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A Multidisciplinary Approach to Resolving the End-Guadalupian Extinction

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A multidisciplinary approach to resolving the end-Guadalupian extinction

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ABSTRACT

The transition from the middle to late Permian (Guadalupian–Lopingian) is claimed to record one or more extinction events that rival the ‘Big Five’ in terms of depletion of biological diversity and reorganization of ecosystem structure. Yet many questions remain as to whether the events recorded in separate regions were synchronous, causally related, or were of a magnitude rivaling other major crises in Earth’s history. In this paper, we survey some major unresolved issues related to the Guadalupian–Lopingian transition and offer a multidisciplinary approach to advance understanding of this under-appreciated biotic crisis by utilizing records in Southern Hemisphere high-palaeolatitude settings. We focus on the Bowen-Gunnedah-Sydney Basin System (BGSBS) as a prime site for analyses of biotic and physical environmental change at high palaeolatitudes in the middle and terminal Capitanian. Preliminary data suggest the likely position of the mid-Capitanian event is recorded in regressive deposits at the base of the Tomago Coal Measures (northern Sydney Basin) and around the contact between the Broughton Formation and the disconformably overlying Pheasants Nest Formation (southern Sydney Basin). Initial data suggest that the end-Capitanian event roughly correlates to the transgressive “Kulnura Marine Tongue” in the middle of the Tomago Coal Measures (northern Sydney Basin) and strata bearing dispersed, ice-rafted gravel in the Erins Vale Formation (southern Sydney Basin). Preliminary observations suggest that few plant genera or species disappeared in the transition from the Guadalupian to Lopingian, and the latter interval saw an increase in floristic diversity.

1. The end-Guadalupian mass extinction

The end-Permian extinction (EPE, c. 252 million years ago, Burgess et al., 2014) was the most severe biotic crisis of the Phanerozoic Eon (Wignall, 2001; Erwin et al., 2002; Stanley, 2016) with more than 60% of marine and terrestrial genera going extinct. The traditional view of the EPE was that it represented a singular global extinction event, but it is now generally recognized that the late Permian was in fact characterized by a series of global disruptions leading up to the main marine kill interval close to the Permian-Triassic boundary, along with subsequent events that delayed biotic recovery in the Early Triassic (Chen et al., 2022). Jin et al. (1994) and Stanley and Yang (1994) recognized an earlier marine extinction event at the middle (Guadalupian)–upper (Lopingian) Permian boundary (herein called the end-Guadalupian Extinction: EGE, c. 259 million years ago), which may in fact represent the first major global disruption leading up to the EPE. Although less prominent than the EPE, the EGE is considered to have entailed major biodiversity loss by some researchers (e.g., Stanley, 2016; Rampino and Shen, 2019) and was ecologically disruptive (Muscente et al., 2018; Day and Rubidge, 2021). Furthermore, some researchers

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have also postulated an even earlier, mid-Capitanian extinction event (MCE; e.g., Bond et al., 2010a; Arefifard and Payne, 2020). This begs the question as to whether the late Permian Earth system was teetering on the brink of planet-wide ecological disruption, its resiliency challenged by the closely spaced preceding extinction events and in effect, “primed” for global collapse. Conversely, since the late Permian biosphere consisted of hardened EGE survivor groups, the severity of EPE ecosystem collapse may have been even worse if not for the EGE. What were the tipping points that triggered the EGE and preceded the EPE, the largest extinction in Earth history?

Currently, considerable uncertainty exists as to whether the EGE represents a global extinction event, and if it entailed one or more crises. The severity, timing and ultimate cause(s) of the EGE and associated perturbations are also disputed. Putative links to global cooling and southern hemisphere glaciation remain unresolved (Isozaki et al., 2007a, 2007b).

Analyses accounting for variable sampling rates over time suggest that global Guadalupian extinction rates among marine taxa are well within background rates for the Phanerozoic (Foote, 2007; Alroy, 2008). Sampling-standardized analyses by Clapham et al. (2009) suggested that the EGE may have been driven by suppressed origination rather than by elevated extinction, or was a ‘depletion event’ (*sensu* Stigall, 2019). Regardless of extinction rates, the EGE was one of the most severe ecological crises of the Phanerozoic (Stanley, 2016) and likely altered ecosystem structure and distribution to a greater degree than did some larger extinction (or depletion) events (McGhee et al., 2013; Muscente et al., 2018; Rampino and Shen, 2019). Raup and Sepkoski (1982) initially placed the onset of the EPE well within the Guadalupian.

In the well-constrained Guadalupian-Lopingian Global Stratotype Section and Point (GSSP) in south China, major losses in both marine macro- and microfauna occurred, but this was during the mid-Capitanian, well before the end-Guadalupian (Shen and Shi, 2009; Wignall et al., 2009a,2009b; Bond et al., 2010a, 2010b). The terrestrial fossil record in South China (Shen, 1995) shows a major overturn in palaeoflora in the Capitanian, consistent with the timing based on marine fossils, although the stratigraphic sampling resolution remains coarse. Thus, Bond et al. (2010a) argued for a “Capitanian Extinction”. Subsequent work established evidence for a second, later extinction event at the Guadalupian-Lopingian boundary at this site and elsewhere (Bond et al., 2015; Huang et al., 2019; Zhong et al., 2020; Song et al.,

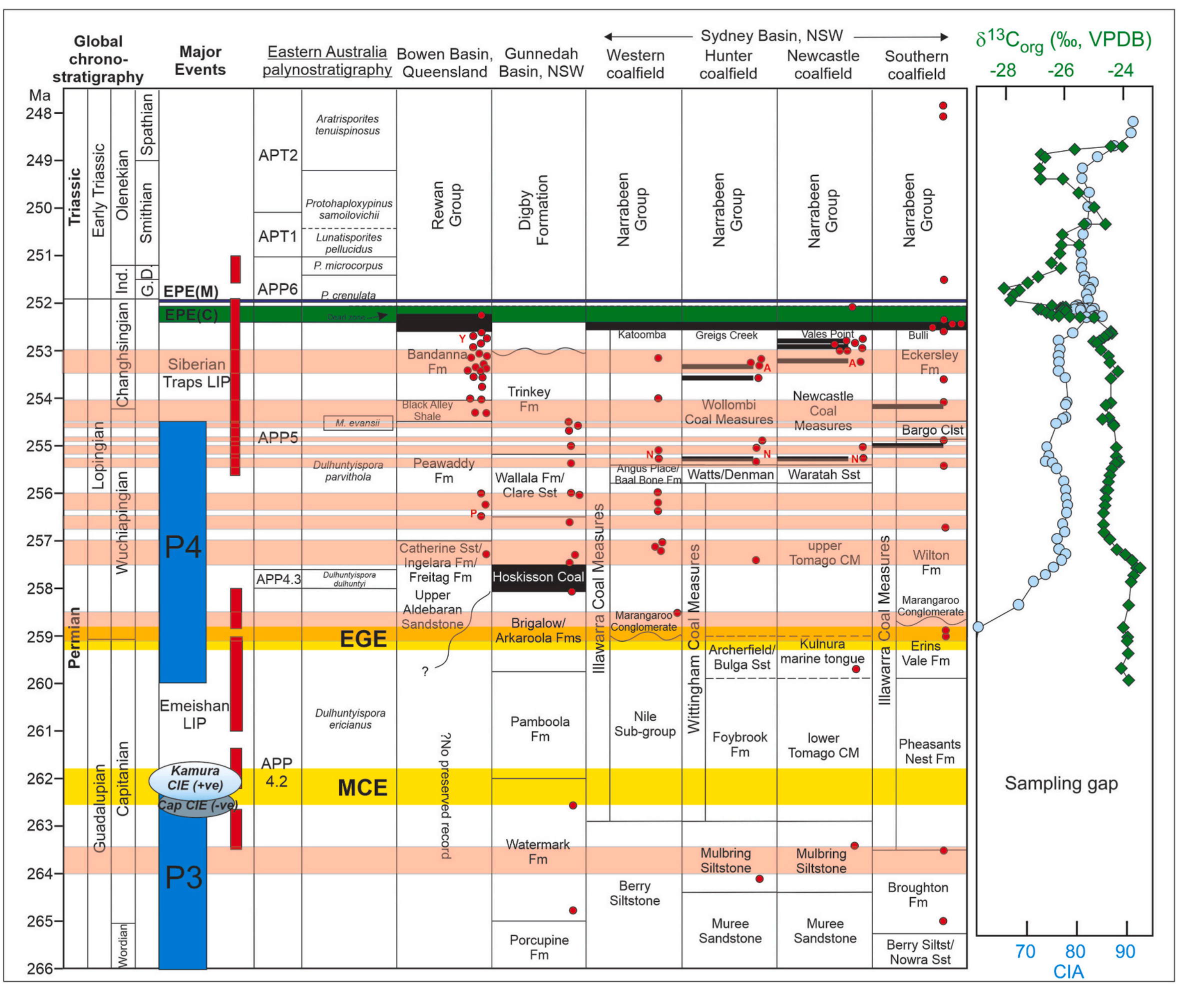

Fig. 1. Stratigraphic framework for the middle–late Permian record of the Bowen-Gunnedah-Sydney Basin System (BGSBS), showing available age (red circles) and other data, and major geological events (modified after Fielding et al., 2022). Horizontal yellow bars denote times of interpreted biotic crises from the literature. Vertical red bars denote time ranges of major LIPs (Burgess and Bowring, 2015; Chen and Xu, 2021). Horizontal pink bars denote clusters of tuff ages within the BGSBS succession (Nicoll, pers. comm.). Stratigraphic data from various sources including Metcalfe et al. (2015), Laurie et al. (2016), Fielding et al. (2019, 2021), and Mays et al. (2020). P3 and P4 are glaciations after Fielding et al. (2023). CapCIE refers to the mid-Capitanian Carbon Isotope Excursion (Zhang et al., 2021), and Kamura CIE to the Kamura event of Isozaki et al. (2007a, b, 2011). MCE – Mid-Capitanian Extinction, EGE – End-Guadalupian Extinction, EPE(M) – End-Permian Extinction (marine), EPE(C) – End-Permian Extinction (continental). Red capital letters denote some prominent tuff beds; A – Awaba, N – Nobbys, P – Platypus, Y – Yarrabee. Geochemical trends are from PHK Bunnerong-1, published by Fielding et al. (2019, 2023). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2023). Retallack et al. (2006) argued for a palaeofloral extinction event at the end-Guadalupian in Antarctica and South Africa, but issues persist over the veracity of both the data used to formulate this interpretation and the timing of events (Bond et al., 2010a: p. 111).

Conflicting interpretations of the extent of extinction during the EGE may point to taxonomic heterogeneity in the effects of the EGE. Analysis of Chinese data by Fan et al. (2020) suggested that depletion at the EGE (from extinction or suppressed origination) was restricted to corals and foraminifera, with a possible correlative loss of plant and terrestrial vertebrate communities (Bond et al., 2010a; Marchetti et al., 2022). Day et al. (2015) found evidence for a major turnover of tetrapods in the Karoo Basin of South Africa at about 260 Ma. Notably, all these groups were key organisms in mid-Permian ecosystems. Bond et al. (2010a, 2015), Isozaki et al. (2007a, b, 2011, their "Kamura Event"), Huang et al. (2019), and Arefifard and Payne (2020) further suggested additional extinction pulses for marine taxa in the mid-Capitanian in records from China, Svalbard, Iran, Japan, and Croatia, converging on c. 262 Ma (Fig. 1). Zhang et al. (2021) found evidence for palaeoceanographic disturbances coincident with the mid-Capitanian faunal turnover at 261.6 $\pm$ 1.6 Ma. The balance of evidence suggests that more than one extinction event affecting both marine and terrestrial ecosystems occurred during the Guadalupian–Lopingian transition. Their pattern and relative timing are well-constrained in the area of the GSSP in South China, but not elsewhere. Whether these die-offs were triggered by warming, cooling or other factors remains unresolved.

Numerous plausible drivers of extinction and ecosystem alteration coincide with the EGE, including: Emeishan Large Igneous Province (ELIP) magmatic activity, circum-Gondwanan explosive volcanism, regression and loss of marine habitat, long-term cooling, ocean anoxia, catastrophic methane outbursts, combustion of terrestrial biomass and shoaling of sulfidic waters (e.g., Wignall et al., 2009a; Zhang et al., 2015; Chapman et al., 2022; Song et al., 2023; Kaiho et al., 2023). Coincidence of all these factors with the ELIP has led to a broad consensus that, like most other global extinction events, environmental perturbations associated with large-volume volcanic eruptions were the principal driver for the EGE (Wignall, 2001; Wignall et al., 2009b; Bond et al., 2010a; Sun et al., 2010; Shellnutt et al., 2012, 2020; Zhong et al., 2020). This is because continental large igneous provinces are exceptional intraplate igneous events in Earth's history and are the only known terrestrial phenomena that can trigger global mass extinction events on land and in the oceans (Bryan and Ferrari, 2013).

Large-scale ecosystem perturbations in the mid-Capitanian predate the main eruptive phase of the ELIP (Chen and Xu, 2021). If an early intrusive phase and associated outgassing in the ELIP occurred (Liu et al., 2021), this may have led to the large-scale emission of significant greenhouse gases and particulates and could have triggered the mid-Capitanian crisis. If the mid-Capitanian timing of this intrusive phase is correct, it would coincide with the close of the P3 glaciation in eastern Australia (Fielding et al., 2008, 2023) (Fig. 1), suggesting that the mid-Capitanian was characterized by global warming. Nonetheless, there are conflicting interpretations of this event, with Bond et al. (2010a) and Zhang et al. (2021) documenting a negative carbon isotope excursion that they interpreted to record warming, whereas Isozaki et al. (2007a, b, 2011, their "Kamura Event") reported a positive carbon isotope excursion that they considered to record cooling (Fig. 1).

The end-Guadalupian (end-Capitanian) extinction (EGE) coincides with the end of the main eruptive phase of the ELIP (Chen and Xu, 2021), and again may have been triggered by release of greenhouse gases and toxic aerosols. However, the EGE also coincides with the early phase of the eastern Australian P4 glaciation (Fielding et al., 2008, 2023) (Fig. 1), suggesting a causal link with global cooling. Yang et al. (2018) proposed that the P4 glaciation in eastern Australia and the potentially global cooling event were caused by the terminal phase of ELIP volcanism and weathering of lavas. Although a timing overlap is observed, generally little evidence exists for the occurrence of large-scale and intense weathering during the emplacement of flood basalt provinces as a viable mechanism to drive relatively rapid global cooling (Bryan, 2021). Available geochronological constraints (Fig. 1) suggest there may be an antithetic relationship between the timing of eastern Australian glaciations P3 and P4 and that of the Emeishan and Siberian Traps LIPs. Nonetheless, uncertainties persist, not least because Emeishan in southwest China and northern Vietnam were in the palaeotropics during the Permian, hence strata in those regions were unaffected by the alpine (valley-confined) nature of the P4 glaciation recorded in the high palaeolatitudes of eastern Australia. Furthermore, continuous sections through the Guadalupian-Lopingian boundary are sparse, in part due to an interpreted global sea-level lowstand at that time (Haq and Schutter, 2008).

2. Deciphering regional vs. global patterns

The causes, effects, and timeline of the MCE and EGE have not been resolved satisfactorily. Furthermore, since a potentially worldwide cooling event is coeval with the EGE, detailed examination of a site that lay in the high southern palaeolatitudes, where a direct record of cold conditions is preserved, is crucial to an improved understanding of the EGE. We posit that the Bowen-Gunnedah-Sydney Basin System (BGSBS) in eastern Australia (Fig. 2) is the ideal site for resolving these uncertainties. The BGSBS was a retroarc foreland basin during the middle and late Permian that accumulated a thick, stratigraphically complete succession along a palaeo-continental margin, spanning the Guadalupian-Lopingian transition (Fielding et al., 2001). Unlike sites in China (equatorial and proximal to Emeishan volcanism) and mid-latitude Svalbard, the Australian record represents high southern palaeolatitudes (40–70°S) that may have been more sensitive to climate changes than lower-latitude locations (Fig. 2D). Our ongoing work aims to: 1. Determine whether the EGE was linked to cooling of marine and lowland continental habitats, 2. Elucidate its ultimate cause, and 3. Determine the extent to which both basin-marginal and distant volcanic activity played a role in this event at high southern latitudes.

A large inventory of new, high-precision, absolute age data from primary volcanic deposits allows unprecedented insight into the timing and pacing of events through the Permian succession of the BGSBS (e.g., Metcalfe et al., 2015; Laurie et al., 2016; Fielding et al., 2019, 2021). New geochronological data have provided the basis for a highly resolved upper Permian stratigraphic framework (Fig. 1), which by means of a refined palynostratigraphic scheme (Laurie et al., 2016; Mays et al., 2020), can be tied to near- and offshore marine successions of Western Australia and Asia. This is a key advancement because a paucity of ammonoid and conodont faunas in Australia had previously hindered correlation of the Australian Permian with the rest of the world. Despite recent efforts targeting principally the late Permian record, however, comparatively few new ages are available to constrain the middle Permian and the Guadalupian-Lopingian boundary (Fig. 1). Timing is key to understanding the relationships of regional and global events through the middle–late Permian. Additional high-precision geochronological anchor points are needed in order to better constrain the timing of key events in the BGSBS, and we have targeted a series of thick tuffaceous beds for U-Pb CA-IDTIMS dating that bracket the target intervals.

The most stratigraphically complete middle–upper Permian succession occurs in the Sydney Basin, which accumulated c. 2000 m of predominantly siliciclastic sediments in the foredeep axis preserved in coastal New South Wales (NSW) between the cities of Sydney and Newcastle (Figs. 1 and 2B). The correlative succession in the Gunnedah Basin in northern NSW is also informative, whereas biostratigraphic data in the absence of absolute age controls suggest that the equivalent interval is missing from the Bowen Basin in Queensland (Figs. 1 and 2). Our work thus far has focused on the foredeep of the Sydney Basin, where the most continuous record is likely to be preserved. Here, we have examined intervals from the lower Capitanian Mulbring Siltstone through the Capitanian to Wuchiapingian Tomago Coal Measures and

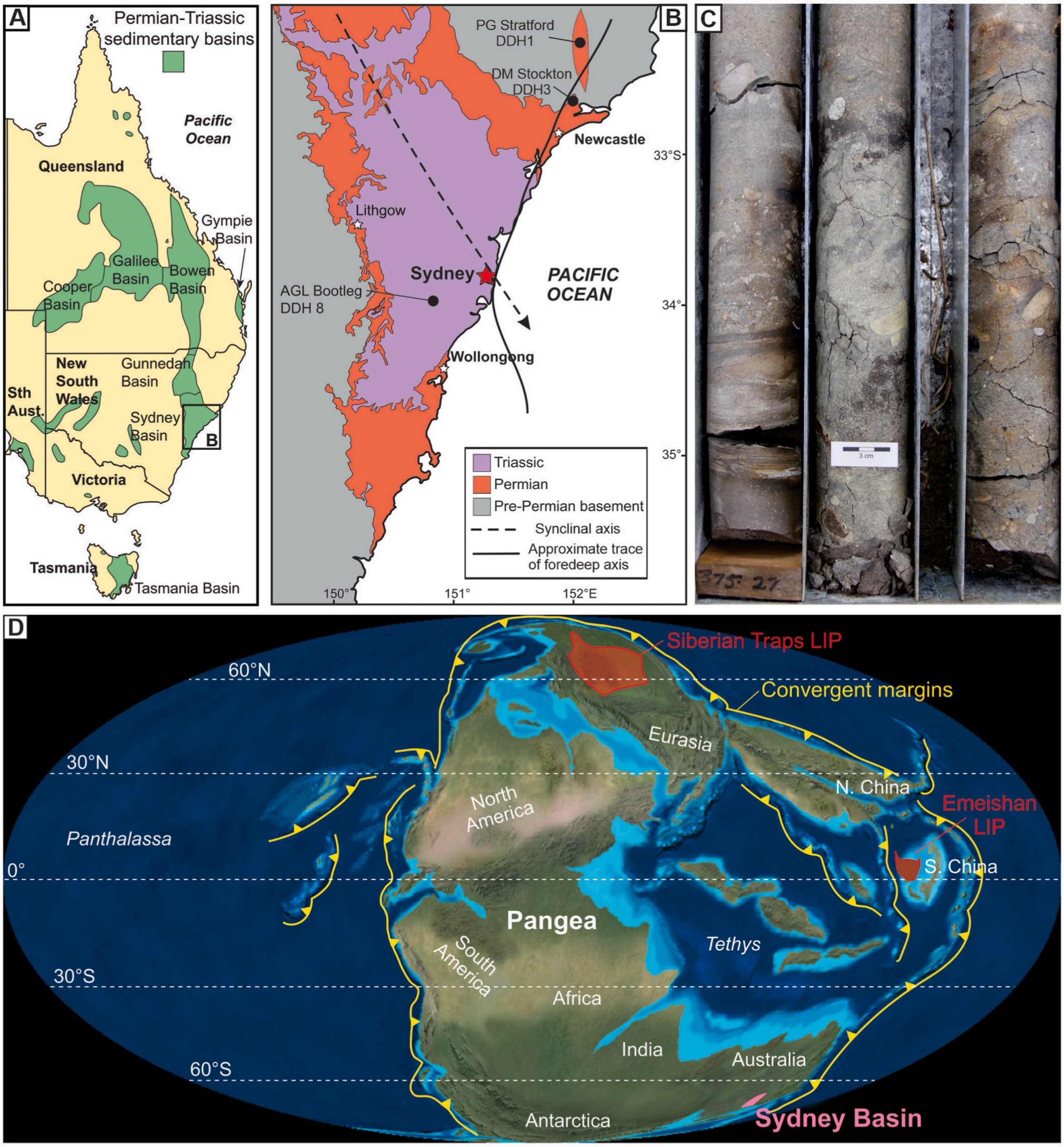

Fig. 2. A) Map showing the location of preserved Permian-Triassic sedimentary basins in eastern Australia. Inset box shows the location of part B. B) Geological map of the Sydney Basin in coastal New South Wales, Australia, showing the location of boreholes mentioned herein. Note that the present-day synclinal axis of the Sydney Basin (NW-SE) is at an acute angle to that of the original retroarc foredeep (broadly N-S) as informed by unit isopachs (Mayne et al., 1974). C) Core image showing a candidate interval for the end-Guadalupian crisis, the "Kulnura Marine Tongue" within the Tomago Coal Measures (Fig. 1) in PG Stratford DDH1. Note the presence of a low diversity trace fossil suite and dispersed gravel in sandy mudrocks, indicative of a stressed shallow marine environment and glacimarine conditions, respectively. D) Palaeogeographic map of Pangea in the late Permian, showing the location of the study area (Sydney Basin) in high southern palaeolatitudes of southeast Pangea, and those of the Emeishan Large Igneous Province (LIP) and Siberian Traps LIP (map based on Blakey, 2016).

their lateral equivalents. Available surface exposures of those units in the Newcastle coalfield area provide limited samples of the full succession but allow detailed observations on stratal geometry and other features. Strategically located drillcores, on the other hand, provide continuous coverage of the entire succession with minimal lateral dimension. Logging of these drillcores informs a facies analysis of the target succession, which is then used to interpret depositional environments and their changes through time.

Correlation of the interpreted timing of mid- and end-Capitanian events with the eastern Australian Permian stratigraphy (Fig. 1) suggests that the former should occur in the basal part of the Tomago Coal Measures and equivalents, and the latter should broadly correlate with the "Kulnura Marine Tongue", a marine interval that separates the lower from the upper Tomago Coal Measures (Fig. 2C). In DM Stockton DDH-3, the contact between the Mulbring Siltstone and overlying lower Tomago Coal Measures coincides with the uppermost occurrence of dispersed gravel and is interpreted to record the end of eastern Australian glaciation P3 in that locality. The base of the lower Tomago Coal Measures is an abrupt contact between offshore marine and coastal plain facies, and may represent a sequence boundary. The time-equivalent contact between the Broughton Formation and overlying basal Pheasants Nest Formation in AGL Bootleg-8 is also disconformable on a similar basis, and the lowermost part of this formation appears to record a highly stressed coastal plain setting (as indicated by the low-diversity, sporadically distributed trace fossil suite dominated by small individual traces). In PG Stratford-1 and AGL Bootleg-8, the Kulnura Marine Tongue and equivalent Erins Vale Formation record a major marine transgression and contain abundant dispersed gravel indicating the onset of eastern Australian glaciation P4 (Fig. 2C). The trace fossil assemblage in this unit is restricted in diversity and contains small individual traces, both indicators of environmental stress, and the top of the marine interval is marked by a pronounced disconformity with coastal plain strata erosionally overlying shoreface deposits. The exact implications of these patterns await the results of other analyses.

3. A multidisciplinary approach

Given the complexity of such key events in Earth's history, we contend that a multidisciplinary approach is essential for identifying and integrating the patterns of biotic turnover and changes in the physical environment during the middle–late Permian. We have sampled well-preserved lithologies from two drillcores for petrography (sandstones), and for major and minor element geochemistry, sulphur content and isotopes, mercury concentrations and isotopes, stable isotopes of carbon and oxygen, biomarkers, and palynology (mudrocks). We have surveyed the drillcores cited above for plant macro- and meso-fossils, and have carried out exhaustive surveys of both marine invertebrate and plant fossils held in collections at the Australian Museum and the Geological Survey of NSW. Terrestrial vertebrate and invertebrate fossils are strikingly sparse in eastern Australia during this interval but enhanced palynostratigraphic controls and radiogenic-isotope dating ought to provide improved correlation with the fauna-rich successions of the Karoo Basin, South Africa (Prevec et al., 2009, 2022; Smith et al., 2020; Gastaldo and Bamford, 2023; Rochín-Bañaga et al., 2023). In addition, quantitative studies of herbivore damage features on fossil leaves and wood provide a gauge of insect feeding guild success through time. Quantitative palynology will reveal compositional and productivity changes in terrestrial and aquatic primary producer communities (plants, algae/acritarchs), and attendant signatures of ecological stress (e.g., enhanced wildfire activity, microbial blooms). Geochemical and biofacies data can be evaluated against the core logs and compared with evidence for palaeoenvironmental change derived from sedimentological data. Mercury, together with sulphur abundances and isotopic values, will be used to evaluate possible roles of both regional (related to the contemporaneous Hunter-Bowen Orogeny) and distant (related potentially to the ELIP) volcanic activity in palaeoenvironmental disturbances.

The broad distribution of eastern Australian volcanic activity over time is plotted on Fig. 1. This is important, because Chapman et al. (2022) proposed that volcanic activity temporally overlapping with the Hunter-Bowen Orogeny may have played a significant role in the somewhat later, and devastating, end-Permian biotic crisis in eastern Australia. Concentrations of volcanic tephra occur at times that may correlate with palaeoenvironmental disturbance (Fig. 1), but this has yet to be evaluated fully. The end-Permian biotic crisis in this region is associated with a negative excursion in $^{13}C_{org}$ values, transient changes in the Chemical Index of Alteration and evidence for increased seasonality and increased surface temperatures, complete loss of the *Glossopteris* flora and of coal, and spikes in the abundances of microbes, fungi, and charcoal (Fielding et al., 2019; Vajda et al., 2020; Mays et al., 2021; Frank et al., 2021; Mays and McLoughlin, 2022). Evidence from the late Permian succession as a whole suggests that while palaeoenvironmental conditions deteriorated in perhaps a stepwise fashion, the major decline in conditions occurred over the last 1 m.y. or less of the Permian Period—an interval during which explosive volcanism was waning in the region (Frank et al., 2021; Fielding et al., 2022; Kerrison, 2022; Mays and McLoughlin, 2022). Similar timespans are indicated for mid- and end-Capitanian events from the research literature (Fig. 1). Retallack et al. (2011) proposed a series of short-lived "greenhouse crises" through the middle and late Permian of the Sydney Basin including a "mid-Capitanian Mass Extinction", but this hypothesis has not yet been rigorously tested.

4. Conclusions and future work

The nature, timing, and even existence of palaeoenvironmental disturbances at the mid- and end-Capitanian (or end-Guadalupian) are surrounded by uncertainty. Resolution of these uncertainties would represent a major step forward in understanding the cataclysmic changes at the close of the Palaeozoic Era and, by integrating geological, geochemical and palaeontological data into palaeoclimate models, would provide potentially useful information for managing and mitigating present and future climate change. Records from various parts of the world currently leave a confusing picture as to when (or even if) faunal and floral extinctions took place in the Capitanian, and none of the existing records is capable of assessing the full range of possible drivers for palaeoenvironmental change. The thick, stratigraphically complete, age-constrained, middle and upper Permian successions of the eastern Australian margin, which lay in high southern palaeolatitudes at the time, offer a unique opportunity to resolve these issues. Such near-polar locations are more likely to record climatic changes faithfully, and they also preserve a clear record of the final cold intervals of the late Palaeozoic Ice Age, allowing evaluation of the role of icehouse conditions in Capitanian palaeoenvironmental changes. A comprehensive evaluation of the palaeontological and geological signals of the EGE and related events in this region is now underway. Preliminary results suggest that the mid-Capitanian event is recorded in the basal Tomago Coal Measures in the northern Sydney Basin and around the contact between the Broughton Formation and the overlying Pheasants Nest Formation in the southern Sydney Basin. Similar data suggest that the end-Capitanian event roughly correlates with the "Kulnura Marine Tongue" in the middle of the Tomago Coal Measures (northern Sydney Basin) and the Erins Vale Formation (southern Sydney Basin). We encourage similar multidisciplinary approaches in other parts of the world to resolve the global patterns and causes of this enigmatic biotic crisis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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