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Anchialine biodiversity in the Turks and Caicos Islands: New discoveries and current faunal composition

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Abstract: Lying at the southernmost point of the Lucayan Archipelago, the Turks and Caicos Islands are amongst the better studied localities for anchialine cave biodiversity. For nearly five decades, novel invertebrate fauna, comprised primarily of crustaceans, have been collected from these tidally influenced pools – but new findings are always on the horizon. Herein we present new records of crustaceans and annelids from anchialine blue holes and horizontal caves of the Turks and Caicos. These findings include two potentially new species of meiofaunal annelids and a new species of remipede collected from a shallow water cave pool. Our 2019 expedition additionally expands known faunal distributions for several taxa across the Caicos islands, and raises the biodiversity of the region to 35 species, 13 of them considered endemic. This is the first comprehensive faunal list for the anchialine systems in the Caicos Bank.

Keywords: subterranean fauna, anchialine, Polynoidae, Nerillidae, Remipedia

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INTRODUCTION

Anchialine ecosystems are characterized as tidal, brackish water bodies with subterranean connections to the sea (Holthuis, 1973). Originally described as tidally influenced pools, cave diving explorations in the late 20th century highlighted that these systems are often associated with extensive subterranean labyrinths (Stock et al., 1986; Iliffe, 2000, 2005). Biological research in anchialine systems continues to yield new and exciting taxa, of uncertain phylogenetic affinities, within classes, orders and families that are often found exclusively in anchialine caves (Iliffe, 1986, 2000). Some of these species are phylogenetically

old, presumably colonizing the anchialine realm in the Tertiary (Iliffe, 2005), while others exhibit close affinities to deep sea groups (Gonzalez et al., 2018; Iliffe & Alvarez, 2018) or represent highly modified members of otherwise interstitial lineages (Worsaae et al., 2004, 2019b; Martínez et al., 2016b).

Anchialine systems are known from the Caribbean, Mediterranean, Indo-Pacific and Atlantic islands including Bermuda, Canary Islands, Ascension and even Iceland (Iliffe et al., 1983; Iliffe & Sarbu, 1990; Biernbaum, 1996; Kristjánsson & Svavarsson, 2007; Martínez García et al., 2009; Pérez-Moreno et al., 2016). The most extensive of these systems in terms of density and size of subterranean passages occur

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in the Northern Caribbean, particularly in the Yucatán Peninsula (Alvarez et al., 2015), Cuba (Orghidan et al., 1973), Jamaica (Kornicker & Iliffe, 1992) and Hispaniola (Trias et al., 1997) as well as in the adjacent Lucayan Archipelago, which includes the Bahamas and the Turks and Caicos Islands (Palmer, 1985).

The Turks and Caicos Islands (Fig. 1A), and the neighboring islands of the Bahamas, are known for their high number of cave adapted anchialine species, prime for scientific exploration (Botosaneanu, 2000). Anchialine water bodies in this karstic area are primarily accessed through blue holes and horizontal caves (Gregor, 1981), harboring a diverse community of locally endemic, cave-limited species dominated by crustaceans, annelids and other invertebrates (Kornicker & Iliffe, 1985; Suárez-Morales & Iliffe, 1996; Koenemann et al., 2007). The first cave adapted species reported from the Turks and Caicos were the shrimp *Barbouria cubensis* (von Martens, 1872) and *Typhlatya garciai* Chace, 1942, discovered in 1975 from easily accessible pools and karstic windows (Buden & Felder, 1977). However, the majority of the diversity was not discovered until after 1982 once scientific cave divers started exploring the subterranean labyrinths (Bowman et al., 1985; Holsinger & Yager, 1985; Kornicker & Iliffe, 1985). We here provide an overview of these discoveries, which we further update with the results of our “2019 Caicos Caves III Expedition” with the aim of obtaining a comprehensive genetic collection of anchialine fauna across cave systems of the Turks and Caicos Islands. A prospective on the general state of knowledge, as well as on potential conservation issues of these ecosystems, are provided.

MATERIALS AND METHODS

Geological settings of the Turks and Caicos Island

The Caicos Islands are the emerged part of the Caicos Bank, the southernmost platform in the Lucayan Archipelago. This large shallow water bank is surrounded by waters reaching oceanic depths, with the present-day Caicos Islands being located along the northern and western margins. Strong easterly trade winds and resulting wind-wave agitation have promoted the development of oolitic sands in the shallow water interior of the platform (Dravis & Wanless, 2008). Washed ashore on the islands, these oolitic sands have piled into Holocene and Pleistocene age ridges, oriented parallel to the shoreline and perpendicular to prevailing easterly trade winds. These shallow water carbonates that comprise the bank have been continuously depositing

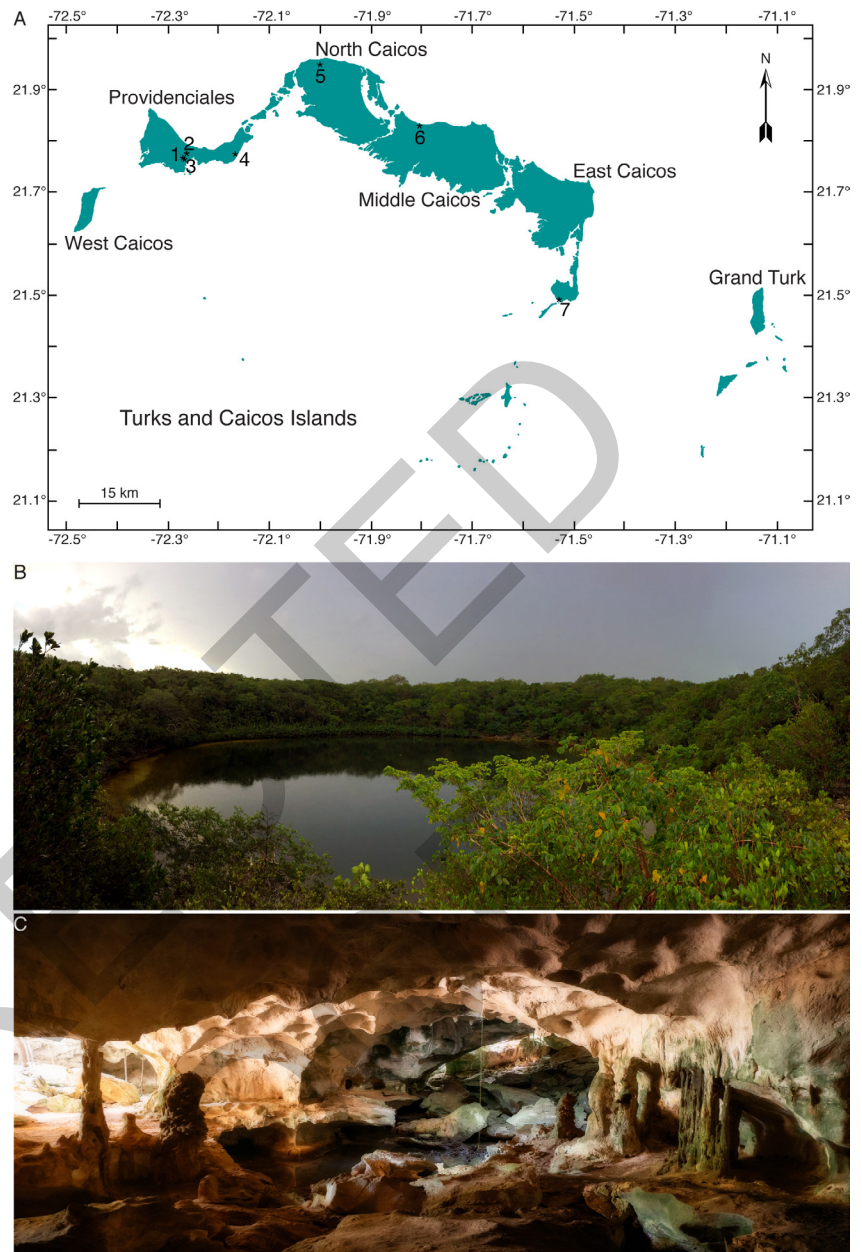


Fig. 1. The Turks and Caicos Islands with examples of cave systems found throughout the islands. A) Islands of the Turks and Caicos with known cave locations mapped: 1. Airport Cave, 2. Old Blue Hill Cave, 3. Snake Cave, 4. The Hole, 5. Cottage Pond, 6. Conch Bar Cave, 7. The Fountain; B) Cottage Pond, North Caicos Island. Photo by Brett C. Gonzalez; C) Conch Bar Cave, Middle Caicos Island. Photo by Joost Daniels.

and subsiding since at least the Cretaceous, but possibly as early as the Jurassic (Schlager et al., 1984), and extend deep into the surrounding sea floor (Dietz et al., 1970). The slow subsidence of the bank due to the continually accumulating weight of new carbonates has maintained the top of the bank near sea level. Yet, during Pleistocene periods of sea level regressions, the entire top of the carbonate bank was exposed to atmospheric weathering, producing the characteristic karst terrain. The climate of the islands is tropical and semi-arid with an average temperature of 26°C and annual rainfall of 730 mm. The karst topography of the islands is dominated by dolines (closed depressions) produced by limestone solution or collapse into underlying caves (Guidry et al., 2007). Collapsed caves on land consist of deep circular pits with a talus cone in the center, while occasional large vertical shafts or blue holes lie in shallow waters of the interior bank. Cavernous porosity underlying the

islands resulted from dissolution along abundant fracture networks, running parallel to the bank margin (Guidry et al., 2007).

History of previous cave expeditions

The initial discovery of cave adapted aquatic fauna from the Caicos Islands occurred in April 1975 when Donald Buden collected the shrimp *B. cubensis* and *T. garciai* from several tidal cave pools on the island of Providenciales (Buden & Felder, 1977). In November 1979, collections made during the Amsterdam Expeditions to the West Indian Islands resulted in the discovery and description of the amphipod *Spelaeonicippe provo* Stock & Vermeulen, 1982. The first cave diving expedition, “Caicos Caves I”, took place in October 1982, led by Thomas M. Iliffe, Jill Yager, Dennis Williams and Paul Hobbs. This trip was extraordinarily productive, yielding nine new cave adapted species: the annelid *Pelagomacellicephala iliffei* Pettibone 1985; copepod *Erebonectoides macrochaetus* (Fosshagen & Iliffe, 1994); amphipod *Bahadzia stocki* Holsinger, 1985; leptostracan *Speonebalia cannoni* Bowman, Yager & Iliffe, 1985; shrimp *Agostocaris williamsi* Hart & Manning, 1986; ostracod *Deeveya spiralis* Kornicker & Iliffe, 1985; remipedes *Godzillius robustus* Schram, Yager & Emerson, 1986 and *Kaloketos pilosus* Koenemann, Iliffe & Yager, 2004; and the stygiomysid *Stygiomysis clarkei* Bowman, Iliffe & Yager, 1984. A year later, in October 1983, Williams found a third remipede, *Lasionectes entrichoma* Yager & Schram, 1986. In May 1991, Iliffe collected the copepod *Fosshagenia ferrarii* Suarez-Morales & Iliffe 1996. Twenty years after “Caicos Caves I”, another significant diving expedition, “Caicos Caves II”, took place in June 2003 and included Iliffe, Mark Parrish, John Garvin, James Hurley and Darcy Gibbons. This project discovered three new copepod species: *Azygonectes plumosus* Fosshagen & Iliffe, 2007; *Bofuriella spinose* Fosshagen & Iliffe, 2007; and *Caiconectes antiquus* Fosshagen & Iliffe, 2007; a new isopod *Bahalana caicosana* Botosaneanu & Iliffe, 2003; and another new remipede, *Micropacter yagerae* Koenemann, Iliffe & van der Ham 2007. Most recently, in January 2019, the Smithsonian “Caicos Caves III” team consisted of Thomas M. Iliffe, Brett C. Gonzalez, Alejandro Martínez, Jørgen Olesen, Katrine Worsaae, Sarit Truskey, Lauren Ballou, Marc Allentoft-Larsen, Joost Daniels, Paul Heinerth and Rhonda Hart.

Sampling collection – Smithsonian “Caicos Caves III”

Our 2019 Caicos Caves III expedition was sponsored by the Smithsonian Institution with the aim of obtaining a comprehensive genetic collection of anchialine fauna across cave systems in the Turks and Caicos Islands. In order to accomplish this, fauna was unbiasedly collected across all available access points, including caves, ponds and wells with different environmental conditions, such as wide-ranging salinities (brackish to fully haline) and varying light exposure (entrance pools, twilight-, constant dark zones). Specific details pertaining to faunal

collections are listed in [Supplemental Table](#) and detailed below.

Cave fauna was collected by scientific cave divers using 20 mL glass scintillation vials or 50 mL plastic falcon tubes. Prior to capture, water-filled vials and tubes were flushed with ambient cave water to prevent osmotic shock. For smaller fauna, plankton nets with removable cod-ends were employed (Iliffe & Alvarez, 2018). Separate cod-ends were used for fresh- and saltwater layers. Upon returning to the surface, samples were placed in lidded cooling boxes until processing. All samples were processed within 24-48 hrs.

Initial processing included photographing and assigning all samples museum voucher numbers. Live specimens were relaxed with an isotonic solution of MgCl₂, then photographed using a mounted Canon EOS 5DSR with dual-slave Speedlite 430EX II strobes. Morphological examinations were done with light microscopy (LM) using Olympus SZX10 and SZX16 microscopes (Olympus, Tokyo, Japan).

Since the primary focus of this expedition was to obtain genomic quality DNA across anchialine fauna, hologenophore vouchers (Pleijel et al., 2008) were prepared to ensure molecular sequences could be tracked back to individual specimens. This semi-destructive approach allows for identification and additional morphological analyses. Morphological vouchers were typically preserved in either 3% glutaraldehyde or 2-4% paraformaldehyde, with the occasional preservation in 96% EtOH when necessitated by downstream protocols. Removal of several taxonomically non-informative structures (pereopods, parapodia, antennae, trunk limbs, etc.) was performed to obtain genomic quality tissue. Dissected parts were placed in alphanumeric tubes preloaded with 150 µL of M2 buffer (AutoGen) and stored at 4°C. Paragenophore vouchers of select individuals were preserved in 96-100% EtOH for DNA analyses and in Trizol or RNAlater for RNA analyses. All paragenophore vouchers were stored at -20°C in the field and transferred to -80°C upon returning to the Smithsonian National Museum of Natural History.

Permissions for specimen collection and export were granted through a scientific research permit (SRP No.: 18-12-01-23) issued by the TCI Department of Environment and Coastal Resources (DECR) issued to TMI. All specimens are deposited at the Smithsonian National Museum of Natural History, Washington, D.C., USA (USNM 1524194-1524351).

RESULTS

Seven anchialine cave systems yielding significant faunal discoveries are known from the Turks and Caicos Islands: four in Providenciales, one in North Caicos, one in Middle Caicos and one in South Caicos. Detailed descriptions for each cave are provided below; exact cave locations have been withheld per the guidelines of our scientific research permit. Specific faunistic information for each cave can be found in [Supplemental Table](#). From this point forward, we

use the term “stygbite/stygbitic” to refer to those species exclusively known from cave systems, while those species that are only recorded from the Turks and Caicos are referred to as “endemic”.

Caicos caves

Caves in Providenciales Island

Airport Cave is located at the crest of a hill overlooking Providenciales International Airport car park. It is about 2 km inland from the coast near the midpoint of the island of Providenciales at the northwestern corner of the Caicos Bank. The cave entrance is a crescent-shaped fissure extending off the side of a much larger, but debris-choked, sinkhole. A narrow ravine-like passage extends down for 20 m to a tidal anchialine pool lying in total darkness. The maximum water depth is 14 m. A colony of bats roost over the pool and their guano makes up much of the sediment. Based on our most recent visit, this cave should be considered biologically ‘dead’ in terms of macrofauna, as water pollution and hydrogen sulfide render the water anoxic and unsuitable for supporting animal life. Seven stygbitic species had been previously recorded from this locality, four of which are endemic (see [Supplemental Table](#)).

Old Blue Hill Cave is 300 m to the northeast of Airport Cave on Providenciales. Two pools on opposite sides of a large collapsed sinkhole are separated by massive breakdown boulders. The largest pool, beneath a 7 m high limestone cliff, opens to sunlight and has several meters of tannic surface water. Below the tannic layer, the water clears and a restricted hole opens into a larger chamber, sloping down and then choked off by a breakdown at 25 m depth. The second pool is sheltered from direct sunlight in a shallow cave and contains clear water. Seven stygbites are known from this locality, four of which are considered endemic (see [Supplemental Table](#)).

Snake Cave is located about 1.5 km inland and 1.1 km north of the airport on Providenciales. It consists of a long and narrow, mostly water-filled, fissure forming the margin of a larger collapsed sink. Although parts of the cave pool are dimly illuminated, the back section remains in total darkness. Maximum water depth is 8 m. Due to its remoteness, this cave is rarely visited, with only one stygbite being recorded (see [Supplemental Table](#)).

The Hole is a deep sinkhole, located at the crest of Long Bay Hills, a prominent ridgeline on the southwestern side of Providenciales. The cave is a 50 m diameter and 18 m deep sinkhole with vertical walls of soft limestone and 200 m from the nearest open water (Juna Sound on the south coast). Sheer walls surrounding a pool show a close resemblance to cenotes found in northern Yucatán Peninsula, México. This 15 m long by 10 m wide pool at the bottom of the depression is open to daylight. It is about 6 to 8 m deep, but the bottom is completely choked by breakdown and surface debris, such that no human-sized cave passages extends off from it. A total of nine stygbites have been recorded from this cave, having the highest diversity on Providenciales (see [Supplemental Table](#)).

Caves in North Caicos Island

Cottage Pond is a submerged sinkhole, located 4 km inland from the north coast of North Caicos Island (Fig. 1B). A shallow, rock-rimmed depression encloses a nearly circular pond, 50 m in diameter. At the surface, murky water limits underwater visibility to about 1–3 m. However, near the center of the pond (20 m depth), a 12 m long horizontal crack opens into a collapsed chamber (70 m in diameter) that reaches water depths of 80 m. A conical debris mound lies directly below the entrance crack (~40 m depth) and extends downward to the bottom of the deep chamber. Evidence of prior subaerial exposure in the form of stalactites and flowstone can be found down to 45 m. Layers of hydrogen sulfide accumulate at around 40 m depth. Currently the best known system in North Caicos, a total of 15 stygbitic (five endemics) are known from Cottage Pond, exhibiting the highest diversity of all known anchialine systems in the Turks and Caicos (see [Supplemental Table](#)).

Caves in Middle Caicos Island

Conch Bar Cave, with over 3 km of horizontal passageways, is the largest subaerial cave in the Lucayan Archipelago (Fig. 1C) (Smart et al., 2008). The cave consists of a series of large chambers and irregular passageways along the southern margin of an eolianite ridge. A series of phreatic formed, elliptical shaped passages with domed ceilings run towards the interior of the ridge. Passage ceiling elevations extending up to 22 m above sea level may be related to former mixing zones (haloclines) or water tables. The centrally located main entrance is in a 40 m diameter collapsed depression. From this breakdown entrance chamber, partially flooded passages extend to the east and north. Clear water in these passages is generally about 0.5–1 m deep, although depths upwards of 15 m are present in several areas farther into the cave. Scattered throughout the cave, many isolated pools fluctuate tidally indicating the presence of subterranean connections between them. Conch Bar Cave has the second highest diversity in the Turks and Caicos, with 14 recorded stygbites, eight of which are endemic from the islands (see [Supplemental Table](#)).

Caves in South Caicos Island

The Fountain is a tidal spring with brackish water flowing from a narrow crack, being used as the water supply to flood neighboring salt flats. This is the only system known from South Caicos, with only a single recorded stygbite (see [Supplemental Table](#)).

Fauna

Based on the review of all published references for the islands, as well as our new results, 35 anchialine species across three phyla have been recorded in the Turks and Caicos. These include three undetermined species from earlier expeditions (see [Supplemental Table](#)), plus three new discoveries during the “Caicos Caves III Expedition”. Crustacea comprise most of the records, being represented by 28 species. Among Crustacea, Copepoda is the most numerous group with 12 species (4 Cyclopoida, 8 Calanoida), of which

five are considered stygobitic (see above). Remipedia is the second largest crustacean group with five species, all stygobitic. Ostracoda and Decapoda have three known species each. While the decapods are all stygobitic, only one ostracod is considered to be stygobitic. Amphipoda is represented by two stygobitic species, while only single species are known for Leptostraca, Stygiomysida and Isopoda.

Other phyla represented in the subterranean environments of the Turks and Caicos Islands are Mollusca, with four species, and Annelida, with three species. All the annelids are considered stygobitic, as opposed to the mollusks, which are exclusively epigeal taxa, only capable of surviving at cave entrances.

During the “Caicos Caves III” faunal investigations, we recovered three new cave exclusive species, including two annelids belonging to the genera *Mesonerilla* and *Speleonerilla*, and a remipede possibly belonging to a new genus.

A detailed overview of the most relevant anchialine species recorded throughout the Turks and Caicos Islands, including newly collected material, is provided below, including their distribution, phylogenetic affinities and some general remarks. These species are selected based on their phylogenetic or ecological relevance (stygobites) within the cave systems. Accidental species, records lacking formal identification or exclusively epigeal species known from cave entrances are only mentioned in [Supplemental Table](#).

Phylum Annelida

Suborder Aphroditiformia

Family Polynoidae

Pelagomacellicephala iliffei Pettibone, 1985

Fig. 2A

Material examined. Turks and Caicos Islands, North Caicos Island, Cottage Pond, 9 January 2019, 33 m, 1 specimen (juvenile), USNM 1524287; 10 January 2019, 33-44 m, 3 specimens, USNM 1524314, USNM 1524315, USNM 1524316.

Distribution. Previously only known from Conch Bar Cave, Middle Caicos Island (type locality), but with new collections from Cottage Pond, North Caicos Island.

Remarks. Stygobitic. This is a very rare species that has only been collected twice after its original species description. It is a predator, typically swimming in saline waters of the cave water column. *Pelagomacellicephala iliffei* originally was known from a single cave locality in Middle Caicos at shallow depths (1–1.5 m), but this latest expedition expands both its distribution and depth range to include Cottage Pond on North Caicos. Individuals putatively identified as *P. iliffei* have been collected throughout the Bahamas, including the islands of Exumas, Eleuthera, Cat and Long, although they differ in body size and number of segments; constituting genetically distinct evolutionary entities (Gonzalez et al., 2017).

Pelagomacellicephala iliffei is closely related to the only other known anchialine cave scale worm, *Gesiella jameensis* (Hartmann-Schröder, 1974) from

La Corona lava tube in Lanzarote, Canary Islands, Spain (Martínez et al., 2016a). Both species are phylogenetically related to members of the subfamily Macellicephalinae (Gonzalez et al., 2018; Martínez & Gonzalez, 2018), and therefore, putatively have a deep sea ancestry (Gonzalez et al., 2018; Zhang et al., 2018).

Family Nerillidae

Mesonerilla sp.

Fig. 2B

Material examined. Turks and Caicos Islands, Middle Caicos Island, Conch Bar Cave, 4 January 2019, 0.5-2.0 m cave pools, 2 specimens, USNM 1524205, USNM 1524206.

Distribution. Only known from Conch Bar Cave, Middle Caicos Island.

Remarks. Stygobitic. Members of this genus typically inhabit interstitial marine sands (Worsaae, 2014). However, in anchialine caves, related species are found in coarse sand sediments or lapilli patches as well as hovering over fine silty sediment (Worsaae et al., 2009). Interstitial or epibenthic species of *Mesonerilla* are deposit feeders, collecting biofilms or deposited organic matter with the help of their club-shaped palps and buccal ciliation. The records presented herein are the first for the genus from the Turks and Caicos.

Mesonerilla sp. is characterized by the presence of a mid-ventral terminal prolongation of the pygidium, a feature shared by the marine interstitial species *M. katharinae* Worsaae, Mikkelsen & Martínez, 2019 and *M. peteri* Worsaae, Mikkelsen & Martínez, 2019 from the Caribbean; as well as for the anchialine species *M. xurxoi* Worsaae, Mikkelsen & Martínez, 2019 from Lanzarote and three undescribed species from Bermuda, México and Cuba (Worsaae et al., 2019a).

Speleonerilla sp.

Fig. 2C

Material examined. Turks and Caicos Islands, Middle Caicos Island, Conch Bar Cave, 4 January 2019, 0.5-2.0 m cave pools, 2 specimens, USNM 1524243, USNM 1524244.

Distribution. Only known from Conch Bar Cave, Middle Caicos Island.

Remarks. Stygobitic. All animals were collected from the water column using a plankton net. This genus was originally described from anchialine caves of Bermuda as *Longipalpa* (Worsaae et al., 2004), but was recently changed to *Speleonerilla* as the previous name was preoccupied (Worsaae et al., 2019b). *Speleonerilla* only inhabits anchialine caves, being found anywhere between brackish and fully haline waters in twilight and constant dark zones. Unlike all other Nerillidae, members of *Speleonerilla* are suspension feeders and live in the water column. This is the first record of the genus in the Turks and Caicos.

Speleonerilla is sister to several interstitial species of the genus *Mesonerilla*, suggesting that the lineage colonized the water column of anchialine caves

from marine interstitial environments (Worsaae, 2005). Phylogenetic analyses have found the genus monophyletic, with *S. isa* Worsaae, Gonzalez, Kerbl, et al., 2018, from Lanzarote, branching near a clade containing the Caribbean species (Worsaae et al., 2019a). *Speleonerilla* sp. from the Turks and Caicos resembles other Caribbean species morphologically, but unpublished DNA sequences indicate that it may represent a new species (Worsaae et al. unpublished). Microscopical examinations of, e.g., gonoducts and ciliation patterns are currently being conducted in search of diagnostic morphological features.

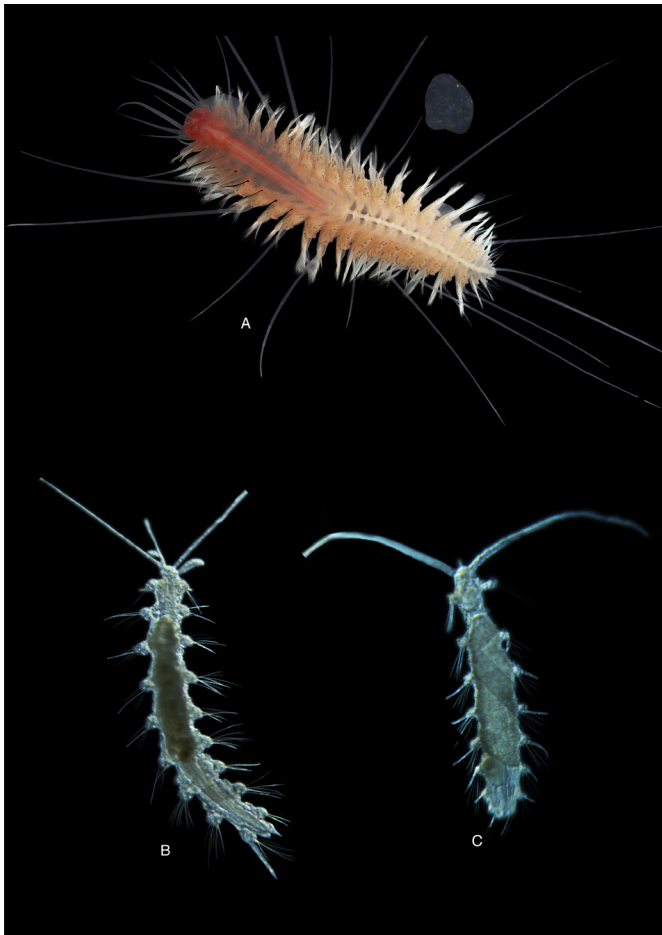


Fig. 2. Anchialine annelids of the Turks and Caicos Islands. A) *Pelagomacellicephala iliffei*; B) *Mesonerilla* sp.; C) *Speleonerilla* sp. Photos by Jørgen Olesen, Brett C. Gonzalez and Katrine Worsaae. Images not to scale.

Phylum Arthropoda

Class Copepoda

Order Calanoida

Family Epacteriscidae

Azygonectes plumosus Fosshagen & Iliffe, 2007
see Fosshagen & Iliffe (2007)

Distribution. The type locality is Cottage Pond, North Caicos Island, Turks and Caicos Islands, but is also known from Old Blue Hill Cave, Providenciales, Turks and Caicos Islands.

Remarks. Stygobitic. Found only in the fully haline water column in constant dark zones. This species has only been collected during its discovery. It can be distinguished from other epacteriscids in the Turks and Caicos by the presence of an extremely long setae V on the left side of the caudal rami.

The only other species described from this genus is *A. intermedius* Fosshagen & Iliffe 2007, exclusively known from caves in Andros and Exuma islands, Bahamas. Both species of *Azygonectes* typically share their habitat with other copepod species, including cyclopoids and ridgewayiid calanoids, which most likely constitute prey items.

Epacteriscidae entirely consists of stygobitic species (Fosshagen & Iliffe, 2004a), except for *Miheptneria abyssalis* Andronov, 2007, which has been recorded in the northeast Atlantic at 4622 m deep. Therefore, a deep-sea affinity can be attributed to the family.

Bofuriella spinosa Fosshagen & Iliffe, 2007
see Fosshagen & Iliffe (2007)

Distribution. Only known from the type locality, Conch Bar Cave, Middle Caicos, Turks and Caicos Islands.

Remarks. Stygobitic. Only collected once from the water column in shallow tidal pools in Conch Bar Cave, most of which are open and exposed to low levels of light. These pools frequently accumulate guano from resident bat populations and range from brackish to fully haline, suggesting its tolerance to varying salinities.

Two additional species in the genus are known from the Bahamas: *B. parvorata* Fosshagen & Iliffe 2007 from Cat Island and *B. vorata* Fosshagen, Boxshall & Iliffe 2001 from the Exuma Cays (Fosshagen et al., 2001; Fosshagen & Iliffe, 2007). As with other epacteriscids, all species of *Bofuriella* are raptorial predators.

Caiconectes antiquus Fosshagen & Iliffe, 2007
see Fosshagen & Iliffe (2007)

Distribution. The type locality is designated as Cottage Pond, North Caicos Island, Turks and Caicos Islands; however, additional specimens have been collected in Conch Bar Cave on Middle Caicos Island, and Old Blue Hill Cave on Providenciales, Turks and Caicos Islands.

Remarks. Stygobitic. *Caiconectes* is a monotypic genus endemic from Caicos Islands (Fosshagen & Iliffe, 2007), found across a wide range of depths and only from the water column. It may be found in entrance pools, twilight or in constant darkness zones. This monotypic species is rarely observed, but has been collected in several localities throughout the Turks and Caicos. Hydrological conditions at the time of collection show high tolerances to variabilities in salinity, temperature and oxygen. *Caiconectes* has the appearance of a typical hyperbenthic calanoid with raptorial feeding.

Erebnectoides macrochaetus (Fosshagen & Iliffe, 1994)

see Fosshagen & Iliffe (1994); Fosshagen et al. (2001)

Distribution. Only known from two caves. The type locality is The Hole, Providenciales, Turks and Caicos Islands, with additional records from Conch Bar Cave, Middle Caicos, Turks and Caicos Islands.

Remarks. Stygobitic. This rare monotypic genus is endemic from Caicos Islands, where it is only known from shallow areas of two anchialine caves with intermittent light levels. It is morphologically similar to *Erebonectes*, represented by the Bermudian endemic species *E. nesioticus* Fosshagen 1985 (Fosshagen & Iliffe, 1985). As other epacteriscids, *E. macrochaetus* is a raptorial predator on small swimming cave organisms.

Family Fosshageniidae

Fosshagenia ferrari Suárez-Morales & Iliffe, 1996
see Suárez-Morales & Iliffe (1996)

Distribution. Only known from the type locality, Conch Bar Cave, Middle Caicos Island, Turks and Caicos Islands.

Remarks. Stygobitic. This rare species is exclusively known from a single collection in the shallow, open pools of Conch Bar Cave (0.5-1 m depth), which are subject to periods of illumination and variability in salinities.

The genus *Fosshagenia* is known from one additional species, *F. suarezi* Fosshagen & Iliffe 2004a, endemic to Grand Bahama (Bahamas) (Fosshagen & Iliffe, 2004a). The family Fosshageniidae also includes deep-sea species of the genus *Temoropia* (Boxshall & Halsey, 2004).

Class Malacostraca

Order Amphipoda

Family Hadziidae

Bahadzia stocki Holsinger, 1985
Fig. 3A

Material Examined. Turks and Caicos Islands, Providenciales, The Hole, 8 January 2019, 4 – 6 m, 9 specimens, USNM 1524279-1524285.

Distribution. This amphipod inhabits several caves on Providenciales, including Airport Cave (type locality), The Hole and Snake Cave.

Remarks. Stygobitic. This species is known from brackish waters in anchialine cave pools and flooded passages, tolerating extremely low oxygen concentrations. *Bahadzia stocki*, while only known from three localities, is quite common, and in Airport Cave, is associated with several other crustaceans including remipedes.

The genus *Bahadzia* includes ten additional species from the Caribbean. Bahamas: *B. obliqua* Stock, 1986 (Cat Islands); *B. setimana* Stock, 1986 (South Andros); and *B. williamsi* Holsinger, 1985 (Grand Bahama and Abaco). Cuba: *B. yagerae* Ortiz & Pérez, 1995 and *B. patilarga* Sawicki, Holsinger, Ortiz & Pérez 2003 (Matanzas, Cuba). Hispaniola: *B. latipalpus* Stock, 1986 (Haiti) and *B. jaraquensis* Jaume & Wagner 1998 (Dominican Republic). México: *B. setodactylus* Holsinger, 1992 (Cozumel) and *B. bozanici* Holsinger 1992 (Cozumel and Yucatán Peninsula). Cayman Islands: *B. caymanensis* Sawicki & Holsinger, 2004 (Grand Cayman). The monophyly of the genus is supported by morphological phylogenies, but a molecular phylogeny of the group is still lacking.

Family Pardaliscidae

Spelaeonicippe provo Stock & Vermeulen, 1982
Fig. 3B

Material examined. Turks and Caicos Islands, Middle Caicos Island, Conch Bar Cave, 4 & 7 January 2019, 0.5 – 2.0 m cave pools, 25 specimens, USNM 1524199, USNM 1524203, USNM 1524215-1524216, USNM 1524246-1524256, USNM 1524260-1524263.

Distribution. This species is widely distributed in the Lucayan Archipelago. From the Turks and Caicos Islands, it occurs in caves on Providenciales, including Airport Cave (type locality, cited as “nameless water hole NW of the airfield” in the original reference), The Hole, Snake Cave and Old Blue Hill Cave, and on Middle Caicos Island from Conch Bar Cave. Additional localities include several Bahamian Islands, including Abaco (Dan’s Cave) and the Exuma Cays – Great Guana Cay (Oven Rock Cave) (Stock & Vermeulen, 1982; van der Ham, 2002).

Remarks. Stygobitic. Specimens were collected in shallow to intermediate depths (~1-10 m) in cave pools where they were found in dimly illuminated to completely dark waters. No obvious morphological differences have been observed between the different cave populations of *S. provo* across the Lucayan Archipelago, but molecular analyses may reveal the presence of cryptic species or evolutionary units as it has been showed in other stygobites with similar distribution patterns (Gonzalez et al., 2017).

The genus *Spelaeonicippe* includes one additional species, *S. buchi* (Andres 1972), endemic to a volcanic cave on Lanzarote, Canary Islands, Spain (Andres, 1975). *Spelaeonicippe provo* and *S. buchi*, along with *Antronicippe serrata* Stock & Iliffe 1990, which is endemic from Grieta de la Caleta de la Torta on Santa Cruz Island, Galapagos (Stock & Iliffe, 1990), belong to the family Pardaliscidae, otherwise entirely consisting of deep-sea species. This suggest a deep sea affinity for species of *Spelaeonicippe*, yet the relationships between deep sea and cave species in these groups have not yet been investigated (Iliffe et al., 1984; Martínez et al., 2016a).

Order Isopoda

Family Cirolanidae

Bahalana caicosana Botosaneanu & Iliffe, 2003
Fig. 3C

Material examined. Turks and Caicos Islands, Middle Caicos Island, Conch Bar Cave, 4 January 2019, 0.5–2.0 m cave pools, 1 specimen, USNM 1524212.

Distribution. The type locality is Cottage Pond, North Caicos Island with additional records from Conch Bar Cave, Middle Caicos Island, Turks and Caicos Islands.

Remarks. Stygobitic. The type material of this isopod was collected from 25-46 m depths in Cottage Pond, as opposed to the shallow depths in Conch Bar Cave in which they were found during the Caicos Caves III expedition. The genus *Bahalana* includes five additional species from the Bahamas and Cuba. Bahamian species include *B. abacoana* Botosaneanu

& Iliffe, 2006 (Abaco), *B. cardiopus* Notenboom, 1981 (Acklins and Mayaguana), *B. exumina* Botosaneanu & Iliffe, 2002 (Exumas) and *B. geracei* Carpenter 1981 (Andros, Abaco, Grand Bahama and San Salvador); while one Cuban species is known, *B. bowmani* Ortiz, Lalana & Pérez 1997 (Ciénaga de Zapata, Matanzas).



Fig. 3. Assorted anchialine crustaceans of the Turks and Caicos Islands. A) *Bahadzia stocki*; B) *Spelaeonicippe provo*; C) *Bahalana caicosana*; D) *Speonebalia* cf. *cannoni*; E) *Stygiomysis clarkeri*. Photos by Jørgen Olesen, Sarit B. Truskey and Brett C. Gonzalez. Images not to scale.

Order Decapoda

Family Agostocaridiidae

Agostocaris williamsi Hart & Manning, 1986

Fig. 4A

Material examined. Turks and Caicos Islands, North Caicos Island, Cottage Pond, 9 January 2019, 12-20 m, 1 specimen, USNM 1524288.

Distribution. Big Fountain Blue Hole, Cat Island, Bahamas is the type locality with additional Bahamian locations, including Old Freetown Cave, Grand Bahama Island. From the Turks and Caicos Islands, individuals have been collected in Airport Cave, Providenciales, as well as Cottage Pond, North Caicos Island.

Remarks. Stygobitic. Our specimens were found swimming in the water column or near the bottom, where the species was comparatively abundant. *Agostocaris bonzanici* has been observed feeding on ground meat in aquaria, suggesting that species of the genus might be scavengers (Mejía-Ortiz, 2010).

The family Agostocaridiidae includes three other cave species: *A. acklinsensis* Álvarez, Villalobos & Iliffe, 2004 from Acklins Island (Bahamas); *A. bozanici* Kensley, 1988 from Yucatán Peninsula (México); and *A. zabaletai* Mejía-Ortiz, Yañez & López-Mejía, 2017 from Cozumel Island (México) (Kensley, 1988; Alvarez et al., 2004; Mejía-Ortiz et al., 2017). Species of the family morphologically resemble those in the anchialine family Anchialocarididae, as well as the deep-sea families Alvinocarididae and Mirocarididae (Alvarez et al., 2004; Mejía-Ortiz et al., 2017), suggesting that ancestors of *Agostocaris* might have colonized anchialine environments from the deep sea.

Family Barbouriidae

Barbouria cubensis (von Martens, 1872)

Fig. 4B

Material examined. Turks and Caicos Islands, Middle Caicos Island, Conch Bar Cave, 4 & 7 January 2019, 0.5–2.0 m deep cave pools, 3 specimens, USNM 1524202, USNM 1524257, USNM 1524259.

Distribution. Widespread throughout the Bahamas, the Turks and Caicos Islands, Bermuda, Cuba, Cayman Islands, Jamaica and in a few locations along the Caribbean coast of the Yucatán Peninsula, México.

Remarks. Stygobitic. Shrimp were collected from shallow cave pools, where they were found swimming near the guano-rich bottom or amongst the crevices. Pools were in total darkness or dimly illuminated and contained brackish waters. This species is probably a scavenger based on their attraction to baited traps, as well as observations from aquaria (Mejía-Ortiz, 2010; Ditter et al., 2015).

Barbouria cubensis is one of the first described anchialine species, initially reported from Cuba (Barbour, 1945) and afterwards throughout the Caribbean from a wide range of habitats, including open pools and dark cave sections containing brackish to fully haline waters. Despite this broad distribution, animals from geographically distant localities show morphological variation but lack genetic structure based on mitochondrial markers (Ditter et al., 2019), suggesting that they disperse across different island banks. Larval dispersal across distant islands has been also suggested for the Indo-Pacific anchialine shrimp *Metabetaus lohena* (Russ et al., 2010).

The family Barbouriidae includes *B. cubensis*, together with the Mexican *B. yanezi* Mejía, Zarza & López, 2008, four species of the genus *Parhippolyte* and the deep sea genus *Ligur*, suggesting a potential deep sea origin for these anchialine shrimp (Hart Jr et al., 1985).

Family Atyidae

Typhlatya garciai Chace, 1942

Fig. 4C

Material examined. Turks and Caicos Islands, Providenciales, Old Blue Hill Cave, 5 January 2019, 01-04 m, 16 specimens, USNM 1524213, USNM 1524219-1524226. Middle Caicos Island, Conch Bar Cave, 4 January 2019, 0.5-2.0 m cave pools,

10 specimens, USNM 1524197-1524198, USNM 1524201, USNM 1524204, USNM 1524207-1524211.

Distribution. The type locality is Cuba, Holguín Province, Banes; however, *T. garciai* has been recorded in the Turks and Caicos from the following localities, Conch Bar Cave, Middle Caicos Island, and Old Blue Hill Cave and Snake Cave on Providenciales. From Cuba, localities include Gran Caverna de Santo Tomás (Pinar del Río), cave “Las Cuatrocientas Rozas” in Potrero de Molino and several casimbas (local name for large cracks and crevices amongst the coralline rocks) around Puerto Pesquero (both in Holguín).

Remarks. Stygobitic. These small shrimp are found in waters of salinities ranging from fresh to fully haline. Large populations can literally carpet the bottom at shallow depths of some illuminated cave pools. Interestingly, Botello et al., (2013) found *T. garciai* to be genetically identical to *T. kakuki* Alvarez, Iliffe & Villalobos, 2005 from caves on Acklins Island in the Bahamas. Given the slight morphological variations, the underlying genetic diversity appears to be low, and population level genetics are needed to understand relationships between individuals from the known localities.

Order Leptostraca

Family Nebaliidae

Speonebalia cannoni Bowman, Yager & Iliffe, 1985
Fig. 3D

Material examined. Turks and Caicos Islands, North Caicos Island, Cottage Pond, 6 & 7 January 2019, 22–44 m, 4 specimens, USNM 1524241-1524242, USNM 1524264-1524265.

Distribution. The type locality is Airport Cave with additional records from The Hole, Providenciales, Cottage Pond, North Caicos Island, and from caves in Great Abaco (Bahamas).

Remarks. Stygobitic. Our specimens were observed swimming in the water column of the cave, in total darkness. Specimens were collected from two caves (The Hole and Cottage Pond), but not in Airport Cave due to water pollution. The wide distribution of this species across the Turks and Caicos and the Bahamas needs to be reinvestigated using molecular methods and more detailed morphological studies.

Class Ostracoda

Order Halocyprida

Deeveya spiralis Kornicker & Iliffe, 1985
see Kornicker & Iliffe (1985)

Material examined. Turks and Caicos Islands, North Caicos Island, Cottage Pond, 7 January 2019, 1 specimen. No museum number assigned.

Distribution. Known from the type locality, The Hole Cave, Providenciales, Turks and Caicos Islands; as well as from Cottage Pond, North Caicos Island.

Remarks Stygobitic. Our specimen was collected using a vial from the water column, where it was seen swimming in total darkness.

Six additional described species make up the genus, all of them from caves in the Bahamas: *D. medix*

Kornicker in Kornicker, Yager & Williams, 1990 from Grand Bahama, Exuma and Abaco; *D. bransoni* Kornicker & Palmer 1987 and *D. hirpex* Kornicker in Kornicker, Yager & Williams, 1990 from Andros; *D. exleyi* Kornicker & Iliffe 1998 from the Exumas; and *D. jillae* Kornicker & Iliffe 1989 from Eleuthera. Molecular studies are needed to further understand relationships between these species.

Order Stygiomysida

Family Stygiomysidae

Stygiomysis clarkei Bowman, Iliffe & Yager, 1984
Fig. 3E

Material examined. Turks and Caicos Islands, Middle Caicos Island, Conch Bar Cave, 4 & 7 January 2019, 0.1 – 2.0 m deep cave pools, 6 specimens, USNM 1524195-1524196, USNM 1524214, USNM 1524258, USNM 1524266, USNM 1524267.

Distribution. Known from Conch Bar Cave (type locality), Middle Caicos Island, and Snake Cave, Providenciales. This species is also known from Lucayan Caverns, Grand Bahama Island, Bahamas (Bowman et al., 1984; Pesce & Iliffe, 2002).

Remarks. Stygobitic. These blind, unpigmented crustaceans were found swimming near the guano and mud bottoms of shallow cave pools. Pools were in total darkness or faintly illuminated.

Stygiomysis is a genus with seven described exclusively stygobitic species distributed throughout the Caribbean and Italy. *Stygiomysis aemete* Wagner, 1992 from Pedernales (Dominican Republic); *S. cokei* Kallmeyer & Carpenter, 1996 from Quintana Roo and Yucatán (Yucatán Peninsula, México); *S. holthuisi* (Gordon 1958) from Anguilla, Saint Martin, Puerto Rico, Grand Bahama, Quintana Roo and Yucatán (México); *S. ibarrae* Ortiz, Lalana & Perez 1996 from Matanzas (Cuba); *S. major* Bowman, 1976 from Jackson Bay (Jamaica); and *S. hydruntina* Caroli 1937 from Puglia (southern Italy).

Class Remipedia

Order Nectiopoda

Family Godzilliidae

Godzillius robustus Schram, Yager & Emerson, 1986
Fig. 5A

Material examined. Turks and Caicos Islands, North Caicos Island, Cottage Pond, 9 January 2019, at 24–51 m depths, 3 specimens, USNM 1524345, USNM 1524347, USNM 1524349.

Distribution. Known only from the type locality, Cottage Pond, North Caicos Island (Schram et al. 1986).

Remarks. Stygobitic. Observed swimming in the water column, together with the remipedes *Kaloketos pilosus* Iliffe & Yager, 2004 and *Lasionectes entrichoma* Yager & Schram, 1986 in deeper waters with total darkness and fully haline salinities.

Godzillius is a remipede genus with two large and robust species distributed in the Caribbean. The other species of the genus is *G. fuchsi* Gonzalez, Singpiel & Schlagner, 2013, described from Dan’s Cave and Ralph’s Sink on Abaco Island, Bahamas, where it co-



Fig. 4. Anchialine decapods of the Turks and Caicos Islands. A) *Agostocaris williamsi*; B) *Barbouria cubensis*; C) *Typlatya garciai*. Photos by Sarit B. Truskey and Brett C. Gonzalez. Images not to scale.

occurs with at least five additional remipedede species (Dan's Cave) (Gonzalez et al., 2013). Currently this is the only remipedede genus known from both the Turks and Caicos and the Bahamas.

Family Cryptocorynetidae

Kaloketos pilosus Koenemann, Iliffe & Yager, 2004

Fig. 5B

Material examined. Turks and Caicos Islands, North Caicos Island, Cottage Pond, 7 & 9 January 2019, at 24-51 m depths, 2 specimens, USNM 1524329, USNM 1524342.

Distribution. Known only from the type locality, Cottage Pond, North Caicos Island (Koenemann et al., 2004).

Remarks. Stygobitic. Observed swimming in the water column, together with the remipededes *G. robustus* and *L. entrichoma* in deeper waters with total darkness and fully haline salinities.

This monotypic genus is so far endemic of Cottage Pond.

Family Speleonectidae

Lasionectes entrichoma Yager & Schram, 1986

Fig. 5C

Material examined. Turks and Caicos Islands, Providenciales, Old Blue Hill Cave, 5 January 2019, at 22 m depth, 4 specimens, USNM 1524318-1524321.

North Caicos Island, Cottage Pond, 7 & 9 January 2019, at 24-51 m depths, 21 specimens, USNM 1524323-1524328, USNM 1524330-1524333, USNM 1524335-1524341, USNM 1524343, USNM 1524346, USNM 1524348, USNM 1524350.

Distribution. Known from three locations in the Turks and Caicos Islands, Old Blue Hill Cave (type locality) and Airport Cave on Providenciales, and Cottage Pond, North Caicos Island.

Remarks. Stygobitic. Observed swimming in the water column, together with the remipededes *G. robustus* and *K. pilosus* in deeper cave waters with total darkness and fully haline salinities. *Lasionectes entrichoma* is by far the most abundant remipedede species collected on this current expedition, particularly in Cottage Pond. This species was absent from Airport Cave, from where it has previously been reported, likely due to water pollution.

Family Micropacteridae

Micropacter yagerae Koenemann, Iliffe & van der Ham, 2007

Fig. 5D

Material examined. Turks and Caicos Islands, Providenciales, Old Blue Hill, 5 January 2019, at 22 m depth, 2 specimens, USNM 1524317, USNM 1524322.

Distribution. Known only from its type locality, Airport Cave, and Old Blue Hill, Providenciales.

Remarks. Stygobitic. Observed swimming in the water column with the remipedede *L. entrichoma*. *Micropacter yagerae* was not collected at its type locality (Airport Cave) during this expedition, which we found degraded and completely depleted of life due to water pollution.

The generic name *Micropacter* means 'tiny hunter' and refers to the small size of the individuals, superficially resembling juveniles of the family Speleonectidae.

Family c.f. Morlockiidae

***Morlockia* sp. nov.**

Fig. 5E

Material examined. Turks and Caicos Islands, Middle Caicos, Conch Bar Cave, 5 & 7 January 2019, at < 0.5 m depth, 3 specimens, USNM 1524194, USNM 1524334, USNM 1524344

Distribution. Known only from the type locality, Conch Bar Cave, Middle Caicos Island.

Remarks. Stygobitic. Our specimens are unusual for remipededes in that they were collected from brackish (21 ppt) surface waters of small, shallow pools, rather than higher salinity water in the deep interior of underwater caves. Only *Speleonectes epilimnius* Yager & Carpenter, 1999 has been found in similar conditions, described from a brackish pool (24-25 ppt) at the back of Major's Cave (San Salvador, Bahamas) (Carpenter, 1999). Our specimens co-occurred with *S. clarkei*.

These specimens are under study, but preliminary attempts to identify the species based on both

morphology and molecular data limited to one marker (16S rRNA) have been so far inconclusive.



Fig. 5. Remipedes of the Turks and Caicos Islands. A) *Godzillius robustus*; B) *Kaloketos pilosus*; C) *Lasioneectes entrichoma*; D) *Micropacter yagerae*; E) *Morlockia* sp. nov. All photos by Jørgen Olesen. Images not to scale.

DISCUSSION

Since the first scientific expedition to the Turks and Caicos Islands in 1975, a total of 32 species of animals have been recorded from aquatic subterranean environments. The Caicos Caves III expedition recorded three additional species, including two new annelids and a new remipede, bringing the total number of known anchialine fauna in the Turks and Caicos to 35, 22 of which are known stygobites. Four of these records lack any formal identification or detailed description, but we have included them as they are historical records that were listed during description of accompanying fauna (Stock & Vermeulen, 1982; Koenemann et al., 2004), providing important information regarding the diversity that these systems sustain (see [Supplemental Table](#)). These records include one mollusk (Cochliopidae) and three copepod crustaceans (Oithonidae, Pseudodiaptomidae, Ridgewayiidae; [Supplemental Table](#)). Some of this unknown diversity had been collected from hand-dug wells breaching the groundwater, which are known to additionally host epigeal freshwater dispersalist species (see for example Pesce 1985; Bowman 1986). Recent expeditions, including Caicos Caves III, omitted

sampling of this type due to sediment infilling of the wells and their limited access to subsurface haline waters, possibly missing numerous representatives (mainly crustaceans) throughout the Turks and Caicos.

As in prior expeditions, we too recovered potentially new species (two annelids and one remipede), as well as new records for the Turks and Caicos. Our report of *Mesonerilla* and *Speleonerilla* (both belonging to family Nerillidae, Annelida) is of particular interest because the only annelid previously known from the Turks and Caicos caves was the polynoid scale worm, *Pelagomacellicephala*. The presence of *Mesonerilla* in Conch Bar Cave is not surprising; it is a widespread genus of annelid, found in both cave and non-cave interstitial habitats throughout the world and typically lacks obvious cave-specific adaptations (Worsaae et al., 2009, 2019a). *Speleonerilla*, in contrast, is a cave-adapted genus, currently known from disjunct localities, including Yucatán Peninsula (México), the Bahamas, Bermuda, Cuba and Lanzarote (Canary Islands), secondarily adapted to feed on suspended organic matter in the water column of anchialine caves (Worsaae et al., 2019b). Currently this is the southernmost record for *Speleonerilla*. Their widespread occurrence in the Caribbean and Atlantic suggests that increased sampling efforts would likely result in the discovery of additional species from anchialine habitats elsewhere in the region.

Our most unexpected discovery of this expedition was the putative new remipede species from Conch Bar Cave, Middle Caicos. Surprisingly, specimens were found in small pools less than 1 m deep. These collections all happened during an incoming tide, reiterating the importance and presence of a spelean corridor, permitting unhindered movements throughout the carbonate platform. Occasionally other species have also been found in shallow anchialine cave pool habitats (i.e., *Morlockia ondinae* García-Valdecasas, 1984 in Lanzarote, Martínez pers. obs.). This is the first record of a remipede from Conch Bar Cave and from the island of Middle Caicos, making it the fifth remipede species for the Turks and Caicos Islands.

Similar to other Caribbean localities (i.e., Yucatán Peninsula and the Bahamas), several of the anchialine species found in this expedition are known from multiple Caicos islands (i.e., Providenciales, Middle, North) or have broader distributions across the Caribbean and Atlantic (see [Supplemental Table](#)). Diving collections from the Caicos Caves III expedition has extended the known range of *P. illiffei* within the Caicos Bank, originally described from shallow cave pools in Conch Bar Cave, Middle Caicos, to now also inhabit deep cave waters in Cottage Pond, North Caicos Island. While specimens from both localities are not currently available for genetic comparisons, morphologically, these annelids appear identical. It remains unknown what degree of connectivity exists between the Turks and Caicos Islands; however, Gonzalez et al., (2017) showed evidence of an active spelean corridor on the island of Eleuthera, Bahamas, whereby genetically identical species of *P. illiffei* were found from caves in excess of 100 km apart.

The idea of a spelean corridor is not new – originally and somewhat flippantly suggested by Chace & Hobbs (1969), the idea was largely overlooked or dismissed until recently. Nevertheless, continued faunal surveys incorporating molecular methods (Alvarez et al., 2015) have shown this concept to be a viable means towards the broad, regional distributions seen in anchialine fauna (Santos, 2006; Hunter et al., 2008; Botello & Álvarez, 2010). In the Turks and Caicos, several crustaceans are also likely utilizing such means for distribution, including *Agostocaris williamsi*, *Barbouria cubensis*, *Lasioneetes entrichoma*, *Stygiomysis clarkei*, *Spelaeonicippe provo* and *Typhlatya garciai*, all of which are found in multiple island and cave localities on the Caicos Bank. Similar to *P. iliffei*, some of these crustaceans are also known from locations outside the Turks and Caicos Islands, including the Bahamas, Yucatán Peninsula, Cuba, Jamaica and the Lesser Antilles, depending on the species. While phylogeographic analyses are lacking for many of these species, it is likely that they comprise different evolutionary histories related to the presence of certain functional traits (i.e., larvae, body size, salinity tolerance) and the age of each lineage.

Considering the new records presented herein, it is evident that substantial undocumented diversity is still to be found in the anchialine realm. New species are constantly described even in relatively well-investigated and easily accessible anchialine systems, including for example those in Yucatán Peninsula and Lanzarote, where six (Rubio et al., 2015; Suárez-Morales et al., 2017b, 2017a; Angyal et al., 2018; Grego et al., 2019; Sánchez & Martínez, 2019) and five new species (Martínez et al., 2016b; Gobert et al., 2019; Worsaae et al., 2019a, 2019b), respectively, have been described within the last five years. These numbers highlight the importance of continued exploration, particularly considering that some anchialine species may use different habitats rather than caves, appearing only occasionally in caves (Martínez et al., 2013). While none of the anchialine species in the Turks and Caicos are currently protected, their small populations, relatively low densities and endemism are sufficient reasons to encourage this situation to change. In addition, a better understanding of anchialine communities would allow us to better predict how these presumably isolated but delicate ecosystems will respond to ongoing environmental change and human impacts (Mammola et al., 2019).

Threats to Caicos Caves and its Biodiversity

Caves are rare and fragile environments that once damaged or destroyed, are lost forever. Low densities of endemic, blind and depigmented organisms, often known from only a single location, are constantly at risk or under threats of extinction (Mammola et al., 2019). Cave waters are particularly susceptible to anthropogenic disturbances as they already exhibit extreme physiochemistries, being characterized as lightless, oxygen and food deprived habitats (Gonzalez et al., 2011). Cave animals living in these environments are often forced to switch for short periods of time to less efficient anaerobic metabolism in order to

survive periods of low oxygen stress (Bishop et al., 2004). These stressors vary in form, but generally, subterranean ground waters are highly susceptible to pollution and contamination through inadequate wastewater disposal, leeching from solid waste landfills or unsanitary use of caves and groundwater (Iliffe, 1979; Martínez et al., 2020).

In 2013, Iliffe became aware that an extension of the Providenciales Airport Parking area was planned near Airport Cave. Previous diving explorations and biological collections from Airport Cave on Providenciales in 1982, 1983 and 2003 resulted in the discovery of five new species of cave-adapted crustaceans making it one of the most biologically significant caves in the country. Letters to governmental departments explaining the importance of this cave and its unique fauna were sent, urging steps be taken to protect and preserve this cave site since the property is owned by the Airport Authority. Completion of the parking area occurred as planned, yet with no obvious or immediate disturbances to the area around the cave entrance. However, upon our most recent 2019 trip to Airport Cave, the entrance pool was found to be devoid of life, likely due to exhaustion of oxygen from the water. Earlier reports several years prior to 2019 from colleagues had similarly reported foul and polluted water conditions for Airport Cave. The exact cause of the oxygen depletion is unclear, but several possibilities exist. Guano from the colony of bats nesting in the cave ceiling may have increased into the pool, resulting in an increase in bacterial utilization. Alternatively, hydrological parameters may have changed as buildup of fine, silty sediments throughout the cave caused a further reduction to subterranean groundwater circulation. However, these two issues are historical processes to caves of the Turks and Caicos Islands, and being that only Airport Cave is afflicted, it is highly suggestive of anthropogenic disturbances. Similar single cave ‘die offs’ have been known elsewhere throughout the Lucayan Archipelago (pers. obs.) and are often traceable back to changes in ground use or water pollution. Perhaps sewage from the adjacent airport complex is further polluting the groundwater, or construction of the airport’s parking lot may have blocked off underground flow channels. Until additional studies are carried out, there is no way to know for sure. Additional concerns and problems and were also observed in 2019 at Old Blue Hill Cave, the only other site on Providenciales where remipedes have been found. While this cave is located in a relatively remote part of the island, a group of people have set up a makeshift encampment, and are using the cave pool for bathing and laundering of clothes. What long-term impact this may have on water quality and the cave fauna is unclear.

In any event, cave species tend to be present in low numbers and constrained to a narrow depth range in small parts of the caves. Due to their highly restricted distribution, low population sizes and environmentally threatened habitats, most Caicos cave animals qualify for classification as endangered. As a result, subterranean environments of the Turks and Caicos Islands are valuable and in need of effective legal

protection, especially as island developments and anthropogenic encroachment continues.

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