Late Eocene tropical sea surface temperatures: A perspective from Panama

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Received 2 November 2000; revised 22 October 2001; accepted 22 January 2002; published 6 August 2002.

[1] We have reconstructed mean annual coastal temperatures and seasonality during the Eocene (Priabonian; 36.6–40 Ma) using oxygen isotope profiles of shallow marine aragonitic gastropods (Gatuncillo Formation, Panama). These data provide a unique opportunity to document low-latitude coastal climates during a preglacial “greenhouse” period. Assuming shell oxygen isotope profiles primarily reflect changes in water temperature, our results indicate water temperatures in a middle to outer shelf setting (20–50 m depth) varied by 6°–8°C, and mean annual temperatures (MAT) were >26°C. These temperatures are in agreement with pollen-based surface temperature reconstructions for the late Eocene and are consistent with other Eocene mollusk-based tropical coastal temperature estimates but are at odds with the few Eocene foraminiferal-based estimates of mean annual tropical sea surface temperatures (≈17°–22°C).

INDEX TERMS: 4267 Oceanography: General: Paleooceanography; 9604 Information Related to Geologic Time: Cenozoic; 1040 Geochemistry: Isotopic composition/chemistry; KEYWORDS: Eocene, stable isotopes, tropical environment, sea surface temperatures, Paleogene, mollusca

1. Introduction

[2] Climate proxy records indicate surface temperatures dramatically changed during the Eocene–early Oligocene from a warm “greenhouse” state to colder “icehouse” conditions. The late Eocene (Priabonian; 36.6–40 Ma) represents a critical transition interval following a long-term cooling trend (beginning in the early Eocene), and precluding the onset of large-scale continental glaciation. Currently it is unclear whether these climate changes were in response to long-term changes in atmospheric greenhouse gas levels [Pearson and Palmer, 2000; Sloan and Rea, 1995; Freeman and Hayes, 1992] and/or to associated shifts in atmospheric/oceanic circulation [Lear et al., 2000; Sloan and Rea, 1995; Rind and Chandler, 1991].

[3] Accurate reconstructions of tropical sea surface temperatures (SST) and the equator-to-pole (E-P) temperature gradient for this interval are useful in evaluating climate experiments designed to evaluate the cause(s) of Eocene-Oligocene global climate shift. Climate theory predicts tropical SST and the E-P surface temperature gradient are extremely sensitive to variations in greenhouse gas levels and meridional heat transport. Specifically, changes in greenhouse gas levels would tend to influence surface temperatures at all latitudes (unequally), whereas changes in circulation would redistribute heat.

[4] Existing paleotemperature records show pronounced surface cooling over land [Wolfe, 1978] and sea [Lear et al., 2000; Zachos et al., 1994] at middle and high latitudes during the Eocene and Oligocene. Whether tropical temperatures cooled, however, is unclear. Oxygen isotope measurements of shallow marine mollusks, marine faunal data, and terrestrial records indicate late Eocene-Oligocene tropical temperatures similar to or slightly warmer than modern [Kobashi et al., 2001; Graham, 1994, 2000; Adams et al., 1990; Greenwood and Wing, 1995], whereas oxygen isotope-based SST records are interpreted as recording a long-term cooling of tropical temperatures from 24°–26°C in the early Eocene to 17°–22°C in the late Eocene [Zachos et al., 1994; Douglass and Savin, 1978]. These oxygen isotope-based SST estimates are controversial because (1) values for the late Eocene differ by as much as 8°C from temperatures estimated using other proxies, (2) Eocene tropical SST estimates are 6°–8°C cooler than Pleistocene and Last Glacial Maximum surface temperatures, when ice volume was greater, and (3) they are based on relatively few data. Additional quantitative surface temperature estimates for the low latitudes during the Eocene may help resolve the discrepancy between these proxy data sets.

[5] Empirical water temperature-shell δ¹⁸O calibrations have been developed for both aragonitic and calcitic mollusks [Grossman and Ku, 1986; Anderson and Arthur, 1983] and are commonly employed in Quaternary paleoclimate studies for reconstructing nearshore paleoenvironments. The primary challenge in obtaining paleotemperature estimates using shallow-water mollusks is to isolate potential salinity and diagenetic effects on δ¹⁸O. Isotope-based paleotemperature reconstructions have been relatively underutilized in coastal settings for the pre-Quaternary, primarily because well-preserved molluscan shell material is rare. However, several recent studies have shown that the preservation of primary geochemical signatures in fossil shells can be determined using both textural and geochemical data. The diagenetic transition of aragonite, a metastable form of calcium carbonate, to low-Mg calcite and of low-Mg calcite to high-Mg calcite is accompanied by distinct changes that can be used as criteria to determine shell preservation [Krantz et al., 1996; Al-Aasm and Veizer, 1986a, 1986b]. Thus it appears that pre-Quaternary climate
can be accurately reconstructed using isotopic data from well-preserved aragonitic mollusks [Andreasson and Schmitz, 1998; Purton and Brasier, 1997].

This study estimates tropical surface temperatures during the late Eocene (Priabonian) using stable isotope profiles of well-preserved fossil mollusk shells. Specimens analyzed are from an outcrop of the Gatuncillo Formation of Panama. Specifically, we use published faunal and geochemical data for this formation to reconstruct the paleoenvironmental setting (depth, salinity, etc.) and estimate seasonality and mean annual temperature (MAT) using oxygen isotope measurements of aragonitic fossil shells.

2. Background

2.1. Lithostratigraphy

The Gatuncillo Formation is a 900 m thick transgressive sequence of terrestrial, brackish water, and marine sediments [Woodring and Thompson, 1949] which outcrops throughout Panama. This sequence unconformably overlies Cretaceous basement (altered volcanic pyroclastic and tuff deposits) and is overlain by deep marine sediments of the Oligocene Bohio Formation (Figure 1). The formation consists primarily of mudstone and siltstone, with thin limestone and sandstone beds [Woodring, 1970, 1957; Woodring and Thompson, 1949].

Benthic foraminifers and mollusks are the dominant fauna in the upper Gatuncillo Formation [Woodring, 1957; P. Franceschi, personal communication, 1999]. Planktonic foraminifers (P. Franceschi, personal communication, 1999) do occur but are rare. In addition, coral [Budd et al., 1992] and echinoids [Cooke, 1948] occur at some localities. Published biostratigraphy based on these faunal data indicate the terrestrial and marine sediments of the Gatuncillo Formation are late middle to late Eocene in age [Escalante, 1990; Graham, 1985; Jenkins, 1964; Woodring, 1957; Woodring and Thompson, 1949].

2.2. Fossil and Locality Description

Specimens were obtained from the invertebrate paleontology collections of the Paleontological Research Institute (PRI) and the Smithsonian Institution’s National
Museum of Natural History (SMITH). PRI specimens are part of the Olsson Collection and were collected from shale and siltstone beds near Rio Terrable (Figure 2), ~50 miles east of Panama City (Olsson [1942], locality 1053). SMITH specimens were collected by Robert and Jay Stewart of the Panama Canal Commission [Stewart et al., 1981] and identified by Woodring [1982, 1970, 1964, 1959, 1957]. SMITH samples analyzed are from both shales and siltstones near the upper course of the Rio Palenque, Palenque, Colon Province (U.S. Geological Survey (USGS) locality 24553) and a sandy limestone near a tributary of the Guaniquito (USGS locality 8286). We chose to analyze specimens from these localities because of the remarkable preservation of shell nacre, growth banding, and ornamentation.

[10] Isotopic analyses were carried out on Hannatoma antyx, Ampullela olssoni, Mytilus terrablensis, and Anomia cf. lisbonensis. Photographs of the gastropods are shown in Figure 3. H. antyx is an extinct cerithid gastropod similar to the modern cerithid Mesalia, which lives in sandy temper-
ate marine waters eating algae and detritus. *A. olssonii* is an extinct naticid gastropod. Modern naticids are predatory, adapted to living in sand, and are common in beach and sandy shallow marine environments. Both species belong to families that precipitate aragonitic shells. The bivalves *M. terrablenesis* and *Anomia* sp. have modern relatives that are predominantly shallow marine epifaunal suspension feeders. Members of the genus *Mytilus* precipitate both aragonitic and bimineralic (calcite and aragonite) shells; anomids only precipitate calcitic shells.

11 Mollusks tend to precipitate skeletal material in oxygen isotopic equilibrium (or near equilibrium) with seawater [Grossman and Ku, 1986]. In addition, isotope studies of modern taxa related to *H. antyx* [Kobashi et al., 2001; Rahimpour-Bonab et al., 1997; Allmon et al., 1994, 1992] and *M. terrablenesis* [Klein et al., 1996; Killingley and Berger, 1979] support our assumption that δ¹⁸O values of fossil shells can be used to reconstruct ambient water conditions. However, it is likely that shell δ¹³C values do record some disequilibrium or “vital” effects [Tanaka et al., 1986].

2.3. Modern Oceanographic Setting of Panama

12 Today the presence of the isthmus results in a strong temperature and salinity contrast between the Pacific and Caribbean coasts [Levitus and Boyer, 1994], which is evident in isotopic profiles of modern mollusks from Panama [Bemis and Geary, 1996; Geary et al., 1992]. The eastern Pacific is fresher than the western Atlantic because of high rates of evaporation in the Caribbean and transport of this moisture-rich air to the Pacific. In addition, intense summer rainfall (508 cm/yr) and associated high runoff rates result in large seasonal salinity variations along the southern (Pacific) coast of Panama. The southern coast is also characterized by winter/spring upwelling. As a result, waters along the Pacific coast of Panama exhibit high interannual temperature and salinity variability relative to the Caribbean coast, where little upwelling is observed and precipitation rates are substantially lower (208.28 cm/yr [Levitus and Boyer, 1994]). The salinity and upwelling differences between the northern and southern coasts of Panama are thought to have evolved as a direct consequence of the uplift of the Central American Isthmus in the Pliocene [Collins, 1996; Teranes et al., 1996].

2.4. Previous Work on Modern and Fossil Mollusks From Panama

13 Studies of modern gastropods and bivalves from several sites in Panama have accurately reconstructed mean annual temperature and seasonality using detailed oxygen isotope profiles of tropical shallow-water mollusks [Bemis and Geary, 1996; Geary et al., 1992]. Bemis and Geary and Geary et al. have shown that shell isotope profiles record seasonal fluctuations in nearshore water δ¹⁸O and δ¹³C on both the Pacific and Caribbean coasts, associated with changes in water salinity and upwelling, respectively. On the basis of the strong correlation between environmental conditions and shell isotope profiles in Panama [Bemis and Geary, 1996; Geary et al., 1992], Florida [Jones and Allmon, 1991], and Mexico [Allmon et al., 1992], several studies have reconstructed tropical water temperatures and coastal upwelling during the Neogene [Teranes et al., 1996; Jones and Allmon, 1995]. These mollusk-based paleoclimate estimates agree with other proxy-based climate reconstructions [Jones and Allmon, 1995].

### Table 1. Partial List of Invertebrate Fauna Found in Gutuncillo Formation

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<th>Taxon</th>
<th>Larger benthic foraminifera&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Other abundant foraminifera&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Echinoids&lt;sup&gt;c&lt;/sup&gt;</th>
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<td>Lepidocyclina chaperi&lt;sup&gt;b&lt;/sup&gt;</td>
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<sup>a</sup> Woodring [1957], Coryell and Embich [1937], Cole [1949, 1952], and Vaughan [1926].

<sup>b</sup> Described as abundant in literature.

<sup>c</sup> Cooke [1948] and Durham [1954].

<sup>d</sup> Woodring [1957], Woodring and Thompson [1949], Olsson [1942], and Coryell and Embich [1937].
**lisbonensis** specimen) were analyzed. Analyses of multiple specimens of each taxa were made to ensure that our paleotemperature estimates reflect long-term averages. Multiple taxa with different ecological niches were analyzed to prevent biases in the data from microenvironmetal differences or seasonal cessation of growth.

[15] X-ray diffraction patterns, cathodoluminescence, scanning electron microscopy (SEM), petrographic analyses, and isotope data were used to determine specimen preservation using the model of *Al-Aasm and Veizer* [1986a, 1986b]. Taxa that precipitated aragonitic shells were chosen for detailed sampling because aragonite is metastable, making alteration relatively easy to detect.

[16] Nine gastropod specimens were sampled at high resolution; bulk samples were taken from the remaining gastropod and bivalve specimens. Powdered carbonate microsamples were drilled from individual growth bands (Figure 3), similar to the sampling technique discussed by Allmon et al. [1992]. Samples were taken at intervals of 0.5–3 mm intervals. Powdered samples weighing between 20 and 100 µg were then analyzed on either a Micromass Prism or a Micromass Optima gas source mass spectrometer with a common acid bath at the University of California, Santa Cruz, Stable Isotope Laboratory. Stable isotope values with a precision of better than 0.000018 for most samples. Six hundred ratios were collected on each sample, resulting in pronounced cyclicity. Several of the *H. antyx* intrashell carbon isotope profiles exhibit a drift toward low values, possibly due to ontogeny or growth rate-related fractionation. *Ampullella olssoni* profiles exhibit δ18O values between −1.5 and −3‰ and δ13C values between 0 and −4.5‰ and do not show any trends as a function of time.

4.4. Strontium Isotope Data

[22] The 87Sr/86Sr and stable isotope data for sample splits are listed in Table 2. *Hannatoma antyx* specimens (n = 18) have an average 87Sr/86Sr ratio of 0.70765 ± 0.00002, and *Ampullella olssoni* specimens (n = 4) average 87Sr/86Sr values are calculated as 0.70757 ± 0.00001. These data are plotted in Figure 6.

5. Discussion

5.1. Chronostratigraphy

[23] The larger foraminifera assemblage (*Lepidocyclina chaperi*, *Lepidocyclina pustulosa*, *Astrocyclus georgiana*, and *Astrocyclus minima*) as well as other taxa present (e.g., echinoid species *Peronella (Neolagumenum) dally*) also occurs in the Ocala Limestone of Florida and in the Yellow Limestone of Jamaica. These taxa clearly indicate sediments are late Eocene (SBZ 19-20; Priabonian) in age [Frost and Langenheim, 1974; Robinson, 1968, 1993]. In addition, *Hantkenina alabamensis* indicates a latest Eocene age.
The local molluscan fauna also occurs in late Eocene and early Oligocene sediments of California, Venezuela, Columbia, and Jamaica [Durham et al., 1949]. Together these faunal data confirm a latest Eocene age (Priabonian). This age estimate for the marine Gatuncillo fauna is consistent with interpretations of palynological data from underlying terrestrial sediments [Graham, 1985] that indicate a late Eocene age.

5.2. Strontium Isotope Data

One obstacle to reconstructing temperatures from the shell chemistry of marine fossils preserved in land-based outcrops is in detecting the effects of meteoric diagenesis, particularly recrystallization that occurs on a microscale. Our gastropod shells exhibit a wide range of strontium isotope values. The highest shell \(^{87}\text{Sr}/^{86}\text{Sr}\) ratios are ~0.7077, which is identical to late Eocene seawater values [Zachos et al., 1999]. Specimens with low Sr isotope values may be older than late Eocene and reworked, or the marine Sr isotope record, which is sparse during the late Eocene, may be overprinted and/or noisy. However, the lowest shell value, 0.70753, is substantially lower than late Eocene seawater and more like values for the middle-upper Cretaceous (~75 million years ago [Howarth and McArthur, 1997]), which is well outside of the range for these fossil mollusks.

Lower shell Sr isotope ratios might reflect the presence of nonlattice bound Sr (e.g., clays and adsorbed Sr), freshwater dilution, and/or diagenetic overprinting. To determine whether there was a noncarbonate component contributing Sr to the samples (i.e., clays and adsorbed Sr), sample splits for specimens 117 and 118 were prepared using a different method (rinsed in an ammonium oxalate solution and dissolved in nitric acid). The cleaning did not appear to affect shell Sr isotope values (Table 2). Thus we conclude that shell carbonate is the dominant source of the strontium analyzed.

Assuming the range in shell Sr isotope values does represent differing amounts of freshwater dilution, water...
Salinity can be estimated using a late Eocene marine $^{87}$Sr/$^{86}$Sr value of 0.7077 and a $^{87}$Sr-depleted freshwater end-member. For the hypothesized freshwater end-member we assume Mesozoic carbonates and/or volcanics were being weathered \cite{Howarth and McArthur, 1997; Faure, 1986}. A potential source of Mesozoic $^{86}$Sr-enriched limestones and volcanics is the Nicoya ophiolite complex (or associated accretionary terranes), currently exposed in Costa Rica and Panama \cite{Di Marco, 1994; Dengo, 1962}. Water salinity estimates are derived by assuming a range of freshwater Sr isotope ratios.

**Figure 5.** Isotope profiles of four gastropod shells sampled in this study. Values are reported in delta notation in units of per mil relative to a VPDB standard. Each specimen is estimated to have lived for 1–3 years on the basis of the number of maxima and minima. Error in isotope analyses is estimated as 0.05% for oxygen and 0.10% for carbon, based on accuracy of standards and precision of standards and sample replicates.

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<th>Species</th>
<th>Sample Name</th>
<th>Method</th>
<th>$^{87}$Sr/$^{86}$Sr ($\pm1\sigma$)</th>
<th>$\delta^{18}$O (VPDB)</th>
<th>$\delta^{13}$C (VPDB)</th>
<th>Preservation</th>
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<td><em>H. antyx</em></td>
<td>SMITH-117 (bulk)</td>
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<td>0.707681 ± 0.000011</td>
<td>-2.66</td>
<td>-1.43</td>
<td>P</td>
</tr>
<tr>
<td><em>H. antyx</em></td>
<td>SMITH-117-1</td>
<td>2</td>
<td>0.707742 ± 0.000018</td>
<td>-2.17</td>
<td>-0.76</td>
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<tr>
<td><em>H. antyx</em></td>
<td>SMITH-117-3</td>
<td>2</td>
<td>0.707726 ± 0.000018</td>
<td>-2.69</td>
<td>-1.49</td>
<td></td>
</tr>
<tr>
<td><em>H. antyx</em></td>
<td>SMITH-117-4</td>
<td>2</td>
<td>0.707635 ± 0.000018</td>
<td>-2.71</td>
<td>-2.73</td>
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<tr>
<td><em>H. antyx</em></td>
<td>SMITH-118 (bulk)</td>
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<td>0.707593 ± 0.000011</td>
<td>-3.02</td>
<td>-2.69</td>
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<tr>
<td><em>H. antyx</em></td>
<td>SMITH-118-1</td>
<td>2</td>
<td>0.707594 ± 0.000018</td>
<td>-3.11</td>
<td>-2.31</td>
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</tr>
<tr>
<td><em>H. antyx</em></td>
<td>SMITH-118-1B</td>
<td>1</td>
<td>0.707565 ± 0.000018</td>
<td>-3.15</td>
<td>-2.34</td>
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<td><em>H. antyx</em></td>
<td>SMITH-118-2</td>
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<td>0.707594 ± 0.000018</td>
<td>-3.09</td>
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<td><em>H. antyx</em></td>
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<td>0.707619 ± 0.000018</td>
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<td>-2.29</td>
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<td>SMITH-3 (bulk)</td>
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<td>0.707694 ± 0.000013</td>
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<td><em>H. antyx</em></td>
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<td>0.707653 ± 0.000030</td>
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<td>P</td>
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<td><em>H. antyx</em></td>
<td>SMITH-5 (bulk)</td>
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<td>0.707660 ± 0.000017</td>
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<td>SMITH-6 (bulk)</td>
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<td>0.707703 ± 0.000013</td>
<td>-3.10</td>
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<td><em>H. antyx</em></td>
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<td><em>H. antyx</em></td>
<td>PRI-6 (bulk)</td>
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<td>0.707740 ± 0.000011</td>
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<td>PRI-21 (bulk)</td>
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<td><em>A. olssoni</em></td>
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</table>

$^{a}$, dissolved in hydrochloric acid; $^{b}$, rinsed in ammonium oxalate and dissolved in nitric acid.

$^{b}$, pristine; ?, questionable preservation.
and concentrations and comparing shell Sr isotope data to mixing curves (Figure 7) using the method of Bryant et al. [1995]. H. antyx shell Sr isotope values correspond to water salinities between 20 and 35. Water salinities between 10 and 20 are estimated using the A. olssonii Sr isotope ratios. This calculation suggests some organisms spent the majority of their life in waters with a salinity of 20, while others (belonging to the same species) were in fully marine waters. If this is true, we would predict that shell strontium isotope values should be correlated to oxygen isotope values. However, shell strontium isotope values do not show a statistically significant correlation to oxygen or carbon isotope values (Figure 6). This implies that different individuals did not grow in waters with radically different water salinities and strontium isotope values. In addition, specimens do not exhibit significant intershell variability in Sr isotope values (Table 2), suggesting that water salinity did not vary significantly over the course of a few years.

[27] The observed range in shell strontium isotope values can be explained by diagenetic alteration of some specimens. Examination of the high-resolution stable isotope and strontium isotope data set for SMITH-117 and SMITH-118 (Table 2 and Figure 5) shows the following: SMITH-117 is characterized by late Eocene marine Sr isotope values and exhibits a range in δ18O and δ13C values of 1.2 and 3.6%, respectively. In contrast, SMITH-118 has a nonmarine Sr isotope signature and does not show as much intershell variability in stable isotope values (Δδ18O of 0.7‰ and Δδ13C of 2.4‰), consistent with shells being diagenetically overprinted. Although we cannot unequivocally demonstrate the presence of secondary carbonate, we must conclude that specimens with shell Sr isotope values with strontium isotope ratios that are lower than an acceptable late Eocene seawater ratio of ~0.70770 ± 0.00005 are suspect, even though bulk mineralogy and mean shell δ18O and δ13C values are similar to values for shells with a higher Sr isotope ratio.

5.3. Paleoenvironmental Setting

[28] Gatuncillo fauna at Rio Palenque include coral, abundant marine mollusks, echinoids, and larger foraminifera [Woodring, 1957]. All the taxa present clearly indicate growth in shallow (<100 m), fully marine, clear tropical waters. The lack of planktonic foraminifera and the excellent preservation of shells (bivalves are articulated; specimens are not abraded) are consistent with in situ deposition and minimal transport. Larger foraminifera are characteristic of tropical waters with little input of terrigenous material (i.e., near islands and away from rivers). The abundance and diversity of these large rotaliine-form, photosymbiont-bearing benthic foraminifera (for example, A. minima, A. georgigana, and L. pustulosa) indicate warm (>22°C), oligotrophic, shallow waters (intermediate photic zone; <100 m) with normal marine salinities of 34 [Hallock and Glenn, 1986]. In addition, the shapes and types of larger foraminifera (i.e., N. striatoreticulatus, O. floreidensis, O. jacksonensis, O. vaughani, A. minima, and L. pustulosa) and the types of shallow water mollusk taxa (i.e., Anomia sp. and Hannatoma antyx) indicate growth in an open marine, middle to outer shelf setting in water depths between 20 and 70 m [Kumar and Saraswati, 1997; Lee et al., 1997; Hallock and Glenn, 1986; Moore, 1964; Woodring, 1957]. In addition, the presence of H. abamemesis [Woodring, 1957; Coryell and Embich, 1937] supports a deeper-shelf depositional setting.
On the basis of the foraminiferal and molluscan faunal assemblages, we interpret these sediments as having been deposited in reef and shallow foreslope settings, in water depths of 20–70 m [Kumar and Saraswati, 1997; Hallock and Glenn, 1986; Setiawan, 1983].

5.4. Freshwater Input

The faunal data discussed in section 5.3 sets some general constraints on the paleoenvironmental setting of Panama and supports the interpretation that the marine strata of the Gatuncillo were deposited in a shallow tropical sea. Furthermore, the taxa present indicate that in general, water temperatures were warm and salinities were close to open marine values. Nonetheless, quantitative estimates of water salinity are needed in order to use shell oxygen isotope data to estimate water temperatures. To quantify paleosalinities, we use published faunal data and shell $\delta^{13}C$ profiles.

The molluscan fauna present in the Gatuncillo consist of taxa that are thought to be fully marine (e.g., Anomia and H. antyx), primarily marine (e.g., Mytilus), and both marine and estuarine (e.g., Tellina). This molluscan assemblage indicates that either conditions were wholly marine or varied from marine to estuarine spatially and/or temporally. More detailed examination of the published foraminiferal data [Coryell and Embich, 1937] suggests growth in fully marine conditions. Examination of the wall structure of the foraminiferal assemblages and comparison to environmental fields for living assemblages [Murray, 1991, 1973] indicate growth in a normal marine environment. In addition, the high biodiversity and the specific genera present suggest growth in a shelf setting characterized by marine salinities [Murray, 1991].

In addition, the presence of several taxa that are restricted to marine-stenohaline environments indicate normal marine salinities [Hudson, 1990]. Specifically, the presence of echinoids [Woodring, 1957; Durham, 1954; Cooke, 1948], coral [Woodring, 1957], larger benthic foraminifera [Woodring, 1957; Coryell and Embich, 1937], and Aturia peruviana [Miller and Furnish, 1939], a Tertiary nautiloid, supports fully marine conditions.

Published faunal data are used to establish marine salinities and argue against freshwater dilution. Using this framework, shell geochemical data are used to confirm whether hydrographic conditions changed appreciably during the year. Directly using shell $\delta^{13}C$ data to interpret water salinities is complex because of several factors. The carbon isotope ratio of mollusk shells reflects the composition of a variety of CO2 sources, including dissolved inorganic carbon (DIC) in ambient waters and CO2 from respiration. In addition, shell $\delta^{13}C$ can be influenced by growth rate and ontogenetic age.

The range in carbon isotope values within each shell is used to estimate the seasonal range in the ambient water DIC $\delta^{13}C$. To do this, we assume the $\delta^{13}C$ of shell material is precipitated in equilibrium with the $\delta^{13}C$ of DIC or offset by a (roughly) constant amount from equilibrium values. The $\delta^{13}C$ values for modern shallow-water turritellid gastropods (closely related to cerithid gastropods) are within the range of predicted equilibrium carbon isotope values and range from 1 to 3% (37 individuals at 22 different locations).

Because river runoff is a source of $^{13}C$-depleted DIC and $^{18}O$-depleted water, shells precipitating in estuarine settings should generally (1) have a larger range in $\delta^{13}C$ than marine shells, (2) have $\delta^{18}O$ ratios that are correlated with $\delta^{18}O$ values, and (3) be extremely depleted in $\delta^{13}C$. A cross plot of $\delta^{13}C$ and $\delta^{18}O$ (Figure 8) shows that most H. antyx specimens exhibit a relatively small $\delta^{13}C$ range, there is no statistically significant correlation between $\delta^{13}C$ and $\delta^{18}O$ (Figure 8) for most of the samples (the exception is

![Figure 8](https://example.com/figure8.png)

Figure 8. Oxygen-carbon isotope cross plot of isotope data for well-preserved gastropod shells. Each symbol represents a different specimen. The heavy isotope values and lack of a significant correlation between the oxygen and carbon isotope data indicate these individuals grew in waters that were not subject to freshwater dilution during most of the year.
SMITH-117; Figure 9), and mean shell isotope values are relatively heavy. We interpret this to mean that the ambient water DIC δ¹³C and water salinity did not change significantly on seasonal and intra-annual timescales for most individuals. Finally, the lack of Sr isotope variability in shells with late Eocene marine values gives us additional confidence in our interpretation of the faunal and carbon isotope data.

5.5. Marine Salinities and δ¹⁸O

[35] Today the north coast of Panama is characterized by waters with high salinity and δ¹⁸O values due to evaporative enrichment of Caribbean waters. This isotopically depleted vapor is transported to the Pacific, resulting in fresher waters with lower δ¹⁸O values. Paleogeographic reconstructions for the Eocene indicate there was open communication between the Atlantic and the Pacific along the Tropical American Seaway. Without the isthmus serving as a barrier between ocean basins, surface waters off of the northern and southern coasts of Panama would be more uniform in isotopic composition and salinity. Water salinities (and δ¹⁸O) along any region of the Panamanian coast would be controlled by the salinity of Caribbean source waters (Atlantic Ocean), local rates of evaporation and precipitation, upwelling, and fluvial inputs. During the late Eocene the relative enrichment of Caribbean waters would be slightly decreased relative to modern because the net transport of freshwater would be much lower (due to the lack of the isthmus), while evaporation rates were probably similar to (or slightly higher than) modern. On the basis of our

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**Figure 9.** Calculated paleotemperatures and stable isotope profiles for well-preserved *H. antyx* specimens (SMITH-117, SMITH-14, SMITH-118, and SMITH-7). Water temperatures are calculated using a δ₁₂O value of −0.8‰ (SMOW) and aragonite paleotemperature equation of Grossman and Ku [1986].
interpretation of the faunal assemblage and isotope data, we assume that upwelling and freshwater input was negligible. Modern surface salinities off the coast of Panama in the Caribbean are 35.0, and in the Pacific they are 32.6 (annual average at 20 m depth [Levitus and Boyer, 1994]). Seasonally, water salinities vary from 34.1 to 35.9 along the Caribbean coast, and along the Pacific coast they vary from 31.2 to 34. We estimate mean annual water salinities at water depths near 10–25 m were around 33.5 ± 0.5 during seasonally by 0.4°C. If we assume that water δ18O values fluctuated seasonally by 0.4‰, a slightly smaller mean annual range in temperature (MART) of 6°C is calculated. Using the salinity-δ18O relationship for the Gulf of Mexico, we calculate average winter and summer temperatures of 25.5 and 33.5°C, respectively. If we assume that water δ18O values fluctuated seasonally by 0.4‰, a slightly smaller mean annual range in temperature (MART) of 6°C is calculated. Using the salinity-δ18O relationship for the Gulf of Mexico, we calculate the same MAT (31°C) and seasonal range in temperatures (6°C–8°C). Even with greatly reduced water salinities (28), mean annual temperatures similar to modern are calculated (26°C–28.5°C; Table 3). Owing to uncertainties associated with reconstructing water salinities and δ18O and potential diagenetic artifacts these temperature calculations cannot be precisely interpreted. With these caveats we infer from these calculations a mean annual temperature >26°C and a seasonality of 6°C–8°C.

5.6. Paleotemperature Reconstruction

Figure 9 shows the oxygen isotope profiles of four well-preserved H. antyx shells analyzed with a corresponding temperature scale (assuming a surface water δ18O of −0.8‰). Water temperatures are calculated using the following equation:

\[ T(°C) = 20.6 - 4.34(\delta^{18}O_a - \delta^{18}O_w), \]

where \( \delta^{18}O_a \) is the oxygen isotopic composition of aragonite relative to the standard VPDB and \( \delta^{18}O_w \) is the isotopic composition of water relative to MOW, or mean ocean water [Grossman and Ku, 1986]. The relationship between SMOW and MOW is

\[ \delta^{18}O_{MOW} = \delta^{18}O_{SMOW} - 0.2‰ \]

A mean annual temperature of 30°C is calculated using the water δ18O relationship, an average H. antyx shell δ18O value of −2.9‰, and an average salinity of 33 (Table 3). Using the mean maximum and minimum shell oxygen isotope values of all the profiles (−1.8 and −3.7‰), we calculate average winter and summer temperatures of 25.5 and 33.5°C, respectively. If we assume that water δ18O values fluctuated seasonally by 0.4‰, a slightly smaller mean annual range in temperature (MART) of 6°C is calculated. Using the salinity-δ18O relationship for the Gulf of Mexico, we calculate the same MAT (31°C) and seasonal range in temperatures (6°C–8°C). Even with greatly reduced water salinities (28), mean annual temperatures similar to modern are calculated (26°C–28.5°C; Table 3). Owing to uncertainties associated with reconstructing water salinities and δ18O and potential diagenetic artifacts these temperature calculations cannot be precisely interpreted. With these caveats we infer from these calculations a mean annual temperature >26°C and a seasonality of 6°C–8°C.

5.7. Warm Late Eocene Tropical Temperatures?

These shallow-water coastal temperatures are similar to terrestrial surface temperature estimates [Graham, 1994, 2000] for Central America (Panama and Jamaica) during the middle Eocene—early Oligocene. On the basis of paleobotanical data, Graham [2000] concluded that mean annual surface temperatures were >26°C and terrestrial environments were characterized by tropical conditions similar to present-day northern Panama. Similarly, Adams et al. [1990] also concluded that low-latitude sea surface temperatures were
warm during this interval on the basis of marine faunal data. However, these temperatures are much warmer than the SST estimates of 17°C–22°C based on the δ18O of late Eocene foraminifera from two low-latitude eastern Pacific deep-sea cores [Zachos et al., 1994]. Currently surface temperatures along the Panama coast (26°C–27°C) are very similar to open ocean temperatures in both the Atlantic and Pacific (26–28°C) and slightly warmer than land surface temperatures (24°–25°C) [Levitus and Boyer, 1994]. This is consistent with basic principles of climate dynamics which prohibit large thermal gradients from persisting in the equatorial regions [Pierrehumbert, 1995]. Farther south, off the Peru and Ecuador coasts, there is a large difference between coastal and open ocean surface temperatures (5°C), primarily due to localized upwelling that results in cooler coastal temperatures. In both central and northern South America, open ocean surface temperatures are either similar to or warmer than coastal temperatures. Because our coastal site was not influenced by upwelling, we estimate Eocene regional surface temperatures for the open ocean were at least 26°C using our calculated minimum coastal winter surface temperature. This suggests tropical surface temperatures were similar to (or slightly warmer than) modern during the late Eocene, and the equator-to-pole surface temperature gradient was steeper than previously thought.

There are several possible explanations for the discrepancy between the different proxy data. The first is that both the coastal and open ocean paleotemperatures are correct and that open marine surface temperatures were significantly cooler than coastal and land surface temperatures. For the reasons discussed above this seems unlikely unless the few open ocean sites in the eastern Pacific were subject to periodic upwelling. The second possibility is that there are errors in the sea surface salinity estimates used to derive SST either in coastal or open ocean. This is also unlikely given that the observed temperature difference (~6–10°C) would require errors in salinity estimates of up to 5–8 ppt (assuming 0.25%o/ppt for low latitudes). Modern surface salinity of the tropics is quite high (~37–38 ppt), and for purely physical reasons it is unlikely that significantly higher salinities could be achieved in the open ocean [Crowley and Zachos, 2000]. A third possibility is that there are biases in open marine foraminifera-based SSTs toward colder temperatures due to unconstrained artifacts such as depth of calcification or preservation-related biases [Crowley and Zachos, 2000; Schrag et al., 1995; Zachos et al., 1994]. We cannot provide evidence currently to eliminate any of these possibilities outright. However, we do note that stable isotopic profiles of Eocene mollusks from a hypothesized paleo-upwelling region along the coast of Nigeria exhibit a large range of stable isotope values, corresponding to a seasonal range in temperatures of 17°C–30°C and MAT of 25°C [Andreasson and Schmitz, 1998]. If upwelled waters at open ocean sites came from the same depth as coastal waters (which is generally true today), then the cool tropical open ocean temperatures (17°C–22°C) may in fact reflect the temperature of these upwelled waters. Moreover, we note that new foraminiferal-derived isotope data from an Atlantic subtropical site for the middle/late Eocene [Wade and Kroon, 1999] yield open ocean surface temperatures warmer than modern. In light of these isotope-based paleotemperature estimates, the published open marine foraminifera-based SSTs may be biased toward cooler temperatures because of the factors discussed above.

5.8. Implications

Our results, in conjunction with published data from other paleoclimate studies (using other types of proxy data and from other sites), imply that the low-latitude, late Eocene coastal ocean was characterized by warm surface temperatures (~26°C in nonupwelling regions). On the basis of these data we infer late Eocene open ocean temperatures were similar to modern at low latitudes. Warm tropical temperatures with warmer than present high-latitude SST imply a relatively steep meridional surface temperature gradient and are consistent with greenhouse forcing being the primary cause of late Eocene warmth. Increased oceanic/atmospheric heat transport (resulting from difference in circulation patterns), on the other hand, should result in low-latitude cooling assuming all other factors remained the same [i.e., Rind and Chandler, 1991].

If tropical SST were warm during the late Eocene, tropical SST may have been even higher in the early Eocene in response to greatly elevated greenhouse gas levels (as implied by pCO2 reconstructions and the extreme high-latitude warmth of that period). At least one foraminiferal-based oxygen isotope record suggests significantly warmer (~5°C) tropical SST in the early Eocene [Bralower et al., 1995] but with the same offsets relative to coastal SST as described in this study. Clearly, further constraints on the evolution of low-latitude surface temperatures during the Eocene are still needed.

6. Conclusions

We have measured the oxygen and carbon stable isotopic composition of primary shell material from fossil specimens of Hannatoma antyx and Ampullella olssonii, Eocene shallow water gastropods, and Mytilus terrabensis and Anomia cf. lisbonensis, marine bivalves. These specimens are from the upper Eocene Gatunillo Formation. We interpret these oxygen isotope profiles as a record of shallow-water temperatures not salinity, based on the salinity tolerances of the Gatunillo fauna (foraminifera, coral, and mollusk) and of isotope profile modeling. On the basis of this work we conclude that tropical temperatures seasonally varied by 6–8°C, and mean annual surface temperatures were >26°C. These temperatures reflect shallow water conditions (middle-outer shelf), probably in the intermediate photic zone. Our results support the findings of palynological tropical surface temperature reconstructions and are inconsistent with the existing low-latitude open ocean SST estimates. Other coastal surface temperature reconstructions for the Eocene and open ocean data from subtropical sites also suggest warm tropical temperatures [Wade and Kroon, 1999; Tripati et al., 1998; Tripati and Zachos, 2000; Andreasson and Schmitz, 1998; Adams et al., 1990].

Acknowledgments. Supported by National Science Foundation grant OCE-9458367 to J. C. Zachos and by a Geological Society of
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