Foraminifera in elevated Bermudian caves provide further evidence for +21 m eustatic sea level during Marine Isotope Stage 11

Peter J. van Hengstum [a,*], David B. Scott [a], Emmanuelle J. Javaux [b]

[a] Department of Earth Sciences, Dalhousie University, Edzel Castle Circle, Halifax, Nova Scotia, Canada, B3H 4J1
[b] Research unit of Paleobotany–Paleopalynology–Micropaleontology, Geology Department, University of Liège, 4000 Sart-Tilman Liège, Belgium

ARTICLE INFO

ABSTRACT

Two hypotheses have been proposed to explain the origin of marine isotope stage (MIS) 11 deposits in small Bermudian caves at +21 m above modern sea level: (1) a +21 m MIS 11 eustatic sea-level high-stand, and (2) a MIS 11 mega-tsunami event. Importantly, the foraminifera reported in these caves have yet to be critically evaluated within a framework of coastal cave environments. After statistically comparing foraminifera in modern Bermudian littoral caves and the MIS 11 Calonectris Pocket A (+21 m cave) to the largest available database of Bermudian coastal foraminifera, the assemblages found in modern littoral caves – and Calonectris Pocket A – cannot be statistically differentiated from lagoons. This observation is expected considering littoral caves are simply sheltered extensions of a lagoon environment in the littoral zone, where typical coastal processes (waves, storms) homogenize and rework lagoonal, reefal, and occasional planktic taxa. Fossil protoconchs of the Bermudian cave stygobite *Caecum caverna* were also associated with the foraminifera. These results indicate that the MIS 11 Bermudian caves are fossil littoral caves (breached flank margin caves), where the total MIS 11 micro-fossil assemblage is preserving a signature of coeval sea level at +21 m. Brackish foraminifera (*Polysaccammina*, *Pseudothurammina*) and anchialine gastropods (~95%, >300 individuals) indicate a brackish anchialine habitat developed in the elevated caves after the prolonged littoral environmental phase. The onset of sea-level regression following the +21 m highstand would first lower the ancient brackish Ghyben-Herzberg lens (<0.5 m) and flood the cave with brackish water, followed by drainage of the cave to create a permanent vadose environment. These interpretations of the MIS 11 microfossils (considering both taphonomy and paleoecology) are congruent with the micropaleontological, hydro-geological and physical mechanisms influencing modern Bermudian coastal cave environments. In conclusion, we reject the mega-tsunami hypothesis, concur with the +21 m MIS 11 eustatic sea-level hypothesis, and reiterate the need to resolve the disparity between global marine isotopic records and the physical geologic evidence for sea level during MIS 11.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

The proposed MIS 11 (400 ka) +21 m eustatic sea-level high-stand has been debated since geologic evidence was first marshaled by Hearty et al. (1999) and supported by reports from other widespread localities (Kaufman and Brigham-Grette, 1993; Lundberg and McFarlane, 2002; Roberts et al., 2007). Problems arose when the physical geologic evidence for a MIS 11 highstand could not be reconciled with marine stable isotopic or atmospheric CO_2 records that suggest sea level during MIS 11 should be homologous to more recent interglacials due to similar oceanic water volumes (i.e., MIS 5e: +4–6 m; Hodell et al., 2000; Karner et al., 2002; Raynaud et al., 2005; Rohling et al., 2008). The islands of Bermuda are ideally suited for sea-level research, because they have remained tectonically and glacio-isostatically stable during the Quaternary (Vacher and Rowe, 1997). To date, Bermudian evidence for the MIS 11 highstand are marine-to-brackish sediments and fossils in karst caves, exposed in four elevated caves surrounding Government Quarry: Calonectris (+21.3 m), UGQ4 (+21 m), UGQ5 (+18 m), and the Land et al. site (~ +21; Land et al., 1967; McMurtry et al., 2007; Olson and Hearty, 2009). These deposits are fossiliferous, containing: molluscs, vertebrates, echinoderms, red algae, coral fragments, and foraminifera. Numerous age determinations (U-series dating on speleothem, amino acid racemization on *Poecilozonites* and *Glycymeris*) from independent laboratories confirm an

* Corresponding author. Tel.: +1 902 494 3604; fax: +1 902 494 6889.
E-mail addresses: vanhengstum@dal.ca (P.J. van Hengstum), dbscott@dal.ca (D.B. Scott), ej.javaux@ulg.ac.be (E.J. Javaux).

MIS 11 age for the sediments and fossils in question (Hearty and Olson, 2008; McMurtry et al., 2008; Olson and Hearty, 2009).

Recently, McMurtry et al. (2007) proposed that the sediments were not developed *in situ*, but were transported into the caves from lower elevations by a mega-tsunami. Their arguments are based on: (1) the range of elevations for the deposits, (2) re-interpretation of isopachous cements as multi-generational and developed in multiple environments—not solely through speleogenesis, (3) generating additional variable U-series ages on the calcite flowstone (although still indicating a MIS 11 age for the sediments), and (4) the occurrence of several species of benthic foraminifers that were interpreted as having been transported by a mega-tsunami because they are supposedly atypical of other Bermudian coastal environments (i.e., lagoons, beaches). Arguments for and against the first three main points have been extensively discussed in publications debating the mega-tsunami hypothesis (i.e., McMurtry et al., 2007, 2008; Hearty and Olson, 2008; Olson and Hearty, 2009), however, the foraminifera have until now received incomplete assessment. The objective of this study is to compare modern populations of Bermudian cave foraminifera on Bermuda to the microfossils preserved in the MIS 11 elevated caves. This comparison will examine if the foraminifera found by McMurtry et al. (2007) were transported by mega-tsunami, or if in fact they are consistent with a MIS 11 sea-level highstand. Without this analysis, the debate surrounding the origin of sedimentary deposits in the elevated Bermudian caves is currently incomplete.

2. Coastal cave environments and foraminifera

There are several different types of coastal cave environments and habitats that require consideration before investigating geological remains in caves (Fig. 1). Importantly, cave environments are not static, but constantly change in response to external and internal factors, such as ongoing speleogenesis (both phreatic and vadose) or sea-level change. In coastal carbonate terrain, local hydrogeology is arguably the greatest ecological control on ecosystems in different coastal cave systems. The groundwater flooding a cave passage is either part of the Ghyben-Herzberg (GH) lens (fresh to brackish water) or basal marine groundwater that is intruding from the coast (Vacher, 1988; Whitaker and Smart, 1990). The GH lens contains meteoric water that is flowing coastward, whereas the basal marine water exhibits more complex subterranean circulation patterns (Vacher, 1988; Whitaker and Smart, 1990; Moore et al., 1992). The interface between these two water masses is the halocline or mixing zone, which is (1) a slightly acidic region, dominantly responsible for phreatic cave dissolution, and (2)

strongly controlled by sea level (see theoretical and practical discussions in: Smart et al., 1988; Vacher and Rowe, 1997; Schneider and Kruse, 2003). Arising from the strong environmental gradients between these two separate water masses (salinity, dissolved oxygen, etc), different aquatic invertebrates have ecological niches in different passages and areas of coastal caves, depending upon which water mass is currently saturating a specific cave passage (e.g., Pohlman et al., 1997).

The Stock et al. (1986) classification of coastal cave environments, and elaborated on herein, is most frequently used to describe phreatic (flooded) cave habitats and ascribe ecological niches to modern aquatic cave fauna (stygobites and stygophiles). First, reef caves are void spaces below modern sea level in modern reef environments. They range in size from small void spaces to dominant cave passages, and are hydrologically dominated by coastal oceanography (e.g., Kitamura et al., 2007). Anchialine caves have a recognizable terrestrial and marine influence, and typically intersect (or are within) the Ghyben-Herzberg (GH) lens. Anchialine caves can have either sub-areal access through a sinkhole (cenote), or subterranean access by a cave passage meandering from the basal saline groundwater into the GH lens (Fig. 1). In contrast, submarine caves have entrances that are below sea level, their passages are completely flooded with saline water, yet they receive active continental influence, not from the terrestrial surface, but through saline groundwater circulation (i.e., Whitaker and Smart, 1990). These caves retain a significant marine character at their entrance, and have arguably received the majority of marine ecological attention. Next, littoral caves occur at sea level in the littoral zone, and are humanly accessible from outside the cave environment. They often contain the air–water interface, which can continue for some distance into the cave. Within a geologic framework, littoral cave environments can be sea caves, or breached flank margin caves—where speleogenesis and wave action have collectively breached a flank margin cave wall. The breeching of a flank margin cave wall is an important environmental event, as the cave habitat instantly evolves from a dark and isolated subterranean void space, to a protected enclosure along a coastline with physical oceanic communication. Because many flank margin caves form significantly close to sea level, they have received considerable geologic attention as a Pleistocene sea-level proxy (Mylroie and Carew, 1990; Labourdette et al., 2007 Mylroie et al., 2008). This classification of coastal cave environments provides a simplified – yet necessary – framework for evaluating cave micropaleontological remains, as sea level and hydrogeological changes will have a concomitant impact on how specific habitats in a phreatic cave evolve.
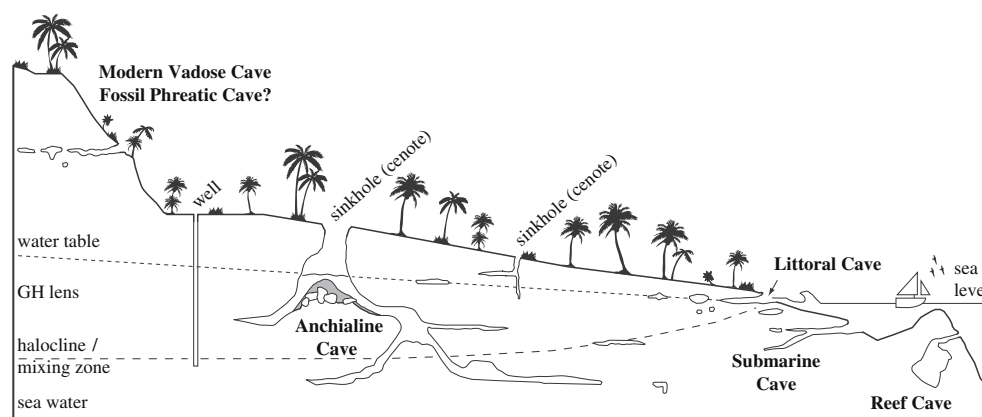

Fig. 1. Classification of coastal cave environments. Note that sinkholes are commonly known as cenotes in Mexico, and this nomenclature is occasionally extended to other global localities.

An important limitation of this scheme is that not all cave environments are adequately described *senso stricto* by this classification. For example, large solitary coastal cave systems may contain several types of cave environments; such as Ox Bel Ha in Mexico, which hosts both anchialine and submarine cave habitats. Furthermore, other types of coastal environments can potentially overprint cave habitats, especially when the cave entrance has evolved into another coastal system (e.g., from a sinkhole into a mangrove swap or lagoon). This classification scheme also omits the relationships between the present cave environment and the geologic mechanisms responsible for cave formation. For example, many modern submarine cave environments are historical former flank margin caves. Despite these caveats, this classification scheme provides an environmental structure for understanding the origin of ancient cave deposits.

Benthic foraminifera (unicellular marine to brackish protists) are particularly important environmental proxies across coastal environments, owing to the excellent preservation potential of their tests in the sedimentary record, and their ecologic sensitivity to critical environmental parameters (e.g., pH, dissolved oxygen, temperature). The sensitivity of foraminifera to salinity has caused specific species to evolve ecological niches at specific elevations relative to modern sea level in salt marshes, which is widely used as an accurate tool for demarcating former sea levels (Scott and Medioli, 1980a, 1978; Scott et al., 1981; Horton and Edwards, 2005). In contrast to their widespread application in coastal research, there has been very little systematic investigation of foraminifera in caves. Documentation of foraminifera in subterranean settings is typically limited to mentioning their sedimentary contribution within the context of a broader analysis, or just documenting their existence (Fig. 2). However, van Hengstum et al. (2009) demonstrated how benthic foraminifera are capable of discriminating historical vertical displacements of the halocline and GH lens in coastal cave environments, whereby microfauna in phreatic caves respond to the evolving cave habitats caused by sea-level change. Most importantly, euryhaline foraminifera and testate amoebae (thecamoebians) can colonize cave passages saturated by the GH lens (fresh to brackish water), which are different from the marine taxa living below the halocline in the saline groundwater (Bermuda: Sket and Iliffe, 1980; Javaux, 1999; Mexico: van Hengstum et al., 2008, 2009).

3. Regional setting

The origin of foraminifera in the MIS 11 elevated Bermudian caves (Calonectris, UGQ4, UGQ5, Land et al., 1967 site) will only be understood after they have been compared with all natural Bermudian coastal environments, including coastal caves (Fig. 3A). In 1993 and 1995, over 170 surface sediment samples (upper 5 cm) were collected from across Bermudian coastal environments: mangroves (Hungry Bay, Mill Share), reefs (Hog Breaker reefs, Twin Reefs, North Lagoon traverse), lagoons (North Lagoon off Devonshire dock, Harrington Sound), protected lagoons with peripheral mangroves (Walsingham Bay, Mangrove Bay), and the entrance to anchialine caves (Leamington Cave, Walsingham Cave System – entrances: Walsingham and Crystal caverns; Javaux, 1999). All of the sampling sites were typically in one environmental category, except a transect that was sampled in the North Lagoon (from the lagoon, into the reef). In addition, 2 samples were collected in early 2009 from a modern littoral cave. This sample collection provides the baseline information to examine the similarity between fossil and modern assemblages of Bermudian coastal foraminifera. Based on the mega-tsunami hypothesis, there should be minimal congruency between the foraminiferal assemblages in modern Bermudian coastal environments and the foraminiferal assemblages in the MIS 11 elevated caves (McMurtry et al., 2007).

The MIS 11 fossil caves are all located in the vicinity of Government Quarry, Bermuda, on the isthmus separating Harrington Sound and Castle Harbor (Fig. 3B). Geologically, this area is commonly referred to as the Walsingham Tract, after the Walsingham Formation. This limestone bedrock is the oldest and most diagenetically mature eolianite on Bermuda (Land et al., 1967) and is famous for both vadose and phreatic caves. Sediment no longer exists in outcrop for either the Land et al. (1967) or the Calonectris
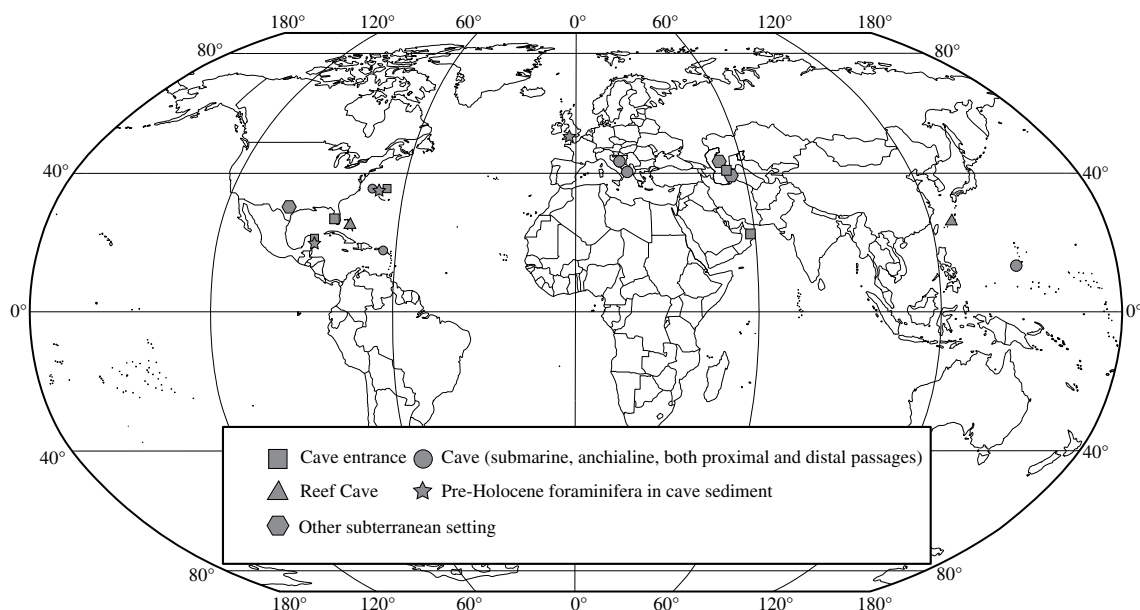

Fig. 2. Global subterranean locations where foraminifera that have been recovered. As reported by: Birstein and Ljovuschkin (1965), Mikhalevich (1976), Sket and Iliffe (1980), Reiswig (1981), Rasmussen and Brett (1985), Longly (1986), Proctor and Smart (1991), Novosel et al. (2002), Javaux and Scott (2003), McMurtry et al. (2007), Kitamura et al. (2007), Denitto et al. (2007), Lewis and Tichenor (2008), E. Reinhardt (Oman – Pers. Com., 2009), van Hengstum et al. (2008, 2009). Foraminifera have yet to be documented in southern hemisphere coastal cave environments.
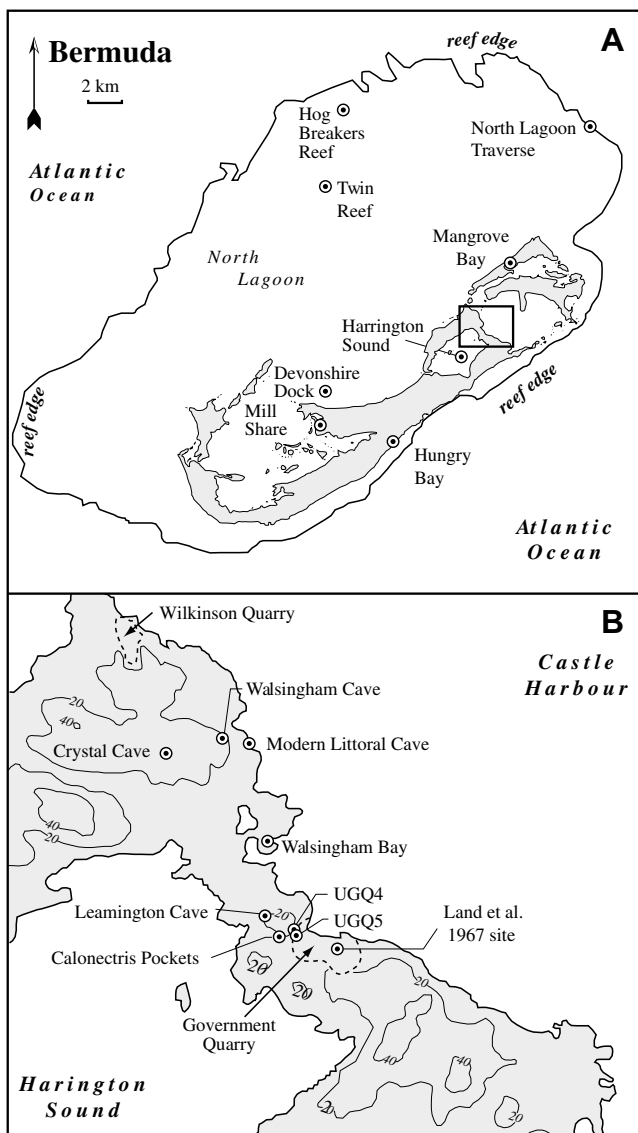
Fig. 3. Surface sediment locations across Bermuda (A) and along the Walsingham Tract (B). Base map and contours (20 m interval) after Vacher et al. (1989).

sites, however, representative sediment samples from Calonectris Pocket A and Pocket B (<50 cm apart) were obtained from the Smithsonian Institution for analysis (see Olson and Hearty, 2009 for detailed outcrop descriptions). Wilkinson (2006) discovered that only very rare foraminifera are preserved in the other elevated MIS 11 caves (UGQ4, UGQ5, Land et al., 1967 site), which are only suitable for a presence/absence-based interpretation (McMurtry et al., 2007). Although foraminifera from every cave are unavailable and unsuitable for multivariate statistical treatment, we re-summarize all the shared microfossils preserved in the Bermudian MIS 11 cave sediments to allow for a holistic interpretation of the foraminifera in question.

4. Methods

Surface sediment samples (10 cm^{-3}, upper 5 cm) were washed over a 63 μm sieve, and approximately 300 foraminifers were wet-enumerated where possible in petri dishes (Javaux, 1999). Approximately 271 separate taxonomic units were originally identified in the surface samples, collectively forming the largest

available database of Bermudian coastal foraminifera. For the MIS 11 Calonectris Pockets, only Calonectris Pocket A contained statistically significant abundances of foraminifera, which are suitable for multivariate statistics analysis, not Pocket B. However, all foraminifera observed from Calonectris Pocket B were noted for their presence, similarly to the other elevated cave sites. Only total assemblages of foraminifera were considered in this analysis (thanatocoenosis), which includes the bias introduced by typical taphonomic processes at each sample site, such as coastal re-working. However, the thanatocoenosis is thought to better characterize average environmental conditions at a sample locale (Scott and Medioli, 1980b) and allows for the inclusion of fossil material into a statistical investigation with the modern samples.

After manually entering the original database from Javaux (1999) into a personal computer, statistically insignificant samples (n = 25) were omitted from the analysis (where: <300 individuals were enumerated, abundances of taxonomic units grossly did not total 100%, insignificant sampling of a separate environmental settings). The original 271 taxonomic units (species) were then amalgamated into genera to smooth any taxonomic inconsistencies (especially in the miliolid group) and create a more robust comparison between environments by desensitizing the analysis to micro-environmental effects within individual ecotopes. Of the original 128 different genera (observations) identified, 38 genera were deemed statistically insignificant and omitted from the final multivariate analysis due to the estimated standard error for the genera being greater than the abundance in all samples (Patterson and Fishbein, 1989). This resulted in a final data matrix of 145 samples, each with 90 observations. Samples were then compared using a Euclidean distance coefficient and amalgamated into clusters using Ward's method of minimum variance and displayed in an hierarchical dendrogram, using the software package *PAST* (Paleontological Statistics, Hammer et al., 2001), which approaches the method of Fishbein and Patterson (1993). Finally, representative microfossil specimens from the modern littoral cave and MIS 11 Calonectris Pockets were imaged using scanning electron microscopy (SEM) to confirm taxonomy, examine shell exteriors, and make detailed visual comparisons.
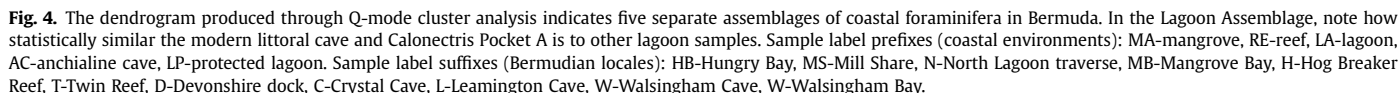
5. Results

5.1. Modern Bermudian coastal foraminifera

The dendrogram produced through the Q-mode cluster analysis indicates five distinct clusters that are interpreted as different assemblages of coastal foraminifera in Bermuda: Mangrove Assemblage, Reef Assemblage, Lagoon Assemblage, Anchialine Cave Assemblage, and the Protected Lagoon Assemblage (Fig. 4). Only a brief overview of these assemblages is provided here, as all the major and subtle ecological and taxonomic nuances of this dataset are provided in Javaux (1999) and Javaux and Scott (2003).

The Mangrove Assemblage contains samples from Mill Share and Hungry Bay and has the lowest diversity of all the assemblages. The dominant genus is *Trochammina*, with *Polysaccamina*, *Miliammina*, *Pseudothurammina*, and *Discorinopsis* present in lower abundances. The Reef Assemblage is dominated by *Homotrema rubrum* at Hog Breaker Reef, Twin Reef, and North Lagoon Reef and has significantly increased diversity in the miliod and rotalid groups as compared with the Mangrove Assemblage. The Reef Assemblage and the Mangrove Assemblage are both very well defined by the cluster analysis, owing largely to the significant overall contribution of *Trochammina* and *Homotrema* to their respective assemblages.

The most diverse samples are in the Lagoon Assemblage, where miliolid genera are dominant. Samples from Devonshire Dock, Harrington Sound, the modern littoral cave, Calonectris Pocket A,

Fig. 4. The dendrogram produced through Q-mode cluster analysis indicates five separate assemblages of coastal foraminifera in Bermuda. In the Lagoon Assemblage, note how statistically similar the modern littoral cave and Calonectris Pocket A is to other lagoon samples. Sample label prefixes (coastal environments): MA-mangrove, RE-reef, LA-lagoon, AC-anchialine cave, LP-protected lagoon. Sample label suffixes (Bermudian locales): HB-Hungry Bay, MS-Mill Share, N-North Lagoon traverse, MB-Mangrove Bay, H-Hog Breaker Reef, T-Twin Reef, D-Devonshire dock, C-Crystal Cave, L-Leamington Cave, W-Walsingham Cave, W-Walsingham Bay.

and two samples from a protected lagoon (Mangrove Bay) are included in this assemblage. Many characteristic reef (*Homotrema*, *Asterigerina*,) mangrove (*Polysaccamina*, *Pseudothurammina*), and planktic taxa are commonly encountered in the lagoons, indicating that coastal processes are constantly re-working foraminiferal tests from across the Bermudian platform. The inclusion of two samples from a protected lagoon site is therefore not surprising, considering the size of the database and that locations within a protected lagoon may actually be more comparable to an open lagoon site, such as the entrances to more open water. The Protected Lagoon Assemblage contains samples from both Walsingham Bay and Mangrove Bay, which are protected by mangroves (*Rhizophora* spp.) around the lagoon periphery. *Discorinopsis*, *Helenina*, *Triloculina*, and *Trochammina* are the most dominant genera in the Protected Lagoon Assemblage, with overall decreased diversity as compared with the open lagoons (Harrington Sound, North Lagoon). Three mangrove swamp samples are similar to the Protected Lagoon Assemblage based on the Q-mode cluster analysis (MA-MS2, MA-HB3, MA-HB4). All of these samples are <30 cm deep in the water and have increased abundances of *Triloculina oblonga* (opportunistic subtidal taxon), *Discorinopsis*, and *Helenina*—common higher-salinity mangrove species. In such shallow settings, evaporation may cause increased salinity (albeit still hyposaline) in smaller pools, environmentally creating a protected lagoon microenvironment within a larger mangrove setting.

The Anchialine Cave Assemblage is best characterized by elevated abundances of *Spiropthalmidium* sp., a taxon that is rarely encountered (<1%) outside the phreatic cave environment (Javaux, 1999). Five samples from outside the cave environment (LA-H16, LA-H17, LA-H18, LA-H6, MA-M23) are most similar to Bermudian anchialine cave samples, all which have the highest abundances of *Ammonia* in the whole database. This preliminary investigation of Bermudian phreatic caves was limited to only the entrances of the larger subterranean cave systems, and did not sample through the full range of environmental variables that exist in a phreatic cave (light gradients, salinity gradients, etc.). This factor explains why the anchialine cave samples share similarity to other open water sample locales. However, this limited sampling of the anchialine caves recovered different living foraminifera in the brackish GH lens than in marine conditions below the halocline (based on rose Bengal staining, Javaux, 1999). *Polysaccammina* and *Pseudothurammina* were found living in the brackish GH lens, although only in samples requiring omission from multivariate statistics because insufficient individuals were originally counted in those samples (Javaux, 1999). These species are diagnostic brackish taxa and only form small populations in marshes, brackish ponds, and the GH lens in Bermuda and Mexico (Scott, 1976; Javaux and Scott, 2003; Roe and Patterson, 2006; van Hengstum et al., 2008). However, despite the removal of these samples from the database, typical marsh foraminifera *Trochammina*, *Polysaccammina*, and *Pseudothurammina* are living in the modern GH lens in the Walsingham Tract (<30 cm thick – Iliffe et al., 1983; Javaux, 1999). Below the halocline in full marine salinity, typical lagoon taxa fauna are living (*Quinqueloculina*, *Rosalina*, *Triloculina*). Lastly, minor abundances of reef, lagoon, and planktic foraminifera are present at the sediment-water interface in the anchialine caves. *Archaias angulatus* and *Articulina* tests were often fractured, and edge rounding and abrasion were common on *Amphistegina* and *Asterigerina* tests. Furthermore, *H. rubrum*, a diagnostic reef taxon, was found inland within the cavern of Walsingham Cave, several hundred meters away from the modern coastline, and several kilometers from the reef. The absence of rose Bengal staining indicates these taxa are not living in modern anchialine caves (Javaux, 1999). Their transport into the cave is attributed to typical coastal processes (waves, hurricanes) re-working these taxa from adjacent coastal environments into the caves.

Most relevant to this study is that neither the samples from the modern littoral cave, nor samples from Calonectris Pocket A, can be statistically differentiated from the modern lagoon based on foraminifera alone. The modern littoral cave samples are statistically most similar to samples collected from Harrington Sound lagoon and the North Lagoon (sample sites off Devonshire dock). Fractured, dead specimens of *A. angulatus* and *Articulina mucronata* were present in the modern littoral cave, along with reef taxa *Amphistegina lessoni* and *Asterigerina carinata*. Therefore, typical coastal processes (waves and storms) are responsible for transporting material from the reefs and lagoons into the modern littoral cave, and demonstrating how littoral caves act as mere sheltered extensions of lagoons with respect to foraminifera. Typical coastal foraminifera dominated the modern littoral cave assemblage (*Quinqueloculina*, *Triloculina*, other rotalids), with lower abundances of *Textularia agglutinans* and stygophilic ostracods (*Loxochonca oculocrista*, *Paranesidea sterreri*). However, the modern littoral cave is also the habitat for the endemic cave gastropod *C. caverna*—which does not live in lagoons—and provides a diagnostic paleoenvironmental marker for a phreatic cave. Many foraminiferal tests have surficial pitting (Plate 1 – M3, M7, M9, M12), not a surprising characteristic because mildly acidic conditions can occur in littoral caves from the mixing of meteoric water in the GH lens with saline marine water (Smart et al., 1988; Mylroie et al., 2008).

5.2. Microfossils in MIS 11 caves

Microfossils preserved in the sediment of MIS 11 Calonectris Pockets included foraminifera, rare ostracods, and rare bryozoan fragments (Plate 1). Statistically insignificant quantities of foraminifera were preserved in Calonectris Pocket B, but typical coastal taxa were observed, including: *Amphistegina*, a sole fractured specimen of *Archaias*, *Asterigerina*, *Bolivina*, *Quinqueloculina*, *Rosalina*, and *Triloculina* (Table 1). Ostracods and other microfossil remains were absent from Pocket B. In contrast, a high abundance of foraminifera ($\sim$832 cm^{-3}) were preserved in Pocket A, including all the taxa from Pocket B, except *Archaias angulatus*, as well as a two planktic foraminifers. The only agglutinated taxon recovered from the Calonectris site was *T. agglutinans* (Plate 1 – F10). After examining Calonectris foraminifera with SEM, several tests contained fractured chambers (Plate 1 – F5, F10) as well as dissolution pitting (Plate 1 – F7)—characteristics also observed in foraminiferal tests from the modern littoral cave (M9, M12). Secondary calcite overgrowth was also observed on the foraminifer tests (Plate 1 – F8), and on the interior of ostracod valves. Additionally, all of the foraminifera documented from the Calonectris Pockets also are present in modern Bermudian caves (Table 1). Pocket A also contained the ostracods *L. oculocrista* and *P. sterreri* (articulated and disarticulated specimens), which are common taxa in modern Bermudian anchialine and littoral caves, and capable of withstanding mesohaline conditions (5–18 psu, Maddocks and Iliffe, 1986). Notably, the genus *Loxochonca* especially favors littoral environments (Van Morkhoven, 1963). Finally, two specimens of the gastropod *C. caverna* were found in Calonectris Pocket A, a protoconch (Plate 1 – F16) and a protoconch with part of the secondary growth stage attached. This gastropod is an aquatic, Bermudian endemic cave taxon (stygobite) that can tolerate salinity from 20 to 35 psu (Moolenbeek et al., 1988). The recovery of this taxon is significant by providing strong evidence that Calonectris Pockets were once phreatic cave environments.

Foraminifera preserved in the other Bermudian MIS 11 caves (UGQ5, UGQ4, Land et al., 1967 site) were previously presented by McMurtry et al. (2007). The only taxon preserved in all the MIS 11 caves is the robust foraminifer *A. lessoni*. The Land et al. (1967) site

Table 1
Preserved MIS 11 microfossils in elevated Bermudian caves compared with modern cave environments. Data for UGQ5 (+18 m), UGQ4 (+21 m), and the Land et al. (1967) site (∼+21 m) from Wilkinson (2006).

	Modern Caves		MIS 11 Caves				
	Anchialine	Littoral	C. Pocket A	C. Pocket B	UGQ4	Land site	UGQ5
Stygobites							
Caecum caverna (gastropod)	•	•	•				
Stygophiles							
Abdidodentrix rhomboidalis	•	•	•				
Bolivina spp.	•	•	•	•			
Cibicides sp.	•	•	•				•
Cymbaloporetta squamosa	•	•	•				
Milionella subrotunda	•	•	•				
Hoeglundina c.f. *elegans*	•	•	•	•	•		
Quinqueloculina candeiana	•	•	•			•	
Quinqueloculina lamarckiana	•	•	•	•			•
Quinqueloculina poeyana	•	•	•				•
Quinqueloculina seminulum	•	•	•			•	•
Quinqueloculina vulgaris	•	•	•			•	•
Quinqueloculina spp.	•	•	•	•			
Planorbulina sp.	•	•	•				
Pyrgo elongata		•	•				
Pyrgo subsphaerica		•	•				
Polysaccammina ipohalina	•					•	
Pseudothurammina limnetis	•					•	
Reophax sp.	•						•
Rosalina spp.	•	•	•	•			
Spiroloculina antillarum	•	•	•				
Textularia agglutinans	•	•	•			•	
Triloculina carinata	•	•	•				
Triloculina oblonga	•	•	•				
Triloculina spp.	•	•	•	•			
Loxochonca sp.	•	•	•			•	
Paranesidea sterreri	•	•	•				
Bryozoan fragments	•	•	•		•	•	•
Transported							
Amphistegina lessoni	•	•	•	•	•	•	•
Archaias angulatus	•	•		•		•	
Articulina spp.	•	•	•				
Articulina pacifica	•	•	•	•			
Asterigerina carinata	•	•	•	•		•	
Gypsina vesicularis	•					•	•
Homotrema rubrum	•	•		•		•	•
Planktic foraminifera	•	•	•			•	
Coral fragments		•					

(+21 m) was previously the most diverse site, containing a planktic foraminifer, reworked *H. rubrum* fragments, *Gypsina* sp., *Quinqueloculina* spp., and very rare *Archaias*, *Asterigerina*, *Textularia*, *Polysaccamina*, and *Pseudothurammina* (Wilkinson, 2006). UGQ5 (+18 m) contained only *Gypsina*, *Quinqueloculina*, and reworked *H. rubrum*. In contrast to the other MIS 11 caves, where typically several taxa are preserved, only one taxon was preserved in UGQ4 (+21 m; *A. lessoni*). The lack of diversity preserved in UGQ4 is not surprising, as neither diverse nor abundant microfossils were preserved in Calonectris Pocket B, which is <50 cm away from the most diverse and abundant assemblages preserved in Calonectris Pocket A. Considering subterranean geochemical processes are not spatially or temporally constant in vadose cave environments, the differential preservation of microfossils between caves sites likely reflects the different taphonomic history endured by microfossils in different cave locales. Importantly, all the microfossils preserved in the MIS 11-aged sediments are similarly present in modern Bermudian cave environments (Table 1).

6. Discussion: sea level or mega-tsunami?

Based on several independent lines of micropaleontological evidence, we must reject the mega-tsunami hypothesis because the MIS 11 foraminifera in the elevated Bermudian caves cannot be attributed solely to a mega-tsunami event. Diverse foraminifera from coastal and pelagic sources are known to characterize modern tsunami deposits (Hawkes et al., 2007). However, Hawkes et al. (2007) were able to differentiate statistically a tsunami foraminiferal assemblage from background foraminiferal assemblages in different coastal environments, across a spatially extensive area, from the same tsunami (2004 Indian Ocean event). In contrast, the MIS 11 foraminifera from Calonectris Pocket A are statistically similar to the expected background microfossil assemblage in a littoral cave environment. Bermudian paleotopography during a +21 m sea-level highstand would have just been several small emergent islands with a shoreline quite proximal (<50 m, Fig. 3) to entrance(s) of the Government Quarry caves, where typical wave and storm activity cannot be ignored as mechanisms for transporting robust calcite grains (reef foraminifera and coral fragments) and pelagic taxa into MIS 11 coastal caves. Considering the foraminifera preserved in Calonectris Pocket A are most statistically similar to modern lagoons, and by corollary to modern littoral cave environments, the vast majority of the foraminifera preserved in Calonectris Pocket A are interpreted as an *in situ* MIS 11 littoral cave assemblage (thanatocoenosis). Despite the lack of statistically significant populations of foraminifera in the other elevated cave sites, all the foraminifera ever recovered in these sites can be accounted for in modern Bermudian coastal cave environments

(Javaux, 1999; Wilkinson, 2006; Table 1). Therefore, we interpret all the Bermudian +21 m caves (UGQ4, UGQ5, Calonectris Pockets, Land et al., 1967 site) as recording a micropaleotological signature of a co-stratigraphic sea level – dated to MIS 11.

Morphologically, shell fragmentation and surface dissolution occur equally on foraminiferal tests from the modern littoral cave and the Calonectris Pockets (Plate 1). The observed shell fragmentation is taphonomically consistent with shells being reworked in the littoral zone, and minor acidity is common at the halocline in modern phreatic caves. This provides supporting evidence for an *in situ* interpretation of these foraminiferal assemblages, as opposed to transport by a mega-tsunami. However, fragmentation can also occur through other transport mechanisms, and acidic conditions can also occur in vadose caves from percolating environmental acids or organic acids derived from the breakdown of organic matter. Regardless of the mechanism that deposited the microfossils, vadose conditions have occurred in the elevated caves since the microfossils were emplaced (e.g., MIS 2). During these times, non-spatially consistent, mild acidy can help explain the differential preservation of microfossils between the different Bermudian elevated caves, as robust foraminifer tests clearly have the greatest preservation potential (*Amphistegina* – Table 1). Therefore, because the shell taphonomy and the selective preservation of microfossils between the caves can equally be attributed to phreatic cave (speleogenic) and high-energy (i.e., tsunami) environmental histories, these characteristics cannot be used as diagnostic evidence for either the MIS 11 +21 m highstand or mega-tsunami hypothesis, as previously argued (McMurtry et al., 2007).

Despite the ambiguous shell characteristics, other micropaleontological evidence recovered from the elevated Bermudian caves unequivocally supports the interpretation of *in situ* phreatic cave environments caused by +21 m sea level. The most convincing evidence is the recovery of the aquatic gastropod *C. caverna* (stygobite) in Calonectris Pocket A (Plate 1). *C. caverna* (gastropod) are common in the sediment of modern Bermudian caves, either solely as the protoconch or with the secondary growth stage attached (Moolenbeek et al., 1988). Considering only one specimen was found in the modern littoral cave sediment (Plate 1), littoral cave

habitats likely reflect the ecological boundary of this stygobite in subterranean environments. However, they are relatively abundant in Bermudian anchialine caves, which is likely their optimum ecological niche. The recovery of this stygobite in Calonectris indicates that marine water once flooded this elevated cave. Littoral and cave-tolerant (stygophiles) ostracods (*L. oculocrista* and *P. sterreri*) were preserved in Calonectris Pocket A, and *Loxochonca* sp. was recovered from the Land et al. (1967) site (Plate 1). These ostracods currently live in modern Bermudian coastal cave environments, and suggest the littoral zone was once present in the elevated caves (Van Morkhoven, 1963; Maddocks and Iliffe, 1986). Lastly, bryozoan skeletal fragments were present in both the modern littoral cave and in Calonectris Pocket A. Living bryozoans and their skeletal remains are quite common in coastal caves, and even stygobitic cave taxa have been described (e.g., Silén and Harmelin, 1976). We find it challenging to envisage how a mega-tsunami coincidently eroded, transported, and deposited (a) cave stygobites, (b) littoral, cave-adapted ostracods, (c) bryozoans, and (d) an assemblage of foraminifera statistically and taphonomically consistent with a littoral cave environment, all into elevated caves during MIS 11. The comprehensive micropaleontolgocal evidence preserved in the elevated Bermudian caves is consistent with the simple explanation that littoral cave environments did exist at +21 m in Government Quarry, Bermuda during MIS 11.

Interestingly, *Polysaccammina ipohalina* and *Pseudothurammina limnetis* were preserved in carbonate clasts from archived museum samples belonging to the destroyed cave of Land et al. (1967) and Wilkinson (2006). This is a surprising recovery in sediments dated to MIS 11, considering these taxa are individually not significantly abundant in modern brackish environments (salt marshes, ponds). Furthermore, due to the largely organic makeup of their tests, these marsh taxa are rarely preserved outside of their usual anoxic marsh environments because their shells easily oxidize or are consumed by bacteria. We find it pressing to believe *Polysaccammina* and *Psuedothurammina* have remained taxonomically identifiable since MIS 11 after enduring: mechanical homogenization in a tsunami, energetic deposition into a vadose cave, subsequent desiccation—but not oxidation or bacterial consumption,
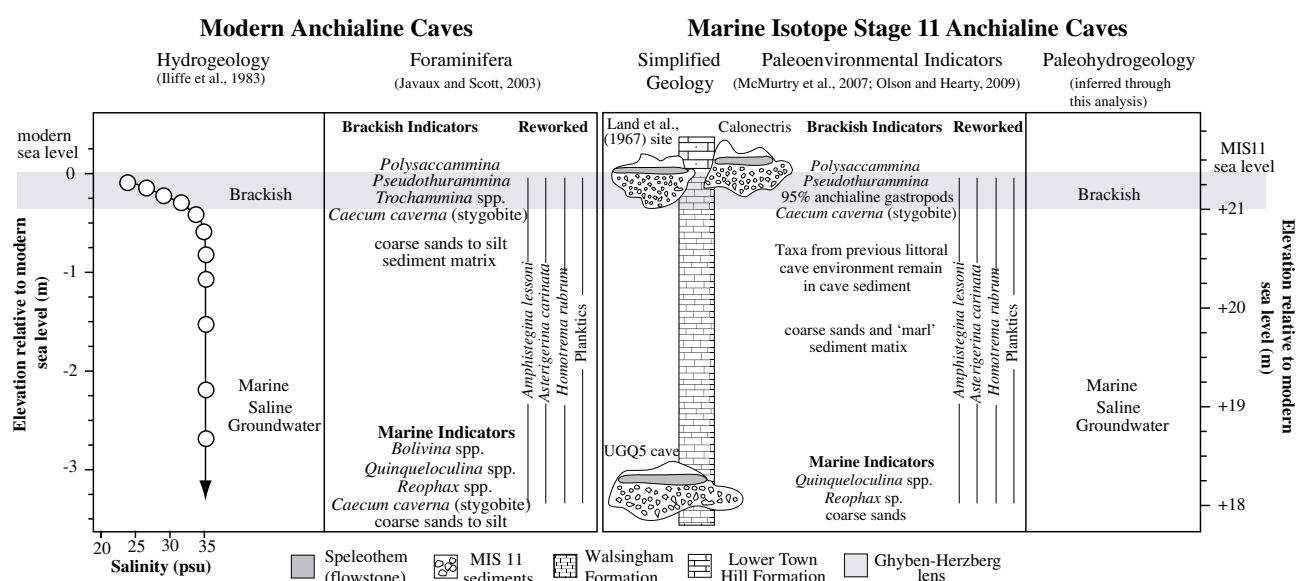

Fig. 5. Diagrammatic representation of the MIS 11 cave environment (microfossils, sediments, groundwater, and GH lens) and MIS 11 sea-level position during development of anchialine environmental conditions. Note the striking similarity between modern and MIS 11 micropaleontological, hydrogeological, and coastal variables in Bermudian coastal caves. Modern salinity data after Iliffe et al. (1983).

and encasement by calcite cements. Although common marsh foraminifera have been previously found in tsunami deposits (*Haplophragmoides*, Hawkes et al., 2007), this example was from an open coastline, not a cave. To our knowledge, there are currently no documented descriptions of the foraminiferal characteristics of known recent tsunami deposits in caves, providing no comparative data. Furthermore, if a tsunami entrained Bermudian mangrove or salt marsh taxa and deposited them into a cave, we would expect to recover *Trochammina* and *Discorinopsis*, which are common Bermudian mangrove genera, similarly to *Haplophragmoides* of Hawkes et al. (2007), not coincidently two extremely rare foraminifers. Therefore, we favor an *in situ* origin for these fragile
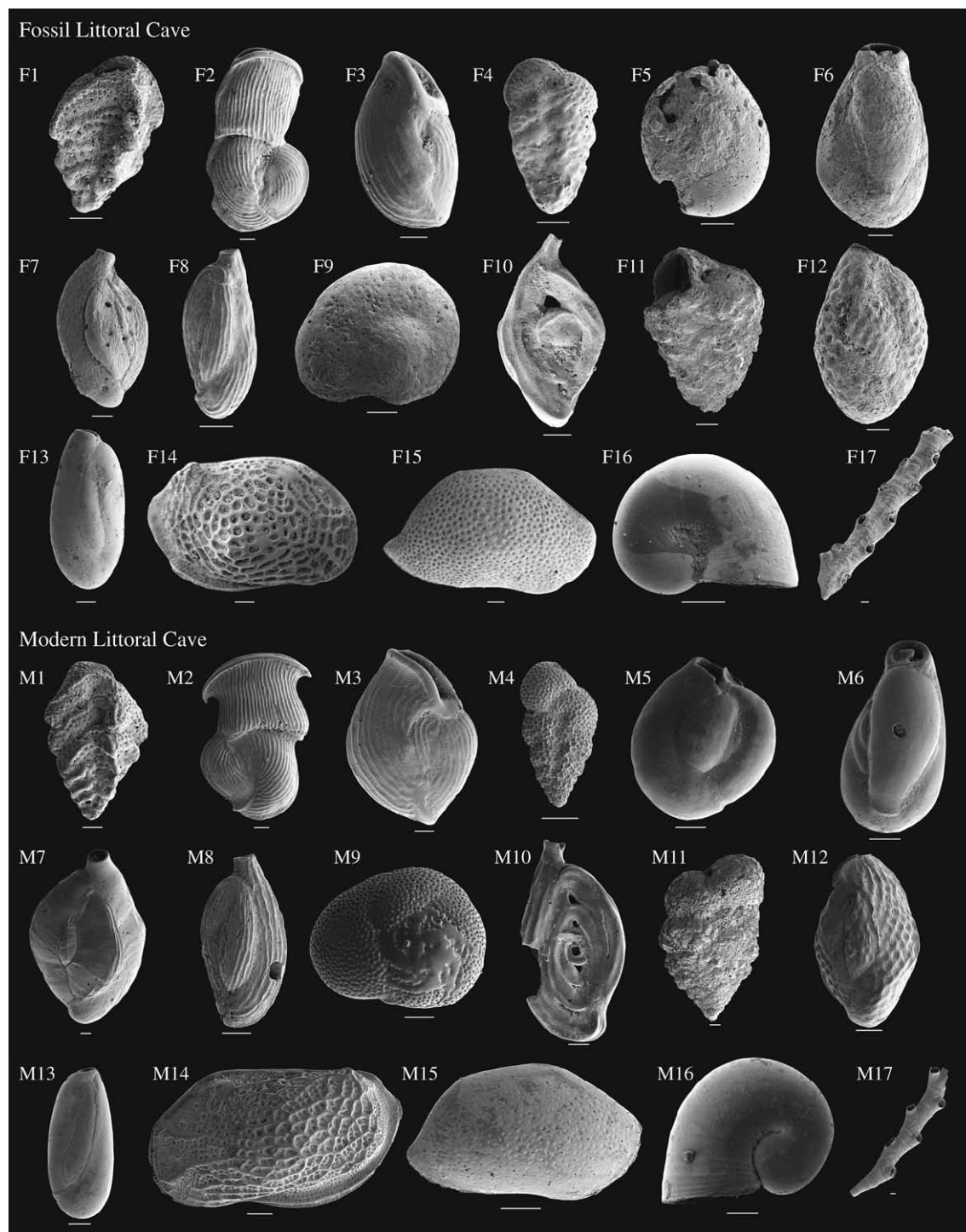

Plate 1. A comparison of MIS 11 littoral cave (Calonectris) microfossils (top half) to the microfossils in the modern littoral cave (bottom half). Foraminifera: F1, M1: *Abdidodentix rhomboidalis* Millett, 1899; F2, M2: *Articulina spp.* d'Orbigny, 1826; F3, M3: *Articulina mexicana* Cushman, 1944; F4, M4: *Bolivina variabilis* Williamson, 1858; F5, M5: *Miliolinella subrotunda* Montagu, 1803; F6, M6: *Pyrgo elongata* d'Orbigny, 1826; F7, M7: *Quinqueloculina candeiana* d'Orbigny, 1839; F8, M8: *Quinqueloculina poeyana* d'Orbigny, 1839; F9, M9: *Rosalina subaracuana* Cushman, 1922; F10, M10: *Spiroloculina antillarum* d'Orbigny, 1839; F11, M11: *Textularia agglutinans* d'Orbigny, 1839; F12, M12: *Triloculina carinata* d'Orbigny, 1839; F13, M13: *Triloculina oblonga* Montagu, 1803. Ostracods: F14, M14: *Loxochonca oculocrista* Teeter, 1975; F15, M15: *Paranesidea sterreri* Maddocks and Iliffe, 1986. Troglobytic gastropod: F16, M16: *Caecum caverna* Moolenbeek et al., 1988. Bryozoan fragment: F17, M17. Scale bar represents 50 μm.

marsh foraminifera, as this interpretation is taphonomically more plausible.

At the onset of sea-level regression following the MIS 11 high-stand, the original littoral cave environments would become saturated by brackish water from the concomitant vertical lowering of the GH lens (Fig. 5). The limited spatial extent of coeval Bermudian paleotopography likely favored the formation of a very thin GH lens during MIS 11 (<0.5 m), analogous to modern hydrogeological conditions along the modern Walsingham Tract (Iliffe et al., 1983). Considering, the strong control of sea level on the absolute elevation of a GH lens on small islands (Schneider and Kruse, 2003), an MIS 11 GH lens <0.5 m thick on Bermuda perched at +21 m also reflects a very similar eustatic sea-level position (Fig. 5). This brackish water would create an anchialine habitat in the elevated Bermudian caves, which would have been particularly suitable to *Polysaccammina* and *Psuedothurammina*, consistent with modern conditions in Bermudian coastal caves (Fig. 5). The recent documentation of a ~95% anchialine gastropod assemblage (>300, only ~5% marine individuals) in the Calonectris cave (+21 m) further corroborates the marsh foraminiferal paleoecology where an anchialine environment developed after a littoral cave environment (Olson and Hearty, 2009). Continual sea-level regression would have ultimately drained the elevated caves to create a vadose cave environment, suitable for the precipitation of speleothem deposits (flowstone) above the MIS 11 cave sediments, which have been repeatedly dated to late MIS 11 or early MIS 10 (McMurtry et al., 2008; Olson and Hearty, 2009).

7. Conclusions

After comparing modern and fossil Bermudian cave foraminifera, the microfossil evidence can no longer support the mega-tsunami hypothesis because they are not unequivocally diagnostic of tsunami. In contrast, the MIS 11 microfossils preserved in the Bermudian elevated caves provide striking evidence for a MIS 11 +21 m sea-level highstand, as tectonic and glacio-isostatic sea-level changes are not major geologic factors contributing to sea-level change in Bermuda. Considering the microfossils within a taphonomic and paleoecologic framework, we conclude: (1) that the Government Quarry Caves were indeed MIS 11 coastal cave environments; (2) typical assemblages of *in situ* littoral cave foraminifera developed due to a co-stratigraphic sea level (+21 m); and (3) sea-level regression following the MIS 11 highstand flooded the caves with a brackish GH lens – creating a suitable ecologic niche for marsh foraminifera and anchialine gastropods. These results indicate that modern cave environments cannot be ignored in any interpretation of sea level or tsunami history in Bermuda, and demonstrate that foraminifera in coastal cave environments have a wider potential as sea-level markers than previously appreciated. Although the risk of tsunami events in the Caribbean is becoming increasingly apparent (Ward and Day, 2001; Teeuw et al., 2009), microfossil evidence for ancient tsunamis still requires stringent evaluation. Lastly, because the Bermudian microfossil evidence in the elevated Government Quarry Caves corroborates the previously presented geologic evidence for a MIS 11 +21 m eustatic sea-level highstand, we suggest a greater focus on resolving the disparity between global marine isotopic records and the physical geologic evidence for sea level during MIS 11.

Acknowledgements

References

Birstein, J.A., Ljovuschkin, S.I., 1965. Fauna of the brackish underground waters of Central Asia. Intern. J. Speleol. 1 (3), 307–320.

Cushman, J.A., 1922. Shallow-water foraminifera of the Tortugas region. Papers from the Department of Marine Biology of the Carnegie Institution of Washington 17, 1–85.

Cushman, J.A., 1944. Foraminifera from the shallow water of the New England Coast. In: Cushman Laboratory for Foraminiferal Research Special Publication, vol. 12, 37 p.

Denitto, F., Terlizzi, A., Belmonte, G., 2007. Settlement and primary succession in a shallow submarine cave: spatial and temporal benthic assemblage distinctness. Mar. Ecol 28 (S1), 35–46.

d'Orbigny, A.D., 1826. Tableau méthodique de la classe des Céphalopodes. Annal. Sci. Naturel. 7, 245–314.

d'Orbigny, A.D., 1839. Foraminifêrs, in sagra, R., de l'histoire physique, politique et naturelle de l'île de Cuba. A Betrand, Paris.

Fishbein, E., Patterson, R.T., 1993. Error weighted maximum likelihood (EMWL): a new statistically based method to cluster quantitative micropaleontological data. J. Paleontol 67, 475–486.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4 (1), 9.

Hawkes, A.D., Bird, M., Cowie, S., Grundy-Warr, C., Horton, B.P., Hwai, A.T.S., Law, L., Macgregor, C., Nott, J., Ong, J.E., Rigg, J., Robinson, R., Tan-Mullins, M., Sa, T.T., Yasin, Z., Aik, L.W., 2007. Sediments deposited by the 2004 Indian Ocean tsunami along the Malaysia–Thailand peninsula. Mar. Geol. 242, 169–190.

Hearty, P.J., Kindler, P., Cheng, H., Edwards, R.L., 1999. Evidence for a +20 m middle Pleistocene sea-level highstand (Bermuda and Bahamas) and partial collapse of Antarctic ice. Geology 27, 375–378.

Hearty, P.J., Olson, S.L., 2008. Mega-highstand or mega-tsunami? Discussion of McMurtry, et al (Elevated marine deposits in Bermuda record a late Quaternary mega-tsunami: Sed. Geol. 200, 2007:155–165). Sed. Geol. 203 (3–4), 307–312.

Hodell, D.A., Charles, C.D., Ninnemann, U.S., 2000. Comparison of interglacial stages in the South Atlantic sector of the southern ocean for the past 450 kyr: implications for Marine Isotope Stage (MIS) 11. Global Planet. Change 24, 7–26.

Horton, B.P., Edwards, R.J., 2005. The application of local and regional transfer functions to the reconstruction of Holocene sea levels, north Norfolk, England. The Holocene 15 (2), 216–288.

Iliffe, T.M., Hart Jr., C.W., Manning, R.B., 1983. Biogeography and the caves of Bermuda. Nature 302, 141–142.

Javaux, E.J., 1999. Benthic foraminifera from the modern sediments of Bermuda: implications for Holocene sea-level studies. PhD thesis, Dalhousie University, Canada.

Javaux, E.J., Scott, D.B., 2003. Illustration of modern benthic foraminifera from Bermuda and remarks on distributions in other subtropical/tropical areas. Paleontol. Electron. 6 (4), 29.

Karner, D.B., Levine, J., Medeiros, B.P., Muller, R.A., 2002. Constructing a stacked benthic $\delta^{18}O$ record. Paleoceanography 17 (3), 1030. doi:10.1029/2001PA000667.

Kaufman, D.S., Brigham-Grette, J., 1993. Aminostratigraphic correlations and paleotemperature implications, Pliocene–Pleistocene high sea level deposits, northwestern Alaska. Quatern. Sci. Rev. 12, 21–33.

Kitamura, A., Yamamoto, N., Kase, T., Ohashi, S., Hiramoto, M., Fukusawa, H., Watanabe, T., Irino, T., Kojitani, H., Shimamura, M., Kawakami, I., 2007. Potential of submarine-cave sediments and oxygen isotope composition of cavernicolous micro-bivalve as a late Holocene paleoenvironmental record. Global Planet. Change 55 (4), 301–316.

Labourdette, R., Lascu, I., Mylroie, J., Roth, M., 2007. Process-like modeling of flank-margin caves: from genesis to burial evolution. J. Sed. Res. 77, 965–979.

Land, L.S., Mackenzie, F.T., Gould, S.J., 1967. The Pleistocene history of Bermuda. Geol. Soc. Am. Bull. 78, 993–1006.

Lewis, R.D., Tichenor, H.R., 2008. Recent foraminifera at the platform margin, Doolittle's Grotto and Double Caves dive sites, San Salvador Island, Bahamas. Geol. Soc. Am. Abstr. Progr. 40 (4), 21.

Longly, G., 1986. The biota of the Edwards Aquifer and the implications for paleozoogeography. In: Abbott, P.L., Woodruff Jr., C.M. (Eds.), The Balcones Escarpment: Geology, Hydrology, Ecology and Social Development in Central Texas, pp. 51–54.

Lundberg, J., McFarlane, D., 2002. Isotope stage 11 sea level in the Netherlands Antilles. Geol. Soc. Am. Abstr. Progr. 9, 8.

Maddocks, R.F., Iliffe, T.M., 1986. Podocopid ostracoda of Bermudian caves. Stygologia 2 (1/2), 26–76.

McMurtry, G.M., Tappin, D.R., Sedwick, P.N., Wilkinson, I., Fietzke, J., Sellwood, B., 2007. Elevated marine deposits in Bermuda record a late Quaternary megatsunami. Sed. Geol. 200, 155–165.

McMurtry, G.M., Tappin, D.R., Sedwick, P.N., Wilkinson, I., Fietzke, J., Sellwood, B., 2008. Reply to "Mega-highstand or megatsunami? Discussion of McMurtry, et al (Elevated marine deposits in Bermuda record a late Quaternary megatsunami: Sed. Geol. 200 (2007) 155–165 by Paul J. Hearty and Stors L. Olson, Sedimentary Geology (2007) 155–165". Sed. Geol. 203, 313–319.

Mikhalevich, V.I., 1976. New data on the foraminifera of the groundwaters of Middle Asia. Intern. J. Speleol. 8, 167–175.

Millett, F.W., 1899. Report on the recent foraminifera of the Malay Archipelago collected by Mr. A. Durrand, F.R.M.S. J. Royal. Microscop. Soc..

Moolenbeek, R.G., Faber, M.J., Iliffe, T.M., 1988. Two new species of the genus Caecum (gastropoda) from marine caves on Bermuda. Studies in Honour of Dr. Pieter Wagenaar Hummelinck. 123, 209–216.

Moore, Y.H., Stoessell, R.K., Easley, D.H., 1992. Fresh-water/sea-water relationship within a groundwater system, northeastern coast of the Yucatan Peninsula. Ground Water 30, 343–350.

Montagu, G., 1803. Testacea Britannica, or Natural History of British Shells, Marine, Land, and Fresh-water, Including the Most Minute. J.S. Hollis, Romsey, England.

Mylroie, J.E., Carew, J.L., 1990. The flank margin model for dissolution cave development in carbonate platforms. Earth. Surf. Proc. Landf. 15 (5), 413–424.

Mylroie, J.E., Mylroie, J.R., Nelson, C.S., 2008. Flank margin cave development in telogenetic limestones of New Zealand. Acta Carsol. 37 (1), 15–40.

Novosel, M., Bakran-Petricioli, T., Požar-Domac, A., Kužić, P., Radić, I., 2002. The benthos of the northern part of the Velebit Channel (Adriatic Sea, Croatia). Natur. Croat. 2 (4), 387–409.

Olson, S.L., Hearty, P.J., 2009. A sustained +21 m sea-level highstand during MIS 11 (400 ka): direct fossil and sedimentary evidence from Bermuda. Quatern. Sci. Rev. 28, 271–285.

Patterson, R.T., Fishbein, E., 1989. Re-examination of the statistical methods used to determine the number of point counts needed for micropaleontological quantitative research. J. Paleontol. 63 (2), 245–248.

Pohlman, J.W., Iliffe, T.M., Cifuentes, L.A., 1997. A stable isotope study of organic cycling and the ecology of an anchialine cave ecosystem. Mar. Ecol. Prog. Ser. 155, 17–27.

Proctor, C.J., Smart, P.L., 1991. A dated cave sediment record of Pleistocene transgressions on Berry Head, Southwest England. J. Quat. Sci. 6 (3), 233–244.

Raynaud, D., Barnola, J.M., Souchez, R., Lorrain, R., Petit, J.R., Duval, P., Lipenkov, V.Y., 2005. The record for marine isotope stage 11. Nature 436 (7047), 39–40.

Rasmussen, K., Brett, C., 1985. Taphonomy of Holocene cryptic biota's from St. Croix, Virgin Islands: information loss and preservational biases. Geology 13, 551–553.

Reiswig, H.M., 1981. Particulate organic carbon of bottom boundary and submarine cavern waters of tropical coral reefs. Mar. Ecol. Prog. Ser. 5, 129–133.

Roberts, D.L., Jacobs, Z., Karkanas, P., Marean, C.W., 2007. Onshore expression of multiple orbitally driven Late Quaternary marine incursions on the ultra-stable southern South African coast. Quatern. Int. 167–168 (3) – 486.345.

Rohling, E.J., Grant, K., Hemleben, C., Hoogakker, B.A.A., Bolshaw, M., Kucera, M., 2008. High rates of sea-level rise during the last interglacial period. Nat. Geosci. 1, 38–42. doi:10.1038/ngeo.2007.28.

Roe, H.M., Patterson, R.T., 2006. Distribution of thecamoebians (testate amoebae) in small lakes and ponds, Barbados, West Indies. J. Foram. Res. 36 (2), 116–134.

Schneider, J.C., Kruse, S., 2003. A comparison of controls on freshwater lens morphology of small carbonate and siliciclastic islands: examples from barrier islands in Florida, USA. J. Hydro. 284, 253–269.

Scott, D.B., 1976. Brackish-water foraminifera from southern California and description of *Polysaccammina ipohalina* n. gen., n. sp. J. Foram. Res. 6, 312–321.

Scott, D.B., Medioli, F.S., 1978. Vertical zonations of marsh foraminifera as accurate indicators of former sea-levels. Nature 272 (5653), 528–531.

Scott, D.B., Medioli, F.S., 1980a. Quantitative studies of marsh foraminiferal distributions in Nova Scotia: implications for sea level studies. Cushman Foundation for Foraminiferal Research No. 17, 57 p.

Scott, D.B., Medioli, F.S., 1980b. Living vs. total foraminiferal populations: their relative usefulness in paleoecology. J. Paleont. 54, 814–831.

Scott, D.B., Williamson, M.A., Duffet, T.M., 1981. Marsh foraminifera of Prince Edward Island: their recent distribution and application for former sea level studies. Maritime Sed. Atlan. Geol. 17, 98–129.

Silén, L., Harmelin, 1976. *Haplopoma sciaphilum* sp.n., a cave-living bryozoan from the Skagerrak and the Mediterranean. Zoolog. Script. 5 (1–4), 61–66.

Sket, B., Iliffe, T.M., 1980. Cave fauna of Bermuda. Int. Rev. Gesam. Hydrobio. 65, 871–882.

Smart, P.L., Dawns, J.M., Whitaker, F., 1988. Carbonate dissolution in a modern mixing zone. Nature 335, 811–813.

Stock, J.A., Iliffe, T.M., Williams, D., 1986. The concept "anchialine" reconsidered. Stygologia 2 (1/2), 90–92.

Teeuw, R., Rust, D., Solana, A., Deweney, C., 2009. Large coastal landslides and tsunami hazard in the Caribbean. EOS 90 (10), 81–88.

Teeter, J.W., 1975. Distribution of Holocene marine Ostracoda from Belize. In: Wantland, K.F., Pusey, W.C. (Eds.), Carbonate Sediments, Clastic Sediments, and Ecology. AAPG Studies in Geology, vol. 2, pp. 400–499.

Vacher, H.L., 1988. Dupuit-Ghyben-Herzberg analysis of strip island lenses. Geol. Soc. Am. Bull. 100 (4), 580–591.

Vacher, H.L., Rowe, M.P., Garrett, P., 1989. The Geological Map of Bermuda. The Ministry of Works and Engineering, The Bermuda Government [map].

Vacher, H.L., Rowe, M.P., 1997. Geology and hydrogeology of Bermuda. In: Vacher, H.L., Quinn, T. (Eds.), Geology and Hydrogeology of Carbonate Islands: Developments in Sedimentology. Elsevier, pp. 35–90.

van Hengstum, P.J., Reinhardt, E.G., Beddows, P.A., Huang, R.J., Gabriel, J.J., 2008. Thecamoebians (testate amoebae) and foraminifera from three anchialine cenotes: low salinity faunal transitions (1.5–4.5 psu). J. Foram. Res. 38 (4), 305–317.

van Hengstum, P.J., Reinhardt, E.G., Beddows, P.A., Schwarcz, H.P., Gabriel, J.J., 2009. Foraminifera and testate amoebae (thecamoebians) in an anchialine cave: surface distributions from Aktun Ha (Carwash) cave system, Mexico. Limnol. Oceanogr. 54 (1), 391–396.

Van Morkhoven, F.P.C.M., 1963. Post-palaeozoic ostracoda: their morphology, taxonomy, and economic use, vol. 2. Elsevier, Amsterdam.

Ward, S.N., Day, S., 2001. Cumbre Vieja Volcano—potential collapse and tsunami at La Palma, Canary Islands. Geophys. Res. Lett. 28, 3397–3400.

Whitaker, F.F., Smart, P.L., 1990. Active circulation of saline ground waters in carbonate platforms: evidence from the Great Bahama Bank. Geology 18, 200–203.

Wilkinson, I.P., 2006. Foraminifera from the putative tsunami deposits at Castle Harbour, Bermuda. British Geological Survey Internal Report, IR/06/001R, 14 p.

Williamson, W.C., 1858. On Recent Foraminifera of Great Britain. Ray Society, London, England.