Permian, such as Microbaculatispora, and the possible osmundalean Horriditribites (Galtier and Taylor, 1994; Figs. 7A–7B and 7E).

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The timing of this abundance increase is in sharp contrast to that of the pleuromeian and selaginel-
laean lycophyte abundance spikes of Greenland
(Loo y et al., 2001) and offshore Norway (Ho-
chuli et al., 2010), which were reported to have
occurred during the initial phase of the terrestrial
extinction interval. Furthermore, this signature is
significantly later than that of the Salt and
Surghar ranges, Pakistan, which reveal the on-
set of a prolonged lycophyte dominated flora as
early as the Dienerian (Herrmann et al., 2011a).
Concurrent with the increase in pleuromeian fos-
sils, the repeated occurrence of spinicaudataans suggests a shift toward seasonal desiccation and
perhaps increased salinity in ephemeral flood-
plain lakes (Gueriau et al., 2016).

The major positive $\delta^{13}$C $\text{org}$ excursion near the
base of the Aratrisporites tenuispinosus Zone, and
subsequent high values throughout the studied
portion of this zone, are similar to the $\delta^{13}$C
signature observed for the Smithian–Spathian
boundary (SSB) from various successions of the
Northern Hemisphere (Galfetti et al., 2007;
Herrmann et al., 2011b; Zhang et al., 2015,
2019; Lindström et al., 2019). The palynologi-
cal record herein is similar to that consistently
associated with the SSB; specifically, lycophyte
dominated assemblages in the latest Smithian
are followed by a rapid shift during the early
Spathian to stable, mixed pteridophyte-gymno-
sperm florais (Barents Sea: Hochuli and Vigran,
2010; Pakistan: Herrmann et al., 2011a, Herrmann
et al., 2012b; Tibet: Schneebeli-Herrmann et al.,
northern Greenland: Lindström et al., 2019).
The age of this substage boundary has not been well-constrained at present. U-Pb ra-
diometric age determinations of zircons from
tuff deposits have indicated that the SSB is older
than $250.55 \pm 0.51$ Ma (Ovtcharova et al., 2006;
Galfetti et al., 2007). However, these age esti-
mates were not derived using the updated U-Pb
age model employed for the Permian–Triassic
type section (Burgess et al., 2014), precluding
their direct comparison with the most recent age
estimates of the PTB. Importantly, these earlier
methods produced large error ranges and tended
to systematically overestimate the U-Pb age val-
cues (Condon et al., 2010). A ca. $248.45$ Ma age
for the SSB was inferred from a combination of
marine biostratigraphic and magnetostratigraph-
ic indices correlated to the global time scale
(Ogg, 2012). The high-precision absolute age
estimates of the Sydney Basin and deposition
rates for the Lower Triassic in this study put the
positive shift in $\delta^{13}$C $\text{org}$ at ca. $249$ Ma, approxi-
ately midway between the SSB estimates in the
aforementioned chronostratigraphic schemes
(Ovtcharova et al., 2006; Galfetti et al., 2007;
Ogg, 2012). We interpret this positive $\delta^{13}$C $\text{org}$
excursion as a tentative marker of the SSB in
the Sydney Basin; therefore, the base of the Ara-
trisporites tenuispinosus Zone is likely coinci-
dent with, or slightly below, the SSB. However,
higher resolution palynological and chronostrati-
graphic analyses of this interval are necessary to
better constrain the placement and floristic charac-
ter of this event at high southern latitudes.

The emergence of herbaceous lycophytes as
the dominant palynomorph group (particularly
Aratrisporites), significant $\delta^{13}$C $\text{org}$ excursion,
and coeval redbed development near the base of
this zone are indicative of significant environ-
mental changes that delayed the re-establish-
ment of complex forest ecosystems. However,
ecological and environmental interpretations of
this zone are presently equivocal. Pleuro-
meian lycophytes, which dominate the base of
this zone, have long been considered herb-
to shrub-sized xerophytic or halophytic plants that
flourished in regions of probable aridity and/or
elevated salinity (Mägdefrau, 1931; Retallack,
1975; Ziqiang and Lixin, 1982). However, Tri-
assic pleuromeian remains have also been found
in wetland settings in some parts of southern
Gondwana (central Transantarctic Mountains;
Bomfleur et al., 2011). Pleuromeians, like their
closest extant relatives Isoëtes (quillworts), may
have preferred consistently or seasonally wet
habitats, and their dominance during various in-
tervals of the Early Triassic in various parts of
the world was possibly favored by other factors.
This could have included greater immunity to
fluctuations in atmospheric gas concentrations
(thereby $\text{CO}_2$ via their root systems), having
slow growth rates with storage of starch in a
large zone of cortical tissues, occupying open
landscapes free from competition, and possibly
having a form of crassulacean acid metabolism
(CAM) and a lycopsid photosynthetic pathway.
All of these features represent specialized ecol-
ogical adaptations to stressed environments.

This interval saw the starvation of coarse se-
diment supply (Cowan, 1993) and intensification
of red-bed development (Bald Hill Claystone and
equivalents) in the Sydney Basin that likely re-
defined the climatic system. Red-bed formation
has been commonly interpreted to reflect semi-arid conditions (Van Houten, 1973)
and/or strongly fluctuating water levels (Dubiel
and Smoot, 1994). The development of ferrugi-
ous mudrock facies in the Lower Triassic of the
Karoo Basin, southern Africa, has been attribut-
ed to increased temperature, seasonality (Smith
and Botha-Brink, 2014), and either an increase
(Retallack et al., 2003) or decrease (Smith
and Botha-Brink, 2014) in overall precipitation.
Although these facies generally constrain the range
of possible deposition conditions, they are not
indicative of any specific paleoenvironments with
out additional proxies (Sheldon, 2005).

However, in the case of the Sydney Basin, the
marked increase in the CIA during this stage of
ecosystem instability (Fig. 11) favors an overall
increase in precipitation (Fielding et al., 2019).
This likely reflects intensification of the Gond-
wana monsoon in the region. More humid con-
ditions have also been inferred for the onset of
Lower Triassic red paleosols of Antarctica (Ret-
tallack and Krull, 1999). Importantly, as per the
lycophyte abundance increase outlined above,
the onset of redbed development appears to
have occurred at disparate times across southern
Gondwana. Ferruginous mudstone facies have
been dated to near the inferred onset of Permian–
Triassic terrestrial extinctions in the Karoo Ba-
sin (Ward et al., 2005; Smith and Botha-Brink,
2014; Gastaldo et al., 2015) and some regions of
the Transantarctic Mountains (collison et al.,
1994). In other Antarctic successions, the first
ferruginous mudrocks occur much higher in
the Lower Triassic successions, in some cases
hundreds of meters above the last evidence of
Permian floras (see McLoughlin et al., 1997;
Retallack and Krull, 1999). This diachrony of
ferruginous strata and coeval pulse of lycophyte
dominance are clearly indicative of shifting cli-
matic belts across much of Pangaea that likely
initiated during the late Permian (McLoughlin
et al., 1997). However, further data will be re-
quired to resolve the precise climatic drivers of
the sedimentary and biotic changes in the late
Early Triassic.

This interval of ecosystem instability initi-
ated with rapid fluctuations in palynomorph
assemblages caused by blooms of specialist
lycophytes. However, following this interval of
lycophyte dominance, the spore-pollen record of
the A. tenuispinosus Zone reflects the establish-
ment of a complex fern-gymnosperm recovery
flora, with assemblages similar in composition
and abundance to those of the L. pellucidus–P.
samoilovichii zones. The high inter-sample vari-
ability of this zone is reflected by the large area it
occupies in the ordination space (Fig. 5).

Toward the end of this stage, fossil leaves of
Dicroidium become much more common in the studied bore
cores and in outcrop throughout the Sydney Ba-
sin (Walkom, 1925; Retallack, 1980) and are
matched by abundance increases of Alisporites
(Falciisporites) and Pteruchipollenites, poll-
len commonly associated with cortysetperms
(Clement-Westerhof, 1974; Balme, 1995). In con-
trast, there is a corresponding reduction in all
taeniate bisaccate pollen to negligible lev-
els. We note a distinct absence of Lepidopteris
(peltsperm) leaves in the cores toward the top
of this zone. However, Lepidopteris madagas-
cariensis remained a sub-dominant element in
macrofloras recovered from equivalent strata in
outcrop of the northern Sydney Basin and the

Permian-Triassic south polar floristic timeline

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The establishment of a new, complex conifer-peripodisperm climax flora was interrupted by a major phase of abiotic stress in the region initiating approximately 2 m.y. after the PTB (ca. 250 Ma; mid-Smithian). This was indicated by a marked rise of pleurocerian lycophytes with specialized ecophysiological traits and a stepwise positive shift in stable carbon isotopes. This was followed by the accumulation of thick packages of ferruginous mudrocks, an increase in chemical weathering, and a major overturn of the palynofloras shortly before the Smithian–Spathian boundary (SSB), the first such stable carbon and palynological records of this boundary from southern Gondwana. The age of the SSB was estimated as ca. 249 Ma by interpolating the sediment accumulation rates from radiogenic-isotope age anchor-points within the Sydney Basin. The specific environmental changes that triggered this environmental transition late in the Early Triassic are presently unclear, but they were likely linked to prolonged climate change and shifting climatic belts across southern Gondwana. Similar changes have been identified in post-EPE successions worldwide but at discrete intervals. The high southern latitudes were likely the last region on Earth to develop these environmental conditions. In summary, the loss of the Permian climax conifer-perispermoid floras represents a major collapse in primary productivity and ecological complexity from which the terrestrial vegetation did not recover until late in the Early Triassic.

ACKNOWLEDGMENTS

This research was funded by collaborative research grants from the National Science Foundation (EAR-1636625 to CRF and TDF). Funding was also received from the Swedish Research Council (grant 2015-4264 to YV, and grants 2014-5234 and 2018-04527 to SM). The authors thank Sam Slater for assistance with the ordination analyses, and Arne Winguth, Cornelia Winguth, Malcolm Bocking, and James Crowley for their input, which provided additional geochronologic and paleoclimatic context. Special thanks to John Laurie for discussions regarding Australian biotstratigraphic schemes. Assistance with sample collection was provided by Mark Ryland and the staff at the Londonderry Drillcore Library, NSW, Australia. We are grateful to Rob Strachan for editing the manuscript and Benjamin Bonfruit and one anonymous reviewer for their constructive reviews, which greatly improved the manuscript.

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Mays et al.


Appendix 1. Additional methodological details for palynological counts and ordination analyses.

**Table A2.** Palynomorph taxa and groups sorted by morphological categories as employed throughout this paper. Note the finer taxonomic divisions for PKHB-1 Count 1. Taxa in bold have been employed herein for regional palynostratigraphic correlation. Morphological categories are based on those of Traverse (2007). “Spp.” includes only other species not already listed.

**Table A3.** Abundance tables of palynomorph groups. All percentages are calculated as a proportion of the respective total palynomorph sample count (N). Average counts for PHKB-1 are calculated from the abundances of both counts 1 and 2. Dashes indicate samples included only in PHKB-1 Count 2. Palynomorph concentration per gram of dried sediment (C) derived by the following calculation (modified from Benninghoff, 1962):

\[ C = \frac{(N \times L_t)}{(L \times M)} , \]

where \( N \) = total palynomorph sample count, \( L_t \) = estimated *Lycopodium* spores per spiked sample (= 9666; standard deviation = 671; Maher, 1981), \( L = Lycopodium \) spores counted, and \( M \) = mass of processed dried sediment.

**Table A4.** Abundance tables of palynofacies groups. All percentages are calculated as a proportion of the respective palynofacies total, either category subtotal (n) or total palynofacies count (N = 500). Palyn = palynomorphs, phyto = phytoclasts, miospores = spores + pollen, - = samples in which *Lycopodium* spore tablets were not included during processing. PHKB-1 palynofacies data are from Fielding et al. (2019).

**Table A5.** Palynomorph categories for ordination analysis applied to all palynomorph count data. Categories employed in this study are numbered.

**Table A6.** Stable carbon isotope data for PKHB-1 and CCC-27. PHKB-1 data are from Fielding et al. (2019).

**Table A7.** List of specimens in Figs 7 and 8, including taxon authorities, sample numbers, slide numbers and England Finder coordinates (Eng. Find. coords); K = kerogen slide.
APPENDIX 1: ADDITIONAL METHODS and REFERENCES CITED

Palynology count methods

Of the 52 palynological samples from PHKB-1, we provide the full palynomorph count data sets of the 44 samples presented by Fielding et al. (2019), including additional data categories that were excluded from that study for brevity; taxa assigned to each taxonomic/morphological category are outlined in Appendix 2. Twenty-four of these samples were counted a second time by CM (‘Count 1’; the remaining specimen counts constitute ‘Count 2’; see Appendix 3) for the purpose of verifying the original results of Fielding et al. (2019). The remaining eight samples from PHKB-1 (S014107, S014111, S014112, S014115, S014121, S014122, S014123, S014149), and four samples from CCC-27 (S014165, S014168, S014169, S014171), were barren of palynomorphs, and excluded from the palynomorph counts. All palynomorph counts incorporated ≥250 individual specimens, except for six samples from PHKB-1 (S014097, S014099, S014100, S014105, S014116 and S014141) and three samples from CCC-27 (S014158, S014166, S014167), which failed to meet the prescribed specimen count. Full palynomorph count data are presented in Appendix 3.

Pollen diagrams of PHKB-1 (Figs. 3 and 4) were produced from a composite data set of counts 1 and 2; in samples where both count data were available, an average was calculated and used. Where only Count 2 data were available, these data were employed. Count 2 did not include monolette spores other than Thymospora spp. and zonate monolette spores (= Aratrisporites spp.). As such, all values of ‘other monolette spores’ for Count 2 were assigned to zero for the purposes of the pollen diagrams.

Kerogen slides of all 78 samples were produced for palynofacies analysis. Palynofacies data were compiled from counts of 500 individual grains (minimum grain diameter = 5 µm). The following palynofacies categories and subcategories were included in the counts (following the classification of Tyson, 1995): 1, palynomorphs ([a] plant spores, [b] pollen, [c] phytoplankton, [d] fungal remains); 2, phytoclasts ([e] opaque including charcoal, [f] tracheids/rays, [g] other translucent phytoclasts, [h] cuticles/membranous tissues); and 3, amorphous organic matter (AOM; [i] particulate, [j] resin). Full palynofacies count data are presented in Appendix 4.

To estimate productivity (a measure of absolute abundance) per sample, a standardized quantity of an exotic marker spore species was added to the samples during palynological processing (Stockmarr, 1971). For these estimates, selected samples were dried, weighed and one spore tablet of extant Lycopodium clavatum per sample was added prior to acidification (for specific samples and lycopodium counts, see appendices 3 and 4). Spore tablets were from Batch 3862, as prepared by the Department of Geology, Lund University (2014); estimated number of spores per tablet = 9,666 ± 6.94% (confidence estimations follow Maher, 1981). These extrinsic Lycopodium spores were counted in addition to the total counts for palynofacies and palynomorphs outlined above. By counting these standard markers in parallel with the palynological counts, we employed the relative changes in palynomorphs or palynofacies as a proxy of palynomorph production or total organic production, respectively, for a given time horizon. Specifically, there is an inverse relationship between the Lycopodium count and total palynomorphs/palynofacies count; hence, an interval of higher palynomorphs/palynofacies productivity should be reflected by a relatively low Lycopodium count. Fluvio-deltaic systems are characterized by variable depositional rates and hydraulic sorting of sediments, including palynomorphs and other organic matter (Brown et al., 2007). Thus, productivity estimates should
only be compared between assemblages from lithofacies of similar grain-size (e.g., claystone, siltstone, or fine sandstone), because these should reflect comparable flow conditions at the site of deposition. In order to control for this variable, siltstone and claystone facies were selected for palynological processing, reflecting minimal depositional transport (Folk, 1980), except where indicated in appendices 3 and 4. Palynomorph concentrations for each sample spiked with *Lycopodium* were calculated by employing the method outlined by Benninghoff (1962; see Appendix 3); however, owing to the low concentrations of counted *Lycopodium* spores, absolute palynomorph concentrations could not be determined reliably for most samples in PHKB-1.

**Ordination data treatment and indices**

For nMDS, the abundance data needed to be standardized across both well successions, and this was conducted in a series of stages. Firstly, within PHKB-1, Count 1 was selected where possible (because of the higher sample counts), and Count 2 data for the remaining samples in that well. Secondly, data categories shared by both successions could be compared without regrouping, whereas more finely-partitioned data required amalgamation into broader morphological categories (‘lumping’) which could then be compared across all count data sets. Thirdly, samples were excluded if they failed to meet the minimum palynomorphs count number of 250, including functionally barren samples (14 samples in total from PHKB-1, seven from CCC-27; see Appendix 3). Finally, palynomorph categories that were recorded from single samples (‘singletons’) were excluded in order to decrease statistical noise.

Ordination analyses were conducted on two versions of the compiled data: 1, relative abundance; and 2, presence/absence. Relative abundances were calculated as a proportion of the total count of each sample, thus standardizing for different count sizes. NMDS ordination analyses were conducted on these relative abundance data, and on two types of transformed fossil data sets: 1, a logarithmic function (e.g., Spicer and Hill, 1979; Slater and Wellman, 2015); and 2, a square root function. These transformations were performed to compress the abundance ranges, without altering their relative rank-orders. The Bray-Curtis similarity index was employed for all variants of the relative abundance data; this is algebraically equivalent to the Bray-Curtis dissimilarity index (Bray and Curtis, 1957). The combination of nMDS and Bray-Curtis index has been demonstrated to be a reliable ordination method for quantitative ecological data (Minchin, 1987). For the presence/absence ordination, all palynomorph group abundances were converted to binary, where the absence of a palynomorph group = 0, and presence = 1. The Jaccard index of similarity was chosen for the presence/absence ordination because it has consistently proven reliable for intergroup differences in binary ecological data (Hubálek, 1982). Ordination analysis was conducted on a binary variant of the data set because, although anomalously high taxon abundances can greatly influence the ordination of abundance data sets, binary data are immune to this effect. A comparison of presence/absence and relative abundance ordinations should reveal which samples are contributing inordinately to the dissimilarity between palynomorph assemblages. Furthermore, both ordination techniques were included in this study because temporal differentiation (biozones) was probably a major factor controlling the differences between assemblages, and these zones are defined partly on taxon acmes and partly on taxon first appearances. Relative abundance ordination is more relevant for differentiating the former, whereas presence/absence ordination should reveal the latter.
REFERENCES CITED


<table>
<thead>
<tr>
<th>De</th>
<th>Hamilton</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aratrisporites</td>
<td>TAENIATE</td>
</tr>
<tr>
<td>Brevitriletes</td>
<td>ECHINATE</td>
</tr>
<tr>
<td>Dulhuntyispora</td>
<td>POLYPLICATE/COSTATE</td>
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<tr>
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<td>Quadrisporites</td>
<td>BISACCATE</td>
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<td>Vitreisporites</td>
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<table>
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<th>Concentration (%)†</th>
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<td>16 6,4</td>
</tr>
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<td>0 0,0</td>
</tr>
<tr>
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</tr>
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<td>3 1,2</td>
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</tr>
<tr>
<td>15 2,6</td>
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</tr>
<tr>
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<td>6 2,4</td>
</tr>
<tr>
<td>5 0,9</td>
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</tr>
<tr>
<td>3 1,2</td>
<td>4 1,6</td>
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| 465 250 | Siltstone |
| 78 31,2 | ‒‒‒‒‒‒ |
| 53 21,2 | ‒‒ ‒ ‒ |
| 53 21,2 | ‒‒ ‒ ‒ |
| 53 21,2 | ‒‒ ‒ ‒ |
| 0 0,0 | 0 0,0 |

| 468 436 | Siltstone |
| 78 31,2 | ‒‒‒‒‒‒ |
| 53 21,2 | ‒‒ ‒ ‒ |
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| Depth (m) | Sand–silt–clay ratio | Sample number | [cm] | total | % | Palynophorids | % | Palynological | % | Planktonic | % | Protistological | % | Other | % | Trachysporites | % | Moscovais | % | Cribrospores | % | Cribrostylid | % | Cribrostylid Spores | % | Cribrostylid Ratio | % | Hirticribrostylid | % | Hirticribrostylid Spores | % |
|----------|----------------------|---------------|------|-------|--|---------------|--|---------------|--|-------------|--|---------------|--|--------|--|---------------|--|-------------|--|-------------|--|-------------|--|---------------|--|-------------|--|---------------|--|-------------|--|---------------|--|-------------|--|---------------|--|
| 334,5 | 0.79 | S014146 | 22,65 | 2.50 | 154 | 7,89 | 133 | 23,07 | 157 | 26,62 | 30,57 | 5,00 | 34,72 | 29 | 5,80 | 40,28 | 46,30 | 18 | 3,60 | 25,00 | 0 | 0,00 | 72 | 14,40 | 74 | 14,80 | 18,18 | 36 | 66,67 | 81,82 | 0,22 | 407 | 81,40 | 21 | 0 | 4,20 | 0 | 0 | 50 | Fine Silt |
| 352,5 | 0.80 | S014147 | 23,55 | 2.60 | 155 | 7,90 | 133 | 23,07 | 157 | 26,62 | 30,57 | 5,00 | 34,72 | 29 | 5,80 | 40,28 | 46,30 | 18 | 3,60 | 25,00 | 0 | 0,00 | 72 | 14,40 | 74 | 14,80 | 18,18 | 36 | 66,67 | 81,82 | 0,22 | 407 | 81,40 | 21 | 0 | 4,20 | 0 | 0 | 50 | Fine Silt |
| 355,5 | 0.81 | S014148 | 24,60 | 2.80 | 153 | 7,88 | 132 | 22,78 | 155 | 25,98 | 29,57 | 5,00 | 34,72 | 29 | 5,80 | 40,28 | 46,30 | 18 | 3,60 | 25,00 | 0 | 0,00 | 72 | 14,40 | 74 | 14,80 | 18,18 | 36 | 66,67 | 81,82 | 0,22 | 407 | 81,40 | 21 | 0 | 4,20 | 0 | 0 | 50 | Fine Silt |
| 357,5 | 0.82 | S014149 | 24,75 | 2.80 | 153 | 7,88 | 132 | 22,78 | 155 | 25,98 | 29,57 | 5,00 | 34,72 | 29 | 5,80 | 40,28 | 46,30 | 18 | 3,60 | 25,00 | 0 | 0,00 | 72 | 14,40 | 74 | 14,80 | 18,18 | 36 | 66,67 | 81,82 | 0,22 | 407 | 81,40 | 21 | 0 | 4,20 | 0 | 0 | 50 | Fine Silt |
| 360,5 | 0.83 | S014150 | 25,90 | 3.00 | 152 | 7,87 | 131 | 22,56 | 154 | 25,96 | 29,57 | 5,00 | 34,72 | 29 | 5,80 | 40,28 | 46,30 | 18 | 3,60 | 25,00 | 0 | 0,00 | 72 | 14,40 | 74 | 14,80 | 18,18 | 36 | 66,67 | 81,82 | 0,22 | 407 | 81,40 | 21 | 0 | 4,20 | 0 | 0 | 50 | Fine Silt |
| 362,5 | 0.84 | S014151 | 26,05 | 3.00 | 154 | 7,89 | 133 | 23,07 | 157 | 26,62 | 30,57 | 5,00 | 34,72 | 29 | 5,80 | 40,28 | 46,30 | 18 | 3,60 | 25,00 | 0 | 0,00 | 72 | 14,40 | 74 | 14,80 | 18,18 | 36 | 66,67 | 81,82 | 0,22 | 407 | 81,40 | 21 | 0 | 4,20 | 0 | 0 | 50 | Fine Silt |

**Table A2. Paleonoeid Counts for the Cenolyser (DS 27, CEC-27), Including Percentages and Palynomorph Concentrations.**
<table>
<thead>
<tr>
<th>POLLEN/ SPORES</th>
<th>POLLEN/COSTATE</th>
<th>POLLEN/MONOCOLPATE</th>
<th>POLLEN/MONOSACCATE</th>
<th>POLLEN/TRIULATE</th>
<th>POLLEN/ZONATE</th>
<th>POLLEN/PHYTOPLANKTON</th>
<th>POLLEN/FUNGUS</th>
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</thead>
<tbody>
<tr>
<td>1. All aleate pollen/spores</td>
<td>2. All costate and polyplicate</td>
<td>3. All monocolpate</td>
<td>4. All monocinate</td>
<td>5. Other non-taeniate monosaccate pollen</td>
<td>6. Lagerista sp.</td>
<td>7. Other taeniate baculate pollen</td>
<td>8. All non-taeniate monosaccate pollen</td>
</tr>
<tr>
<td>Depth (m)</td>
<td>Height (m from top of Bulli Coal seam)</td>
<td>$\delta^{13}C_{\text{org}}$ (%o V-PDB)</td>
<td></td>
<td></td>
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