THECAMOEBIANS (TESTATE AMOEBAE) AND FORAMINIFERA FROM THREE ANCHIALINE CENOTES IN MEXICO: LOW SALINITY (1.5–4.5 psu) FAUNAL TRANSITIONS

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ABSTRACT

This study presents the first systematic documentation of thecamoebians and foraminifera in anchialine cenotes (sinkholes) from Quintana Roo, Mexico. Thirty-three surface sediment samples (upper 5 cm) were collected from cenotes Carwash (1.5 psu), Maya Blue (2.9 psu) and El Eden (>3.3 psu). Q-mode cluster analysis of the faunal distributions isolated four low-diversity (Shannon diversity index 1.0–1.5) and salinity-controlled assemblages. Assemblage 1 (1.5 psu) is dominated by the thecamoebians Centropyxis aculeata “aculeata” (53%) and Arcella vulgaris (21%). Assemblage 2 (2.9 ± 0.2 psu) is dominated by Centropyxis aculeata “discoides” (41%) and Centropyxis aculeata “aculeata” (27%). Dwarfed (~50 μm) Centropyxis constricta “aerophila” (20%) with an autogenous test and Jadammina macrescens (29%) dominate Assemblage 3 (3.4 ± 0.2 psu). Finally, Ammonia tepida (51%), Tritaxis sp. (29%) and Elphidium sp. (11%) dominate Assemblage 4 (3.7 ± 0.4 psu). Thecamoebian and foraminiferal populations in the subtropical cenotes are distributed according to salinity variations as found in other temperate paralic systems. The centropyxid taxa trended towards ecophenotypes without spines with increasing salinity, and dwarfed and autogenous-shelled Centropyxis constricta “aerophila” were determined as the most euryhaline thecamoebian, persisting at the ecological boundary of the group (~3.3 psu). Importantly, the transition from the thecamoebian-dominated assemblage to a foraminiferal-dominated assemblage occurs at a salinity of approximately 3.5 psu.

INTRODUCTION

The Yucatan Peninsula of Mexico is an expansive (75,000 km²), low-lying limestone platform that separates the western Caribbean Sea from the Gulf of Mexico (Fig. 1A). Speleogenesism has resulted in extensive and hydraulically active cave networks interconnected to coastal water. The karst landscape includes thousands of collapse sinkholes, known locally as cenotes (from the Mayan word “dz’odon”), which provide physical access to the aquifer and subterranean cave systems. The cenotes are described as anchialine because they are meromictic, coastal environments where basal saline water is stratified from superior freshwater (Fig. 1B). The term anchialine was coined by Holthuis (1973) to describe tidally influenced surface pools containing brackish to salt water with no surface connection to marine water. Cenotes and the underlying phreatic cave networks collectively form unique aquatic ecosystems where primary productivity in the cenotes supports endemic cave populations (stygobites). Documentation of cenote biota began during scientific expeditions of the Carnegie Institution of Washington in the 1930’s (Pearson and others, 1936). Only recently have advances in scuba diving technology allowed for more extensive documentation of cenote and cave fauna, resulting in new inventories of zooplankton, macrocrustaceans and fish (Sanchez and others, 2002; Schmitter-Soto and others, 2002; Iliffe, 1992; Lopez-Adrian and Herrera-Silveira, 1994). Even though foraminifera have been well documented in the Gulf of Mexico (e.g., Osterman 2003; Denne and Sen Gupta, 1993; Gary and others, 1989; Culver and Buzas, 1983; Peag, 1981; Bandy, 1956; Bandy, 1954), neither foraminifera nor thecamoebians have ever been documented in the cenotes of Mexico. Recently, foraminifera and thecamoebians have been documented as being able to live in the unique phreatic cave environment of the Yucatan karst landscape (van Hengstum, 2008).

Foraminifera (marine to brackish water) and thecamoebians (brackish to freshwater) are environmentally sensitive and form simple secreted (CaCO₃, mucopolysaccharide, SiO₂) or agglutinated tests. Foraminifera are ubiquitous in most marine environments from abyssal depths to upper salt marshes and exhibit considerable ecological zonation with respect to various environmental parameters (Murray, 2006). In contrast, thecamoebians (also called testate amoebae) are found in most freshwater settings (i.e., lakes, bogs and soil) and are useful environmental indicators of moisture content, pH changes and lake trophic status (Mitchell and others, 2008; Patterson and Kumar, 2002; Scott and others, 2001; Charman, 2001; Charman and others, 2000). Both taxonomic groups remain well preserved in the Holocene sedimentary record, thereby contributing to their wide usage as paleoenvironmental proxies.

An area of active research is to characterize the zonation between these two taxonomic groups in oligohaline conditions (0.5–5 psu), such as in salt marshes (i.e., Gehrels and others, 2001; Riveiros and others, 2007). These investigations have provided significant insight into the salinity tolerance of thecamoebians, but intrinsic characteristics of the salt marsh environment may be obscuring more detailed taxonomic gradation. First, the known dominant factors that control thecamoebians are salinity, water saturation, percent moisture (Charman and others, 2000; Scott and others, 1980) and pH (Escobar and others, 2008). As such, isolating salinity as the dominant factor controlling thecamoebian taxa is challenging in environments with large temporal and diurnal fluctuations in
multiple parameters. Second, soil thecamoebian taxa become established in extreme high marsh zone where pedogenic processes begin, and these taxa have the potential to taphonomically bias lower salt marsh assemblages. This problem further confounds attempts to isolate gradations from the lacustrine thecamoebians to foraminifera with increasing salinity. Third, the sharp faunal gradations observed in salt marshes are not as gradational as desired to observe thecamoebian taxonomic subtleties (Gehrels and others, 2001). As such, additional environments are needed to further study these faunal transitions. Although salt marshes cannot be directly compared to cenotes due to the many differences between these two environments, the oligohaline cenote may be another setting in conjunction with salt marshes to resolve low salinity effects on thecamoebians and foraminifera. The objectives of this study were to (1) characterize and develop baseline data on distributions of thecamoebians and foraminifera in Yucatan anchialine cenotes and (2) investigate the species succession between thecamoebians and foraminifera in oligohaline conditions.

CENOTE PHYSIOGRAPHY AND STUDY SITES

The Yucatan Peninsula is composed of diagenetically immature reefal limestone with Eocene rock in the interior grading seaward to a Quaternary coastline overlain by unconsolidated Holocene sediments (Weidie, 1985). The limestone retains ~25% porosity (Harris, 1984) allowing effective infiltration and drainage of precipitation and subsequently contributes to a lack of rivers in the Yucatan. Speleogenesis has been an ongoing process on the Yucatan Peninsula since the late Neogene in both phreatic and vadose settings. The geologic processes controlling cenote formation are (1) sub-aerial dissolution of limestone in the vadose zone through carbonic acid percolation during precipitation; (2) subterranean dissolution and collapse of cave ceilings from karst dissolution at the CO$_3^-$ undersaturated halocline (Smart and others, 1988); and (3) dominantly through the collapse of cave ceilings due to the removal of a hydraulic buoyant force during sea level regressions (Smart and others, 2006; Schmitter-Soto and others, 2002). Cenote morphology most commonly contains a circular or elliptical opening with limestone blocks forming a central breakdown pile on the cenote floor (Fig. 1B). Sediment accumulations at the bottom of the cenote have been recently investigated by Gabriel and others (in press) and determined to record environmental evolution in the cenote.

The eastern Yucatan receives a mean annual rainfall of 1.5 m/yr, with up to 85% lost through evapotranspiration based on calculations from mean annual air temperatures. The remaining 15% of annual rainfall is drained through the freshwater lens (Alcocer and others, 1998; Moore and others, 1992; Hanshaw and Back, 1980). The modern aquifer on the Yucatan is density-stratified; a freshwater lens is buoyant and floats above the marine water intruding from the coast (Moore and others, 1992). Both fresh and saline waters circulate through the caves at 1–10 km/day. While the fresh water in the lens actively migrates coastward, the marine water incursion exhibits diurnal landward migration within larger subsurface convection cells (Beddows and others, 2007; Moore and others, 1992). The halocline separating the fresh and marine water dissolves the limestone in a phreatic setting, resulting in anastomosing, phreatic caves (Smart and others, 1988; 2006). Sea level oscillations throughout the Neogene have regularly shifted the relative position of the halocline, subsequently causing cave development at different elevations in the subsurface. Local variations in hydrogeology throughout the Yucatan cause significant variability in cenote water chemistry (e.g., pH: 6.3–10.4, dissolved oxygen: 0.6–7.4 mg/L, temperature: 22–33.5°C, chlorophyll-a: 0.11–97.4 mg/m$^3$; Schmitter-Soto and others, 2002).

CARWASH CENOTE

The Carwash Cenote (CW) is the main access into the Aktun Ha (Carwash) Cave System, located ~8.5 km west of the Caribbean coast, within 40 m of the highway (Fig 1A). The sinkhole has an elliptical opening with an average length of 46 m, width of 15 m and depth of 5 m (Fig. 3). The submerged central breakdown pile on the bottom is generally flat, with only one large boulder located in the northern end of the sinkhole, although there are many submerged tree trunks and branches around the periphery. The sediment accumulation on the breakdown pile and the cenote response to rising Holocene sea-level was documented by Gabriel and others (in press) and the deeper cave thecamoebians and foraminifera in van Hengstum and others (in press). The benthic environment
contains a dense cover of algal mats and abundant fish (especially *Astyanax mexicanus*). During the rainy season, algal blooms characterize the surface water, where active primary productivity creates vibrant green surface water. Dissolved oxygen (2.4 ml L\(^{-1}\)) is above the ecological requirements of most aerobic foraminifera (>1 ml L\(^{-1}\)), but the salinity of 1.5 psu inhibits most taxa (Murray, 2006). The top of the local halocline is seasonally stationary at 21 m depth, which is significantly below the range of sampling depths (Fig. 2). Detailed water-quality data for the Carwash Cenote is given in Alcocer and others (1998).

**MAYA BLUE CENOTE**

The Maya Blue Cenote (MB) is one of several sinkholes in the Naranjal-Maya Blue Cave System, located ~5.6 km west of the Caribbean coast (Fig. 1A). The water-filled sinkhole is crescent-shaped, with an average length of 50 m, width of 10 m and depth of 3.5 m. Large blocks of limestone ~6–10 m in width are exposed at the bottom and are interspersed with sediment that is visibly abundant in diatoms and organic matter. A larger area of exposed sediment occurs at the center of the cenote, where several macrophytes have become established. The Maya Blue Cenote is more oligotrophic than the Carwash Cenote, with a notable absence of reoccurring pelagic algal blooms and year-round water clarity. Salinity is 2.9 psu, and dissolved oxygen is above the normal metabolic requirements for foraminifera in the range of sampling depths.

**EL EDEN CENOTE**

El Eden Cenote (EE) is situated 1.8 km inland from the Caribbean coast and is a popular tourist snorkeling attraction in Quintana Roo (Fig. 1). The cenote averages 37 m by 15 m in length and width and is one of several cenotes found in the larger Ponderosa Cave System. Large blocks of limestone strata, collapsed during cenote formation, characterize the benthic environment. Along the periphery, a few of these limestone blocks intersect the water interface and have developed into miniature islands colonized by ferns and grasses. This creates a high degree of variability in depths across the cenote bottom from 1 to 8 m. The diversity of fish fauna is greater at El Eden Cenote compared to the other two cenotes. The halocline is the shallowest at this locale, being at 11.5 m depth, with a subtly increasing salinity from the surface (3.3 psu) to the halocline. Dissolved oxygen (>2.0 ml L\(^{-1}\)) and hydrologic flow rates (3 cm/s) of the freshwater lens are greater at El Eden Cenote as compared to the other two sites. The configuration of the breakdown blocks, which range down...
into the saline water, combined with increased flow rates, visibly induce turbulence and enhanced mixing of the saline water into the freshwater lens at El Eden Cenote.

**METHODS AND ANALYSIS**

Thirty-three surface sediment samples (upper 5 cm) were collected from the Carwash Cenote (CW; n = 7), the Maya Blue Cenote (MB; n = 12) and El Eden Cenote (EE; n = 14) by scuba diving in August 2006 (Fig. 3), capturing the range of cenote subenvironments. Depth profiles of salinity, pH, dissolved oxygen and temperature were collected through the aquifer at each cenote locale with a submersible multi-parameter probe (YSI 600XLM) to characterize current hydrologic conditions. Sediment samples were washed on a 45-μm screen to retain thecamoebians and foraminifera. Remaining sediment residues were wet-split as required and all samples were picked wet. Thecamoebian taxonomy generally follows Medioli and Scott (1983) and Reinhardt and others (1998). A total of eight thecamoebian and eleven foraminifera taxa were identified in the three cenotes (Plate 1, Table 1). Thecamoebians and foraminifera were considered collectively in this study, where relative fractional abundance (\( F_i \)) of each taxonomic unit was calculated by

\[
F_i = \frac{C_i}{N_i},
\]

where \( C_i \) is the number of specimens of a species counted and \( N_i \) is the total number of specimens counted in the sample.

As an exploratory tool, shell categories (thecamoebians, agglutinated foraminifera and calcite foraminifera) were plotted on a ternary diagram, a useful technique to describe different foraminiferal environments (i.e., Murray, 2006). With thecamoebians, agglutinated foraminifera and calcite foraminifera representing the lacustrine to marine salinity continuum, a ternary diagram can provide insight into the distributions in environments with the most marginal salinity. The recovered taxa were categorized as above using the fractional abundance and plotted on a standard ternary diagram.

The standard error (\( S_{F_i} \)) of sampling (for a two-tailed alpha of 0.05) for each taxon was used to determine statistically significant taxa. If the calculated standard error for a taxon was greater than the fractional abundance in all the samples, then that particular taxon was deemed statistically insignificant and excluded from further multivariate analysis (Patterson and Fishbein, 1989). Standard error was calculated through the following formula, where \( t \) is Student’s \( t \):

\[
S_{F_i} = \frac{t \sqrt{F_i(1 - F_i)} / \sqrt{N_i}}{N_i}.
\]

Additionally, the Shannon-Weaver diversity index (SDI; Shannon and Weaver, 1949) was calculated for each sample to quantify the environmental stability at each sample location (stable conditions are \( > 2.5 \), transitional conditions are \( 1.5 - 2.5 \) and ‘harsh’ conditions are \( < 1.5 \); Patterson and Kumar, 2002). Although these ranges were used by Patterson and Kumar (2002) exclusively for thecamoebians, Riveiros and others (2007) used these SDI ranges to successfully describe collective thecamoebian and foraminiferal assemblages from a Canadian salt marsh. Since the SDI is strongly influenced by the species richness in a sample and in oligohaline settings the species richness of both thecamoebians and foraminifera decreases, the meaning of the numeric ranges presented by Patterson and Kumar (2002) is preserved in oligohaline conditions. The index is calculated through the following formula, where \( S \) is the species richness for each sample:

\[
SDI = -\sum_i \left( \frac{F_i}{N_i} \right) \ln \left( \frac{F_i}{N_i} \right)
\]

Q-mode cluster analysis is used to characterize statistically similar assemblages using the statistical freeware package PAST (Hammer and others, 2001). Of the total 21 taxonomic units recovered, three thecamoebian taxa (Bullinularia indica, Diffugia oblonga, Lagenodiffugia vas) and two foraminiferan taxa (Bolivina variabilis and Textularia earlandi) were statistically insignificant due to large standard error and therefore omitted from further multivariate analysis (Patterson and Fishbein, 1989). Samples were compared using a simple Euclidean distance coefficient and amalgamated into clusters using Ward’s method of minimum variance; the results are displayed in an hierarchical dendrogram (Fig. 4). The bioenosis was not quantified, but the combined bio- and thanatocoenosis is thought to better characterize average conditions at a sample site (Osterman, 2003; Scott and Medioli, 1980a).

**RESULTS**

The dendrogram produced by the Q-mode cluster analysis indicates four distinct salinity-controlled clusters that are interpreted as separate assemblages (Fig. 4). All seven samples recovered from CW form Assemblage 1 (A1) with a mean depth of 4.6 m and a salinity of 1.5 psu. A1 is characterized by abundant Centropyxis aculeata (74%) and Arcella vulgaris (21%). Notably, the thecamoebian strain C. aculeata “aculeata” (with spines, 53%) dominates over the strain without spines, C. aculeata “discoides” (21%). Only one sample in CW contains a small number of Jadalmmina macrescens (2%). Very low diversity (mean SDI = 1.05, Table 2) indicates the environment deviates from optimal growth conditions for both lacustrine testate amoebae and foraminifera (where SDI > 2). On the ternary diagram, all the samples plot at or near the apex due to the large relative abundance of thecamoebians (mean 99.6%; Fig. 5).

The majority of samples from Assemblage 2 (A2) come from MB. The A2 samples were found at a mean depth of 3.5 m and a salinity of 2.9 ± 0.2 psu. Centropyxid taxa dominate (mean 82%), however, there are subtle taxonomic shifts at the species and strain (ecophenotype) level. Centropyxis aculeata “aculeata” decreases (mean 27%), whereas C. aculeata “discoides” increases (41%). There is a significant decrease in the contribution of Arcella vulgaris (mean 2 ± 3%; high SD due to larger inter-sample variability) to the populations compared to that in A1. Centropyxis
Table 1. Relative abundance and standard error ($\pm 1$ s) for taxonomic units.

<table>
<thead>
<tr>
<th>Sample</th>
<th>E1</th>
<th>E2</th>
<th>E3</th>
<th>E5</th>
<th>E6</th>
<th>E7</th>
<th>E8</th>
<th>E9</th>
<th>E10</th>
<th>E11</th>
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<tr>
<td>Depth (m)</td>
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<td>6.4</td>
<td>1.8</td>
<td>5</td>
<td>3</td>
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<td>5.5</td>
<td>2.4</td>
<td>1.8</td>
</tr>
<tr>
<td>Salinity (psu)</td>
<td>3.5</td>
<td>4.2</td>
<td>3.4</td>
<td>3.7</td>
<td>3.5</td>
<td>3.6</td>
<td>3.4</td>
<td>3.5</td>
<td>3.5</td>
<td>3.4</td>
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<tr>
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<td>179</td>
<td>327</td>
<td>496</td>
<td>259</td>
<td>394</td>
<td>1075</td>
<td>462</td>
<td>219</td>
<td>193</td>
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<td>Individuals/ft</td>
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<td>131</td>
<td>50</td>
<td>104</td>
<td>79</td>
<td>430</td>
<td>185</td>
<td>88</td>
<td>25</td>
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<tr>
<td>Shannon diversity index ($H$)</td>
<td>1.965</td>
<td>1.187</td>
<td>1.28</td>
<td>1.078</td>
<td>0.997</td>
<td>1.232</td>
<td>1.529</td>
<td>1.41</td>
<td>1.143</td>
<td>1.666</td>
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</table>

<table>
<thead>
<tr>
<th>Species</th>
<th>abundance</th>
<th>standard error ($\pm$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Arcella vulgaris</em></td>
<td>1.81</td>
<td>0.61</td>
</tr>
<tr>
<td><em>Bullinula indica</em></td>
<td>1.44</td>
<td>0.85</td>
</tr>
<tr>
<td><em>Centropyxis aculeata</em> aculeata</td>
<td></td>
<td></td>
</tr>
<tr>
<td>standard error ($\pm$)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Centropyxis aculeata</em> discoides</td>
<td></td>
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</tr>
<tr>
<td>standard error ($\pm$)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Centropyxis constricta</em> aerophila</td>
<td></td>
<td></td>
</tr>
<tr>
<td>standard error ($\pm$)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Centropyxis constricta</em> constricta</td>
<td></td>
<td></td>
</tr>
<tr>
<td>standard error ($\pm$)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Centropyxis constricta</em> 'constricta'</td>
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<td></td>
</tr>
<tr>
<td>standard error ($\pm$)</td>
<td>-</td>
<td>-</td>
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<tr>
<td><em>Doliva striatula</em></td>
<td>3.83</td>
<td>0.60</td>
</tr>
<tr>
<td><em>Doliva variabilis</em></td>
<td>2.01</td>
<td>-</td>
</tr>
<tr>
<td><em>Elphidium sp.</em></td>
<td>3.02</td>
<td>2.23</td>
</tr>
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<td><em>Elphidium spinosa</em></td>
<td>0.30</td>
<td>0.61</td>
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<tr>
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<td>1.21</td>
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<td>26.68</td>
<td>66.06</td>
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<td><em>Miliammina fusca</em> var. juvenile</td>
<td></td>
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</tr>
<tr>
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<td>0.59</td>
<td>0.85</td>
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<td>66.06</td>
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<td>4.71</td>
<td>7.21</td>
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<td><em>Polyacanthonia tophalina</em></td>
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<tr>
<td>standard error ($\pm$)</td>
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<td>-</td>
</tr>
<tr>
<td><em>Rosalia subaracana</em></td>
<td>-</td>
<td>2.79</td>
</tr>
<tr>
<td><em>Spirillina vivipara</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Textularia eriolandi</em></td>
<td>0.60</td>
<td>-</td>
</tr>
<tr>
<td><em>Triloculina oblonga</em></td>
<td>0.60</td>
<td>-</td>
</tr>
<tr>
<td><em>Tritaxis fusca</em></td>
<td>2.72</td>
<td>27.37</td>
</tr>
<tr>
<td><em>Tritaxis fusca</em></td>
<td>1.75</td>
<td>6.53</td>
</tr>
<tr>
<td><em>Jadammina macrescens</em></td>
<td>10.27</td>
<td>2.79</td>
</tr>
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<td><em>Jadammina macrescens</em></td>
<td>3.27</td>
<td>2.41</td>
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</table>

The abundance of *Jadammina macrescens* is no longer a dominant species in A3, and the abundance of the Centropyxis constricta doubles (mean 28%). The abundance of *Jadammina macrescens* (30%) and *Miliammina fusca* (3%) also increase. *Tritaxis* sp. (mean 4 ± 4%)
and *Ammonia tepida* (mean 13 ± 10%) contribute to populations, but there is large intra-sample variability. Aberrant tests were recorded in four samples (E1, E8, E10, E12), where 2% of *Ammonia tepida*, 35% of *Elphidium* sp. and 5% of *J. macrescens* had irregular test morphologies.

All samples from Assemblage 4 (A4) come from EE at a mean depth of 4.5 m and salinity of 3.7 ± 0.4 psu. Thecamoebian taxa decrease significantly (mean 9%) with large intra-sample variability (±13%). *Ammonia tepida* (mean 51%) is the dominant taxon, with *Tritaxis* sp. (21%) and *Elphidium* sp. (mean 11 ± 12%) contributing to the assemblage and increasing the diversity. The dominance of hyaline foraminifera in A4 causes the samples to plot in the lower right apex of the ternary diagram. Diversity is low (SDI = 1.284) from continual environmental stress in the low salinity conditions. In samples where test aberrancy was recorded (E5, E7, E9), 17% of *Elphidium* sp. contained irregular chambers and 25% of *Jadammina macrescens* in E9.

**DISCUSSION**

**COMPARISON BETWEEN CENOTES**

The greatest dominance of thecamoebians occurs in CW (mean 99.6%), which is to be expected, as this cenote has salinity (1.5 psu) values closest to the ideal thecamoebian habitat of fresh water. In the ternary diagram, all the samples from CW plot at the apex, reflecting the dominance

**TABLE 1. Continued.**

<table>
<thead>
<tr>
<th>Sample</th>
<th>E13</th>
<th>E14</th>
<th>E15</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
<th>M4</th>
<th>M5</th>
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<tr>
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<td>1.8</td>
<td>5.49</td>
<td>2.7</td>
<td>4</td>
<td>1.8</td>
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<tr>
<td>Salinity (psu)</td>
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<td>3.4</td>
<td>4.4</td>
<td>2.9</td>
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<tr>
<td><em>Sum (N)</em></td>
<td>215</td>
<td>93</td>
<td>242</td>
<td>382</td>
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<td>233</td>
<td>328</td>
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<td>186</td>
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<td><em>Shannon diversity index (H)</em></td>
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<td>1.124</td>
<td>1.139</td>
<td>1.625</td>
<td>1.242</td>
<td>1.146</td>
<td>1.298</td>
<td>1.277</td>
<td>1.731</td>
<td>1.049</td>
</tr>
</tbody>
</table>

**Table 1. Continued.**

**Arcella vulgaris**
- standard error (±) 2.01 - - 0.72 - 3.68 - 0.80 0.77

**Bullinaria indica**
- standard error (±) - - - 0.72 - - - - -

**Centropyxis aculeata “aculeata”**
- standard error (±) 8.84 12.90 0.41 25.39 12.82 4.72 4.28 2.72 5.32 6.20 4.31 4.25

**Centropyxis aculeata “discoidea”**
- standard error (±) 5.58 3.23 - 35.60 59.83 64.38 64.38 38.11 55.56 34.15 0.40

**Centropyxis constricta “aerophila”**

**Centropyxis constricta “constricta”**
- standard error (±) 6.19 - 0.81 2.82 1.66 2.60 1.95 - 2.08 2.22 5.84

**Diffugia globulus**
- standard error (±) - - - - 0.43 0.30 - 0.84 0.60 - 0.80

**Diffugia oblonga**
- standard error (±) - - - - - - - - - -

**Lagenodifflugia vas**
- standard error (±) - - - - - - - - - -

**Ammonia tepida var. juvenile**
- standard error (±) 0.47 - 0.41 0.52 - - - - - 0.41

**Ammonia tepida**
- standard error (±) 11.16 19.35 49.59 - - - - - - 0.62

**Bolivina striatula**
- standard error (±) 4.21 8.12 6.30 - - - - - - 1.21

**Bolivina variabilis**
- standard error (±) - - - - - - - - - -

**Elphidium sp.**
- standard error (±) - - 2.48 - 1.71 - - - - - 1.22

**Miliammina fusca**
- standard error (±) 1.86 - - 4.97 17.09 0.43 2.13 3.70 4.70 6.16

**Polysaccammina iophalina**
- standard error (±) 2.33 - 2.15 - - - - - - -

**Rosalina subaracuana**
- standard error (±) - - - - - - - - - -

**Spirillina vivipara**
- standard error (±) - - - - - - - - - -

**Textularia earlandi**
- standard error (±) - - - - - - - - - -

**Triloculina oblonga**
- standard error (±) 0.47 - - - - - - - - -

**Tritaxis fusca**
- standard error (±) 3.72 1.08 36.36 0.26 - - - - - -

**Jadammina macrescens**
- standard error (±) 11.16 61.29 9.50 4.19 3.42 0.43 1.52 3.70 11.79 0.40

**Table 1. Continued.**

and *Ammonia tepida* (mean 13 ± 10%) contribute to populations, but there is large intra-sample variability. Aberrant tests were recorded in four samples (E1, E8, E10, E12), where 2% of *Ammonia tepida*, 35% of *Elphidium* sp. and 5% of *J. macrescens* had irregular test morphologies.

All samples from Assemblage 4 (A4) come from EE at a mean depth of 4.5 m and salinity of 3.7 ± 0.4 psu. Thecamoebian taxa decrease significantly (mean 9%) with large intra-sample variability (±13%). *Ammonia tepida* (mean 51%) is the dominant taxon, with *Tritaxis* sp. (21%) and *Elphidium* sp. (mean 11 ± 12%) contributing to the assemblage and increasing the diversity. The dominance of hyaline foraminifera in A4 causes the samples to plot in the lower right apex of the ternary diagram. Diversity is low (SDI = 1.284) from continual environmental stress in the low salinity conditions. In samples where test aberrancy was recorded (E5, E7, E9), 17% of *Elphidium* sp. contained irregular chambers and 25% of *Jadammina macrescens* in E9.

**DISCUSSION**

**COMPARISON BETWEEN CENOTES**

The greatest dominance of thecamoebians occurs in CW (mean 99.6%), which is to be expected, as this cenote has salinity (1.5 psu) values closest to the ideal thecamoebian habitat of fresh water. In the ternary diagram, all the samples from CW plot at the apex, reflecting the dominance...
of thecamoebians over foraminifera in that cenote (Fig. 5). One sample plots slightly down the left axis, reflecting the minor contribution of *Jadammina macrescens* at that sampling site. At MB, there is a larger contribution of agglutinated foraminifera (13%) causing the samples from that location to plot along the left axis of the ternary diagram. Thecamoebians are still the dominant fauna (85%) in MB, although the slightly higher salinity (2.9 psu) is more conducive to textularid populations than in CW. Since both of these cenotes have similar benthic conditions, hydrologic flow (1.5 cm/s), pH, oxygen and temperature (Fig. 2), the difference in salinity is likely the dominant abiotic factor contributing to the observed faunal variations.

In contrast to MB and CW, the samples from EE are more evenly distributed over the ternary diagram than the other two cenotes. In addition to thecamoebians (mean 28%) and agglutinated foraminifera (mean 29%), EE is also a habitat for calcite-shelled foraminifera (mean 43%). The halocline is shallowest at EE, and hydrologic flow is greater (3 cm/s) when compared to the other sites. The higher salinity at EE (3.3 psu), associated with the proximity to the coast, allows euryhaline calcite taxa to become established (i.e., *Ammonia tepida*) and suppresses larger thecamoebian populations. Intra-sample variability can be explained in several ways: (1) subtle increases in salinity with depth in the freshwater lens; (2) complex bathymetry creating many microenvironments that might be influenced

\[
\text{TABLE 1. Continued.}
\]

<table>
<thead>
<tr>
<th>Sample</th>
<th>M9</th>
<th>M10</th>
<th>M11</th>
<th>M12</th>
<th>C1</th>
<th>C2</th>
<th>C3</th>
<th>C4</th>
<th>C5</th>
<th>C6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth (m)</td>
<td>3.6</td>
<td>2.4</td>
<td>4.6</td>
<td>2.4</td>
<td>5.5</td>
<td>4.9</td>
<td>4.6</td>
<td>4.3</td>
<td>3</td>
<td>5.9</td>
</tr>
<tr>
<td>Salinity (psu)</td>
<td>2.9</td>
<td>2.9</td>
<td>2.9</td>
<td>2.9</td>
<td>1.5</td>
<td>1.5</td>
<td>1.5</td>
<td>1.5</td>
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<tr>
<td>Sum (N)</td>
<td>429</td>
<td>169</td>
<td>260</td>
<td>120</td>
<td>294</td>
<td>157</td>
<td>223</td>
<td>90</td>
<td>286</td>
<td>106</td>
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<tr>
<td>Individuals</td>
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<td>135</td>
<td>208</td>
<td>96</td>
<td>78</td>
<td>31</td>
<td>45</td>
<td>29</td>
<td>57</td>
<td>84</td>
</tr>
<tr>
<td>Shannon diversity index (H)</td>
<td>1.22</td>
<td>1.636</td>
<td>1.672</td>
<td>1.18</td>
<td>1.005</td>
<td>0.901</td>
<td>1.0379</td>
<td>0.924</td>
<td>1.174</td>
<td>1.037</td>
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</tbody>
</table>

\[
\text{Arcella vulgaris}
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\[
\text{standard error (±)}
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\[
\text{Bullimunaria indica}
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\[
\text{standard error (±)}
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\[
\text{Centropyxis aculeata “aculeata”}
\]
\[
\text{standard error (±)}
\]
\[
\text{Centropyxis aculeata “discoides”}
\]
\[
\text{standard error (±)}
\]
\[
\text{Centropyxis constricta “aerophila”}
\]
\[
\text{standard error (±)}
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\[
\text{Centropyxis constricta “constricta”}
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\[
\text{standard error (±)}
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\[
\text{Difflugia globulus}
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\text{standard error (±)}
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\[
\text{Difflugia oblonga}
\]
\[
\text{standard error (±)}
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\[
\text{Lagenodifflugia vas}
\]
\[
\text{standard error (±)}
\]
\[
\text{Ammonia tepida var. juvenile}
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\[
\text{standard error (±)}
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\[
\text{Ammonia tepida}
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\[
\text{standard error (±)}
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\text{Bolivina striatula}
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\text{standard error (±)}
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\text{Bolivina variabilis}
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\text{standard error (±)}
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\text{Elphidium sp.}
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\text{standard error (±)}
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\text{Miliammina fusca}
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\text{standard error (±)}
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\text{Polysaccammina iophalina}
\]
\[
\text{standard error (±)}
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\[
\text{Rosalina subaracuana}
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\text{standard error (±)}
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\text{Spirillina vivipara}
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\text{standard error (±)}
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\[
\text{Textularia earlandi}
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\text{standard error (±)}
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\[
\text{Triloculina oblonga}
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\[
\text{standard error (±)}
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\[
\text{Tritaxis fusca}
\]
\[
\text{standard error (±)}
\]
\[
\text{Jadammina macrescens}
\]
\[
\text{standard error (±)}
\]
TABLE 2. Average Shannon diversity index, salinity, dominant cenote of origin, depth and relative abundance for each taxon in the four assemblages.

<table>
<thead>
<tr>
<th>Assemblage</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
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</thead>
<tbody>
<tr>
<td>Shannon diversity index ($H$)</td>
<td>1.034</td>
<td>1.367</td>
<td>1.509</td>
<td>1.284</td>
</tr>
<tr>
<td>Salinity (psu)</td>
<td>1.5</td>
<td>2.9 ± 0.2</td>
<td>3.4 ± 0.2</td>
<td>3.7 ± 0.4</td>
</tr>
<tr>
<td>Dominant location of assemblage</td>
<td>CW</td>
<td>MB</td>
<td>EE</td>
<td>EE</td>
</tr>
<tr>
<td>Mean sample depth (m)</td>
<td>4.6</td>
<td>3.5</td>
<td>2.5</td>
<td>4.5</td>
</tr>
</tbody>
</table>

THECAMOEBIANS

*Arcella vulgaris* | 21 ± 12 | 2 ± 3 | <1 | <1 |
*Centropyxis aculeata* “aculeata” | 53 ± 8 | 27 ± 18 | 8 ± 5 | 3 ± 3 |
*Centropyxis aculeata* “discoides” | 21 ± 6 | 41 ± 19 | 3 ± 2 | 5 ± 9 |
*Centropyxis constricta* “aerophila” | <1 | 3 ± 1 | 20 ± 17 | <1 |
*Centropyxis constricta* “spinosa” | <1 | 9 ± 6 | 15 ± 15 | <1 |

FORAMINIFERA

*Jadammina macrescens* | 2 ± 4 | 3 ± 4 | 29 ± 28 | 3 ± 2 |
*Tritaxis* sp. | 0 | <1 | 3 ± 4 | 21 ± 13 |
*Ammonia tepida* | 0 | <1 | 13 ± 10 | 51 ± 9 |
*Elphidium* sp. | 0 | <1 | <1 | 11 ± 12 |

FIGURE 4. A Q-mode dendrogram indicating four distinct assemblages. The mean salinity with 1 standard deviation for each assemblage is provided. Sample labels follow those of Figure 3.
through seasonal temperature changes; and (3) sediment re-
spension and transport through tourist disturbance and
higher hydrologic flow rates. These environmental variables
are biologically relevant for amoebae, which can tempo-
rarily encyst during ecologically unfavorable conditions.
Since these characteristics are not as prevalent at MB or
CW as at EE, more consideration is given to these intrinsic
characteristics when interpreting samples from EE.

**ASSEMBLAGE 1 (1.5 PSU)**

Assemblage 1 is located only at the CW, an environment
suitable for only the most euryhaline of the thecamoebians.
Therefore, *Centropyxis aculeata* dominates A1 and other
more stenohaline thecamoebians are excluded (i.e., *Dif-
flugia oblonga* “triangularis”). The increased primary
productivity in CW seems to promote the secondary
dominance of *Arcella vulgaris*. This qualitative assessment
is based on other studies where *A. vulgaris* becomes the
dominant taxon when there is increased nutrient loading or
primary productivity (Reinhardt and others, 2005). Rare
*Jadammina macrescens* are also present with minimal test
aberrancy, indicating some environmental stress on the
species. These results are similar to those from other coastal
and lacustrine studies in which (1) *Centropyxis* spp. are
shown to be opportunists and the most euryhaline of the
testate amoebae (i.e., Riveiros and others, 2007; Scott and
others, 2001); (2) *A. vulgaris* is an indicator of environ-
mental stress from nutrient loading (i.e., Roe and Patterson,
2006; Reinhardt and others, 2005; Patterson and others,
2002); and (3) rare *J. macrescens* persists at its ecological
freshwater boundary of 1.5 psu (Murray, 2006).

**ASSEMBLAGE 2 (2.9 ± 0.2 PSU)**

Between A1 and A2, there are taxonomic and environ-
mental transitions. All the samples plot in the top-most
region of the ternary diagram, indicating thecamoebians are
still dominant contributors to the overall assemblage.
*Jadammina macrescens* is still the only foraminiferan, with
only a minor increase in abundance from A1. In the
thecamoebians, there is a change in the dominant strain of
the species *Centropyxis aculeata*. In the A2, there is a
change to a dominance of *C. aculeata* “discoides” (41%) over
*C. aculeata* “aculeata” (27%).

The change to a dominance of *Centropyxis aculeata*
“discoides” over *C. aculeata* “aculeata” from A1 to A2 is
a noteworthy observation. Reinhardt and others (1998)
divided *C. aculeata* and *Centropyxis constricta* into
ecophenotypes or ‘strains’ based on the presence or absence
of spines: (1) *C. aculeata* “aculeata” is ornamented with
spines on the aboral (fundus) region—we have observed up
to 18; (2) *C. aculeata* “discoides” is circular, without spines;
(3) *C. constricta* “aerophila” is lacking in spines on the
aboral region; (4) *C. constricta* “constricta” is ornamented
with 1–3 aboral spines; and (5) *C. constricta* “spinosa” is
ornamented with >3 aboral spines. In previous lake studies,
attributing these centropyxid strains to a definitive abiotic
variable has proven problematic, although evidence does
suggest that multiple environmental factors play a role in
the phenotype expressed by a species (e.g., Reinhardt and
others, 1998; Medioli and Scott, 1983).

To retain consistency among the entire *Centropyxis* genus
in this study, our taxonomic strain concept of *C. aculeata*
is consistent with that of Reinhardt and others (1998), but *C.
constricta* is modified as follows: (1) *C. constricta* “spinosa”
is characterized by the presence of aboral spines (we have
observed up to 8); and (2) *C. constricta* “aerophila” is
characterized by the absence of aboral spines. In A2, which
has a slightly elevated salinity over A1, the *C. aculeata* test
morphology without spines predominates (*C. aculeata*
“discoides”). This relationship has also been observed in
other global non-tropical settings. In the British Columbian
salt marshes studied by Riveiros and others (2007), the
ecophenotypes “discoides” (mean 12.5%) and “aerophila”
(14%) dominate over “aculeata” (7%) and “spinosa” (8%)
in the saline-stressed High Marsh Assemblage. In UK salt
marshes (Gehrels and others, 2001), *C. constricta* “aerophila”
(designated as *C. platystoma*, but reported by the
authors as equivalent to the “aerophila” morphotype) is the
most euryhaline of the thecamoebians (see Fig. 5 in Gehrels
and others, 2001). These results indicate that in oligohaline
environments, a thecamoebian ecophenotype without
spines on the aboral region has an ecological advantage
over their counterparts with spines. However, since spines
are also expressed on thecamoebians in limnetic environ-
ments, other ecological or environmental factors may be
controlling the expression of spines in the absence of stress
related to salinity (such as pH, percent moisture or factors
related to reproduction).

**ASSEMBLAGE 3 (3.4 ± 0.2 PSU)**

*Centropyxis constricta* form the largest thecamoebian
component (35%) in A3, with foraminifera emerging as the
Thecamoebians: 1 *Arcella vulgaris*, autogenous test (x341); 2 *A. vulgaris*, (x341); 3 *Centropyxis aculeata* – xenogenous test (x406), note that the taxonomic criterion for angle between aperture face and body wall is to be <45° (Medioli and Scott, 1983; x600); 4 *C. constricta* specimen with spines on xenogenous test (x300), note that the taxonomic criterion for angle between aperture face and body wall is to be >60° (Medioli and Scott, 1983; x600); 5 *C. aculeata* “aculeata” (x462); 6 *C. aculeata* “aculeata” (x388); 7 *C. aculeata* “discoides” (x462); 8 Impoverished and dwarfed *C. constricta* “aerophila” with autogenous test (x425); 9 *C. constricta* “spinosa,” autogenous test (x300); 10 *C. constricta* “aerophila,” xenogenous test (x425). 11–26 Foraminifera: 11 *Ammonia tepida*, spiral side (x388); 12 *A. tepida*, umbilical side (x462); 13 *A. tepida* var. juvenile, proloculus and first two chambers, a consistent morphology (x775); 14 *Ammonia tepida*, aberrant test shape, arrow points to abnormal additional chamber (x150); 15 *Ammonia tepida*, aberrant test shape, complex form (x150); 16 *Elphidium sp.* (x150); 17 *Elphidium sp.* , aberrant test shape, arrow points to abnormal additional chamber (x150); 18 *Elphidium sp.* - aberrant test shape, complex form (x150); 19, 20 *Miliammina fusca* (x150); 21 *Jadammina macrescens* (x150); 22 *J. macrescens*, apertural view (x203); 23 *J. macrescens*, aberrant test displaying a twinned tests (x186); 24 *Tritaxis sp.*, spiral view (x170); 25 *Tritaxis sp.*, umbilical view (x231); 26 *Tritaxis sp.*, side view (x156). See Figure 4 of Geslin and others (2000) for categorization of morphological abnormalities. Scale bars represent 50 µm.
dominant taxonomic grouping in the assemblage. Plate 1 illustrates the separation of the species C. aculeata and C. constricta based on the geometric angle between the apertural face and the test wall (after Fig. 10 in Medioli and Scott, 1983; see Plate 1). In A3, the test of C. constricta is consistently autogenous; the strain without spines dominates the assemblage (C. constricta “aerophila”, 20%); and they have an overall dwarfed size (45–63 μm).

As such, this morphotype of C. constricta “aerophila” is interpreted as the most euryhaline of the thecamoebians, persisting at the ecological boundary of the group. Again, we interpret the lack of spines in C. constricta “aerophila” as physiologically advantageous over the ecophenotype with spines.

The locations where A3 is recovered are more suitable habitats for foraminifera than A2 or A1, as indicated by an increase in the abundance of Jadammina macrescens (29%) and Tritaxis sp. (3%). Ammonia tepida and Elphidium sp. are also present, and the occurrence of aberrant tests indicates some ecological stress on these populations. The salinity increase from A2 to A3 is sufficient to make the environment more favorable for euryhaline foraminifera over thecamoebians. Longer-term salinity data in the cenote indicate very minor shifts over time (Beddows, in preparation), however, the shallow average depth for A3 (~2.5 m) introduces the possibility of micro-environmental control on the distributions from the formation of seasonally-controlled cap layers of lower-salinity water. The fresher surface water during the rainy season would negatively affect the health of hyaline foraminifera, but positively affect thecamoebians (especially opportunists such as the centropyxids). In contrast, evaporation during the dry season would slightly increase salinity, creating conditions that are more favorable for foraminifera. This likely explains the small amount of C. aculeata in the assemblage and large intra-sample variability in the relative abundance of Elphidium sp. and Tritaxis sp. in A3. This assemblage represents the ecological boundary of thecamoebians in the cenotes.

**Assemblage 4 (3.7 ± 0.4 psu)**

The most saline assemblage is A4 (mean 3.7 psu), in which foraminifera dominate and thecamoebians are only a minor contribution through Centropyxis aculeata (mean <10%). Since this cenote is a popular tourist area (i.e., snorkeling, scuba diving) with appreciable hydrologic flow rates (3 cm/s), the possibility of thecamoebian tests being disturbed through recreational activity (post-mortem re-suspension) and transported to another deeper locale cannot be ignored. The reworking and transport of tests from shallower depths is a likely explanation of the variable abundance of thecamoebian tests in A4 and further explains the high intra-sample variability (standard deviations) in the mean abundance of taxa. The foraminifer Ammonia tepida (51%) dominates A4, an unsurprising result considering the adaptability of this genus and its reputation for being present in other oligohaline environments (i.e., Wennrich and others, 2007, and references therein). The second most abundant foraminifer in A4 is Tritaxis sp. (21%), an enigmatic observation as it is more commonly known from coastal shelves and bathyal sediments (e.g., Martin, 2008). It will be interesting to learn if more shelf-to-bathyal foraminifera are common in other mesohaline cenotes. The general trend in the cenotes of decreasing Jadammina macrescens and increasing abundance of other halophiles with increasing salinity is consistent with other reports of foraminiferal ecology (Scott and Medioli, 1978, 1980b).

The subtle salinity variation between A3 (mean 3.4 psu) and A4 (mean 3.7 psu) is due to the average sampling depths, where A3 is shallower (mean 2.5 m, mean of 51% total foraminifera in each sample) than A4 (mean 4.5 m, mean of 91% foraminifera in each sample). When comparing the three cenotes, the halocline is the shallowest at EE, and there is a subtle concomitant increase in salinity with depth (Fig. 2). The deeper saline water in EE is interpreted as a favorable environment for foraminifera and not thecamoebians, as apparent through larger abundances of foraminifera in A4. Future characterization of only the biocoenosis in the cenotes would likely decrease some of the variability in the different assemblages by eliminating taphonomic effects (i.e., excluding reworked specimens).

Aberrant foraminiferal tests have been widely observed in response to anthropogenic influences such as pollution and natural variability in temperature, salinity, dissolved oxygen, pH, nutrition and other factors at the ecological boundary of a species (Geslin and others, 2000; Yanko and others, 1994; Boltovskoy and others, 1991). In the cenotes, dissolved oxygen, pH and temperature are all within the ecological requirements for healthy foraminiferal growth. The frequency of aberrant tests is fewer in the cenotes than in other studies (e.g., Wennrich and others, 2007), thereby suggesting only minor ecological stress on the foraminiferal populations. However, the marginal salinities are interpreted as being the dominant ecological stress causing the observed test aberrancy.

**CONCLUSIONS**

Foraminifera and thecamoebians were recovered from the cenotes (sinkholes) on the Yucatan Peninsula, Mexico. The recovered foraminifera and thecamoebians (testate amoebae) from this subtropical setting are responding to local environmental controls in the same way as they do in previously investigated temperate systems. The anchialine nature of cenotes is an additional environment in which to study thecamoebian and foraminiferal ecology in oligohaline settings. In contrast to other coastal systems where thecamoebians and foraminifera co-occur, cenotes remain a permanently aquatic habitat with hydrology more stable than that in intertidal settings. Furthermore, cenotes remain energetically sheltered from large-scale, coastal perturbations (e.g., hurricanes), and microfossils in this environment are less exposed to taphonomic processes typical of neritic environments (e.g., wave action). Hence, thecamoebian populations in cenotes are dominantly influenced by aquatic conditions, as opposed to percent moisture or pedogenesis as in some intertidal settings.

The thecamoebian morphotypes without spines dominated over the morphotypes with spines as salinity increased in the cenotes. The environmental influence on the presence or absence of spines is additional evidence for
the morphological fluidity and ecophenotypes in individual thecamoebian species. An important transition from thecamoebian-dominated populations to foraminiferan-dominated populations occurs at a salinity of ~3.5 psu. This is the first paper to report such an ecological boundary for thecamoebians, and the boundary needs further evaluation in other environments. However, this evidence further supports salt marsh research that documents thecamoebians surviving in more saline conditions than historically believed. In the cenotes, dwarf (45–63 μm), autogenous Centropyxis constricta “aerophila” persisted as the most euryhaline thecamoebian. This ecophenotype is interpreted as the most favorable centropyxid morphology under stressed conditions imposed through elevated salinity.

Finally, there are few environments where thecamoebians and foraminifera can ecologically co-exist in the same populations. Since foraminifera and thecamoebians play important roles in the nutrient transfer from lower to higher trophic levels (Finlay and Estaban, 1998; Lipps and Valentine, 1970), their interspecific interactions within the same ecological niche warrants further investigation. These results indicate that anhaline cenotes are another paralic environment, in addition to the salt marsh, where the collective ecology of the thecamoebians and foraminifera can be examined. In these unique oligohaline settings, the ecological interactions between fauna in the total rhizopod population—the thecamoebians and foraminifera—are currently unknown.

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