





Preservation of plant-wax biomarkers in deserts: implications for Quaternary environment and human evolutionary studies

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ABSTRACT: Analysis of plant-wax biomarkers from sedimentary sequences can enable past environmental and hydrological reconstruction and provide insights into past hominin adaptations. However, biomarker preservation in desert contexts has been considered unlikely given the sparse nature of the vegetation within the landscape. Here we evaluate the preservation of *n*-alkanes and fatty acids collected from four depositional sequences associated with archaeological contexts in the Nefud Desert, Saudi Arabia, and the Thar Desert, India. Pleistocene and Holocene samples were selected to understand the effects of age on preservation. The results of molecular distribution patterns and indices, particularly the high carbon preference index and average chain length, show the preservation of plant-wax biomarkers in both the Holocene and Pleistocene desert sequences, while $\delta^{13}\text{C}$ values and organic content provide insights into the vegetation contributing to the plant-wax organic pool. This study provides a baseline for understanding human–environment interactions and for reconstructing changes in arid land habitats of relevance to hominins during the Quaternary. © 2024 The Authors. *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: India; *n*-alkanes; *n*-alkanoic acids; palaeoenvironments; Saudi Arabia

Introduction

Plant-wax biomarkers and their stable carbon ($\delta^{13}\text{C}$) and hydrogen ($\delta^2\text{H}$) isotope ratios are now frequently analysed proxies for studying past climates, vegetation and environments on global, regional and local scales. In particular, the use of *n*-alkanes (*n*-alk) and *n*-alkanoic acids (fatty acids; FA) preserved in soil/sediments and palaeosols from archaeological sites or regionally relevant lake and marine cores has increased considerably, providing both 'off-' and 'on-site' palaeoenvironmental records of past climate and landscape change of relevance to hominin populations over the last 5 Ma (deMenocal, 2011; Jha et al., 2020; 2021; Lupien et al., 2021; Patalano et al., 2021; Villaseñor et al., 2023).

Much plant-wax research undertaken to study past terrestrial ecosystems has focused on either palaeosols or lake sediments due to the potentially higher preservation of organic matter (OM; Eglinton and Hamilton, 1967; Chikaraishi and Naraoka, 2006; Castañeda and Schouten, 2011; Jha et al., 2020; Lupien et al., 2021). However, plant-wax preservation in desert sediments has not been widely investigated due to large sediment grain size, high temperature and perceptions of limited wax production on these vegetation-sparse landscapes. Nevertheless, these factors are yet to be explored systematically in terms of their biomarker preservation potential. For the first time, we attempted to analyse Pleistocene and Holocene sediments from desert contexts to assess the preservation of plant-wax biomarkers.

Here, we use widely accepted molecular indices such as distribution patterns, carbon preference index (CPI), average chain length (ACL), *n*-alk and FA concentration to evaluate the preservation of *n*-alk and FA in sediments collected from archaeological sequences in the Nefud Desert, Saudi Arabia,

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and the Thar Desert, India (Figure 1). These regions were selected because they are geographically located along much-discussed hominin dispersal routes (Petraglia et al., 2010, 2012; Roberts and Stewart, 2018; Blinkhorn et al., 2020; Groucutt et al., 2021). Moreover, both regions hold essential information in relation to past hominin adaptive capacities (Petraglia et al., 2010, 2012; Roberts and Stewart, 2018). We also measured the bulk $\delta^{13}\text{C}$ and total organic content of the sediment samples to provide a holistic understanding of plant-wax preservation in these deserts and their potential for palaeoenvironmental reconstruction. We specifically sought to evaluate the preservation of long-chain *n*-alk ($\geq\text{C}_{25}$) and FA ($\geq\text{C}_{22}$) compounds because they are primarily derived from terrestrial plant-waxes in sediment archives (Eglinton and Hamilton, 1967; Marzi et al., 1993; Jha et al., 2020). We make qualitative inferences based on several molecular indices (Struck et al., 2020; Knief et al., 2020). However, we do not attempt to

provide any quantified estimate of past environment and vegetation change in this paper.

Background

Morphological and physiological adaptations, such as increasing specific leaf areas, lower water conductance and increasing epicuticular wax content (Falcão et al., 2015), enable plants to adapt to water-limited contexts. Leaf epicuticular wax, rich in organic compounds such as long-chain aliphatic hydrocarbons, plays a crucial role in regulating stomata for gas exchange, preventing water loss and protecting leaves (Kerstiens, 1996). Plant-waxes are a mixture of straight long-chain hydrocarbons and their derivatives. Additionally, some branched and cyclic hydrocarbons with secondary metabolites form a minority group in the composition of plant-wax. However, the chemical

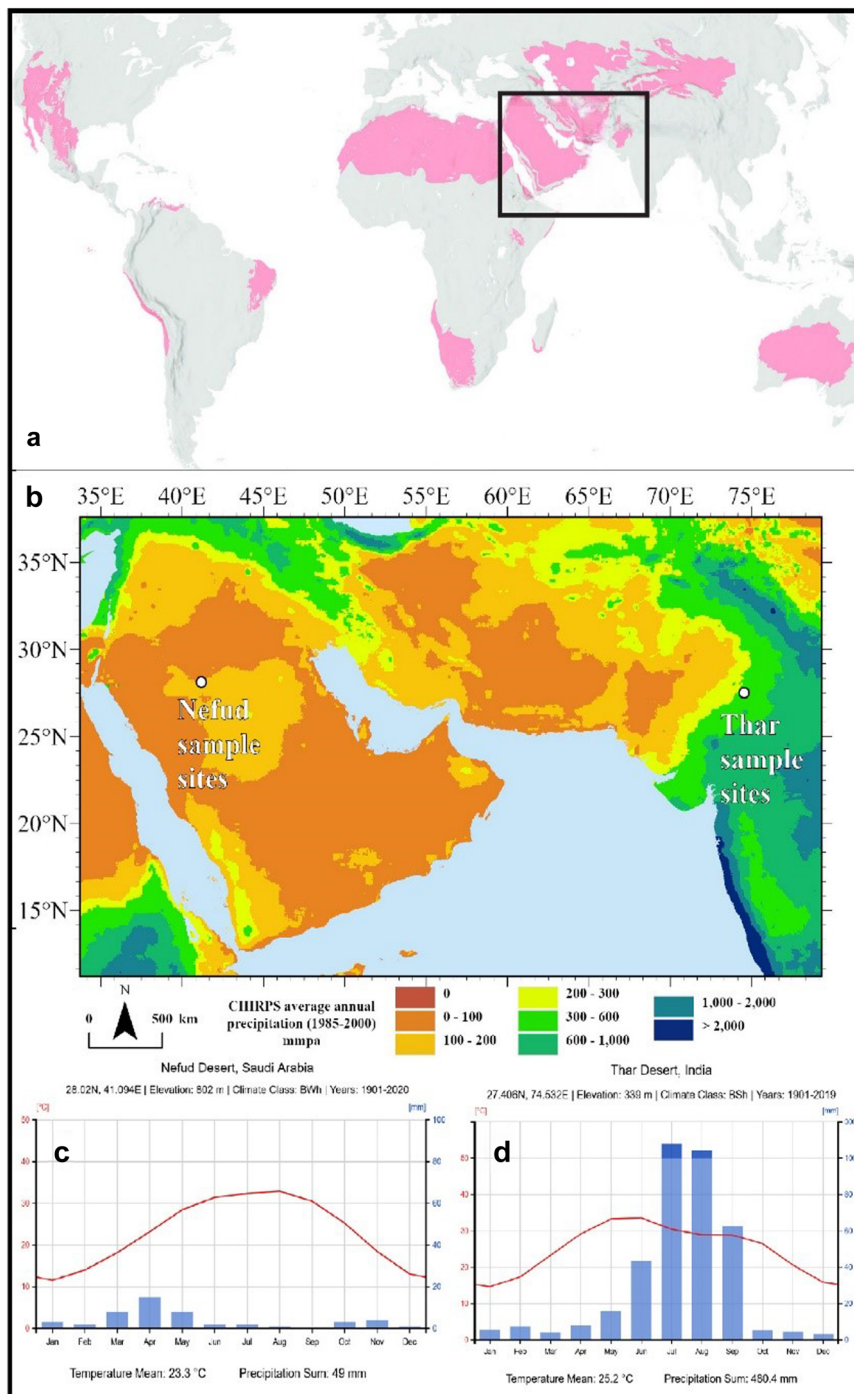


Figure 1. (a) Location of the Nefud and Thar deserts. (b) Modern climatic context of the region. Climatograms of the Nefud (c) and Thar (d) deserts show temperature and precipitation variability (1901–2020). The graph was prepared using <https://climatecharts.net/>. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

composition and distribution of a given plant-wax depend on several factors, including species, environment, growing season temperature and aridity (Dodd and Poveda, 2003; Bush and McInerney, 2013; Alfarhan et al., 2020; Jha et al., 2024). For example, Bush and McInerney (2015) observed that leaves growing in arid regions show comparatively higher ACL values than vegetation from temperate zones.

A recent study of biomarker preservation and OM sourcing in modern sediments along an elevational transect through different temperature and humidity regimes in the Atacama Desert, Chile, demonstrated the potential of plant-wax compounds in storing environmental information in hyper-arid regions (Knief et al., 2020). Additionally, studies from modern topsoil of the hyper-arid Atacama and Gobi Desert in Mongolia provide vital insights into plant-wax preservation in arid environments (Struck et al., 2020; Knief et al., 2020). Studies from the Atacama Desert (Wilhelm et al., 2017) and Black Rock Desert, USA (Lerch et al., 2018), have also explored biomarker preservation in clay-rich older sediments. However, the prospect of plant-wax preservation over deeper timescales in arid regions has not been widely explored.

Plant-waxes deposited in soils represent a time-averaged signal of biosynthetic sources and local climate parameters (Eglinton and Hamilton, 1967; Wu et al., 2019; Jha et al., 2020). Soil OM receives input from C₁₀ to C₄₀ carbon-chains belonging to *n*-alk and FA produced by bacteria, phytoplankton and terrestrial plants (Cranwell et al., 1987). A dominance of C₂₇ to C₃₅ *n*-alk with odd-over-even preference (OEP) and C₂₄ to C₃₄ FA with even-over-odd preference (EOP) is often considered to be a characteristic signature of terrestrial plants (Eglinton and Hamilton, 1967; Supporting Information Fig. S1). Meanwhile, short- and mid-chain compounds (\leq C₂₅) are interpreted mainly as the product of algae, photosynthetic bacteria and aquatic plants (Cranwell et al., 1987). However, plant-waxes incorporated into sediments can be impacted by diagenesis, which can affect the characteristic distributions (OEP and EOP) of higher plants, limiting the use of plant-waxes as a palaeo-proxy (Chikaraishi and Naraoka, 2006). Therefore, it is essential to verify the preservation of plant-waxes in different settings before using them for palaeoenvironmental reconstructions.

Study regions and sample collection

Nefud Desert

The Nefud Desert is situated in northern Arabia, at a critical nexus in the Saharo-Arabian arid belt (Figure 1). Previous research from the region has indicated frequent climatic oscillations that intermittently shaped past ecological and hydrological habitats across the region (Breeze et al., 2017; Roberts Stewart, Alagaili, et al., 2018; Groucutt et al., 2021). The Pleistocene and Holocene sediments of Saudi Arabia have preserved abundant archaeological sites (Petraglia et al., 2012, 2019; Groucutt et al., 2015, 2021; Breeze et al., 2017; Jennings et al., 2016; Scerri et al., 2018). Nevertheless, the exact nature of the hominin-inhabited landscapes at different points in time remains unclear (Roberts, Stewart, Alagaili, et al., 2018).

Samples were collected from the dated palaeo-lake sequences of JB-1 (a quarry site; Fig. S2) at Jebel Qatar (<37.6 ka; Petraglia et al., 2012; Parton et al., 2018) and at a sedimentary sequence (PE-1; Fig. S3) which has similar stratigraphy and comparable chronology to Jebel Qatar 200 (JQ-200; <11.7 ka; Crassard et al., 2013). Samples were collected from different depths covering different sedimentary and archaeological phases (see Text S1). The age of the samples was determined according to

previously published age–depth models (Crassard et al., 2013; Parton et al., 2018).

Thar Desert

The Thar Desert in western South Asia (Figure 1b) shares a boundary with the Oriental zone and Saharo-Arabian Belt (Holt et al., 2013; Blinkhorn, 2021). This region has evidence for some of the earliest modern human populations expanding and moving eastwards across Late Pleistocene Asia (Blinkhorn et al., 2013, 2019). The region is located at the threshold of the Indian summer monsoon system of South Asia. Due to its location, depending on the prevailing conditions in the past, the Thar Desert would have provided a terrestrial biogeographical gateway to the remainder of South and Southeast Asia (Blinkhorn et al., 2020).

Samples were collected from a pedogenically stabilized dune (16R dune) locality (Fig. S4), which was previously dated to between ~187 and 6 ka (Achyuthan et al., 2007; Singhvi et al., 2010), and the Jankipura site (Fig. S5), a Mid- to Late Holocene lake sequence preserved near to a pond (Table S1).

Ten samples were selected and analysed from the Nefud (*n*=5) and Thar (*n*=5) deserts representing four sites and covering the Mid-Pleistocene to Late Holocene (Table S1). Detailed lithological descriptions, chronology, archaeological contexts and an overview of the modern climate and vegetation types of the study regions are provided in Text S1.

Methodology

Extraction and chromatography of plant-wax

Total lipid extraction (TLE) and separation was done following the method described by Patalano et al. (2020) and Jha et al. (2020). Briefly, dry, homogenized sediments (~55 g) were extracted with a Büchi (E-916) Speed Extractor using 9:1 (v/v) dichloromethane/methanol. TLEs were separated into three fractions using silica-gel chromatography by elution with hexane (F1), dichloromethane (F2) and methanol (F3) solvents. The F1 fraction contained *n*-alks and F3 fractions were methylated using a 2% solution of HCl in methanol kept at 70°C for 20–24 h. Further purification of FA methyl esters (FAMES) was performed with silica-gel chromatography with dichloromethane and hexane as eluents.

The *n*-alk and FA samples were analysed using a gas chromatography (Agilent 7890B) system coupled to an Agilent 5977A Series Mass Selective Detector at the Max Planck Institute of Geoanthropology (MPI-GEA), Germany. Detailed methodology and instrument conditions are provided in Text S1 (section 3).

Characterization of plant-wax compounds

The source characterization of *n*-alk and FA was done using different indices such as CPI (Marzi et al., 1993) and ACL (Eglinton and Hamilton, 1967), which have been calculated according to the equations:

$$\text{ACL}(n\text{-alk or FA}) = \frac{\sum C_n \times n}{\sum C_n} \quad (1)$$

where $n \geq 24$ to 35 and C_n is the concentration of *n*-alk or FA with *n* carbons; and

$$\text{CPI}(n\text{-alk}) = 0.5 \times \left[\frac{\sum \text{even}}{\sum \text{odd}} + \frac{\sum \text{odd}}{\sum \text{even}} \right] \quad (2)$$

$$\text{CPI(FA)} = 0.5 \times \left[\frac{\sum \text{odd}}{\sum \text{even}} + \frac{\sum \text{even}}{\sum \text{odd}} \right] \quad (3)$$

where the concentration of carbon chains ranges from 25 to 35 for *n*-alk and 24 to 34 for FA.

Total organic carbon and $\delta^{13}C_{bulk}$ of sediment

Dried and powdered sediment (~1 g) was reacted with 2 M HCl to decarbonate the samples and neutralized using Milli-Q water. The HCl-treated samples were introduced into a Thermo Scientific Flash 2000 Elemental Analyser coupled to a Thermo Delta V Advantage Isotope Ratio Mass Spectrometer at the MPI-GEA. Details of the method are provided in Text S1 (section 3.3).

Results

Nefud Desert

The molecular distribution, shown by OEP in *n*-alk and EOP in FAs, is well preserved in the sediment samples (Figure 2a). The concentration of higher chain *n*-alk (C_{25} to C_{35}) and FA (C_{24} to C_{34}) varied from 162.2 to 2230.8 $ng\ g^{-1}$ and 268.1 to 1243.2 $ng\ g^{-1}$ of dry sediment, respectively (Figure 2d). The C_{27} *n*-alk is the maximum carbon number (CN_{max}) for all samples. The C_{26} FA is the CN_{max} for the all three samples of site PE-1 whereas C_{28} and C_{24} FA are dominant in JB-1-1 and JB-1-2 samples, respectively (Table S1). The CPI and ACL

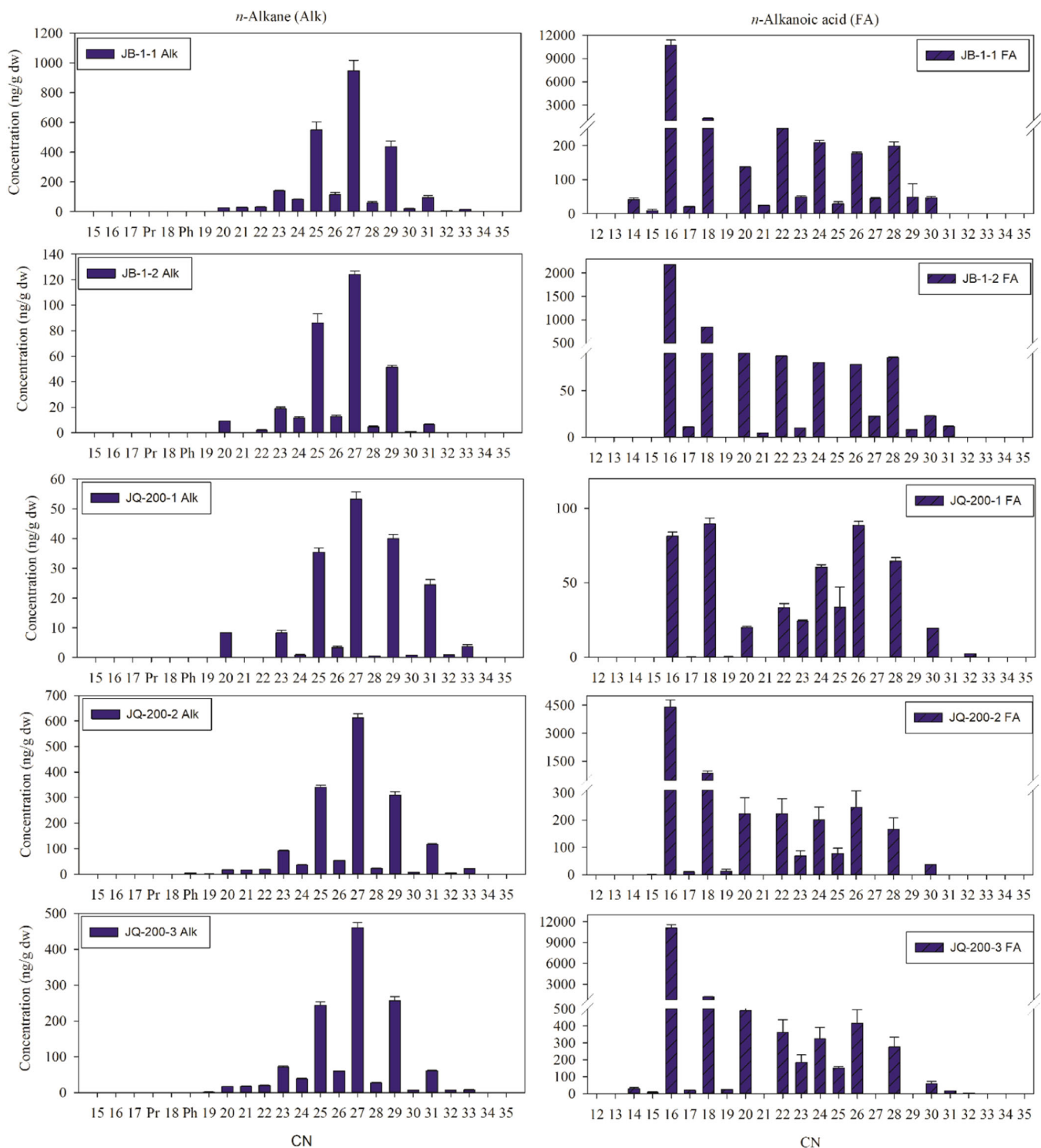


Figure 2. Distribution of plant-wax biomarker compounds (*n*-alk and FA) in sediments collected from Nefud Desert, Saudi Arabia. See Table S1 for sample description. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

values ranged from 9.1 to 25.2 and 26.8 to 27.8 for *n*-alk and 4.7 to 6.4 and 26.1 to 26.4 for FA, respectively (Figure 2; Table S1). The $\delta^{13}\text{C}_{\text{bulk}}$ and TOC of the sediment samples varied from -25.0 to -17.9% and 1.1 to 10.2%, respectively (Table S1).

Thar Desert

The OEP in *n*-alk and EOP in FA are well preserved in the sediments (Figure 3). The concentration of long-chain (C_{25} – C_{35})

n-alk and FA (C_{24} – C_{34}) varied from 43.5 to 279.3 ng g^{-1} and 70.8 to 6341.7 ng g^{-1} of dry sediment, respectively (Figure 3). C_{31} is the dominant *n*-alk in all samples except in a younger sample (J18) where C_{29} is dominant. The CN_{max} in FA varies between C_{24} and C_{30} in each sample (Table S1). The CPI and ACL values ranged from 2.9 to 3.7 and 29.9 to 31.4 for *n*-alk and from 4.4 to 7.4 and 27.4 to 29.4 for FA, respectively (Table S1; Figs. 3 and S2). Total organic carbon and $\delta^{13}\text{C}_{\text{bulk}}$ values of the samples varied from 0.01 to 0.4% and -25.7 to -16.4% , respectively (Figs. 3 and S2; Table S1).

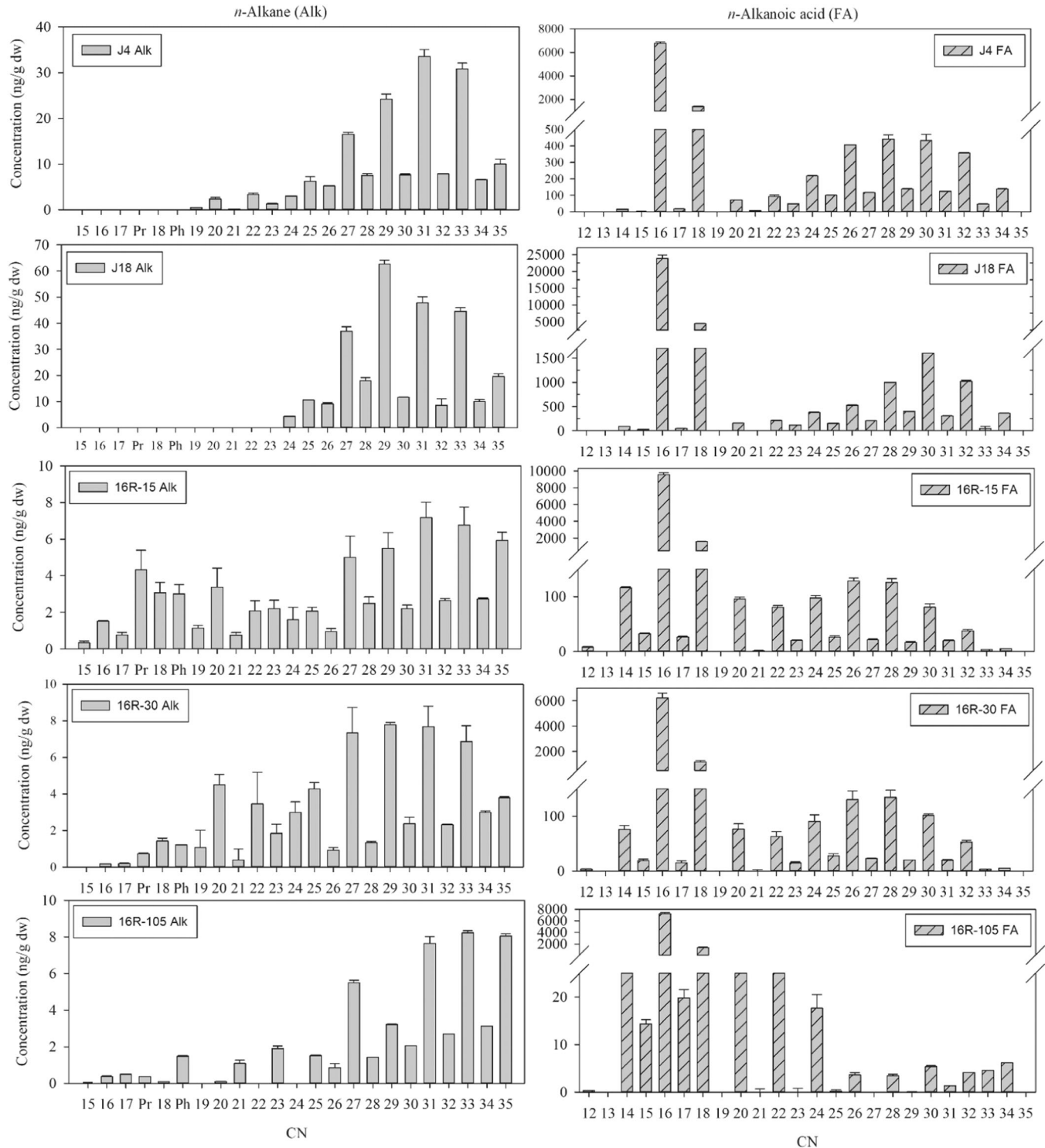


Figure 3. Distribution of plant-wax biomarker compounds (*n*-alk and FA) in sediments collected from Thar Desert, India. See Table S1 for sample description.

Discussion

We examined the preservation of plant-waxes in Holocene and Pleistocene sediments collected from archaeological sites in the Nefud and Thar Deserts of Saudi Arabia and India, respectively (Figure 1). The distribution pattern of *n*-alk and FA (Hoefs et al., 2002) of older sediment samples (Figs. 2, 3 and S2) are comparable to the distribution pattern of modern plants from the Banni and Gangetic Plains, India (Jha et al., 2020; Sarangi et al., 2022; Roy and Sanyal, 2022), as well as the topsoil distribution of *n*-alk seen in the Atacama and Mongolia regions (Knief et al., 2020; Struck et al., 2020). The comparison suggests that these biomarkers are potentially well preserved in the Nefud and Thar Desert sediments.

CPI is a proxy for degradation and diagenesis in sedimentary environments (Cranwell, 1981; Marzi et al., 1993). Generally, a CPI close to ~1 in sediment samples is considered to indicate a degraded sample or a sample dominated by petrogenic sources (Cranwell, 1981; Marzi et al., 1993; Polissar et al., 2021). Observational data have indicated that the degradation of higher odd-chain *n*-alk ($\geq C_{25}$) and even-chain FA ($\geq C_{22}$) compounds, or the microbial production of shorter/mid-chain compounds, can lead to decreased CPI values in sediment (Cranwell, 1981; Marzi et al., 1993; Grimalt et al., 1988; Brittingham et al., 2017). Recent research suggests that CPI values may also be lowered due to leaf burning during fire events (Sarangi et al., 2022). Particularly in desert environments, arid conditions with limited moisture prevents

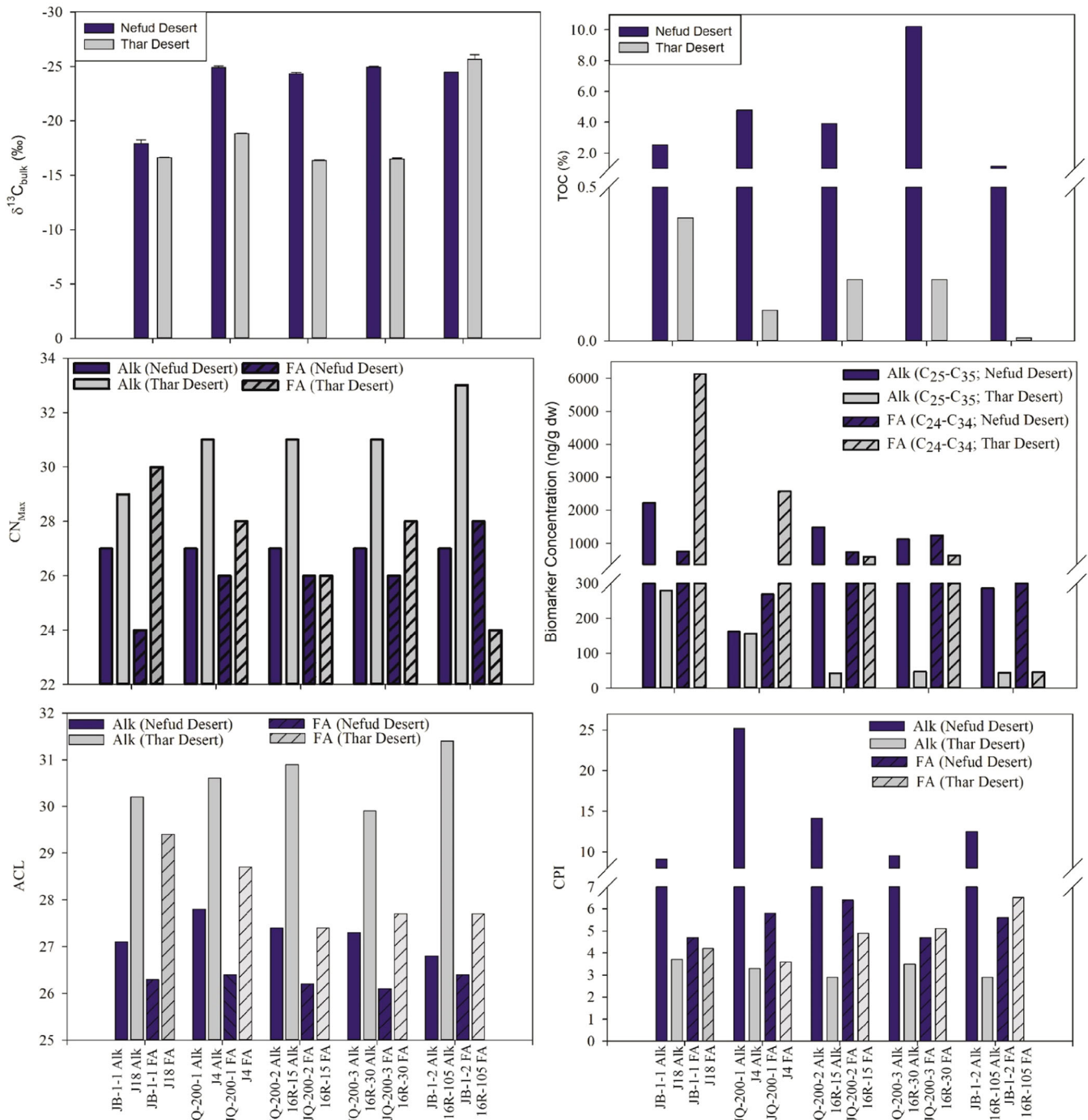


Figure 4. Bulk stable carbon isotope, total organic content, carbon chain (CN_{max}) length (*n*-alk and FA), biomarker concentration (*n*-alk and FA), ACL and CPI values of 10 samples from the Nefud (*n*=5) and Thar (*n*=5) deserts. These suggest preservation potential of plant-waxes from sediments in contemporary arid regions for paleoenvironmental reconstruction. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

extensive microbial degradation of chemical compounds. Indeed, higher CPI (>1), along with well-defined OEP and EOP in sediments, indicate that *n*-alk and FA are well-preserved biomarker signals (Cranwell, 1981; Marzi et al., 1993). The average CPI values obtained in our study are 14.1 (*n*-alk) and 5.4 (FA) for the Nefud desert and 3.3 (*n*-alk) and 4.9 (FA) for the Thar Desert (Table S1), which indicate a clear predominance of well-preserved plant-wax in the sediment, with minimal influence from microbial degradation or fire-related processes in the sampled locales of the Nefud and Thar Desert (Figure 4; Table S1; Marzi et al., 1993; Polissar et al., 2021; Sarangi et al., 2022; Roy and Sanyal, 2022).

Qualitative assessment of the compounds suggests that the FA concentrations (ng g^{-1}) are much higher in the Thar Desert and lower in Nefud Desert samples than *n*-alk (Table S1; Figure 4). Generally, concentrations of FA and *n*-alk vary considerably both at the species level and among different plant types (C_3 vs. C_4) (Diefendorf et al., 2011; Freimuth et al., 2019; Sarangi et al., 2022; Roy and Sanyal, 2022; Jha et al., 2024). Furthermore, abundant carbon chains (CN_{max}) of *n*-alkyl compounds, particularly from *n*-alk, has been used to distinguish the contribution of trees and shrubs (C_{27} , C_{29} and C_{31}) and grasses (C_{33} and C_{35}) in different contexts in Africa, India, Australia, North America, Europe and Mongolia (Bush and McInerney, 2013; Garcin et al., 2014; Ankit et al., 2017; Pillai et al., 2017; Aichner et al., 2018; Bliedtner et al., 2018; Struck et al., 2020; Knief et al., 2020). However, recent studies on the plant-wax composition of modern C_3 trees and shrubs, and C_4 grasses from India suggest that conventional theories regarding *n*-alk and FA production in plants might not be accurate for every region and need to be verified using region-specific modern analogues (Roy and Sanyal, 2022; Sarangi et al., 2022; Jha et al., 2024).

Most trees and shrubs follow C_3 pathways, and grasses follow C_4 pathways, except in the temperate zone where C_3 grasses can also be seen (Griffith et al., 2015). The proportion of C_4 grasses in an environment is recorded in the higher abundance of C_{33} and C_{35} in sedimentary deposits (Garcin et al., 2014), but temperature and aridity can also control CN_{max} selection in plant-wax distributions (Liu et al., 2018). Broadly, long-chain (C_{33} and C_{35}) *n*-alk are considered to be tracers of grassy biomes on the landscape, whereas C_{31} is found equally across plant types, and C_{27} and C_{29} are favoured in trees and shrubs (Schwark et al., 2002; Meyers, 2003; Jansen et al., 2006; Garcin et al., 2014; Schäfer et al., 2016; Magill et al., 2019; Polissar et al., 2021; Jha et al., 2024). Our data indicate the dominance of C_{27} and C_{31} for *n*-alk and C_{26} and C_{28} for FA in the Nefud and Thar Desert samples, which reflects a probable contribution from mixed C_3 – C_4 and C_3 /CAM (Crassulacean acid metabolism) flexible plants (Table S1). Temporal variation in the biomarker indices (ACL, CPI and CN_{max}), TOC and $\delta^{13}\text{C}_{\text{bulk}}$ values suggest the two sampled records may show changes in palaeoenvironmental conditions during the Pleistocene and Holocene in these regions (Table S1). Nevertheless, given issues of diagenesis (Polissar et al., 2021; Sarangi et al., 2022), compound-specific isotope analysis (CSIA) is required to confirm this in future and we focus on preservation assessment in the current paper.

ACL is derived from the abundance of long-chain *n*-alkyl compounds (Poynter and Eglinton, 1990) and has been broadly used to reconstruct past climate and environments (Castañeda et al., 2009; Bliedtner et al., 2018). ACL values have been shown to correlate with higher growing season temperature and aridity (Dodd and Poveda, 2003; Bush and McInerney, 2015). The vital assumption for using ACL values as a proxy is that plant-waxes deriving from dry, warm grassy biomes would have more abundant longer chain lengths

than those from forests (Cranwell, 1981; Jansen et al., 2006). However, Wang et al. (2015) performed a systematic examination (26 sites, 823 plants) of modern plants and demonstrated a lack of a statistical difference between woody and non-woody vegetation in this regard, suggesting ACL values may not always act as a reliable proxy for past vegetation (Wang et al., 2015). The ACL values in our studies are ≥ 26.8 and ≥ 29.9 (*n*-alk) and ≥ 26.1 and ≥ 27.4 (FA) in the Nefud and Thar Deserts, respectively (Figure 4; Table S1). The qualitative assessment of ACL values when coupled with inferences from CPI, chain length distribution, OEP and EOP suggest the prevalence of vegetation communities dominated by herbs, shrubs and grasses relative to trees (Figure 4, Table S1; Bush & McInerney, 2013; Garcin et al., 2014; Bliedtner et al., 2018). Further, the sample with the lowest $\delta^{13}\text{C}_{\text{bulk}}$ values has the highest CN_{max} (C_{33}) and ACL values (31.4) in *n*-alk, which could be explained either due to the presence of abundant C_3 grasses or contributions from CAM plants following C_3 photosynthetic pathways (Figure 4; Table S1). However, the quantitative estimate of vegetation type and photosynthetic pathways can only be determined by conducting future studies using CSIA.

Conclusion

Overall, the preservation of plant-wax biomarkers in desert sediments offers a valuable opportunity to gain insights into the environment and adaptation of past human societies. In the Holocene epoch, the Nefud Desert exhibits lower $\delta^{13}\text{C}_{\text{bulk}}$ values, lower ACL and higher CPI compared to the Thar Desert. These qualitative data suggest, in a broad sense, that humans were inhabiting and exploiting mixed C_3 – C_4 environments in the Nefud Desert, while the Thar Desert was seemingly predominantly characterized by a grassland (C_4)-dominated environment during the Holocene.

We also note that the data presented here only show the preservation of long-chain *n*-alk and FA compounds, and the inferences presented are qualitative in nature. For future quantitative estimation of past environments and vegetation, biomarker assessment of modern plants and CSIA from the studied deserts is recommended.

We demonstrate the preservation of plant-wax in Holocene and Pleistocene sediments taken from archaeological sites in Saudi Arabia's Nefud Desert and India's Thar Desert. Our data highlight the potential of these biomarkers to provide high-resolution quantitative palaeoenvironmental signatures. We recommend plant-specific biomarkers and their CSIA from archaeological sites preserved in desert biomes as a potential means for developing holistic understandings of past human interactions with changeable, arid-land environments.

Declaration of competing interest

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

Author contributions—D.K.J. P.R. and M.P. conceptualized the research. D.K.J. performed the laboratory work. D.K.J., R.P., J.I. and P.R. interpreted the data. D.K.J., H.A., R.D., J.B., N.B., P.R. and M.P. planned the Thar Desert fieldwork. A.M.A., S.A., N.B., P.S.B., N.D., H.S.G., M.G. and M.P. planned and conducted fieldwork in Nefud Desert. D.K.J. prepared the original draft, and wrote the manuscript with R.P. and P.R., including input from all co-authors. M.P.

and P.R. supervised the research. All authors have read and agreed to the final version of the manuscript.

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Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article

Supporting information

Additional supporting information can be found in the online version of this article.

Fig. S1. Total ion chromatogram (TIC) of GCMS analysis of *n*-alk and FA fractions from sediment samples of the Thar Desert, India. This raw data highlights the presence of plant-waxes in the analysed sediments.

Fig. S2. Field photograph of JB-1 site and visible lithological variation of upper 3 m sequence. The yellow dots represent depth of the studied samples.

Fig. S3. Field photograph of site PE-1 (JQ200) showing lithological variations with a scale. The yellow dots represent depth of the studied samples.

Fig. S4. New geological trench near 16R dune locality. It is an 18 m thick deposit that was first excavated in the 1980s. The yellow dots represent depth of the studied samples.

Fig. S5. Field photograph of Jankipura site (J) showing lithological variation and position of sample collections. The charcoal layer is visible at the top 30 cm of the site.

Table S1. Archaeological site, chronological context, geochemical and biomarker data from Nefud and Thar desert samples.

Abbreviations. ACL, average chain length; CAM, Crassulacean acid metabolism; CN, carbon number; CPI, carbon preference index; CSIA, compound-specific isotope analysis; EOP, even-over-odd preference; FA, fatty acids; FAME, fatty acid methyl ester; *n*-alk, *n*-alkanes; OEP, odd-over-even preference; OM, organic matter; TLE, total lipid extract; TOC, total organic carbon.

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