A NEW SPECIES OF BENTHIC FORAMINIFERA FROM AN INLAND BAHAMIAN CARBONATE MARSH

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ABSTRACT

A new benthic foraminifer, Helenina davescottensis nov. sp., is described from an oligohaline carbonate marsh (palustrine environment) located in a sinkhole on Grand Bahama Island, The Bahamas. The uppermost stratigraphy in the sinkhole is characterized by up to 260 cm of peat, which is overlain by 5–10 cm of carbonate sediment that contain Helenina davescottensis. Ontogenetic variability is illustrated with a full sequence of individuals from two chambers (proloculus + first chamber) through eight chambers. Chamber arrangement is planispiral evolute in juveniles that have fewer than three chambers, but arrangement changes to trochospiral evolute when the fourth chamber is added. Adults rarely exceeded 6–7 chambers and were never observed with more than 8 chambers. Supplementary apertures are common and diverse, and multichambered individuals typically achieve 100–200 μm in diameter. Helenina davescottensis was found co-occurring with other low-oligohaline microfossils (Jadammina macrescens, testate amoebae, charophytes, and hydroid gastropods), but not other common euryhaline hyaline foraminifera (e.g., H. anderseni, Ammonia tepida). Given the sinkhole stratigraphy, perhaps Helenina davescottensis was an early colonizer of a recently generated palustrine environment.

INTRODUCTION

The Bahamian archipelago is an extensive network of carbonate islands and shallow banks in the tropical North Atlantic Ocean that cover ~300,000 km² (Carew & Mylroie, 1997). The two largest carbonate banks in the northwestern Bahamas are the Little Bahama Bank and Great Bahama Bank, which remain separated from each other by the Northwest Providence Channel. Geophysical and subsurface-drilling surveys indicate that the shallow-water carbonates primarily comprising these banks likely began forming in the late Jurassic or early Cretaceous (Meyerhoff & Hatten, 1974; Sheridan et al., 1988; Melim & Masaferro, 1997), and they are now at least 5 km thick (Mullins & Lynts, 1977). The modern surficial geology of the northern Bahamas is characterized by large eolianite ridges (Kindler & Hearty, 1997), with abundant carbonate sediment production in the adjacent shallow marine environments (Neumann & Land, 1975; Milliman et al., 1993; Maloof & Grotzinger, 2012).

Extensive dissolution and modification of these ancestral carbonates over geologic time has created a mature karstified landscape in the Bahamas, which is characterized by abundant dissolution features such as karren, epikarst, sinkholes and blueholes, caves, and coastal biokarst (Cunliffe, 1985; Harris et al., 1995; Mylroie et al., 1995b; Walker et al., 2008). Deep, steep-walled sinkholes (Mylroie et al., 1995a) receive considerable attention for their preservation of Quaternary vertebrate fossils, Lucayan remains, and terrestrial paleoclimate records (Kjellmark, 1996; Steadman et al., 2007; Slayton, 2010), and they appear conspicuously on satellite imagery in both subaerial (e.g., 26.2176°N, 77.2104°W) and shallowly-submerged settings (e.g., 23.7804°N, 77.7195°W). From a hydrogeologic perspective, deep sinkholes and blue holes can permit observation of a complete groundwater profile, so they have been traditionally targeted to study the circulation and chemistry of subterranean aquifers (Moore et al., 1992; Whitaker & Smart, 1997).

Most ecosystem research in coastal karst basins (caves, sinkholes) is focused on the biology and biogeography of their endemic metazoans (Iliffe et al., 1983; Gonzalez et al., 2013; Jaume et al., 2013) and bacteria (Gonzalez et al., 2011), with considerably less attention devoted to understanding their protistan communities. However, diverse assemblages of benthic foraminifera and testate amoebae (i.e., thecamoebians) have been described in North Atlantic coastal karst basins (van Hengstum et al., 2008; 2009; van Hengstum & Scott, 2011). With the limited knowledge gained thus far from modern distributional studies, cave foraminifera and testate amoebae have been successfully used to reconstruct and evaluate groundwater circulation, salinity changes, and groundwater-level rise through the Holocene in response to sea-level and climate forcing (van Hengstum et al., 2010, 2011; van Hengstum & Scott, 2012; Collins et al., 2015). However, additional research on modern foraminiferal ecology and distributions in karst basins is needed to fully realize the potential of benthic foraminifera in this emerging capacity.

In addition to deep, flooded sinkholes, there are also shallow and inconspicuous sinkholes on the Bahamian subaerial landscape (e.g., 26.4913°N, 77.11384°W; 26.4431°N, 77.1236°W; or 26.4307°N, 77.1462°W). Some of these sites may have formed by dissolution during the Marine Isotope Stage 5e transgression (Harris et al., 1995), but others may be deep sinkholes that have become infilled with sediment. Despite their inland position, these shallow sinkholes may contain fresh to slightly brackish marsh environments, and they can be colonized by sawgrass, Rhizophora (mangrove), and even freshwater microbialites. In contrast to wetlands along the shoreline, the ocean does not regularly inundate these inland wetlands. Instead, they are ephemeral or perennially flooded by the uppermost sector of the local freshwater lens (or aquifer) in the topographic low on the antecedent karst topography (Gentry & Davis, 2006). Not surprisingly, peat deposits have been identified in successions recovered from...
Floridian (Lane et al., 2011), Bahamian (Kovacs et al., 2013), and Mexican sinkholes (Gabriel et al., 2009). However, the physical emplacement histories of these peat deposits are varied (detrital versus in situ origin), and not necessarily attributable to a paleo marsh or swamp environment. These inland marshes located within shallow Bahamian sinkholes could be categorized as interior marshes as described by Monty & Hardie (1976), but they can also be described as palustrine environments when local groundwater conditions promote abundant carbonate deposition (Alonso-Zarza & Wright, 2010). Since the absolute elevation of the groundwater itself is ultimately controlled by base-level change, these now partially-inundated sinkhole marshes represent just one type of environment that may (e.g., Gabriel et al., 2009), or may not (e.g., Alverez Zarikian et al., 2005), exist within a sinkhole basin during a transgressive or regressive cycle.

Here we describe Helenina davescottensis, a new species of benthic foraminifera from a shallow oligohaline sinkhole on Grand Bahama Island (26.606383° N, 78.406433° W). The sinkhole is located 650 m from the coastline, and it is currently occupied by a carbonate marsh habitat with a maximum water depth of 10 cm (Fig. 1). Extensively weathered relict speleothems are present on the northwest wall of the basin, which suggests the site was originally a cave that has experienced roof collapse.

METHODS

The shallow sinkhole was surveyed in June 2014 as a potential modern analog for an inland sinkhole that has recently been flooded by concomitant groundwater-level and sea-level rise. A staff was used to probe and examine sediment thickness and character in the sinkhole. Several short push cores (<30 cm) and surface samples were collected to examine microfossils in the upper sediment layers. Wet sediment samples and short push cores (<20 cm long) were transported back to the lab, wet sieved over a 45-μm mesh, and examined wet under a stereomicroscope. Microfossils were also examined in samples that were dried overnight, however, microfossils with fragile tests were poorly preserved after desiccation (e.g., Helenina davescottensis, testate amoebae). As such, microfossils were wet-picked, mounted and gold-sputter coated for scanning electron microscopy (SEM) on a desktop Hitachi TM3000 desktop SEM. No attempt was made to distinguish living from dead individuals.

RESULTS

The uppermost stratigraphy in the sinkhole is characterized by a peat deposit that passes into a thin veneer (<10 cm) of carbonate sediments. The subsurface peat deposit thickens from ~50 cm in the southeast to >260 cm in the northwest (Fig. 1). The uppermost sediment of the peat deposit contained no microfossils, which suggests a terrestrial or freshwater setting. The peat deposit was not subject to further analysis for this study. The laminated carbonate sediment is most likely derived from freshwater microbially, which are well known from the northern Bahamas (Monty, 1972; Monty & Hardie, 1976).
Previously, shallow (<2 m to littoral), freshwater wetlands characterized by carbonate deposition from calcium bicarbonate-saturated groundwater have been described as palustrine marshes or environments (Alonso-Zarza & Wright, 2010). Evidence of recurrent wetting and drying in palustrine environments is typically preserved in the subsurface stratigraphy as desiccation features (e.g., calcium carbonate crusts, mudcracks) or evidence of pedogenesis (Monty & Hardie, 1976, Alonso-Zarza & Wright, 2010). However, such features were only observed along the periphery of the sinkhole and not in the central regions. This perhaps indicates that the study site is perennally from the long-term inundation by the local groundwater, or sufficient regional precipitation prevents prolonged desiccation. Stratigraphic outcrops of Mesozoic palustrine environments also commonly contain gyrogonites from freshwater charophytes, rare freshwater ostracodes, and freshwater gastropods (Alonso-Zarza & Wright, 2010). The uppermost carbonate sediment in the Grand Bahamas study site also contains these microfossils, in addition to testate amoebae [e.g., Centropyxis aculeata (Ehrenberg), Centropyxis constricta (Ehrenberg)] and a previously unknown benthic foraminifer (Fig. 2) that we describe in detail below (Fig. 3).

SYSTEMATICS

Order ROTALIIDA Lankester, 1885
Superfamily DISCORBACEA Ehrenberg, 1838
Family ROTALIILLIDAE Loeblich & Tappan, 1964
Genus Helenina (Saunders, 1961)
Helenina davescottensis nov. sp.

Description. Test is hyaline-calcareous, translucent, free, perforate, and globular with a roughly biconvex appearance in the adult (Fig. 2). Chamber arrangement is planispiral evolute from the proloculus until addition of the third chamber; thereafter chamber arrangement becomes generally trochospiral evolute. The primary aperture in adults is an interiomarginal opening with a distinctive lip, but the primary aperture in juveniles (<4 chambers) is more slit-like. Previous apertures remain open on both the dorsal and ventral side from the evolute chamber arrangement (i.e., relict supplementary apertures), and this creates salient circular to globular openings into the test. After addition of the fifth chamber, additional supplementary apertures with a simple flap-like apertural modification (arrows on Figs. 2.19, 2.23, 2.24) can be present on the periphery of adult tests (six to eight chambers). The initiation of the shift to the trochospiral evolute arrangement varied between the 4th to 6th chambers, and this characteristic promoted some variability in the external shape. The type population was comprised of individuals that were primarily 4–6 chambers in size, and individuals achieving 7–8 chambers were rarely observed.


Etymology. To honor the extensive contributions by Dr. David B. Scott (Professor Marine Geology and Micropaleontology, Dalhousie University, Canada) to our understanding of marsh foraminifera.

Holotype. A specimen that is morphologically identical to Figure 2.18 was designated, and archived in the Cushman Collection at the Smithsonian Institution (USNM number: 616980).

Paratypes. Archived in the Cushman Collection at the Smithsonian Institution (USNM number: 616981–616984).

Distribution. In addition to the modern population at the type locality on Grand Bahamas, the new species is also present in Torreblanca Marsh in Spain (see discussion). Subfossil H. davescottensis have also been recovered from ~1.25 m below the sediment-water interface from sediment cores extracted from No Man’s Land, which is also a sinkhole basin on Abaco Island (26.5924’N, 77.2797’W) in the northern Bahamas. The occurrence of H. davescottensis in No Man’s Land is at a lithologic contact between peat and carbonate mud, which is similar to the type locality. Details on this occurrence will be discussed elsewhere.

DISCUSSION AND CONCLUSIONS

Outside of the Bahamas, the other known occurrence of this species is in the brackish Torreblanca Marsh (40.1811’N, 0.1973’W) in eastern Spain on the Mediterranean coast (Guillem, 2007), where it co-occurs with other brackish foraminifera [e.g., Trichohyalus aguayoi (Bermúdez)]. The individuals from both the Grand Bahamas study site and Torreblanca Marsh are small, typically fewer than eight chambers, and evolve throughout ontogeny. Guillem (2007) placed his individuals within “Discorbis” bulbosus (Parker, 1954) based on similarity to individuals (as Discorbis bulbosus) in Loeblich & Tappan (1987, p. 557, figs. 10–11). This was a tentative placement, however, as Guillem (2007) did note that the aperture differed between the individuals observed in Torreblanca Marsh and those imaged by Loeblich & Tappan. Parker (1954) imaged the coiling pattern of “Discorbis” bulbosa (pl. 8, figs. 10–12) as trochospiral, with an evolute dorsal side and an involute ventral side. In contrast, the individuals from Torreblanca Marsh (Guillem, 2007, pl. 13, figs. 1–6) and from the Grand Bahamas, are evolute on both the dorsal and ventral sides. The new species in question (Fig. 2) also attains fewer chambers than “Discorbis” bulbosa, which Parker (1954) describes as having 8–12 chambers, yet Helenina davescottensis from the Grand Bahamas was never observed with more than eight chambers. In addition, “Discorbis” bulbosa was never described with supplementary apertures or the salient relict apertures on the dorsal and ventral surface. Therefore, the “Discorbis” bulbosa described by Parker (1954) is unique, and we consider the individuals described by Guillem (2007) as conspecific with Helenina davescottensis described here.

Several taxonomic characteristics differentiate Helenina anderseni (Warren, 1957) from H. davescottensis. In Loeblich & Tappan (1964, p. C580), H. anderseni is described as involute on the umbilical side and evolute on the dorsal side, with the final chamber of H. anderseni...
FIGURE 2. *Helenina davescottensis* nov. sp. ontogenetic series. 1–4 Proloculus and first chamber. 5–6 Three chambers, ventral view. 7–8 Three chambers, dorsal view. 9 Four chambers, dorsal view. 10 Four chambers, ventral view with large apertural flap. 11 Four chambers, dorsal view with apertures from second and fourth chambers visible. 12 Four chambers, side view emphasizing initiation of trochospiral chamber arrangement. 13 Five chambers, dorsal view. 14 Five chambers, side view with trochospiral character. 15 Five chambers, ventral view with apertures from previous chambers open. 16 Five chambers, side view. 17 Five chambers, dorsal view. 18–21 Six chambers, dorsal view. 22 Six chambers, ventral and side view to emphasize slight trochospiral character and open apertures of previous chambers. 23 Seven chambered individual with wide apertural opening and two supplemental apertures. 24 Eight chambers, but note the inconsistency in the trochospiral coiling in the seventh and eighth chamber to give an almost planispiral appearance. Arrows point to supplementary apertures (19, 23). All specimens are sized proportionally to the scale bars that are located in the corners.
extending over and covering the umbilical region (see figs. 1C, 3C, 4C in Gennari et al., 2011). In contrast, the flap-like apertural modification in H. davescottensis does partially extend over the umbilical area, just not sufficiently to make the umbilical region involute (Fig. 2.10, 2.15). As such, the chamber arrangement of H. davescottensis is more evolute throughout ontogeny (Fig. 2), and does not achieve a completely involute stage on the umbilical side.

The different primary-aperture morphology and supplementary apertures between the two species are also taxonomically significant. First, the interomarginal aperture of H. anderseni extends across the peripheral margin and onto the dorsal side and ventral side where it follows the suture line to create a crescentic to sinuate, slit-like opening into the test. In contrast, additional globular chambers are added in H. davescottensis such that openings on the dorsal side of the test are circular (not sinuate). Even juvenile individuals of H. anderseni retain elongated to sinuate openings on the dorsal surface (see fig. 5 in Gennari et al., 2011), as described for the adults by Loeblich & Tappan (1964). Secondly, H. davescottensis has supplementary apertures on the periphery of final chambers (e.g., Figs. 2.19, 2.24), which to our knowledge, have not been described for H. anderseni. The total number of chambers also differentiates the two species: H. davescottensis typically achieved only 6–7 chambers in the thousands of individuals observed from the type locality, whereas H. anderseni commonly exceeds ten (e.g., Gennari et al., 2011). Given the taxonomically important features described above, H. davescottensis warrants designation as a new species of foraminifera.

A reasonable question is whether our multiple geographic observations of H. davescottensis are simply aberrant tests of some other previously described species living in the northern Bahamas, given that benthic foraminifera typically develop test abnormalities in stressed environments such as those with low salinity. However, when foraminifera with test anomalies are encountered, they are typically co-observed with individuals exhibiting a normal external morphology within a pre-existing species concept, even in sinkholes (van Hengstum et al., 2008). No other hyaline foraminifera were observed at the study site and H. davescottensis is characterized by a predictable and repetitive morphology. This is in contrast with the random external morphologies of abnormal foraminiferal tests. It should also be noted that H. anderseni was not observed cohabiting the other localities where H. davescottensis has been observed (Torreblanca Marsh in Spain, and No Man’s Land on Abaco Island), which would be expected if the new species described here (H. davescottensis) represented an aberrant morphology of H. anderseni. Furthermore, the observation of H. davescottensis on either side of the North Atlantic in a similar environment (i.e., a marsh habitat flooded by groundwater) does suggest a stabilized phenotype. It remains possible that a microspheric versus

\begin{figure}[h]
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\caption{Other co-occurring microfossils. 1 Centropyxis aculeata var. spinosa. 2-3 Centropyxis constricta var. spinosa. 4 Centropyxis constricta var. aerophila. 5 Jadammina macrescens. 6-7 gyrogonites from charophytes. 8 Hydrobia sp. A scale bar is provided for each microfossil group.}
\end{figure}
megalouspheric relationship (i.e., schizont-gamont dimorphism) may yet be determined between these two different species of Helenina. However, it remains prudent to taxonomically differentiate these individuals for their potential value in reconstructing paleoenvironmental conditions in karst basins until further culturing or molecular systematics work can confidently resolve these issues.

Other small rotalids share some characteristics with Helenina davescottensis, but its unique chamber arrangement, supplementary apertures, and aperture structure warrant its designation as a new species. Ammonia tepida (Cushman) is another euryhaline benthic foraminifer that occurs in Caribbean inland sinkholes (van Hengstum et al., 2008). However, even by addition of the third and fourth chamber, the interiormarginal aperture of Ammonia tepida is not covered by a flap-like projection like that of H. davescottensis, and A. tepida does not have supplementary apertures on the dorsal side like H. davescottensis.

Nonionella is another common coastal genus that is partially evolute on the spiral side, but this taxon is involute on the umbilical side, and lacks an apertural lip. Metarotaliella simplex (Grell, 1979) is another small rotalid from marsh-like brackish habitats on carbonate platforms that can easily be confused with H. davescottensis, but the different coiling pattern and grooved umbilical surface in M. simplex clearly differentiates the two. Given the test characteristics of H. davescottensis (e.g., small, thin and fragile, often destroyed through desiccation) and abundance in typically under-sampled environments, we suggest that H. davescottensis has been previously overlooked or that rare individuals have been designated as juveniles of more ubiquitous coastal taxa.

The other common smaller benthic foraminifer that occurs in both carbonate sinkholes and caves in Torreblanca Marsh, Spain, is Paraphysalidida paralica (Guillem & Usera, 2012). Paraphysalidida paralica is a small, 3-chambered benthic foraminifer that inhabits oligohaline to mesohaline (1.5–18) conditions, in both modern and fossil settings (Guillem, 2007; Gabriel et al., 2009; Blázquez & Usera, 2010; van Hengstum et al., 2010; and Collins et al., 2015 as Physalidida simplex). It was first observed widely in Torreblanca Marsh, Spain, but has since been observed in Mexican (Yucatan) and Bermudian coastal karst basins. Guillem & Usera (2012) erected the new genus and species because the original hand-drawn holotype of Physalidida simplex Heron-Allen & Earland, which can be viewed in the Ellis and Messina Catalog, is morphologically very different from the individual subsequently imaged by Loeblich and Tappan (1964, 1987). The type locality of Physalidida simplex Heron-Allen & Earland is a shallow marine lagoon in the Pacific Ocean, which has very different environmental conditions from the brackish groundwater habitats where Paraphysalidida paralica is abundant. As such, it is surprising that P. paralica was not observed in the study site, given that P. paralica commonly occurs in oligohaline tropical environments inundated by groundwater. Some still question whether P. paralica represents a juvenile of some pre-existing euryhaline foraminifera. However, Guillem & Usera (2012) clearly imaged a cylindrical or tubular canal between the 2nd and 3rd chamber, a taxonomically significant feature that is not observed in other common euryhaline foraminifera such as Ammonia tepida, H. anderseni, or the new H. davescottensis described here (Fig. 2).

Ecologically, the other microfossils associated with H. davescottensis in the carbonate marsh suggest that this site remains within the low oligohaline salinity range (0.5–3.5). However, the absence of other euryhaline foraminifera suggests stressful environmental conditions for these taxa. Although no viability indicator was employed, the ubiquitous presence of H. davescottensis suggests that this species lives in these marsh conditions for at least part of a given year. The only other benthic foraminifer observed at the study site was the rare occurrence of Jadamina macrescens (Brady) (Fig. 3.5). This is somewhat curious considering other euryhaline foraminifera [e.g., Ammonia tepida Cushman, Trichohauly alus aguoyi (Bermudez), Tiphotrocha compromitata (Cushman & Brönnimann), Trochammina inflata (Montagu)] are widely observed in brackish tropical and subtropical sinkholes, caves, mangroves, and ponds (Avanzini & Scott, 2003; Roe & Patterson, 2006, van Hengstum et al., 2008; van Hengstum & Scott, 2011). In our samples, three species (or formae) of testate amoebae (i.e., thecamoebians) were observed, all within the same genus: Centropyxis aculeata (Ehrenberg) var. spinosa (Fig. 3A), Centropyxis constricta (Ehrenberg) var. spinosa (Figs. 3B, 3C), and Centropyxis constricta (Ehrenberg) var. aerophila (Fig. 3D). These thecamoebians have been previously observed in Mexican oligohaline sinkholes, but only in sinkholes that are flooded by groundwater with a salinity of less than ~3.5 (van Hengstum et al., 2008). Also observed were gyrogonites from charophytes, which are non-marine green algae (Figs. 3F, 3G: Garcia, 1994), and the cosmopolitan freshwater gastropod Hydrobia (Fig. 3H).

The occurrence of H. davescottensis could potentially be linked to groundwater conditions, or to an oligohaline carbonate marsh environment. The fact that H. davescottensis was recovered from a sinkhole may only be happenstance, as carbonate marshes need not be confined to a sinkhole basin and typically occur over wider geographic areas. In Spain, the Torreblanca Marsh is constructed upon a Pliocene and Quaternary-aged sedimentary infill, and its hydrology is linked to the Opressa Plain coastal aquifer (Giménez & Morell, 1997). In 1993, the annual temperature, salinity, and pH variability at several locations in Torreblanca Marsh had a range of 10–30°C, 6.6–13.4 psu, and an average pH of 7.5–8.1, respectively (Guillem, 2007, p. 76–80). This is slightly higher salinity than in the Grand Bahamas, but both locales are influenced by groundwater. Lastly, these results suggest that tropical sinkholes with carbonate marshes may provide a modern analog for ancient palustrine outcrops. Additional analysis will be required, however, to answer some of the ecological, environmental and taxonomic questions not resolved here.

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REFERENCES


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