





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

DEEPAK KUMAR JHA,<sup>1\*</sup>  ROBERT PATALANO,<sup>2,3</sup> JANA ILGNER,<sup>1</sup> HEMA ACHYUTHAN,<sup>4</sup> ABDULLAH M. ALSHAREKH,<sup>5</sup>  SIMON ARMITAGE,<sup>6,7</sup> JAMES BLINKHORN,<sup>6</sup> NICOLE BOIVIN,<sup>1,8,9</sup> PAUL S. BREEZE,<sup>10</sup> RAVINDRA DEVRA,<sup>11</sup> NICHOLAS DRAKE,<sup>10</sup> HUW S. GROUCUTT,<sup>1,12,13,14</sup> MARIA GUAGNIN,<sup>1</sup> PATRICK ROBERTS<sup>1,3</sup>  and MICHAEL PETRAGLIA<sup>8,9,15</sup> 

<sup>1</sup>Department of Archaeology, Max Planck Institute of Geoanthropology, Jena, Germany

<sup>2</sup>Department of Biological and Biomedical Sciences, School of Health and Behavioral Sciences, Bryant University, Smithfield, RI, USA

<sup>3</sup>isoTROPIC Research Group, Max Planck Institute of Geoanthropology, Jena, Germany

<sup>4</sup>Centre for Environmental Studies, Anna University, Chennai, India

<sup>5</sup>Department of Archaeology, College of Tourism & Archaeology, King Saud University, Riyadh, Saudi Arabia

<sup>6</sup>Centre for Quaternary Research, Royal Holloway, University of London, London, UK

<sup>7</sup>SFF Centre for Early Sapiens Behaviour (SapienCE), University of Bergen, Bergen, Norway

<sup>8</sup>School of Social Science, Saint Lucia, QLD, Australia

<sup>9</sup>Human Origins Program, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

<sup>10</sup>Department of Geography, King's College, London, UK

<sup>11</sup>Department of Humanities and Social Sciences, Indian Institute of Science Education and Research Mohali, Punjab, India

<sup>12</sup>Department of Classics and Archaeology, University of Malta, Msida, Malta

<sup>13</sup>Extreme Events Research Group, Chemical Ecology, and Biogeochemistry, Jena, Germany

<sup>14</sup>Institute of Prehistoric Archaeology, University of Cologne, Cologne, Germany

<sup>15</sup>Australian Research Centre for Human Evolution, Griffith University, QLD, Australia

Received 6 April 2023; Revised 29 December 2023; Accepted 14 January 2024

**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,

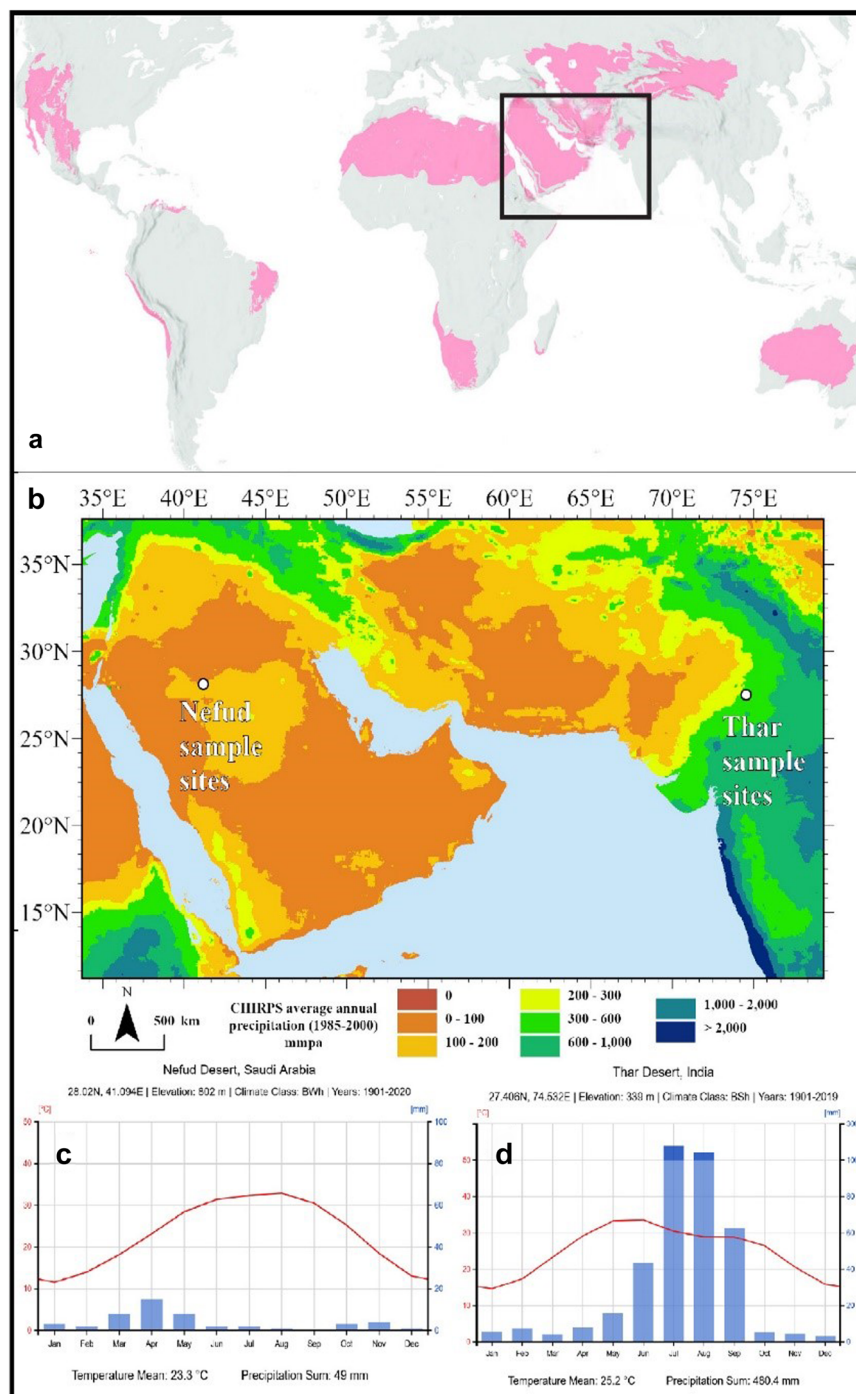
\*Correspondence: Deepak Kumar Jha, as above.  
Email: jha@gea.mpg.de

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 C<sub>10</sub> to C<sub>40</sub> carbon-chains belonging to *n*-alk and FA produced by bacteria, phytoplankton and terrestrial plants (Cranwell et al., 1987). A dominance of C<sub>27</sub> to C<sub>35</sub> *n*-alk with odd-over-even preference (OEP) and C<sub>24</sub> to C<sub>34</sub> 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 ( $\leq C_{25}$ ) 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:

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

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

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

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

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

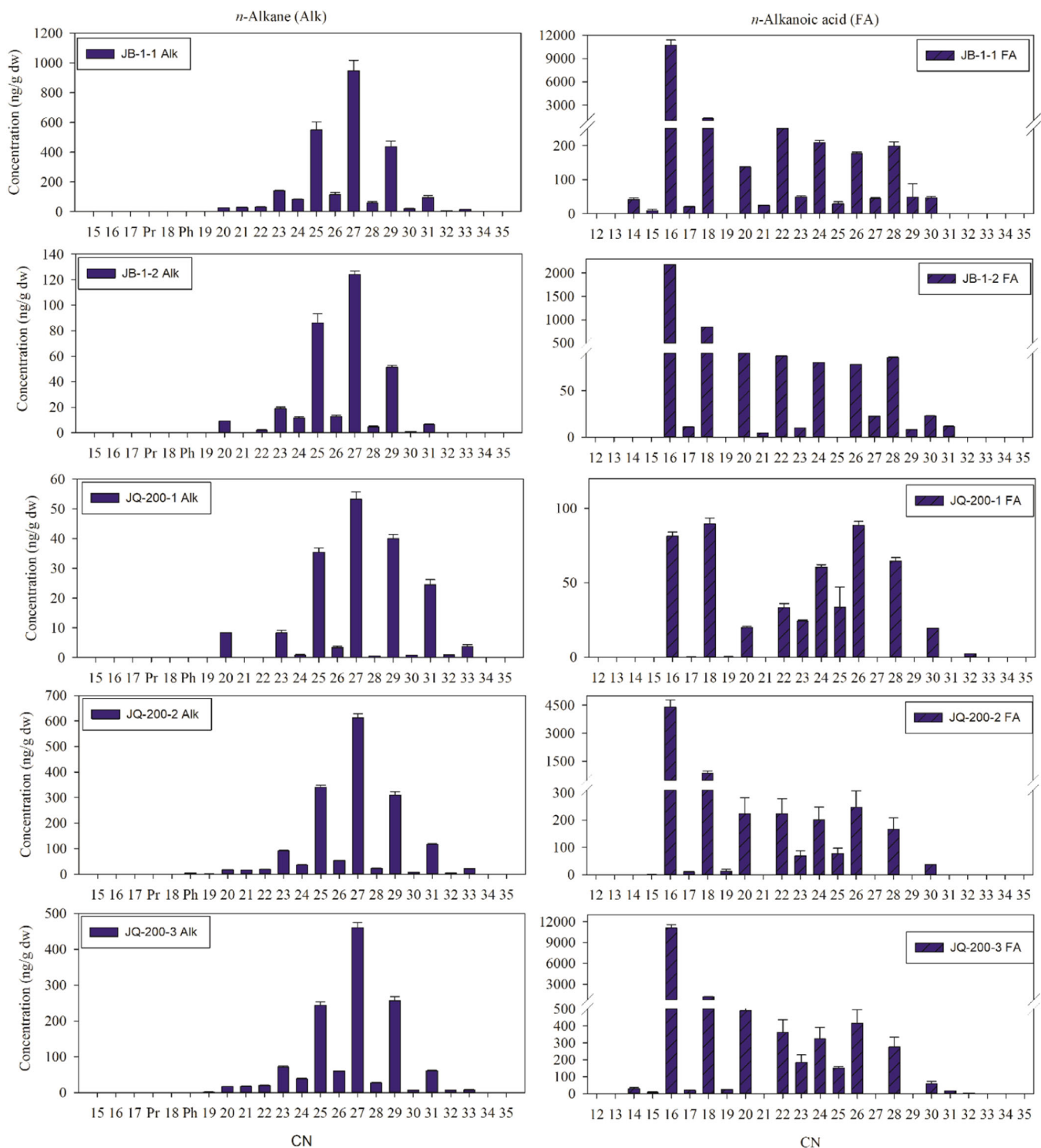
### Total organic carbon and $\delta^{13}C_{bulk}$ of sediment

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



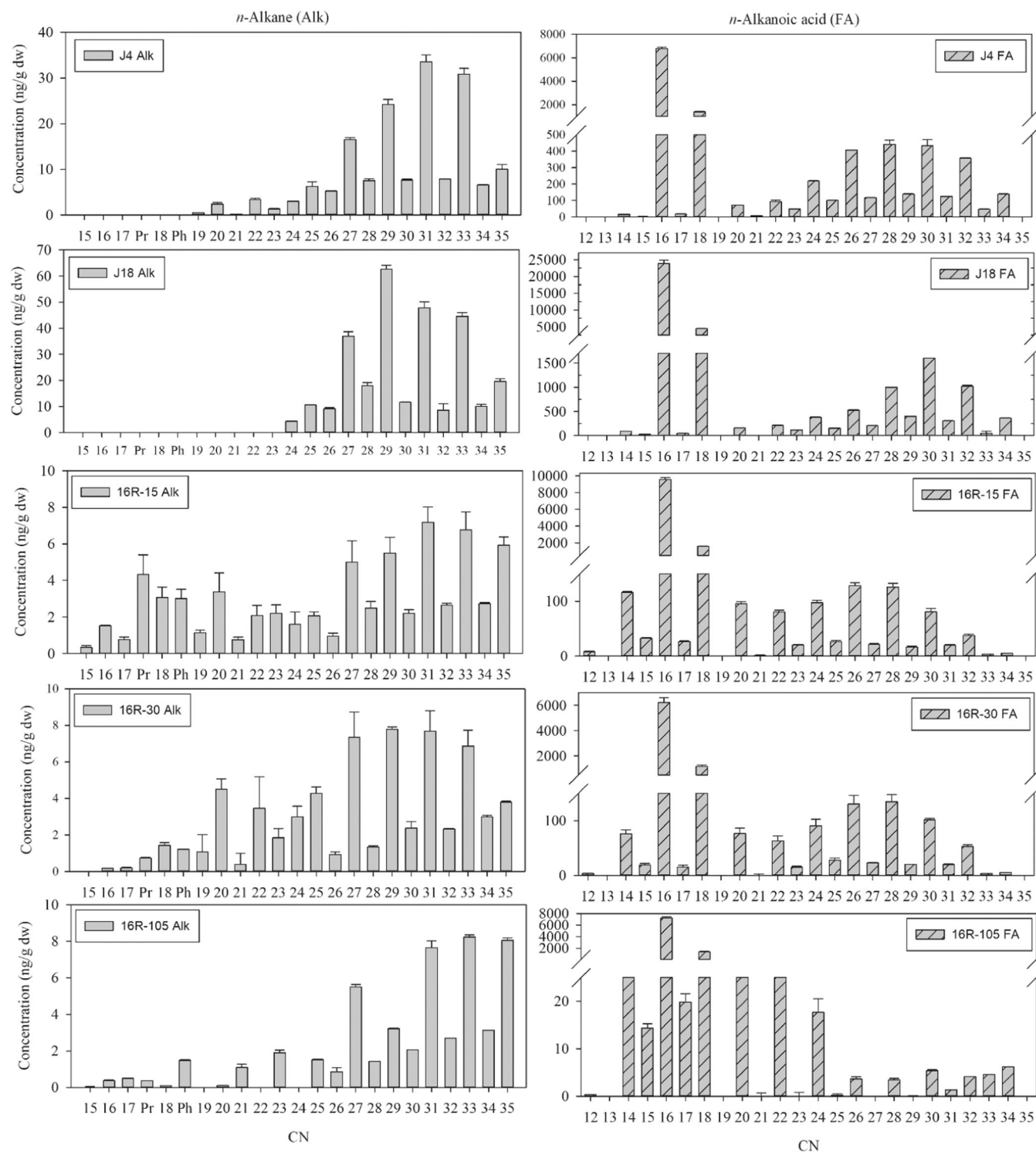
**Figure 2.** Distribution of plant-wax biomarker compounds (*n*-alk and FA) in sediments collected from Nefud Desert, Saudi Arabia. See Table S1 for sample description. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

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 ( $\text{C}_{25}$ – $\text{C}_{35}$ )

*n*-alk and FA ( $\text{C}_{24}$ – $\text{C}_{34}$ ) varied from 43.5 to 279.3  $\text{ng g}^{-1}$  and 70.8 to 6341.7  $\text{ng g}^{-1}$  of dry sediment, respectively (Figure 3).  $\text{C}_{31}$  is the dominant *n*-alk in all samples except in a younger sample (J18) where  $\text{C}_{29}$  is dominant. The  $\text{CN}_{\text{max}}$  in FA varies between  $\text{C}_{24}$  and  $\text{C}_{30}$  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).

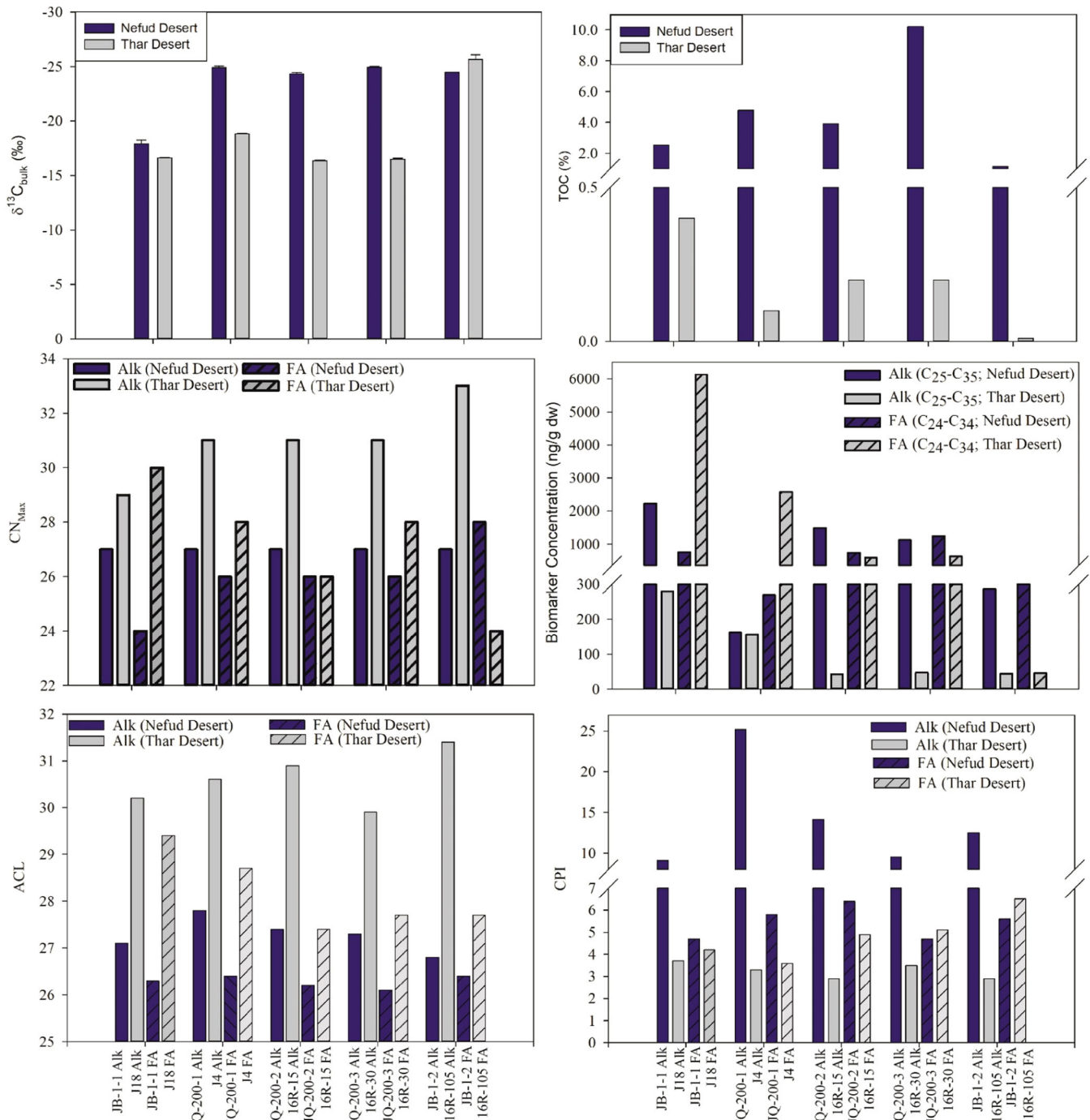


**Figure 3.** Distribution of plant-wax biomarker compounds (*n*-alk and FA) in sediments collected from Thar Desert, India. See Table S1 for sample description.

## 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)]

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 ( $\text{ng g}^{-1}$ ) 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 ( $\text{CN}_{\text{max}}$ ) 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  $\text{CN}_{\text{max}}$  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  $\text{CN}_{\text{max}}$ ), 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  $\geq 26.8$  and  $\geq 29.9$  (*n*-alk) and  $\geq 26.1$  and  $\geq 27.4$  (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  $\text{CN}_{\text{max}}$  ( $C_{33}$ ) 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.

**Acknowledgements.** Funding for this project was provided by the Max Planck Society. Fieldwork in the Nefud Desert was supported by the Heritage Commission, Ministry of Culture, Saudi Arabia. We thank HH Prince Badr Bin Abdullah Bin Farhan Al-Saud, Minister of Culture, for permission to work in the area as well as Dr Jasir Alherbish, CEO of the Heritage Commission, and Dr Abdullah al-Zahrani, General Director for Archaeological Excavations. We thank Mr Purushottam Gupta (GSI, Jaipur), Dr Anoop Ambili (IISER Mohali), Dr Parth Chauhan (IISER Mohali) and Prof. Prasanta Sanyal (IISER Kolkata) for scientific discussion and logistical support during fieldwork in Thar Desert. D.K.J. and R.D. would like to thank Sub Divisional Magistrate office and villagers of the Didwana for their hospitality and cooperation during the geological field camp in Thar Desert, India. A.M.A. acknowledges support of the Researchers Supporting Project (RSP-2023/126), King Saud University, Riyadh, Saudi Arabia. P.S.B. acknowledges support from Leverhulme Trust (ECF-2019-538). S.J.A.'s contribution to this work was partly supported by the Research Council of Norway, through its Centres of Excellence funding scheme, SFF Centre for Early Sapiens Behaviour (SapienCE), project number 262618. We acknowledge the editor and two anonymous reviewers for their constructive comments and suggestions, which enhanced the quality of the manuscript. Open Access funding enabled and organized by Projekt DEAL.

### 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.

### References

Achyuthan, H., Quade, J., Roe, L. & Placzek, C. (2007) Stable isotopic composition of pedogenic carbonates from the eastern margin of the Thar Desert, Rajasthan, India. *Quaternary International*, 162–163, 50–60. Available at: <https://doi.org/10.1016/j.quaint.2006.10.031>

Aichner, B., Ott, F., Stowiński, M., Noryskiewicz, A.M., Brauer, A. & Sachse, D. (2018) Leaf wax *n*-alkane distributions record ecological changes during the Younger Dryas at Trzechowskie paleolake (northern Poland) without temporal delay. *Climate of the Past*, 14(11), 1607–1624. Available at: <https://doi.org/10.5194/cp-14-1607-2018>

Alfarhan, A.H., Rajakrishnan, R., Al-Shehri, M.A., Al-Tamimi, A.S.M., Al-Obaid, S. & Khalaf, S. (2020) Analysis of the cuticular wax composition and ecophysiological studies in an arid plant-Ziziphus nummularia. *Saudi Journal of Biological Sciences*, 27(1), 318–323. Available at: <https://doi.org/10.1016/j.sjbs.2019.09.030>

Ankit, Y., Mishra, P.K., Kumar, P., Jha, D.K., Kumar, V.V., Ambili, V. et al. (2017) Molecular distribution and carbon isotope of *n*-alkanes from Ashtamudi Estuary, South India: Assessment of organic matter sources and paleoclimatic implications. *Marine Chemistry*, 196, 62–70. Available at: <https://doi.org/10.1016/j.marchem.2017.08.002>

Bliedtner, M., Schäfer, I.K., Zech, R. & von Suchodoletz, H. (2018) Leaf wax *n*-alkanes in modern plants and topsoils from eastern Georgia (Caucasus) – implications for reconstructing regional paleovegetation. *Biogeosciences*, 15(12), 3927–3936. Available at: <https://doi.org/10.5194/bg-15-3927-2018>

Blinkhorn, J. (2021) The gateway to the oriental zone: Environmental change and palaeolithic behaviour in the Thar Desert. *Quaternary International*, 596, 79–92. Available at: <https://doi.org/10.1016/j.quaint.2020.11.021>

Blinkhorn, J., Achyuthan, H., Jaiswal, M. & Singh, A.K. (2020) The first dated evidence for Middle-Late Pleistocene fluvial activity in the central Thar Desert. *Quaternary Science Reviews*, 250, 106656. Available at: <https://doi.org/10.1016/j.quascirev.2020.106656>

Blinkhorn, J., Achyuthan, H., Petraglia, M. & Ditchfield, P. (2013) Middle Palaeolithic occupation in the Thar Desert during the Upper Pleistocene: the signature of a modern human exit out of Africa? *Quaternary Science Reviews*, 77, 233–238.

Blinkhorn, J., Ajithprasad, P., Mukherjee, A., Kumar, P., Durcan, J.A. & Roberts, P. (2019) The first directly dated evidence for Palaeolithic occupation on the Indian coast at Sandhav, Kachchh. *Quaternary Science Reviews*, 224, 105975.

Breeze, P.S., Groucutt, H.S., Drake, N.A., Louys, J., Scerri, E.M.L., Armitage, S.J. et al. (2017) Prehistory and palaeoenvironments of the western Nefud Desert, Saudi Arabia. *Archaeological Research in Asia*, 10, 1–16. Available at: <https://doi.org/10.1016/j.ara.2017.02.002>

Brittingham, A., Hren, M.T. & Hartman, G. (2017) Microbial alteration of the hydrogen and carbon isotopic composition of *n*-alkanes in sediments. *Organic Geochemistry*, 107, 1–8.

Bush, R.T. & McNerney, F.A. (2013) Leaf wax *n*-alkane distributions in and across modern plants: Implications for paleoecology and chemotaxonomy. *Geochimica et Cosmochimica Acta*, 117, 161–179.

Bush, R.T. & McNerney, F.A. (2015) Influence of temperature and C4 abundance on *n*-alkane chain length distributions across the central USA. *Organic Geochemistry*, 79, 65–73. Available at: <https://doi.org/10.1016/j.orggeochem.2014.12.003>

Castañeda, I.S., Mülitz, S., Schefuss, E., Lopes Dos Santos, R.A., Sinninghe Damsté, J.S. & Schouten, S. (2009) Wet phases in the Sahara/Sahel region and human migration patterns in North Africa. *Proceedings of the National Academy of Sciences of the United States of America*, 106(48), 20159–20163. <https://doi.org/10.1073/pnas.0905771106>

Castañeda, I.S. & Schouten, S. (2011) A review of molecular organic proxies for examining modern and ancient lacustrine environments. *Quaternary Science Reviews*, 30(21–22), 2851–2891.

Chikaraishi, Y. & Naraoka, H. (2006) Carbon and hydrogen isotope variation of plant biomarkers in a plant–soil system. *Chemical Geology*, 231(3), 190–202. Available at: <https://doi.org/10.1016/j.chemgeo.2006.01.026>

Cranwell, P.A. (1981) Diagenesis of free and bound lipids in terrestrial detritus deposited in a lacustrine sediment. *Organic Geochemistry*, 3(3), 79–89.

Cranwell, P.A., Eglinton, G. & Robinson, N. (1987) Lipids of aquatic organisms as potential contributors to lacustrine sediments—II. *Organic Geochemistry*, 11(6), 513–527. Available at: [https://doi.org/10.1016/0146-6380\(87\)90007-6](https://doi.org/10.1016/0146-6380(87)90007-6)

Crassard, R., Petraglia, M.D., Drake, N.A., Breeze, P., Gratuze, B., Alsharekh, A. et al. (2013) Middle Palaeolithic and Neolithic



- occupations around Mundaflan palaeolake, Saudi Arabia: Implications for climate change and human dispersals. *PLoS One*, 8(7), e69665. Available at: <https://doi.org/10.1371/journal.pone.0069665>
- deMenocal, P.B. (2011) Climate and Human Evolution. *Science*, 331(6017), 540–542. Available at: <https://doi.org/10.1126/science.1190683>
- Diefendorf, A.F., Freeman, K.H., Wing, S.L. & Graham, H.V. (2011) Production of *n*-alkyl lipids in living plants and implications for the geologic past. *Geochimica et Cosmochimica Acta*, 75(23), 7472–7485. Available at: <https://doi.org/10.1016/j.gca.2011.09.028>
- Dodd, R.S. & Poveda, M.M. (2003) Environmental gradients and population divergence contribute to variation in cuticular wax composition in *Juniperus communis*. *Biochemical Systematics and Ecology*, 31(11), 1257–1270. Available at: [https://doi.org/10.1016/S0305-1978\(03\)00031-0](https://doi.org/10.1016/S0305-1978(03)00031-0)
- Eglinton, G. & Hamilton, R.J. (1967) Leaf Epicuticular Waxes. *Science*, 156(3780), 1322–1335. Available at: <https://doi.org/10.1126/science.156.3780.1322>
- Falcão, H.M., Medeiros, C.D., Silva, B.L.R., Sampaio, E.V.S.B., Almeida-Cortez, J.S. & Santos, M.G. (2015) Phenotypic plasticity and ecophysiological strategies in a tropical dry forest chronosequence: A study case with *Poincianella pyramidalis*. *Forest Ecology and Management*, 340, 62–69. Available at: <https://doi.org/10.1016/j.foreco.2014.12.029>
- Freimuth, E.J., Diefendorf, A.F., Lowell, T.V. & Wiles, G.C. (2019) Sedimentary *n*-alkanes and *n*-alkanoic acids in a temperate bog are biased toward woody plants. *Organic Geochemistry*, 128, 94–107. Available at: <https://doi.org/10.1016/j.orggeochem.2019.01.006>
- Garcin, Y., Schefuß, E., Schwab, V.F., Garreta, V., Gleixner, G., Vincens, A. et al. (2014) Reconstructing C3 and C4 vegetation cover using *n*-alkane carbon isotope ratios in recent lake sediments from Cameroon, Western Central Africa. *Geochimica et Cosmochimica Acta*, 142, 482–500. Available at: <https://doi.org/10.1016/j.gca.2014.07.004>
- Griffith, D.M., Cotton, J.M., Powell, R.L., Sheldon, N.D. & Still, C.J. (2017) Multi-century stasis in C3 and C4 grass distributions across the contiguous United States since the industrial revolution. *Journal of Biogeography*, 44(11), 2564–2574.
- Grimalt, J.O., Torras, E. & Albaigés, J. (1988) Bacterial reworking of sedimentary lipids during sample storage. *Organic Geochemistry*, 13(4–6), 741–746.
- Groucutt, H.S., White, T.S., Clark-Balzan, L., Parton, A., Crassard, R., Shipton, C. et al. (2015) Human occupation of the Arabian Empty Quarter during MIS 5: Evidence from Mundaflan al-Buhayrah, Saudi Arabia. *Quaternary Science Reviews*, 119, 116–135. Available at: <https://doi.org/10.1016/j.quascirev.2015.04.020>
- Groucutt, H.S., White, T.S., Scerri, E.M.L., Andrieux, E., Clark-Wilson, R., Breeze, P.S. et al. (2021) Multiple hominin dispersals into southwest Asia over the past 400,000 years. *Nature*, 597(7876), 376–380. Available at: <https://doi.org/10.1038/s41586-021-03863-y>
- Hoefs, M.J.L., Rijpstra, W.I.C. & Sinninghe Damsté, J.S. (2002) The influence of oxic degradation on the sedimentary biomarker record I: Evidence from Madeira Abyssal Plain turbidites. *Geochimica et Cosmochimica Acta*, 66(15), 2719–2735. Available at: [https://doi.org/10.1016/S0016-7037\(02\)00864-5](https://doi.org/10.1016/S0016-7037(02)00864-5)
- Holt, B.G., Lessard, J.P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D. et al. (2013) An update of Wallace's zoogeographic regions of the World. *Science*, 339(6115), 74–78. Available at: <https://doi.org/10.1126/science.1228282>
- Jansen, B., Nierop, K.G.J., Hageman, J.A., Cleef, A.M. & Verstraten, J.M. (2006) The straight-chain lipid biomarker composition of plant species responsible for the dominant biomass production along two altitudinal transects in the Ecuadorian Andes. *Organic Geochemistry*, 37(11), 1514–1536.
- Jennings, R.P., Parton, A., Clark-Balzan, L., White, T.S., Groucutt, H.S., Breeze, P.S. et al. (2016) Human occupation of the northern Arabian interior during early Marine Isotope Stage 3. *Journal of Quaternary Science*, 31(8), 953–966. Available at: <https://doi.org/10.1002/jqs.2920>
- Jha, D.K., Hirave, P., Ghosh, S., Dasgupta, B. & Sanyal, P. (2024) Does leaf wax isotopic characterisation of gymnosperms and angiosperms capture environmental gradients in Himalayas? *Organic Geochemistry*, 187, 104720. Available at: <https://doi.org/10.1016/j.orggeochem.2023.104720>
- Jha, D.K., Samrat, R. & Sanyal, P. (2021) The first evidence of controlled use of fire by prehistoric humans during the Middle Paleolithic phase from the Indian subcontinent. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 562, 110151. Available at: <https://doi.org/10.1016/j.palaeo.2020.110151>
- Jha, D.K., Sanyal, P. & Philippe, A. (2020) Multi-proxy evidence of Late Quaternary climate and vegetational history of north-central India: Implication for the Paleolithic to Neolithic phases. *Quaternary Science Reviews*, 229, 106121. Available at: <https://doi.org/10.1016/j.quascirev.2019.106121>
- Kerstiens, G. (1996) Plant cuticles—An integrated functional approach. *Journal of Experimental Botany*, 47(Suppl.1), 50–60. Available at: <https://doi.org/10.1093/oxfordjournals.jxb.a022915>
- Knief, C., Bol, R., Amelung, W., Kusch, S., Frindte, K., Eckmeier, E. et al. (2020) Tracing elevational changes in microbial life and organic carbon sources in soils of the Atacama Desert. *Global and Planetary Change*, 184, 103078. Available at: <https://doi.org/10.1016/j.gloplacha.2019.103078>
- Lerch, M., Bliedtner, M., Roettig, C.B., Schmidt, J.U., Szidat, S., Salazar, G. et al. (2018) Lipid biomarkers in aeolian sediments under desert pavements—potential and first results from the Black Rock Desert, Utah, USA, and Fuerteventura, Canary Islands, Spain. *E&G quaternary science journal*, 66(2), 103–108. Available at: <https://doi.org/10.5194/egqsj-66-103-2018>
- Liu, J., An, Z. & Liu, H. (2018) Leaf wax *n*-alkane distributions across plant types in the central Chinese Loess Plateau. *Organic Geochemistry*, 125, 260–269. Available at: <https://doi.org/10.1016/j.orggeochem.2018.09.006>
- Lupien, R.L., Russell, J.M., Subramanian, A., Kinyanjui, R., Beverly, E.J., Uno, K.T. et al. (2021) Eastern African environmental variation and its role in the evolution and cultural change of Homo over the last 1 million years. *Journal of Human Evolution*, 157, 103028.
- Magill, C.R., Eglinton, G. & Eglinton, T.I. (2019) Isotopic variance among plant lipid homologues correlates with biodiversity patterns of their source communities. *PLoS One*, 14(2), e0212211. Available at: <https://doi.org/10.1371/journal.pone.0212211>
- Marzi, R., Torkelson, B.E. & Olson, R.K. (1993) A revised carbon preference index. *Organic Geochemistry*, 20(8), 1303–1306. Available at: [https://doi.org/10.1016/0146-6380\(93\)90016-5](https://doi.org/10.1016/0146-6380(93)90016-5)
- Meyers, P.A. (2003) Applications of organic geochemistry to paleolimnological reconstructions: A summary of examples from the Laurentian Great Lakes. *Organic Geochemistry*, 34(2), 261–289. Available at: [https://doi.org/10.1016/S0146-6380\(02\)00168-7](https://doi.org/10.1016/S0146-6380(02)00168-7)
- Parton, A., Clark-Balzan, L., Parker, A.G., Preston, G.W., Sung, W.W., Breeze, P.S. et al. (2018) Middle-late Quaternary palaeoclimate variability from lake and wetland deposits in the Nefud Desert, Northern Arabia. *Quaternary Science Reviews*, 202, 78–97. Available at: <https://doi.org/10.1016/j.quascirev.2018.10.010>
- Patalano, R., Roberts, P., Boivin, N., Petraglia, M.D. & Mercader, J. (2021) Plant wax biomarkers in human evolutionary studies. *Evolutionary Anthropology: Issues, News, and Reviews*, 30(6), 385–398. Available at: <https://doi.org/10.1002/evan.21921>
- Patalano, R., Zech, J. & Roberts, P. (2020) Leaf wax lipid extraction for archaeological applications. *Current Protocols in Plant Biology*, 5(3), e20114. Available at: <https://doi.org/10.1002/cppb.20114>
- Petraglia, M.D., Alsharekh, A., Breeze, P., Clarkson, C., Crassard, R., Drake, N.A. et al. (2012) Hominin dispersal into the Nefud desert and Middle Palaeolithic settlement along the Jubbah palaeolake, northern Arabia. *PLoS One*, 7(11), e49840. Available at: <https://doi.org/10.1371/journal.pone.0049840>
- Petraglia, M.D., Breeze, P.S. & Groucutt, H.S. (2019) Blue Arabia, Green Arabia: Examining human colonisation and dispersal models. In: Rasul, N., (Ed.) *The Red Sea, II*. Berlin: Springer. pp. 675–683.
- Petraglia, M.D., Haslam, M., Fuller, D.Q., Boivin, N. & Clarkson, C. (2010) Out of Africa: New hypotheses and evidence for the dispersal of Homo sapiens along the Indian Ocean rim. *Annals of Human Biology*, 37(3), 288–311. Available at: <https://doi.org/10.3109/03014461003639249>
- Pillai, A.A.S., Anoop, A., Sankaran, M., Sanyal, P., Jha, D.K. & Ratnam, J. (2017) Mid-late Holocene vegetation response to climatic drivers and biotic disturbances in the Banni grasslands of western India. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 485, 869–878. Available at: <https://doi.org/10.1016/j.palaeo.2017.07.036>

- Polissar, P.J., Uno, K.T., Phelps, S.R., Karp, A.T., Freeman, K.H. & Pensky, J.L. (2021) Hydrologic changes drove the Late Miocene expansion of C4 grasslands on the northern Indian subcontinent. *Paleoceanography and Paleoclimatology*, 36(4), e2020PA004108. Available at: <https://doi.org/10.1029/2020PA004108>
- Poynter, J. & Eglinton, G. (1990) Molecular composition of three sediments from hole 717c: The Bengal Fan. In: Proceedings of the Ocean Drilling Program: Scientific Results, 116.
- Roberts, P. & Stewart, B.A. (2018) Defining the “generalist specialist”-niche for Pleistocene *Homo sapiens*. *Nature Human Behaviour*, 2(8), 542–550. Available at: <https://doi.org/10.1038/s41562-018-0394-4>
- Roberts, P., Stewart, M., Alagaili, A.N., Breeze, P., Candy, I., Drake, N. et al. (2018) Fossil herbivore stable isotopes reveal Middle Pleistocene hominin palaeoenvironment in “Green Arabia”. *Nature Ecology & Evolution*, 2(12), 1871–1878. Available at: <https://doi.org/10.1038/s41559-018-0698-9>
- Roy, B. & Sanyal, P. (2022) Isotopic and molecular distribution of leaf-wax in plant–soil system of the Gangetic floodplain and its implication for paleorecords. *Quaternary International*, 607, 89–99. Available at: <https://doi.org/10.1016/j.quaint.2021.09.004>
- Sarangi, V., Roy, S. & Sanyal, P. (2022) Effect of burning on the distribution pattern and isotopic composition of plant biomolecules: Implications for paleoecological studies. *Geochimica et Cosmochimica Acta*, 318, 305–327. Available at: <https://doi.org/10.1016/j.gca.2021.12.003>
- Scerri, E.M.L., Shipton, C., Clark-Balzan, L., Frouin, M., Schwenninger, J.L., Groucutt, H.S. et al. (2018) The expansion of later Acheulean hominins into the Arabian Peninsula. *Scientific Reports*, 8(1), 17165. Available at: <https://doi.org/10.1038/s41598-018-35242-5>
- Schäfer, I.K., Lanny, V., Franke, J., Eglinton, T.I., Zech, M., Vysloužilová, B. et al. (2016) Leaf waxes in litter and topsoils along a European transect. *Soil*, 2(4), 551–564.
- Schwark, L., Zink, K. & Lechterbeck, J. (2002) Reconstruction of postglacial to Early Holocene vegetation history in terrestrial Central Europe via cuticular lipid biomarkers and pollen records from lake sediments. *Geology*, 30(5), 463–466. Available at: [https://doi.org/10.1130/0091-7613\(2002\)030<0463:ROPTEH>2.0.CO;2](https://doi.org/10.1130/0091-7613(2002)030<0463:ROPTEH>2.0.CO;2)
- Singhvi, A.K., Williams, M.A.J., Rajaguru, S.N., Misra, V.N., Chawla, S., Stokes, S. et al. (2010) A ~ 200 ka record of climatic change and dune activity in the Thar Desert, India. *Quaternary Science Reviews*, 29(23–24), 3095–3105. Available at: <https://doi.org/10.1016/j.quascirev.2010.08.003>
- Struck, J., Bliedtner, M., Strobel, P., Bittner, L., Bazarradnaa, E., Andreeva, D. et al. (2020) Leaf waxes and hemicelluloses in topsoils reflect the  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  isotopic composition of precipitation in Mongolia. *Frontiers in Earth Science*, 8, 343. Available at: <https://doi.org/10.3389/feart.2020.00343>
- Villaseñor, A., Uno, K.T., Kinyanjui, R.N., Behrensmeyer, A.K., Bobe, R., Advokaat, E.L. et al. (2023) Pliocene hominins from East Turkana were associated with mesic environments in a semiarid basin. *Journal of Human Evolution*, 180, 103385.
- Wang, M., Zhang, W. & Hou, J. (2015) Is average chain length of plant lipids a potential proxy for vegetation, environment and climate changes? *Biogeosciences Discussions*, 12(7), 5477–5501.
- Wilhelm, M.B., Davila, A.F., Eigenbrode, J.L., Parenteau, M.N., Jahnke, L.L., Liu, X.L. et al. (2017) Xeropreservation of functionalized lipid biomarkers in hyperarid soils in the Atacama Desert. *Organic Geochemistry*, 103, 97–104. Available at: <https://doi.org/10.1016/j.orggeochem.2016.10.015>
- Wu, M.S., West, A.J. & Feakins, S.J. (2019) Tropical soil profiles reveal the fate of plant wax biomarkers during soil storage. *Organic Geochemistry*, 128, 1–15. Available at: <https://doi.org/10.1016/j.orggeochem.2018.12.011>