Molecular and isotopic evidence reveals the end-Triassic carbon isotope excursion is not from massive exogenous light carbon

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The negative organic carbon isotope excursion (CIE) associated with the end-Triassic mass extinction (ETE) is conventionally interpreted as the result of a massive flux of isotopically light carbon from exogenous sources into the atmosphere (e.g., thermogenic methane and/or methane clathrate dissociation linked to the Central Atlantic Magmatic Province [CAMP]). Instead, we demonstrate that at its type locality in the Bristol Channel Basin (UK), the CIE was caused by a marine to nonmarine transition resulting from an abrupt relative sea level drop. Our biomarker and compound-specific carbon isotopic data show that the emergence of microbial mats, influenced by an influx of fresh to brackish water, provided isotopically light carbon to both organic and inorganic carbon pools in centimeter-scale water depths, leading to the negative CIE. Thus, the iconic CIE and the disappearance of marine biota at the type locality are the result of local environmental change and do not mark either the global extinction event or input of exogenous light carbon into the atmosphere. Instead, the main extinction phase occurs slightly later in marine strata, where it is coeval with terrestrial extinctions and ocean acidification driven by CAMP-induced increases in Pco2; these effects should not be conflated with the CIE. An abrupt sea-level fall observed in the Central European basins reflects the tectonic consequences of the initial CAMP emplacement, with broad implications for all extinction events related to large igneous provinces.

Significance

The end-Triassic mass extinction that occurred ∼202 Ma is one of the “Big Five” biotic crises of the Phanerozoic Eon. It is also accompanied by an organic carbon isotopic excursion that has long been interpreted as the result of a global-scale carbon cycle disruption. Rather than being due to massive inputs of exogenous light carbon into the ocean–atmosphere system, the isotopic excursion is shown here to reflect regional sea-level change that caused a transition from a marine ecosystem to a less saline, shallow-water, microbial-mat environment and resultant changes in the sources of organic matter. The mass extinction that occurred slightly later, caused by abrupt injection of volcanogenic CO2, is accompanied by only modest changes in organic carbon isotopic composition.
an epicontinental sea with restricted circulation. Based on lithology and fossil evidence in the Westbury and Llithostroformations, the northern parts of this seaway (including the United Kingdom) had fluctuating salinity (14). Located on the northern flank of the CAMP (Fig. 1), the Central European Basin contains no lava flows or ash beds, hindering direct correlation with paroxysmal magmatic events. A well-documented cycle of sea-level fall and then rise throughout the basin occurred in the few hundred thousand years of the latest Rhaetian (15). It is within this environmental context that the BCB CIE, and its more southern correlatives, formed close in time to the ETE and initiation of the CAMP.

Results and Discussion

Sea-Level Fall Resulted in Microbial Mat Emergence and Ecological Stress. Biomarker data for both the St. Audrie’s Bay and Llithostro sections of the BCB (SI Appendix, Fig. S1) suggest that the BCB CIE is a feature driven by ecological community changes forced by decreasing water depth and salinity within the basin and, by extension, to the European basin as a whole. We describe the biomarker results in stratigraphic (i.e., chronological) order as follows.

After an extended interval of predominantly nonmarine red-bed deposition spanning most of the Triassic, the BCB was flooded by marine waters of abnormally low salinity, which deposited the dark mudstones of the Westbury Formation in the Rhaetian (14). Both sections show a relatively abrupt upward transition to the lighter-colored lower Cotham Member of the Llithostro Formation, characterized by fewer marine fossils and abundant oscillation ripples, indicating a shallowing water depth but without much change in faunal composition. The lower Cotham and uppermost Westbury were subjected to folding and brecciation attributed, at least in part, to syndepositional megaseismic event(s) (16). Through the Westbury to Cotham lithological transition, perturbations in biomarker-inferred ecological and redox conditions are apparent. C29 steranes (24-n-propyl cholestanes), compounds derived from marine pelago-phyte algae, show a constant decrease to zero (Fig. 2). Except for low-diversity marine bivalves identified in the lower part of the Cotham Member in Lavernock Point, South Wales, a near absence in marine fossils throughout the Cotham Member supports a transition from a residual sea to a restricted shallow non-marine environment (7, 17). Furthermore, declining values of the gammacerane index and ratios of isorenieratane/triaromatic steroids signify the termination of stratification (18) and disappearance of photic zone euxinia (a condition in which hydrogen sulfide is present in the sun-lit region of the water column) (19–22), respectively (Fig. 2). This is likely caused by the strong mixing of shallow water that recharges oxygen throughout the water column. Additionally, strong shifts in the relative abundances of C27, C28, and C29 steranes that generally represent red, chlorophyll c-containing, and green algae, respectively, are observed (SI Appendix, Fig. S2), implying an unstable environment sensitive to ambient perturbations, a common observation associated with shallowing water.

Truncating the folded lower Cotham seismite is an erosional surface downward from which intrude deep desiccation cracks (~1 m), at which level, the BCB CIE and the upper Cotham Member begins (Fig. 2). This sedimentological feature, as well as other evidence of desiccation with smaller crack length, wave ripples (Fig. 2), and possible rain imprint (7), indicates the CIE is recorded during maximum regression and centimeter-scale
Contrastingly, the pustular and smooth microbial mats in the hy-
equally contributed by cyanobacteria and
evidence of microbial mats and Highborne Cay stromatolites (Bahamas) show modern Laguna Guerrero Negro (Baja California) hypersaline
ter environments (25, 26). In the context of microbial systems, the associated (i.e., soil, wood degradation), terrestrial, and freshwa-
compared to other sources such as marine cyanobacteria are minor producers of 2-methylhopanoids (23, 24), preserved as
2-MeHs in sediments, complicating interpretations of the 2-MeH index values (Fig. 2) are also observed.

Although 2-MeH is typically used as a biomarker for cyanobac-
ter, other organisms, exemplified by
other prokaryotes in the mats (27). Whether
hpnP genes from a predominantly cyanobacterial source despite a major contribution of α-proteobacteria in the mats (27). Whether primarily sourced from cyanobacteria or α-proteobacteria, increases in the 2-MeH index in the lower CIE interval most simply interpreted to constitute a microbial-mat source. Additionally, a well-mixed water column at the lower CIE is evidenced by low gam-
and α-light-adapted brown-pigmented GSB, respectively, are barely detectable (SI Appendix, Fig. S8). Increasing relative abundances of low light-adapted brown-pigmented GSB, indicated by ratios of isorenieratane/triaromatic steroids, are also observed (Fig. 2) (29, 30); however, such increases are mostly an order of magnitude lower compared to those above and below the CIE. Altogether, these changes strongly argue for the initiation of freshening and shallowing conditions populated by thin, microbial-mat communities containing oxygenic cyanobacteria and/or α-proteobacteria and point to the dramatic perturbations to the ecosystem and environment at the lower CIE stage.

Nearly absent C30 steranes in the upper CIE, except one outlier sample, corroborate the interpretation of a nonmarine environment throughout the Cotham Member. Another line of evidence is the elevated ratios of (renieratane and renierapurpurane)/isorenieratane ([ren+rnp]/iso) (Fig. 2). Renieratane and renierapurpurane are carotenoid biomarkers sourced from numerous strains of cyanobacteria (31, 32) and high (ren+rnp)/iso ratios, as observed in the upper CIE, are typical of Phanerozoic lacustrine settings with low sulfate inventories (33). Increases in chlorobactane and okenane, pigment-derived biomarkers for high light-adapted anoxygenic phototrophic green-pigmented green (GSB) and purple (PSB) sulfur bacteria (20, 28), respectively, are barely detectable (SI Appendix, Fig. S8). Increasing relative abundances of low light-adapted brown-pigmented GSB, indicated by ratios of isorenieratane/triaromatic steroids, are also observed (Fig. 2) (29, 30); however, such increases are mostly an order of magnitude lower compared to those above and below the CIE. Altogether, these changes strongly argue for the initiation of freshening and shallowing conditions populated by thin, microbial-mat communities containing oxygenic cyanobacteria and/or α-proteobacteria and point to the dramatic perturbations to the ecosystem and environment at the lower CIE stage.

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Fig. 2. Biomarker evidence of depositional facies change at St. Audrie’s Bay (orange circles and solid lines) and Lilstock (blue squares and dashed lines) compared to the δ13Corg and TOC records. The BCB CIE is displayed in light green (lower CIE) and pink (upper CIE), while newly proposed extinction onset is highlighted in light purple. The interpreted meaning of each biomarker-based proxy is indicated in bold above each column. Full details of the biomarker measurements are in SI Appendix. PCA loosely represents an index of integrated variability corresponding to microbial-mat formation and is represented here by PC-2. Note that PCA was carried out for all samples except two samples from Blue Lias Formation, to avoid large bias introduced by the outliers, and that the isorenieratane/triaromatic steroids are plotted in log scale. More information with regard to the comparison between PC-1 and PC-2 is available in SI Appendix.
microbial mats beneath surficial cyanobacterial layer(s) (Fig. 2). The cooccurrence of all these carotenoids requires redox stratification, a niche most parsimoniously attributed to a microbial-mat source (29). Additionally, the gammacerane index increases in the upper CIE further support microbial-mat formation and/or freshwater input. Although typically used as a stratification proxy in marine or hypersaline lagoon settings (18), increases of gammacerane in the upper CIE likely result from other source(s) of tetrahymanol (i.e., gammacerane precursor), such as phototropic bacteria (34) and/or freshwater ciliates (35). Notably, many α-proteobacteria that produce 2-methylhopanoids also have the capacity to produce tetrahymanol, and an inverse relationship is observed between these compounds (24, 36). Thus, upper CIE gammacerane index increases are interpreted to be a direct response to ecological and environmental changes different from the lower CIE. Some of the largest and most dramatic changes in the relative abundances of the predominant C27, C28, and C29 steranes and the ratio of algae to bacteria are also observed in the upper CIE at lowest δ13Corg values (SI Appendix, Fig. S2). The oligotrophic and shallow water conditions of the upper Cotham Member support a habitat in which photosynthetic microbial mats could thrive alongside the observed generally oligohaline or freshwater biota (37), including darwinulid ostracodes, spinocaudatan crustaceans, and the bryophyte Naiadita lanceolata (7–9).

The transition from the lower CIE to the upper CIE witnessed a significant reformation of the aquatic microbial community, with the upper CIE hosting the lowest δ13Corg values (Figs. 2 and 3). In addition, a principal component analysis (PCA) of the biomarkers interpreted to relate to a microbial-mat source during the CIE (Fig. 2) reveals that most of the variability occurs during the upper CIE and that 55 to 65% of variation can be explained in the first (PC-1) and second (PC-2) principal components (SI Appendix, Supplementary Text and Fig. S9).

The coeval Cotham Marble (covering 2,000 km² elsewhere in the SW United Kingdom) also contains the remains of microbial-mat habitats during the CIE. Comprised of microbialites and laminar and thrombolytic stromatolites, this unit also displays a negative carbon isotopic profile (38, 39). Similar biomarkers have been attributed to microbial mats in the Chicxulub crater core that were transported from a carbonate platform by seiches and tsunamis after an asteroid impact (40). Accompanying the upper Cotham low-stand is the replacement of the marine biota by a nonmarine flora and fauna (7, 9, 13). Although the extinction horizon is conventionally placed at this level at the CIE, the absence of marine Triassic taxa cannot be attributed to extinction because those taxa would be absent in the nonmarine BCB even if the ETE never occurred.

**Return to Marine Conditions.** The termination of the CIE in the lower Langport Member is accompanied by a transgressive event that led to the reestablishment of a transitional marine environment, evidenced by a rise in C30 steranes and a return of the diagnostic carotenoid isorenieratane as the dominant photosynthetic pigment (Fig. 2). The synchronous responses in bulk isotope, C30 steranes, and other proxies (discussed later) strongly argue that the termination of the CIE is related to local depositional environment shifts (Fig. 2 and SI Appendix, Fig. S2). For example, this boundary witnessed a rise in 2MeH, sudden decline in freshwater ciliates and/or phototropic bacteria (gammacerane index), elimination of aromatic carotenoid-producing cyanobacteria ([ren+rnp]/iso), resurgence of brown-pigmented GSB (isorenieratane/triaromatic steroids) (Fig. 2), and a strong methane cycle modulated by methanotrophs (3Me-H) (SI Appendix, Fig. S2). Additionally, minor perturbations in eukaryotic communities are observed based on C27–29 sterane compositions (SI Appendix, Fig. S2). Interestingly, C30 steranes anticorrelate with the relative density of cyanobacteria/α-proteobacteria vs. aerobic methanotrophs (SI Appendix, Fig. S3), a relationship that is contrary to common observations, as summarized in ref. 41. In our case, this pattern is most reasonably explained as reflecting the demise of the freshwater nitrogen-fixing cyanobacteria and/or α-proteobacteria present in microbial mats brought about by

**Fig. 3.** Compound-specific isotope analysis of pristane and phytane from St. Audrie’s Bay and Lilstock and n-alkanes from Lilstock. δ13C17, 18, 19 indicates isotopic values of C17, C18, and C19 n-alkanes displayed in different color intensities. Av. δ13C17, 18, 19-Av. δ13C(pr, ph) represents isotope mean value offsets between C17,18,19 n-alkanes and pristane + phytane used to investigate autotrophy (auto.) vs. heterotrophy (hetero.). St. Audrie’s Bay palynology data were previously reported in ref. 13 and are correlated here to Lilstock through lithological changes. The inferred meaning of each compound is indicated in bold above each column. BL, Blue Lias Formation; L, Langport Member; LIL, Lilstock; SAB, St. Audrie’s Bay; UC, Upper Cotham Member; VPBD, Vienna Pee Dee Belonemite.
the marine transgression. Dynamic shifts in almost all biomarkers and PCA scores are observed in one sample of the Langport Member at Lilstock without significant change in δ^13Corg composition (Fig. 2 and SI Appendix, Fig. S9). However, this interval is deposited within a heavily bioturbated level not observed at St. Audrie’s Bay and is therefore considered a likely outlier. A shift back toward marine conditions in the middle to upper Langport Member is also indicated by a return of marine bivalve taxa, several of which disappeared at the base of the freshwater input at the CIE. Although several of these bivalve taxa persist into the overlying Blue Lias Formation, there are also several regional local appearances (10, 11). The uppermost mollusk-bearing Langport Member resembles the bioturbated marlstone and limestone facies that occur cyclically in the overlying Blue Lias Formation, reflecting a return to fully marine conditions (Fig. 1). Conodonts occur for the first time in this unit, only to have their last occurrence in the overlying basal Blue Lias Formation (12), which also contains the last occurrence of the characteristic Late Triassic reptile clad Phytosaurusia (42).

The Langport Member-to-Blue Lias Formation transition, a previously debated flooding event (43, 44) corroborated here by the largest increase in the C38 sterane index (Fig. 2), is characterized by a negative shift in δ^13Corg and significant changes in biomarkers, including a switch from aerobic methanotrophy to cyanobacterial dominance and shifts in the proportion of C29 and C30 steranes (Fig. 2). The base of the Blue Lias Formation is marked by microlaminated organic matter-rich mudstones (“paper shales”), the basal 2 cm of which contains a “Lilliput Assemblage” (45) of tiny (millimeter-scale) bivalves (SI Appendix, Fig. S4). The succeeding finely laminated paper shales and remaining Preplanorbis zone (lowermost Blue Lias Formation, lacking ammonites, specifically Psiloceras planorbis) are characterized by a pronounced positive δ^13Corg shift (Fig. 1) (4) and numerous levels of abundant completely decalcified and poorly preserved bivalves of low diversity (SI Appendix, Fig. S5), most simply interpreted as the results of a calcification crisis in which no aragonitic and few calcitic mollusks are preserved. Negative δ^13Corg values return with the reappearance of ammonites, particularly P. planorbis that preserve the aragonitic nacre (Fig. 1). A marked microfloral swing with an acme of the conifer pollen form *Classopolis meyeriana* also occurs at the base of the Blue Lias Formation. The appearance of P. planorbis along with the sporomorph taxon Ceratophollenites thiagarriti within the extensive C. meyeriana acme marks the approximate base of the Hettangian (13). Previously interpreted as a product of another major disruption in the exchangeable reservoirs between the terrestrial and marine realms at the ETE (4), and used as a chemostratigraphic marker (main CIE), this negative shift is now recognized as a change to long-term relatively negative δ^13Corg values lasting through the Hettangian Age, rather than a single event (44, 46).

**Compound-Specific Isotope Analysis of the CIE Supports Its Environmental Origin.** Compound-specific isotope analysis (CSIA) of biomarkers provides insight into how ecological change(s) contribute to the δ^13Corg record, as well as the complex array of sources and related processes affecting δ^13Corg values.

Biomarkers investigated by CSIA include pristane and phytane typically derived from chlorophylls *a* and *b* (cyanobacteria and/or algae) (47), C17–19 n-alkanes from microbes including bacteria and algae (48), C23–25 odd carbon-numbered n-alkanes from bryophytes (49) and other submergent plants (50, 51), and C25 odd carbon-numbered n-alkanes from land plants (52) (SI Appendix, Table S1).

Major differences in the biomarker δ^13C values observed between both sections occur at the onset of the CIE. For instance, at St. Audrie’s Bay, pristane exhibits the largest isotopic shift (~5.1‰) that seemingly mirrors an equal shift in the bulk δ^13Corg record, whereas at Lilstock, the largest compound-specific isotopic shifts are recorded in the C21–29 odd-numbered n-alkanes (~4.12 to ~6.0‰), albeit lesser than the ~8.1‰ bulk δ^13Corg excursion (Fig. 3 and SI Appendix, Fig. S6 and Table S1).

In addition, during the termination of the CIE at Lilstock, some of the largest isotopic shifts occur in the C21–29 odd-numbered n-alkanes with >5‰ positive shifts that are not mirrored in the bulk δ^13Corg record (3.6‰) (Fig. 3 and SI Appendix, Fig. S6 and Table S1). Such discrepancies exemplify the CIE reflects a more complex, endogenic origin related to ecological change(s).

The covariation of δ^13Corg and δ^13Cphytane values through the CIE indicates that the CIE can primarily be explained by microbial-community changes (Fig. 3). Specifically, within the CIE the most negative δ^13Corg values coincide with most negative δ^13Cphytane values (~34.8‰ and ~33.9‰) at St. Audrie’s Bay and Lilstock, respectively. Although pristane has its primary contributions from chlorophylls *a* and *b* in the water column, phytane has multiple predominant sources including cyanobacteria and methanogenic archaea residing in microbial mats as well as those from chlorophyll *a* and *b*-containing photoautotrophic algae that reside in the water column. For example, phytane-related isoprenoids released after the cleavage of polar lipids have been detected in abundance in the hypersaline microbial mats of Shark Bay, Western Australia, and Laguna Guerrero Negro, Mexico (53, 54). Originating from archaeol, microbial mats of Shark Bay, Western Australia, and Laguna Guerrero Negro, Mexico (53, 54). Originating from archaeol, such compounds are indicative of methanogens found in a range of environments including microbial mats (55–57). In these mats, n-alkyl lipids (e.g., C17–19 n-alkanes) are depleted in 13C compared to the cooccurring isoprenoids by ~1.5‰, whereas in bacteria, the opposite pattern is observed (ref. 58 and references therein). Based on increases in heterotrophy given by the positive isotopic offsets between n-alkanes (C17–19) and isoprenoids (pristane and phytane) and the ~2‰ offsets between δ^13Cpristane and δ^13Cphytane during the CIE onset (Fig. 3), negative shifts in δ^13Cphytane are associated with increased bacterial activity of microbial mats. Enhanced preservation of phytane associated with microbial-mat formation explains low CIE pristane/phytane ratios, typically associated with more reducing conditions (59), during red-bed oxic deposition (SI Appendix, Fig. S2). Therefore, the incongruity of the interpretation of redox conditions based on lithologic observation and biomarkers suggests that the pristane/phytane ratio is a source indicator associated with microbial mat, rather than being simply an indicator of redox conditions (Fig. 2 and SI Appendix, Fig. S2).

Microbial mats are known to produce lipids with greater 13C-depletion compared to those of phytoplankton (60). Investigations into the isotopic composition of phospholipid fatty acids in modern freshwater microbialites have shown lipids greatly depleted in 13C (61, 62), and biomarkers of sulfate-reducing bacteria (important contributors in microbial-mat communities) in the carbonate matrix of concretions are also considerably 13C-depleted (δ13C values ranging between ~40.5 and 42.0‰).
Further, the recycling of $^{13}$C-depleted autotrophic biomass by lower-residing heterotrophic layers within freshwater microbialites is required to explain changes in microbialite vertical $\delta^{13}$C profiles and calcium carbonate precipitation equations whereby the local $\delta^{13}$Ca/Ca becomes increasingly negative as a result of microbial respiration (64, 65). Thus, the $^{13}$C-depleted organic carbon associated with freshwater microbial mats and respiration-induced release of $^{13}$C-depleted carbon to the inorganic carbon pool and its reassimilation would be essential drivers of the CIE and possibly account for the minor offsets between the isotopic composition of pristane and phytane. Furthermore, methanogenic bacterial metabolism important in microbial mats produces methane in large quantities (37), meaning that microbial-mat emergence in the SW United Kingdom could constitute an important methane source unrelated to the CAMP.

In the same interval at Lüstone, odd-numbered mid- to long-chain $n$-alkanes ($C_{31} \ldots C_{37}$) show isotopic values more depleted than those of phytane, ranging between $-34.8$ and $-36.3\%e$ (SI Appendix, Table S1 and Fig. S6). The $^{13}$C-depleted midchain-length $n$-alkanes may be attributed to bryophytes and possibly other submerged/ floating plants, as corroborated by fossil evidence that includes the aquatic bryophyte (liverworts) Naiadita and Hepaticites (along with freshwater to brackish Crustacea) in the Cotham Member (7, 9). The $^{13}$C-depletion of long-chain $n$-alkanes with odd over even preference within the CIE has been cited as evidence of an input of light carbon into the atmosphere (66), based on data from Austrian sections. These sections, while having an overall similar lithostratigraphy (Fig. 1) and similar patterns in $n$-alkanes differ from those of the BCB in having high total organic carbon (TOC) values in the CIE. Furthermore, the longer-chain $n$-alkane isotopic record fluctuates cyclically (67) through the St. Audrie’s section (SI Appendix, Fig. S7), with more shifts in $n$-alkane than bulk organic $\delta^{13}$C, an observation more parsimoniously explained by episodic floral changes tied to cyclical climate rather than multiple changes in atmospheric composition. Pollen and spore data from St. Audrie’s Bay track mid- to long-chain $n$-alkane isotope values (Fig. 3 and SI Appendix, Fig. S6 and Table S1) through the CIE (13). The CIE onset closely correlates with a greater abundance of pollen (dominated by C. meyeriana) and terminates with a greater abundance of spores, the largest turnover in sporomorph taxa (Fig. 3). Spore-bearing plants such as lycophytes and monilophytes can exhibit higher carbon isotopic discrimination compared to pollen-bearing plants (e.g., gymnosperm and angiosperm) by up to $\sim 5\%e$ in $^{13}$C values (68). Variation in plant inputs, although unlikely being the primary explanation of the CIE, most possibly is a consequence of local hydrologic/ climatic shifts amplifying isotopic shifts and contributing to the CIE (69). The shifts between autotrophic algae vs. heterotrophic bacteria together with cyclical land plant inputs (58, 70) during the CIE explain geochemical variations and differences, highlighting that local environmental changes triggered the onset and termination of the CIE. Supporting that the CIE is endemic in its origin.

Following the CIE, the $\delta^{13}$C of pristane and phytane in the middle Langport Member are relatively constant, and phytane is interpreted as being sourced largely from chlorophylls a and b. $\delta^{13}$C values of the C17 to C19 and C29 $n$-alkanes are generally more positive, with the exception of one negative excursion that has a negligible effect on the $\delta^{13}$Corg record and is coincident with pollen and spore changes and heavy bioturbation. Above this, across the upper Langport-to-Blue Lias transition, the $\delta^{13}$C of pristane and phytane become relatively less stable, particularly at St. Audrie’s Bay, and all n-alkanes, particularly C19 and C29, show a negative excursion coincident with increases in Classopollis pollen and a negative shift in the $\delta^{13}$Corg record (Fig. 3).
correlation such as magnetostratigraphy, U-Pb geochronology, and astrochronology.

Conclusions

Biomarker and compound-specific isotopic data from the BCB at St. Audrie’s Bay and Lilstock, United Kingdom, show that the iconic CIE preceded the main ETE and that the CIE itself is a record of freshwater microbial-mat development and other ecological changes driven by a geologically transient, regional sea-level change. Use of the BCB CIE and its European correlates as a global isochronous chronostratigraphic marker is therefore not tenable. The succeeding younger negative-isotopic excursion at the onset of the biocalcification event, associated with the last conodonts and the last phytosaurs, might be such a global isochronous marker. This interpretation of the CIE requires a reanalysis of global correlations at a tens of thousands of years resolution with independent correlation methods and should lead to a better understanding of the regional vs. global effects of the CAMP on one of the largest mass extinctions in Earth’s history.

Materials and Methods

For δ^{13}C_{org} and TOC analyses, carbonates were removed from samples (dry weight, ~0.5 g) by acid digestion and measured using a Delta V Plus mass spectrometer connected to a Thermo Flash 1112 via a Conflu IV and a carbon, hydrogen, nitrogen, and sulfur elemental analyzer at the West Australian Biogeochronology Centre, University of Western Australia. For biomarker analysis, bitumens were isolated from dry-sediment samples (30 to 180 g) by solvent extraction using a Milestone Start-E microwave extraction system in 50 mL of 9:1 dichloromethane:methanol (DCM:MeOH) using a temperature program of 21 to 80 °C over 10 min (held for 15 min). Elemental sulfur was removed using activated copper turnings, and bitumen compounds were separated into saturate (n-hexane), aromatic (3:1 n-hexane:DCM), and polar (9:1 DCM:MeOH) fractions using column chromatography with activated silica gel. St. Audrie’s Bay saturate fractions were analyzed using an Agilent 6890N gas chromatograph (GC) connected to a Micromass AutoSpec Ultima multiple reaction-monitoring mass spectrometer (MRM-MS). St. Audrie’s Bay aromatic and Lilstock combined saturate and aromatic fractions were analyzed using an Agilent 7890B GC connected to an Agilent 7010A triple quadrupole (QQQ) tandem MS. All GC-MRM-MS and GC-QQQ-MS analyses were conducted at R.E.S.’s laboratory, Massachusetts Institute of Technology. Details on quality control regarding multiple-instrument measurements are expanded in SI Appendix. Compound-specific isotope analysis was conducted at Curtin University using a Thermo Trace GC Ultra connected to a Thermo Delta V Advantage isotope-ratio MS via a GC Isolink and Conflo IV. For full materials and methods, see SI Appendix.

Data Availability. All study data are included in the article and supporting information.

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