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MODERN AND FOSSIL CALLIANASSID BURROWS OF THE BAHAMAS: COMPARISONS AND IMPLICATIONS FOR PALEOENVIRONMENTAL ANALYSIS

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ABSTRACT. Deep-burrowing callianassid shrimp are common and dominant as bioturbators in modern intertidal to shallow subtidal, sandy carbonate substrates of the Bahama Archipelago, wider Caribbean, and beyond. Likewise, *Ophiomorpha*, the distinctive, three-dimensional, branched, and lined burrow with pelleted exterior walls attributed to the burrowing activities of callianassids is the most common trace fossil found in Pleistocene subtidal grainstones throughout the Bahamas.

Polyester-resin casts were made of callianassid burrows from three different shallow-marine settings around San Salvador Island in order to determine burrow system architectures for comparison with *Ophiomorpha* from subtidal Pleistocene deposits throughout the Bahamas and elsewhere. At Graham's Harbour, on the island's north coast, subtidal, heavily burrowed, open-sand areas are interspersed with thick *Thalassia* seagrass beds. Casts taken here revealed complex, overall U-shaped burrows with tiered, branching pouch-like structures, numerous nodes, and occasional loops. The burrow maker has been identified as *Neocallichirus maryae.*

Our intertidal site was on the large, muddy-sand flats that border parts of Pigeon Creek lagoon on the southeast coast of San Salvador. Here mounded topography is generated by the deep-burrowing callianassid, *Glypturus acanthochirus.* Burrow casts have a complex, downward spiraling form that is highly distinctive. Our second subtidal site was in Long Bay on the island's west coast. This site generally experiences somewhat greater wave energy than normally present in Graham's Harbour and grass beds are absent. Burrow casting efforts were less successful here, but shallow excavations uncovered the upper parts of burrow shaft and tunnel systems that revealed a different architecture from those at the other two sites and are similar in size and form to at least some Pleistocene *Ophiomorpha* specimens.

The architecture of modern callianassid burrows is species specific, but comparisons of modern burrow systems with potential fossil counterparts are hampered by lack of full knowledge of the modern burrows and of identification of their tracemaker species. Distal structures of *Ophiomorpha* found at localities on Harry Cay, Little Exuma; Devil's Point, Great Inagua; and Rum Cay reveal complex burrow forms different from those of *Neocallichirus maryae* and *Glypturus acanthochirus.* Successful casts of modern callianassids in Long Bay may reveal the presence of similar basal structures, thus establishing a match. Further progress in matching modern and fossil callianassid burrow architectures will significantly improve understanding of the infaunal dynamics of modern tropical, shallow-subtidal environments and will provide better means to differentiate the paleoenvironmental settings of ancient tropical shallow-subtidal carbonates.

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INTRODUCTION

Snorkelers and scuba divers exploring the shallow marine waters and all-carbonate sedimentary environments around San Salvador and other islands of the Bahama Archipelago almost always encounter sandy-bottom areas with numerous burrow openings of various sizes, ranging up to about 4 cm in diameter. Some areas are dominated by conical mounds, each with a small opening at the top, and adjacent funnel-shaped depressions with larger burrow openings.

These areas commonly are near seagrass beds dominated by turtle grass (*Thalassia testudinum*). Along protected, mangrove-fringed coastal areas such as those bordering Pigeon Creek lagoon on San Salvador, large sand mounds of coalesced cones surrounded by funnel-shaped depressions with basal openings are exposed at low tide. Other bare-sand areas on the shallow offshore shelves of the islands, commonly in close proximity to coral patch reefs also can exhibit numerous fairly large burrow openings.

These cones, mounds, funnel-shaped depressions, and large burrow openings all are the products of ghost shrimps of the Family Callianassidae (Arthropoda: Malacostraca: Decapoda: Axiidea). Formerly this family was assigned to the Infraorder Thalassinidea, but recent phylogenetic research indicates that this taxon actually represents two distinct lineages, so assignment of the family to the Infraorder Axiidea now is preferred (see Dworschak et al., 2012, for a current systematics review; "thalassinideans" remains useful as a broad reference term). Callianassids are primarily burrowers in marine sediments and have global distribution except for the polar seas. They achieve greatest diversity in shallow subtidal settings of the tropics, with species occurrence numbers decreasing toward the poles (Dworschak, 2000, 2005). At present more than 200 species of callianassids have been identified in the scientific literature (Dworschak, 2005, and pers. comm., 2010). The most recent and comprehensive review of callianassid biology, including ecology and ethology, is by Dworschak et al. (2012).

Callianassids are fossorial in that they spend their entire lives in complex, deep (up to ~2 m), and extensive burrow systems. In the tropics, they can occur in high densities and are a powerful agent of bioturbation within sandy substrates. Their ability to create a mounded topography, such as along intertidal reaches of the margins of Pigeon Creek on San Salvador, qualifies them as true "ecosystem engineers" (Curran and Martin, 2003), capable of influencing "the whole sedimentology

and geochemistry of the seabed" (Dworschak, 2004). Examples of prodigious bioturbation by callianassids in tropical, all-carbonate settings were provided by Tudhope and Scoffin (1984, Great Barrier Reef area, Australia), Tedesco and Wanless (1991, South Florida and Caicos Platform), and Curran (2007, Bahamas).

The fossilized burrows of callianassids are most commonly assigned to the ichnogenus *Ophiomorpha*, characterized by three-dimensional branching and thick walls that are smooth on the inside and mammillated on the exterior by discoid to ovoid pellets generated by the shrimp in construction of their complex burrow systems. *Ophiomorpha* is the dominant trace fossil in late Pleistocene (MIS 5e) shallow subtidal grainstones or calcarenites throughout the Bahama Archipelago, and its presence can create a distinctive ichnofabric that commonly reaches maximum level on the Droser-Bottjer Ichnofabric Index scale (Droser and Bottjer, 1989; Knaust et al., 2012, Fig. 10).

The present study was designed to investigate the distribution of modern callianassids around the island of San Salvador. Our goal was to make complete representative casts of the callianassids present at the three study sites and to capture specimens at each site for species identification. The overall architecture of a well-formed callianassid burrow system has been demonstrated to be species specific (Suchanek, 1985, and later studies), so with knowledge of the characteristics of a given modern burrow system and its tracemaker identified, our hypothesis is that it then should be possible to match late Pleistocene *Ophiomorpha* burrows with their modern counterparts. If this can be accomplished, the value of a given *Ophiomorpha* occurrence for paleoenvironmental interpretation would be significantly enhanced. Of course, this goal is much easier stated than achieved. At this point, we have had only partial success, as reported here. More work needs to be done to completely fulfill our goal, but the initial findings are promising, and
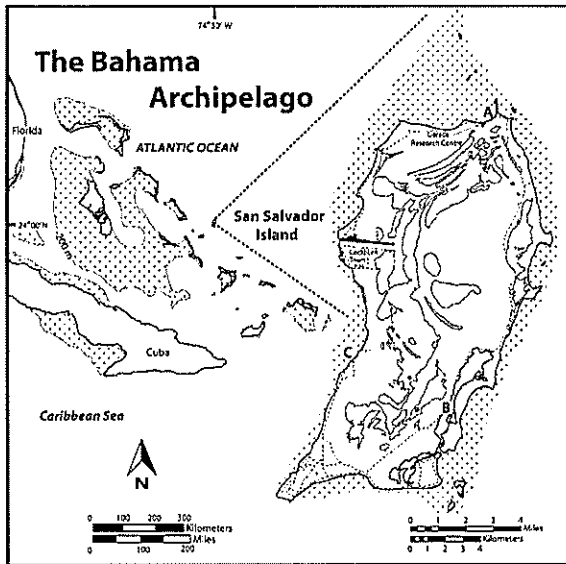
Figure 1. Index map to the Bahama Archipelago, San Salvador, and the callianassid burrows study sites: A – Graham's Harbour; B – Pigeon Creek; C – Long Bay.

we hope to be able to continue this line of research to completion in the future.

STUDY SITES AND SETTINGS

Three sites in significantly different settings around the periphery of San Salvador were selected for study of modern callianassid burrows (Figure 1) and are described below.

Graham's Harbour

Located off the north coast of San Salvador, Graham's Harbour is a large, high-energy, windward lagoon bounded to the northeast by North Point, to the north by Gaulin's bank-barrier coral reef and offshore cays, and largely open to the west. The Holocene history of the lagoon and its sediment facies were documented by Colby and Boardman (1989). A more detailed sediment distribution study by Randazzo and Baisley (1995) revealed the presence of three ecologic zones in the southeastern part of Graham's Harbour. Although not shown on their maps, our study area would be in the nearshore, Sparsely Vegetated Zone of
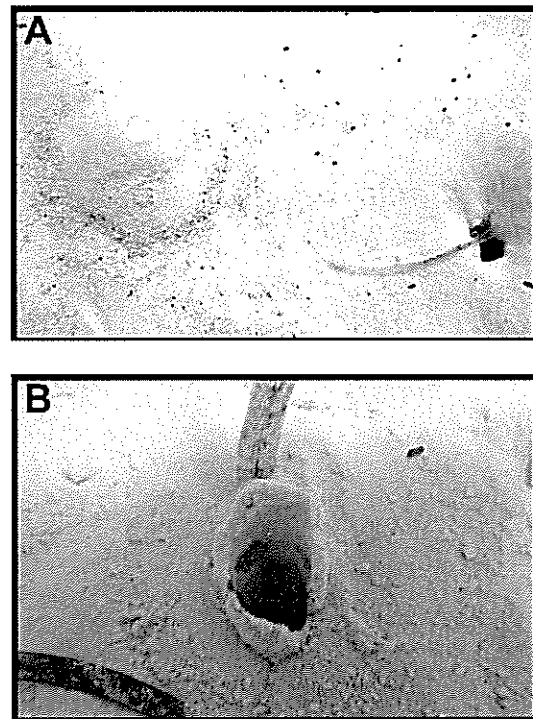

Figure 2. Surface characteristics of callianassid burrows found in shallow water at Site A in Graham's Harbour: A) Callianassid burrow cone (excurrent flow) and adjacent funnel (incurrent flow, burrow diameter ~ 2.5 cm) at about 2 m water depth; dark specks at upper right are callianassid fecal pellets. B) Top part of a callianassid burrow wall exposed by wave current erosion and diver-hand excavation. Outside diameter of burrow is 3 cm; note the presence of Thalassia testudinum seagrass leaves and a single callianassid fecal pellet in upper right of photo.

Randazzo and Baisley, characterized by well sorted, medium-grained sand with dominantly aggregate and skeletal grains and a lesser percentage of non-skeletal grains.

Our Site A is located just a short distance offshore from the Gerace Research Centre (GRC) beach, across the road and opposite the second full-sized telephone pole east of the GRC Main Laboratory building. A narrow path leads to the beach, and our staging area was a short distance to the east on rocks just above the high tide line

Figure 3. Characteristic mounded topography produced by the deep-burrowing callianassid, Glypturus acanthochirus, *along the wide intertidal carbonate-sand flats bordering parts of Pigeon Creek lagoon. Mounds here commonly have widths of 1+ m and lengths of coalesced mounds can be up to several meters.*

(Figure 1; N24°07.201', W74°27.747'). Offshore and just beyond seaward dipping beachrock, a clean sandy bottom is present going out for several 10s of meters before thick beds of seagrass (dominantly turtlegrass, *Thalassia testudinum*) are encountered (see profile showing surface and subsurface relationships across this area by Curran, 1997, Ichno-locality-2, his Figure 1). Callianassid burrows begin to appear a short distance seaward of the low tide line. The callianassids living here have complex, U-shaped burrows (to be discussed in detail later), and form a sediment cone ("volcano") at the excurrent end; the incurrent flow commonly is via a funnel-like depression with an opening of ~2 to 4 cm (Figure 2A).

Water depths are shallow, up to ~3 m depending on the level of the tide (semi-diurnal with a range of ~0.75 to 1 m). The density of burrows increases offshore to the edge of the seagrass beds; our burrow casting was done in the sandy bottom area about 30 to 50 m offshore. Some callianassids burrow within the grass beds, but their burrow openings are hard to isolate, so such areas are unfavorable for initial investigation. The appearance of the sandy bottom at this site is highly variable. If recent storms have not scoured the bottom, it will exhibit mound and crater topography owing to the cumulative burrowing activity of the callianassids. If soon after a storm, only new, small cones will be present, and the incurrent openings will be near level with the plane of the bottom. Callianassid burrows are lined by the shrimps, which form a firm burrow wall consisting of a mixture of fine sand, mud, and organic material. With some scouring, the burrow walls can be seen around openings and commonly will stand up in partial relief (Figure 2B). Occasionally one will see a shrimp at the incurrent opening to its burrow, but callianassids are fossorial and presumably do not leave their burrows willingly.

Pigeon Creek

Site B (Figure 1; N23°59.131', W74°29.101') is located on the western edge of the northern part of the Pigeon Creek tidal lagoon, on a large intertidal sand flat fringed on the landward side by red mangroves (*Rhizophora mangle*). The sand flat is close to the Queen's Highway and a short distance north of the abandoned houses marked as "Old Place Settlement" on the Bahamas Land and Surveys topographic map (1972). At low tide, the distinctly mounded topography of the flat is revealed (Figure 3). These mounds are the result of deep-burrowing activity of the callianassid *Glypturus acanthochirus*, and the microbial mat-stabilized mounds support a diverse community of shallow-tier burrows (Curran, 1997, Ichno-locality 5; Curran and Martin, 2003).

The sedimentology of Pigeon Creek was described in detail by Mitchell (1987) and Cummins et al. (1995), who also included analysis of molluscan taphonomy. Mitchell (1987) defined 12 lithofacies within Pigeon Creek based on mean grain size and dominant grain morphotypes. The Site B sand flat is within Mitchell's *Halimeda*-sand lithofacies. Although the Cummins et al. (1995) study did not extend to the Creek's north arm, the

sediments of our study area would fall within their *Halimeda*-rich 'packstone' facies.

Tide range in Pigeon Creek is variable and up to about 0.75 m depending on precise location, and the best time to visit this study site is at full low tide when the callianassid mounds are fully exposed. There is a tide lag in Pigeon Creek, and in our experience the mounds do not become well exposed until at least 45 minutes to as much as two hours or more past the predicted low tide time for San Salvador. On any given day, if wind conditions or other factors hold tide waters in, the mounds may not emerge much at all. Surfaces of the large mounds are generally firm, with the low areas in between much softer and occupied by a thin cover of turtle grass (*Thalassia testudinum*) and the large incurrent, funnel-shaped burrow openings of callianassids.

Long Bay

Site C (Figure 1; N24°00.493', W74°31.831') is located offshore of the beach at Long Bay. Here sediments of the lower foreshore and shallow offshore consist of clean, well sorted, fine skeletal and peloidal sand (Clark et al., 1989). The shallow offshore area also is devoid of seagrass beds and typically displays ripple marks and small sand waves as well as numerous openings of burrows formed by callianassids. These circular burrow openings range from 3-4 mm up to 2-3 cm in diameter, depending on whether or not the very top part of the burrow is intact or has been eroded away. A complete callianassid burrow normally will be constricted at its opening, whereas if eroded, the full diameter of the burrow will be exposed, including parts of the burrow-wall lining. This lining is typically darker in color owing to the presence of organic matter incorporated into it by the shrimp during burrow construction. Our burrow-casting area was between 20 to 30 m offshore at low tide in clear water of about 2 m depth. Here large burrow openings were common.

METHODS

A prime objective of this study was to make sets of complete resin casts of callianassid burrows from each of the three study sites. We used Hi-Bond boatyard polyester resin as our casting medium. This material is denser than seawater, so it will flow to the deepest parts of burrow systems, and it has been used successfully for casting burrows in subtidal or otherwise wet conditions for some time (Shinn, 1968; Atkinson and Chapman, 1984). This resin and accompanying hardener is relatively inexpensive and widely available.

At our shallow subtidal sites (A & C), casting was a two-person operation requiring a scuba diver to do the actual casting and a snorkeler to assist as needed. After establishing a suitable staging area well above the high tide line for all needed gear, we scouted the seafloor directly offshore for an area where burrow openings were common. Once identified, the casting area was marked with a well-anchored float. Care was taken to ensure that the anchor weight for the float was sufficient to hold position and that the line had enough slack so that the float would not be lifted and moved with high tide. The prospective open burrows for casting were then selected and marked. We used flagging tape wrapped around pieces of beachrock to mark burrows for casting; numbers can be written on the tape with a waterproof marker as needed.

Once all is ready for casting, resin was mixed with hardener at the staging area on the beach. We used a plastic pitcher with a handle and spout as our resin container, and we mixed only 50% of the recommended hardener amount per volume (1 oz. hardener per 1 gal. of resin recommended; we mixed about ½ gallon batches and used ¼ oz. of hardener per batch). This slows the hardening process and allows more time for the diver to find burrows and pour resin into them. We allowed at least 24 hrs. for hardening prior to excavation of casts. The diver must be set to go as the assistant mixes resin and hardener; upon

entering the water, the diver has about 20 minutes to complete cast-pouring operations. Obviously some trial and error is involved; typically we could pour 5 to 10 burrows per casting dive.

The next step is burrow cast excavation, and for this operation we used an airlift attached to a scuba tank (Figure 4A). The airlift consists of a PVC pipe with a 6 cm inner diameter fitted with a connector for a scuba tank. Excavation of a complete burrow cast is a real challenge because callianassid burrows can go deep, over 0.5 m. Digging by hand also is required, and the whole process can take over an hour for a single burrow excavation. Nonetheless, the effort is worth it, as
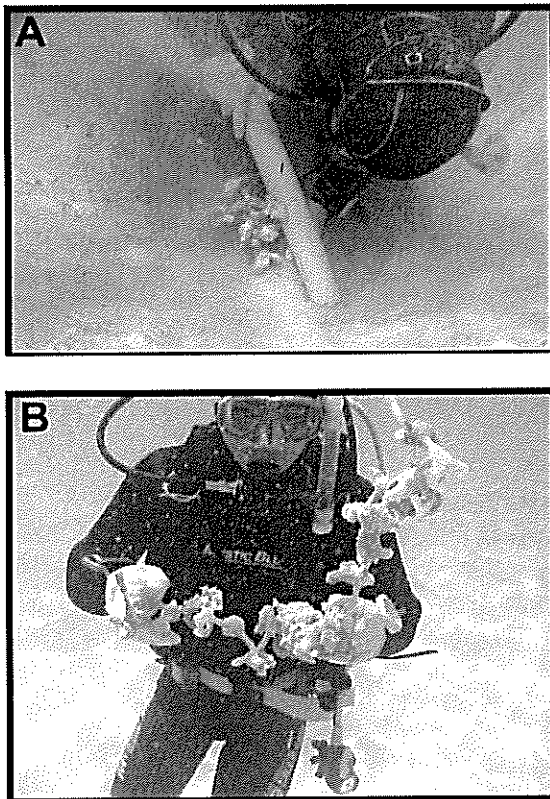

Figure 4. Underwater casting activity and casts from the Graham's Harbour site: A) Diver Koji Seike excavating a burrow cast using an airlift attached to a scuba tank; note top of cast to left of the airlift tube. Cloudy background is from excavated sediment suspended in the water column. B) Koji with the large, near-complete callianassid burrow cast shown in Figure 6A.

large, near-complete casts can be obtained (Figure 4B).

The biggest casting problem is poor resin penetration into the burrow. A burrow may appear fresh and with a clean burrow opening, but it is virtually impossible to know if any given burrow is blocked at depth by sediment, seagrass leaves, or a combination of the two. This can be frustrating and wasteful because all too commonly casting appears to be going well, when in fact, the burrow blocked at depth. Failed casts do not reveal much about true burrow form (Figure 5), and valuable time and resin have been lost. If a method for cleaning burrows prior to resin pouring could be devised, perhaps the problem of blocked burrows could be solved or at least reduced.

A second problem is offshore wave action. When working in the shallow offshore, even relatively small waves (sub-whitecap wave heights) can inhibit operations, owing to both lowered visibility and difficulty of holding position. Although the weather was generally fine in early February 2011 when this study was conducted, it was windy, and offshore conditions were often less than ideal, so our overall yield of burrow casts was less than what we had hoped it would be.

Another goal of our study was to capture callianassids for taxonomic identification. These shrimp are notoriously difficult to catch given their deep-burrowing capabilities and quickness of movement. We used a stainless steel "yabby" pump (or bait pump) designed and manufactured in Australia. "Yabby" is the slang Australian term for callianassids. In Australia, yabbies are caught in coastal areas and used for fish bait. Our pump was made by Alvey fishing supplies company. For the do-it-yourselfer, instructions are available over the internet for making "yabby" pumps from PVC pipe. We were successful in capturing callianassids in two of our three study areas (no catch in Long Bay). Species identifications of our harvested specimens were made from close-up images of the specimens by Dr. Peter Dworschak, Natural History Museum, Vienna, Austria.

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Locality & Setting	Surface Expression of Burrows	Burrow Cast Form	Probable Burrow Maker	Probable Feeding Mode
Graham's Harbour (shallow subtidal) (see Figs. 2, 4, 5, & 6)	Two burrow openings; conical sediment mounds with small excurrent openings and adjacent funnel-shaped depressions with large incurrent openings.	Near-complete burrow casts have broad U-shape; incurrent shaft leads to tiered, branching pouch-like structures; base of U has complex arrangement of burrow nodes and loops; shaft to excurrent opening incomplete.	*Neocallichirus maryae* (*N. cacahuate* also present; no burrow casts yet)	Deposit feeding with likely use of seagrass blades.
Pigeon Creek (intertidal to shallow subtidal) (see Figs. 3, 7)	Two burrow openings; large, coalesced mounds stabilized by microbial mats with adjacent large funnel-shaped depressions and large incurrent openings.	Burrow casts have complex spiral shaft from incurrent opening with branching to short, blunt-ended tunnels; simpler connecting shaft to excurrent opening not well recorded.	*Glypterus acanthochirus* (*Neocallichirus grandimana* also present; no burrow casts yet)	Deposit feeding with significant use of organic matter indirectly derived from microbial mats on mound surfaces.
Long Bay (shallow subtidal) (see Fig. 8)	Single small burrow openings with small sediment cones in fair weather; burrow openings enlarged after wave-generated erosion events remove burrow tops.	No casts; form not fully known, appears to be shaft and tunnel dominated.	Unknown	Presumed deposit feeding.

Table 1. *Settings and characteristics of callianassids and their burrows around San Salvador Island, Bahamas.*

BURROW CASTING RESULTS AND DISCUSSION

Our overall goal was to obtain complete casts of callianassid burrows from each of our three study sites for comparison of modern burrow architectures with those of fossil forms previously illustrated and described and in the literature. Although the casting difficulties and weather problems mentioned above did not allow us to obtain as many complete casts as we had hoped, we were able to obtain meaningful results from all of our sites, as discussed below. Comparisons of San Salvador callianassids and their burrows are summarized in Table 1.

Callianassids are obligate burrowers, and individuals are virtually never seen outside of their burrows, which are species specific and noted for their architectural complexity (see Dworschak et al., 2012, Figure 69.31, for a sampling of the burrow forms of callianassids and closely related groups). Although considered to be deposit feeders in the broad sense, the food preferences of callianassids and their precise modes of feeding are complex and quite varied, ranging from picking through
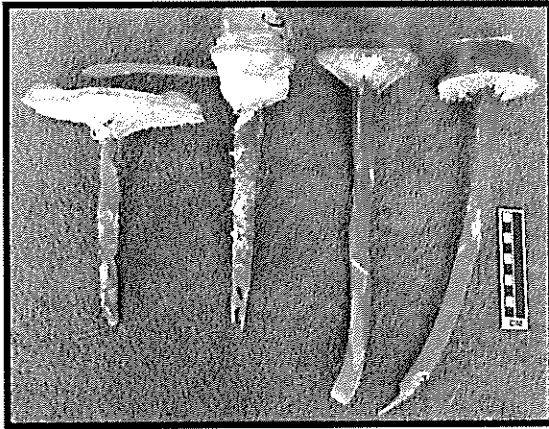
Figure 5. Failed burrow-cast tops from the Graham's Harbour site. Blockage of callianassid burrows by sediment and grass blades a short distance within the burrows was a persistent casting problem.

sediment deposits for organic debris, to ingestion of organic-rich burrow-wall material, to active collection of seagrass leaves and storage in burrow chambers for direct consumption or to serve as substrate for the growth of microbes ("farming" activity) and their later consumption (Abed-Navandi and Dworschak, 2005; Abed-Navandi et al., 2005; Nickell and Atkinson, 2005).

This complexity led to attempts to classify the feeding modes of modern thalassinideans, including callianassids, based on their burrow architectures and the presence or absence of seagrass beds (Suchanek, 1985; Griffis and Suchanek, 1991, their Figure 1). An even more complex classification of thalassinidean trophic modes based on twelve specific burrow features was devised by Nickell and Atkinson (1995). These schemes have been criticized as being too rigid given the sometimes mixed nature of feeding modes for any given species (Dworschak and Ott, 1993; Dworschak et al., 2012), but the Nickell and Atkinson scheme may permit conclusions about trophic modes from consideration of multiple burrow characteristics.

From the paleontological perspective, the reliance of the Griffis and Suchanek (1991) classification scheme on seafloor surface features

such as presence or absence of burrow mounds is not practical because such features are not normally preserved in the fossil or stratigraphic records. However, if more information about individual fossil callianassid burrows (*Ophiomorpha* and other trace fossils believed to be of thalassinidean origin) can be compiled and overall burrow architectures recognized, then it may be possible to identify burrow features of trophic significance and thus paleoecologic importance in the future.

Graham's Harbour

Two large, nearly complete, and spectacularly complex burrow casts (Figure 6) were recovered from our Graham's Harbour site, in addition to several incomplete casts. Both burrow casts have a broad U-shape; the largest cast (Figure 6A) reached a depth of 53 cm below the seafloor and has a width of 37 cm. After an initial extension of the shaft downward for about 10 to 12 cms, the casts of both burrows revealed the presence of distinctive, branching, pouch-like structures that are slightly downward-directed and have a tiered arrangement along the vertical length of the burrow, with the branching pouches separated by short shaft segments. Seven tiered, pouch-like structures are present in the largest cast (Figure 6A).

Similar pouch structures were figured by Suchanek (1983, 1985) for burrows identified as constructed by *Callianassa rathbunae* in the U.S. Virgin Islands in fine-grained carbonate sands adjacent to *Thallasia testudinum* seagrass beds, a setting very much like that present in Graham's Harbour. In subsequent taxonomic reorganization and reassignment, *C. rathbunae* was renamed as, *Neocallichirus maryae* (Karasawa, 2004). Voucher specimens from Graham's Harbour have been identified as *N. maryae*. This species is known to be distributed throughout the wider Caribbean region, including south Florida and the Bahama Archipelago, and ranges from Bermuda to northern Brazil (Abed-Navandi, 2000).

The Graham's Harbour casts differ from the burrow form figured by Suchanek (1983, 1985)

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in several important respects. Our casts reveal a broad, U-shaped burrow architecture, not just a downwardly directed, tiered shaft ending at depth as shown by Suchanek (1983, Figure 4). After downward extension to maximum depth of penetration, the burrow cast turns laterally and a series of nodes are present, connected by the main tunnel (Figure 6A, B). In both burrow casts, the tunnel forms a distinct loop in at least one place, as best shown in Figure 6B. The tunnel extends laterally for several 10s of centimeters and then turns upward as a shaft (Figure 6A) that presumably continued without interruption to an excurrent opening at the surface. Note that a shrimp was trapped by resin in this part of the shaft. Although two burrow casts is not a large sample, both reveal the same basic burrow form. We think this form is a more accurate representation than the burrow reconstruction of Suchanek (1983, Figure 4), which may have been assembled from parts of casts and thus could not show the full U-shape of the burrow with its complex nodes and loops that are present along with the tiered, branching pouches.

Some of our partial casts reveal that the branching pouches can be surprisingly large structures (Figure 6C), with branch diameters of several centimeters. Although these pouches were obviously open when burrow casts were made, the casts commonly had seagrass leaves within or
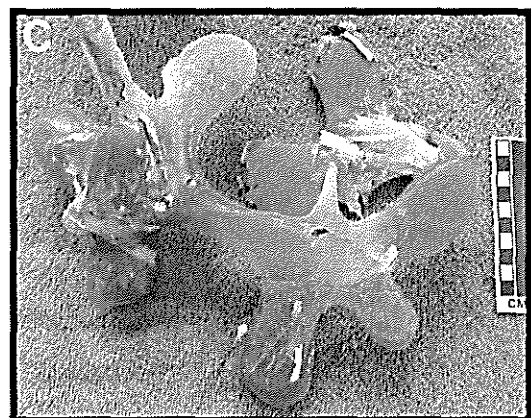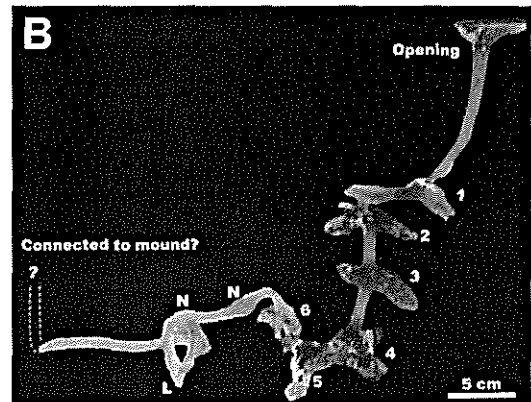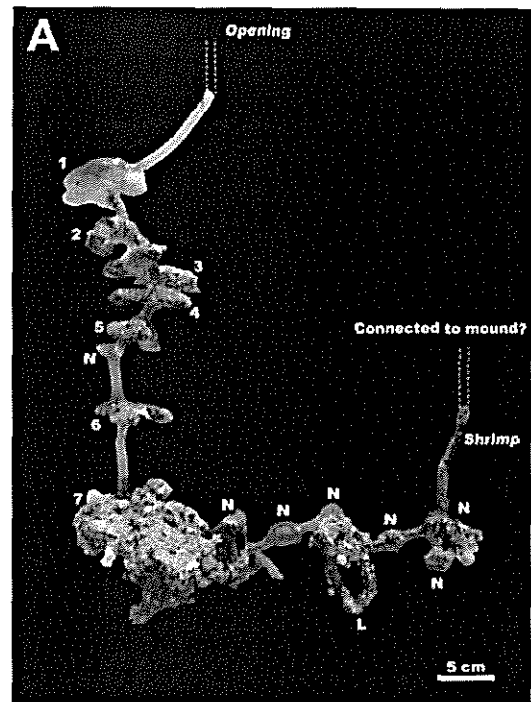

Figure 6 (right). Characteristics of the complex callianassid burrow casts from the Graham's Harbour site: A & B) Near-complete casts; "opening" indicates the funnel-shaped end of the burrow and the incurrent flow direction; the excurrent flow would be from the smaller opening at the top of a mound. Numbers indicate each tier of pouch-like branches from surface to depth of about 50 cm; N denotes burrow nodes, and L indicates a loop structure characteristic of this burrow form. The tracemaker species for this burrow form is Neocallichirus maryae. *C) Close-up of three tiers of the large, branching, pouch-like structures; note the presence of* Thalassia testudinum *blades on and within the hardened cast resin.*
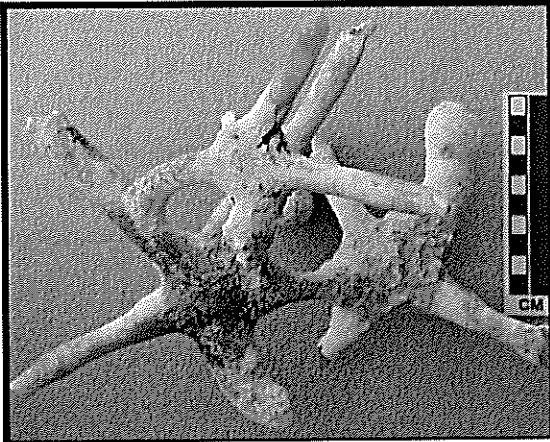
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Figure 7. Cast of the downward-spiraling burrow shaft of Glypterus acanthochirus *from the Pigeon Creek site; large structure closest to scale is the downward end of the burrow cast. These complex burrows can penetrate to depths of more than 1 m below the surface.*

attached to the resin, indicating that seagrass was present within the burrow systems. Suchanek (1983, 1985) and Griffis and Suchanek (1991) characterized *Neocallichirus maryae* (formerly *Callianassa rathbunae*) as a deposit feeder, and indicated that the pouches were storage places for coarse-grained sediment debris and also seagrass, which may form an important part of the shrimp's diet, either directly or indirectly via "farming activity."

In addition to *Neocallichirus maryae*, our identifications of callianassid specimens from Graham's Harbour indicate that a second species, *Neocallichirus cacahuate*, also is present in this area. In the future, we hope to be able to enlarge our collection of burrow casts from this site and to confirm the burrow form of this second species. It is certainly possible that even more species of callianassids reside in Graham's Harbour.

Pigeon Creek

The previous identification by Curran and Martin (2003) of *Glypturus acanthochirus* as the large, mound-forming species of callianassid present at Pigeon Creek was confirmed by our new

voucher specimens. Sediment cones formed around the excurrent openings of *G. acanthochirus* burrows coalesce to form large, semi-permanent mounds stabilized by thin microbial mats. The large mounds are separated by multiple funnel-shaped depressions that include incurrent burrow openings and a thin cover of *Thalassia testudinum*. This distinctive topography is characteristic of the intertidal flats that are common around parts of the margin of Pigeon Creek and other, similar tidal creek areas throughout the Bahama Archipelago (Figure 3).

Glypturus acanthochirus is a powerful bioturbator that forms deep (up to 1.6 m or more) and complex burrows (Dworschak and Ott, 1993; Curran and Martin, 2003). The most distinctive aspect of *G. acanthochirus* burrows is the spiral form of the main burrow shaft, with short branches leading off the main shaft and terminating in blunt dead-ends (Figure 7). Large, near-complete casts of *G. acanthochirus* burrows in Belize were made by Dworschak and Ott (1993, Figure 7). Similar casts, identified as from generic "*Callianassa*" burrows, were made by Shinn (1968) from the Florida Keys and western Bahamas and by Tedesco and Wanless (1991) from the Caicos Platform. Based on their distinctive form, these casts also represent the burrows of *G. acanthochirus* and indicate the presence of this species throughout the wider Caribbean. All three studies also reported that the burrow chambers of *G. acanthochirus* were commonly filled with shelly, coarse sediment that entered the burrow system through the funnel openings. This infilling process can change the original fabric of underlying deposits and create a new and distinctive ichnofabric, as demonstrated by Tedesco and Wanless (1991) and Dworschak and Ott (1993).

Dworschak and Ott (1993) postulated that *Glypterus acanthochirus* is primarily a deposit feeder, as this callianassid is virtually continuously processing sediment and organic debris that comes into its burrow through the funnel-shaped incurrent opening. In a more recent study using C and N

Figure 8. Upper part of a diver hand-excavated callianassid burrow in fine sand at about 2 m water depth at the Long Bay site. Note the characteristic pelleted exterior and smooth interior surface of the burrow wall. The callianassid species that constructs burrows at this site is as yet unknown. Lens cap is 5 cm in diameter.

Figure 9. Representative specimens of Ophiomorpha *from Upper Pleistocene shallow subtidal grainstones of the Bahamas: A) Closely packed* Ophiomorpha *shafts and tunnels (Ichnofabric Index 5 on Droser-Bottjer scale), Cockburn Town fossil coral reef, west coast of San Salvador; burrow diameters and wall characteristics here are consistent with diameters of modern callianassid burrows excavated at the Long Bay site. B) An* Ophiomorpha *specimen from Harry Cay, Little Exuma; these complex, large-diameter, branched tunnel structures with blunt, typically somewhat enlarged termini are common at the Little Exuma site and known to occur elsewhere in the Bahamas, suggesting the existence of a Pleistocene callianassid tracemaker not presently identified from modern Bahamian environments.*

stable isotope signatures of available food items, Abed-Navandi and Dworschak (2005) determined that organic material indirectly derived primarily from the microbial mats that form on the surfaces of the large burrow mounds was the single most important food source for *G. acanthochirus*, with mangrove leaves, deeper sediment, and the burrow wall itself not relevant as food sources for this species. In a sense, this further emphasizes the role of this callianassid as an ecosystem engineer in that the burrowing activity of the shrimp creates a topographic surface favorable for development of the microbial mats from which the shrimp derives a significant amount of its food.

In addition to *Glypterus acanthochirus*, we have identified specimens of *Neocallichirus grandimana* from the spit-like sand-bar deposits around the inlet area of Pigeon Creek, and *N. maryae* also may be present in the inlet area in and around extensive seagrass beds. We have not yet been able to successfully cast their burrows here, but we hope to be able to do so in the future.
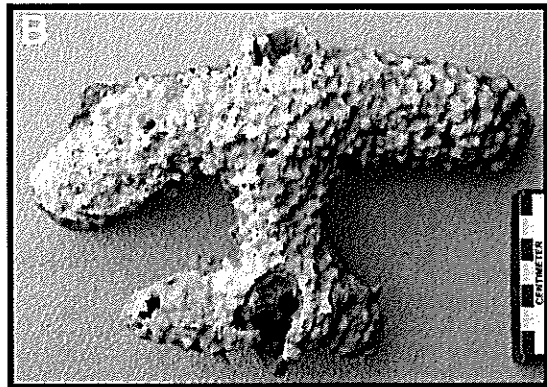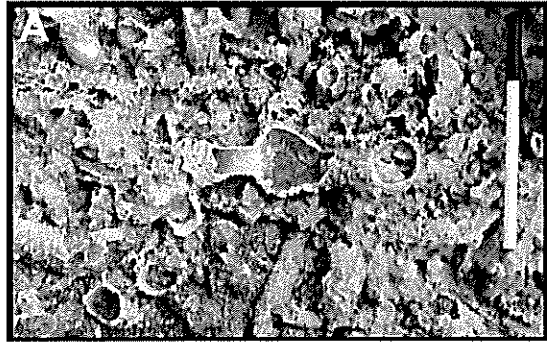
Long Bay

Callianassid burrows are common in the large open sandy areas between the patch reefs of Long Bay. In fair weather conditions, small sediment cones can form around burrow openings, but adjacent funnel-shaped depressions are not

present, so these burrows appear to be single-opening systems. During our fieldwork period, the eroded tops of callianassid burrows (diameter = 2 to 3 cm) were numerous. Unfortunately, we had poor resin-casting results owing to persistent wavy conditions. The open burrows that we did attempt to cast apparently were blocked by sediment at depth because we had very poor resin penetration. However, we were able to excavate the tops of several burrows by hand, and the results were revealing.

These callianassid burrows have a constricted surface opening for excurrent flow and then widen and turn sharply to extend laterally as a tunnel for 10 to 12 cm before turning downward as a steeply inclined shaft (Figure 8). It is likely that branching occurs at depth. The burrow walls are substantial, up to 5 mm thick, and have a clearly pelleted exterior and smooth interior (Figure 8), as is typical for callianassid burrows. We also were unable to capture shrimp at this site, so the burrow-maker species remains unknown. Making successful burrow casts at this site is a top priority for the future. There are no seagrass beds in Long Bay, so the feeding mode of these callianassids most likely is generalist deposit feeding.

Fossil Callianassid Burrows

Callianassid burrows are commonly preserved as trace fossils in the Pleistocene shallow subtidal grainstones of the Bahamas. These fossil burrows are assigned to the ichnogenus *Ophiomorpha*, a three-dimensional, branching burrow system of shafts and tunnels that are thickly lined, with smooth inner wall surfaces and characteristically pelleted exterior surfaces (Curran, 2007). *Ophiomorpha* shafts and tunnels can impart a distinctive ichnofabric to Bahamian shallow subtidal grainstones that can reach the maximum on the Droser-Bottjer ichnofabric scale (Figure 9A; Droser and Bottjer, 1989; Knaust et al., 2012, Figure 10).

The *Ophiomorpha* shafts and tunnels at the Cockburn Town fossil coral reef site on San Salvador (Figure 9A; Curran, 1997) have burrow diameters and wall characteristics consistent with diameters of the modern callianassid burrows from our Long Bay site. Furthermore, they do not exhibit the distinctive architectures of the burrow systems from Graham's Harbour and Pigeon Creek. The unidentified callianassid that is common in Long Bay today is a likely candidate as the tracemaker of *Ophiomorpha* at the fossil coral reef site and at other Pleistocene localities in the Bahamas.

A distinctive *Ophiomorpha* structure (Figure 9B) consisting of large diameter, branched tunnels with blunt, typically somewhat enlarged termini that formed a basal part of the burrow system are common at several Pleistocene subtidal grainstone localities in the Bahamas, including Harry Cay on Little Exuma, Devil's Point on Great Inagua, and Rum Cay, as well as the Miami Limestone (Pleistocene) of south Florida (Curran, 2007; Mylroie et al., 2008). However, these structures have not been found at the Cockburn Town site, very likely because the exposures there reveal only the upper parts of the *Ophiomorpha* burrow systems. If complete casts from the modern burrows in Long Bay can be successfully made, and if they reveal branching, blunt-ended termini, then a definitive Pleistocene to modern link will be confirmed, and a useful paleoenvironmental indicator established.

CONCLUSIONS

The results of this study indicate that there are several species of deep-burrowing callianassids inhabiting the intertidal to shallow subtidal environments around San Salvador Island in the Bahamas, with the real possibility that other species are present and await full documentation. It is clear that the burrowing activity of callianassids is the major source of bioturbation in the shallow subtidal carbonate sediments of San Salvador and likely throughout the Bahama Archipelago. In like manner, *Ophiomorpha*, the fossil burrow of callianassids, is the dominant trace fossil in late

Pleistocene subtidal grainstones of the Archipelago. Our specific finding are:

1. There are at least four species of callianassids in the modern shallow subtidal environments around the periphery of San Salvador Island: *Neocallichirus maryae* (formerly known as *Callianassa rathbunae* or *Neocallichirus rathbunae*) and *Neocallichirus cacahuate* in Graham's Harbour, *Glypterus acanthochirus* and *Neocallichirus grandimana* in Pigeon Creek, and an as yet unidentified species in Long Bay. Each of these species form large burrow systems with distinctive and unique architectures.

2. *Ophiomorpha*, the fossilized burrow of callianassids, has wide distribution in Pleistocene shallow subtidal grainstones throughout the Bahama Archipelago. Distinctive basal structures of *Ophiomorpha* found at localities on Harry Cay, Little Exuma; Devil's Point, Great Inagua; and Rum Cay reveal a complex burrow architecture different from those of *N. maryae* and *G. acanthochirus*. Future casts of modern callianassid burrows in Long Bay may reveal the presence of similar basal structures, thus establishing a match.

3. Future research will include continued identification of callianassid species present throughout the Bahamas and casting of their burrows in order to define their species-specific burrow system architectures. In addition, the effort to find new Pleistocene subtidal localities should continue, with the hope of finding *Ophiomorpha* specimens that will shed new light on overall burrow architectures. When matches can be made with confidence between modern and fossil burrow architectures of callianassids, useful new paleo-environmental indicators will have been created.

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