Lipid and DNA Evidence of Dominance of Planktonic Archaea Preserved in Sediments of the South China Sea: Insight for Application of the TEX₈₆ Proxy in an Unstable Marine Sediment Environment

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The marine planktonic archaea are dominated by Thaumarcheotal Marine Group I, which is characterized by the lipid biomarker thaumarchaeol. The marine benthic archaea are characterized by greater diversity of currently unknown species whose lipid biomarker signatures are uncertain. In this study, a sediment core from the northwestern part of the South China Sea (SCS) (water depth 1474 m) was analyzed using molecular DNA and lipid biomarker approaches. While 16S rRNA gene analysis showed changing archaeal community structures with sediment depth, this change had little impact on the fossil record of archaeal lipids that are characteristic of the planktonic community. As a result, the fossil archaeal lipids recorded paleo sea surface temperature of the SCS since the last glacial maxima by the TEX₈₆ proxy, which agreed generally with the winter temperature recorded by planktonic foraminiferas collected from the same area of the SCS that hosted mass-transported deposits. This suggests that this deep water deposit may have partially preserved paleoclimate record reflecting seasonal temperature variation in a near shore setting, which is in contrast to annual sea surface temperature or sub sea surface temperature variation recorded by TEX₈₆ in the open ocean.

Keywords: mass-transported deposits, paleotemperature, planktonic archaea, South China Sea, TEX₈₆, thaumarchaeol, thaumarchaeota

Introduction

Archaea are ubiquitous in the environment and play an important role in the global carbon and nitrogen cycle (Schleper et al. 2005). They biosynthesize isoprenoid glycerol dialkyl glycerol tetraethers (GDGTs) as major membrane lipids, which include a series of compounds with zero to four cyclopentyl moieties (Figure 1) (Schouten et al. 2002). In Thaumarcheota a cyclohexyl moiety also exists along with other four cyclopentyl rings, which makes the compound a special name called thaumarchaeol, previously known as crenarchaeol (Figure 1) (Schouten et al. 2002; Sinninghe Damsté et al. 2002). Culture experiments show that the distribution of isoprenoid GDGTs with cyclopentyl moieties increases with temperature (Boyd et al. 2011; Lai et al. 2008; Uda et al. 2001). Schouten et al. (2002) introduced the TEX₈₆ index (tetraether index of tetraethers consisting of 86 carbons) as a sea surface temperature (SST) proxy based on the relative abundance of isoprenoid GDGTs, which has been widely used but many questions remain in terms of the climate interpretations of the TEX₈₆ temperature records (Jia et al. 2012; Schouten et al. 2007; Schouten et al. 2013; Wei et al. 2011).

For example, Kim et al. (2008) showed that TEX₈₆ values corresponded well with annual mean temperature of upper mixed layer of the ocean on the basis of analysis of 287 global core-top sediments; other studies have shown that TEX₈₆ reflected the temperature of a particular season of the year (Castaneda et al. 2010; Herfort et al. 2006; Huguet et al. 2011; Leider et al. 2010) and TEX₈₆ also may have corresponded to subsurface temperature better than SST (Jia et al. 2012; Li et al. 2013; Wuchter et al. 2006; Yamamoto et al. 2012).

GDGT distributions in the ocean can be affected by lateral transport of isoprenoid GDGTs (Kim et al. 2009; Shah et al. 2003).
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2008) and changes in nutrients and pH (Pearson et al. 2008; Turich et al. 2007b), which may compromise the application of TEX$_{86}$ as an SST proxy (Turich et al. 2007). TEX$_{86}$ also can be biased by GDGT inputs from soil archaea (Weijers et al. 2006; Zhu et al. 2011) and benthic archaea in hydrate rich environments (Liu et al. 2011; Zhang et al. 2011). Furthermore, other studies have shown that TEX$_{86}$ values for intact polar lipid (IPL) GDGTs are consistently higher than those from core lipid GDGTs even in normal marine sediments (Lipp and Hinrichs 2009; Wei et al. 2011).

Mass-transported deposits (MTDs) are an important component of deep water deposition system, which often occur in deep water basins around the world and play an important role in petroleum exploration and production (Moscardelli and Wood, 2008; Shao et al. 2010; Wang et al., 2009). The South China Sea (SCS) is the largest marginal sea of the western Pacific Ocean. The Qiongdongnan Basin is located in the present shelf, slope and abyssal environments (Xie et al. 2006) with the slope environment containing one of the gas hydrate prospecting zones in the northern SCS (Yang et al. 2013). Wang et al. (2009) showed that MTDs are widely distributed in Quaternary sedimentary sequences of the continental slope in the Qiongdongnan Basin of SCS. Many paleoclimatic studies have been conducted in the SCS, which are commonly based on temperature proxies such as foraminiferal oxygen isotope ratios and Mg/Ca ratios, foraminiferal transfer function, or the U$_{37}$w methods (Jian et al. 2000; Jian et al. 2003; Zhao et al. 2006). Recently, the TEX$_{86}$ proxy has been used to reconstruct temperature records in SCS (Ge et al. 2013; Jia et al. 2012; Li et al. 2013; Wei et al. 2011; Zhang et al. 2013), however, the impact of MTDs on paleoclimate records, especially on the TEX$_{86}$ index, is poorly known.

In this study, we analyzed GDGT lipids and molecular DNA from sediments in the Qiongdongnan Basin of the SCS. We also compared polar (P)-GDGT contents that were measured by liquid chromatography-mass spectrometry (LC-MS) to those calculated from archaeal 16S rRNA gene copies (a proxy for cell abundance) in order to evaluate the effect of intact polar GDGTs in sediments on TEX$_{86}$. Our results show that despite the samples being from the hydrate-rich region, the lipids in the sediments are predominantly from planktonic archaea, and the calculated TEX$_{86}$ indicates winter sea surface temperature during the last 24 Ka years. The effect of MTDs on TEX$_{86}$ is also evaluated in this study.

Material and Methods

Site Description and Sampling

A sediment core (HQ08-48PC; 16°57.5134′N, 110°31.5809′E, 1,474 m; Figure 2) was obtained during the cruise HY4-2008-1 in the Qiongdongnan Basin of the northern SCS. Sediment samples were collected using the R/V Haiyang No. 4. The core was 7.14 m long, soft, rich in foraminifera and made up of silty clay. Eleven sediment samples were obtained aseptically with each sample collected every 70 cm along the core. These samples were collected into 50-mL centrifuge tubes and stored at −80°C until analysis.
**Environmental and Bulk Parameter Analysis**

**Pore water**

Pore waters were obtained by centrifuging the sediments and were filtered through a 0.22-μm pore size, 4-mm diameter filter prior to analysis. Sulfate and chlorine were analyzed with an Ion Chromatogram (DX-600, Dionex, USA). Methane was analyzed using a Gas Chromatograph (6890 N series, Agilent Technologies, USA) on board the ship.

**TOC, TN and carbon isotopes of TOC**

About 5-g sediment was decarbonated using 10% HCl and neutralized by repeated washing with distilled and deionized water before analysis. Part of the dried bulk sediment was used for analysis of total organic carbon (TOC) using an element analyzer (EA1110, Carlo Erba). The carbon isotopes of the TOC were then determined on the GV-Isoprime EA IRMS with a precision of 0.1‰ for δ^{13}C (VPDB), which is defined as

\[
\delta^{13}C = \left(\frac{^{13}C/^{12}C}_{sa}/^{13}C/^{12}C_{std} - 1\right) \times 1000
\]

where “sa” stands for sample and “std” for standard.

**DNA Analysis**

**DNA isolation and amplification**

Bulk DNA was extracted from sediment samples using PowerSoil DNA Isolation Kit (Mo Bio Laboratories, Carlsbad, CA) in accordance with the manufacturer’s instructions. Archaeal 16S rRNA gene fragments were amplified using primers Arch21F (5′-TTCCGGTTGATCCYGCCGCCGGA-3′) and Arch958R (5′-YCCGCGGCTTGAMTCCAATT-3′) as previously described (DeLong 1992). The conditions for amplification of archaeal 16S rRNA genes were the following: initial denaturation at 95°C for 3 min; 30 cycles of denaturing (1 min at 94°C), annealing (1 min at 55°C), and extension (1.5 min at 72°C); and a final extension at 72°C for 10 min. The PCR products were purified with a QIAquick PCR Purification kit (Qiagen Inc., Irvine, CA) according to the manufacturer’s suggested protocol.

**Quantitative PCR**

Quantitative PCR was performed using the StepOne real-time system (Life Technologies) and a 20 μl reaction mixture that consisted of 2 μl (1 to 10 ng) of DNA as the template, 0.4 μl (10 μM) of each primer, 0.4 μl ROX Reference Dye (50×) and 10 μl of SYBR® Premix Ex Taq (2×) (TAKARA). Archaeal 16S rRNA genes were quantified using the primers 344F (5′-ACGCGGGCCGACGAGGGCAGA-3′) and 518R

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Fig. 2. Map showing the location of core HQ08-48PC in this study. Blue dot is from a previous study (Jiang and Li 2003).
(5'-ATTACCGCGGCTGCTGG-3') (Ovares et al. 1998) and the following thermal profile: 30 sec at 95°C, followed by 40 cycles of 5 sec at 95°C, 1 min at 60°C; 15 sec at 95°C, 1 min at 60°C, and 15 sec at 95°C to make the melting curve.

Cloning and restriction fragment length polymorphism (RFLP) analysis

The PCR product was ligated into the pMD-18T vector (TaKaRa) and transformed into Escherichia coli DH5α competent cells. The transformed cells were plated on Luria-Bertani plates containing 100 µg/mL of ampicillin, 80 µg/mL of X-Gal (5-bromo-4-chloro-3-indolyl-β-D-galactopyranoside), and 0.5 mM IPTG (isopropyl-β-D-thiogalactopyranoside) and incubated overnight at 37°C. Resulting PCR products were screened for the correct size and purity by 1% agarose gel electrophoresis.

The PCR-amplified inserts were digested with the restriction endonucleases MspI (Fermentas) for 3 h at 37°C. The resulting products were separated by gel electrophoresis on a 3.0% agarose gel in TAE buffer. A total of 206 clones were analyzed and at least one phylotype from each group (determined by RFLP banding pattern and/or ≥ 97 sequence similarity) was subject to complete nucleotide sequencing.

Phylogenetic analysis

The 16S rRNA gene sequences were grouped into operational taxonomic units (OTUs) at 3% distance cut-off using the DOTUR program (Schloss and Handelsman 2005). Sequence similarity searches were performed using the BLAST network service of the NCBI database (http://www.ncbi.nlm.nih.gov/BLAST). The sequences were tested for chimeras by using the Ribosomal Database Project (Thompson et al. 1997). Phylogenetic trees were constructed using the MEGA program version 3.0 (Kumar et al. 2004) with the Kimura two-parameter algorithm and the neighbor-joining method.

Accession number of nucleotide sequences

The sequences have been deposited in the GenBank database under accession numbers: HQ611174 - HQ611227.

Lipid Extraction and Analysis

The original sample was spiked with an internal standard (C_{46}, 974.08 ng) before the extraction procedure began. The freeze-dried sediment sample spiked with the internal standard was extracted ultrasonically five times with a mixture of dichloromethane (DCM): methanol (MeOH) (3:1, v/v). The total extract was transferred into a KOH-MeOH solution (6%) for overnight and then extracted by n-hexane five times. Lipid analysis by HPLC-MS followed previously described procedures (Wei et al. 2011).

Briefly, the GDGTs were first eluted isoctratically with (A) n-hexane and (B) isopropanol as follows, 99% A: 1% B for 5 min, then a linear gradient to 1.8% B in 45 min. Flow rate was 0.2 mL/min. After each analysis the column was cleaned by back flushing with n-hexane/isopropanol (90:10, vol: vol) at 0.2 mL/min for 10 min. Conditions for APCI/MS were as follows: nebulizer pressure 60 psi, vaporizer temperature 400°C, drying gas (N_{2}) flow 5 L/min and temperature 200°C, capillary voltage −3.5 kV, corona 5 µA (3.2 kV). Single ion monitoring (SIM) mode was used to detect eight isoprenoidal GDGT signals (m/z 1302, 1300, 1298, 1296, 1292, 1050, 1036, 1022) and the C_{46} internal standard (m/z 744), with a dwell time of 237 ms per ion.

GDGT Proxies

(1) TEX_{86} was calculated based on the equation from Schouten et al. (2002) and Kim et al. (2010):

\[ \text{TEX}_{86} = \frac{\text{GDGT}-2 + \text{GDGT}-3 + \text{Thaum.}}{\text{GDGT}-1 + \text{GDGT}-2 + \text{GDGT}-3 + \text{Thaum.}} \]

(2)TEX_{86}-derived sea surface temperatures (SST) were calculated according to Kim et al. (2010):

\[ \text{SST} = 68.4 \times \text{TEX}_{86}^\text{H} + 38.6 \]

(3) BIT and MI index were calculated according to Hopmans et al. (2004) and Zhang et al. (2011), respectively:

\[ \text{BIT} = \frac{\text{I} + \text{II} + \text{III}}{\text{I} + \text{II} + \text{III} + \text{Thaum.}} \]

\[ \text{MI} = \frac{\text{GDGT}-1 + \text{GDGT}-2 + \text{GDGT}-3}{\text{GDGT}-1 + \text{GDGT}-2 + \text{GDGT}-3 + \text{Thaum.} + \text{Thaum.'}} \]

GDGT Abundance Calculated from Cell Numbers

We assumed that each living archaeal cell would contain one 16S rRNA gene and the GDGT per cell maximum would be 8.5 fg IP-GDGT cell^{-1} (Huguet et al. 2010). Thus IP-GDGT abundances were calculated on the basis of the archaeal 16S rRNA gene copy numbers.

Results and Discussion

Geochemical and Biological Profiles Supporting the Applicability of TEX_{86} in the SCS

Because the Qiongdongnan Basin is one of the most prospective areas for gas hydrate explorations in the northern continental slope of the SCS, TEX_{86}-derived temperatures may not be valid where high rates of anaerobic oxidation of methane occur (Pancost et al. 2001; Schouten et al. 2002; Wakeham et al. 2007; Zhang et al. 2011). Thus geochemistry profiles were first obtained to evaluate the application of TEX_{86} in this region of the northern SCS.
The CH$_4$ concentrations in all samples ranged from 0.82 to 3.68 mM (Figure 3, Supplementary Table S1), which are in the lower end of normal marine sediments (Van Dover 2000) and were low compared to methane concentrations in hydrate locations (Levin 2005).

Porewater sulfate concentrations ranged from 26.49 to 31.31 mM, indicating low activity of sulfate reduction; the Cl$^-$ concentrations ranged from 620.3 to 742.6 mM, indicating a lack of hydrate dissociation that may release fresh water to dilute the Cl$^-$ concentration (Figure 3, Supplementary Table S1). The TOC concentrations ranged from 0.88 to 1.29% and the $\delta^{13}$C of TOC remained relatively constant averaging $-21.49/\text{permil}$ (Figure 3, Supplementary Table S1), which indicates a signature of normal marine TOC. This is further supported by the MI values (0.18 to 0.21), which are in the range of 0–0.3 for normal marine conditions (Zhang et al. 2011). BIT values were less than 0.2 in all samples (Figure 3), which are in the range of open marine sediments (Hopmans et al. 2004).

We also investigated the archaeal diversity and community structures that provided independent information on methane oxidation by archaea. All the archaeal sequences belonged to either Crenarchaeota/Thaumarcheota or Euryarchaeota (Figure 4a, Supplementary Table S2). The former group consisted of Marine Group I (MGI) of Thaumarchaeota, and Miscellaneous Crenarchaeotal Group (MCG), Marine Benthic Group A (MBGA), Marine Benthic Group B (MBGB) and C3 of Crenarchaeota (Figure 4a, Supplementary Table S2). The other group consisted of the Marine Benthic Group D (MBGD), the South African Gold Mine Euryarchaeotal Group (SAGMEG), Novel Euryarchaeotic Group (NEG), Miscellaneous Euryarchaeotal Group (MEG), Deep-Sea Hydrothermal Vent Euryarchaeotic Group 6 (DHVE6) and the Marine Benthic Group E (MBGE) of Euryarchaeota (Figure 4a, Supplementary Table S2).

Archaeal community structure changed with depth along the sediment core (Figure 4a). The upper layer was dominated by uncultivated archaeal lineages (38% of MGI and 26% of MBGB), the intermediate layer had the archaeal lineages relatively evenly distributed (35% of MBGB, 20% of MCG, 20% of MBGD and 16% of C3), and the deeper layer was mainly composed of uncultivated archaeal lineages (51% of MCG and 34% of MBGD) (Figure 4a, Supplementary Table S2).

MCG and MBGD increased in phylotypes with increasing depth of the core, indicating their potential importance in deeper marine subsurface. However, none of the samples showed the presence of ANME groups that are associated with anaerobic oxidation of methane commonly occurring in cold seep or gas hydrate locations (Harrison et al. 2009; Knittel et al. 2005; Teske et al. 2002).

Collectively, the low CH$_4$ concentrations, relatively high concentrations of porewater sulfate, $\delta^{13}$C of TOC characteristic of nonmethane oxidation and low MI, and the lack of ANME groups suggest that sediment in core HQ08-48PC was deposited under normal marine conditions. Therefore, the TEX$_{86}$-derived temperatures from our samples were unlikely to be biased by methane-metabolizing archaea (Zhang et al. 2011).

**IP-GDGT Effect on TEX$_{86}$ of C-GDGT**

**GDGT distribution**

All samples showed a characteristic marine archaeal GDGT profile, with abundant thaumarchaeol (51.5–60.8%) and GDGT-0 (20.0–30.3%) and less contributions of GDGT-1 to GDGT-3 and the thaumarchaol regioisomer among the different samples. This observation was consistent with our previous findings in the SCS (Ge et al. 2013; Wei et al. 2011). Cluster analysis showed that the compositions of the archaeal C-GDGTs in the post glacial (PG) period were clearly different from those in the Last Glacial Maximum (LGM) period (Figure 5).

**IP-GDGT Effect on TEX$_{86}$ of C-GDGT**

The number of archaeal 16S rRNA genes in our samples averaged $2.1 \times 10^4$ copies/g (n = 11) and ranged from $1.08 \times 10^4$ to $4.1 \times 10^4$ copies/g (wet weight) (Figure 6). The archaeal copies reached the highest value of $1.08 \times 10^4$ copies/g (wet weight) in the uppermost sample.

IP-GDGT abundance calculated according to archaeal 16S rRNA gene copies ranged from 0.4 to 9.2 ng/g (Figure 6).
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Fig. 4. Frequency of the archaeal lineages and Neighbor-joining tree of the archaeal 16S rRNA genes. (a) Frequency of archaeal lineages in clone libraries constructed from samples collected at 0–20 cm, 350–370 cm and 630–650 cm in the sediment core HQ08-48PC. (b) Phylogenetic tree constructed using archaeal 16S rRNA genes recovered from the upper, intermediate and deeper sediments of the core. The unique archaeal 16S rRNA sequences obtained in this study were grouped at 0.03 distance cutoff using the DOTUR program. The scale bar represents a 5% sequence difference. The archaeal 16S rRNA sequences obtained in this study are shown in bold, along with their distribution in each clone library as depicted in the parentheses.

In contrast, C-GDGT abundance averaged 705.6 ng/g (n = 11) and ranged from 378.7 to 1055.7 ng/g (Figure 6). The calculated IP-GDGT abundance was thus several orders of magnitude lower than that of C-GDGT. This is consistent with results from Lengger et al. (2012) who compared IP-GDGT with C-GDGT by direct LC-MS analysis.

TEX$_{86}$ value can be affected by IPL derived from in situ production by benthic heterotrophic archaea in sediments (Lipp and Hinrichs 2009). Some studies showed that TEX$_{86}$ values for IPL GDGTs were consistently higher than those from core lipid GDGTs (Lipp and Hinrichs 2009; Liu et al. 2011; Wei et al. 2011). In this study, abundance of IP is less than 1% of total GDGTs, which suggests that in situ production in the subsurface sediment does not substantially influence the TEX$_{86}$ of the C-GDGT.

Indication of TEX$_{86}$ SST

The SST derived from TEX$_{86}$ was calculated according to Kim et al. (2010) and ranged from 21.1°C to 27.4°C along the sediment core. TEX$_{86}$ SST had a narrow range of 26.7 to 27.4°C between 0 and 140 cm, following a rapid decrease to 21.2°C from 140 cm to 280 cm and then maintained a relatively constant value of 21.3°C (Figure 7). A sediment core (SA12-19) near HQ08-48PC had been drilled for paleoclimate study, and foraminiferal transfer functions (Jiang and Li 2003)
showed distinct winter and summer SSTs changes during the last glacial-Holocene transition (Figure 7). Supposing that HQ08-48PC and SA12-19 had the same sedimentary rate because both cores were very close and had similar water depth, the age model of core SA12-19 was applied to core HQ08-48PC.

The SST derived from TEX$_{86}$ in this study agrees in general with the winter temperature recorded by planktonic foraminifera (Jiang and Li 2003); however, a large difference can occur at different depths (Figure 7). There may be several possibilities for the difference between the two temperature proxies.

First, samples of TEX$_{86}$ proxy has lower resolution than those of planktonic foraminifera (PF)-based temperatures so that some detail temperature changes were not revealed in core HQ08-48PC. The sampling interval for TEX$_{86}$ was 70 cm; whereas the sampling interval for PF-based temperature was 10 cm in average. Second, the standard deviation of TEX$_{86}$ temperature was 2.5°C whereas the standard deviation of PF-based temperature was 1.39°C (Jiang and Li 2003). However, the largest difference between TEX$_{86}$ and PF-based winter temperature is $>4$°C, which cannot be explained by the poor resolution of the TEX$_{86}$. Third, TEX$_{86}$ may be a mixed signal of archaeal biomass from different water depths or seasons. Previous studies have indicated that TEX$_{86}$ values may reflect a specific season of the year in different sites (Schouten et al. 2013).

Leider et al. (2010) showed that the TEX$_{86}$-based temperatures reflected winter SSTs for the nearshore sites on the southern Italian shelf but corresponded to summer SSTs at

![Fig. 5. Clustering analysis of relative abundances of GDGTs in archaeal core lipids from HQ08-48PC of the South China Sea. PG and LGM stand for Post Glacial and the last Glacial Maximum period, respectively.](image)

![Fig. 6. Depth profiles of archaeal 16S rRNA gene copies and GDGT lipid contents. 16S rRNA gene copies were obtained using quantitative PCR; IP-GDGT was calculated on the basis of the archaeal 16S rRNA gene copy numbers and single cell GDGT lipid content (Huguet et al. 2010); The content of C-GDGTs were analyzed using LC-MS directly.](image)
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Fig. 7. Paleo temperature variation since the last glacial maxima in the northern SCS. TEX86-based SST was reconstructed according to Kim et al. (2010) from the Core HQ08-48PC (in green dash line); SSTs in winter (red line) and summer (blue line) were calculated based on planktonic foraminifera (PF) in core SA12-19 using palaeoecological transfer functions (Jiang and Li 2003).

the most offshore sites (>733 m). Ge et al. (2013) and Zhang et al. (2013) also showed that TEX86-based temperature values near shore reflect wintertime SST in the northern SCS. It also has been argued that the sediment GDGTs are deposited from the whole water column above the sediment (Schouten et al. 2002; Wuchter et al. 2006). In the SCS, previous studies have also suggested that the TEX86 index reflect subsurface temperature (Jia et al. 2012; Li et al. 2013), which would be lower than summer SST, but possibly close to winter SST for the site. Fourth, the core may be a mixture of shallow and deep water sediments as a result of MTDs.

Wang et al. (2009) show that MTDs are widely distributed in Quaternary sedimentary sequences of the continental slope in the Qiongdongnan Basin of SCS and led to effective transport of shallow sediment to the deep water (Li et al. 2011; Wang et al. 2009), suggesting the GDGTs signals may have originated mainly from near shore sediments. The core in-
deep recorded mostly near shore environment in the northern continental slope of the SCS, which is also supported by the high input of land-derived material from the near shore in the northern SCS (Chen et al. 1998; Shao et al. 2010; Xie et al. 2006). Overall, the discrepancy between TEX86 proxy and the PF proxy indicate the complex hydrological and depositional environment in the Qiongdongnan Basin.

It is important to notice that MTDs affect TEX86 in continental margins. Further work is necessary to better understand sediment depositional and transport processes from near shore to open oceans in the marginal sea and thus to better understand the changes in past sea temperature during geological history.

Conclusions

In this study we employed molecular DNA and lipid biomarker approaches to evaluate IP-GDGT effect on TEX86 in a hydrate-prospect zone in the South China Sea. The results showed that the sediment had little impact of hydrate dissociation and the archaeal community structures exhibited significant change with depth with IP-GDGTs being too small a quantity to affect TEX86 values derived from C-GDGTs. Therefore, the fossil archaeal lipids reasonably recorded the changes in past sea temperature of the near shore environment in the SCS since the last glacial maxima, which agrees generally with the winter temperature recorded by planktonic foraminifera collected from the same area of the SCS. However, due to the complex hydrological and depositional conditions of the Qiongdongnan basin, the TEX86 proxy should be used with caution in this geological unstable region.

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Supplemental Material

Supplemental data for this article can be accessed on the publisher’s website.
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