A nutrient control on fluctuating oceanic redox conditions during the early Cambrian radiation of animals

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ABSTRACT

The early Cambrian witnessed an increase in metazoan ecosystem complexity, likely linked to enhanced oxygen and nutrient availability. Ocean redox chemistry exerts a strong control on the biogeochemical cycling of the limiting nutrient phosphorus, but the response of phosphorus cycling to redox dynamics in the early Cambrian ocean remains poorly resolved. Here, we report phosphorus phase association data for three sections documenting a bathymetric marine transect through terminal Ediacaran to early Cambrian Stage 2 (<538–521 Ma) on the Tarim Block, China. During the terminal Ediacaran to middle Fortunian, a fluctuating ferruginous-dysoxic OMZ developed, with ferruginous conditions promoting phosphorus recycling in deeper water parts of the OMZ. Combined with enhanced upwelling, this stimulated high primary production and organic matter burial, resulting in the development of better oxygenated conditions during the late Fortunian to early Stage 2. The development of oxic-dysoxic conditions at this time promoted phosphorus burial in association with iron minerals, and combined with waning upwelling, the reduced supply of nutrients helped maintain these conditions. This likely promoted diversification of small shelly fossils (SSFs) in the late Fortunian. However, efficient phosphorus burial also suppressed oxygenic photosynthesis. Thus, the overall expanded oxygenation was punctuated by episodes of subsequent deoxygenation during Cambrian Stage 2, which were driven by relatively enhanced upwelling and an increased supply of bioavailable phosphorus from continental weathering during pulsed eustatic transgression. Enhanced P burial from early Stage 2 onwards contributed to more stable and longer-lived oxic episodes, helping to facilitate the development of more complex ecosystem structures.

Keywords: Nutrient cycling; primary productivity; Early Cambrian; Tarim Basin

INTRODUCTION

Phosphorus (P) is generally considered to be the ultimate limiting nutrient for primary productivity on geological timescales (Tyrrell, 1999). The bioavailability of P has thus exerted a key control on organic carbon production, and ultimately oxygenation dynamics, throughout much of Earth's history (e.g., Van Cappellen and Ingall, 1996). This includes the early Cambrian, where it is increasingly apparent that the early radiation of animal life occurred against a backdrop of highly dynamic oceanic oxygen levels (Alexander et al., 2025). However, the role of key nutrients such as P in driving oxygenation dynamics during the early Cambrian has seldom been explored in detail (see Liu et al., 2024).

Phosphorus concentrations in the surface ocean reflect a balance between the sources of P and subsequent removal processes to the sediments. As a first order control, the intensity of chemical weathering impacts the riverine influx of dissolved P (Planavsky et al., 2010; Wang et al., 2020). However, on the modern Earth, the upwelling flux of remineralized P from the deep sea to the surface ocean may be several orders of magnitude higher than the riverine influx (Schlesinger and Bernhardt, 2013), highlighting the key control that upwelling exerts on primary productivity.

An additional source of P may arise from redox-promoted recycling of P from the sediments (Algeo and Ingall, 2007; Ingall et al., 1993; Poulton, 2017). Initially, potentially bioavailable P is mainly removed to the sediments by biological uptake and sinking of

biomass (in the form of organic matter or skeletal remains), and via uptake in association with Fe (oxyhydr)oxide minerals (Slomp et al., 1996a), with the latter process potentially being particularly significant under ferruginous (anoxic, Fe(II)-containing) conditions (Bowyer et al., 2020; Guilbaud et al., 2020; Reinhard et al., 2017). During diagenesis, the anaerobic remineralization of organic matter (Ingall et al., 1993) and the reductive dissolution of Fe (oxyhydr)oxide minerals (Slomp et al., 1996b) remobilizes P into porewaters. A proportion of this P may undergo 'sink switching' to authigenic phases, such as carbonate fluorapatite (CFA) (Ingall et al., 1993; Ruttenberg and Berner, 1993) or Fe phosphate minerals (e.g., vivianite; Dijkstra et al., 2016; Jilbert and Slomp, 2013; Xiong et al., 2019), while P may also be retained in the sediment via adsorption to iron (oxyhydr)oxide minerals near the sediment-water interface (Slomp et al., 1996a). However, a proportion of the released P may also be recycled back to the water column, particularly under euxinic (anoxic and sulfidic) bottom water conditions, potentially driving a positive productivity feedback (Van Cappellen and Ingall, 1996). Extensive P recycling may also occur under ferruginous bottom water conditions, particularly where sulfidic porewaters develop close to the sediment-water interface (Alcott et al., 2022; Qiu et al., 2022).

It is generally thought that the Neoproterozoic witnessed a global increase in oceanic phosphate concentrations during the Cryogenian (Planavsky et al., 2010; Reinhard et al., 2017) and Ediacaran (Dodd et al., 2023; Laakso et al., 2020; Shimura et al., 2014; Yang et al., 2024), and elevated phosphate levels may have persisted into the early Cambrian, leading to the formation of major phosphorite deposits (Gao et al., 2024; Zhang et al., 2024). Increased oceanic phosphate concentrations are generally considered to have been derived from

upwelling (Gao et al., 2024; Zhang et al., 2024), continental weathering (Li et al., 2022; Peng et al., 2025) and/or volcanism (Gao et al., 2018; Zhu et al., 2021), but redox-driven recycling of P from the sediments is an additional potentially significant source that has largely been ignored. Phosphorus recycling may exert a positive feedback on primary productivity and hence oxygen production, thereby impacting animal evolution (Liu et al., 2024). However, although a recent compilation of the phosphorus content of marine sediments suggests little secular change in median values from the Neoproterozoic through the Paleozoic (Laakso et al., 2020), few studies have investigated P cycling in the early Cambrian in detail, particularly with regard to specific links to oxygenation dynamics and animal evolution (see Creveling et al., 2014; Liu et al., 2024).

To evaluate the potential impact of redox-driven P cycling on productivity, oxygenation dynamics and animal evolution, we provide a detailed geochemical study of P cycling in the Tarim Basin, Northwest China. The succession documents marine sedimentation during the terminal Ediacaran and early Cambrian (Fortunian and Stage 2; ≤538 Ma to ~521 Ma), and includes a rich record of Cambrian-type small shelly fauna (SSF) preserved during a major phase of SSF emergence and diversification (Qian and Xiao, 1984; Qian et al., 2009; Yao et al., 2005; Yue and Gao, 1992). We build upon a recent detailed study of redox dynamics across a bathymetric transect in the basin (Wei et al., 2025), which provides the context for exploring the role of P cycling via phase association analyses (Thompson et al., 2019). This allows a detailed exploration of the potential roles of P recycling, upwelling and weathering in driving oxygenation dynamics across the basin, and hence links to biological evolution, during this critical interval in the earliest Cambrian.

GEOLOGICAL BACKGROUND

The Tarim Basin (Fig. 1A) is one of the oldest cratonic blocks in China, with an area larger than 600,000 km^2. Following the Neoproterozoic break-up of the Rodinia supercontinent, the Tarim lithosphere evolved into a rift basin (Turner, 2010). At the end of the late Ediacaran, the Tarim Basin continued to separate from the Gondwana continent and gradually evolved from a rift setting into a passive continental margin. On the northwestern margin of the Tarim Basin, in the Aksu area (Fig. 1A), the Yurtus Formation records deposition in a continental shelf environment, which was linked to the infant southern Tianshan Ocean to the north (Yu et al., 2009). The area entered the post-rift subsidence stage when large-scale transgression occurred, leading to the deposition of cherts and black shales with phosphatic nodules (Fig. 1B).

The Yurtus Formation unconformably overlies the Ediacaran Qigebulake Formation, which is dominated by dolostone (Fig. 1B), and conformably underlies the Xiaoerbulake Formation, composed of thin-bedded dolostones with fossiliferous layers containing trilobites (Yue and Gao, 1992). Generally, the Yurtus Formation consists of three SSF-bearing lithological units: (1) a lower unit consisting of chert and interbedded shale with phosphatic nodules; (2) a middle unit of black shale with carbonate interbeds, passing to grey shale and carbonate alternations; and (3) an upper unit comprising thin-bedded carbonates, occasionally with interbedded calcareous shales (Fig. 1B).

Regional paleobathymetric reconstructions that incorporate insight from outcrop and drill core sections suggest that the Sugaitebulake (SGTB) section (40°53'46"N, 79°29'45"E)

represents the shallowest water depth, the Kungaikuotan (KGKT) section (40°49'17"N, 79° 27'08"E) represents an intermediate-depth setting, and the Shiairike (SARK) section (40° 59'19"N, 80°00'22"E) represents the deepest water setting (Fig. 1A, C; Zhu et al., 2018). Specifically, the SARK section is considered to have been deposited below storm wave base, while the SGTB and KGKT sections were deposited above storm wave base, likely in a sub-tidal environment (Gao et al., 2022). The overall lithostratigraphic architecture is therefore consistent with thickening of the basal Yurtus siliceous-shale facies, in this area of the Tarim Basin, to the south and east with distance from the SGTB section (Fig. 1A; Zhou et al., 2014). Despite extremely condensed deposition, with an estimated sedimentation rate of 0.2 cm/ka (<30 m representing ≥15 m.y.; Wei et al., 2025), the entirety of the Yurtus Formation can be correlated to the terminal Ediacaran to early Cambrian Stage 2, through global carbon isotope systematics and biostratigraphic constraints based on SSFs (Wei et al., 2025). Given the absence of the diagnostic basal Cambrian ichnospecies *Treptichnus pedum*, the Ediacaran-Cambrian boundary in the Tarim succession is tentatively placed immediately above the lowest carbonate carbon isotope values in the lowermost interval of the Yurtus Formation, which are preliminarily correlated with the negative carbon isotope excursion that immediately underlies the first appearance of *T. pedum* in globally distributed successions (Nelson et al., 2023; Bowyer et al., 2024).

METHODS

A total of 92 samples (shales, cherts and carbonates) were collected at regular intervals of ~0.6 m from the Yurtus Formation across the three sections. After avoiding veins,

potential weathered surfaces and visible pyrite nodules, fresh samples were carefully trimmed and powdered using an agate mill. Total phosphorus (P) and micro-nutrient analyses (Ba, Ni, Cu and Zn) were conducted at the China University of Geosciences, Beijing. Phosphorus phase partitioning analyses were performed at the University of Leeds, UK. All other data have been published previously (Wei et al., 2025).

Micro-nutrient analyses

For micro-nutrient analyses, ~40 mg of powdered sample was weighed into a 7 mL PFA (perfluoroalkoxy) digestion vessel. A mixture of 2 mL concentrated HNO_3 and 2 mL concentrated HF was then added to each vessel, and the vessels were then sealed and placed in a high-pressure, Teflon-lined steel digestion bomb system. The bombs were heated in an oven at 190°C for 48 h to completely dissolve refractory minerals. After cooling, 1 mL of concentrated HNO_3 was added, which was then then heated to dryness. Following this, 2 mL of HNO_3 and 2 mL of deionized water were added, and the vessel was reheated at 165°C for 24 h. Finally, the solution was transferred to a 50 mL polyethylene bottle and diluted 2000-fold with deionized water. Reference materials and blanks were processed in the same way, and samples were analysed by inductively coupled plasma-mass spectrometry. Analytical precision monitored by standards AGV-2, BHVO-2, W-2, GSR-1 and GSR-3 was <5% Ba, and<10% for Cu, Zn and Ni, with an accuracy of within 10% for all elements.

To determine total P contents, ~100 mg of each sample was weighed into a Teflon high-pressure digestion vessel. To each vessel, 3 mL of HNO_3, 2 mL of HF, and 1 mL of $HClO_4$ were sequentially added. The vessels were then sealed and heated in an oven at 180°

C for 48 h. After cooling to room temperature, the vessels were opened and placed on a hotplate at 150℃ to evaporate to incipient dryness. The residue was then re-dissolved in 5 mL of 4% HNO_3 and transferred to a 50 mL polyethylene bottle. Finally, the solution was diluted with deionized water to yield a total dilution factor of 500, followed by analysis by inductively coupled plasma optical emission spectrometry at the China University of Geosciences (Beijing). Reference materials and procedural blanks were prepared identically to the samples. Analyses were within 10% of international standards AGV-2, GSR-1 and GSR-5, with a relative standard deviation (RSD) of <5%.

Phosphorus phase partitioning

Sedimentary P is dominantly composed of iron-bound P (P_{Fe}), authigenic carbonate fluorapatite (CFA), biogenic apatite and carbonate-associated P (P_{auth}), detrital P (P_{det}) and organic P (P_{org}) (Ruttenberg, 1992), which in ancient rocks may be operationally quantified via the sequential extraction scheme of Thompson et al. (2019). Initially, poorly crystalline Fe (oxyhydr)oxide-bound P (P_{Fe1}) was extracted with a sodium dithionite solution at pH 7.6 for 8 h at room temperature. Authigenic P (P_{auth}) was then extracted via a sodium acetate solution at pH 4 for 6 h at room temperature, followed by dissolution of detrital apatite (P_{det}) using a 10% HCl solution for 16 h at room temperature. Phosphorus associated with magnetite (P_{mag}) was then extracted with an ammonium oxalate solution for 6 h at room temperature, followed by the dissolution of P associated with more crystalline Fe (oxyhydr)oxide minerals (P_{Fe2}) using a dithionite-citrate-acetate solution at pH 4.8 for 6 h at room temperature. Finally, to liberate organic-bound P (P_{org}), the residue was ashed (550°C

for 2 h) and reacted with 10% HCl solution for 16 h at room temperature. Here, P_{Fe} comprises the sum of P_{Fe1} + P_{Fe2} + P_{mag}. An extended discussion on the potential impact of recrystallization of P_{auth} to P_{det} is included in the Supplementary Information (Fig. S1). The solutions obtained during the extractions were measured for P content using the molybdate blue method (Strickland and Parsons, 1972), except for the P_{Fe1}, P_{mag} and P_{Fe2} solutions, which were measured by inductively coupled plasma optical emission spectrometry due to interference with the extractant reagents when using the spectrophotometric method (Thompson et al., 2019). Replicate analyses of in-house reference materials (n = 5) yielded a relative standard deviation (RSD) of<6% for each step.

RESULTS

Phosphorus geochemistry

Total P concentrations show a particularly wide range in the KGKT (135 to 6684 ppm; average = 1588 ± 1794 ppm; 1σ, n = 19) and SARK (78 to 13811 ppm; average = 3857 ± 9900 ppm; 1σ, n = 43). The SGTB section displays a relatively stable total P range in the lower half of the section (3249 ± 2184 ppm, n = 23) before decreasing to lower values towards the top (574 ± 342 ppm, n = 7; Fig. 2), and this overall decrease is also evident in the KGKT and SARK sections. However, when normalized to Al, relatively constant values of 0.07 ± 0.04 (wt%/wt%) are apparent in the SGBT section, and all ratios are elevated relative to the UCC average (Mclennan, 2001) of 0.009 wt%/wt% (Fig. 2). Relatively stable P/Al ratios are also evident in the upper parts of the KGKT and SARK sections, although as with total P contents, P/Al ratios fluctuate widely in the lower part of these sections, with values that

sometimes plot below the UCC average (Fig. 2). The P pool that comprises phases considered to be potentially reactive in surface environments (P_{reac}, calculated as the sum of P_{Fe} + Fe_{aut} + P_{org}) is shown normalized to Al in Fig. 2. P_{reac}/Al ratios are relatively constant (0.04 ± 0.02 wt%/wt%) throughout the SGBT section, but ratios are much more variable in the SARK (0.18 ± 0.38 wt%/wt%) and KGKT (0.23 ± 0.54 wt%/wt%) sections (Fig. 2).

Most data from the three sections have highly elevated molar C_{org}/P_{org} ratios (4709 ± 5953, n = 54; Fig. 2), considerably above the Redfield ratio of 106/1 (open symbols on Fig. 3). In the SGTB section, with the exception of one sample exhibiting higher values of 113.2 at 17.7 m, molar C_{org}/P_{reac} ratios (26.2 ± 18.3, n = 29) are significantly lower than the Redfield ratio throughout the Yurtus Formation, but with an increasing trend upwards (Fig. 2A). The C_{org}/P_{reac} ratios through Interval I in the SARK and KGKT sections fluctuate above and below the Redfield ratio, ranging from 19-1271 (average = 368 ± 401, n = 18) and 2-176 (average = 101.1 ± 72.5, n = 4), respectively (Figs. 2B, C, 3A). The C_{org}/P_{reac} ratios in Intervals II and IV in the KGKT section and Interval II in the SARK section are all lower than 106 (27.2 ± 19.1 and 17.3 ± 21.3, respectively; Figs. 2B, C, 3B, C, D), although limited P phase partitioning data are available for these particular intervals. This is due to the dominant dolostone lithology, where P extractions were not performed due to the potential for additional direct P drawdown via substitution into the carbonate lattice (Dodd et al., 2023), which complicates consideration of P phase association data.

Micro-nutrient and productivity data

Similar to the P/Al profile (0.07 ± 0.04 wt%/wt%), Ba/Al, Ni/Al, Cu/Al and Zn/Al ratios in

the SGTB section generally plot close to UCC thresholds throughout intervals I-III, with relatively constant values (B/Al = 0.006 ± 0.006 wt%/wt%; Ni/Al = 0.0008 ± 0.0004 wt%/wt%; Cu/Al = 0.0003 ± 0.0002 wt%/wt%; Zn/Al = 0.0006 ± 0.0003 wt%/wt%; Fig. 4A). However, Ni/Al, Cu/Al and Zn/Al ratios (and possibly Ba/Al) then show a distinct increase in Interval IV, followed by a subsequent decrease. The Ba/Al, Ni/Al, Cu/Al and Zn/Al trends in the KGKT and SARK sections are also similar to the respective trends in P/Al (Fig. 4B, C). Specifically, interval I is characterized by generally high (and particularly fluctuating in the case of KGKT) Ba/Al (2.79 ± 7.14 wt%/wt%), Ni/Al (0.008 ± 0.006 wt%/wt%), Cu/Al (0.009 ± 0.01 wt%/wt%) and Zn/Al (0.028 ± 0.03 wt%/wt%) values (Fig. 4B, C). These ratios then decrease with increasing stratigraphic height in Interval II, with some values falling below UCC values, before an increase to moderate values in the upper part of Interval II. The overlying Interval III is generally characterized by moderate ratios (P/Al = 0.66 ± 0.75 wt%/wt%; Ba/Al = 0.04 ± 0.038 wt%/wt%; Ni/Al = 0.004 ± 0.007 wt%/wt%; Cu/Al = 0.002 ± 0.004 wt%/wt%; Zn/Al = 0.013 ± 0.025 wt%/wt%; note that limited data are available for this interval at KGKT), but there is a distinct shift to higher values in the upper part of Interval III and through Interval IV (Interval IV is not present at SARK).

DISCUSSION

P drawdown and recycling across the Tarim Basin

Previously reported iron speciation and redox-sensitive trace metal data (Wei et al., 2025; Zhu et al., 2022) have revealed a highly dynamic oxygen minimum zone (OMZ) in the Tarim Basin, evolving from an unstable condition with a ferruginous core (mainly at SARK

and KGKT) during the late Ediacaran to middle Fortunian, to less intense dysoxic-oxic episodes from the late Fortunian onwards, with another anoxic incursion mainly recorded at SGTB during late Stage 2 (Figs. 2, 5; redox terminology is according to Algeo and Li, 2020). Redox conditions in the Tarim Basin thus deviate from the more severe case of mid-depth euxinia that has been proposed for other regions of the global ocean at this time (e.g., Li et al., 2010). Under ferruginous conditions, bioavailable P may be effectively scavenged from the water column through co-precipitation with iron (oxyhydr)oxides (e.g., Slomp et al., 1996b) or via the formation of vivianite or green rust (Xiong et al., 2023). However, biogeochemical modelling has suggested that an increase in oceanic sulfate concentrations in the early Cambrian ferruginous ocean may have led to enhanced phosphate recycling from the sediments, due to increased release of P during organic matter remineralization by sulfate-reducing bacteria (Laakso et al., 2020). Such recycling may promote a positive productivity feedback (Van Cappellen and Ingall, 1994), and hence we next evaluate controls on P drawdown and cycling across the Tarim Basin.

The positive relationship between highly reactive Fe and total P in the SGTB section (Fig. 6A) suggests that a significant proportion of P was delivered to the Yurtus sediments via an Fe-P shuttle (Fig. 5). The low molar C_{org}/P_{reac} ratios (below the Redfield ratio) throughout the SGTB section provide direct support for this, and also demonstrate minimal P recycling back to the water column, despite extensive release of P from organic matter during anaerobic remineralization (indicated by highly elevated molar C_{org}/P_{org} ratios; Fig. 2A). Indeed, the dominance of P_{aut} phases (primarily carbonate fluorapatite) over P_{Fe} and P_{org} (Table S1) demonstrates that the P released from both organic matter and Fe

(oxyhydr)oxides during early diagenesis was largely incorporated into secondary phases via 'sink switching' (e.g., Ruttenberg, 1993). This is consistent with the development of dysoxic-oxic conditions at SGTB throughout most of the Terreneuvian (Fig. 5), which would have limited recycling of P back to the water column due to re-adsorption to Fe (oxyhydr)oxides close to the sediment-water interface (e.g., Slomp et al., 1996a). However, somewhat higher C_{org}/P_{reac} values in Interval IV (Figs. 2A, 3D) may imply relatively minor P recycling back to the water column, consistent with the development of a ferruginous core to the OMZ that fluctuated in its spatial extent at this time (Fig. 5D). Under such conditions, the development of sulfidic pore waters close to the sediment-water interface, which diminishes the near-surface Fe (oxyhydr)oxide trap for P mobilized during diagenesis, may stimulate P recycling even under ferruginous conditions (Alcott et al., 2022; Qiu et al., 2022).

By contrast, the lack of a relationship between highly reactive Fe and total P in the KGKT and SARK sections (Fig. 6B, C) suggests that P cycling was largely de-coupled from Fe minerals in these deeper water settings. However, an initial drawdown flux of P in association with Fe minerals cannot be entirely discounted for these sections, as P recycling back to the water column (indicated by elevated C_{org}/P_{reac} ratios in Interval I; Figs. 2B, C, 3A) would have impacted the primary relationship between Fe_{HR} and total P. Nevertheless, the particularly high organic carbon contents in Interval I at SARK and KGKT (Fig. 2B, C) imply that organic P was likely the dominant drawdown pathway during the late Ediacaran to middle Fortunian, consistent with the deeper water anoxic setting that would have limited sequestration of Fe (oxyhydr)oxides (and associated P) formed via precipitation at the oxycline (Fig. 5A). Therefore, the P recycling evident in ferruginous SARK and KGKT samples

deposited during Interval I again likely reflects the development of sulfidic pore waters close to the sediment-water interface.

The extent to which the KGKT section experienced P recycling during Interval I appears to have been minimal relative to the deeper water SARK section during the late Ediacaran to middle Fortunian, as indicated by lower C_{org}/P_{reac} ratios (<176 at KGKT; <1271 at SARK; Figs. 2C, 3A). Thus, a depth gradient is apparent in terms of the intensity of P recycling to the water column during the late Ediacaran to middle Fortunian, which appears to have been controlled by the intensity of reducing conditions in the water column (Fig. 5A).

During Interval II (Late Fortunian to early Stage II), the available data suggest that P was effectively sequestered in the sediments across the entire bathymetric transect (C_{org}/P_{reac} below the Redfield ratio; Figs. 2, 5B). The general paucity of available data in the two deeper water sections from middle to late Stage II (Intervals III-IV) precludes a direct assessment of P cycling. However, the general persistence of less intensely reducing conditions across the bathymetric transect at this time (Fig. 5C, D), implies that P was likely dominantly fixed in the sediments under dysoxic-oxic conditions, with the potential for relatively minimal P recycling at the site of the fluctuating ferruginous core during late Stage II.

Controls on marine redox and nutrient dynamics

Multiple shallow oceanic oxygenation events (OOEs) have been suggested to have occurred from Cambrian middle Stage 2 to Stage 4, based on $\delta^{13}C_{carb}$ compositions and sulfur isotopes in carbonate associated sulfate ($\delta^{34}S_{CAS}$) from Siberian Platform carbonates (Alexander et al., 2025; He et al., 2019). This raises the question of what caused and

maintained the OMZ redox structure apparent on the Tarim Block, which aligns with OMZ conditions reported elsewhere over this interval (e.g., Guilbaud et al., 2018; Hammarlund et al., 2017). Evidence from micronutrient (Ni/Al, Cu/Al, Zn/Al) and Ba/Al (an indicator of the relative intensity of productivity; Schoepfer et al., 2015; Tribovillard et al., 2006) profiles suggests that the outer-middle shelf in the Tarim Basin experienced high primary productivity during the late Ediacaran to middle Fortunian (Interval I), followed by low productivity during the late Fortunian to early Stage 2 (Interval II), with a recovery to higher levels during middle Stage 2 (Interval III) (Fig. 4B, C). By contrast, the inner shelf maintained a low level of productivity throughout deposition of the Yurtus Formation, with the exception of an apparent increase during late Stage 2 (Fig. 4A).

To explain these observations, we invoke an upwelling flux of phosphorus to the shelf associated with eustatic transgression, with an initiation recorded in time-equivalent strata of North America near the base of the Sauk Megasequence, which records diachronous transgressive flooding of the Laurentian craton (Sloss, 1963). This initially enhanced primary productivity and organic matter remineralization in the water column, leading to the spatial heterogeneity in ferruginous-dysoxic conditions observed across the OMZ setting during the late Ediacaran to middle Fortunian (Wei et al., 2025). The subsequent extent and intensity of local deoxygenation and primary productivity was further controlled by local drawdown of P into the sediments and the intensity of recycling back into the water column. We next explore in more detail the role of P cycling in the context of external inputs of P from upwelling and continental weathering.

Marine eutrophication during the terminal Ediacaran to middle Fortunian

During the late Ediacaran to middle Fortunian (Interval I), P is considerably enriched (relative to the average UCC value) across the three sections, while P_{reac}/Al values at SARK (and to a lesser extent at KGKT) are generally more variable and elevated than in the SGTB section (Fig. 2). This suggests an effective P drawdown mechanism from a water column that was rich in phosphate, in addition to enhanced bio-available P recycling from the sediments in deeper water parts of the OMZ, as supported by elevated C_{org}/P_{reac} ratios (Fig. 2). Low chemical index of alteration (CIA) values (Fig. 4; Wei et al., 2025), which reflect the intensity of chemical weathering (Nesbitt and Young, 1982), suggest that the continental weathering influx of P was unlikely to have been particularly high at this time. This leaves enhanced upwelling during the late Ediacaran to middle Fortunian as a more likely source of elevated P concentrations in the water column.

We evaluate this possibility by considering trends in Co × Mn values, whereby sediments in upwelling systems are commonly characterized by Mn and Co depletion (<0.4 ppm·wt%), while sediments from restricted basins tend to have elevated values (>0.4 ppm·wt%) (Böning et al., 2004; Sweere et al., 2016). The low Co × Mn values observed across the shelf (Fig. 4; Wei et al., 2025) are thus consistent with high intensity upwelling, suggesting that upwelling was the primary source of enhanced nutrients to the region. Notably, however, generally lower Co × Mn values in the SARK and KGKT sections relative to SGTB (Fig. 4) indicate that the middle-outer shelf experienced more intense upwelling (Wei et al., 2025). Nevertheless, despite a lower P influx from upwelling at SGTB, P contents, P/Al ratios and P_{reac}/Al ratios remain high (Fig. 2A), likely due to extensive drawdown of P in

association with Fe (oxyhydr)oxide minerals precipitating at the chemocline, as discussed above.

We thus propose the operation of a redox-controlled nutrient shuttle across the shelf, whereby recycled P from sediments at SARK, and to a lesser extent at KGKT, was upwelled along with the deeper ocean P flux and sequestered at SGTB (Fig. 5A). The drawdown of P during Fe mineral precipitation under dysoxic-oxic conditions at SGTB then suppressed local primary productivity, as indicated by the lower Ba/Al, Ni/Al, Cu/Al and Zn/Al ratios, which would also have helped maintain dysoxic-oxic conditions (Figs. 4A, 5A). By contrast, the extensive P recycling (indicated by high C_{org}/P_{reac} ratios) in the SARK section, and more limited P recycling (indicated by slightly elevated C_{org}/P_{reac} ratios) in the KGKT section (Figs. 2, 3), appear to have driven enhanced local marine primary productivity, as indicated by particularly high Ba/Al, Ni/Al, Cu/Al and Zn/Al ratios (Fig. 4A, B). Therefore, while enhanced upwelling initially promoted primary productivity and the development of ferruginous-dysoxic conditions across the shelf (Wei et al., 2025), the consequent recycling of P from middle-outer shelf sediments increased surface water productivity. As a result, the dual source of bioavailable P from upwelling and redox-dependent recycling resulted in high organic carbon burial, and promoted the observed general increase in $\delta^{13}C_{carb}$ values that occurs through Interval I (Fig. 2; Wei et al., 2025). This likely contributed to subsequent gradual atmospheric and shallow ocean oxygenation (He et al., 2019), resulting in the more widespread dysoxic-oxic conditions that developed during Interval II (Fig. 5B; see below).

The high water column phosphate concentrations proposed for this interval occurred broadly coincident with the earliest global appearance of small shelly fauna, which may

391 have utilized phosphate in their growth and are commonly preserved as phosphatic
392 sclerites, consistent with an abundance of phosphatic anabaritids and protoconodonts in
393 the lower Yurtus Formation (Fig. 7; Qian and Xiao, 1984; Qian et al., 2009). This may imply a
394 causal link, whereby abundant phosphate and enhanced primary productivity associated
395 with upwelling, which initially promoted regional palaeoredox heterogeneity and OMZ-type
396 conditions, may together have been partly responsible for the first appearance and rapid
397 diversification of 'Cambrian-type' SSFs, as documented in the lower Yurtus Formation (Xiao
398 and Duan, 1992; Yao et al., 2005). At this time, efficient sedimentation of P in skeletal
399 material and faecal pellets resulted in a major global interval of phosphorite deposition (Fig.
400 1; Cook and Shergold, 1984; Brasier, 1990a; Brasier, 1990b; Knoll, 1994).
401
402 ***Oligotrophic conditions during the late Fortunian to early Stage 2***
403 During the Late Fortunian to early Stage 2 (Interval II), the combination of lower Ba/Al,
404 Ni/Al, Cu/Al and Zn/Al ratios (Fig. 4), along with lower TOC contents (Fig. 2), in the SARK and
405 KGKT sections, indicate decreased primary productivity (Fig. 5B). This coincides with P/Al
406 ratios at KGKT and SARK that commonly plot near to the UCC value (Fig. 2B, C), which may
407 be a consequence of either generally low phosphate availability in the water column, or P
408 recycling from the sediments back to the water column (Poulton, 2017). Effective drawdown
409 of seawater phosphate at KGKT and SARK is evidenced by very low C_{org}/P_{reac} ratios
410 ($\ll$106/1, Figs. 2B, C, 3B), giving no evidence for P recycling, as expected under the
411 dysoxic-oxic conditions that developed at this time (Fig. 5B). Therefore, the occurrence of
412 low P/Al values, despite evidence for effective P drawdown to the sediments, indicates that

the mid-outer shelf was depleted in phosphate (e.g., Guilbaud et al., 2020), and this limited primary productivity (Fig. 5B).

The decline in phosphate concentrations may have initially been triggered by decreased upwelling, as indicated by a general increase in Co × Mn values, particularly in the deeper water SARK section (Fig. 4; Wei et al., 2025). Waning upwelling would have led to an enhanced dependence on nutrients supplied from continental weathering. However, in this context, the highly fluctuating CIA values observed across the three sections through Interval II (Fig. 4) provide no persuasive evidence for a particularly strong enhancement of continental weathering (Fig. 4, Wei et al., 2025). Thus, overall, there is compelling evidence for the development of oligotrophic conditions across the shelf at this time, driven by low P supply from both upwelling and continental weathering (Fig. 5B).

Oligotrophic conditions would have helped maintain a better oxygenated water column through decreased C_{org} remineralization, leading to a diminished OMZ that was characterized by dysoxic conditions throughout, rather than the spatial development of anoxic-ferruginous conditions suggested for the late Ediacaran to middle Fortunian (Figs. 5, 7). These oligotrophic conditions occur broadly coincident with an inferred global OOE near the base of Stage 2 (Alexander et al., 2025; Bowyer et al., 2024; He et al., 2019; Wei et al., 2025), and may imply that enhanced organic carbon burial driven by active P recycling in the terminal Ediacaran, and especially the late Ediacaran to middle Fortunian, ultimately led to this OOE.

The resultant OOE in lower Stage 2 may have helped to facilitate the major diversification of SSFs documented in this interval (Liu and Algeo, 2025; Maloof et al., 2010),

in addition to more intrinsic biological processes associated with ongoing ecosystem restructuring (Mills and Canfield, 2014). The latter likely included the filter-feeding activity of sponges, which transfer oxygen demand from the water column to the sediment by clearing picoplankton (Perea-Blazquez et al., 2012) and dissolved organic carbon (de Goeij et al., 2008). Sponges, body fossils of which are now known from as early as the terminal Ediacaran (Wang et al., 2024), often yield spicules that are abundant constituents of lower Cambrian SSF assemblages (Chen et al., 2023; Chang et al., 2019; Yi et al., 2022), and recent evidence even points to an early Cambrian first appearance of archaeocyath sponges within the Fortunian (Wang et al., 2025). The preferential removal of picoplankton may have exerted a selective pressure for larger eukaryotic phytoplankton and promoted more efficient organic carbon export, thereby further transferring oxygen demand from shallow waters to the sediments and deeper water settings. This is also consistent with the occurrence of planktonic algae-like sphaerodinoflagellate and benthic red algae across this interval in the Tarim Basin (Li et al., 2022). Lastly, efficient removal of organic carbon from the water column through production of rapidly sinking faecal pellets, may also have aided more efficient water column oxygenation (Logan et al., 1995; Lenton et al., 2014).

The variety of mechanisms that enhanced oxygenation of bottom waters would have further promoted P removal and may have triggered a positive feedback on oceanic oxygenation. This appears to be consistent with falling $\delta^{13}C_{carb}$ (5n) and $\delta^{34}S_{CAS}$ values in the immediate aftermath of the 5p $\delta^{13}C_{carb}$ peak during Interval II (Fig. 2; Wei et al., 2025), which may reflect progressively decreasing organic carbon and pyrite burial as a consequence of an OOE (He et al., 2019). However, the retention of P in the sediments

would ultimately have restricted net oxygen production through reduced organic carbon and pyrite burial, which may have stalled or slowed continued atmospheric oxygenation on the shelf (Boyle et al., 2014). As a result, only longer duration OOEs followed by transient anoxic events occurred, instead of persistent oxygenation from Stage 2 onwards. This is consistent with both rising $\delta^{13}C_{carb}$ and $\delta^{34}S_{CAS}$ prior to peak 6p in middle Stage 2 (Fig. 2; Wei et al., 2025), which may reflect marine deoxygenation conducive to the progressive burial of organic carbon and pyrite (He et al., 2019).

Nutrient-replete conditions during middle to late Stage 2

During middle Stage 2 (Interval III), the progressive increase in micronutrients observed in the SARK section (Fig. 4C) supports a gradual increase in productivity, although this did not immediately result in enhanced TOC burial at the deeper water site (Fig. 2). Generally low Co × Mn values in Interval III in the SARK section (Fig. 4C) suggest that this increase in productivity was driven by a return to more intense upwelling, but this upwelling did not significantly impact the shallower water SGTB site at this time (indicated by high Co × Mn values in Interval III; Fig. 4A).

By late Stage II (Interval IV), however, higher micronutrient ratios in the SGTB and KGKT sections (Fig. 4A, B) support enhanced productivity (Fig. 5D), driven by phosphate supplied via both upwelling (indicated by low Co × Mn values) and potentially also continental weathering (indicated by high CIA values Fig. 4A, B). However, while there are relatively few data points, low C_{org}/P_{reac} ratios through Interval IV in both the SGBT and KGKT sections, suggest that P drawdown in association with Fe minerals precipitating under dysoxic-oxic

conditions (Fig. 5D) exerted a negative productivity feedback (e.g., Guilbaud et al., 2020). Thus, despite an overall increase in nutrient supply, which was sufficient to result in the development of ferruginous anoxia at the heart of the OMZ (Fig. 5D), the overall intensity of primary production was relatively limited compared to the prevailing conditions that occurred during the terminal Ediacaran to middle Fortunian (Interval I). Hence, TOC burial was maintained at a relatively low level (Fig. 2).

This interval records widespread colonization of carbonate platforms by archaeocyaths and novel SSFs, including brachiopods (Fig. 7, Maloof et al., 2010; Qian et al., 2009; Zhuravlev et al., 2023). It also corresponds to the onset of another major pulse of eustatic transgression that led to widespread flooding of shallow marine settings (e.g., Bowyer et al., 2023), which is also captured by stratal stacking patterns in the Tarim Basin succession (Fig. 7, Wei et al., 2025). This final platform-wide flooding appears to mark a major transition in the Tarim Basin record, from an earlier interval dominated by transgression-induced nutrient upwelling, to a later interval where nutrient input and attendant productivity and palaeomarine redox dynamics were affected to a greater extent by continental weathering, and were at least partially disconnected from nutrient input linked to sea level change (Fig. 7). This may reflect the combined effects of ongoing second-order sea level rise and global warming during the Terreneuvian (Hearing et al., 2018).

CONCLUSIONS

Our multi-proxy approach demonstrates a complex and evolving interplay between oceanic redox conditions, nutrient availability, upwelling, and continental weathering in the

Tarim Basin during the early Cambrian radiation of animals. Initial high intensity upwelling during the terminal Ediacaran to middle Fortunian promoted high primary productivity and thus the development of anoxic conditions in the deeper waters of an OMZ setting. This, in turn, promoted redox-driven P recycling back to the water column in deeper water portions of the OMZ, hence resulting in a positive productivity feedback. Combined with the intense upwelling, this promoted high organic matter burial in deeper shelf settings, with the subsequent oxygen production likely contributing to the OOE documented at the peak of the 5p carbon isotope excursion during the late Fortunian to early Stage 2.

This then led to the development of dysoxic-oxic conditions across the OMZ in the Tarim Basin, which ultimately promoted P burial and a negative productivity feedback. Combined with decreased upwelling, this resulted in oligotrophic conditions, which in turn, resulted in better oxygenated conditions, that may have facilitated ongoing diversification of SSFs. However, the retention of sedimentary P also suppressed oxygenic photosynthesis, and thus transient anoxic events punctuated the expanding oxia. As a result of these feedbacks, an OOE occurred, rather than persistent oxygenation from Stage 2 onwards.

During middle to late Stage 2, enhanced upwelling coupled with more intense continental weathering again supplied sufficient nutrients to stimulate higher rates of primary production, although this was not as intense as during the terminal Ediacaran to middle Fortunian. Phosphorus burial under dysoxic-oxic water column conditions maintained the longer-lived and more stable oxic pulses through this interval. Finally, our dataset shows a transition in the middle-upper part of Stage 2, from nutrient input that was dominated by upwelling promoted during transgressive episodes, towards nutrient input

dominated by continental chemical weathering, which may reflect the combined effects of ongoing second-order sea level rise and global warming during the Terreneuvian.

ACKNOWLEDGMENTS

This study was financially supported by the National Natural Science Foundation of China Grant No. (41961144023 and 41730424) and Chinese Scholarship Council (CSC) funding. SWP acknowledges support from NERC grants NE/T008458/1 and NE/Z000122/1, and FB acknowledges funding from UKRI grant EP/Y008790/1.

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FIGURE CAPTIONS

Figure 1. Geological details and geographic position of the Yurtus Formation in the Tarim Basin. (A) Geological map of the Tarim Basin (modified after Zhou et al., 2014); (B) Stratigraphy of the Lower Cambrian Yurtus Formation and sea level curve (modified after Zhou et al., 2014); (C) Paleo-bathymetric locations of the Kungaikuotan (KGKT), Sugaitebulake (SGTB) and Shiairike (SARK) sections (modified after Zhu et al., 2018).

Figure 2. Stratigraphic distribution of total organic carbon (TOC), carbonate carbon isotope

($\delta^{13}C_{carb}$), P, P/Al (wt%/wt%) and P_{reac}/Al (wt%/wt%), alongside molar C_{org}/P_{org} and C_{org}/P_{reac} ratios. (A) The Sugaitebulake section (SGTB); (B) The Kungaikuotan (KGKT) section; (C) The Shiairike (SARK) section. Dashed line on the P/Al plots (mass ratio of 0.009 wt%/wt%) represents the average Upper Continental Crust value (Mclennan, 2001); dashed line on C/P plots denote the Redfield ratio (106/1). Data for redox conditions, TOC and $\delta^{13}C_{carb}$ are modified from Wei et al. (2025). Intervals I, II, III and IV correspond to the terminal Ediacaran to middle Fortunian (I), the late Fortunian to early Stage 2 (II), middle Stage 2 (III), and late Stage 2 (IV).

Figure 3. Molar C_{org} versus P_{reac} and P_{org} cross plots for the Kungaikuotan (KGKT), Sugaitebulake (SGTB) and Shiairke (SARK) sections in the Tarim Basin during the terminal Ediacaran to middle Fortunian (A), the late Fortunian to early Stage 2 (B), middle Stage 2 (C), and late Stage 2 (D). The black lines represent the Redfield C/P ratio of 106/1.

Figure 4. Stratigraphic profiles for primary productivity (Ba/Al, P/Al, Ni/Al, Cu/Al and Zn/Al; data from this study), and chemical weathering (CIA) and upwelling (Co × Mn) (from Wei et al., 2025) across the three sections in the Tarim Basin. (A) The Sugaitebulake section (SGTB); (B) The Kungaikuotan (KGKT) section; (C) The Shiairike (SARK) section. Intervals I, II, III and IV correspond to the terminal Ediacaran to middle Fortunian (I), the late Fortunian to early Stage 2 (II), middle Stage 2 (III), and late Stage 2 (IV). Dashed lines on the nutrient plots represent UCC values; dashed line on the Co × Mo plot represents the threshold of 0.4 ppm·wt% to differentiate upwelling from a restricted setting (Sweere et al., 2016).

Figure 5. Proposed model for P burial and recycling. Thickness of the arrows indicates the relative flux. (A) the terminal Ediacaran to middle Fortunian, active nutrient shuttling where remobilized dissolved P from the ferruginous outer shelf was recycled by upwelling to the middle to inner shelf. Here, drawdown of recycled P through uptake by Fe (oxyhydr)oxide particles occurred in the inner shelf at SGTB, while for KGKT a small degree of P recycling back to the water column occurred after initial drawdown of P associated with organic carbon. Both upwelling and recycling promoted local productivity and organic carbon burial, leading to subsequent shallow marine oxygenation; (B) the late Fortunian to early Stage 2, dysoxic-oxic conditions were initiated by decreased upwelling and maintained by P burial across the three sections. Phosphorus derived from continental weathering was effectively fixed in the inner shelf, resulting in a more oligotrophic environment at the distal KGKT and SARK sites; (C) middle Stage 2, enhanced upwelling and continental influx led to high primary productivity. Persistent dysoxic-oxic conditions were maintained by consistent P burial at SGTB. The dashed light red arrows reflect possible P burial mechanisms (given the lack of P partitioning data) for the KGKT and SARK sections; (D) late Stage 2, continued upwelling and an enhanced continental influx caused a small enhancement of ferruginous conditions, leading to limited P burial and some recycling back to the water column at SGTB, with a resultant increase in primary productivity. Here, most P burial occurred at KGKT. Redox conditions are modified from Wei et al. (2025).

Figure 6. Cross-plots of highly reactive Fe contents versus total P concentrations for the

Kungaikuotan (KGKT), Sugaitebulake (SGTB) and Shiairke (SARK) sections in the Tarim Basin.

Figure 7. Proposed temporal correlation for chemostratigraphic and biostratigraphic data from the Tarim Basin, Northwest China (modified after Wei et al., 2025). Global composite $\delta^{13}C_{carb}$ framework, mean generic richness dataset and lowest fossil occurrence information are summarized, alongside important radioisotopic ages (after Bowyer et al., 2024 and references therein). Published fossil occurrences for the SGTB section are also shown (Xiao and Duan, 1992). VPDB—Vienna Peedee belemnite. Note that this global framework follows recent updates to the timescale, whereby the lowest temporally-calibrated occurrence of *T. pedum* is set at ~533 Ma (Nelson et al., 2023).

[1]Supplemental Material. *[Table S1 and Figure S1]*. Please visit https://doi.org/10.1130/XXXX to access the supplemental material, and contact editing@geosociety.org with any questions.