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Key Points:

- On the Barents Shelf, uppermost Permian and Lower Triassic sedimentary rocks record peak C_{33} - n -alkylcyclohexane and phytanyl toluene contents
- C_{33} - n -alkylcyclohexane from phytoplankton indicates blooms of certain primary producers during the Permian–Triassic environmental crisis
- Phytanyl toluene and C_{33} - n -alkylcyclohexane may be derived from organisms occupying a similar ecological niche

Supporting Information:

Supporting Information may be found in the online version of this article.

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Phytoplankton Blooms on the Barents Shelf, Svalbard, Associated With the Permian–Triassic Mass Extinction

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Abstract Mid- to higher-latitude shallow marine environments are suggested to serve as refugia for organisms during intervals of rapid environmental change associated with hyperthermals. To understand the role of these environments during hyperthermals, we herein investigate the Permian–Triassic environmental crisis, which led to the most severe mass extinction event in the Phanerozoic. Our analysis of siliciclastic deposits from the Boreal Ocean from Lusitaniadalen, Svalbard, reveals a distinct increase of the lipid biomarkers C_{33} - n -alkylcyclohexane (C_{33} - n -ACH) and phytanyl toluene following the extinction event. This increase does not appear to reflect facies changes. Rather, it coincides with the extinction horizon, and persists into the lowermost Triassic (Griesbachian). Our findings suggest that neither C_{33} - n -ACH nor phytanyl toluene are linked to short periods of photic zone euxinia recorded at Lusitaniadalen, but rather are derived from a specific group of phytoplankton. This indicates that higher-latitude ecosystems may have supported regional blooms of unknown primary producers after the Permian–Triassic mass extinction, thus explaining the selective survival of some marine organisms. We also identify (albeit in lower abundance) C_{33} - n -ACH and its pseudohomologs in northern Italy, which is the first report of n -ACHs in the tropical Tethys region across the Permian–Triassic transition outside of South China, highlighting the wide paleogeographic distribution of this biomarker. Phytanyl toluene, however, is found exclusively in deposits recording higher-latitude ecosystems, and is likely linked to organisms occupying a similar ecological niche as the source organism of C_{33} - n -ACH in these settings.

Plain Language Summary Environmental changes can have detrimental effects on marine ecosystems. Studying Earth's history can help us to understand how ecosystems respond to environmental changes. The Permian–Triassic mass extinction, the biggest mass extinction in Earth's history, is linked to rapid environmental changes. Here, we analyze two molecular fossils (lipid biomarkers), C_{33} - n -alkylcyclohexane (C_{33} - n -ACH) and phytanyl toluene, that are associated with this mass extinction, from samples from different paleolatitudes and paleo-oceans. These biomarkers increase several-fold in the aftermath of the extinction in higher-latitude settings, such as Svalbard, while we detect only traces of C_{33} - n -ACH in tropical settings, if any. Although the organisms producing these biomarkers are unknown, they were likely synthesized by organisms able to survive the harsh environmental conditions during this interval of Earth's history. This is particularly true for higher-latitude ecosystems, which may have experienced less severe environmental stress, such as less extreme (though potentially greater changes in) temperatures, compared to tropical ecosystems. C_{33} - n -ACH mirrors patterns of other biomarkers indicative of increased primary productivity during the same time interval, suggesting that it could be another molecule produced by a specific group of phytoplankton. Phytanyl toluene was probably produced by different phytoplankton found in the Boreal Ocean but not the tropical locations.

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1. Introduction

Rapid environmental changes can lead to biodiversity crises and mass extinctions. To understand the response of organisms to these changes, plasticity, adaptation or range shifts of modern species or populations can be studied (e.g., Donelson et al., 2019). However, ecosystem responses are highly complex and depend on multiple factors that are challenging to fully capture through laboratory experiments. To better understand the long-term effects of rapid environmental changes on communities, past hyperthermal events can be studied, such as the Paleocene–Eocene Thermal Maximum (e.g., McInerney & Wing, 2011) and the Permian–Triassic environmental crisis; the latter triggered the most severe mass extinction in the Phanerozoic, often referred to as the Permian–Triassic mass extinction or end-Permian mass extinction (e.g., Dal Corso et al., 2022; Payne & Clapham, 2012).

During the Permian–Triassic mass extinction, ca. 252 million years ago, approximately 81% of marine species went extinct globally (Stanley, 2016), but extinction patterns and functional diversity were geographically variable (Foster & Twitchett, 2014). The mass extinction event in marine ecosystems is constrained to 60 ± 48 kyr in well-dated sections in China (Burgess et al., 2014), and was accompanied by a sharp negative carbon isotope ($\delta^{13}\text{C}$) excursion, observed globally (Korte & Kozur, 2010). This $\delta^{13}\text{C}$ excursion reflects a perturbation to the carbon cycle, which remained volatile for the following ca. 500 kyr before $\delta^{13}\text{C}$ values returned to pre-extinction levels (Burgess et al., 2014). Hence, although the extinction event (i.e., elevation in extinction rates) occurred in a geologically relatively short time interval, the environmental crisis culminating in the mass extinction probably lasted much longer. A variety of environmental factors are hypothesized to have acted as extinction drivers in marine ecosystems, such as global warming (e.g., Gliwa et al., 2022; Joachimski et al., 2012; Schobben et al., 2014) and changes in temperature gradients (Sun et al., 2024), the expansion of oxygen minimum zones (e.g., Cao et al., 2009; Penn et al., 2018; Xiang et al., 2020; F. Zhang et al., 2020), and changes in nutrient cycling (Grasby et al., 2020; Sun, 2019, 2024). Several marine ecosystems are thought to have acted as refugia for marine life during the environmental crisis, such as deep-water thermal refugia (Foster et al., 2023; Godbold et al., 2017). Similarly, modern mid- to high-latitude ecosystems may provide opportunities for equatorial taxa to escape (sub-) tropical thermal stress (Poloczanska et al., 2016). Cool-water ecosystems can, therefore, exhibit characteristic community compositions during past crises. These are reflected in the geological record, for example, in the aftermath of the Permian–Triassic mass extinction, when the northwestern shelf of Pangea was characterized by a diverse ichnofauna (Beatty et al., 2008) and contained taxa that either migrated to the Boreal Ocean or whose geographic ranges contracted to this ecosystem (Foster et al., 2023; Nakrem & Mørk, 1991), thereby flattening latitudinal diversity gradients in the extinction aftermath (e.g., Beatty et al., 2008; Foster & Twitchett, 2014; Song et al., 2020; Twitchett & Barras, 2004).

While previous studies have focused particularly on biomineralizing micro- and macrofossil communities, this study exclusively investigates molecular fossils (lipid biomarkers), aiming to enhance our understanding of ecosystem responses, particularly among primary producers, to the Permian–Triassic environmental crisis. By assessing the appearance and prevalence of the molecular fossils C_{33} -*n*-alkylcyclohexane (C_{33} -*n*-ACH) and phytanyl toluene, we aim to document differences across paleolatitudes, and determine their environmental significance in different paleo-ocean basins. Our findings therefore offer new insights into the mechanisms underlying ecosystem resilience and recovery after severe environmental perturbations.

2. Materials and Methods

2.1. Geological Setting and Sample Acquisition

The molecular fossil inventories from different Permian–Triassic successions were investigated across paleolatitudes including sites around the Tethys, with a focus on Boreal sites recorded by the sedimentary succession of Svalbard (Figure 1). These deposits are of special interest, because Svalbard has been migrating north from the equator since the Devonian, currently occupying a high-latitude position ($74\text{--}81^\circ\text{N}$), whereas it was situated at a paleolatitude of approximately 50°N during the Permian–Triassic transition (Elvevold et al., 2007; Smyrak-Sikora et al., 2025). Due to its location on the Barents Shelf in the Boreal Ocean at the northern margin of Pangea, it was isolated from the warm, equatorial water of the Tethys Ocean, thus representing a relatively cold-water shallow-marine ecosystem (e.g., Beauchamp & Baud, 2002; Worsley, 2008) contrasting with Permian–Triassic sections recording tropical settings in the Paleo- and Neotethys (Figure 1a). In the west of the main island of Svalbard's archipelago, Spitsbergen, the strata are tilted, folded and thrust in the West Spitsbergen Fold and Thrust Belt (Dallmann et al., 1993), which represents a more proximal part of the shelf at that time (Mørk

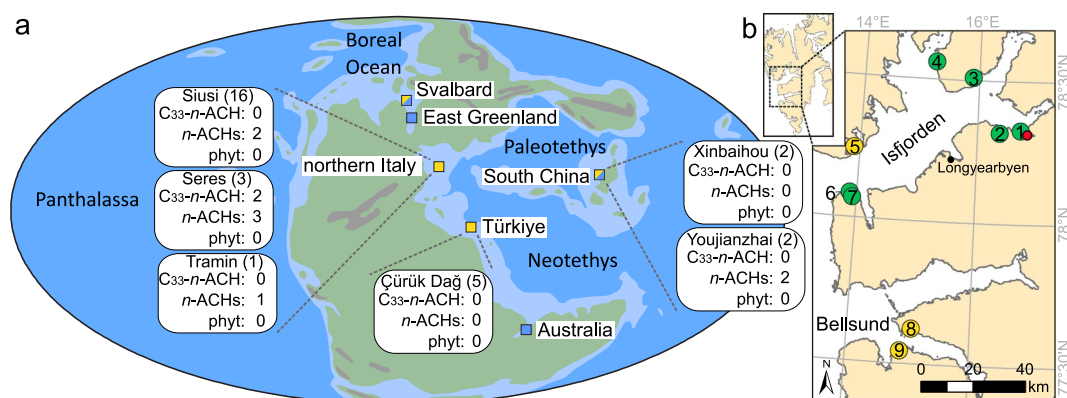


Figure 1. Sample locations. (a) Paleogeographic reconstruction of continental configuration at the Permian/Triassic boundary (map modified from Blakey, 2012). Yellow: sections studied here and summary of the findings (number of samples in parentheses after the section's name, and number of samples in which a compound was found is given); n-ACH—n-alkylcyclohexane; phyt—phytanyl toluene; blue: C₃₃-n-ACH findings from other studies (Svalbard: Grotheer et al., 2017; Nabbefeld et al., 2010; East Greenland and Australia: Grice et al., 2005; Hays et al., 2012; South China: Saito et al., 2022; Xie et al., 2017). (b) Sampling locations on Spitsbergen, Svalbard (Base map projection: WGS 84/Arctic Polar Stereographic); 1: Lusitaniadalen; 2: Ledalen; 3: Høgskulefjellet; 4: Kongressfjellet; 5: Selmaneset; 6: Festningen (Vardebukta); 7: Starostinaksia; 8: Bravaisberget; 9: Reinodden. Green: C₃₃-n-ACH and pseudohomologs detected; yellow: only pseudohomologs of C₃₃-n-ACH detected; red point next to (1): Deltadalen.

et al., 1982). In contrast, the Permian–Triassic sedimentary successions in the more distal part of the shelf in central Spitsbergen are horizontally bedded and have undergone only small to moderate thermal alteration (Olaussen et al., 2025).

A key section for studying the Permian–Triassic transition from multiple perspectives is Lusitaniadalen (Figure 1b). The Kapp Starostin Formation and the lowermost overlying Vikinghøgda Formation record the Changhsingian, whereas most of the Vikinghøgda Formation represents the Early Triassic (Mørk et al., 1999; Zuchuat et al., 2020). We place the Kapp Starostin/Vikinghøgda formation boundary according to the definition by Nagy et al. (2025) on top of the last glauconitic sandstone bed. Due to the scarcity of macro- and microfossils in uppermost Kapp Starostin Formation, the extinction horizon at Lusitaniadalen was previously determined based on the absence of complex bioturbation in strata overlying the last glauconitic sandstone bed (Foster et al., 2023; Nabbefeld et al., 2010; Uchman et al., 2016). The transition from the last glauconitic sandstone to the very fine-grained sandstones of the Vikinghøgda Formation also records an abrupt negative organic carbon isotope excursion at Lusitaniadalen (Nabbefeld et al., 2010), that has been observed globally to coincide with the extinction event (e.g., Cao et al., 2009; Sephton et al., 2005; Xie et al., 2007). The Permian/Triassic boundary, however, is not well-constrained in Lusitaniadalen, but in Deltadalen, the adjacent valley to the east (Figure 1b), it is placed approximately 2.40 m above the last glauconitic sandstone bed based on a tephra layer dated to 252.13 ± 0.62 Ma, deposited just above the local First Appearance Datum of the conodont *Hindeodus parvus* (Zuchuat et al., 2020).

Thirty-two samples were collected at Lusitaniadalen, Svalbard, from the succession of alternating bioturbated mudstones and silica-rich fine-grained sandstones (−41.51 to −30.58 m below the formation boundary) and from the uppermost glauconitic sandstone beds (−0.86 to −0.23 m) of the Kapp Starostin Formation prior to the extinction, as well as from the overlying laminated siltstones and very fine-grained sandstones from the post-extinction interval of the Vikinghøgda Formation (0.51–29.70 m), in which abundant concretionary horizons can be found. Samples were collected from unweathered outcrop exposures and wrapped in aluminum foil to avoid contamination. In particular, we focused on intervals of the Kapp Starostin Formation below the glauconitic sandstones, as the bioturbated mudstones deposited here represent conditions prior to the Permian–Triassic environmental crisis, but are lithologically comparable to the lowermost Vikinghøgda Formation. This enabled us to better account for a potential bias in the biomarker inventory introduced by the lithological change at the extinction horizon. In addition to Lusitaniadalen, eight other sections in western and central Spitsbergen were sampled to identify regional patterns in biomarker signals (Figure 1b). Lastly, we compared data from Spitsbergen with results from Tethyan sections, including data from northern Italy (western Paleotethys), the Great

Bank of Guizhou in South China (eastern Paleotethys), and the Taurus Mountains in Türkiye (western Neotethys) (Figure 1a). These tropical sections are predominantly carbonate successions with thick microbialites formed in the post-extinction interval in Türkiye and South China. A more detailed description of the geological setting in northern Italy (Broglio Loriga et al., 1990; Farabegoli et al., 2007; Groves et al., 2007; Horacek et al., 2010; Massari et al., 1994; Noé, 1987; Posenato, 2010; Prinoth & Posenato, 2023), South China (Foster et al., 2018, 2019; Lehrmann et al., 1998, 2001, 2003, 2005, 2007; Payne et al., 2006), and Türkiye (Altiner & Zaninetti, 1980; Angiolini et al., 2007; Baud et al., 2005, 2007; Crasquin-Soleau et al., 2002, 2004; Lys & Marcoux, 1978; Marcoux & Baud, 1988; Özgül, 1984, 1997; Richoz, 2006; Şahin & Altiner, 2019; Stampfli et al., 1991) can be found in Supporting Information S1.

2.2. Sample Preparation and Data Processing

We analyzed molecular fossils from both carbonate (23 samples) and siliciclastic (66 samples) settings. To extract molecular fossils from carbonates (the majority of the samples from the Tethys), the surfaces were cut off and samples were cleaned three times with acetone to remove any contaminants from the surfaces prior to being dissolved by slowly pouring 10% hydrochloric acid onto approximately 1 cm³-sized pieces following the procedure by Birgel et al. (2006). The siliciclastic samples were cleaned with acetone and then manually powdered in an agate mortar. The total lipid extract was retrieved by extracting the samples four times with dichloromethane: methanol (3:1, v:v) for 15 min in an ultrasonic bath, and separate them into maltenes (*n*-hexane soluble fraction) and asphaltenes (*n*-hexane insoluble fraction). The maltene fraction was further separated by polarity (fractions F1–F4) using solid-phase column chromatography with a NH₂-modified silica gel column (Birgel & Peckmann, 2008). The hydrocarbons (F1) were predominantly composed of *n*-alkanes. For a better identification and quantification of the two compounds of interest (C₃₃-*n*-ACH and phytanyl toluene), the *n*-alkanes were removed from the hydrocarbons with a molecular sieve (pore size of 5 Å), following the procedure described by Sabino et al. (2021). The compounds of interest were identified using coupled gas chromatography-mass spectrometry (GC-MS; Thermo Scientific Trace Ultra GC and Thermo Scientific DSQ II MS), searching for *m/z* = 83 and *m/z* = 106 for identification of C₃₃-*n*-ACH and phytanyl toluene, respectively (Figure 2), and comparison with published spectra (McIlldowie & Alexander, 2005). The aromatic hydrocarbon fraction (F2) was also scanned for phytanyl toluene, but it was not detected. For quantification, hydrocarbons were measured on a gas chromatograph coupled to a flame ionization detector (GC-FID; Thermo Scientific Trace 1310 GC). Quantification was achieved using Chromeleon 7 (version 7.2.10; Thermo Fisher Dionex) by calculating compound quantity in relation to 5α(H)-cholestane, the co-injection standard, and normalizing it to the sample's TOC content. For TOC determination (Figure S1 in Supporting Information S1), samples were de-carbonated with 100 µL 1M HCl and analyzed with a Euro EA 3000 (Euro Vector) elemental analyzer with a precision of ±0.05% and standard deviations <0.08. C₃₃-*n*-ACH and phytanyl toluene could only be quantified in samples from Lusitaniadalen. In other sections both targeted compounds either co-elute with other compounds or their content was too low to be quantified. Where only trace amounts were identified, only the presence or absence is reported. Correlations between the content of biomarkers were determined with the software R (version 4.3.2) (2023). The maturity of the samples was estimated with the methylphenanthrene index (MPI) after Cassani et al. (1988) by using the peak areas of 1-, 2-, 3- and 9-methylphenanthrene (MP) from *m/z* = 192, and phenanthrene (P) from *m/z* = 178 in the mass chromatogram of the F2 fraction, following $MPI = 1.89(2-MP + 3-MP)/[P + 1.26(1-MP + 9-MP)]$. Due to incomplete chromatographic separation, a proportion of phenanthrene and the methylphenanthenes often co-eluted in the F1 fraction. However, a recalculation of the MPI from the F1 fraction revealed that methylphenanthrene and phenanthrene co-eluted proportionally, and the general pattern per region (central Svalbard, western Svalbard, northern Italy, South China, Türkiye) is preserved (Figure S2 in Supporting Information S1).

3. Results and Discussion

3.1. Occurrence and Paleogeographic Distribution of C₃₃-*n*-Alkylcyclohexane and Phytanyl Toluene

The content of C₃₃-*n*-ACH in samples from Lusitaniadalen, Svalbard, shows a more than ten-fold increase from 8.1 to 43.3 µg/g TOC in the pre-extinction samples to values up to 513.5 µg/g TOC right above the extinction horizon (Figure 3a). Although the pre-extinction samples may have experienced stronger microbial degradation than post-extinction samples as indicated by the larger hump of the unresolved complex mixture (UCM; Figure 2), the signal of increased post-extinction abundance of C₃₃-*n*-ACH is also preserved in the ratio of C₃₃-*n*-ACH and *n*-C₃₄ (Figure S1 in Supporting Information S1). Since *n*-ACHs are more resistant to biodegradation

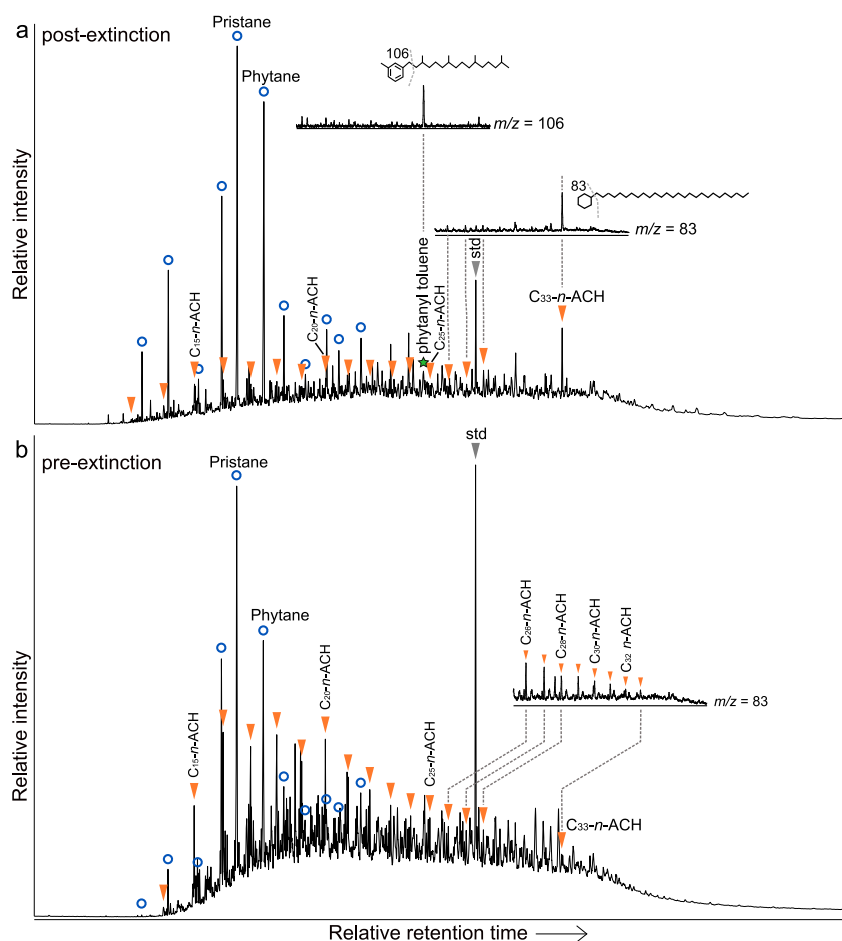


Figure 2. Total ion chromatograms of molecular sieve-treated hydrocarbon samples from Lusitaniadalen, Svalbard. (a) Post-extinction: 0.51 m above the extinction horizon; (b) pre-extinction: -36.87 m below the extinction horizon; orange triangles: C_{33} - n -alkylcyclohexane (C_{33} - n -ACH) and its pseudohomologs; green star: phytanyl toluene; blue circles: pseudohomologous series of head-to-tail linked C_{15-25} -isoprenoids; gray triangle: $5\alpha(H)$ -cholestane standard (std). The mass ranges of $m/z = 83$ to scan for C_{33} - n -ACH and its pseudohomologs and $m/z = 106$ to scan for phytanyl toluene are shown.

than n -alkanes (Koma et al., 2003; Perry & Gibson, 1977), the higher post-extinction ratios cannot be attributed to differential degradation, but instead point to a genuine increase in C_{33} - n -ACH. The content of C_{33} - n -ACH within the first 30 m above the extinction horizon remains elevated, which indicates persistently favorable environmental conditions for the producers of C_{33} - n -ACH or its unknown precursor molecule during the Permian–Triassic environmental crisis. Furthermore, n -ACHs with shorter ($<C_{33}$) alkyl-chains are detected, and show a similar sharp increase in abundance from 156.0 to 710.7 $\mu\text{g/g}$ TOC (sum of C_{14-28} - n -ACH) before the environmental crisis to up to 4,948 $\mu\text{g/g}$ TOC above the extinction horizon (Figure 3b). Similar to the early diagenetic shortening of the alkyl-chains of acyclic isoprenoids (Moldowan & Seifert, 1979) and hopanoids (Rohmer et al., 1980), microbial activity and early diagenetic fragmentation may result in a series of pseudohomolog n -ACHs (Luo et al., 2013; Saito et al., 2022), that derived from the same precursor. We find a strong correlation between C_{33} - n -ACH and shorter-chain C_{14-28} - n -ACH above the extinction horizon (correlation coefficient $r = 0.73$ – 0.97 , Figure S3 in Supporting Information S1). However, correlations are generally weaker between C_{33} - n -ACH and C_{18-28} - n -ACH (correlation coefficient $r = 0.60$ – 0.83), and insignificant for C_{14-17} - n -ACH below the extinction horizon (Figure S3 in Supporting Information S1). The strong correlation above the extinction horizon suggests that C_{14-28} - n -ACH are degradation products and pseudohomologs of C_{33} - n -ACH. The weaker correlations below the extinction horizon suggest that an additional source of n -ACHs potentially contributed to the n -ACH pool, such as degraded fatty acids (e.g., Rubinstein & Strausz, 1979; Shimoyama & Johns, 1972). Also, post-depositional carbon chain elongation may have contributed minor amounts of n -ACHs originating from shorter-chain fatty acids, although shortening of the carbon chain is the dominant reaction during diagenesis and thermal maturation,

and carbon chain elongation has never been observed for alkyl-chains longer than C_{28} (Shimoyama & Johns, 1972). However, even in pre-crisis samples where both C_{33} - n -ACH and shorter-chain n -ACHs are detected, a proportion of these shorter-chain n -ACHs are likely pseudohomologs of C_{33} - n -ACH. This implies that the absence of C_{33} - n -ACH does not necessarily indicate that the source organism(s) were absent, but may suggest enhanced degradation of the precursor molecule for instances in which shorter n -ACHs are present.

Phytanyl toluene is absent in the samples taken from horizons preceding the onset of the Permian–Triassic environmental crisis, except for the last sample below the extinction horizon at -0.23 m with 75.9 $\mu\text{g/g}$ TOC (Figure 3c). Above the extinction horizon at Lusitaniadalen, phytanyl toluene occurs with a maximum content of 425.4 $\mu\text{g/g}$ TOC in the lowest post-extinction sample at 0.51 m. Its content varies but, except for the sample at 13.73 m, remains elevated throughout the section between 12.2 and 216.0 $\mu\text{g/g}$ TOC, thereby resembling the Lower Triassic C_{33} - n -ACH content (correlation coefficient $r = 0.75$, Figure S3 in Supporting Information S1).

The occurrence of C_{33} - n -ACH and its pseudohomologs at Lusitaniadalen is not restricted to samples above the extinction horizon; it also occurs in uppermost Permian pre-crisis samples. Compared to previous studies on lipid biomarkers at Lusitaniadalen (Grotheer et al., 2017; Nabbefeld et al., 2010), this study provides a temporally extended record of the Lusitaniadalen profile. This extended record into the Lower Triassic possibly accounts for the differences in the absolute content of post-extinction C_{33} - n -ACH compared to that reported by Nabbefeld et al. (2010; Figure S4 in Supporting Information S1), who may have captured only the onset of the increase in the content of this biomarker. Additionally, the extended sampling range of our study allows for the establishment of a pre-extinction biomarker base line, and a decoupling of biotic from abiotic (e.g., facies-related) effects on the biomarker inventory, such as a lithological control on biomarker preservation (Peters, 1986; Peters et al., 2005), and the actual biotic change by comparing the C_{33} - n -ACH and phytanyl toluene content below and above the extinction horizon from similar lithologies and depositional environments. Previously reported content changes of C_{33} - n -ACH and phytanyl toluene across the extinction horizon at Lusitaniadalen were limited to the glauconitic sandstones for the pre-crisis signal (Grotheer et al., 2017; Nabbefeld et al., 2010), raising the possibility that the reported changes may have resulted from lithological rather than environmental change. Our new data clearly support that lithology was not the main control on the C_{33} - n -ACH and phytanyl toluene content. Instead, the source organism(s) of C_{33} - n -ACH showed resilience to the significant environmental perturbations across the

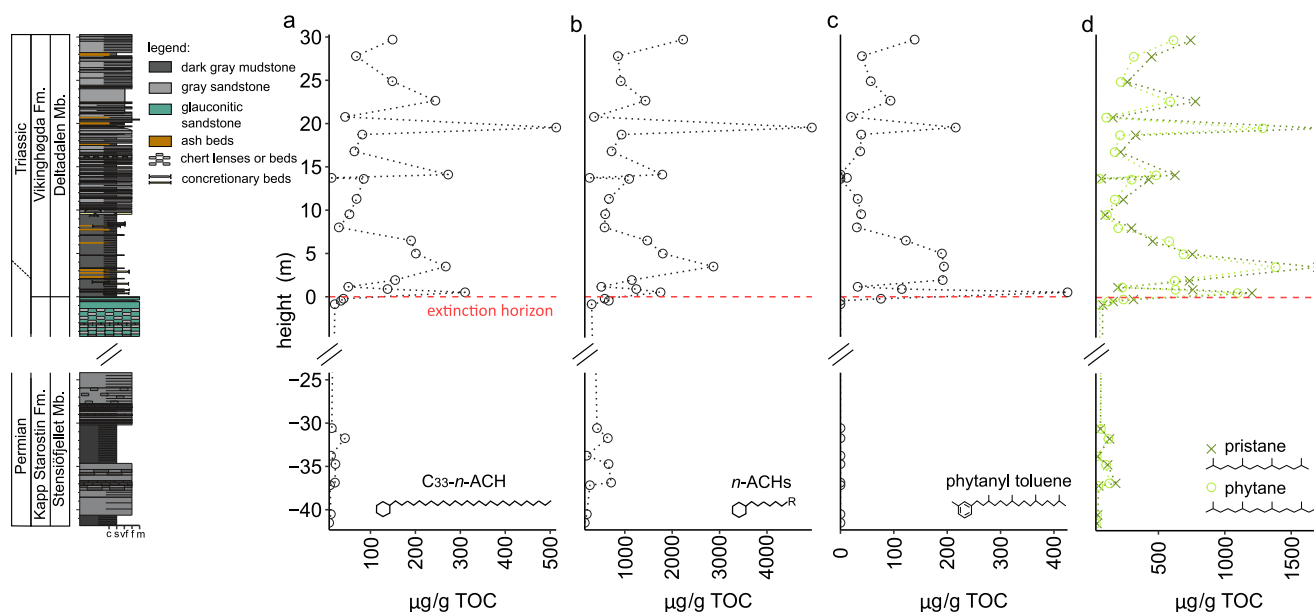


Figure 3. Biomarker profiles across the siliciclastic Permian–Triassic succession at Lusitaniadalen, Svalbard. (a) content of C_{33} - n -alkylcyclohexane (C_{33} - n -ACH); (b) sum of the content of shorter-chain pseudohomologs of C_{33} - n -ACH (C_{14-28} - n -ACH quantified; C_{29-32} - n -ACH are present in the samples but co-elute with other compounds, and cannot be quantified); (c) content of phytanyl toluene; (d) content of pristane (head-to-tail linked C_{19} -isoprenoid) and phytane (head-to-tail linked C_{20} -isoprenoid). The red dashed line marks the extinction horizon (Foster et al., 2023; Nabbefeld et al., 2010; Uchman et al., 2016). Note that the y-axis is broken (as indicated by parallel diagonal line segments) to focus on sampling intervals; similar pre- and post-extinction lithologies were targeted to control for potential lithofacies bias on the biomarker data. c—claystone; s—siltstone; vf—very fine-grained sandstone; f—fine-grained sandstone; m—medium-grained sandstone.

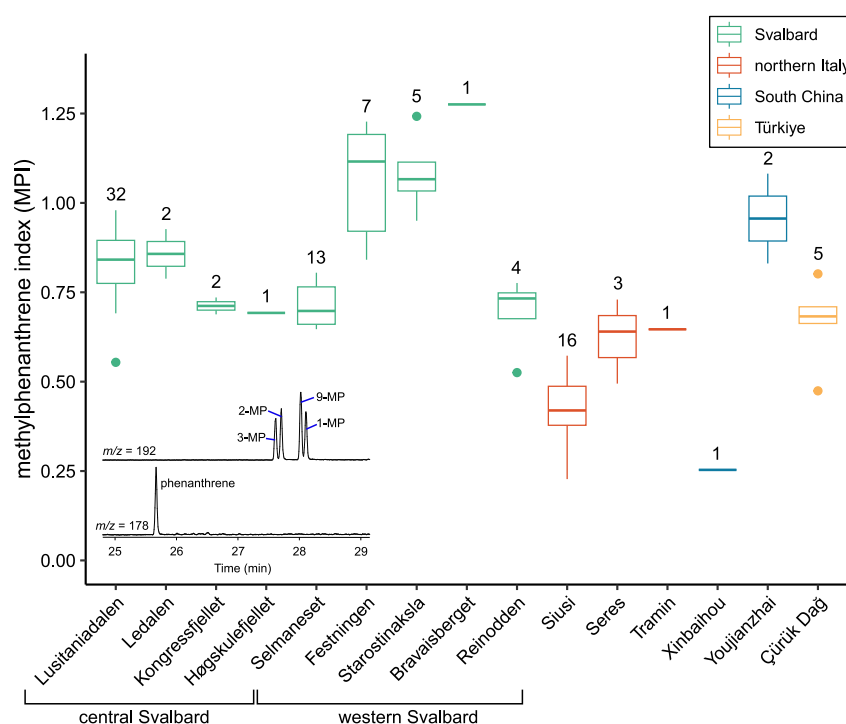


Figure 4. Methylphenanthrene index (MPI) for an estimation of thermal maturity across all investigated sections. The numbers on the boxes denote the total number of analyzed samples per section that contained all compounds required to calculate the MPI. $MPI = 1.89(2-MP + 3-MP)/[P + 1.26(1-MP + 9-MP)]$; MP = peak area of methylphenanthrene from $m/z = 192$ mass chromatogram; P = peak area of phenanthrene from $m/z = 178$ mass chromatogram (see inserted example of mass chromatograms).

Permian/Triassic boundary, and the source organisms of both C_{33} - n -ACH and phytanyl toluene thrived in the post-extinction ecosystem.

C_{33} - n -ACH and its pseudohomologs were not only detected in Lusitaniadalen, but also in other Permian–Triassic sites from central Spitsbergen, including Kongressfjellet and Høgskulefjellet, and in the Olenekian at Ledalen (Figure 1b). From western Spitsbergen, at Starostinaksela and Festningen (Figure 1b), C_{33} - n -ACH is only detected above the extinction horizon, but pseudohomologs are nonetheless abundant in underlying strata prior to the environmental crisis. Three other western Spitsbergen sections (Reinodden, Bravaisberget, Selmaneset) contain only trace amounts of pseudohomologs that are commonly co-eluted with other compounds in the molecular sieve-treated samples. The apparently enhanced preservation of C_{33} - n -ACH in central Spitsbergen compared to western Spitsbergen is likely caused by the lower maturity of the material in central Spitsbergen. In the western Spitsbergen sections, enhanced tectonic activity during the formation of the West Spitsbergen Fold and Thrust Belt in the Eocene (Braathen et al., 1999; Leever et al., 2011; Saalman & Thiedig, 2001) led to higher temperature and pressure, which in turn increased maturity and the degradation of sedimentary organic molecules (cf. Peters et al., 2005). As the methylphenanthrene index (MPI) exhibits a non-linear relationship with thermal maturity with a maximum MPI at a vitrinite reflectance (R_o) of 1.35% (Boreham et al., 1988; Radke & Welte, 1983), we infer that the lower MPI in samples from central Spitsbergen, compared to the higher MPI in western Spitsbergen sites reflects thermally less mature material (Figure 4). Except for an outlier at 13.73 m, the MPI at Lusitaniadalen is within a relatively narrow range (MPI = 0.69–0.98; Figure S1 in Supporting Information S1), indicating a similar thermal history across the section. However, as the shorter-chain n -ACHs are likely derived from the degradation of C_{33} - n -ACH (especially above the extinction horizon), the source organism(s) appear to have thrived across a range of depositional environments from the more distal area in central Spitsbergen to the more proximal area in western Spitsbergen (Mørk et al., 1982). Phytanyl toluene, however, was detected in samples from all sites in central Spitsbergen (Lusitaniadalen, Kongressfjellet, Høgskulefjellet, Ledalen; Figure 1b), but could not be detected in western Spitsbergen samples. This absence may

suggest greater susceptibility to degradation during maturation of the host lithologies, or the exclusion of the source organism(s) from the more proximal part of the basin.

The increased content of C_{33} - n -ACH above the extinction horizon agrees with previous findings, primarily from temperate settings like Western Australia and East Greenland (Grice et al., 2005; Hays et al., 2012) and earlier work from Svalbard (Grotheer et al., 2017; Nabbefeld et al., 2010). In contrast, phytanyl toluene was less frequently recognized across the Permian/Triassic boundary than C_{33} - n -ACH. It has thus far been detected in sections cropping out in Svalbard, Western Australia and East Greenland, whereas it is absent in sites recording lower-paleolatitude ecosystems like the Meishan section in South China (Cao et al., 2009; Grotheer et al., 2017) and other tropical settings in the Tethys Ocean investigated in this study. Both compounds, therefore, represent valuable geochemical markers of the Permian–Triassic environmental crisis and the Early Triassic in higher-latitude ecosystems. However, the distinctly high abundance of the C_{33} - n -ACH homolog seems to be restricted to Permian–Triassic successions, whereas phytanyl toluene is less temporally restricted and has also been recognized from deposits formed during other geological intervals (e.g., Jurassic: Plet et al., 2020; Cretaceous: Moura et al., 2019; Neogene: Sinninghe Damsté et al., 1993).

Existing reports of C_{33} - n -ACH in paleo-(sub)tropical ecosystems are restricted to South China (Shangsi section: Xie et al., 2017; Chaohu section: Saito et al., 2022). In this study, pseudohomologs of C_{33} - n -ACH in South China were only found in samples from Youjianzhai (Figure 1a). However, the thermal maturity of the organic matter at Youjianzhai is rather high (mean MPI = 0.96), and methylphenanthrenes were only present in one of the samples from Xinbaihou, the second section in South China (Figure 4). These samples may record a post-mature signal, also reflected in the very low MPI of 0.25 of the sample from Xinbaihou. While neither C_{33} - n -ACH nor n -ACHs were recorded across the Permian/Triassic boundary in the Taurus Mountains in Türkiye, we detected pseudohomologs of C_{33} - n -ACH and minor traces of C_{33} - n -ACH in pre-extinction samples from northern Italy, which is the first report of late Permian n -ACHs in the Tethys region outside South China. However, contents were too low for quantification and the pseudohomologs commonly co-elute with other compounds. C_{33} - n -ACH has only been quantified in the Tethys region at Shangsi, with an increase from 0 $\mu\text{g/g}$ TOC prior to the Permian–Triassic environmental crisis to up to 35.08 $\mu\text{g/g}$ TOC above the extinction event (Xie et al., 2017). This post-extinction content at Shangsi is within the same order of magnitude as the pre-crisis content at Lusitaniadalen. Although no pseudohomologs are reported from Shangsi accounting for degraded C_{33} - n -ACH, the low C_{33} - n -ACH content suggests less favorable conditions for the source organism(s) to proliferate at this equatorial site.

While the studied sections from the Boreal Ocean are exclusively siliciclastic successions, the Tethys sections analyzed for C_{33} - n -ACH and phytanyl toluene are carbonate-dominated deposits. Carbonate and clastic systems vary in their pore water chemistry, cementation or sedimentation rate and adsorption of organic matter to minerals, which might affect the preservation of organic compounds (e.g., Hemingway et al., 2019; Peters et al., 2005). Hence, a depositional control on the preservation of biomolecules cannot be excluded. To fully understand factors controlling the geographic variability in both C_{33} - n -ACH and phytanyl toluene content, their abundance needs to be constrained in tropical siliciclastic deposits such as the Bódvaszilas Sandstone Formation in Hungary (Hips, 1996) or the Yinkeng Formation in Meishan, South China (Yin et al., 2001).

3.2. Potential Sources of the Extinction Markers

Although the absolute content of C_{33} - n -ACH and its pseudohomologs is several-fold smaller in the tropical Tethys region compared to the Boreal Ocean and higher-latitude regions, an increase of this biomarker after the onset of the Permian–Triassic environmental crisis can be globally observed, but its source organism(s) remain enigmatic. Dong et al. (1993) suggested that n -ACHs were formed by cyclization of long-chain ($>C_{25}$) fatty acids during diagenesis. Long-chain fatty acids and n -alkanes are important components of leaf waxes of land plants (Buschhaus & Jetter, 2011), and would therefore imply terrestrial plant material as the source of long-chain n -ACHs. In such a case, the n -ACHs would originate from the same precursor molecules as n -alkanes with the same carbon number, which would be reflected in a similar carbon number distribution of n -ACHs and n -alkanes. However, unlike C_{33} - n -ACH, the n - C_{33} alkane does not record peak abundances compared to other n -alkanes above the extinction horizon (Figures S1 and S5 in Supporting Information S1). A terrestrial plant source is therefore unlikely.

Others have suggested a phytoplankton source of C_{33} - n -ACH, as its content shows a similar stratigraphic trend to that of the chlorophyll-derived biomarkers pristane and phytane, although the absolute contents differ (Nabbefeld

et al., 2010), as well as increased abundance of the spinose acritarch genera *Michrystidium* and *Veryhachium* at the onset of the C_{33} -*n*-ACH increase (Grice et al., 2005). In addition, C_{33} -*n*-ACH exhibits a similar $\delta^{13}C$ composition as phytane with -33.4‰ and -32.7‰ , respectively (Grice et al., 2005). At Lusitaniadalen, strong correlations between the content of pristane and C_{33} -*n*-ACH (correlation coefficient $r = 0.91$; Figure S3 in Supporting Information S1) and between phytane and C_{33} -*n*-ACH (correlation coefficient $r = 0.90$; Figure S3 in Supporting Information S1) are recorded. Both pristane and phytane contents increase several fold from 28.8 to 312.3 $\mu\text{g/g}$ TOC prior to the environmental crisis to 1,204 $\mu\text{g/g}$ TOC and 1,096 $\mu\text{g/g}$ TOC, respectively, immediately above the extinction horizon (Figure 3d). Notably, the highest pre-crisis content of pristane and phytane at Lusitaniadalen is recorded in the penultimate glauconitic sandstone bed at -0.23 m below the extinction horizon. This aligns with the lowermost detection of phytanyl toluene in the same bed, indicating a gradual increase in the presence of the source organism(s) of phytanyl toluene, rather than an abrupt onset. In addition to chlorophyll and algal tocopherols, pristane and phytane can also derive from the degradation of archaeal isoprenoid compounds (Rontani & Bonin, 2011; Rowland, 1990). Indeed, head-to-tail linked isoprenoid pseudohomologs from C_{21} up to C_{25} were detected in the samples (Figure 2), potentially representing degradation products of extended archaeol (Vandier et al., 2021). However, the abundance of pristane and phytane strongly exceeds the usual ratios of phytanyl to sesterterpanyl-chains in archaea producing extended archaeol in seawater (cf. Vandier et al., 2021) (Figure 2). This suggests that the majority of pristane and phytane in our samples can be interpreted as derived from phototrophic source organisms rather than from the degradation of membrane lipids of archaea, which might only partially contribute to the total pristane and phytane pools.

Additionally, the source organism(s) of C_{33} -*n*-ACH have been previously assumed to be associated with euxinic conditions, based on increased content of green sulfur bacteria-derived biomarkers, aryl isoprenoids, which indicate photic zone euxinia within two meters across the extinction horizon at Lusitaniadalen (Nabbefeld et al., 2010). Instead of anoxygenic green sulfur bacteria, we suggest oxygenic phytoplankton as the source of C_{33} -*n*-ACH, particularly in the post-extinction interval at Lusitaniadalen. This interpretation is supported by the diverse pelagic and benthic fauna, including radiolarians, sponges, bivalves, gastropods, brachiopods and ammonoids, preserved in the basal Vikinghøgda Formation (Foster et al., 2017, 2023). The presence of these aerobic, heterotrophic organisms excludes persistent anoxic or euxinic conditions in either the water column or bottom waters at Lusitaniadalen. Furthermore, redox conditions reconstructed from independent geochemical proxies indicate that the persistence of anoxic and euxinic conditions in Svalbard was comparatively short-lived; these signals disappear approximately 10 m above the extinction horizon (Grasby et al., 2015; Zuchuat et al., 2020). In contrast, both C_{33} -*n*-ACH and phytanyl toluene contents generally remain elevated throughout the investigated interval up to 30 m above the extinction horizon, indicating the source organism(s) were able to grow in oxygenated water. Nonetheless, waxing and waning of photic zone euxinia could have been an important control during the environmental crisis, and the aryl isoprenoids detected by Nabbefeld et al. (2010) as well as variability in extents and styles of burrowing (Rodríguez-Tovar et al., 2021) could indicate intermittent pulses of oxygen stress. Even during episodes of expanding euxinia, oxygenic phototrophs could have persisted and bloomed in an oxygenated surface water layer (e.g., Kasprak et al., 2015; Słowakiewicz et al., 2015). Enhanced remobilization of phosphorus from the seafloor during euxinic or anoxic periods during the Permian–Triassic environmental crisis in Svalbard (Schobben et al., 2020) could have provided otherwise limited nutrients that fertilized phytoplankton blooms. With specific (albeit of unknown affinity) photoautotrophic primary producers able to cope with and even thrive under Early Triassic environmental conditions, blooms of these organisms may have helped sustain planktic food webs and the comparatively less depauperate benthic communities recorded in the Svalbard fossil record (Foster et al., 2017, 2023) through sufficient organic carbon export to the seafloor. Yet, the small size of benthic species and large number of premature and larval shells also suggest that the environmental crisis persisted into the Griesbachian, preventing full ecological recovery.

A change in the composition of primary producers and an increased flux of marine algal material to the sediment, potentially indicating increased primary productivity, was also recognized across the extinction event in the Canadian Sverdrup basin (Algeo et al., 2012). In contrast, in South China, in sections recording a tropical setting, and in which we found C_{33} -*n*-ACH and phytanyl toluene to be less abundant or absent, an abrupt decline in primary productivity was observed right before the onset of the extinction (Y. Zhang et al., 2018). A follow-up meta-analysis has identified this decline as a potential factor explaining the severe loss of biodiversity during the Permian–Triassic environmental crisis (Foster et al., 2024). Hence, primary productivity was likely geographically variable across a range of paleolatitudinal settings (Algeo et al., 2013). Productivity and the community

composition of primary producers are influenced by diverse factors, such as nutrient availability, growth temperature, depth of the photic zone, or oxidant availability, as shown by studies of modern primary productivity (e.g., Arrigo, 2005; Domingues & Barbosa, 2023; Grimaud et al., 2017; Pajares & Ramos, 2019; Wong et al., 2023). An interplay of these factors likely also affected the phototrophic community across the Permian–Triassic transition (e.g., Algeo et al., 2012; Grasby et al., 2016, 2019; Schobben et al., 2020; Shen et al., 2015). Factors such as global warming likely played a role in shaping the phototrophic community composition and gross primary productivity during the Permian–Triassic environmental crisis (e.g., Gliwa et al., 2022; Joachimski et al., 2012), but regional factors must also be considered. For example, terrestrial erosion has been proposed to have increased during the Permian–Triassic environmental crisis in the Paleotethys (Sephton et al., 2005; Wu et al., 2023) and a large delta plain developed on the Early Triassic Barents Shelf, discharging massive amounts of terrestrial material to the shelf (Eide et al., 2018; Gilmullina et al., 2022). Although these terrestrial inputs could provide an important nutrient source and may fertilize phytoplankton (e.g., Putland et al., 2014), increased turbidity may have alternatively impeded increased productivity or led to changes in the primary producer community composition (e.g., Domingues & Barbosa, 2023). Hence, changes in past productivity remain challenging to reconstruct, due to a paucity of direct proxy records and dependence on the complex interplay of many factors. Thus, although a phytoplankton bloom is indicated in the Boreal Realm at Svalbard, we cannot directly infer a local change in primary productivity. However, the post-extinction increases of the chlorophyll-derived biomarkers pristane and phytane as well as relatively diverse higher trophic levels suggest that regional primary productivity was maintained, if not even promoted.

While the tropical Tethys Ocean may have experienced a decrease in primary productivity (Algeo et al., 2013; Y. Zhang et al., 2018), tropical carbonate successions are often characterized by the formation of microbialites (e.g., Foster et al., 2020; Kershaw et al., 2012). These have been attributed to a cyanobacterial origin, for example, in Türkiye, Iran (Heindel et al., 2018) and South China (Xie et al., 2010), which suggests benthic microbial mats contributed to primary production. Neither C_{33} - n -ACH nor phytanyl toluene have been previously reported from these Lower Triassic microbialites in Türkiye, Iran, and South China, but shorter-chain n -ACHs have been detected at Cili, South China, by Luo et al. (2013), who found distinctly elevated relative abundances of C_{21} - n -ACH compared to C_{20} - n -ACH. Furthermore, an increase of characteristic cyanobacterial biomarkers such as n - C_{17} compared to other n -alkanes, or mono-, di- and trimethylated alkanes (e.g., Coates et al., 2014; Gelpi et al., 1970; Heindel et al., 2018; Plet et al., 2020) was not found in samples with increased contents of C_{33} - n -ACH or phytanyl toluene (this study). Consequently, a cyanobacterial source of C_{33} - n -ACH and phytanyl toluene is unlikely.

The source organism(s) of phytanyl toluene remains enigmatic. Phytanyl benzenes were previously hypothesized to originate from diagenetically altered carotenoids (Gallegos, 1981; Grotheer et al., 2017; Summons & Powell, 1987) or isoprenoid quinones (Sinninghe Damsté et al., 1988). In the case of phytanyl toluene, this would suggest a defunctionalized and demethylated benzoquinone (an isoprenoid quinone with a single benzene ring) as a potential precursor molecule. However, quinones are ubiquitous across the domains of life, especially in archaea and bacteria (Collins & Jones, 1981), but also in eukaryotes (Nowicka & Kruk, 2010). The strong correlation of phytanyl toluene and C_{33} - n -ACH observed at Lusitaniadalen supports that both compounds derived from organisms with similar ecological requirements. However, phytanyl toluene is absent throughout most of the investigated interval prior to the environmental crisis whereas C_{33} - n -ACH was detected in pre-extinction strata at selected sites, which suggests that although the source organisms of phytanyl toluene and C_{33} - n -ACH were likely different, they may have occupied a similar ecological niche during the Permian–Triassic environmental crisis. Both compounds were most likely derived from phototrophic algae.

4. Conclusions

The biomarker data for C_{33} - n -ACH and phytanyl toluene presented here extend their record in Svalbard temporally and spatially, enabling the decoupling of lithological change at the extinction horizon from changes in the biomarker inventory. The increased content of both biomarkers above the extinction horizon is interpreted as a response to the Permian–Triassic environmental crisis rather than being driven by changes in the depositional environment. However, their preservation is likely substantially influenced by enhanced degradation at thermally more altered sites, underscoring the importance for careful evaluation when biomarkers are absent. Our findings challenge the previous hypothesis that the source organism(s) of C_{33} - n -ACH are associated with photic zone euxinia as we found no evidence of extended euxinic conditions during the whole interval of increased C_{33} - n -

ACH content. Instead, C_{33} - n -ACH was likely produced during blooms of specific planktonic oxygenic phototrophs in the Boreal Ocean and at higher paleolatitudes in the Early Triassic, potentially forming the base of a resilient ecological community, reflected in the diverse Early Triassic fossil assemblage in Svalbard. Phytanyl toluene, exclusively observed in higher paleolatitude siliciclastic successions and absent in tropical carbonate deposits, appears to have a different source than C_{33} - n -ACH. The spatial disparity in their paleogeographic distribution may reflect differences in environmental requirements, depositional settings, or the distribution of their source organism(s).

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The biomarker data, metadata and R code used in the study are available at Zenodo (Buchwald et al., 2025: <https://www.doi.org/10.5281/zenodo.16032548>).

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