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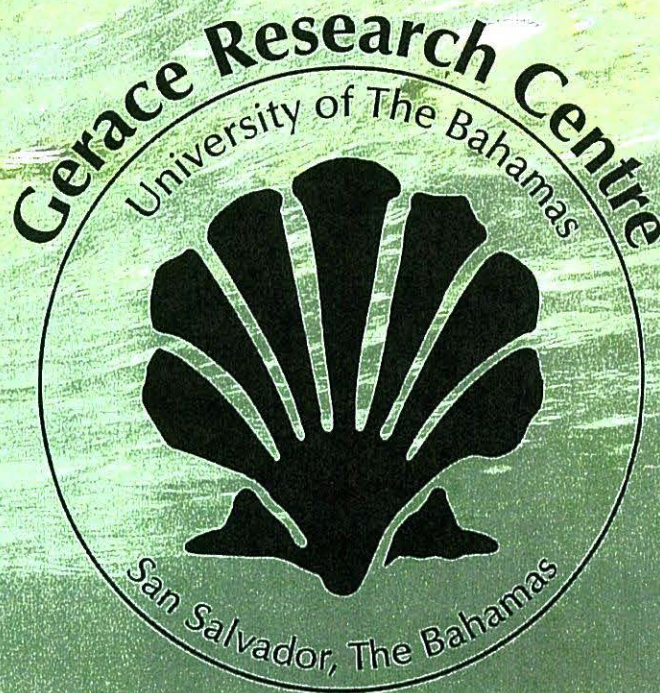
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Callianassid shrimp diversity around San Salvador Island, Bahamas: Why marine biologists and geologists should care

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1. Abstract

Deep-burrowing callianassid shrimp (Decapoda: Axiidea: Callianassidae) are dominant bioturbators in modern intertidal to shallow subtidal, sandy carbonate substrates throughout the Bahama Archipelago and beyond. Nonetheless, callianassids in the Bahamas are poorly known with respect to species present, burrow forms, and general ecology. Goals of our study were to determine what callianassid species inhabit the shallow-marine environments around San Salvador, their environmental preferences, and burrow characteristics. To date, four species of callianassids have been identified from four study sites, with polyester-resin casts made of burrows from three of the sites. Callianassid burrow systems are large, complex, and species specific. Our geological-paleontological goal is to establish matches between modern burrow forms and those of the trace fossil *Ophiomorpha*, attributed to callianassids and found in marine Pleistocene deposits throughout the Bahamas and beyond. At our Graham's Harbour site, burrowed, open-sand areas are interspersed with seagrass beds. *Neocallichirus maryae* (formerly *N. rathbunae*) and *N. cacahuate* are present in sandy areas. *Neocallichirus maryae* casts document a U-shaped burrow form with large, tiered, pouch-like structures. Efforts to cast *N. cacahuate* burrows were unsuccessful, but hand excavations revealed robust, thickly-lined, branching burrows. Two predominately intertidal sites are in Pigeon Creek lagoon. Muddy-sand flats border parts of northern Pigeon Creek, where mounded topography is present, generated by *Glypturus acanthochirus*. Burrow casts have a distinctive, downward spiraling form. Our second Pigeon Creek site is marginal to a sand-spit on the lagoon's south arm, near the inlet to the open Atlantic. Here *Neocallichirus grandimana* is common, and burrow casts reveal an architecture of multiple, robust shafts and tiered horizontal branches that end in bulbous chambers stuffed with marine vegetative matter. Long Bay on the island's west coast is our second subtidal site; wave energy is greater than in Graham's Harbour, and grass beds are absent. Burrows probably made by *N. cacahuate* are common, and hand excavation revealed burrows similar to some present in Graham's Harbour around the old government dock. Any future successful matching of modern callianassid burrow architectures with those of *Ophiomorpha* will aid significantly in differentiating paleoenvironmental settings of ancient tropical, shallow-marine carbonates.

2. Introduction

When making a snorkel or SCUBA dive to explore the shallow-marine waters and sedimentary environments around San Salvador or other islands of the Bahama Archipelago, one likely will encounter sandy-bottom areas with numerous burrow openings of various sizes, ranging up to ~4 cm in diameter. Conical mounds can be common, each with a small opening at the top and an adjacent funnel-shaped depression with a larger burrow opening. Such areas commonly occur near seagrass beds dominated by turtle grass (*Thalassia testudinum*). Along protected, mangrove-fringed, intertidal areas such as 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 open-sand areas on the shallow offshore shelves of the islands, commonly in close proximity to coral patch reefs, also typically exhibit numerous, obvious and sometimes large burrow openings, again up to ~4 cm diameter.

These cones, mounds, funnel-shaped depressions, and large burrow openings all are the products of shrimp of the Family Callianassidae, commonly referred to as ghost shrimp (Arthropoda: Malacostraca: Decapoda: Axiidea, Figure 1; see Dworschak et al. 2012 for current systematics review, including callianassid general biology, ecology, and ethology). Callianassids are primarily burrowers in marine sediments and have global distribution except for high latitude seas. Greatest diversity occurs in shallow subtidal settings of the tropics (Dworschak 2000, 2005). At present more than 200 species of callianassids have been identified in the scientific literature (Dworschak 2005, and pers. comm., 2010).

Callianassids are fossorial, spending essentially their entire lives beyond the larval stages in complex, deep (up to ~2 m), and extensive burrow systems. In the tropics, callianassids can occur in high densities and

are a powerful agent of bioturbation within sandy substrates. With the ability to create a mounded topography, callianassids qualify as true "ecosystem engineers" (Curran and Martin 2003), capable of influencing "the whole sedimentology and geochemistry of the seabed" (Dworschak 2004). Examples of significant bioturbation by callianassids in tropical carbonate settings were described by Tudhope and Scoffin (1984, Great Barrier Reef, Australia), Tedesco and Wanless (1991, South Florida and Caicos Platform), and Curran (2007, Bahamas).

Fossilized burrows of callianassids are usually 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 pellets generated by the shrimp in construction of their burrow systems. *Ophiomorpha* is the dominant trace fossil in late Pleistocene (MIS 5e or Eemian, ~130,000 to 115,000 years ago) shallow subtidal grainstone deposits throughout the Bahama Archipelago (Curran 2007; Knaust et al. 2012), with good examples preserved in the Cockburn Town fossil coral reef sequence on San Salvador (Curran and White 1985; Curran 1997).

Figure 1. Callianassids are characterized by their elongate form and large major cheliped. This is *Glypterus acanthochirus* from North Pigeon Creek on San Salvador.

The present study focused on distribution of modern callianassids in the shallow marine waters around San Salvador. Our goals were to capture specimens for species identification and to make representative casts of the callianassid burrows present at each of our four study sites (Figure 2). This paper is an updated version of Curran and Seike (2016) and was designed primarily to provide marine biologists and others interested in marine invertebrates around San Salvador with basic information on callianassids. The architecture of a callianassid burrow system is known to be species specific (Suchanek 1985, and later studies), so with knowledge of a given modern burrow system and its tracemaker identified, it may be possible to match late Pleistocene *Ophiomorpha* burrows with modern counterparts. If accomplished, a given *Ophiomorpha* occurrence would provide enhanced value for paleoenvironmental interpretation. This goal is much easier stated

than achieved, but preliminary results are encouraging.

3. Methods

3.1. Study Sites and Settings

Four sites in different shallow-marine settings around the periphery of San Salvador were selected for study of modern callianassid burrows (Figure 2), as described below.

3.1.1. Graham's Harbour

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. Holocene history of the lagoon and its sediment facies were documented by Colby and Boardman (1989) and a detailed
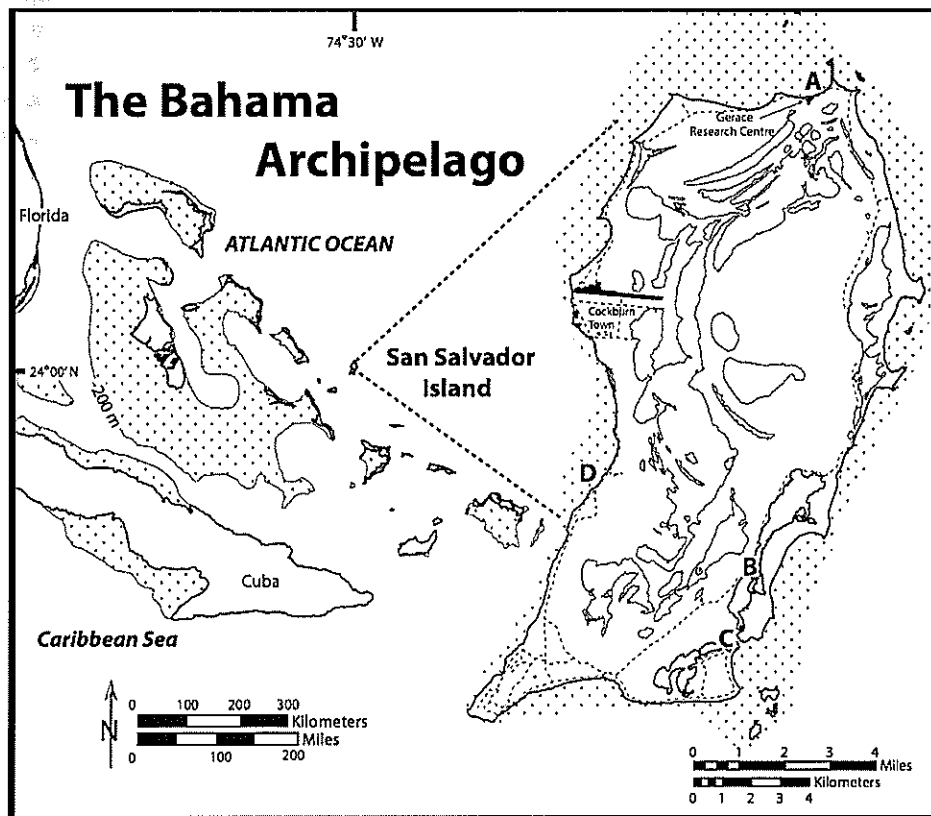

Figure 2. Index map to the Bahama Archipelago, San Salvador, and the callianassid burrows study sites: A – Graham's Harbour; B – North Pigeon Creek; C – South Pigeon Creek; D – Long Bay.

sediment distribution study by Randazzo and Baisley (1995).

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 (N24°07.201', W74°27.747'). A narrow path leads to the beach, and offshore, just beyond seaward dipping beachrock, a clean sandy bottom goes out for 30 to 40 meters to thick beds of seagrass (dominantly *Thalassia testudinum*; see a profile showing surface and subsurface relationships across this area (Curran 1997, his Ichno-locality 2 and Figure 1).

Callianassid burrows begin to appear a short distance seaward of the low tide line. Formed by *Neocallichirus maryae*, the burrows manifest as a sediment cone ("volcano") at the excurrent end, with the incurrent flow commonly via a funnel-like depression with a basal opening of ~2 to 4 cm (Figure 3A). Density of burrows increases offshore to the edge of the seagrass beds, and the appearance of the sandy bottom is highly variable owing to wave-energy conditions. Under fair weather conditions, particularly during late spring to early fall, the area will exhibit mound and crater topography owing to the cumulative callianassid burrowing activity.

If soon after a storm, only new, small cones will be present, and incurrent openings will be near level with the plane of the bottom. The shrimps form a firm burrow wall, dark in color, and consisting of a mixture of fine sand, mud, and organic material. With scouring, burrow walls commonly stand out in partial relief around openings (Figure 3B). Occasionally, a shrimp will be seen at one of the openings to its burrow, but callianassids normally do not leave their burrows. This strip of clean sand bottom extends east to the old Government Pier area, where we also have collected callianassid specimens on either side of the pier, including a second species, *Neocallichirus cacahuate* (burrows to be described later).
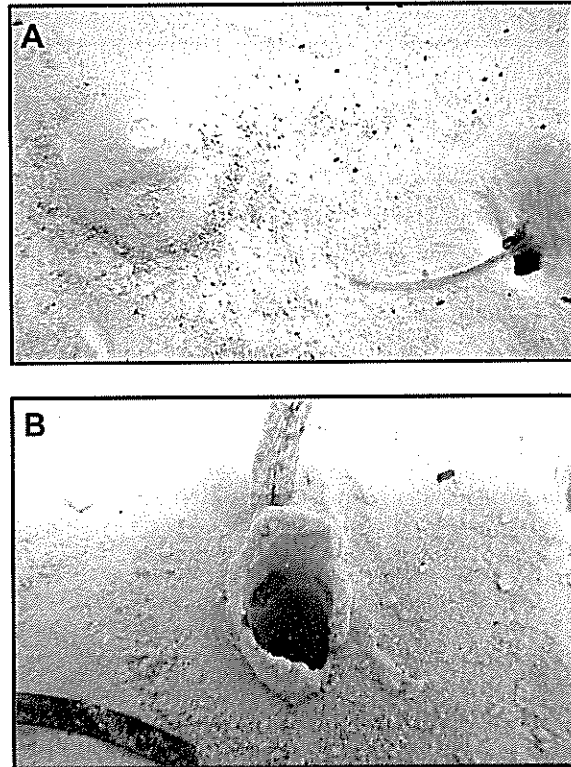

Figure 3. Shallow subtidal surface characteristics of callianassid burrows at Site A in Graham's Harbour: A) Callianassid burrow cone (excurrent flow) and adjacent funnel (incurrent flow, burrow diameter ~ 2.5 cm) at about 2 m water depth; dark specks at upper right are callianassid fecal pellets. B) 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.

3.1.2. Pigeon Creek

Site B (N23°59.131', W74°29.101') is located on the western edge of the northern arm of Pigeon Creek lagoon, on a large intertidal sand flat fringed on the landward side by red mangroves (*Rhizophora mangle*). This sand flat is close to the Queen's Highway, and, at low tide, the distinctly mounded topography of the flat is fully exposed (Figure 4). These mounds are the result of deep-burrowing activity of *Glypturus acanthochirus*, and the

microbial mat-stabilized mounds support a diverse community of shallow-tier burrows (Ichno-locality 5 of Curran 1997; Curran and Martin 2003).

The sedimentology of Pigeon Creek was described in detail by Mitchell (1987) and Cummins et al. (1995), who also included an analysis of molluscan taphonomy. Tidal range in Pigeon Creek is variable and up to about 0.75 m, depending on day in the lunar cycle and precise location. The best time to visit the study sites in Pigeon Creek is at full low tide when callianassid mounds and burrow openings are fully exposed. There is a tide lag in Pigeon Creek, and the mounds at Site B do not become well exposed until at least 45 minutes to as much as two hours past the predicted low tide time. On any given day, if wind conditions or other factors hold tide waters in, the mounds at Site B may not emerge much at all. Surfaces of large mounds are generally firm, with the low areas in between much softer and occupied by a thin cover of turtle grass and the incurrent, funnel-shaped burrow openings of *G acanthochirus*.

Our Site C is a small, intertidal sand flat on the east side of the proximal end of the south arm of Pigeon Creek, marginal to an active sand spit and very close to the inlet to the open Atlantic (N23°57.839', W74°29.265'). Access is via a short, presently overgrown and debris-littered path leading from the abandoned "Ocean House" and then turning south around a patch of red mangroves to the sand-flat area. At low tide, numerous large burrow openings (~ 2 cm diameter) are exposed, but without cones and funnels. These burrows are formed by *Neocallichirus grandimana*. Nearby, the shallow subtidal sandy areas near seagrass beds commonly exhibit mounds and funnels of *N. maryae*.

3.1.3. Long Bay

Site D (N24°00.493', W74°31.831') is located offshore of the beach at Long Bay. The shallow offshore area is sandy, devoid of seagrass beds,
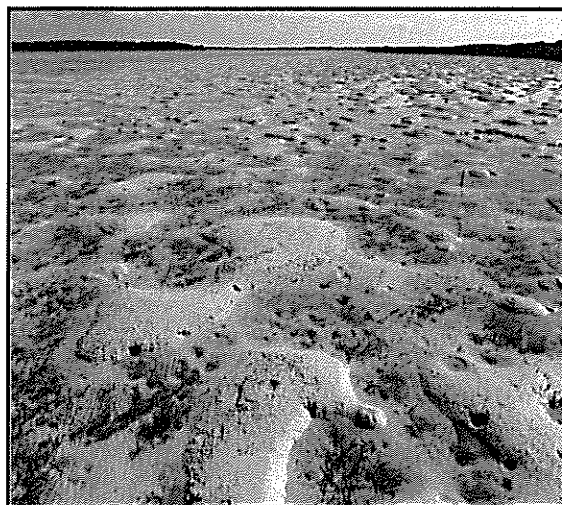

Figure 4. Mounded topography produced by the deep-burrowing callianassid, *Glypturus acanthochirus*, along the wide intertidal carbonate-sand flats bordering parts of North Pigeon Creek lagoon at Site B. Mounds commonly have widths of 1+ m and lengths of coalesced mounds can be up to several meters.

and typically displays ripple marks and small sand waves as well as numerous openings of burrows formed by callianassids, likely *Neocallichirus cacahuate*. 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, and if eroded, the full diameter of the burrow will be exposed, including parts of the burrow-wall lining. 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 usually are common.

3.2. Burrow casting methods

A prime objective of our study was to make complete resin casts of callianassid burrows from each of the four study sites. We used Hi-Bond boatyard polyester resin as our casting medium. The resin 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 available in Nassau by order from GRC.

At our shallow subtidal sites (A & D), casting was a two-person operation requiring a SCUBA diver to do the actual casting and a snorkeler to assist. After establishing a suitable staging area well above the high tide line, we scouted the seafloor directly offshore for areas where burrow openings were common. Once identified, the casting area was marked with a well-anchored float. The open burrows for casting were then selected and marked.

Once all is ready for casting, resin was mixed with hardener at the staging area. 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, allowing more time, usually about 20 minutes, for the diver to cast the burrows. Obviously some trial and error is involved; typically we could pour 5 to 10 burrows per casting dive. We allowed at least 24 hrs. for hardening prior to excavation of casts.

The next step is burrow cast excavation, and for this we used an airlift attached to a scuba tank. 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 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 excavation of a single burrow. Nonetheless, with care, large, near-complete casts can be obtained.

The biggest casting problem is poor resin penetration – a burrow may appear fresh and and clean, but it is virtually impossible to know if any given burrow is blocked at depth by sediment, seagrass leaves, or both. Failed casts

reveal little about true burrow form. A second problem is offshore wave action, with even relatively small waves (sub-whitecap wave heights) inhibiting operations, owing to both lowered visibility and difficulty of holding position.

Another goal of our study was to capture callianassids for taxonomic identification, although they are notoriously difficult to catch given their deep-burrowing capabilities and quickness of movement. We used a stainless steel "yabby" or bait pump designed and manufactured in Australia by Alvey fishing supplies company ("yabby" is the slang Australian term for callianassids). Species identifications of our harvested specimens were verified by Dr. Peter Dworschak, Natural History Museum, Vienna, Austria, from close-up images of the specimens.

4. Results and Discussion

A primary goal was to obtain complete casts of callianassid burrows from all of our study sites for comparison of modern burrow architectures with those of fossil forms previously known from the literature. A listing of San Salvador callianassids and comparisons of their burrows and environmental settings are summarized in Table 1.

Callianassids burrows are species specific and noted for architectural complexity (see Dworschak et al. 2012, his Figure 69.31, for examples of a range of callianassid burrow forms). Although considered as deposit feeders in the broad sense, food preferences of callianassids and their precise modes of feeding are complex and varied, ranging from picking through sediment 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) for 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 burrow architectures and presence or absence of seagrass beds (Suchanek 1985; Griffis and Suchanek 1991, their Figure 1). Nickell and Atkinson (1995) proposed an even more complex trophic modes classification utilizing twelve specific burrow features. These schemes have been criticized as being too rigid given the sometimes multiple feeding modes for any given species (Dworschak and Ott 1993; Dworschak et al. 2012).

Reliance of the Griffis and Suchanek (1991) classification scheme on seafloor surface features, such as presence or absence of burrow mounds, is not practical from the paleontological perspective because such features are not normally preserved in the fossil/stratigraphic record. However, if more information about individual fossil callianassid burrows (*Ophiomorpha* and other similar trace fossils) can be compiled and overall burrow architectures recognized, then it may be possible to identify burrow features of trophic and thus paleoecologic importance in the future. What follows is a review and discussion of the callianassid burrow casts of this study.

4.1. Graham's Harbour

Two large, nearly complete, and complex burrow casts (Figure 5) were recovered from the Graham's Harbour site, in addition to several incomplete casts. Both casts have a broad U-shape; the largest reached a depth of 53 cm below the seafloor and has a width of 37 cm. After initial extension of the shaft downward for ~10-12 cm, both casts exhibit 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. Seven tiered, pouch-like structures are present in the largest cast.

Similar pouch structures were figured by Suchanek (1983, 1985) for burrows of *Callianassa rathbunae* from the U.S.

Virgin Islands occurring in carbonate sands adjacent to *Thalassia testudinum* seagrass beds, a setting very much like that present in Graham's Harbour. In subsequent taxonomic reassignment, *C. rathbunae* was renamed *Neocallichirus maryae* (Karasawa 2004). This species is distributed throughout the wider Caribbean region, including south Florida and the Bahama Archipelago, and ranges from Bermuda to northern Brazil (Abed-Navandi 2000).

Graham's Harbour casts differ from the burrow form figured by Suchanek (1983, 1985) 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, his Figure 4). After downward extension to maximum depth of penetration, the Graham's Harbour casts turn laterally, with a series of nodes present, connected by the main tunnel (Figure 5). In both casts, the tunnel forms a distinct loop in at least one place and extends laterally for ~25-35 cm. In the more complete cast, the tunnel turns upward as a shaft that presumably continued to an excurrent opening at the surface. 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, thus not showing the full U-shape of the burrow with its complex nodes and loops, along with the tiered, branching pouches.

Our partial casts revealed that branching pouches can be surprisingly large structures, with branch diameters of several centimeters. Although the pouches obviously were open during casting, the casts commonly had seagrass leaves within or attached to the resin, indicating the presence of seagrass within the burrows. Suchanek (1983, 1985) and Griffis and Suchanek (1991) characterized *Neocallichirus maryae* as a deposit feeder and
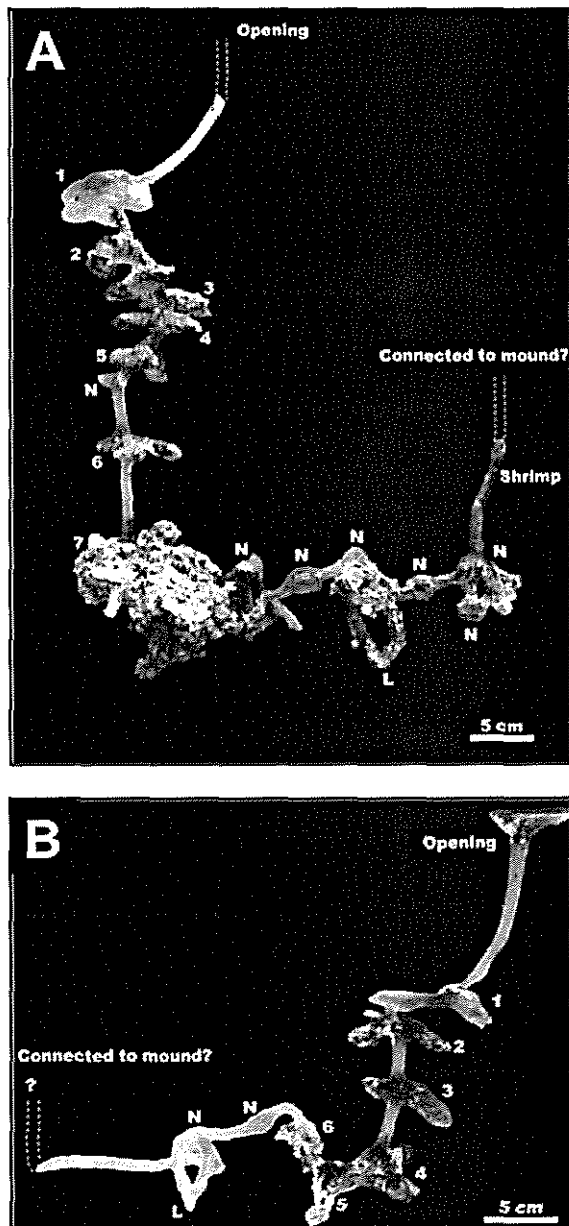
Figure 5. A, B) Near-complete casts of the complex burrows of *Neocallichirus maryae* from Site A in Graham's Harbour. "Opening" indicates funnel-shaped end of burrow and incurrent flow direction; excurrent flow would be from a smaller opening at top of a mound. Numbers indicate each tier of pouch-like branches from surface to depth of about 50 cm; N denotes burrow nodes, and L indicates a loop structure, all characteristic features of this burrow form.

suggested that 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 collections of specimens from Graham's Harbour made from the large sandy areas near the old Government Dock indicate that a second species of callianassid, *Neocallichirus cacahuate*, is also present. However, our attempts to cast this burrow have been unsuccessful to date.

4.2. Pigeon Creek

Glypturus acanthochirus was previously identified as the large, mound-forming species of callianassid present at our Site B on Pigeon Creek (Curran and Martin 2003), and this was confirmed by newly collected voucher specimens. Sediment cones formed around excurrent openings of *G. acanthochirus* burrows coalesce into large, semi-permanent mounds stabilized by thin microbial mats. Mounds are separated by multiple funnel-shaped depressions with incurrent burrow openings and a thin cover of *Thalassia testudinum*. This distinctive topography is characteristic of intertidal flats present around parts of the margin of Pigeon Creek and other, similar tidal creek areas throughout the Bahamas (Figure 4).

As a powerful bioturbator, *Glypturus acanthochirus* forms deep (up to 1.6 m or more), complex burrows (Dworschak and Ott 1993; Curran and Martin 2003). The main shaft of these burrows has a distinctive spiral form, with short branches terminating in blunt dead-ends (Figure 6). Large, near-complete casts of *G. acanthochirus* burrows were made by Dworschak and Ott (1993, their Figure 7) in Belize. 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. The distinctive form of these casts indicates the presence of *G*.

acanthochirus throughout the wider Caribbean.

Dworschak and Ott (1993) postulated that *Glypterus acanthochirus* is primarily a deposit feeder, as this callianassid continuously processes sediment coming into its burrow through the funnel-shaped incurrent opening. In a more recent study using C and N stable isotope signatures of available food items, Abed-Navandi and Dworschak (2005) determined that organic matter 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, sediment, and the burrow wall itself not relevant as food sources. This supports the ecosystem engineer role of these shrimp in that their burrowing activity creates a topographic surface favorable for development of microbial mats from which they harvest a significant amount of their food.

At our Site C in Pigeon Creek, we collected specimens of *Neocallichirus grandimana* from the spit-like sandbar deposits around the east side of the inlet area. *Neocallichirus maryae* also may be present in the inlet area in and around the extensive seagrass beds. In February 2015, we successfully cast two large *N. grandimana* burrows. Both casts had extensive and robust shafts and tunnels with diameters of 2 to 3 cm, and both represented broad burrow systems that extended to considerable depth. The largest cast had a width of 90 cm, extended to >40 cm, and had a total length of 5.1 m, including all shaft and tunnel segments (Figure 7). Neither cast could be completely extracted, and the basal parts of each had to be broken off and left in the substrate. The smaller of the two casts reached a depth below surface of >60 cm. Enlarged junctures of shafts and tunnels and bulbous endings of tunnels stuffed with vegetative matter were distinctive features in both casts, with the former likely as turnaround areas for the shrimp, and the latter indicating use of plant matter as a direct food source or for microbe "farming."
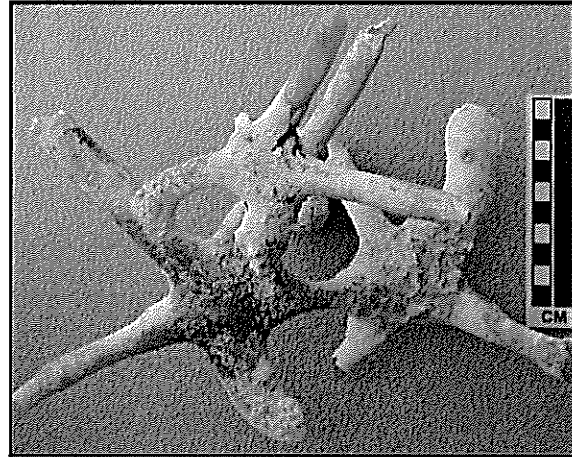

Figure 6. Cast of the incurrent, downward-spiraling burrow shaft of *Glypterus acanthochirus* from North Pigeon Creek Site B; large structure closest to scale is the downward end of the burrow cast. These complex burrows can penetrate to depths of well over 1 m below the surface.

4.3. Long Bay

Callianassid burrows are common here in the large, open sandy areas between patch reefs. In fair weather conditions, small sediment cones form around burrow openings, but adjacent funnel-shaped depressions are not present, so these burrows appear to be single-opening systems. Eroded tops of callianassid burrows (2-3 cm diameter) can be numerous. Unfortunately, we have had poor resin-casting results in Long Bay owing to persistent wavy conditions, and no casts of any significant length have been recovered. However, we were able to excavate the top parts of several burrows by hand, and these short burrow segments provided some useful information.

As with most callianassids, these burrows have a constricted surface opening for excurrent flow and then widen just below the surface. The distinctive feature of the upper part of the Long Bay burrows is that they turn sharply just below the surface and extend laterally as a tunnel for 10 to 12 cm before turning downward as a steeply inclined shaft (Figure 8). Branching probably occurs at depth. The burrow walls are substantial, up to 5 mm thick, and have
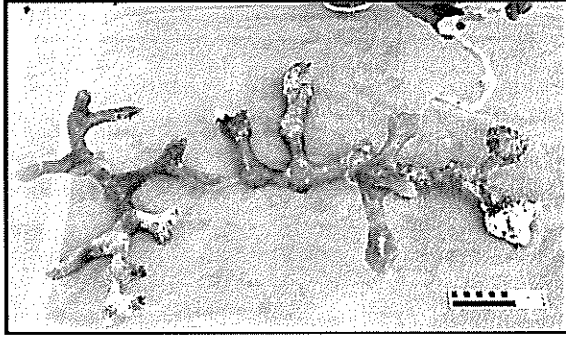
Figure 7. Cast of *Neocallichirus grandimana* burrow from South Pigeon Creek Site C. This is one of two large casts made at this site. This burrow system had a width of 90 cm and extended to at least 40 cm below the surface; unfortunately a deeper segment of the cast broke off during extraction and could not be retrieved. Total length of all segments of this burrow cast = 5.1 m.

a pelleted exterior and smooth interior, as is typical for callianassid burrows. Seagrass beds in Long Bay are sparse at best, so the feeding mode of these callianassids most likely is as generalist deposit feeders. The identity of two shrimp specimens collected from this locality is unconfirmed, but likely *Neocallichirus cacahuate*.

4.4. Geological Utility of 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 well-known ichnogenus *Ophiomorpha*, representing three-dimensional, branching burrow systems of shafts and tunnels that are thickly lined, with smooth inner wall surfaces and characteristically pelleted exterior surfaces (Curran 2007, and earlier reports cited therein).

Ophiomorpha and callianassids in general are important and of interest to geologists working in the Bahamas and similar carbonate regions for the following reasons:

1. The presence of *Ophiomorpha* is a reliable indicator of marine, shallow-subtidal beds in stratigraphic sequences throughout the Bahamas.

2. Callianassids are powerful bioturbators and can modify significantly the original textures and sedimentary structures of modern grainstone deposits, as well as similar ancient sedimentary strata from the Jurassic onward (Buatois et al. 2016).

3. *Ophiomorpha* shafts and tunnels can impart a distinctive ichnofabric to Bahamian shallow subtidal grainstones that can reach maximum level on the Droser-Bottjer ichnofabric scale, such that no new burrow can be formed without cross-cutting a previously existing burrow (Figure 9A; Droser and Bottjer 1989; Knaust et al. 2012, their Figure 10).

4. Dense occurrences of *Ophiomorpha* in ancient carbonate sequences can significantly increase the porosity and permeability of ancient carbonate sequences, as has been documented for the Biscayne Aquifer in the Miami, Florida area (Cunningham et al. 2009).

5. The modern and distinctive callianassid burrow-system forms, documented in this study from different environments around San Salvador, have high preservation potential and could serve as excellent paleoenvironmental indicators if recognized and identified from the fossil record.

As an example of point 5 above, *Ophiomorpha* shafts and tunnels at the Cockburn Town fossil site on San Salvador (Figure 9A; Curran 1997) have burrow diameters and wall characteristics consistent with diameters of modern callianassid burrows from our Site D in Long Bay. 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, similar Pleistocene localities in the Bahamas.

Finally, the distinctive *Ophiomorpha* structure (Figure 9B) consisting of large diameter, branched tunnels with blunt, typically

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 exposures there reveal only upper parts of the *Ophiomorpha* burrow systems. If complete casts from 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.

4.5. Conclusions

This study confirms that at least four species of deep-burrowing callianassid shrimp inhabit the intertidal to shallow subtidal environments around San Salvador Island, with the possibility that other species are also present and await discovery. The burrowing activity of callianassids is the major source of bioturbation in shallow subtidal carbonate sediments of San Salvador and undoubtedly also throughout the Bahama Archipelago. Likewise, *Ophiomorpha*, the fossil burrow of callianassids, is the dominant trace fossil in late Pleistocene subtidal grainstones of the Archipelago and has modified these deposits in significant ways.

The species of callianassids present in the modern shallow subtidal environments of San Salvador Island are distributed as follows: *Neocallichirus maryae* (formerly known as *Callianassa rathbunae* or *N. rathbunae*) and *Neocallichirus cacahuate* in Graham's Harbour, *Glypterus acanthochirus* and *Neocallichirus grandimana* in Pigeon Creek, and possibly *N. maryae* as well, and an as yet unidentified species in Long Bay, likely *N. cacahuate*. Each of these species form large burrow systems with distinctive and unique architectures.

Figure 8. Upper part of diver hand-excavated callianassid burrow in fine sand at about 2 m water depth, Long Bay, Site D. Note the pelleted exterior and smooth interior surface of the burrow wall, characteristic of callianassids. The species that constructs burrows at this site remains unidentified; *Neocallichirus cacahuate* is a likely candidate. Lens cap = 5 cm diameter.

Ophiomorpha, the fossilized burrow of callianassids, has wide distribution in Pleistocene shallow subtidal grainstones throughout the Bahama Archipelago. The distinctive basal structures of *Ophiomorpha* preserved at several localities in the Bahamas reveal a complex burrow architecture different from that of *Neocallichirus maryae, N. grandimana*, and *Glypterus acanthochirus*. Successful casting of modern callianassid burrows in Long Bay may reveal the presence of basal structures similar to the fossil forms, thus establishing a fossil-modern match.

Our future research will include continued collection of specimens and identification of callianassid species present throughout the Bahamas and casting of callianassid 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. Matches made with confidence between modern and

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