

## RESEARCH ARTICLE OPEN ACCESS

# Elevated Tropical Sea Surface Temperatures During the Globally Warm Miocene Caused Heat Stress for Caribbean Coral Reefs

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## ABSTRACT

The warm Miocene (23.0–5.3 Ma) is considered a model case for the global climate of the near future. In view of the current coral reef crisis, studies on Miocene reefs can contribute to predictions regarding the stress resilience of today's reefs against global warming. A Late Miocene (6.2–5.5 Ma) reef coral fauna from Hispaniola Island (Caribbean) characterised by ecologically tolerant taxa was originally interpreted to reflect cool-eutrophic waters. However, the associated planktonic foraminifer assemblage and new TEX<sub>86</sub><sup>H</sup>-based temperature reconstructions document an oligotrophic shallow-water environment harbouring 30–31°C. Thus, in conjunction with unusually low vertical growth rates and erratic trace element signatures of massive reef corals, the coral fauna documents critically high temperatures and a response to heat stress rather than cool upwelling. The findings demonstrate the relevance of understanding shallow-water ecosystems from past warm periods for developing scenarios of a future, warmer world.

## 1 | Introduction

The deep-sea geological record has provided astronomically calibrated time series of Cenozoic climate history (Westerhold et al. 2020). Reconstructions of sea surface temperatures (SSTs) are based on inorganic proxies, such as oxygen isotope ratios (expressed as  $\delta^{18}\text{O}$  values) or the Mg concentration (expressed as Mg/Ca ratios) of the calcite shells of planktonic foraminifers (Herbert et al. 2016; Zachos et al. 2001) while molecular biomarker-based SST-proxies  $\text{U}^{\text{K}}_{37}$  and TEX<sub>86</sub> (Prah and Wakeham 1987; Schouten et al. 2002) are based on complex organic molecules finely dispersed in the sediment. In contrast to the high-resolution SST reconstructions from the deep-sea record, complementary information on SST trends from shallow-water deposits are scarce. The concept of differentiating

warm- and cool-water shallow-marine carbonates (photozoan and heterozoan carbonates) (James 1997; Michel, Borgomano, and Reijmer 2018) allows for broad SST estimates above or below  $\sim 18^\circ\text{C}_{\text{winter}}$  only (James 1997). However, the application of the concept to eu- and mesotrophic tropical habitats is not straightforward, as heterozoan facies may have spatially co-existed with reef coral communities in meso- and eutrophic tropical waters, termed Tropical Transitional Carbonate System (TTCS) (Ortega-Ariza et al. 2023). Further complications to the concept arise from non-reefal shallow-marine carbonates that have formed during geological warm periods at critically high SSTs above the actual reef window SST (Scheibner and Speijer 2008).

For paleotemperature reconstructions of shallow-water carbonates, the use of inorganic proxies ( $\delta^{18}\text{O}$ , Mg/Ca, Sr/Ca) is

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limited by mineralogical transformations upon limestone diagenesis (Brachert et al. 2020). The tetraether index of 86 carbon atoms ( $\text{TEX}_{86}$ ) is a molecular paleothermometer based on the distribution of isoprenoidal glycerol dialkyl glycerol tetraether (GDGT) molecules in marine sediments (Schouten et al. 2002). GDGT molecules, forming the plasma-membrane of specific archaeal microbes that occur ubiquitously in marine environments, allow adaption to variable dwelling temperatures by cyclisation of the isoprenoidal chain linking the glycerol units (Schouten et al. 2002; see review in Inglis and Tierney 2020). The degree of cyclisation is expressed as the  $\text{TEX}_{86}$  ratio, which based on core-top calibrations can be converted in paleo-sea surface temperatures, whereby for tropical waters the  $\text{TEX}_{86}^{\text{H}}$ -ratio and corresponding calibration is applied (see review in Inglis and Tierney 2020). The  $\text{TEX}_{86}^{\text{H}}$  proxy was shown to be insensitive to carbonate diagenesis and applied successfully to shallow-marine carbonates (Petrick et al. 2023). This approach allows testing the effects of SST on fossil shallow-marine benthic communities with a view to warmer-than-present global temperatures in the geological past.

For the globally warm Miocene (23.0–5.3 Ma), an expansion of the reef belt to latitudes of  $\sim 45^\circ\text{N}$  is well documented (Auderset et al. 2022; Perrin 2002). This pattern is well known from the subtropical Mediterranean region, where coral reefs no longer occur (Perrin 2002). In that example, Late Miocene low generic diversity of reef corals, low growth rates (extension rates) of massive corals and frequent warm-water carbonate/cool-water carbonate changes are consistent with a location close to the outer edge of the global reef belt and frequent overshooting/undershooting of the thermal tipping point between photozoan and heterozoan carbonates (Brachert et al. 1996; Sánchez-Almazo et al. 2007). In contrast, for the warm Middle Miocene Climate Optimum,  $\text{TEX}_{86}^{\text{H}}$  records from the North Atlantic suggest critically high SSTs for reef corals/coral reefs to have been reached in the larger Mediterranean

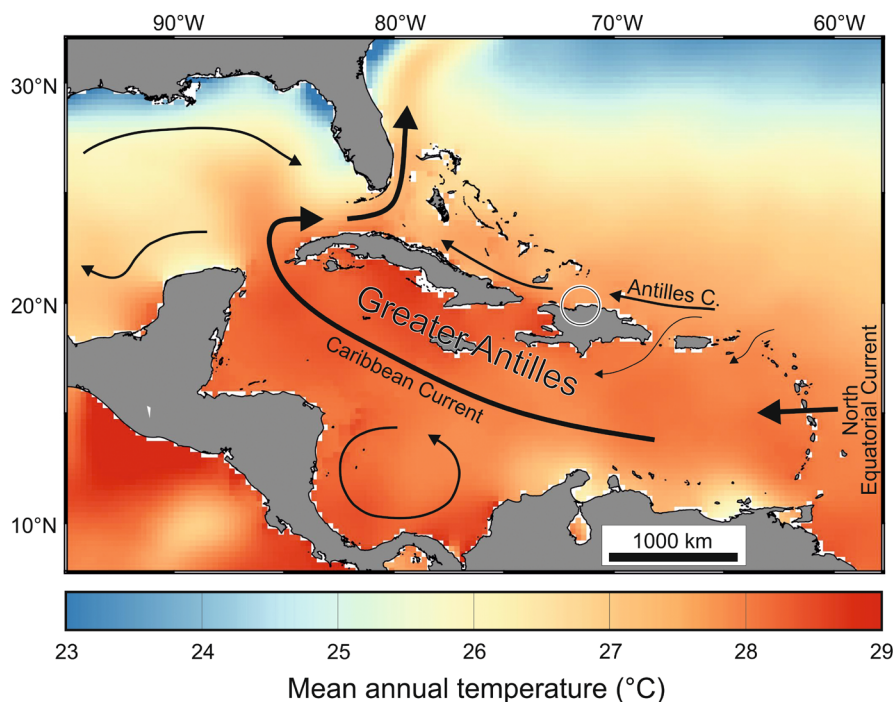
region (Super et al. 2020). Paradoxically though, widespread Miocene TTCS are reported from the tropical Caribbean region, suggested to reflect adverse effects on reef coral growth by upwelling of cool-eutrophic waters (Ortega-Ariza et al. 2023).

Here we present  $\text{TEX}_{86}^{\text{H}}$ -derived SSTs for Mio-/Pliocene TTCS from the island of Hispaniola, NW Caribbean (Figure 1) to discuss possible manifestations of thermal stress in past tropical reef communities, as currently occurring during heat waves and expected to occur as chronic stress by the end of the century. The samples were collected from shallow-marine, mixed clastic-carbonate sediments of the Cibao Basin, northern Hispaniola and imply long-term mean SSTs of 30–31°C (max. 32.6°C) for fossil coral reefs and level-bottom coral communities (Klaus and Budd 2003; McNeill et al. 2011). In addition to the new  $\text{TEX}_{86}^{\text{H}}$  data, we use a published planktic foraminifer (PF) dataset (Lutz et al. 2008; supplement) to discuss the structural differences between the region's present day coral reefs and their Miocene precursors, originally interpreted as reflections of high water turbidity and cool upwelling waters (Johnson and Pérez 2006; Ortega-Ariza et al. 2023) versus possible manifestations of heat stress. While Miocene cool SSTs or local upwelling is documented in the SW Caribbean (Huguet, Jaeschke, and Rethemeyer 2022; Steph et al. 2006), little paleoceanographic information exists for the northern side of Hispaniola (Cibao Basin).

## 2 | Material and Methods

### 2.1 | Regional Geology of the Cibao Basin, Northern Hispaniola

On the Caribbean island Hispaniola (Greater Antilles), the Cibao Basin (CB) acted as a sedimentary basin since the Late Miocene,  $\sim 10$  Ma (McNeill et al. 2011) (Figure 1, Figure S1), comprising in



**FIGURE 1** | Annual sea surface temperature of the Greater Caribbean Region averaged over the 1991–2020 period (Reagan 2023). The open circle denotes Cibao Basin, northern Dominican Republic. Black arrows delineate surface currents (Jouanno et al. 2008; Steph et al. 2006). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

its lower part a sediment wedge of non-marine to brackish and shallow-marine siliciclastics with contributions by reefal carbonates prograding northward towards the Western Equatorial Atlantic (McNeill et al. 2011). Out of these, the middle Messinian (6.6–5.9 Ma) Cercado Fm. consists of ~200 m of cross-bedded sands that grade into calcareous facies with abundant reef biota of an open marine environment in the upper part. The ~400 m thick Gurabo Fm. representing the late Messinian to Zanclean (5.6–4.0 Ma) comprises a sequence of calcareous silts with intercalated beds rich in reef corals (McNeill et al. 2011). Reefal facies of both formations were formed by a highly diverse coral fauna, with massive and robust branching forms typically preserved in life position (Klaus and Budd 2003; Klaus et al. 2007; Maier et al. 2007). Many of the coral taxa are considered ecologically tolerant in terms of (cool) SSTs and trophic grade (Edinger and Risk 1994; Ortega-Ariza et al. 2023).

Middle Messinian sediments were sampled at Arroyo Bellaco reef (AB, sites 463–465,  $n=5$ ) (Maier et al. 2007) (Figure 2, Figure S1, Table S1). The reef framework comprises branching and massive corals, interfilled with greenish, fossiliferous sandy mud that points to a more or less turbid and/or quite-water environment. Water depth at the shallowest parts of the reef section was ~5 m but even the deepest water zones with free-living corals never exceeded 20–30 m (Klaus and Budd 2003; Klaus et al. 2007; Maier et al. 2007). For the Gurabo Fm., samples were taken from the Gurabo section at site 455 ( $n=3$ ), which is characterised by a fossiliferous, greenish sandy mud with abundant reef corals in life position (Figure S1, Table S1). Previous estimates of the paleo-water depth for this site were ~30 m (Denniston, Penn, and Budd 2008). A re-evaluated dataset of PFs from the Cercado and Gurabo Fms. (Lutz et al. 2008) described in the electronic supplement was used in this study to identify paleo-hydrography (stratification vs. upwelling) and trophic state (oligotrophic vs. eutrophic surface water).

## 2.2 | GDGT Analysis and Determination of $\text{TEX}_{86}^H$

For analyses of glycerol dialkyl glycerol tetraethers (GDGTs), sediments were solvent-extracted and the alcohol fraction

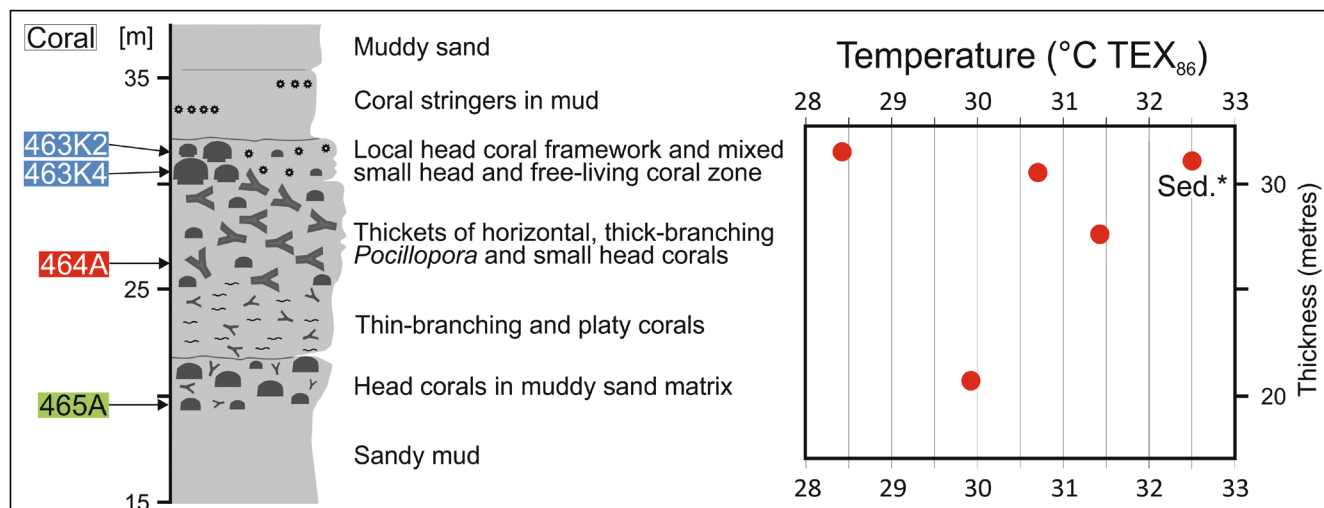
containing the GDGTs isolated, following procedures as in Petrick et al. (2023). GDGTs were analysed by LC/MS and the  $\text{TEX}_{86}^H$  calculation and calibration applied for SST reconstructions, as described in the supplement.

## 3 | Results and Discussion

The  $\text{TEX}_{86}$  values from sediment samples ( $n=8$ ) from the Cercado and Gurabo Fms. range between 0.71 and 0.82 with a mean of  $0.78 \pm 0.01$  and  $0.76 \pm 0.01$  for both formations (Table 1). Using the  $\text{TEX}_{86}^H$  calibration for temperatures  $>15^\circ\text{C}$  (Kim et al. 2010), these values are equivalent to  $30.5 \pm 0.2^\circ\text{C}$  (max.  $32.6^\circ\text{C}$ ,  $n=5$ ) for the Cercado Fm. and  $31.0 \pm 0.3^\circ\text{C}$  (max.  $31.1^\circ\text{C}$ ,  $n=3$ ) for the Gurabo Fm. (Table 1, Figure 2). A GDGT data quality assurance (O'Brien et al. 2017) to evaluate non-thermal effects on  $\text{TEX}_{86}$  (Table 1) gave BIT indices for the Gurabo Fm. of  $0.46 \pm 0.02$  and  $0.31 \pm 0.02$  for the Cercado Fm., typical for coastal marine sediments lacking major contributions from soil microbes affecting the  $\text{TEX}_{86}$  values. The GDGT-0/crenarchaeol ratios yielded values of  $0.32 \pm 0.03$  for both formations and were considered inconspicuous with no evidence for non-thermal influences and/or deviations from modern archaea analogues. The Methane Index (MI) remained  $\leq 0.3$  for all samples excluding any effects from methane oxidation (Table 1).

The samples scraped from the surface of massive corals and from within large lithophagan borings represent estimates averaged over years or probably decades, which may be reflected in the rather uniform SSTs of  $\sim 30$ – $\sim 31^\circ\text{C}$  found for the Cercado and Gurabo Fms. Since sub-annually resolved SST reconstructions based on oxygen isotope ( $\delta^{18}\text{O}$ ) data from close to site 455 of the Gurabo Fm. provided a SST seasonality of  $2^\circ\text{C}$  (Denniston, Penn, Budd 2008) (Figure S1), a fundamental seasonal change in the oceanographic situation (e.g. upwelling/stratification) and distortion of the  $\text{TEX}_{86}^H$ -derived SSTs by overemphasising one particular season is unlikely.

PFs of the Cercado and Gurabo Fms. having drifted from offshore into CB were dominated by warm-oligotrophic species



**FIGURE 2** | Stratigraphic column of the Arroyo Bellaco reef unit, Hispaniola, Greater Antilles (Maier et al. 2007, simplified), together with SSTs inferred from  $\text{TEX}_{86}^H$ . Sed\* = sediment sample; the exact position relative to the other samples from site 463 is not known. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

**TABLE 1** | TEX<sub>86</sub>-derived sea surface temperatures (triplicate analysis), Cibao Basin (Dominican Republic).

Field number	Formation	Age (Ma)	SST°C	TEX <sub>86</sub>	BIT	GDGT-0/Cren	Cren/Cren'	MI
455-B-1	Gurabo	5.5	31.00 ± 0.28	0.77 ± 0.01	0.42 ± 0.02	0.29 ± 0.03	13.79 ± 1.10	0.29 ± 0.02
455-D-2	Gurabo	5.5	31.00 ± 0.25	0.77 ± 0.01	0.51 ± 0.02	0.34 ± 0.02	13.75 ± 0.05	0.29 ± 0.01
455-F-3	Gurabo	5.5	31.13 ± 0.29	0.78 ± 0.01	0.47 ± 0.01	0.32 ± 0.01	11.86 ± 1.26	0.27 ± 0.01
Mean ± 1STD			31.04 ± 0.28	0.78 ± 0.01	0.46 ± 0.02	0.32 ± 0.02	13.13 ± 0.80	0.28 ± 0.01
463-K2	Cercado	6.2	28.46 ± 0.08	0.71 ± 0.00	0.22 ± 0.02	0.28 ± 0.02	12.89 ± 0.68	0.22 ± 0.01
463-K4	Cercado	6.2	30.22 ± 0.30	0.75 ± 0.01	0.22 ± 0.01	0.26 ± 0.02	9.36 ± 0.19	0.19 ± 0.01
463-sediment	Cercado	6.2	32.55 ± 0.22	0.82 ± 0.01	0.43 ± 0.03	0.44 ± 0.03	6.50 ± 0.37	0.19 ± 0.02
464-A	Cercado	6.2	31.51 ± 0.17	0.79 ± 0.01	0.22 ± 0.01	0.24 ± 0.02	8.25 ± 0.85	0.29 ± 0.01
465-B	Cercado	6.2	29.66 ± 0.35	0.74 ± 0.01	0.44 ± 0.02	0.33 ± 0.04	8.49 ± 0.07	0.30 ± 0.02
Mean ± 1STD			30.48 ± 0.22	0.76 ± 0.01	0.31 ± 0.02	0.31 ± 0.03	9.10 ± 0.43	0.24 ± 0.01

Note: GDGT-quality assurance indices BIT, GDGT-0/Cren, Cren/Cren' and MI remain below threshold values indicative of non-thermal influences on TEX<sub>86</sub> ratios. TEX<sub>86</sub><sup>H</sup> is considered to truly reflect Miocene paleo-SSTs.

(50%–60%) while species diagnostic of cool-eutrophic waters contributed with <10% (Lutz et al. 2008) (Table S2). The minor proportion of the cool-eutrophic assemblage to the total PF fauna does not support previous concepts of upwelling having caused cool-eutrophic conditions and the spread of TTCS (Ortega-Ariza et al. 2023), because enhanced production during the upwelling season would bias the sedimentary record towards dominance of the cool-eutrophic PF assemblage (Repschläger et al. 2023). For that reason, warm-oligotrophic (or possibly mesotrophic) waters prevailed off Hispaniola when the Cercado and Gurabo Fms. formed. Given annual SSTs 30–31°C (max. 32.6°C) by TEX<sub>86</sub><sup>H</sup> and SST seasonality ~2°C by a sub-annually resolved stable isotope record from a reef coral next to site 455 of the Gurabo Fm. (Denniston, Penn, and Budd 2008), seasonal upwelling is highly unlikely to have occurred (Spreter et al. 2022; Tudhope et al. 1996). Thus, the reefal deposits of the Cercado Fm. formed in a low-nutrient environment (Maier et al. 2007) and it is likely that this also applies to the Gurabo Fm., in particular site 455. This scenario is consistent within a context of warm-saline water masses of the North Equatorial Current (NEC) and Antilles Current (AC) striving northern Hispaniola (Huguet, Jaeschke, and Rethemeyer 2022; Steph et al. 2006) (Figure 1).

### 3.1 | Significance of the Miocene TEX<sub>86</sub><sup>H</sup> Records From the Cibao Basin

The TEX<sub>86</sub><sup>H</sup>-reconstructed SSTs presented here agree with a very warm, oligotrophic setting that was shallow enough (5–30m depth) to house reef corals (Klaus and Budd 2003; Klaus et al. 2007; Maier et al. 2007). Also, fine-grained, siliciclastic sediments in combination with massive coral growth forms (Denniston, Penn, and Budd 2008; Klaus et al. 2007) indicate growth at very shallow depths and good light availability but low wave energy (Geister 1983). For most modern tropical shallow-water corals, a critical thermal maximum is reached between ~26 and ~29°C annual temperature (Jokiel and Coles 1977; Lough and Cantin 2014), which is still above present day SSTs off Hispaniola Figure 1, though below those of the Miocene (Auderset et al. 2022; Herbert et al. 2016). According to modern standards, annual mean SSTs of 30–31°C (max. 32.6°C) as inferred from the TEX<sub>86</sub><sup>H</sup> records would imply chronic heat stress for the Mio-/Pliocene corals. Thus, the presence of many ecologically tolerant coral taxa (Edinger and Risk 1994; Ortega-Ariza et al. 2023) together with small extension rates by massive corals are likely not due to cool-eutrophic and turbid waters (Denniston, Penn, and Budd 2008; Johnson and Pérez 2006). Rather, a main characteristic of coral skeletal growth beyond the critical thermal maximum is a strongly reduced performance in skeletal extension (Lough and Cantin 2014; DeCarlo and Cohen 2017). In line with heat stress causing stunted skeletal growth, discrepant results of the δ<sup>18</sup>O- and Sr/Ca-thermometers regarding seasonal SST contrasts and inter-annual SST variations (Denniston, Penn, and Budd 2008; Weiss et al., 2017), are also the likely manifestation of physiological stress that causes anomalous trace element geochemical signatures (Clarke et al. 2019, 2017; D'Olivo and McCulloch 2017).

Results shown here imply Mio-/Pliocene coral growth in the tropical Greater Antilles province of the Caribbean at critically high SSTs. Current concepts in carbonate sedimentology only foresee a warm-water facies with a biogenic photozoan association and



cold-water facies with a heterozoan association plus TTCS representing an intermediate stage (James 1997; Michel, Borgomano, and Reijmer 2018; Ortega-Ariza et al. 2023). Accordingly, current concepts of the shallow-marine carbonate record of the tropics and subtropics for the Warm- or Hothouses of the geological past need revision with regard to scenarios pertaining to a warmer-than-present world.  $\text{TEX}_{86}^{\text{H}}$ -derived SSTs for a classic example of cool-water carbonates imply the upper limit of the reef window (Petrick et al. 2023). This is consistent with non-reefal, larger benthic foraminifer-dominated shallow-marine carbonates from the Eocene Hothouse climate as a representation of a temperature regime above the reef window temperature (Scheibner and Speijer 2008). Here, it is proposed to re-interpret the Mio-/Pliocene coral accumulations of the Cibao Basin as TTCS (Ortega-Ariza et al. 2023), but at the upper SST-end of the reef window characterised by heat stress-related slow-growing and ecologically tolerant coral taxa (Edinger and Risk 1994).

## 4 | Conclusions

The late Miocene to early Pliocene Cercado and Gurabo Fms. of the Cibao Basin (Hispaniola, Greater Antilles) represent shallow-marine, mixed clastic-carbonate depositional systems. Coral reefs and level-bottom coral communities, intercalated with marine clastics, are characterised by a diverse but ecologically tolerant reef coral fauna. A quantitative reassessment of the associated planktonic foraminifer fauna has shown that a warm-oligotrophic community dominated, but a subordinate cool-eutrophic community occurred in parallel. To resolve this contradiction, we applied the  $\text{TEX}_{86}^{\text{H}}$  molecular paleothermometer to sediment samples collected from coral surfaces and bivalve borings within coral skeletons.  $\text{TEX}_{86}^{\text{H}}$  data imply that long-term SSTs of 30–31°C (max. 32.6°C) prevailed. Consistently, the low extension rate of massive reef corals and incompatible signatures of the  $\delta^{18}\text{O}$  and Sr/Ca coral-paleothermometers as well as the predominance of ecologically tolerant coral species indicate heat stress. In contrast to previous views, the reef coral occurrences of the Cercado and Gurabo Fms. would thus not be an expression of SSTs near the lower threshold temperature of the reef window but rather at its upper limit. This study demonstrates the capacity of the  $\text{TEX}_{86}^{\text{H}}$ -method for SST reconstruction in carbonate environments that, in combination with proxy analyses of fossil reef corals, can provide intriguing contributions to estimating the stress resilience of coral reefs in the warming world of the nearer future.

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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.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.