Journal of Foraminiferal Research, v. 41, no. 3, p. 201–229, July 2011

ECOLOGY OF FORAMINIFERA AND HABITAT VARIABILITY IN AN UNDERWATER CAVE: DISTINGUISHING ANCHIALINE VERSUS SUBMARINE CAVE ENVIRONMENTS

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ABSTRACT

Seventy-five surface (<4 cm) sediment samples were collected throughout Green Bay Cave System, Bermuda to investigate foraminiferal ecology and habitat variability in underwater coastal caves. This cave is ideal for studying different cave environments because it consists of an anchialine cave environment connected to a submarine cave environment. Each sediment sample was analyzed for foraminifera, $\delta^{13}C_{org}$, C:N, organic matter content, $CaCO_3$, and granulometry. Measurements of pH, salinity, dissolved oxygen, and temperature in the coastal aquifer distinguished the meteoric lens and saline groundwater. Q-mode cluster analysis on the foraminifera produced a dendrogram that segregates the anchialine and submarine cave environments, and subdivides each environment into distinct habitats consistent with local hydrogeology and sedimentology. The anchialine cave environment near the sinkhole is characterized by two groups of foraminifera: 1) the Meteoric Lens Assemblage living in the brackish meteoric lens within 60 cm of sea level, and 2) the Anchialine Cave Assemblage living in the saline groundwater. *Helenina anderseni*, *Discorinopsis aguayoi*, and other marsh foraminifera can persist in the brackish meteoric lens, which transitions into a more diverse assemblage dominated by *Bolivina striatula* and *Rosalina globularis* below the halocline. The boundary between the anchialine (terrestrially dominated) and submarine cave (marine-dominated) environments is demarcated by gross foraminiferal and sedimentary changes ($\delta^{13}C_{org}$ from −24‰ to −18‰, C:N from 11.2 to 8.3) that correspond to the maximum point where terrestrial influences routinely impact the cave benthos. Three assemblages of foraminifera inhabit the submarine cave environment: 1) the Entrance Assemblage in the first ~60 m of the submarine cave, dominated by *Quinqueloculina*; 2) the Circulated Submarine Cave Assemblage dominated by *Spirillina vivipara* and *Triloculina oblonga*, and 3) the Isolated Submarine Cave Assemblage dominated by *Spirophthalmidium emaciatum*. Planktic tintinnids suggest that tidally forced saline groundwater circulation is transporting more nutrients and particulate organic matter to the Circulated Submarine Cave Assemblage than the Isolated Submarine Cave Assemblage. These results indicate that coastal caves are partitioned into specific environments that can be further subdivided into habitats by groundwater masses, sediment fluxes (terrestrial versus marine), and groundwater circulation. This implies that that cave foraminifera can be useful paleohydrogeologic, paleoclimatic, and Quaternary sea-level proxies.

INTRODUCTION

Very little paleoenvironmental or paleoecological research has been done in underwater (phreatic) coastal caves despite their global distribution. Most phreatic cave research concentrates on biology and hydrogeology, with geologic research focused generally on speleogenesis (i.e., Ford and Ewers, 1978; Mylroie and Mylroie, 2007). Marine geology in phreatic caves is a research avenue independent of speleothem analyses for Quaternary climate and sea-level data (e.g., Harmon and others, 2007; Dutton and others, 2009; Baldini, 2010; Dorale and others, 2010). Speleothems can provide information about caves in the vadose zone, or the switch between phreatic and vadose states, but they cannot provide information on environmental change in coastal caves when they are flooded by groundwater. Preliminary research indicates that phreatic cave sediments represent an emerging source of paleoclimate and sea-level data (van Hengstum and others, 2009b; Yamamoto and others, 2009; van Hengstum and others, 2010). Despite these efforts, more information on the modern marine geological processes and microfossils in underwater caves is required so their sediments can be confidently applied to Quaternary sea-level and climate problems.

Information on foraminifera in subterranean settings is currently scarce. The earliest documentation of cave foraminifera, to our knowledge, is by Birnstein and Ljovuschkin (1965). They recovered *Borovina*, *Miliammina*, and *Trochamminita* from a brackish pool (salinity 11) in Kaptar-Khana Cave (Turkmenistan). Cave foraminifera have since been documented elsewhere (e.g., Mikhalevich, 1976; Sket and Iliffe, 1980, Kitamura and others, 2007), but detailed ecologic descriptions of assemblages and taxa have remained unavailable. Javaux and Scott (2003) completed a preliminary sampling in a few Bermudian caves, and discovered diverse foraminiferal communities unlike those in other local coastal environments. Because they sampled only cave entrances, however, the intrinsic underwater cave habitats remained unknown. Fossil foraminifera in both vadose and phreatic caves have also been documented, but interpretations remain unsupported by modern ecological studies (e.g., Proctor and Smart, 1991; van Hengstum and others, 2009a). This study aims to investigate the ecology of foraminifera living in an underwater cave, with specific attention given to distinguishing anchialine versus submarine cave environments, habitats, and faunas, and the processes operating in these environments.

COASTAL CAVE ENVIRONMENTS

Coastal caves are classified into different environments based on inherited geomorphology, hydrogeology, magnitude of terrestrial influence, and coastal position (Fig. 1). Coastal aquifers can be grossly divided into two separate

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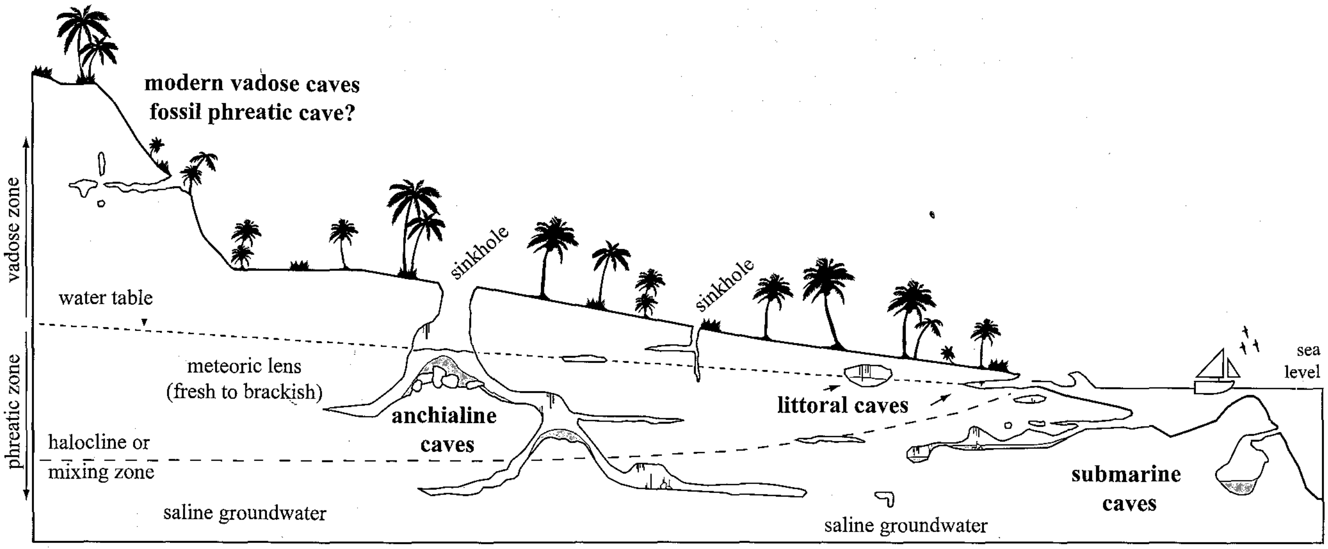

FIGURE 1. Classification of coastal cave environments. On Caribbean terrestrial karst terrain, sinkholes are commonly called cenotes in Mexico and blue holes in the Bahamas. Stalactites and stalagmites that formed during sea-level lowstands often decorate underwater caves.

groundwater masses, the meteoric lens and saline groundwater, which are separated by a halocline (or mixing zone). The meteoric lens can vary from fresh (e.g., salinity 1.5 on the Yucatan) to very brackish (e.g., salinity >20 in some areas of Bermuda), whereas saline groundwater is marine (salinity ~35). These groundwater masses flood porous coastal karst platforms and their abundant caves.

Coastal caves are generally categorized into one of four environments: vadose, littoral, anchialine, or submarine (Fig. 1). Subaerial access into caves is typically through collapse features such as sinkholes or fissures, which often form during sea-level regressions. Sinkholes provide physical "karst windows" into otherwise oligotrophic subterranean habitats, which allow for the influx of terrestrial nutrients, sediments, and non-cave-dwelling organisms. Vadose caves occur above the water table in the unsaturated vadose zone, and although they are not modern aquatic ecosystems, their sediment may contain marine microfossils such as foraminifera (e.g., Proctor and Smart, 1991). Littoral caves occur at sea level and contain an air-water interface throughout most of the cave system. This is caused by the cave passage transecting the water table. Littoral caves that open directly to the sea can have increased hydrodynamics from the attenuation of wave action (Denitto and others, 2007). However, speleothems such as calcite rafts may be the only evidence of the water table in distal cave passages because littoral caves are often environmentally dominated by a meteoric lens (Taylor and Chafetz, 2004; Dorale and others, 2010). Anchialine caves are defined as having restricted atmospheric access, noticeable marine and terrestrial influences, and subterranean connection to the ocean (Stock and others, 1986). Anchialine caves can also transect through the meteoric lens, saline groundwater, or both. Finally, submarine caves are more-narrowly defined as having entrances that are located below sea-level passages flooded only by saline groundwater. Presently, cavities in reef frameworks are considered a specialized type of submarine cave environment, despite their unique role in carbon cycling (De Goeij and Van Duyl, 2007).

This classification scheme is not without limitations. For example, a single cave system can simultaneously host more than one type of cave environment, such as Ox Bel Ha, Mexico, and cave environments are defined based on at one point in time. As such, the environment within a specific cave will evolve during Quaternary sea-level change, or in response to any other processes causing environmental change (e.g., anthropogenic pollution). This classification is also independent of speleogenesis, which may be contemporary with the cave environments. Superimposed upon this classification is that each cave environment comprises spatially variable habitats related to local physico-chemical gradients. For example, different habitats can be created in underwater cave environments from salinity variations between groundwater masses in the coastal aquifer, or attenuating bulk organic matter with increasing distance away from cave entrances (Fichez, 1990, van Hengstum and others, 2009a).

Despite the wide usage of this classification scheme, many questions surround the actual boundary conditions between the different cave environments and their habitats. Because both anchialine and submarine caves can equally exist in saline groundwater, what differentiates anchialine from submarine cave environments in saline groundwater? What is the relative impact of terrestrial versus marine organic matter on the cave benthos? Is there an ecological response to littoral conditions created deeper in the cave when cave passages intersect the water table? Foraminifera are quite sensitive to physical and chemical variables in other coastal systems (e.g., salinity, organic matter, pH), so we hypothesized that they will be helpful for distinguishing coastal cave environments and their endemic habitats.

STUDY SITE GEOLOGY AND HYDROGEOLOGY

Bermudian caves are collapsed karst features in a Carbonate Cover Island according to the Carbonate Island Karst Model (Mylroie and Mylroie, 2007). This is because

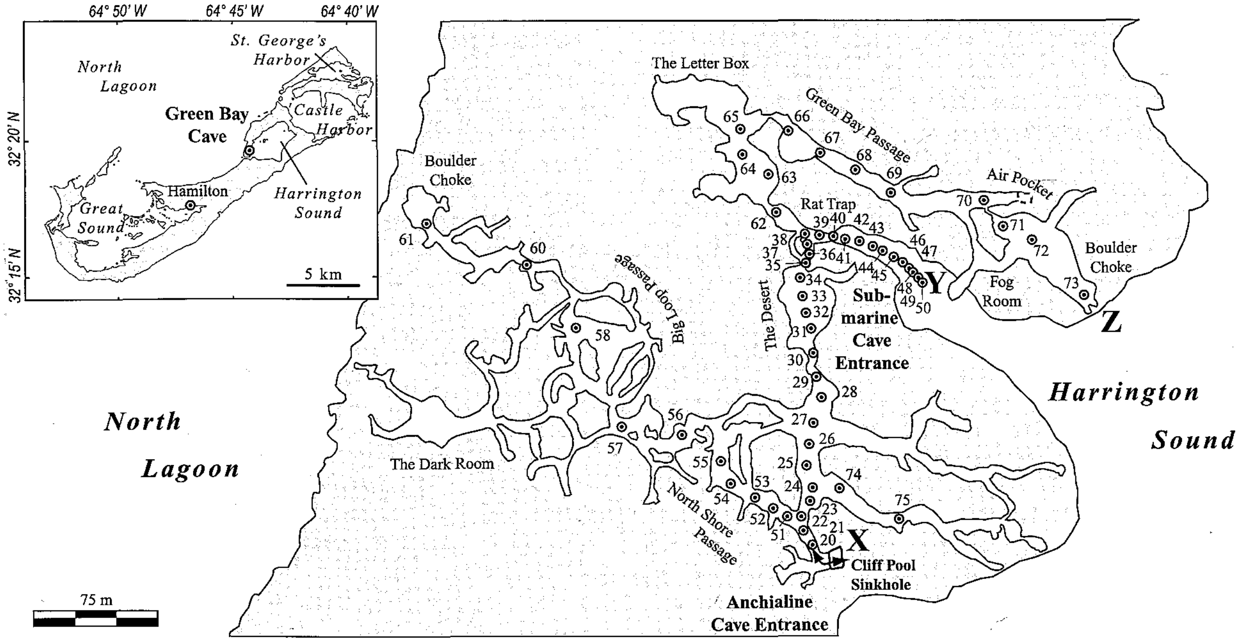

FIGURE 2. The location of Green Bay Cave on Bermuda with a detailed cave survey depicting sample locations. Cliff Pool Sinkhole provides the only subaerial access into the cave, the Trunk Passage physically links the anchialine and submarine cave entrances (Stock and others, 1986), and the Air Pocket is the only location with an air-water interface in the cave. The arrow near Cliff Pool Sinkhole represents the distribution of samples 1 to 19, which are too close together to illustrate with individual markers. Cave survey adapted after original sketch by Robert Power.

Bermudian geology is characterized by a basalt core overlain by alternating eolianites and paleosols that developed during Late Quaternary sea-level highstands and lowstands, respectively (Land and others, 1967; Gees and Medioli, 1970; Hyndman and others, 1974; Vacher and others, 1989, 1995; Hearty, 2002). Bermudian caves formed by three primary processes: (a) vadose dissolution concentrated at the basalt-eolianite contact during Quaternary sea-level lowstands, (b) further modification and enlargement by phreatic dissolution during Quaternary sea-level highstands, and (c) subsequent collapse events triggered by glacial regressions (Mylroie and others, 1995). These processes have created modern caves characterized by large chambers connected by fissures and tunnels. Modern underwater caves in Bermuda are those caves that were re-flooded by rising groundwater associated with Holocene sea-level rise. Five freshwater lenses (i.e., meteoric lenses with salinity <1) characterize Bermudian hydrogeology, but Quaternary speleogenesis has been focused in northeast Bermuda where these freshwater lenses are currently absent (e.g., Vacher and Wallis, 1992; Mylroie and others, 1995; Vacher and Rowe, 1997).

Green Bay Cave was selected as the study site because it includes both anchialine and submarine cave environments as described by Stock and others (1986). It is located on the north shore of Harrington Sound, transecting both the Lower Town Hill and Belmont formations (Fig. 2). The anchialine cave environment begins at Cliff Pool Sinkhole and transects the two different groundwater masses, the meteoric lens and saline groundwater. Cliff Pool Sinkhole has physical characteristics typical of other Bermudian anchialine ponds, including: a very narrow tidal range (<0.5 m), ubiquitous algae, and the anchialine gastropod *Cerithium lutosum* (Thomas and others, 1991). In contrast, the submarine cave environment begins at the cave entrance opening below sea level in Harrington Sound. The Trunk Passage connects these two different environments, thereby providing an ideal location in which to investigate the difference between anchialine and submarine cave environments.

The groundwater that floods Green Bay Cave is typical of most Bermudian caves, where a thin brackish meteoric lens (<0.6 m, salinity >20) is buoyed on saline groundwater (e.g., Sket and Iliffe, 1980). The submarine cave entrance opening into Harrington Sound allows for direct tidal exchange of seawater between the lagoon and saline groundwater in the cave (Fig. 2; Morris and others, 1977; Cate, 2009). However, only ~60% of the seawater that flows into the submarine cave entrance during a tidal cycle returns as outflow into Harrington Sound (Cate, 2009). This indicates that there is a daily diffuse outflow of saline groundwater through the limestone bedrock into the coastal waters. Groundwater current velocities are very low throughout the internal cave passages, but flow velocities can reach a maximum of 1.5 m s^{-1} in the narrow submarine cave entrance during tidal peaks (Cate, 2009).

METHODS

All ecological interpretations herein are based on total assemblages (rose Bengal-stained + unstained individuals) because: 1) annual monitoring experiments on total versus living wild populations indicate that total assemblages better represent average environmental conditions (Buzas and others, 1977; Scott and Medioli, 1980a); 2) total assemblages provide an averaged taphonomic perspective, which is most directly applicable to paleoecological research (Buzas, 1968; Debenay and others, 2001; Debenay and Guillou, 2002; Osterman, 2003; Tobin and others, 2005; Melis and Violanti, 2006); and 3) it is widely recognized that rose Bengal stains both living and recently dead cellular protoplasm, requiring a conservative approach in its application (Bernhard, 1988; Bernhard and others, 2006). Nevertheless, rose Bengal is still required to verify that total cave populations accurately represent the modern fauna (van Hengstum and others, 2009a).

Seventy-five surface sediment samples (each ~35 cm^3 of the top 4 cm) were collected throughout Green Bay Cave (Fig. 2) using self-contained underwater breathing apparatus (SCUBA). For foraminiferal analysis of each sample, a 5-cm^3 subsample was wet-sieved through a 45-µm screen and the residue was immersed in a rose Bengal solution (1 g l^{-1} of 4% buffered formalin). As an a priori requirement for this study, at least one stained individual from each taxonomic unit in each sample required categorical observation (in the bulk sedimentary sample or enumerated subsample) for that species to be reported as part of the modern total assemblage and included in multivariate analysis. This procedure both verifies that the recovered foraminifera are actually living in the cave and recognizes fossil taxa. Previously, van Hengstum and others (2009a) used this method in a Mexican cave to differentiate Pleistocene versus Holocene foraminiferal assemblages. Although we present rose Bengal-based estimates for absolute abundance of living foraminifera in this study, interpretations are based on total assemblages and relative abundances to avoid bias from time-averaging.

Samples were wet-split, wet-picked, sorted by species, and taxonomically enumerated to create an original data matrix of 75 samples × 136 species (Appendix 2). The only rose Bengal-stained planktic microfossils observed were tintinnids, which were counted because they are a useful proxy for particulates in the water column (Scott and others, 1995). After calculating the relative abundance and standard error for each species in every sample, 30 statistically insignificant species were omitted from further multivariate analysis because the standard error was greater than relative abundance in all samples or the species was represented in only one sample (Patterson and Fishbein, 1989). Samples in the final data matrix (75 samples × 106 species) were then compared by Q-mode cluster analysis using a Euclidean similarity measure and Ward's Method of minimum variance in the freeware package *PAST* (Hammer and others, 2001). Lastly, Fisher alpha (F_α) and Shannon-Wiener Diversity Index (*H*) were calculated for each sample to estimate diversity.

Sediments were analyzed for mean grain size, bulk organic matter, calcium carbonate content ($CaCO_3$), and organic matter geochemistry ($\delta^{13}C_{org}$ and C:N ratio). Grain size analysis was determined to identify external influences on the cave passages near the entrances, such as the maximum influence of wave action and tidal currents or terrestrial erosion. Undigested cave sediment was analyzed to retain a complete signature of localized sedimentary processes (Donnelly and Woodruff, 2007; Donato and others, 2009) using a Beckman Coulter LS 230, which has an analytical precision better than ±2 µm on replicate samples and standards (15 µm garnet; see van Hengstum and others, 2007). Bulk organic matter and $CaCO_3$ (weight %) were determined on ~1.5 g dried-sediment subsamples by Loss on Ignition (LOI) for 4.5 hours at 550°C and 2 hours at 950°C, respectively. Analytical precision on replicate LOI samples ($n = 19$) was better than ±1.7% (Heiri and others, 2001). Lastly, $\delta^{13}C_{org}$ and C:N were measured to determine whether the source of the bulk organic matter at each sample site was predominantly terrestrial or marine (Lamb and others, 2006, Perdue and Koprivnjak, 2007; Diz and Francés, 2008; Weijers and others, 2009; Kemp and others, 2010). Bulk sediment was treated with a 10% HCl carbonate digestion, rinsed to neutrality, desiccated, and then ground into a homogenous powder. Stable carbon isotopes and C:N ratio data were measured on subsamples in a Costech elemental analyzer connected to a Thermo-Finnigan DeltaPlus XP mass spectrometer. Carbon isotope ratios were measured against several international and internal standards, and expressed in the standard delta (δ) notation in per mil (‰) against Vienna PeeDee Belemnite (VPDB) with an analytical precision on replicates of ±0.2‰. Sediment variables for each sampling station are included in Appendix 2.

Hydrogeologic properties (dissolved oxygen, salinity, pH, temperature) were measured just above the sediment-water interface in the cave with an independent submersible multiparameter probe (YSI 600XLM). The lead diver of a two-person team carried the probe to measure an undisturbed water column.

RESULTS

ENVIRONMENTAL VARIABLES

Hydrogeological Variables

Two different groundwater masses are discernable at Cliff Pool Sinkhole: a shallow (0.6 m) meteoric lens of brackish water and saline groundwater (Fig. 3). Salinity is ~24, pH is 7.6 in the meteoric lens, and the temperature of ~19°C is slightly cooler than the saline groundwater. Below the halocline, the saline groundwater is marine (salinity 35.5, pH 8.1), and slightly warmer (>20°C) than the meteoric lens. Heliothermic heating near the day of measurement perhaps caused groundwater warming just below the halocline in Cliff Pool Sinkhole. The entire cave system is oxic, as dissolved oxygen is 3 ml l^{-1} in the meteoric lens, >5 ml l^{-1} throughout the saline groundwater, and 6.1 ml l^{-1} in Harrington Sound. On the day of measurement, the salinity and pH of the saline groundwater in the cave approached the oceanic conditions in Harrington Sound.

Sediment Grain Size, Bulk Organic Matter, and $CaC0_3$

Coarse-grained and organic-rich sediment accumulates near the cave entrances, while fine-grained carbonate mud with less organic matter characterizes the cave interior. At Cliff Pool Sinkhole, a poorly sorted diamict with mean grain size of 255 µm occurs down the slope into the cave, which contains abundant terrestrial material (sticks, leaves,

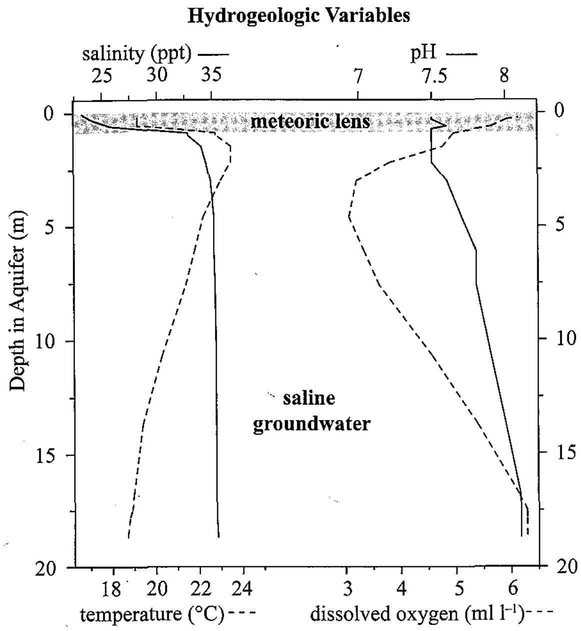

FIGURE 3. Hydrologic variables through the aquifer at Cliff Pool Sinkhole as measured in January 2009. The changes in pH and salinity transition across important ecological thresholds for benthic foraminifera.

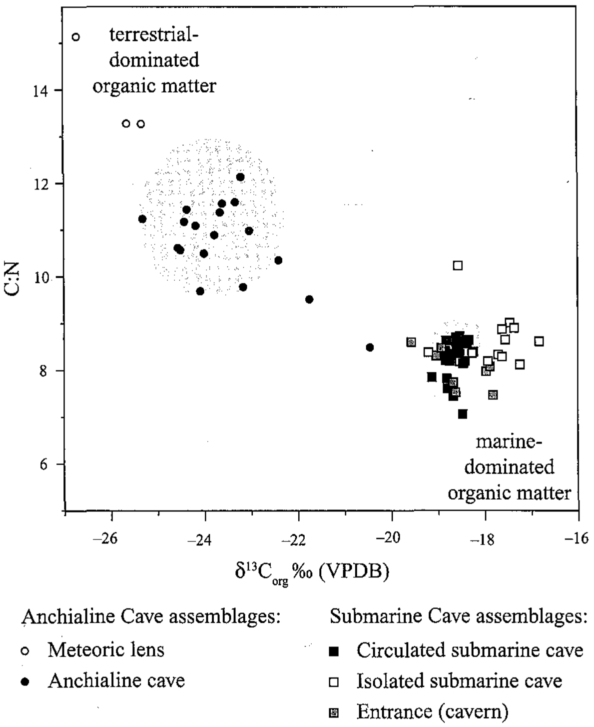

FIGURE 4. A biplot of C:N and $\delta^{13}C_{org}$ indicates that two different types of organic matter are deposited in Green Bay Cave. Sample stations that are dominated by terrestrial organic matter (OM) are colonized by the ML and AC assemblages; whereas, stations that are dominated by marine organic matter are colonized by the CSC, ISC, and E assemblages. The shaded area represents 2σ about the mean (see Results).

livestock bones, etc.), fossil marine bivalves (*Arca*), and sand- to cobble-sized fragments of limestone. The coarse-grained sediment near Cliff Pool Sinkhole changes in the Trunk Passage from S20 to S22 (Fig. 2). These include: 1) a grain-size shift from 225 μm to ~10 μm, 2) a color change from light brown to grayish, 3) bulk organic matter decreases from over >10% to <8%, and 4) $CaCO_3$ increases from 37% to 50%. Fine-grained carbonate mud with a mean grain size of <15 μm (fine silt) dominates the other investigated cave passages beyond the transition from S20 to S22. In the distal cave passages, fine carbonate silt accumulates as infill between boulders derived from ceiling collapses (e.g., Green Bay Passage).

Another sedimentary change occurs in the cave passage between The Desert and the Rat Trap, where carbonate mud in The Desert transitions into a coarse shell hash in the Rat Trap. Mean grain size shifts from 9 μm (S32) to 221 μm (S40), and bulk organic matter increases from <5% to 20%. A fine to medium sand (mean 218–356 μm) with abundant shell material extends from the submarine cave entrance in Harrington Sound down into the Rat Trap. The presence of coral fragments and lagoonal bivalves indicates that waves and tidal currents are transporting some lagoonal sediment from Harrington Sound into the submarine cave entrance.

There are two notable cave-specific sedimentary observations of interest. First, some distal cave passages, such as S71, contained orange- to yellow-hued sediment. Similarly colored sediment also occurs in eastern Yucatan and Mallorcan caves, but the coloration and sedimentary geochemistry has not yet been attributed to a marine geologic or hydrogeologic process (Fornós and others, 2009; van Hengstum and others, 2009a). The sediment at S71 contained modern foraminifera consistent with the adjacent assemblages in the carbonate mud (discussed below). Second, calcite rafts are present at S70, which are a speleothem that precipitates on the water table (Taylor and Chafetz, 2004; Fornós and others, 2009). Their presence was expected because there is a water table almost directly above this sample station in the Air Pocket. No other places in the modern cave contain an air–water interface. Calcite rafts were not laterally transported away from the direct vicinity of the Air Pocket, which is probably due to the low current velocities of groundwater in the cave interior.

$\delta^{13}C_{org}$ *and C:N*

The $\delta^{13}C_{org}$ value for terrestrial organic detritus is −26‰ with C:N ratios exceeding 10. This is because terrestrial plants using the C_3 photosynthetic pathway create ^{13}C-depleted and nitrogen-poor plant tissues (Lamb and others, 2006). The most $\delta^{13}C_{org}$-depleted sample with the highest C:N ratio (15.1) is from Cliff Pool Sinkhole (S03: −26.7‰), at a water depth of 0.6 m (Fig. 4). These geochemical data accord with the sample location because the shallow sinkhole would be expected to receive a high influx of terrestrial organic matter and sediments from surface erosion. In contrast, the most isotopically enriched sample is S72 (−16.8‰), collected near the terminus of the Green Bay Passage (Fig. 2). In general, marine organic matter is relatively more ^{13}C-enriched and nitrogen-rich than

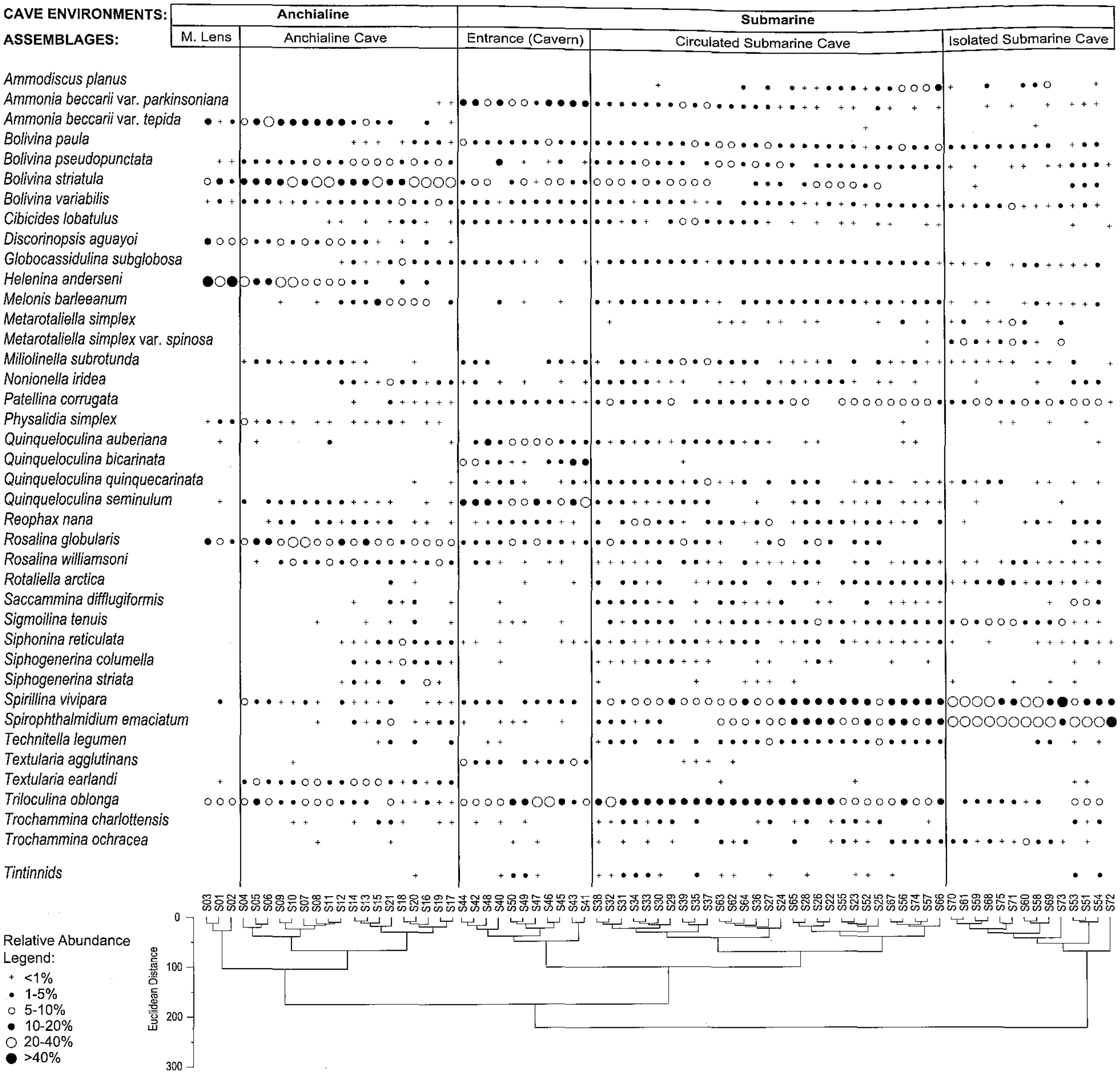

FIGURE 5. Dendrogram produced by Q-mode cluster analysis on the statistically significant taxa in the surface sediment samples. A three-cluster interpretation (Euclidean distance = 150) of the dendrogram distinguishes the anchialine versus submarine cave environments, and a five-cluster interpretation (Euclidean distance = 100) identifies foraminiferal assemblages colonizing different habitats within the cave environments. Only taxa that occurred at >5% in at least one sample are figured to emphasize the significant fauna. M. Lens: Meteoric Lens.

terrestrial organic matter (Lamb and others, 2006). The geochemical signature of the organic matter at S61 is consistent with a marine origin, as the inherited geomorphology provides little opportunity for the influx of terrestrial organic matter at the sample site (Fig. 2). Beyond these two stable carbon-isotopic end members, the rest of the samples generally comprise two clusters in the biplot (Fig. 4). The more carbon-isotopically depleted and nitrogen-poor group (n = 21, mean $\delta^{13}C_{org} = -23.9$, C:N = 11.2) represents samples where the organics are predominantly derived from terrestrial sources (Fig. 5). In contrast, the more carbon-isotopically enriched and nitrogen-rich group (n = 53, $\delta^{13}C_{org} = -18.4$, C:N = 8.3) represents samples where organics are predominantly derived from marine sources.

FORAMINIFERAL ASSEMBLAGES

Abundant benthic foraminifera (living + dead) are present in Green Bay Cave sediments with a mean 2492 individuals per cm^3 (min. 106, max. 6822). No endemic cave species of foraminifera were discovered, but three assemblages (Anchialine Cave, Circulated Submarine Cave, and Isolated Submarine Cave) are distinct from those of other Bermudian coastal environments (Javaux, 1999; van Hengstum and others, 2009b). Not surprisingly, larger benthic foraminifera with photosynthetic symbionts were absent in these dark caves, although rare specimens were found at the submarine cave entrance.

Rare infillings (molds or steinkerns) and degraded foraminifera that eroded out of the limestone were easily

TABLE 1. Arithmetic mean of environmental variables and relative abundance of dominant foraminifera in each assemblage.

Cave Environments:	Anchialine		Submarine		
Assemblages:	Meteoric lens	Anchialine cave	Circulated submarine cave	Isolated submarine cave	Entrance
Hydrogeological variables					
salinity (g l^{-1})	24.6	34.5	35.5	35.5	35.5
pH	7.5	7.8	8.1	8.1	8.1
dissolved oxygen (ml l^{-1})	6.1	5.2	6.2	6.2	6.3
temperature (°C)	19.2	20.7	19.1	19	18.8
Sediment properties					
mean grain size (μm)	224.8	225	14.6	7.1	302.7
OM (wt %)	23.5	14.0	8.0	6.9	9.8
$CaC0_3$ (wt %)	35.2	37.0	50.9	50.8	51.6
C:N	12.0	11.0	8.2	8.6	8.0
$\delta^{13}C_{org}$ (VPDB)	−24.4	−23.8	−18.7	−17.8	−18.6
Foraminifera					
Total foraminifera per cm^3	133	887	3209	2849	3390
Living foraminifera per cm^3	8	20	132	62	210
Shannon-Wiener diversity index (*H*)	1.7	2.8	3.3	2.4	3.2
Fisher alpha diversity index (F_α)	4.1	9.2	16.8	9.4	16.9
Helenina anderseni	**50.9**	7.4			
Textularia earlandi	<1.0	4.3			
Discorinopsis aguayoi	**8.8**	**9.9**			
Bolivina striatula	**7.9**	**18.5**	3.7	<1.0	4.0
Rosalina globularis	2.9	**9.2**	2.5	<1.0	3.8
Triloculina oblonga	<1.0	5.2	**13.4**	1.8	**11.9**
Spirillina vivipara	1.1	1.3	**11.3**	**22.0**	1.2
Spirophthalmidium emaciatum		1.0	**7.4**	**30.7**	<1.0
Patellina corrugata		<1.0	4.5	**5.2**	1.5
Quinqueloculina spp.	<1.0	1.4	4.0	<1.0	**26.0**
Sigmoilina tenuis		<1.0	2.0	5.1	<1.0
Ammonia beccarii var. *parkinsoniana*			2.0	<1.0	**10.0**

recognized and not included in the total assemblages (Appendix 2). Foraminiferal steinkerns were also observed by van Hengstum (2008) in Mexican cave sediments, which likely eroded out of the surrounding limestone during speleogenic processes (see fig. 10 in Fornós and others, 2009). Samples S61 and S63 had non-infilled fossil lagoonal taxa that were mostly *Archaias* (Appendix 2). These were considered allochthonous and excluded from the total assemblage because they were unstained by rose Bengal, and they exhibited characteristics of transport despite the low groundwater flow velocity at these sample sites (greater than stage 2–3 abrasion and breakage as per Cottey and Hallock, 1988).

The dendrogram produced by cluster analysis provided a hierarchical division of the foraminifera, first into cave environments and then into cave habitats. Three groups (or clusters), isolated at a Euclidean distance of 150, represent the classification of anchialine versus submarine cave environments described by Stock and others (1986, Fig. 1). At a Euclidean distance of 100, however, there are five groups that we interpret as separate assemblages colonizing distinct cave habitats. These habitats accord with the measured sedimentologic, organic-geochemical, and hydrogeologic variables. The five assemblages are named by habitat: Meteoric Lens (ML), Anchialine Cave (AC), Circulated Submarine Cave (CSC), Isolated Submarine Cave (ISC), and Entrance (Fig. 5), as described in detail below.

Meteoric Lens (ML) Assemblage

The ML Assemblage has the lowest diversity (mean *H* 1.7), and the lowest absolute abundance (mean 133 specimens cm^3) among the recovered assemblages. The three samples (S01, S02, S03) that yield this assemblage are located in the shallow, brackish meteoric lens at Cliff Pool Sinkhole (<0.6 m deep, mean salinity 24.6). This assemblage has the highest bulk organic matter (mean 23.5%), which is predominantly derived from the terrestrial surface as indicated by the stable carbon isotopes and C:N ratio data (mean −24.4‰, C:N ratio mean 12; Fig. 4). Euryhaline and stress-tolerant foraminifera dominate the assemblage and include *Helenina anderseni* (mean 50.9%), *Bolivina striatula* (mean 7.9%), *Discorinopsis aguayoi* (mean 8.8%), and *Ammonia beccarii* var. *tepida* (mean 5%; Table 1). This is also the only assemblage where *Haplophragmoides wilberti* (max. 2.6%), *Trochammina macrescens* (max. 2%), *T. inflata* (max. 3.2%), and *Miliammina fusca* (max. 1.5%) have statistically significant populations (Appendix 2).

Anchialine Cave (AC) Assemblage

The Anchialine Cave (AC) Assemblage is located below the halocline in the saline groundwater in cave passages proximal to Cliff Pool Sinkhole. Foraminiferal diversity increases from an *H* of 1.7 to 2.8 with increasing water depth below the halocline into the saline groundwater (salinity of 34.5). *Bolivina striatula* (mean 18.5%), *Rosalina globularis* (mean 9.2%), and *Discorinopsis aguayoi* (mean 9.9%) dominate the AC Assemblage, but *Ammonia beccarii* var. *tepida* (mean 8.2%) and *Textularia earlandi* (max. 9.6%) are also common. Still deeper into the coastal aquifer and cave, other shelf and coastal taxa increase in relative abundance, including *Melonis barleeanum* (max. 10%), *Siphogenerina striata* (max. 9%), *Hopkinsina atlantica* (max. 4%), *Nonionella iridea* (max. 5.5%), and *Fursenkoina compressa* (max. 4.7%). Many taxa reach their highest relative abundance in the AC Assemblage. This assemblage is associated with a finer-grained sediment (mean ~225 μm) with less bulk organic matter (mean 14%) than the ML Assemblage, and the organic geochemical proxies indicate that the organics are primarily derived from terrestrial sources (Fig. 4; $\delta^{13}C_{org}$ −23.8‰, C:N 11). Miliolids are also present in the AC assemblage, but they do not form a significant fraction of the assemblage (e.g., *Quinqueloculina* spp. mean 1.4%). *Physalidia simplex* is also most predominant in the AC Assemblage, which is a common taxon in Yucatan anchialine caves (Gabriel and others, 2009; van Hengstum and others, 2009a). Tintinnids in the AC Assemblage never exceed 2% of the total assemblage (Fig. 5).

Circulated Submarine Cave (CSC) Assemblage

This assemblage has the highest diversity ($H = 3.3$, $F_\alpha = 16.8$) of any those recovered from Green Bay Cave, and is dominated by *Triloculina oblonga* (mean 13.4%), *Spirillina vivipara* (mean 11.3%), and *Spirophthalmidium emaciatum* (7.4%; Table 1). Other common species in the assemblage include *Technitella legumen* (max. 5.8%), *Bolivina striatula* (mean 3.7%), and *Patellina corrugata* (mean 4.5%). Of all the Green Bay Cave assemblages, tintinnids were most abundant in the CSC Assemblage, indicating that sufficient particulate is present in the water column to support these planktic ciliates (Fig. 5, Garrabou and Flos, 1995; Scott and others, 1995). The pH (mean 8.1), temperature (19.1°C), dissolved oxygen (6.2 ml l^{-1}), and salinity in the saline groundwater approach oceanic conditions, indicating that the groundwater is not stressing the foraminifera. The substrate for this assemblage is typically carbonate mud (fine silt, mean grain size 14.6 μm, mean $CaCO_3$ = 50.9%), with lower organic matter content (mean 8.2%) than the ML Assemblage. The organic matter is more carbon isotopically enriched (mean −18.7‰) than that of the ML Assemblage, indicating that the organic matter is predominantly marine (Fig. 3). The C:N ratio indicates that more nitrogen-rich plant tissues are present in the sediment associated with this assemblage than the AC and ML assemblage (mean 8.2).

Isolated Submarine Cave (ISC) Assemblage

The ISC Assemblage is dominated by *Spirophthalmidium emaciatum* (mean 30.7%), which has a maximum of 80% in S72. Other significant taxa include *Patellina corrugata* (mean 5.2%) and *Spirillina vivipara* (mean 22%), and less-abundant constituents such as *Rotaliella arctica* (max. 13%) and *Bolivina variabilis* (max. 7%). This assemblage is less diverse than the CSC (mean *H* of 2.4). Only samples S53 and S54 (Fig. 2), located between CSC Assemblage sites, had tintinnids. Most of the substrate consists of fine-grained carbonate mud (mean 7.1 μm, mean $CaCO_3$ 50.8%), similar to that of the CSC Assemblage, except for orange-hued carbonate mud at S71. Bulk organic matter content is slightly less in the ISC Assemblage (mean 6.9%), and is comprised of the most carbon isotopically enriched and nitrogen-rich organic matter in the entire cave, indicating a marine origin (mean: $\delta^{13}C_{org}$ 17.8‰ and C:N 8.6). As with the CSC Assemblage, the saline groundwater mass approached oceanic values (means: 8.1 pH, 18.8°C, 6.3 ml l^{-1} dissolved oxygen).

Entrance Assemblage

The Entrance Assemblage is located up to ~60 m into the cave from the submarine cave entrance at the northwestern end of Harrington Sound. The Entrance Assemblage extends from the light-limited "twilight" zone, colloquially referred to as the "cavern", to the completely dark Rat Trap (Fig. 2). This assemblage consists of typical lagoonal foraminifera dominated by *Quinqueloculinia* spp. (mean 26%), *Triloculina oblonga* (mean 11.9%), and *Ammonia beccarii var. parkinsoniana* (mean 10%). Foraminiferal diversity is similar to the CSC Assemblage (mean *H* 3.2). As with the ISC and CSC assemblages, the saline groundwater flooding the Entrance Assemblage approaches oceanic conditions and is not ecologically limiting to foraminifera. Samples S47, S48, S49, and S50 were obtained from the lagoon just outside the cave and cluster with the Entrance Assemblage in the dendrogram (Fig. 5), suggesting a close affinity between foraminifera living in the lagoon and in the submarine cave entrance. The substrate typically consists of poorly sorted, medium-sand shell hash (mean grain size 302 μm), with a mean organic matter content of 9.8%. The mean values of $\delta^{13}C_{org}$ (8.6‰) and C:N (8) are similar to those for the ISC and CSC assemblages, indicating that the organic matter is predominantly marine.

DISCUSSION

TAPHONOMY: ARE CAVE FORAMINIFERA TRANSPORTED OR IN SITU?

A limitation of using total assemblages to derive ecological information is that one must consider possible taphonomic effects on the final assemblages. van Hengstum and others (2009a) found unstained late Pleistocene foraminifera in surface sediment from distal passages of Aktun Ha Cave, Mexico. Their presence was likely due to the very low to absent sedimentation rates in the distal cave passages of Aktun Ha that led to significant time-averaging. Conversely, abundant rose Bengal-stained specimens consistent with the total assemblage were found in every surface sample from Green Bay Cave. This indicates that the foraminiferal assemblages recovered from Green Bay Cave represent recent conditions at the sampling sites. The degree of time-averaging, however, is unknown because sedimentation rates throughout the cave have not been quantified. Nevertheless, the abundance of stained specimens provides strong evidence that the total assemblages reported herein, excluding those of S73 and S61 as discussed below, represent the recent fauna of Green Bay Cave.

Cave entrances open to the ocean are influenced by wave action and, in the case of Green Bay Cave, strong tidal currents from the restricted geomorphology. These processes are transporting sediment, nutrients, and foraminifera from the lagoon into the submarine cave, thus causing the coarse-grained shell hash to accumulate in the first 50 m of the cave. With increasing distance into the cave, rapidly decreasing current velocities facilitate a grain-size shift to fine carbonate mud with few shell fragments. The substrate change is also coincident with the faunal change from the Entrance Assemblage to the CSC Assemblage. The rarity of foraminifera with photosymbionts in the Entrance Assemblage, which are common in Bermudian lagoons (Javaux, 1999), indicates that the incoming tidal current is not causing wholesale transport of foraminifera from the lagoon into the cave. The Entrance Assemblage also includes stained foraminifera consistent with the total assemblage, which confirms that most of the assemblage is in situ. On the slope and at the base of Cliff Pool Sinkhole, some foraminifera may be derived from gravitational transport, but the infrequency of sinkhole taxa at the base of the Cliff Pool Sinkhole suggests that this is a minor factor. Lastly, several taxa in Green Bay Cave (e.g., *Ammodiscus planorbis, Labrospira evoluta, Parvigenerina* spp.) have not been previously reported from Bermuda, and the Anchialine Cave Assemblage is distinct from all other foraminiferal assemblages in Bermudian coastal environments. Based on the available evidence, the recovered foraminifera are living in Green Bay Cave, and the different assemblages are colonizing endemic cave habitats.

THE ANCHIALINE CAVE ENVIRONMENT

Salinity, dissolved oxygen, and food resources (quantity and source) are perhaps the most important variables influencing benthic foraminiferal ecology (e.g., Jorissen and others 1995; Jorissen and Wittling, 1999; Morigi and others, 2001; Scott and others, 2001; Debenay and Guillou, 2002; Murray, 2006). Dissolved oxygen in the groundwater is not controlling foraminifera in Green Bay Cave because it is only ecologically limiting to foraminifera if <2 ml l^{-1} (Bernhard and Sen Gupta, 1997; Osterman and others, 2008), and the entirety of Green Bay Cave is currently well-oxygenated (Fig. 3). Both the ML and AC assemblages have similar C:N and $\delta^{13}C_{org}$ values, which indicates that both assemblages receive regular inputs of terrestrial organic matter (Fig. 3, Table 1). These results suggest that neither dissolved oxygen nor the source of organic matter is causing segregation of these assemblages (and habitats) in the anchialine cave environment. By definition, anchialine cave environments can be located in the meteoric lens, the saline groundwater, or both (Fig. 1). In Green Bay Cave, the halocline divides the anchialine cave environment into two categorically different habitats that are colonized by different foraminiferal assemblages. The ML assemblage colonizes a habitat flooded by the brackish meteoric lens; whereas the AC assemblage colonizes a habitat flooded by the saline groundwater mass.

Euryhaline foraminifera dominated by *Helenina anderseni* and *Ammonia beccarii* var. *tepida* are common in the brackish meteoric lens of Cliff Pool Sinkhole (mean salinity 24.6), which is the assemblage with the lowest diversity (mean *H* of 1.7). Debenay and Guillou (2002) describe *Helenina anderseni* as nearly obligate brackish because it is cosmopolitan in tropical and subtropical mangroves, cold-temperate salt marshes, and marine–freshwater transitions (e.g., Scott and Medioli, 1980b; Scott and others, 1991; Hayward and Hollis, 1994; Debenay and others, 1998). *Discorinopsis aguayoi* is also a typical inhabitant of tropical brackish ponds and mangroves (Arnold, 1954; Javaux and Scott, 2003). Other diagnostic brackish-water indicators in the ML assemblage are common salt marsh taxa, such as *Trochammina inflata*, *T. macrescens*, *Miliammina fusca*, and *Haplophraphmoides wilberti* (Scott and Medioli, 1980b; Horton and Edwards, 2006). Only salinity in the meteoric lens crosses an ecological threshold for benthic foraminifera (Murray, 2006; Table 1), which indicates that this groundwater mass provides a stressed habitat suitable only for euryhaline taxa common to other pH- and salinity-stressed marginal-marine settings (e.g. Scott and Medioli, 1980b; Javaux and Scott, 2003; Horton and Edwards, 2006). Therefore, the meteoric lens is a specific habitat within the anchialine cave environment because it is terrestrially impacted both (a) hydrogeologically by precipitation and surface runoff into the meteoric lens, and (b) sedimentologically from the high quantities of terrestrial organic matter eroding into Cliff Pool Sinkhole.

The foraminifera in the sinkhole of Green Bay Cave are slightly different than those that van Hengstum and others (2008) found in the Yucatan cenotes (sinkholes). These faunal differences are most likely related to salinity because Cliff Pool Sinkhole is polyhaline (within the salinity range of 18–30) while the described Mexican cenotes are oligohaline (within the salinity range of 0.5–5). Euryhaline taxa are common in both regions, such as *Ammonia beccarii* var. *tepida, Miliammina fusca,* and *Trochammina* spp. However, *Ammonia beccarii* var. *tepida* and thecamoebians dominate the Mexican cenotes, whereas *Helenina anderseni* and *Discorinopsis* dominate Cliff Pool Sinkhole. It is well known that *Ammonia* is tolerant to the oligohaline to mesohaline conditions present in the cenotes, which has been verified through culturing experiments and field observations elsewhere (e.g., Bradshaw, 1961; Boltovskoy and Lena, 1971), perhaps at the expense of *Helenina* and *Discorinopsis*. The Mexican cenotes are also inhabited by the most brackish-tolerant thecamoebians *Centropyxis* and *Arcella* when salinity is <3.5 (van Hengstum and others, 2008). No oligohaline sinkholes are known in Bermuda.

In Cliff Pool Sinkhole, foraminifera rapidly diversify below the halocline in the saline groundwater (mean *H* of 2.8 below 0.6 m). The Anchialine Cave (AC) Assemblage is dominated by *Bolivina striatula* (mean 18.5%) and *Rosalina globularis* (mean 9.2%) and is a previously undocumented assemblage living in Bermudian coastal waters. Its dominant taxa are also common in the saline habitats flooded by the upper oxic layer above the hydrogen sulphide layer in Mecherchar Jellyfish Lake (Palau, Lipps and Langer, 1999; Kawagata and others, 2005), a location some also consider is anchialine. With increasing depth in the coastal aquifer at

Cliff Pool Sinkhole, there is a decrease in euryhaline taxa (e.g., *Helenina, Ammonia, Discorinopsis*) and an increase in stenohaline taxa (e.g., *Siphogenerina, Nonionella iridea, Fursenkoina*) because the saline groundwater will favor marine foraminifera. Hydrogeologic mixing, vertical tidal oscillation of the halocline, and complete loss of the meteoric lens during droughts likely create variable brackish conditions to a depth of ~1 m in the coastal aquifer where the euryhaline taxa persist in Cliff Pool Sinkhole.

Based on the results from Green Bay Cave, haloclines separate habitats in both coastal caves and in stratified lagoons (e.g., Debenay and others, 1998). This causes euryhaline foraminifera to colonize habitats flooded by the upper brackish water, while stenohaline taxa live below the halocline (Debenay and others, 1998; Debenay and Guillou, 2002). However, habitats both above and below the halocline in stratified lagoons are still considered part of the greater lagoon environment. In contrast, foraminifera living below the halocline in the distal cave may actually be part of the submarine cave environment, and not necessarily part of the anchialine cave environment (Fig. 1, Stock and others, 1986). This distinction is important because although the halocline is a critical environmental feature in phreatic caves, subterranean habitats flooded by groundwater cannot be simply considered as subterranean stratified lagoons or estuaries. They are a distinct class of coastal environments with unique ecosystems and marine geological processes.

Determination of $\delta^{13}C_{org}$ and C:N can identify both the quality and source (terrestrial versus marine) of organic matter, which can then be correlated to the faunal assemblages (Fig. 4; Lamb and others, 2006). The source of organic matter is an important ecological variable for benthic foraminifera because it can cause differential resource partitioning, chemical gradients in the sediment, and microhabitat dysoxia (e.g., Jorissen and others, 1995; De Rijk and others, 2000; Morigi and others, 2001; Abu-Zied and others, 2008; Diz and Francés, 2008; Mojitahid and others, 2009). For example, Mojitahid and others (2009) found that the quality, quantity, and source of organic matter in the Rhône River prodelta (France) controlled benthic foraminifera. Their study demonstrated that different taxa colonized the terrestrial (more refectory) versus marine (more labile) organic matter. Furthermore, Diz and Francés (2008) found that seasonal phytodetritus caused a rapid response in benthic foraminifera in the shallow (<20 m) Ria de Vigo embayment (Spain) because specific taxa rapidly adjusted to the availability of new food resources (labile phytodetritus). It may be noted that as Cliff Pool Sinkhole is a point source for both abundant terrestrial materials (e.g., sediments, organic matter) and inputs from primary productivity, organic matter gradients will be generated from the sinkhole down into the cave. This point source of nutrients is anticipated to influence foraminiferal ecology in the anchialine cave environment similarly to how nutrient fluxes affect benthic foraminifera in other coastal environments.

The depleted $\delta^{13}C_{org}$ values associated with the AC and ML assemblages indicate that their bulk organic matter is primarily derived from terrestrial sources (Lamb and others, 2006; Mojitahid and others, 2009; Fig. 4). Aquatic plant material from the sinkhole may be contributing some $\delta^{13}C_{org}$-depleted organic matter to the cave, but this is likely minor considering both the small size of the sinkhole and the large quantity of terrestrial sediments entering into the cave. The $\delta^{13}C_{org}$ value of sediments associated with the AC assemblage (−23.8‰), however, is slightly more enriched than that of the ML assemblage (−24.4‰). This indicates that the AC assemblage receives slightly more marine organic matter (Table 1, Fig. 6). This result is supported by a lower C:N ratio in the AC assemblage because marine organic matter is more nitrogen enriched than terrestrial organic matter (Lamb and others, 2006). This relationship was expected because primary productivity does occur in the light-limited cave near Cliff Pool Sinkhole. Dense, green algae blooms occur seasonally on the surface of Cliff Pool Sinkhole, providing an additional resource of organic matter entering the cave at Cliff Pool Sinkhole. Consequently, the AC assemblage occupies a distinct habitat in the saline groundwater that receives more varied sources of organic matter in favorable marine conditions. It still remains part of the broader anchialine cave environment, however, because it is still dominated by terrestrial processes.

The foraminifera inhabiting the anchialine environment below the halocline in Cliff Pool Sinkhole must be capable of tolerating large quantities of more-refectory terrestrial organic matter with pulsed supplies of more-labile marine phytodetritus. For example, *Rosalina globularis*, which is common in the AC assemblage, passively grazes when food is readily available, but switches to active foraging as food resources diminish (Sliter, 1965). *Bolivina striatula* is a eutrophic species that becomes associated with *Buliminella elegantissima* when terrestrial organic matter is abundant (Patterson and others, 2000; Eichler and others, 2003; Abu-Zied and others, 2008). Both of these taxa are common in the Green Bay Cave AC assemblage, and in the Pleistocene anchialine cave assemblage observed by van Hengstum and others (2009a). Abundant organic matter in the benthos causes dysoxia within millimeters below the sediment-water interface (Corliss, 1991; Bernhard and Sen Gupta, 1997; Diz and Francés, 2008). Although dissolved oxygen in the sediments was not measured in this study, infaunal taxa comprising the AC assemblage, such as *Fursenkoina, Hopkinsina*, and *Bolivina,* are known to be tolerant to dysoxia (Kaiho, 1994; Bernhard and Sen Gupta, 1997; Bernhard and others, 1997). The high quantity of refectory terrigenous organic matter, pulsed phytodetritus, and likelihood of sedimentary dysoxia would also explain the high relative abundance of *Textularia earlandi* (max. 9.2%). This is a highly opportunistic taxon known to tolerate dysoxia (Alve and Goldstein, 2010), and in Green Bay Cave it was found only in the AC assemblage. The high volume of terrigenous organic matter entering the cave at Cliff Pool Sinkhole is perhaps the most significant environmental control on habitats colonized by the AC assemblage.

Terrestrial organics and sediments attenuate in Green Bay Cave with increasing distance from Cliff Pool Sinkhole. This is easily observed in the cave using SCUBA and in the sedimentary proxies (Fig. 6). Less than 60 m along the Trunk Passage in the transect from Cliff Pool Sinkhole to Harrington Sound, the Circulated Submarine Cave assem-

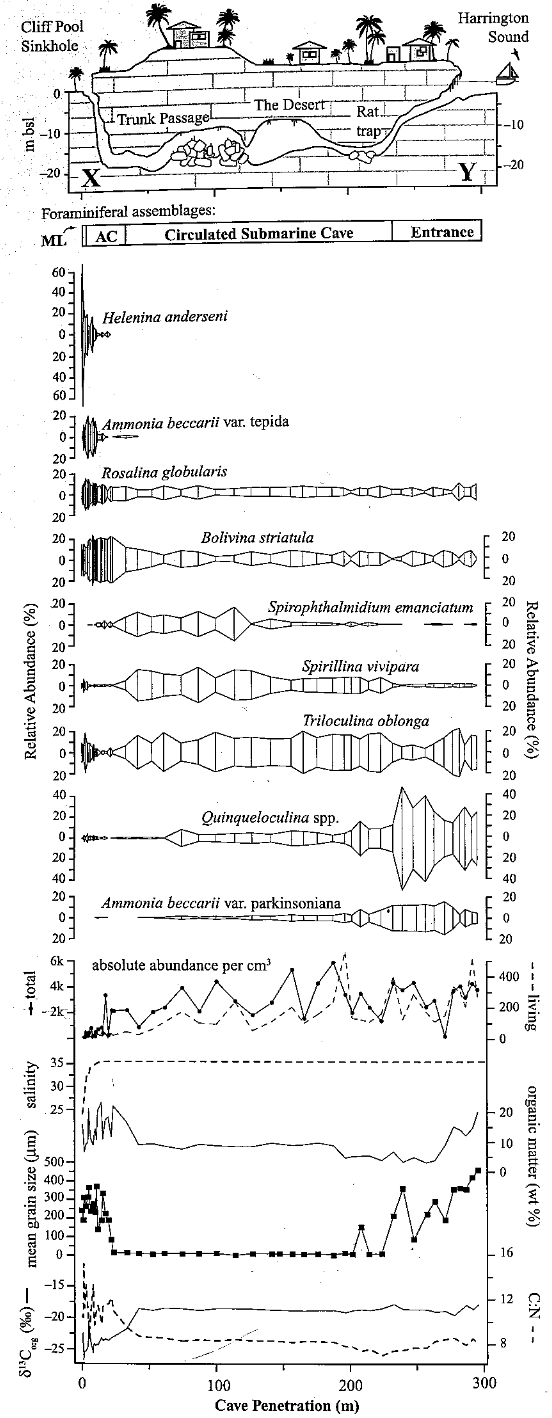

FIGURE 6. Relative abundance of dominant foraminifera along the transect from Cliff Pool Sinkhole (X) to Harrington Sound (Y). This transect along the Trunk Passage crosses the boundary between the anchialine and submarine cave environments (S20–S22), which reflects a loss of terrestrial influence on the cave benthos. This is evidenced by changing foraminiferal, geochemical, and sedimentological proxies at the same position in the passage (see Table 1). ML: Meteoric Lens, AC: Anchialine Cave.

blage begins (Fig. 2, Fig. 6). This change in foraminiferal assemblages is coincident with sedimentary and geochemical changes in the cave benthos, but *not* hydrogeological changes in the coastal aquifer.

THE BOUNDARY BETWEEN ANCHIALINE AND SUBMARINE CAVE ENVIRONMENTS

The idea that coastal cave environments can be differentiated from each other is an established concept (Stock and others, 1986). However, a quantitative division between anchialine and submarine cave environments, and their intrinsic heterogeneous habitats, has not been addressed because coastal cave research has generally focused on the ecology of macro-invertebrates and prokaryotes. This issue is only compounded by the limitations imposed on researchers of having to observe and sample on SCUBA. As a consequence, the subdivision of coastal cave environments in the literature and in practice can be quite confusing.

Stock and others (1986) stated that a prerequisite for anchialine cave environments is that they are terrestrial influenced by either meteoric water or by the influx of terrestrial nutrients. Habitats flooded by the meteoric lens are easily categorized as anchialine because their hydrogeology is terrestrially influenced by precipitation (meteoric water), which inevitably transports dissolved terrestrial chemicals. In addition, sinkholes receive a constant flux of terrestrial sediment from overwash events and erosion, which allows for an intuitive anchialine designation. A problem arises, however, when classifying coastal caves in the saline groundwater mass because both submarine and anchialine cave environments can be flooded by saline groundwater (Fig. 1). Some authors prefer the occurrence of tidal influence as diagnostic evidence for anchialine caves and sinkholes (Holthuis, 1973), but the fact remains that submarine caves also experience tidal influence because underwater caves are open systems (e.g., Kitamura and others, 2007; Yamamoto and others, 2009; van Hengstum, 2010). Elsewhere, the indiscriminate term "glacioeustatic cave pools" has been used to collectively refer to all phreatic coastal cave environments (e.g., Ginés and Ginés, 2007). However, this term excludes the natural extension of caves and their environments above the water table (into the vadose zone), and prevents the organizing of organisms, ecosystems, and physical processes into specific environments. Similar to Stock and others (1986), we favor an approach that discriminates coastal cave environments based upon the totality of natural processes operating in coastal caves, which in turn controls local ecosystems. We further extend the classification to span the vadose-to-phreatic continuum (Fig. 1).

Based on the definition of Stock and others (1986), distinguishing anchialine versus submarine cave environments is possible if the magnitude of both terrestrial and marine influences is quantified. In our view, the dominant manifestations of marine versus terrestrial influence on underwater caves can be hydrogeological, sedimentological, or chemical. In the coastal zone, the meteoric lens or terrestrial sediments and chemicals entering sinkholes can terrestrially influence underwater caves. In contrast, underwater caves may be marine influenced by saline groundwater, or marine sediments and chemicals entering submarine cave entrances. We argue that coastal cave environments are differentiated by the summation of environmental conditions, including hydrogeological, sedimentological, and ecological variables. Therefore, any phreatic cave or sinkhole dominated by terrestrial influences and processes is an anchialine environment, including those flooded by saline groundwater. Under this new premise, anchialine and submarine cave environments can now be quantitatively distinguished using ecological, sedimentological, and geochemical proxies.

Green Bay Cave is ideal for investigating the difference between anchialine and submarine cave environments. This is because an anchialine sinkhole entrance is separated from a submarine cave entrance by >250 m of flooded cave passage (Fig. 5). Based on the totality of environmental parameters, the boundary between the anchialine to submarine cave environment occurs in the Trunk Passage from S20 to S22. That is also where the foraminiferal community transitions from the AC to the CSC assemblage. Sedimentologically, both mean grain size and bulk organic matter decrease, and geochemical proxies ($\delta^{13}C_{org}$ and C:N) indicate sedimentary organic matter is no longer predominantly terrestrial. The foraminifera must be responding to the totality of environmental parameters in the cave because there is no significant hydrogeologic change coincident with these sedimentary changes. Sample station 21 is the most distal site where the cave benthos is routinely impacted by terrestrial nutrients, sediments, and organic matter entering the cave at Cliff Pool Sinkhole, and marine processes begin to dominate beyond this point (Figs. 2 and 6). Based on the quantified change from a terrestrial-dominated to a marine-dominated cave environment at S21, we argue that this represents the boundary between the anchialine and submarine cave environment in the Green Bay Cave System.

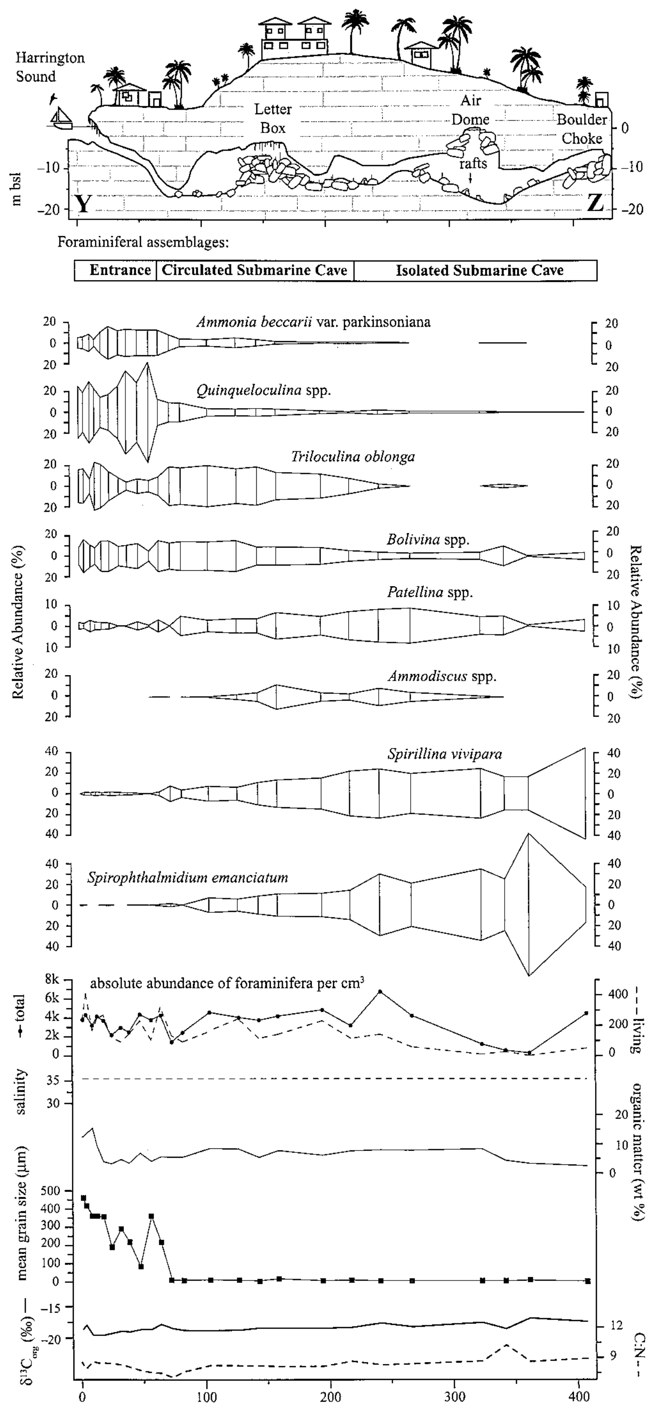

FIGURE 7. Relative abundance of dominant foraminifera along the transect from Harrington Sound (Y) to the end of the Green Bay Passage (Z). These data evidence the impact of attenuating sedimentological and nutrient gradients with increasing distance into a submarine cave environment. Note that the Boulder Choke is actually proximal to the ocean through the cave wall (Fig. 2). The abundance of fossil *Archaias* in the sediments at the Boulder Choke suggests that this cave passage once exited into Harrington Sound (Fig. 2), but has since been isolated by a cave collapse.

THE SUBMARINE CAVE ENVIRONMENT

Of all categories of coastal caves, submarine caves have arguably received the most attention by marine ecologists because they host intriguing taxonomic gradations in many phylogenies, often related to light availability. The submarine cave entrance to Green Bay Cave begins at Harrington Sound (Fig. 7). The inability of Q-mode cluster analysis to differentiate the lagoon samples (S47–S50) from the samples in the submarine cave entrance (S40–S46) attests to the similarity of foraminifera between the submarine cave entrance and the lagoon. *Quinqueloculina* and other miliolids dominate the Entrance Assemblage, similar to lagoonal assemblages worldwide (e.g., Haig, 1988; Javaux and Scott, 2003). *Quinqueloculina* are generally epifaunal and intolerant of dysoxia (Corliss, 1991), so the waves and currents impacting the submarine cave entrance must keep the upper sediment layers oxygenated to support their high relative abundance. There is an overall attenuation in organic matter with increasing distance into the submarine cave from Harrington Sound (Fig. 7), which is similar to Tremies Cave, a submarine cave in France (Fichez, 1990, 1991). Based on $\delta^{13}C_{org}$ and C:N, the organic matter in all submarine cave habitats is derived from marine sources (Table 1, Fig. 4). The coarse sediment at the submarine cave entrance in Green Bay Cave is similar to Daidokutsu Cave in Japan, wherein the entrance is also characterized by coarse sediment (Omori and others, 2010). The submarine cave entrance of Green Bay Cave opens into Harrington Sound and allows for waves and tidal currents to displace lagoonal sediments into the cave. Omori and others (2010) used photosymbiont-bearing foraminifera such as *Amphistegina* to document decreasing light conditions within Daidokutsu Cave over the last 7 kyr. In contrast, only rare photosymbiont-bearing foraminifera were found in Green Bay Cave in sediments near the submarine cave entrance. This difference between the caves is perhaps related to the size of the cave entrance, or the location of Daidokutsu Cave on an offshore forereef slope. In summary, the Entrance Assemblage in Green Bay Cave colonizes habitats in the disphotic to aphotic submarine cave entrance, which is completely flooded by saline groundwater, yet remains influenced by waves, tidal currents, and sediments from the lagoon.

The Circulated Submarine Cave Assemblage begins at the Rat Trap, along with a sedimentary shift from a coarse-grained shell hash to fine-grained carbonate-mud (mean grain size 14.9 μm), reduced bulk organic matter (mean 8%), and increased $CaC0_3$ (mean 50.9%). Fine carbonate mud also characterizes the inner substrate of Daidokutsu Cave (see Omori and others, 2010). The CSC Assemblage is dominated by *Triloculina* and *Spirillina*, and is the most diverse assemblage in Green Bay Cave. The faunal change from the cave entrance to the Rat Trap must be due to some variable other than groundwater salinity, dissolved oxygen, or the nitrogen-rich labile marine organic matter.

The submarine cave entrance opening into Harrington Sound allows for constant hydrographic communication between the cave environment and coastal ocean. This is expected because daily tidal circulation transports ~1960 m^3 of seawater from the lagoon into cave (Cate, 2009), along with particulate organic matter and dissolved nutrients. Some dissolved nutrients likely enter the submarine cave environment at Cliff Pool Sinkhole, but tidal circulation of the saline groundwater is the dominant mechanism for transporting nutrients throughout the cave. The CSC cave Assemblage inhabits a separate habitat within the submarine cave environment because it is found in passages that are completely flooded by saline groundwater and predominantly influenced by marine sedimentological processes, as previously discussed. We suggest that tidally forced circulation of saline groundwater provides a constant supply of particulate organic matter and nutrients to the areas inhabited by the diverse CSC Assemblage.

Tintinnids provide strong supporting evidence that lagoon nutrients transported by saline groundwater circulation enhances the habitat with the CSC Assemblage. In general, plankton diversity and biomass attenuate with increasing distance into underwater caves (Garrabou and Flos, 1995), which can provide a proxy for nutrients in the water column of the cave. Tintinnids are the only planktic protists preserved in Green Bay Cave. Although the low number of tintinnids precludes a detailed interpretation of their individual species abundances (Patterson and Fishbein, 1989), their presence-absence data is useful. Tintinnids are generally present in The Desert, Trunk Passage, and Green Bay Passage (up to The Letterbox), and partially present in the North Shore Passage (Fig. 2). A main source of food for tintinnids is particulate matter (Scott and others, 1995), which indicates that the water column above the CSC assemblage is regularly supplied with sufficient particulate matter to support tintinnid populations. The presence of tintinnids in Green Bay Cave proximal to cave entrances agrees with sediment trap data from Tremies Cave (France), where the quantity of particulate matter attenuates with increasing distance into the cave (Fichez, 1991). The only sample sites containing tintinnids in the ISC assemblage are S53 and S54 in the North Shore Passage. These are at the transition between the ISC and CSC assemblages, perhaps indicating partial mixing of the water column in that area (Fig. 2). Tintinnids were not recovered with the ISC Assemblage located farther into the cave (e.g., past the Letter Box), which suggests that tidal currents are not transporting nutrients into the distal cave. However, data is needed on the distribution of dissolved nutrients throughout Green Bay Cave to test this hypothesis.

The Isolated Submarine Cave (ISC) Assemblage inhabits the most distal passages of the cave and is dominated by *Spirophthalmidium emaciatum*, *Spirillina vivipara*, *Patellina corrugata*, and bolivinids. Both the ISC and CSC assemblages are dominated by known epiphytic taxa such as *Rosalina* and spirillinids (Langer, 1993), even though there are no plants or light for photosynthesis in the distal cave. The lowest quantity of bulk organic matter occurs in sediments with the ISC assemblage, and its the $\delta^{13}C_{org}$ and C:N values indicate that it is the most marine in the entire cave system (Fig. 4). These sediments are even more carbon isotopically enriched than the lagoonal sediments in Harrington Sound (Vollbrecht, 1996), emphasizing the isolation of the ISC Assemblage from terrigenous influences. Fine carbonate mud characterizes the substrate in the distal cave, similar to that of CSC Assemblage. Clearly, the ISC Assemblage colonizes a separate habitat within the submarine cave environment because it is completely flooded by saline groundwater and dominated by marine processes, yet the foraminifera are responding to different environmental conditions than the CSC or E Assemblages.

Foraminifera that favor high organic matter content are not abundant in the distal cave with the ISC Assemblage. For example, *Melonis barleeanum* is typically <1% in samples of the ISC Assemblage. This taxon is known to favor high organic matter (Caralp, 1989), and reaches its highest relative abundance in substrates with higher bulk organic matter, such as those of the AC and CSC assemblages (Fig. 5). The environmental conditions present in the distal cave likely favor epifaunal suspension feeders or infaunal foragers. *Patellina* (mean 5.2%) and *Spirillina* (mean 22%) are known to exhibit epifaunal suspension feeding (Langer, 1993), which suggests they are suited to opportunistically gathering suspended food resources transported to the distal cave by saline groundwater circulation. An alternative hypothesis is that perhaps *Spirillina* and *Pattellina* are well suited to using abundant high quality, nitrogen-rich marine organic matter (i.e., labile) that is present in the distal cave benthos (Fig. 4). Bolivinids are shallow-infaunal (0–2 cm) detritivores common in fine-grained sediments (Corliss, 1991; Murray, 2006; Teodoro and others, 2010), so their common abundance in the ISC Assemblage is not unusual.

The most abundant taxon in the ISC Assemblage is *Spirophthalmidium emaciatum* (mean 30.7%), which has a rare observational record that includes New Guinea (Haig, 1988), the Mediterranean (Cimerman and Langer, 1991), and the deep Pacific (Brady, 1884). *Spirophthalmidium acutimargo* is a very closely related species that some consider the senior synonym (Haynes, 1973; see Appendix 1), which is common in the deep North Atlantic (Hermelin and Scott, 1985) and in assemblages indicative of high oxic and oligotrophic conditions (Kuhnt and others, 2007). The poor record of *Spirophthalmidium* in coastal settings is not surprising, as it is quite fragile and likely prone to rapid degradation. The distal isolated cave where *S. emaciatum* reaches its highest relative abundance (>75%) is perhaps indicating that this is an oligotrophic miliolid in its preferred habitat, where it is not outcompeted by other lagoonal miliolids. The horizontal distance from the cave to the ocean through the eolianite (porous karst) does not appear to impact the foraminifera assemblages. For example, the terminus of the North Shore Passage is less than ~30 m to the ocean through the cave wall, yet foraminiferal diversity is low in that area and the high abundance of *S. emanciatum* is suggestive of more oligotrophic conditions. These results indicate that dissolved nutrients from the lagoon are not being transported into the cave directly through the karst wall at these localities. This interpretation is consistent with the observed daily net diffuse discharge of saline groundwater from inside Green Bay Cave through the porous karst into coastal lagoons (Cate, 2009), which would also be amplified by any upwelling of saline groundwater through the local strata (Whitaker and Smart, 1990). This further emphasizes that nutrients (particulate matter, dissolved chemicals) transported into Green Bay Cave through the submarine cave entrance would have a strong impact on the cave benthos.

The Air Pocket that is caused by the cave intersecting the water table has no apparent effect on the foraminifera (Fig. 2). There is sedimentary evidence for the existence of the water table, however, because calcite rafts are accumulating below the Air Pocket and they are not laterally transported in the cave passage. Calcite rafts only precipitate at air–water interfaces in caves, which is also observed in littoral caves of Mallorca (Taylor and Chafetz, 2004; Fornós and others, 2009, fig. 9). Alternatively, if the water table was distributed widely throughout a passage in Green Bay Cave and it impacted internal environmental conditions, then such a cave passage should be referred to as littoral cave environment (Fig. 1). These conditions are not met in the modern environments in Green Bay Cave. Because the Air Pocket in Green Bay Cave is spatially limited (<3 m width) and marine geological processes associated with submarine cave environments dominant the cave benthos, this area remains best described as part of the modern submarine cave environment.

Tests of the photosymbiotic genus *Archaias* were found in samples S73 and S61 but are not part of the modern total assemblage in the cave because they never stained with rose Bengal, as previously described. Samples S73 and S61 are from thin veneers (<3 cm) of sediment on collapsed limestone breakdown piles at the termini of the North Shore and Green Bay Passages, and are the most distal stations from any cave opening. Elsewhere, *Archaias* was only present in the disphotic-to-aphotic submarine cave entrance. These abraded and fragmented tests from S73 and S61 indicate that they were previously subjected to high-energy conditions that probably no longer occur in these passages. Based on the collapsed cave ceilings, the absence of any live *Archaias* in the cave, and the taphonomic indications of transport, these are perhaps subfossil specimens from a time when the passages were open to the ocean. This would have allowed for the transport of photosymbiotic taxa from an adjacent lagoon into a submarine cave, which would have most likely occurred during a Quaternary highstand.

FOSSIL CAVE FORAMINIFERA AND QUATERNARY SEA LEVEL

The results from Green Bay Cave indicate that fossil cave foraminifera can be used as sea-level proxies. Flank margin caves, which form between the meteoric lens and the saline groundwater as a result of $CaCO_3$-undersaturation at the halocline (Smart and others, 1988), are often used as Quaternary sea-level indicators (Mylroie and Carew, 1990; Mylroie, 2008; Mylroie and Mylroie, 2009). However, Quaternary sea-level oscillations have repeatedly flooded coastal caves with groundwater during highstands, causing continual reversion of coastal caves to phreatic habitats suitable for aquatic invertebrates and microfossils. This implies that coastal caves can preserve more sea-level information than has been previously recognized or used, beyond first-order approximation of sea level during flank margin cave development.

The first step in relating coastal cave sediments to prior sea levels is to associate their microfossils with a specific type of coastal cave environment (Fig. 1). For example, Proctor and Smart (1991) found *Bolivina*, *Ammonia*, *Cibicides*, and *Cassidulina* in Corbridge Cave (UK) sediments at 5.8 m and 7.2 m above present sea level, and constrained them with U-series dating to 155–116 kya and >210 kya, respectively. By analogy with foraminifera in Green Bay Cave, the Corbridge Cave microfossils can be attributed to a fossil anchialine cave environment that existed during the sea-level highstands of Marine Isotope Stages 5 and 7. Similarly, a fossil foraminiferal assemblage in Aktun Ha Cave, Mexico dominated by *Bolivina* and *Rosalina* was ascribed to a late Pleistocene anchialine cave environment by van Hengstum others (2009a), which is also consistent with the anchialine environment in Green Bay Cave.

In a more specific scenario, the meteoric lens habitat within the anchialine cave environment can also be detected if diagnostic brackish-water indicators are present (e.g., *Trochammina inflata, T. macrescens*). Because the elevation of the meteoric lens is very closely related to sea level, a fossil meteoric lens assemblage can constrain sea level. For example, Wilkinson (2006) found fossil *Polysaccammina* and *Pseudothurammina* in elevated (+21 m) marine caves in Bermuda dated to Marine Isotope Stage 11 (~400 ka). These taxa colonize modern meteoric lens habitats in Bermuda and Mexico (Javaux, 1999; van Hengstum and others, 2008; this study). Consequently, van Hengstum and others (2009b) interpreted the brackish-water fossils as evidence of paleometeoric lens elevated to +21 m by a sea-level highstand. Lastly, an assemblage dominated by fossil *Helenina anderseni* is present in Maya Blue Cave, Mexico (van Hengstum and Reinhardt, unpublished data). Based on comparison with the assemblages in Cliff Pool Sinkhole, the *Helenina* in Maya Blue Cave may be indicative of a paleometeoric lens concurrent with a pervious Quaternary sea-level highstand. In summary, cave foraminifera will provide no less than a proxy for the lowest position of Quaternary sea level.

CONCLUSIONS

1. Benthic foraminifera colonize phreatic coastal caves, and can differentiate both phreatic coastal cave environments and their intrinsic habitats.
2. The anchialine cave environment consists of two habitats colonized by two different foraminiferal assemblages: (a) the Meteoric Lens Assemblage, dominated by euryhaline foraminifera in the brackish meteoric lens (e.g., *Helenina*, *Ammonia*, *Trochammina*), and (b) the Anchialine Cave Assemblage, characterized by a more diverse assemblage dominated by *Rosalina* and *Bolivina* living below the halocline in the saline groundwater near Cliff Pool Sinkhole. Salinity differences in the coastal aquifer (meteoric lens versus saline groundwater) appear to be the primary ecological control on foraminifera in anchialine environments. Secondary factors are the sources and flux of terrigenous sediments and organic matter entering the cave at Cliff Pool Sinkhole.
3. The submarine environment consists of three habitats colonized by three different foraminiferal assemblages: (a) the Entrance Assemblage, dominated by typical lagoon foraminifera (e.g., *Quinqueloculina*) on a coarser-grained substrate impacted by waves, (b) the diverse Circulated Submarine Cave Assemblage, dominated by spirillinids on a carbonate mud substrate that constantly receives lagoon-derived nutrients from saline groundwater circulation, and (c) the Isolated Submarine Cave Assemblage, dominated by *Spirophthalmidium emaciatum* that is inhabiting the distal oligotrophic cave passages most deprived of nutrients and particulate organic matter.
4. Sedimentological variables ($\delta^{13}C_{org}$, C:N, bulk organics, granulometry) can be used to quantify the terrestrial influence on the cave environment, which has a concomitant impact on foraminiferal ecology. By corollary, the boundary between the anchialine and submarine environments were identified as applied in Green Bay Cave. Therefore, global cave passages flooded only by saline groundwater can now be sorted into submarine and anchialine environments based on sediment and microfossil proxies.
5. These results introduce confidence for attributing ecological interpretations to subfossil foraminifera preserved in cave sediments. For example, Pleistocene cave foraminifera can be associated with previous Quaternary sea levels, and foraminifera in cave sediment cores should be reliable proxies for Quaternary climate and hydrogeological changes.

ACKNOWLEDGMENTS

The research was only possible with the generous field support from the Bermuda Cavers Group (Bruce Williams, Gil Nolan, Leon Kemp, and Paul Larrett), technical support from Tom Iliffe, and support from the Tucker family. The Johanna M. Resig Fellowship from the Cushman Foundation for Foraminiferal Research and an *NSERC* Alexander Graham Bell Canada Graduate Scholarship to PvH provided primary research support. Student research grants to PvH from the Geologic Society of America, the Cave Research Foundation, Bermuda Zoological Society, and the Sigma Xi Scientific Research Society provided further support. All samples were collected in accordance with a special permit from the Bermuda Department of Environmental Protection (SP081103). The suggestions of two anonymous reviewers and editorial contributions from Ken Finger are appreciated for improving an earlier draft of this manuscript. This is contribution #176 from the Bermuda Biodiversity Project, Bermuda, Museum, Aquarium, and Zoo.

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Received 2 February 2010
Accepted 17 December 2010

APPENDIX 1

Taxonomic list of species, including original designations, primary references, and remarks pertinent to this study. The accompanying scanning electron micrographs reflect the emphasis of this study on cave fauna. Generic assignments of foraminifera generally follow Loeblich and Tappan (1964, 1987), and species identifications were based on type descriptions in the Ellis and Messina Catalogue of Foraminifera (1940 et. seq.) and, in some cases, illustrations in more recent literature. Tintinnid taxonomy follows Kofoid and Campbell (1929), upon which modern tintinnid taxonomy is based (e.g., Shackleton and Moore, 1954). Bold parenthesised figure numbers refer to illustrations in this article.

Foraminifera

Abditodentrix rhomboidalis (Millet) = *Textularia rhomboidalis* Millet, 1899, p. 559, pl. 7, fig. 4a, b. **(Figs. 8.1, 8.2)**

Ammobaculites foliaceus (Brady) = *Lituola* (*Haplophragmium*) *foliaceum* Brady, 1881, p. 304, pl. 33, figs. 20–25. **(Fig. 8.3)**

Ammodiscus planorbis Höglund, 1947, p. 125, pl. 8, fig. 4, pl. 28, figs. 13–16. **(Figs. 8.4, 8.5)**

Ammodiscus tenuis (Brady) = *Trochammina* (*Ammodiscus*) *tenuis* Brady 1884, p. 332, pl. 38, figs. 4–6. **(Figs. 8.6, 8.7)**

Ammonia beccarii (Linné, 1758) var. *parkinsoniana* (d'Orbigny) = *Rosalina parkinsoniana* (d'Orbigny, 1839a). **(Figs. 8.10, 8.11)**

Ammonia beccarii var. *tepida* (Cushman) = *Ammonia beccarii* (Linné, 1758) forma *tepida* Cushman, 1926. *In* Hayward and others, 2003, p. 353, pl. 1, figs. 1–8. **(Figs. 8.8, 8.9)**

Amphistegina lessonii d'Orbigny, 1826, p. 304, no. 3, pl. 17, figs. 1–4.

Archaias angulatus (Fichtel and Moll) = *Nautilus angulatus* Fichtel and Moll, 1798 (1803, 2nd edn.), p. 112, pl. 21, 23.

Articulina lineata Brady, 1884, p. 183, pl. 12, fig. 19–21. **(Fig. 8.13)**

Articulina multilocularis Brady, Parker and Jones, 1888, p. 215, pl. 40, fig. 10. **(Figs. 8.14, 8.15)**

Articulina pacifica Cushman, 1944, p. 17, pl. 14–18, figs. 15, 16. **(Fig. 8.16)**

Articulina sagra d'Orbigny, 1839a, p. 160, pl. 9, figs. 23–26. **(Figs. 8.17, 8.18)**

Asterigerina carinata d'Orbigny, 1839a, p. 118, pl. 5, fig. 25; pl. 6, figs. 1, 2.

Bolivina paula Cushman and Cahill, 1932 (in Cushman and Ponton, 1932), p. 84, pl. 12, fig. 6. **(Figs. 8.19, 8.20)**

Bolivina pseudopunctata Höglund, 1947, p. 273, pl. 24, fig. 5a, b; pl. 32, figs. 23, 24. **(Figs. 8.21–8.23)**

Bolivina striatula Cushman, 1922, p. 27, pl. 3, fig. 10. **(Figs. 8.24–8.26)**

Bolivina tortuosa Brady, 1881, p. 57, pl. 52, figs. 31–34. **(Fig. 8.27)**

Bolivina variabilis (Williamson) = *Textularia variabilis* Williamson, 1858, p. 76, pl. 6, figs. 162, 163. **(Figs. 8.28–8.30)**

Broeckina orbitolitoides (Hofker) = *Praesorites orbitolitoides* Hofker, 1930, p. 149, pl. 55, figs. 8, 10, 11, pl. 57, figs. 1–5; pl. 61, figs. 3, 14.

Bulimina consectata (McCulloch) = *Neobulimina consectata* McCulloch, 1977, p. 242, pl. 106, figs. 1a, b. **(Figs. 9.1, 9.2)**

Bulimina marginata d'Orbigny, 1826, p. 269, pl. 12, figs. 10–12. **(Fig. 8.31)**

Bulimina elegantissima d'Orbigny, 1839b, p. 51, pl. 7, figs. 13, 14. **(Fig. 8.32)**

Cancris sagra (d'Orbigny) = *Rotalina sagra* d'Orbigny, 1839a, p. 77, pl. 5, figs. 13–15. **(Figs. 9.3. 9.4)**

Cibicides lobatulus (Walker and Jacob) = *Nautilus lobatulus* Walker and Jacob, 1798, p. 642, pl. 14, fig. 36. **(Figs. 9.5, 9.6)**

Clavulina tricarinata d'Orbigny, 1839a, p. 111, pl. 2, figs. 16–18. **(Fig. 9.7)**

Cyclogyra involvens (Reuss) = *Operculina involvens* Reuss, 1850, p. 370, pl. 46, fig. 20. **(Figs. 9.8, 9.9)**

Cymbaloporetta squammosa (d'Orbigny) = *Rosalina squammosa* d'Orbigny, 1839a, p. 91, pl. 3, figs. 12–14.

Dentalina communis (d'Orbigny) = *Nodosaria* (*Dentaline*) *communis* d'Orbigny, 1826, pl. 1, fig. 4. **(Figs. 9.10, 9.11)**

Discorinopsis aguayoi (Bermúdez) = *Discorbis aguayoi* Bermúdez, 1935, p. 204, pl. 15, figs. 10–14. **(Figs. 9.12, 9.13)**

Eggerella scabra (Williamson) = *Bulimina scabra* Williamson, 1858, pl. 5, figs. 136–147. **(Fig. 9.14)**

Elphidium advenum (Cushman) = *Polystomella advena* Cushman 1922, p. 56, pl. 9, figs. 11, 12. **(Figs. 9.15, 9.16)**

Elphidium crispum (Linné) = *Nautilus crispus* Linné, 1758, p. 709, pl. 1, figs. 2d–f.

Elphidium excavatum (Terquem) = *Polystomella excavata* Terquem, 1876, p. 429, pl. 2, figs. 4a, b. **(Figs. 9.21–9.24)**

Elphidium cf. *E. frigidum* Cushman, 1933b, p. 5, pl. 1, figs. 8a, b. **(Figs. 9.17, 9.18)**

Elphidium norvangi Buzas, Smith, and Beam, 1977, p. 96, pl. 7, figs. 1–4. **(Figs. 9.19, 9.20)**

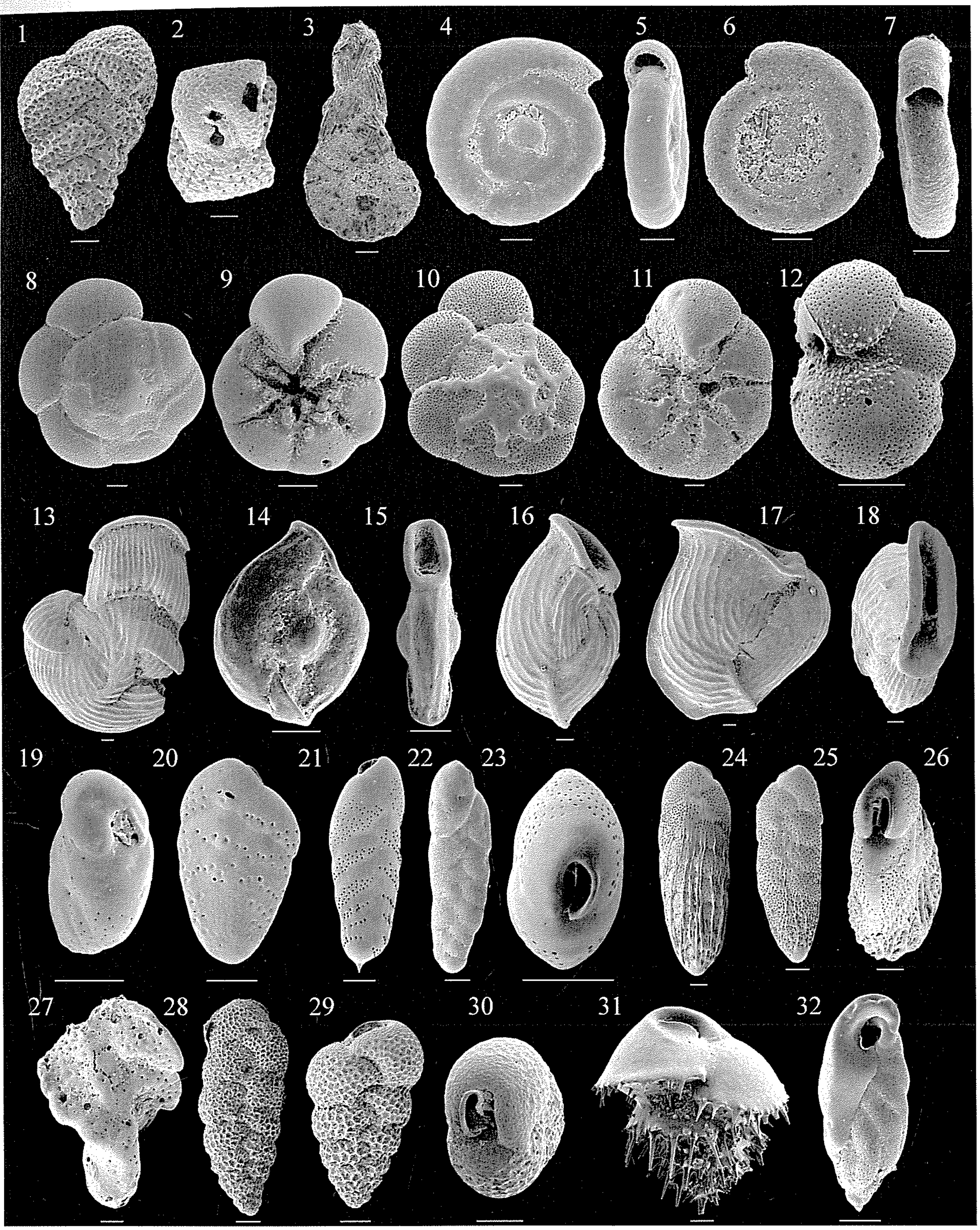

FIGURE 8. **1, 2** *Abditodentrix rhomboidalis*; **3** *Ammobaculites foliaceus*; **4, 5** *Ammodiscus planorbis*; **6, 7** *Ammodiscus tenuis*; **8, 9** *Ammonia beccarii* var. *tepida*; **10, 11** *Ammonia beccarii* var. *parkinsoniana*; **12** juvenile *Ammonia beccarii*; **13** *Articulina lineata*; **14, 15** *Articulina multilocularis*; **16** *Articulina pacifica*; **17, 18** *Articulina sagra*; **19, 20** *Bolivina paula*; **21–23** *Bolivina pseudopunctata*; **24–26** *Bolivina striatula*; **27** *Bolivina tortuosa*; **28–30** *Bolivina variabilis*; **31** *Bulimina marginata*; **32** *Buliminella elegantissima*. Scale bar = 50 μm.

Elphidium sagra (d'Orbigny) = *Polystomella sagra* d'Orbigny, 1839a, p. 55, pl. 6, figs. 19, 20. **(Figs. 9.25, 9.26)**

Epistominella pulchra (Cushman) = *Pulvinulina pulchra* Cushman, 1933a, p. 92, pl. 9, fig. 19. **(Figs. 9.27–9.29)**

Eponides antillarum (d'Orbigny) = *Rotalina antillarum* d'Orbigny, 1839a, p. 75, pl. 5, figs. 4–6. **(Figs. 10.1, 10.2)**

Fissurina lucida (Williamson) = *Entosolenia marginata* (Montagu) var. *lucida* Williamson, 1848, p. 17, pl. 2, fig. 17. **(Figs. 10.3, 10.4)**

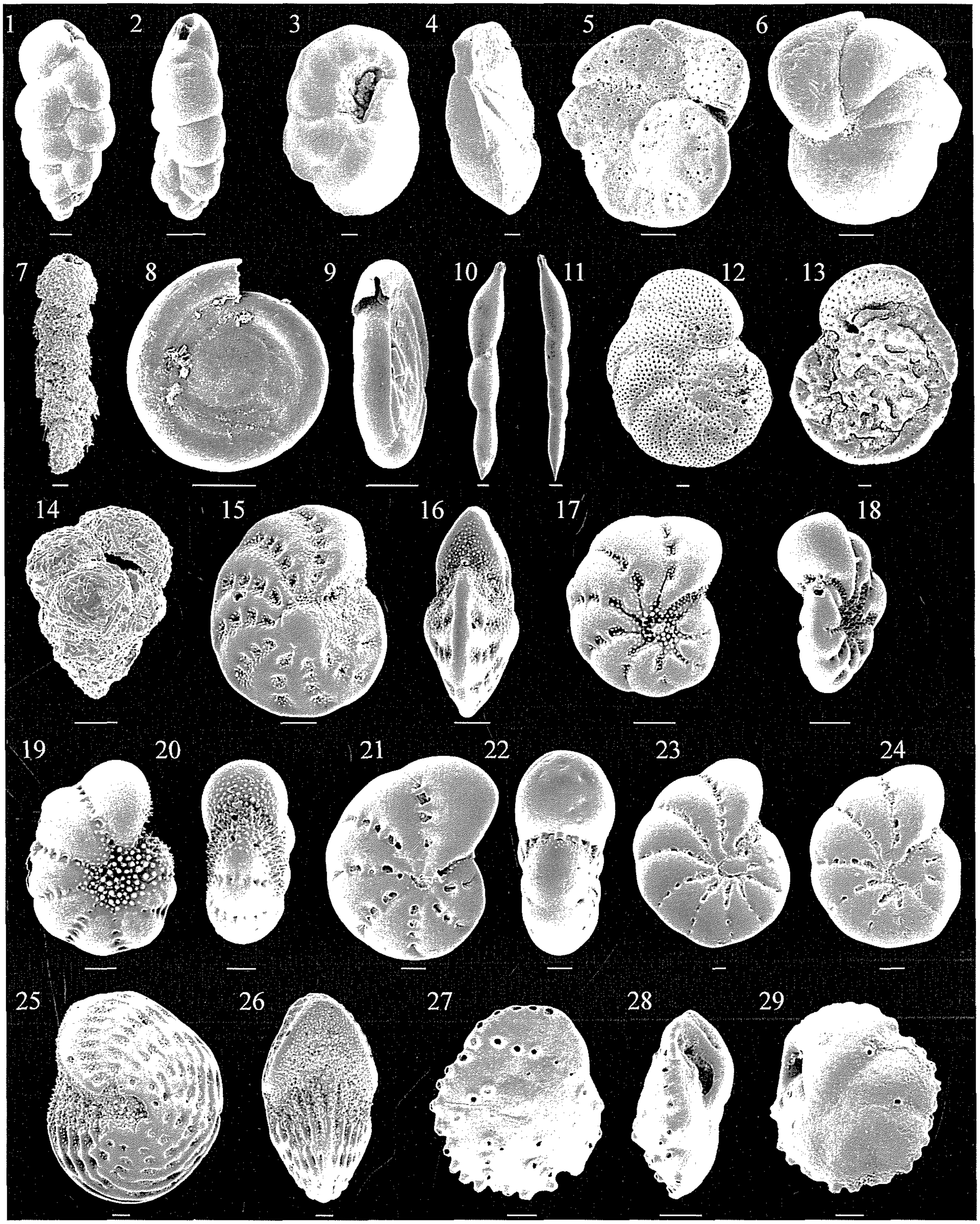

FIGURE 9. **1, 2** *Bulimina consectata*; **3, 4** *Cancris sagra*; **5, 6** *Cibicides lobatulus*; **7** *Clavulina tricarinata*; **8, 9** *Cyclogyra involvens*; **10, 11** *Dentalina communis*; **12, 13** *Discorinopsis aguayoi*; **14** *Eggerella scabra*; **15, 16** *Elphidium advenum*; **17, 18** *Elphidium frigidum*; **19, 20** *Elphidium norvangi*; **21–24** *Elphidium excavatum*; **25, 26** *Elphidium sagra*; **27–29** *Epistominella pulchra*. Scale bar = 50 μm.

Fissurina evoluta McCulloch, 1977, p. 104, 105, pl. 58, figs. 11, 12, 18. **(Fig. 10.6)**

Fissurina sp. These rare individuals were not identified to the specific level. **(Fig. 10.5)**

Fursenkoina compressa (Bailey) = *Bulimina compressa* Bailey 1851, p. 12, pl. 12, figs. 35–37. **(Figs. 10.7, 10.8)**

Globocassidulina subglobosa (Brady) = *Cassidulina subglobosa* Brady, 1881, p. 60, pl. 54, figs. 17a–c. **(Figs. 10.9, 10.10)**

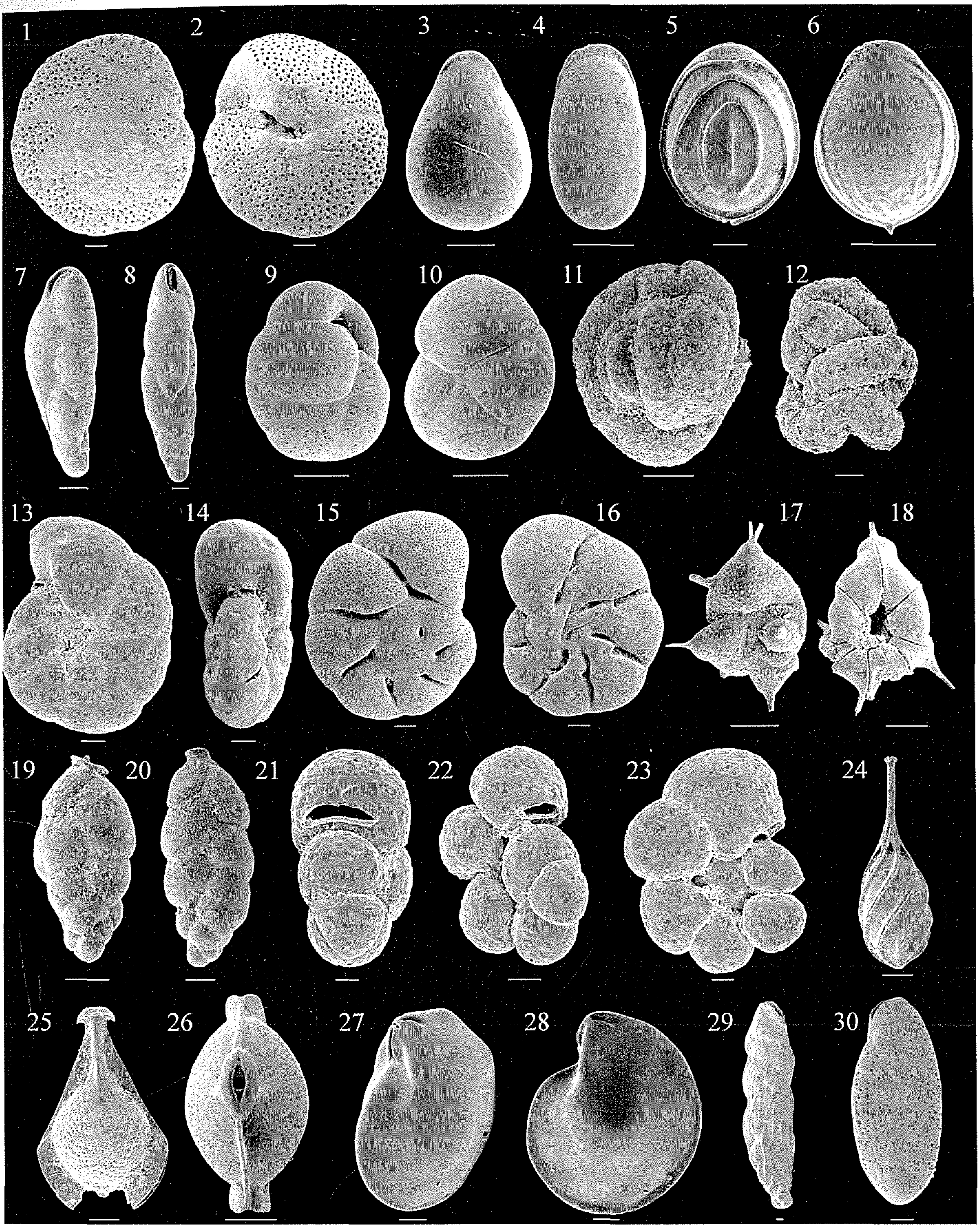

FIGURE 10. **1, 2** *Eponides antillarum*; **3, 4** *Fissurina lucida*; **5** *Fissurina* sp; **6** *Fissurina evoluta*; **7, 8** *Fursenkoina compressa*; **9, 10** *Globocassidulina subglobosa*; **11** *Glomospira charoides*; **12** *Glomospira irregularis*; **13, 14** *Haplophragmoides wilberti*; **15, 16** *Helenina anderseni*; **17, 18** *Rotaliella arctica*; **19, 20** *Hopkinsina pacifica*; **21–23** *Labrospira evoluta*; **24** *Lagena spiralis*; **25, 26** *Lagenosolenia* sp.; **27, 28** *Lenticulina iota*; **29** *Loxostoma mayori*; **30** *Loxostoma rostrum*. Scale bar = 50 µm.

Glomospira charoides (Jones and Parker) = *Trochammina squamata* Jones and Parker var. *charoides* Jones and Parker, 1860, p. 304. **(Fig. 10.11)**

Glomospira irregularis (Grzybowski) = *Ammodiscus irregularis* Grzybowski, 1898, p. 285, pl. 11, figs. 2, 3. **(Fig. 10.12)**

Haplophragmoides wilberti Anderson, 1953, p. 21, pl. 4, fig. 7. **(Figs. 10.13, 10.14)**

Helenina anderseni (Warren) = *Pseudoeponides anderseni* Warren, 1957, p. 39, pl. 4, figs. 12–15. **(Figs. 10.15, 10.16)**

Homotrema rubrum (Lamarck) = *Milipora rubra* Lamarck, 1816, p. 202.

Hopkinsina pacifica Cushman, 1933a, p. 86, pl. 8, fig. 16. **(Figs. 10.19, 10.20)**

Labrospira evoluta (Natland) = *Haplophragmoides evoluta* Natland, 1938, p. 138, pl. 3, figs. 5, 6. **(Figs. 10.21–10.23)**

Lagena spiralis Brady, 1884, p. 448, pl. 114, fig. 9. **(Fig. 10.24)**

Lagenosolenia sp. **(Figs. 10.25, 10.26)**

Lenticulina iota (Cushman) = *Cristellaria iota* Cushman, 1923, p. 111, pl. 70, figs. 4–6. **(Figs. 10.27, 10.28)**

Loxostoma mayori (Cushman) = *Bolivina mayori* Cushman 1922, p. 40, pl. 3, figs. 5, 6. **(Fig. 10.29)**

Loxostoma rostrum Cushman, 1933a, p. 82, pl. 8, figs. 13a, b. **(Fig. 10.30)**

Melonis barleeanum (Williamson) = *Nonionina barleeana* Williamson, 1858, p. 32, pl. 3, figs. 68, 69. **(Figs. 11.1, 11.2)**

Metarotaliella simplex (Grell) = *Rotaliella simplex* Grell, 1979, p. 11, pl. 2, figs. 1–4. Loeblich and Tappan, 1987, p. 564, pl. 616, figs. 1–3; Usera and others, 2002, p. 145, fig. 3.7. We observed two variants of this species, one with spines **(Figs. 11.6, 11.7)**, and one without spines. **(Figs. 11.3–11.5)**

Metarotaliella simplex (Grell) var. *spinosa* van Hengstum and Scott, n. var. The spinose and non-spinose variants always co-existed, therefore we are not confident this represents a new species at this stage; the characteristics of the aperture are identical to *M. simplex*. **(Figs. 11.6, 11.7)**

Miliammina fusca (Brady) = *Quinqueloculina fusca* Brady, 1870, p. 286, pl. 11, figs. 2, 3. **(Figs. 11.8, 11.9)**

Miliolinella circularis (Bornemann) = *Triloculina circularis* Bornemann, 1855, p. 349, pl. 19, figs 4a–c. **(Figs. 11.10, 11.11)**

Miliolinella subrotunda (Montagu) = *Vermiculum subrotundum* Montagu, 1803, p. 521. **(Figs. 11.12, 11.13)**

Mychostomina revertens (Rhumbler) = *Spirillina vivipara* (Ehrenberg) var. *revertens* Rhumbler, 1906, p. 32, pl. 2, figs. 8–10. **(Figs. 11.14, 11.15)**

Nonion pauperata Balkwill and Wright, 1885, p. 353, pl. 13, figs. 25, 26. **(Figs. 11.16–11.18)**

Nonionella atlantica Cushman, 1947, p. 90, pl. 20, figs. 4, 5. **(Figs. 11.19–11.21)**

Nonionella iridea Heron-Allen and Earland, 1932, p. 438, pl. 16, figs. 14–16. **(Figs. 11.22, 11.23)**

Parvigenerina arenacea (Heron-Allen and Earland) = *Bifarina porrecta* (Brady) var. *arenacea* Heron-Allen and Earland, 1922, p. 132, p. 4, figs. 23–26. **(Figs. 11.24, 11.25)**

Parvigenerina bigenerinoides (Lacroix) = *Textularia bigenerinoides* Lacroix, 1932, p. 24, pl. 24, fig. 27; pl. 25, figs. 28–31. **(Figs. 11.26, 11.27)**

Patellina corrugata Williamson, 1858, p. 46, pl. 3, figs. 86–89. **(Figs. 12.1–12.3)**

Patellina corrugata Williamson var. *spinosa* = *Patellina spinosa* Zheng, 1979, p. 177, 178, pl. 21, figs. 12a–c. Although *P. spinosa* was described as a separate species, we suspect it is a morphotype of *P. corrugata*. **(Fig. 12.4)**

Peneroplis carinatus d'Orbigny, 1839b, p. 33, pl. 3, figs. 7, 8.

Peneroplis pertusus Forskål, 1775, p. 125 (not figured). **(Fig. 12.8)**

Peneroplis proteus (d'Orbigny) = *Peneroplis protea* d'Orbigny, 1839a, p. 60, pl. 7, figs. 7–11.

Physalidia simplex Heron-Allen and Earland, 1928, p. 288, pl. 1, figs. 1, 2. This taxon was misidentified as juveniles of *Ammonia beccarii* var. *tepida* in van Hengstum (2008, fig. 3, S3.18), van Hengstum and others (2008, p. 314, pl. 1, fig. 13), Gabriel and others (2009, not figured), and van Hengstum and others (2009a, not figured). Every specimen observed by one of us (PvH) in Mexico and Bermuda was planispiral, evolute (never trochospiral), and had only three chambers with an interiomarginal aperture; they are identical to those figured by Loeblich and Tappan (1987), Usera and others (2002), and Guillem (2007). **(Figs. 12.6, 12.7)**

Planorbulina mediterranensis d'Orbigny, 1826, p. 280, pl. 14, figs. 4–6. **(Fig. 12.5)**

Planulina exorna Phleger and Parker, 1951, p. 32, pl. 18, figs. 5–7; 8a, b.

Planulina wuellerstorfi (Schwager) = *Anomalina wüllerstorfi* Schwager, 1866, p. 258, pl. 7, figs. 105, 107.

Pyrgo denticulata (Brady) = *Biloculina ringens* (Lamarck) var. *denticulata* Brady, 1884, p. 143, pl. 3, figs. 4, 5. **(Fig. 12.12)**

Pyrgo elongata (d'Orbigny) = *Biloculina elongata* d'Orbigny, 1826, p. 298 (not figured).

Quinqueloculina auberiana d'Orbigny, 1839a, p. 193, pl. 12, figs. 1–3. **(Figs. 12.9–11)**

Quinqueloculina bicarinata d'Orbigny, 1878, p. 68, pl. 7, fig. 10. **(Figs. 12.13–12.15)**

Quinqueloculina bosciana d'Orbigny, 1839a, p. 191, pl. 11, figs. 22–24. **(Fig. 12.16)**

Quinqueloculina candeiana d'Orbigny, 1839a, p. 199, pl. 12, figs. 24–26. **(Fig. 12.17)**

Quinqueloculina collumnosa Cushman, 1922, p. 571, pl. 10, fig. 10.

Quinqueloculina contorta d'Orbigny, 1846, p. 298, pl. 20, figs. 4–6. **(Figs. 12.18, 12.19)**

Quinqueloculina exsculpta (Heron-Allen and Earland) = *Miliolina exsculpta* Heron-Allen and Earland, 1915, p. 567, pl. 42, figs. 23–26.

Quinqueloculina funafutiensis (Chapman) = *Miliolina funafutiensis* Chapman, 1901, p. 178, pl. 19, figs. 6, 6a. **(Figs. 12.20, 12.21)**

Quinqueloculina laevigata d'Orbigny, 1826, p. 143, pl. 3, figs. 31–33. **(Figs. 12.22, 12.23)**

Quinqueloculina poeyana d'Orbigny, 1839a, p. 191, pl. 11, figs. 25–27.

Quinqueloculina polygona d'Orbigny, 1839a, p. 198, pl. 12, figs. 21–23. **(Fig. 12.31)**

Quinqueloculina quinquecarinata Collins, 1958, p. 360, pl. 2, figs. 8a–c. **(Figs. 12.26–12.28)**

Quinqueloculina seminulum (Linné) = *Serpula seminulum* Linné, 1758, p. 786. **(Figs. 12.29, 12.30)**

Quinqueloculina spp. Includes rare species and juveniles.

Quinqueloculina subpoeyana Cushman, 1922, p. 66 (not figured). **(Figs. 12.24, 12.25)**

Quinqueloculina sulcata d'Orbigny, 1826, p. 301 (not figured).

Quinqueloculina tenagos Parker, 1953, new name for *Q. rhodiensis* Parker and others, 1953, p.12, pl. 6, figs. 3a–c. **(Fig. 12.32)**

Reophax nana Rhumbler, 1911, p. 182, pl. 8, figs. 6–12. **(Figs. 13.1, 13.2)**

Reophax scottii Chaster, 1892, p. 57, pl. 1, fig. 1. **(Figs. 13.3, 13.4)**

Reophax subfusiformis Earland, 1933, p. 74, pl. 2, figs. 16–19. **(Figs. 13.5, 13.6)**

Reussella atlantica Cushman = *Reussella spinulosa* var. *atlantica* Cushman, 1947, p 91, pl. 20, figs. 6, 7.

Rosalina globularis d'Orbigny, 1826, pl. 13, figs. 1–4. Misidentified as *R. subaraucana* (Cushman) in van Hengstum (2008, fig. 3, S3.30) and van Hengstum and others (2009a, not figured). **(Figs. 13.9, 13.10)**

Rosalina vilardeboana d'Orbigny, 1839b, p. 44, pl. 6, figs. 13–15.

Rosalina williamsoni (Parr) = *Discorbis williamsoni* Parr, 1932, p. 226, pl. 21, fig. 25. **(Figs. 13.11, 13.12)**

Rosalina spp.

Rotaliella arctica (Scott and Vilks) = *Glabratella arctica* Scott and Vilks, 1991, p. 30, pl. 2, figs. 10–12, which is synonymous with

FIGURE 11. **1, 2** *Melonis barleeanum*; **3–5** *Metarotaliella simplex*; **6, 7** *Metarotaliella simplex* var. *spinosa*; **8, 9** *Miliammina fusca*; **10, 11** *Miliolinella circularis*; **12, 13** *Miliolinella subrotunda*; **14, 15** *Mychostomina revertens*; **16–18** *Nonion pauperata*; **19–21** *Nonionella atlantica*; **22, 23** *Nonionella iridea*; **24, 25** *Parvigenerina arenacea*; **26, 27** *Parvigenerina bigenerinoides*. Scale bar = 50 μm.

Rotaliella keigwini (Pawlowski, 1991, p. 168, pl. 2, fig. 2), the only other observation of this taxon. **(Figs. 10.17, 10.18)**

Saccammina difflugiformis (Brady) = *Reophax difflugiformis* Brady, 1879a, p. 51, pl. 4, figs. 3a, b. **(Figs. 13.7, 13.8)**

Sigmoilina tenuis (Czjzek) = *Quinqueloculina tenuis* Czjzek, 1848, p. 149, pl. 13, figs. 31–34. **(Figs. 13.31, 13.32)**

Siphogenerina columellaris (Brady) = *Uvigerina columellaris* Brady, 1881, p. 64, pl. 75; figs. 15–17. **(Figs. 13.14–13.16)**

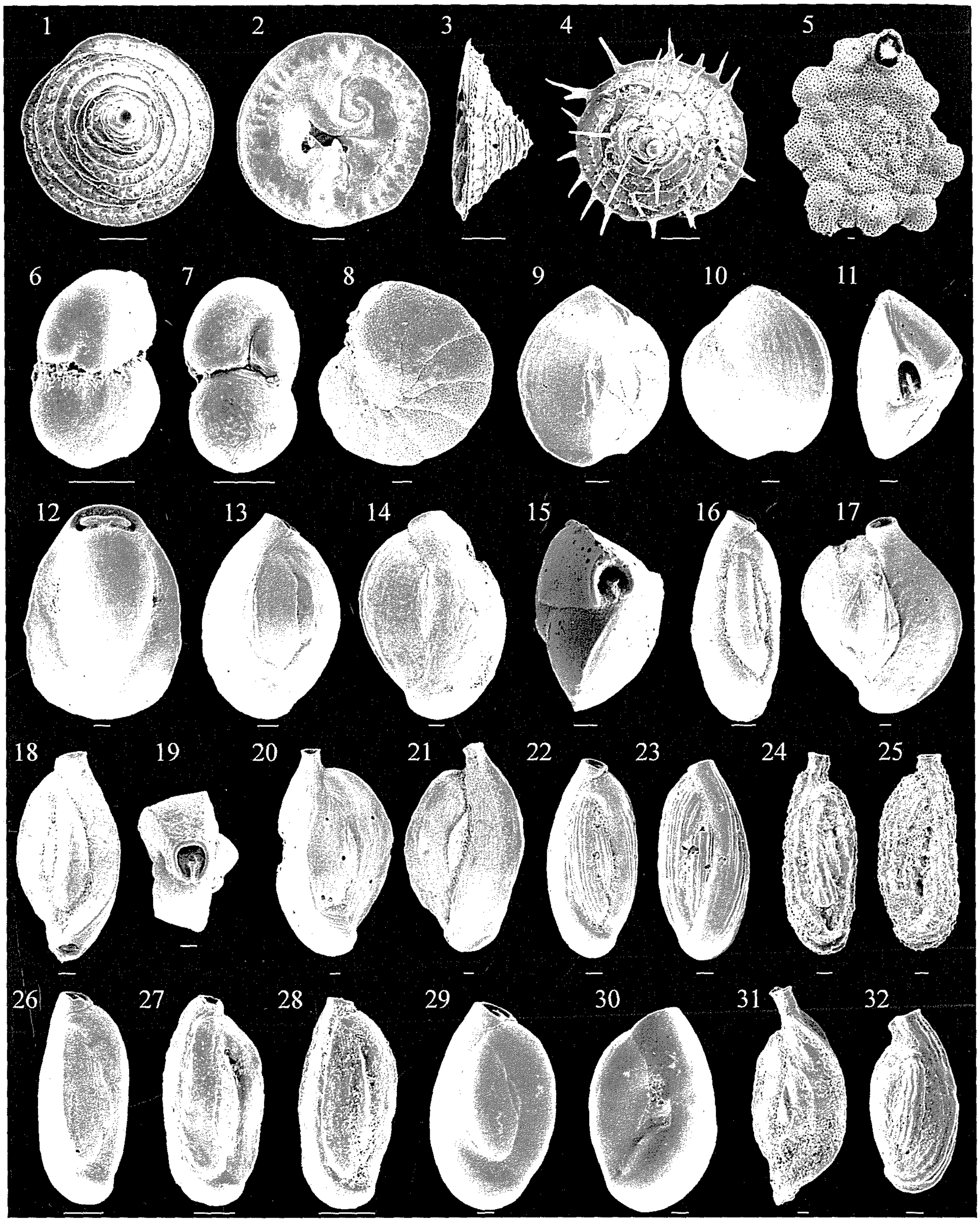

FIGURE 12. **1–3** *Patellina corrugata*; **4** *Patellina corrugata* var. *spinosa*; **5** *Planorbulina mediterranensis*; **6, 7** *Physalidia simplex*; **8** *Peneroplis pertusus*; **9–11** *Quinqueloculina auberiana*; **12** *Pyrgo denticulata*; **13–15** *Q. bicarinata*; **16** *Q. bosciana*; **17** *Q. candeiana*; **18, 19** *Q. contorta*; **20, 21** *Q. candeiana*; **22, 23** *Q. laevigata*; **24, 25** *Q. subpoeyana*; **26–28** *Q. quinquecarinata*; **29, 30** *Q. seminulum*; **31** *Q. polygona*; **32** *Q. tenagos*. Scale bar = 50 μm.

Siphogenerina striata (Brady) = *Sagrina striata* Brady, 1884, p. 584, pl. 75, figs. 25, 26. **(Figs. 13.17, 13.18)**

Siphonina reticulata (Czjzek) = *Rotalina reticulata* Czjzek, 1848, p. 145, pl. 13, figs. 7–9. **(Figs. 13.19, 13.20)**

Siphonina temblorensis Garrison, 1959, p. 669, pl. 86, figs. 4a–c. All individuals are small without an acute periphery or keel. **(Figs. 13.21, 13.22)**

Siphoninella soluta (Brady) = *Planorbulina* (*Truncatulina*) *soluta* Brady, 1881. **(Fig. 13.23)**

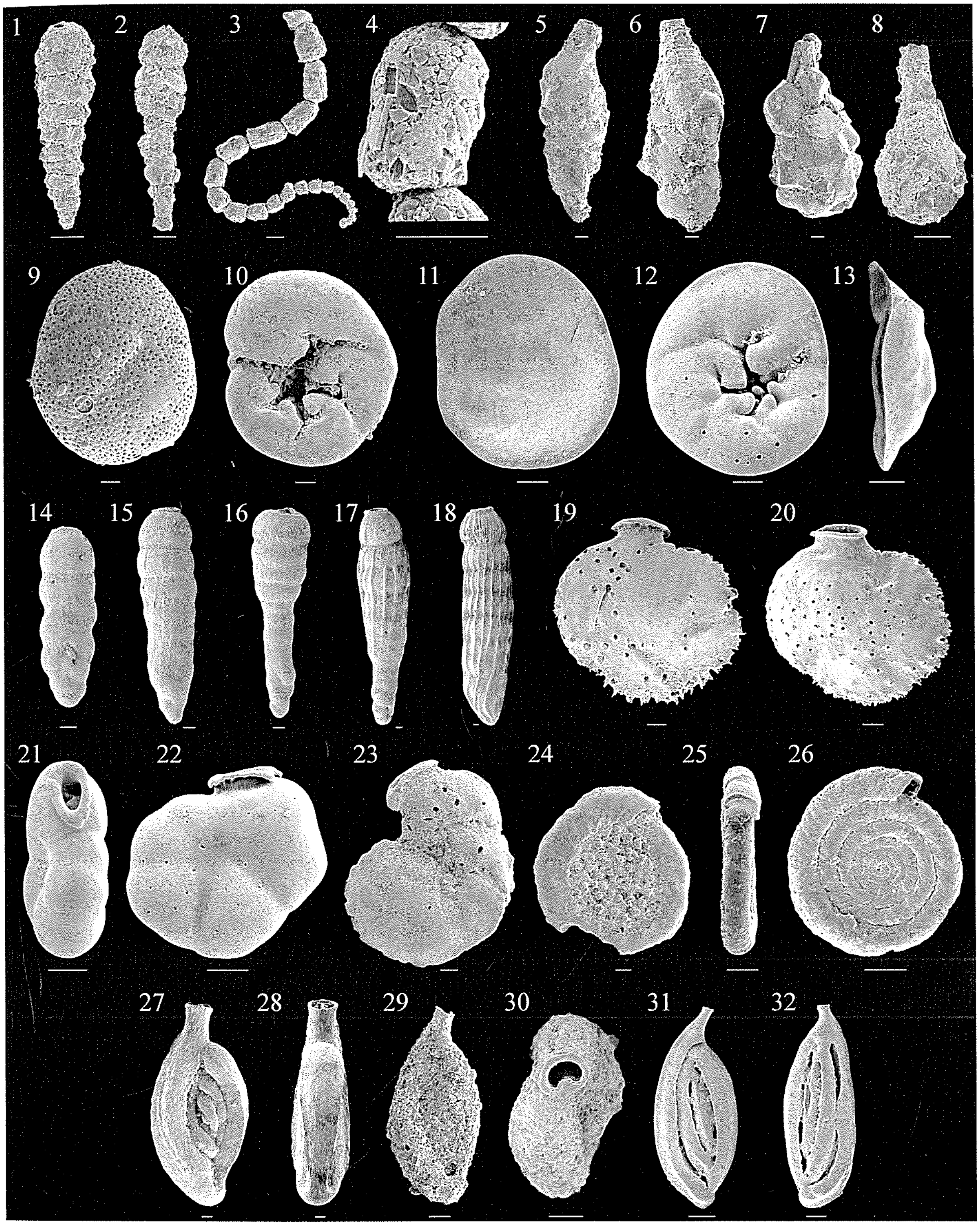

FIGURE 13. **1, 2** *Reophax nana*; **3** *Reophax scottii*; **4** magnified chamber of *R. scottii* showing diatoms incorporated into the test wall; **5, 6** *Reophax subfusiformis*; **7, 8** *Saccammina difflugiformis*; **9, 10** *Rosalina globularis*; **11–13** *Rosalina williamsoni*; **14–16** *Siphogenerina columellaris*; **17, 18** *Siphogenerina striata*; **19, 20** *Siphonina reticulata*; **21, 22** *Siphonina temblorensis*; **23** *Siphoninella soluta*; **24** *Spirillina tuberculata*; **25, 26** *Spirillina vivipara*; **27, 28**; *Spiroloculina antillarum* **29, 30**; *Spiroloculina arenata* **31, 32** *Sigmoilina tenuis*. Scale bar = 50 μm.

Sorites marginalis (Lamarck) = *Orbulites marginalis* Lamarck, 1816, p. 196.

Spirillina tuberculata Brady, 1879b, p. 279, pl. 8, figs. 28a, b. **(Fig. 13.24)**

Spirillina vivipara Ehrenberg, 1843, p. 422, pl. 3, fig. 41. **(Figs. 13.27, 13.28)**

Spiroloculina antillarum d'Orbigny, 1839a, p. 166, pl. 9, figs. 3, 4. **(Figs. 13.29, 13.30)**

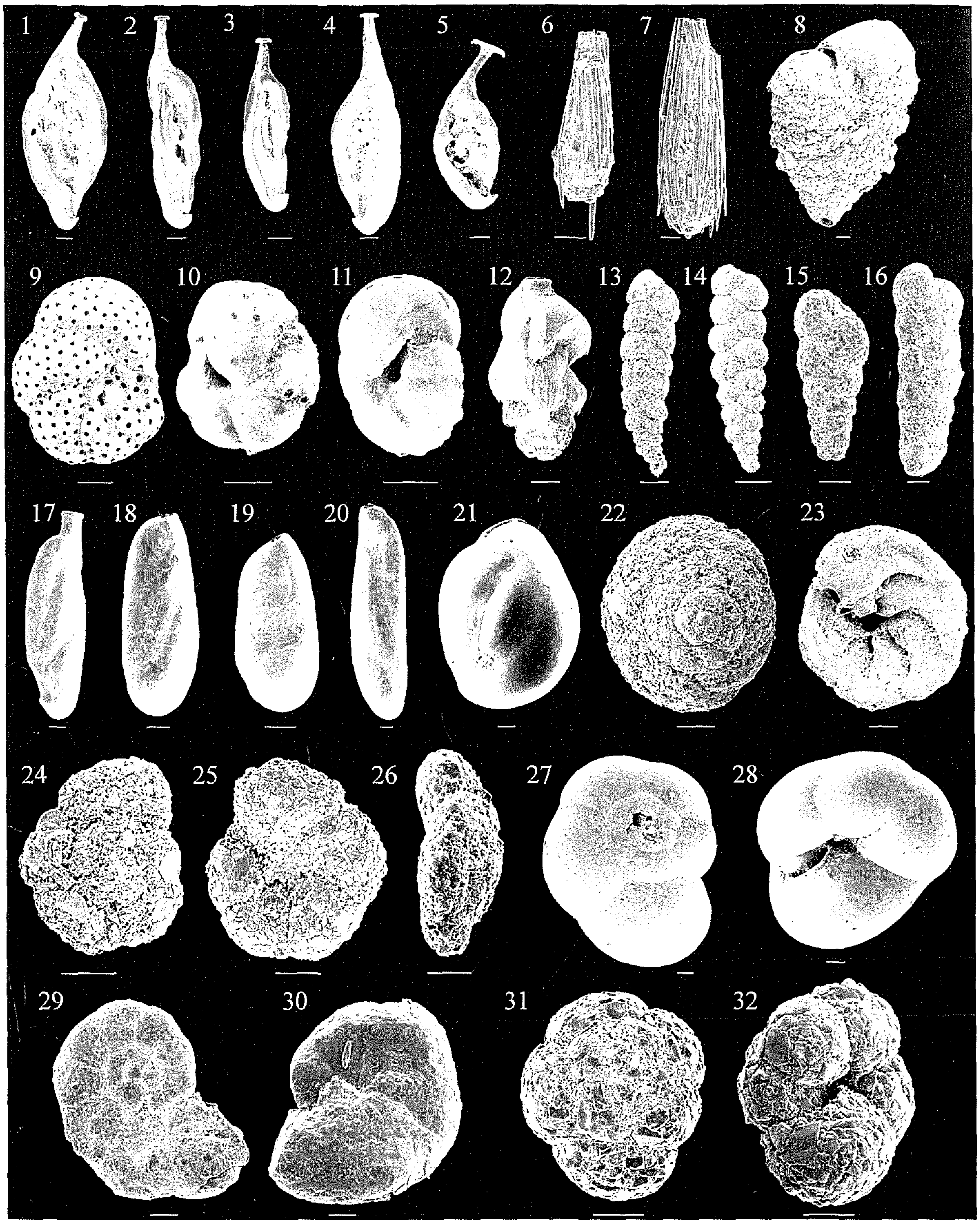

FIGURE 14. **1–5** *Spirophthalmidium emaciatum*; **6, 7** *Technitella legumen*; **8** *Textularia agglutinans*; **9–11** *Svratkina australiensis*; **12** *Trifarina occidentalis*; **13, 14** *Textularia earlandi*; **15, 16** *Textularia* sp.; **17** *Triloculina nasuta*; **18–20** *Triloculina oblonga*; **21** *Triloculina bermudezi*; **22, 23** *Trochammina ochracea*; **24–26** *Trochammina charlottensis*; **27, 28** *Trochammina inflata*; **29, 30** *Trochammina macrescens*; **31, 32** *Trochammina quadriloba*. Scale bar = 50 μm.

Spiroloculina arenata Cushman, 1921, p. 63, pl. 14, fig. 17. **(Figs. 13.25, 13.26)**

Spiroloculina sp. Rare individuals not identified to the specific level.

Spirophthalmidium emaciatum Haynes = *Spirophthalmidium acutimargo* (Brady) var. *emaciatum* Haynes, 1973, new name for *Spiroloculina acutimargo* Brady, 1884, pl. 10, fig. 14 (not figs. 12, 13, and 15). Brady described his fig. 14 with a phialine lip as a juvenile, and the other figures without the phialine lip as adults. Haynes (1973) regarded Brady's fig. 14 as variants of *S. acutimargo*. Cave phenotypes always had an aperture on an elongated neck (of variable length) with a fragile phialine lip.

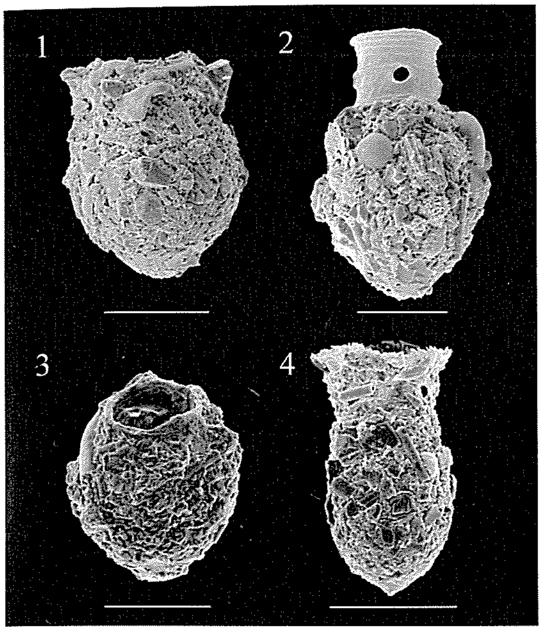

FIGURE 15. **1** *Codonella acutula*; **2** *Codonellopsis americana*; **3** *Stenosemella avellana*; **4** *Codonella elongata*. Scale bar = 50 µm.

Therefore, we elevate Haynes' variant to species level. **(Figs. 14.1–14.5)**

Svratkina australiensis (Chapman, Parr, and Collins) = *Discorbis tuberculata* var. *australiensis* Chapman, Parr, and Collins, 1934, p. 169, pl. 8, fig. 9. Because of its small size and infrequency in the literature, we note synonymies with *S. bubnanensis* McCulloch (1977, pl. 153, figs. 3, 11; Loeblich and Tappan, 1994: p. 161, pl. 353, figs. 10, 11), and the indeterminate species of *Svratkina* in Hottinger, Halicz, and Reiss, (1993, p. 138, pl. 196, figs. 7–10). **(Figs. 14.9–14.11)**

Technitella legumen Norman, 1878, p. 279, pl. 16, figs. 3, 4. **(Figs. 14.6, 14.7)**

Textularia agglutinans d'Orbigny 1839a, p. 144, pl. 1, figs. 17, 18, 32–34. **(Fig. 14.8)**

Textularia earlandi Parker, 1952, new name for *T. elegans* Lacroix, 1931, p. 14, pl. 3, figs. 21–30. **(Figs. 14.13, 14.14)**

Textularia sp. This species differs from *T. earlandi* in being smaller, golden-brownish, and prevalent in the submarine cave environment. Its aperture is within a small depression on the apertural face. **(Figs. 14.15, 14.16)**

Trifarina occidentalis (Cushman), 1923 = *Uvigerina angulosa* Cushman 1922, p. 34, pl. 5, figs. 3, 4. **(Fig. 14.12)**

Triloculina bermudezi Acosta, 1940, p. 37, pl. 4, figs. 1–5. **(Fig. 14.21)**

Triloculina carinata d'Orbigny, 1839a, p. 158, pl. 10, figs. 15–17.

Triloculina nasuta Cushman, 1935, p. 5, pl. 2, figs. 1–3. **(Fig. 14.17)**

Triloculina oblonga (Montagu) = *Vermiculum oblongum* Montagu, 1803, p. 522, pl. 14, fig. 9. **(Figs. 14.18–14.20)**

Triloculina rotunda d'Orbigny, 1826, p. 299.

Triloculina suborbicularis d'Orbigny, 1839a, p. 177, pl. 10, figs. 9, 10.

Trochammina charlottensis Cushman, 1925, p. 39, pl. 6, fig. 4. **(Figs. 14.24–14.26)**

Trochammina inflata (Montagu) = *Nautilus inflatus* Montagu, 1808, p. 81, pl. 18, fig. 3. **(Figs. 14.27, 14.28)**

Trochammina macrescens Brady = *Trochammina inflata* (Montagu) var. *macrescens* Brady, 1870, p. 290, pl. 11, fig. 5. **(Figs. 13.29, 13.30)**

Trochammina ochracea (Williamson) = *Rotalina ochracea* Williamson, 1858, figs. 112, 113. **(Figs. 13.22, 13.23)**

Trochammina quadriloba Höglund, 1948, new name for *T. pusilla* Höglund, 1947, p. 201, pl. 17, figs. 4a–c. **(Figs. 13.31, 13.32)**

Tubinella funalis (Brady) = *Articulina funalis* Brady, 1884, p. 185, pl. 13, figs. 6–11.

Wiesnerella auriculata (Egger) = *Planispirina auriculata* Egger, 1893, p. 245, pl. 3, figs. 13–15.

TINTINNIDA

Codonella acutula Kofoid and Campbell, 1929, p. 52, fig. 104. **(Fig. 15.1)**

Codonella elongata Kofoid and Campbell, 1929, p. 59, fig. 102. **(Fig. 15.4)**

Codonellopsis americana Kofoid and Campbell, 1929, p. 75, fig. 159. **(Fig. 15.2)**

Stenosemella avellana (Meunier) = *Tintinnopsis avellana* Meunier, 1919, p. 30, pl. 22, fig. 37. **(Fig. 15.3)**

APPENDIX 2

Supplementary data (original counts, relative abundance, standard error, taphocoenosis). This table can be found on the Cushman Foundation website in the JFR Article Data Repository (http://www.cushmanfoundation.org/jfr/index.html) as item number JFR_DR201105.