A population history of indigenous Bahamian islanders: Insights from ancient DNA

Vanessa Forbes-Pateman1 | Aram Yardumian2 | Miguel Vilar3,4 | Tanya M. Simms5 | Michael P. Pateman1 | William Keegan6

1Bahamas Maritime Museum, Freeport, Grand Bahama, The Bahamas
2Department of History and Social Sciences, Bryn Athyn College, Bryn Athyn, Pennsylvania, USA
3Department of Anthropology, University of Maryland, College Park, Maryland, USA
4Department of Anthropology, University of Pennsylvania, Philadelphia, Pennsylvania, USA
5School of Chemistry and Life Sciences, University of The Bahamas, Nassau, The Bahamas
6Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA

Correspondence
Vanessa Forbes-Pateman, Bahamas Maritime Museum P.O. Box F43119, Freeport, Grand Bahama, The Bahamas.
Email: valianeforbes@gmail.com

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Abstract
Objectives: The Bahamas is an archipelago in the western Atlantic Ocean that stretches over 1000 km, just north of Cuba and east of the Florida Peninsula. Modern DNA studies show that contemporary Bahamians are genetic descendants of European and African ancestors, unlike Cuba, Dominican Republic, and Puerto Rico, where Indigenous descendancy is well documented. For The Bahamas little was known about the genetic ancestry of the Indigenous Lucayans (AD 700–1600) and their relationship to other Indigenous Caribbean populations. In this study, we investigated genetic diversity in Indigenous Lucayans from the Bahamas Archipelago to better understand the phylogeography of their genetic lineages, and to determine their relationship with other Indigenous Caribbean populations.

Materials and methods: We characterized genetic diversity across two uniparental markers in 31 ancient individuals from burial sites on seven Bahamian islands.

Results: We observed significant homogeneity in Lucayan paternal lineages, with only two haplogroups (Q-M902 and Q-Z781) found among them. Mitochondrial lineages were more diverse, with individuals belonging to haplogroup A2, B2, C1b, and C1d1. Four were assigned to a previously unidentified C1d lineage. Of the B2 samples, 7 of 11 belonged to the rare South America/Caribbean haplogroup B2e. This haplogroup was the most prevalent in the Northwest Bahamas while C1, particularly C1d, was more prevalent in the Central and Southern Bahamas.

Discussion: These findings document a complex genetic history with an initial migration from Hispaniola beginning 1300 years ago, and possible gene flow from Cuba to Andros in late Bahamian prehistory.

KEYWORDS
aDNA, Bahamas, Caribbean, haplogroup, Lucayan, mtDNA, Y-chromosome

1 INTRODUCTION

The Bahamas bears the distinction among Caribbean archipelagos of being both the last to be populated by Indigenous Caribbean people and the first to be encountered by and subsequently depopulated by Europeans (Dunn & Kelley, 1989). European explorers observed a distinct array of Indigenous Caribbean peoples when they arrived in the islands at the end of the 15th century. Today, we infer that the diversity of these groups likely reflected multiple dispersion events that date back millennia and originated from various locations in the Caribbean basin (Callaghan, 2003; Granberry & Vescelius, 2004; Rouse, 1992; Wilson, 2007). The biological and cultural connections to these various possible source populations (Rodríguez Ramos, 2013; Rodríguez Ramos et al., 2013), as well as the diversity that occurred...
within the Caribbean itself, are matters of ongoing research with new anthropological genetics studies published each year confirming the general notion that multiple waves of Amerindian peoples traversed and settled the insular Caribbean (Haak & Cooper, 2009; Martínez-Cruzado et al., 2005; Mendizabal et al., 2008; Vilar et al., 2014; Schroeder et al., 2018; Paulino-Ramirez et al., 2019; Fernandes et al., 2021; Nägele et al., 2020; Nieves-Colón et al., 2019). The main outcome is the identification of at least two distinct waves of population expansion (Rouse, 1986, 1992), the first of which occurred around 6000 years ago and is associated with an Archaic Age migration from Central and/or South America. Regarding this wave, it should be noted that a recent genome-wide study reported evidence for two migrations into Cuba at this time (Nägele et al., 2020), however, a more comprehensive analysis of the data refuted this conclusion (Fernandes et al., 2021). The second migration, which began about 2500 years ago, is represented by a Ceramic Age colonization of the Antilles from South America. Both of these unrelated population expansions have been noted using genome-wide data (Fernandes et al., 2021; Nägele et al., 2020) as well as 3D facial (Ross et al., 2020; Ross & Ubelaker, 2010) and dental morphology (Coppa et al., 2008). Interestingly, none of these studies have found evidence for the movement of peoples into the islands from the southern United States, including Florida (cf. Ulloa Hung & Valcárcel Rojas, 2013), but there currently are too few genetic samples from North America to be definitive. Finally, none of these studies have adequately addressed the issue of population movements within the Bahamian archipelago itself.

The earliest evidence for seasonal exploitation in the Bahama archipelago is dated to around 1300 years ago on Grand Turk, Turks and Caicos Islands (TCI) (Carlson, 1999), and was soon followed by permanent occupations in open-air and cave sites. The commencement of permanent settlement in the central Bahamas also has been dated to nearly 1300 years ago (Berman et al., 2013, p. 265) although this date is controversial. The earliest securely dated contexts indicate a wide dispersion of individuals across the entire archipelago by 1000 years ago (Schulting et al., 2021). The first Indigenous inhabitants were called Lucayans, an anglicized version of the Spanish name for the Bahamian archipelago, “las Islas de los Lucayos.” The Spanish name Lucayo is derived from the Arawakan words Lukku Cairi, which glosses as “people of the islands” (Granberry & Vescelius, 2004). It is the only authentic Indigenous ethnonym we have for a Caribbean culture. Although the directionality of early settlement in the Lucayan Islands has not yet been established, two routes have been proposed: one from Cuba to the central Bahamas (possibly arriving first at Exuma or Long Island and then dispersing north and south through the rest of the islands); and a second from Hispaniola to the TCI and then northward up the island chain (Berman & Gnivecki, 1995; Granberry & Vescelius, 2004; Sears & Sullivan, 1978).

Although the larger islands and many smaller cays were settled by AD 1000, the archaeological evidence is equivocal concerning the Lucayan homeland (Berman et al., 2013; Keegan, 1992; Keegan & Hofman, 2017). A limited number of radiocarbon dates point to possible early settlements in both the southern and central islands, and the distribution of nonlocal pottery (identified in terms of style and temper sources) illustrates exchange with both Cuba and Hispaniola. Locally produced Palmetto ware pottery has design motifs that can be classified with the contemporaneous Meilacciad series pottery produced in both Cuba and Hispaniola. Although there is a shift to more interior settlements in Cuba and Hispaniola, the Lucayans maintained a strong preference for coastal settings and lived in smaller villages and hamlets. Like their neighbors, they were tropical horticulturalists who cultivated a variety of crops including manioc, maize, sweet potatoes (Ciofalo et al., 2018; Ciofalo et al., 2019; Sauer, 2008), and obtained the majority of their animal protein from fish and mollusks. In sum, material culture alone is not sufficient to identify their original homeland.

In the centuries after the arrival of Christopher Columbus on San Salvador Island (Bahamas) in 1492, the Lucayans were said to have been enslaved en masse and transported to Spain, Hispaniola, Puerto Rico, and possibly Cuba (Granberry, 1979–1981; Sauer, 2008; Keegan, 1992; Anderson-Córdova, 2017). Peter Martyr, a contemporary of Columbus, reported that 40,000 Lucayans were removed from these islands in the early 1500s (Martir de Angleria, 1899), however, there are no known records of how many Spanish slaving expeditions reached The Bahamas or how these slave raids were conducted. Although some individuals were carried to Hispaniola from Spain, many more were sold and sent to work in the Spanish pearl industry on the islands off the north coast of Venezuela (Granberry, 1979–1981). In 1513, Ponce de Leon reported that the natives of The Bahamas were extinct, except for one elderly woman, La Vieja, who he encountered on Bimini or Grand Bahama (Craton & Saunders, 1999, p. 56). Additionally, in 1521, Secretaries of the Audiencia Lucas Vazquez and Diego Cavallero hired Francisco Gordillo by licenciado to conduct slave raids in the Lucayan Islands. He systematically attempted as much for “three and a half months,” but due to previous expeditions “picking the islands clean” found none (Hoffman, 1990, p. 6). There is not one mention of any Indigenous inhabitants when the British began to settle in The Bahamas in the 17th century (Craton & Saunders, 1999). Nevertheless, recent radiocarbon dates suggest that at least some Lucayans survived into the 17th century, possibly overlapping with British and pirate expeditions (Berman & Gnivecki, 2019; Morsink, 2015; Schulting et al., 2021).

### 1.1 Caribbean genetic diversity

Although no comprehensive mitochondrial DNA study has been previously published for the islands of The Bahamas, genealogical data provided in The Bahamas DNA project (www.familytreedna.com/groups/bahamas-dna) reveal that of the 156 contemporary Bahamian samples included for mtDNA analysis, 28.2% exhibit predominantly African haplogroups (L0, L1, L2, and L3) and 69.9% are characterized by Western Eurasian derived lineages (H, J, K, T, and U). Although the database reports an additional five samples (3.14%) that are characterized by Indigenous Amerindian mtDNA haplogroups A, B4, and C1, only one of these is a contemporary Bahamian islander. The other
four represent ancient remains from Preacher's Cave that were published in 2009 by Haak and Cooper and reanalyzed recently by Fernandes et al. (2021), Native American Y-DNA lineages (Q-M3, Q-L54), on the other hand, are completely absent among contemporary Bahamians (Simms et al., 2011; www.familytreedna.com/groups/bahamas-dna). When compared to The Bahamas, four of the six major Indigenous mtDNA haplogroups (A2, B2, C1b, and D1) have been reported across modern groups in neighboring Cuba, Hispaniola and Puerto Rico (Martínez-Cruzado et al., 2005; Mendizabal et al, 2008; Paulino-Ramírez et al., 2019; Vilar et al., 2014) as well as in contemporary populations from the Lesser Antillean islands of Dominica, St. Vincent, and Trinidad (Benn Torres et al., 2007, 2015) while only a very low frequency (4%) of haplogroup B2 has been reported in The Maroons from Jamaica (Madrilleo et al., 2015). Conversely, the Indigenous Y-DNA haplogroup Q-M3 has been observed in low levels in Trinidad and St. Vincent (Benn Torres et al., 2015). The limited presence of Indigenous mtDNA and Y-haplogroups in modern Bahamians is likely the result of the complete extirpation of the Lucayan inhabitants in the century following the Spanish invasion.

The first skeletal research in the Bahamian archipelago was conducted by Brooks (1889) who described three crania found in caves throughout the islands. Given that caves played a vital role in the lifestyle and spiritual beliefs of the Lucayans, it should be no surprise that cave sites represent a significant aspect of the archaeological record. Caves exist in two forms, wet (including blue holes and caves with a direct connection to the water table) and dry; however, regardless of the form, they contain a myriad of artifacts that have not been preserved in open-air settings including most human burials, petroglyphs and pictographs, certain faunal and botanical remains, and a variety of wooden artifacts (De Booy, 1913; Hoffman, 1973; Keegan, 1982; Pateman, 2007; Pateman & Keegan, 2019; Rainey, 1934; Winter & Pearsall, 1991). It is through the exploration of caves throughout the archipelago that the majority of Lucayan burials are known.

Recent mtDNA work examining the pre-contact remains discovered in caves and blue holes on several Bahamian islands documented the occurrence of haplogroups A2, B2, and C1b and C1d (Fernandes et al., 2021; Haak & Cooper, 2009; Schroeder et al., 2018). The presence of the above haplogroups, in combination with the absence of D1, D4h3a, which are prevalent throughout North and South America and the North American specific haplogroup X2a, indicates that limited Amerindian lineages were present in the pre-colonial Bahamas. This suggests that genetic diversity in the archipelago was greater in the past than today, Fernandes et al. (2021) concluded that the Lucayans have an ancestry that is strongly related to a widespread Caribbean_Ceramic clade. This clade is associated with a single Ceramic Age migration from South America to Puerto Rico and from there to Hispaniola, The Bahamas and then Cuba. They found no evidence for the migration of peoples with different genetic ancestries into the Caribbean during the Ceramic Age. They did, however, identify unexplained genetic substructures in The Bahamas and Ceramic Age Cuba (BahamasCuba_Ceramic subclade) and in the southeastern Dominican Republic (SECoastDR_Ceramic subclade) that are sufficient to identify these as subclades within the broader Caribbean_Ceramic clade.

In the same study, genetic associations between The Bahamas and several neighboring Caribbean islands were also documented via Runs of Homozygosity (ROH) (Fernandes et al., 2021: Extended Data Table 2). The ROH analysis, which examines long strands of genetic code inherited from shared ancestors, identified 19 pairs of distant cousins via the male X-chromosome. The Lucayans accounted for 13 of these pairs and were affiliated in six relationships with individuals buried on other islands: (1) Eleuthera with Abaco, with El Soco and with Juan Dolio (Dominican Republic), and with Monserrate (Puerto Rico); (2) Crooked Island with two individuals from Sanctuary Blue Hole (Andros, Bahamas), and with Vega Baja (Puerto Rico); (3) Sanctuary Blue Hole with El Soco and with Cabo Rojo 11 (Puerto Rico); (4) Sanctuary Blue Hole with La Caleta and with Andrés (Dominican Republic); (5) Abaco with La Caleta, and with Atajadizo (Dominican Republic); and (6) Rolling Heads, Long Island with Cueva de los Esqueletos 1 (Cuba). The mean of these genetic relationships is still under investigation, but the authors document a strong connection to the Dominican Republic and Puerto Rico, and a possible linkage with Cuba. The relationship with Ceramic Age Cuba implied by the identification of a BahamasCuba_Ceramic subclade may reflect migration from a common homeland and not the movement of people between Cuba and The Bahamas.

While not genetic, Strontium (Sr) isotope analysis provides a more direct method for identifying non-local individuals at burial sites (Laffoon et al., 2017; Price et al., 2020). The Sr isotope results for 19 Bahamian burials identified two outliers (Schulting et al., 2021), both of whom are from Sanctuary Blue Hole, Andros, and both of whom were male (as determined genetically; Fernandes et al., 2021). Their Sr isotope values suggest that these individuals may not have been local to the archipelago and came to The Bahamas from Cuba or Hispaniola. These outliers are the subject of ongoing investigation.

In sum, genome-wide data clustered The Bahamas and Ceramic Age Cuba as comprising a well-defined subclade, but this does not account for ancestral connections with Hispaniola that are more clearly observed in distant/cousin relationships. The Sr isotope data, while limited, hints at inter-island mobility. We next look specifically at patterning in the distribution of uniparental markers to bring into focus the genetic relationships between The Bahamas and other islands of the Caribbean as well as within the Bahamian archipelago itself. Our efforts to identify the Lucayan homeland begin with a discussion of genetic diversity, with an emphasis on uniparental markers. We next review locations in The Bahamas where the samples were obtained, and the methods employed to generate and analyze the genetic material as well as pertinent associated analyses (e.g., AMS radiocarbon dating). The results of these analyses are then described with regard to the distribution of uniparental markers in time and space. Finally, we address our questions regarding Lucayan origins and mobility. Specifically, we aim to answer the following questions: Did the Lucayans arrive from neighboring Hispaniola, Cuba, or both? Is there genetic evidence for prehistoric mobility within The Bahamas?
2. **MATERIALS AND METHODS**

### 2.1 | Sample collection

Although the data used in this study were previously reported (Fernandes et al., 2021; Schulting et al., 2021), this is the first detailed examination of the Y-chromosomal and mtDNA haplogroups for ancient samples from The Bahamas and the first effort to relate genetic and Sr isotope data in the region. We acknowledge the ancient individuals whose skeletal remains were analyzed, present-day people who have an Indigenous Bahamian legacy, and Caribbean-based scholars who were centrally involved in this work (see Alpaslan-Rooodenberg et al., 2021).

Skeletal remains for 30 of the 31 ancient individuals in this study were secured from museum collections in either the Yale Peabody Museum of Natural History (PMNH) or at the National Museum of The Bahamas (Table 1). Permission to transport and analyze the samples was granted by the director of the National Museum of The Bahamas. One sample [PCS37] was previously published in Schroeder et al. (2018). All of the laboratory work was performed in dedicated ancient DNA clean room facilities at the Harvard Medical School, the University College Dublin, and the University of Vienna. All of the Bahamian human remains in the PMNH examined in previous studies (Keegan, 1982; Schaffer, 2015) and the current investigation were collected by Froelich G. Rainey. In January 1934, Rainey visited The Bahamas to locate and excavate archeological sites and examine cultural materials found by local Bahamians. Rainey recovered human skeletons from 13 dry cave sites on Abaco and the surrounding cays, Eleuthera, San Salvador, Rum Cay, Long Island, and Crooked Island (Rainey, 1934). Although Rainey referred to the survey and excavations in The Bahamas in his field diary, he did not write a report or provide detailed field notes of their recovery or context (Granberry, 1978). The exact location for several burial caves is no longer known, and a number of these remains had reportedly been thrown outside of the caves by cave-earth diggers. Similarly, numerous human skeletal remains have been recovered in wet caves by SCUBA divers and explorers with little regard to proper archeological methods and protocols (Pateman & Keegan, 2019). Systematic recovery under archeological supervision has commenced recently at burial sites on Andros, Abaco, Eleuthera, Grand Bahama, and Long Island. Long Island is the only site where burials were located in a sand dune and not a cave context (Hanna et al., 2021; Keegan et al., 2021).

### 2.2 | DNA extraction, library preparation, and DNA sequencing

For all 31 samples, DNA was extracted from the cochlea, ossicles, phalanx, or teeth following protocols in Pinhasi et al. (2015) and Sirak et al. (2020). The DNA was then used to prepare dual-barcoded double-stranded or dual-indexed single-stranded DNA libraries (Gansauge et al., 2017; Gansauge et al., 2020; Rohland et al., 2015). These were subsequently used to sequence the entire mitochondrial genome and ~1.24 million genome-wide SNPs (Fernandes et al., 2021; Nägele et al., 2020; Schroeder et al., 2018). It is important to note that the DNA for three of these samples (I13557, I13740, and I13741) was not amenable to whole genome sequencing but was sufficient in quantity for typing the mitochondrial genome and Y-chromosomal SNPs. These three individuals increased the sample size but did not significantly impact our analysis.

### 2.3 | Radiocarbon dating

Radiocarbon AMS dates ($^{14}$C) for 25 out of the 31 individuals examined in this study were obtained during previous analyses (Fernandes et al., 2021; Hanna et al., 2021; Keegan et al., 2021; Nägele et al., 2020; Schroeder et al., 2018; Schulting et al., 2021). The dates, which have a 2-sigma range from AD 1000 to 1600 (Schulting et al., 2021), are reported in this article as uncalibrated years before present (BP) because the studies are not consistent in their calibration methods nor in reporting the carbon and nitrogen isotopes.

### 2.4 | Phylogenetic analysis

#### 2.4.1 | mtDNA diversity

Mitochondrial DNA haplogroup frequency data for indigenous Native American haplogroups A2, B2, C1, and D1 in both ancient and contemporary populations collected from the Lesser and Greater Antilles as well as from South America were gathered from the literature (Table 2). This haplogroup frequency data was then analyzed using the Arlequin version 3.5.2 program (Excoffier & Lischer, 2010) to generate pairwise Fst genetic distances, which were subsequently utilized to construct a multidimensional scaling (MDS) graph with the aid of IBM SPSS version 25 (IBM Corp., 2017). Further, to establish the genetic diversity present in and around ancient Bahamian samples and to examine directionality of gene flow into the islands from other Greater and Lesser Antillean groups, Median Joining Network diagrams were generated (excluding hyper-variable mutations listed in www.phylotree.org mtDNA tree Build 17) for the two major haplogroups (B2 and C1) found in the archipelago, using the NETWORK program version 10 (Bandelt et al., 1999, http://www.fluxus-engineering.com).

#### 2.4.2 | Y-chromosome diversity

Y-haplogroups were designated by typing a target of 30,000 SNPs across the Y-chromosome (Fernandes et al., 2021). Unfortunately, Y-chromosomal Short Tandem Repeat (YSTR) haplotypes were not generated for the ancient samples given the degree of degradation.
<table>
<thead>
<tr>
<th>Sample #</th>
<th>Island</th>
<th>Lab ID</th>
<th>14C year (bp)</th>
<th>Burial setting</th>
<th>Burial information</th>
<th>Sex</th>
<th>Mt-hg</th>
<th>Y-hg</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Abaco</td>
<td>I13320b</td>
<td>947 ± 24d</td>
<td>Cave</td>
<td>Imperial Lighthouse Cave (#4683)</td>
<td>M</td>
<td>B2e</td>
<td>Q-M902</td>
</tr>
<tr>
<td>2</td>
<td>Abaco, Elbow Cay</td>
<td>I14922b</td>
<td>1119 ± 19d</td>
<td>Dune</td>
<td>Hopetown</td>
<td>F</td>
<td>B2e</td>
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<tr>
<td>3</td>
<td>Abaco, Lubber's Quarters</td>
<td>I14875b</td>
<td>1161 ± 19d</td>
<td>Cave</td>
<td>Bill Johnson's Cave</td>
<td>M</td>
<td>B2</td>
<td>Q-M902</td>
</tr>
<tr>
<td>4</td>
<td>Abaco, Moore's Island</td>
<td>I14923b</td>
<td>609 ± 13d</td>
<td>Cave</td>
<td>Randy's Cave</td>
<td>F</td>
<td>B2e</td>
<td>—</td>
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<tr>
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<td>Crooked Island</td>
<td>I13318b</td>
<td>—</td>
<td>Cave</td>
<td>Burial Cave #1 (#4694)</td>
<td>M</td>
<td>C1b</td>
<td>Q-M902</td>
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<td>I13319b</td>
<td>—</td>
<td>Cave</td>
<td>Gordon Hill Cave, Chamber #1 (#4695)</td>
<td>F</td>
<td>C1b</td>
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<tr>
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<td>Eleuthera</td>
<td>I13321b</td>
<td>—</td>
<td>Cave</td>
<td>Wemyss Bight Cave (#4685)</td>
<td>M</td>
<td>C1b2</td>
<td>Q-M902</td>
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<tr>
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<td>F</td>
<td>C1b</td>
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<td>—</td>
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<td>Garden Cave (Back Chamber)</td>
<td>F</td>
<td>C1d1</td>
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<td>F</td>
<td>C</td>
<td>—</td>
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<td>I14876b</td>
<td>675 ± 20d</td>
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<td>M</td>
<td>B2</td>
<td>Q-M902</td>
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<td>F</td>
<td>B2</td>
<td>—</td>
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<td>669 ± 25d</td>
<td>Cave</td>
<td>Garden Cave (Skull 2)</td>
<td>F</td>
<td>C1d</td>
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<td>745 ± 20d</td>
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<td>Garden Cave (unknown)</td>
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<td>C1d</td>
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<td>Preacher’s Cave</td>
<td>F</td>
<td>B2</td>
<td>—</td>
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<tr>
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<td>PCV001c</td>
<td>—</td>
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<td>F</td>
<td>C1d</td>
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<td>991 ± 22a</td>
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<td>Preacher’s Cave</td>
<td>M</td>
<td>B2</td>
<td>Q-M902</td>
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<tr>
<td>18</td>
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<td>PCV004c</td>
<td>—</td>
<td>Cave</td>
<td>Preacher’s Cave</td>
<td>F</td>
<td>C1d1</td>
<td>—</td>
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<td>19</td>
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<td>1127 ± 19d</td>
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<td>Clarence Town Burial Cave (#4687)</td>
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<td>C1d1</td>
<td>—</td>
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<td>855 ± 15b</td>
<td>Dune</td>
<td>Clarence Town, Rolling Heads (#1)</td>
<td>M</td>
<td>B2e</td>
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<td>595 ± 15b</td>
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<td>660 ± 20d</td>
<td>Dune</td>
<td>Clarence Town, Rolling Heads (#3)</td>
<td>F</td>
<td>B2e</td>
<td>—</td>
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<td>Ragged Island</td>
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<td>1096 ± 20d</td>
<td>Cave</td>
<td>Flamingo Cay Cave</td>
<td>M</td>
<td>C1b2</td>
<td>—</td>
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<td>South Andros</td>
<td>I13558b</td>
<td>593 ± 19d</td>
<td>Blue Hole</td>
<td>Sanctuary Blue Hole (#15)</td>
<td>F</td>
<td>C1b2</td>
<td>—</td>
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<td>South Andros</td>
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<td>502 ± 19d</td>
<td>Blue Hole</td>
<td>Sanctuary Blue Hole (#11)</td>
<td>M</td>
<td>B2e</td>
<td>Q-Z781</td>
</tr>
<tr>
<td>26</td>
<td>South Andros</td>
<td>I13560b</td>
<td>712 ± 18d</td>
<td>Blue Hole</td>
<td>Stargate Blue Hole</td>
<td>M</td>
<td>B2e</td>
<td>Q-M902</td>
</tr>
<tr>
<td>27</td>
<td>South Andros</td>
<td>I14880b</td>
<td>572 ± 20d</td>
<td>Blue Hole</td>
<td>Sanctuary Blue Hole (#5)</td>
<td>M</td>
<td>A2h</td>
<td>Q-Z781</td>
</tr>
<tr>
<td>28</td>
<td>South Andros</td>
<td>I14881b</td>
<td>584 ± 20d</td>
<td>Blue Hole</td>
<td>Sanctuary Blue Hole (#6)</td>
<td>F</td>
<td>A2</td>
<td>—</td>
</tr>
<tr>
<td>29</td>
<td>South Andros</td>
<td>I14882b</td>
<td>685 ± 20d</td>
<td>Blue Hole</td>
<td>Sanctuary Blue Hole (#7)</td>
<td>M</td>
<td>A2</td>
<td>—</td>
</tr>
<tr>
<td>30</td>
<td>South Andros</td>
<td>I14883b</td>
<td>571 ± 20d</td>
<td>Blue Hole</td>
<td>Sanctuary Blue Hole (#2)</td>
<td>M</td>
<td>A2</td>
<td>Q-M902</td>
</tr>
<tr>
<td>31</td>
<td>South Andros</td>
<td>I14879b</td>
<td>700 ± 20d</td>
<td>Blue Hole</td>
<td>Sanctuary Blue Hole (#3)</td>
<td>M</td>
<td>C1d</td>
<td>Q-Z781</td>
</tr>
</tbody>
</table>

Note: The text in bold signifies a previously unnamed C1d mt-dna branch. This is discussed in the results and conclusion sections. It does not have to be bold in the table as the word (new) is also included.

Schroeder et al. (2018).
Fernandes et al. (2021).
Nägele et al. (2020).
Schulting et al. (2021).
3 | RESULTS

The distribution of the Y-chromosomal and mtDNA haplogroups throughout the Bahamian archipelago is shown in Figures 1 and 2, respectively. As Figure 1 illustrates, Y-chromosome haplogroup Q and its derivatives (Q-M902 and Q-Z781) are homogeneous across the islands while mtDNA diversity varies substantially (Figure 2). In this figure, mtDNA haplogroup A2 is restricted to the Central Bahamian Island of Andros, whereas haplogroup C1 is found in both central and southern islands. Haplogroup B2, in contrast, is not limited to a specific region but is present throughout the entire archipelago and was the most common mtDNA haplogroup observed in this study. Until recently (Schroeder et al., 2018), this haplogroup had not been reported in any ancient Caribbean samples, and, to date, it remains the rarest of the four pre-contact haplogroups present in the Greater and Lesser Antilles. Of the 12 B2 samples in The Bahamas, seven were characterized as B2e, a lineage otherwise rare in the Americas, and previously reported only in ancient samples from Saint Lucia (Fagundes et al., 2008). As of 2020, the only other Caribbean location where haplogroup B2e has been identified archeologically is at the Lavoutte site in Saint Lucia (Nägele et al., 2020). All other five B2 lineages in The Bahamas formed a small group (previously unpublished) and thus is still unnamed in mtDNA databases. The average radiocarbon dates generated for the samples derived for mtDNA haplogroup B2 were the oldest, with an average age of ~850 bp (Table 3).

The second most common major mtDNA haplogroup was C1, specifically sub haplogroups C1b and C1d. Both subgroups are present at high frequencies across the Greater Antilles, in both ancient samples and modern populations, although C1b is found in greater proportions in the islands of Hispaniola and Puerto Rico, while C1d has been reported at much lower frequencies, yet ubiquitously, across most of the region (Fernandes et al., 2021; Vilar et al., 2014). Within The Bahamas, C1b and C1d were observed in the central and southern islands, although C1b was present at higher frequencies in Long/Ragged Island and Crooked Island (both are part of the Southern Bahamas). C1d, on the other hand, displays a widespread distribution pattern very similar to that of haplogroup B2. Radiocarbon dating of the human skeletal remains suggests that mtDNA haplogroups C1b (~766 bp) and C1d (~767 bp) may be, on average, slightly younger than B2 (~850 bp) (Table 3). However, the age differences could also
be the product of insufficient sampling, and not necessarily the direct consequence of separate migrations into the islands. Further sampling and age testing may help elucidate this pattern.

Haplogroup A2, in contrast, was only detected in the island of Andros at a frequency there of 50%. Within the Caribbean, this haplogroup is common in Cuba, Hispaniola, Puerto Rico, Curacao and some of the Lesser Antillean islands including St. Vincent and Trinidad (Benn Torres et al., 2007, 2015, 2019; Martinez-Cruzado et al., 2005; Mendizabal et al., 2008; Paulino-Ramirez et al., 2019; Vilar et al., 2014). The restricted presence of this haplogroup to Andros suggests possible direct gene flow to this island from one or more of these sources. Moreover, average radiocarbon dates of the human skeletal remains derived for this haplogroup indicate that it is the youngest mtDNA lineage in The Bahamas, with an average age of only ~603 bp (Table 3). The age and limited geographic distribution of haplogroup A2 could suggest a different migration pattern into the island chain than for the other mtDNA haplogroups.

In the MDS graph (Figure 3), two clusters are apparent. The first of these, which is on the left side of the graph, consists of Abaco, ancient Venezuelans, and a modern Arawak-speaking group (Machiguenga) from the Altiplanos in west-central South America while the other cluster, which spans the entire right side of the graph, is comprised of the Central and Southern Bahamian groups as well as those from South America and the Greater and Lesser Antilles. Interestingly within the latter cluster there is clear distinction between the samples from Andros and those from the remaining Bahamian islands examined. Andros is found in the upper right quadrant, where it segregates with the ancient samples from Puerto Rico but also displays genetic affinities to other Greater and Lesser Antillean populations, including the modern collections from Puerto Rico and Guadeloupe as well as the ancient samples from Saint Lucia. The samples from Long/Ragged Island, Eleuthera, and Crooked Island, in contrast, form a subgroup in the lower right quadrant, displaying genetic affinities to the modern groups from Brazil (Yanomami Indians) and Saint Vincent (Garifuna), as well as to the ancient samples analyzed from Cuba and Guadeloupe.

Given the high frequency of B2 and C1 in the ancient Bahamian samples, mitochondrial genome network diagrams (Figures 4 and 5, respectively) were constructed for both major haplogroups. In the median joining B2 network (Figure 4), the Bahamian samples were found to form two distinct clusters branching from a common ancestral B2 root. This B2 root, which is more than 16,000 years old (Behar et al., 2012), suggests that these two
branches were already distinct long before their arrival in the archipelago. The first of these (i.e., the unnamed B2 branch) is composed only of Bahamian and Hispaniolan samples, the former are specifically from Eleuthera and Abaco. In the other branch, the B2e cluster, five Bahamian individuals share a common set of mutations defining a derived lineage for haplogroup B2e, inclusive of novel mutations 982G, 11419C, and 15894A. Branching from this uniquely Bahamian parental cluster are individuals from Long/Ragged Island, and Abaco. The two other ancient B2e samples from Saint Lucia (Nägele et al., 2020) do not have these uniquely Bahamian mutations, indicating that they likely evolved separately from the ancestral B2e type from South America. The local, in-situ diversity within the uniquely Bahamian B2e cluster suggests that it may have been present in The Bahamas early in its history and remained there for a long time, a finding that is supported by the network estimate for time of coalescence for B2e at 2070 ±1035 years (Bandelt et al., 1999) an age that is slightly higher but within the range of the oldest human remains found in the archipelago.

In the C1 network (Figure 5), the Bahamian samples were found to occupy all four branches of the network, displaying genetic affinities primarily with the samples from Hispaniola and Puerto Rico, and secondarily to Cuba, the latter specifically for C1d1 types. For example, the C1b and C1b2 samples (i.e., the clusters to the right) from Eleuthera, Long/Ragged Island and Crooked Island group together with those from Curaçao, Hispaniola and Puerto Rico, although one branch (C1b+) is specific to the ancient Bahamian samples. The previously unnamed (C1d+) cluster, which consists of nine samples from Hispaniola and three from The Bahamas (Eleuthera and Long Island/Ragged Island), share the same mutations, indicating a close genetic relationship between the two
regions. Finally, in the C1d1 branch to the left of the network, there are only two Bahamian samples, one from Long/Ragged Island and the other from Eleuthera, and these samples also display genetic affinities to those from Cuba and Hispaniola, respectively, albeit more distant relationships and the regions share no haplotypes.

In this study, we also were interested in any evidence for population continuity between pre-contact and modern Bahamian populations. However, such a connection could not be made based solely on the available uniparental data. We intend to return to this question in the near future.
CONCLUSIONS

4.1 Did the Lucayans originate from neighboring Hispaniola, Cuba, or both?

The genome-wide analysis of 263 individuals from Venezuela, Saint Lucia, Guadeloupe, Puerto Rico, Dominican Republic, Haiti, Cuba, and The Bahamas identified a genetically homogenous migration from south to north (Caribbean_Ceramic clade) (Fernandes et al., 2021; Nägele et al., 2020). Genetic substructure sufficient to identify subdivisions within that Ceramic Age group was also recognized, including one subclade composed of individuals from The Bahamas and Ceramic Age Cuba (BahamasCuba_Ceramic). This subclade, however, was found to reflect a bottleneck in western Hispaniola where the migrants to both areas originated. It still remains to be determined whether this migration reached Cuba and The Bahamas separately or whether the migrants passed through one island to reach the other. This ancestral relationship also does not indicate whether or not individuals moved freely between the two.

In contrast, the haploid (uniparental) data suggest that an early group that migrated into the Bahamian archipelago likely carried three (or four) major types of maternal haplogroups, namely B2 (including B2e), and possibly C1b and C1d. Haplogroups B2 and B2e probably arrived first (circa 1160 bp) and were followed years later by C1b and C1d types, but the difference in AMS dates is not statistically significant. The presence of all these major haplogroups in the same population at the same time is not unusual given that communities composed of exogamous lineages typically have more than one type of mtDNA haplogroup. Haplogroup B2 is rare (>2%) across ancient Caribbean samples and modern Caribbean peoples in contrast to A2 and C1 (>20% in some Greater Antilles) (Paulino-Ramirez et al., 2019; Vilar et al., 2014). The dominance and widespread geography of B2 lineages in the Northwest Bahamas shows that population expansion across the entire archipelago occurred rapidly, and that there was not a single propagule but waves of migration from a coherent homeland over a period of perhaps a century (see Fall et al., 2021). Genetic relationships with Hispaniola, and to a lesser degree Puerto Rico, also demonstrate that the Bahamian archipelago likely had stronger influences from Hispaniola than from any other place. Furthermore, Hispaniola is the only other island in the Caribbean where lineages identical to the ancient Bahamian B2 and C1b2 types have been observed.

We further identified what we interpret to be the secondary movement of people from Cuba into Andros Island late in the archipelago’s prehistory (c. 685 bp). Although four individuals from Andros have the ubiquitous B2e and C1 mtDNA haplogroups, as well as Y-haplogroup Q-M902 (n = 8), three individuals from Sanctuary Blue Hole have rare haplogroup combinations of A2 and C1d+ (“new”) mtDNA and the less common Y-haplogroup Q-Z781 mutation. Interestingly, both of these mtDNA haplogroups as well as the rare Y Q-Z781 lineage, occur in Cuba (Fernandes et al., 2021; Nägele et al., 2020), suggesting a possible recent influx of persons from there to the neighboring South Andros Island more recently. The sample size, however, is too small to determine whether this reflects individual or group mobility. Julian Granberry (1991) noted that toponyms for the Lucayan Islands, which were recorded by the Spanish, point to

FIGURE 5 A median-joining network of ancient Caribbean mtDNA haplogroup C1 sequences
the movement of people from Cuba to The Bahamas. These Indigenous place names are consistent with the observed late appearance of Cuban haplogroups on Andros Island.

4.2 Is there genetic evidence for prehistoric mobility within The Bahamas?

Our findings indicate a rapid migration of persons into and within the Bahamian archipelago (Fall et al., 2021; Keegan, 2010), most likely from Hispaniola. This is evident in the distribution of mtDNA haplogroups, which illustrates that the oldest haplogroup, B2, is found primarily in the northernmost islands. This suggests that haplogroup B2 may have been partially replaced or augmented a short time later by persons possessing haplogroup C1b and C1d. However, the radiocarbon AMS dates for the two haplogroups are not significantly different so it is possible that both arrived in The Bahamas at the same time. Most recently, Andros received genetic input from Cuba in the form of haplogroup A2 (Table 3). Rather than a large movement of people, the Andros individuals may reflect a movement of even just a few adult males from Cuba who moved to The Bahamas and were interred on Andros in a blue hole. This pattern is supported by the strontium data as well. Evidence for these migrations into and within The Bahamas is also supported by the MDS (Figure 3), where we see partitioning of the islands in separate quadrants as well as in the network analyses (Figures 4 and 5) which show genetic affinities of the Bahamians to the Greater Antillean samples from Cuba, Hispaniola, and Puerto Rico.

With regard to mobility within The Bahamas, the genome-wide evidence identified stronger genetic similarities between particular individuals on different islands than to the other Bahamian samples (Fernandes et al., 2021). One individual buried on Crooked Island at the South/Central boundary and two individuals from Sanctuary Blue Hole on Andros Island in the Central were identified as genetic distant cousins. This distant/cousin relationship was also observed between an individual from Eleuthera Island (Central) and one from the Abaco Islands (Northwest). These south to central and central to north connections may reflect the initial northward expansion of the population. Alternatively, such affinities could have been maintained by marital and exchange relationships between persons living on the different islands (Keegan, 2015). Future efforts to document interisland mobility will require determining the degree of relationship and relative age for a larger number of individuals encompassing additional locations in the archipelago.

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AUTHOR CONTRIBUTIONS

Vanessa A Forbes-Pateman: Conceptualization (lead); data curation (equal); writing – original draft (equal); writing – review and editing (equal). Aram Yardumian: Conceptualization (supporting); data curation (equal); writing – original draft (equal); writing – review and editing (equal). Miguel G Vilar: Conceptualization (supporting); data curation (equal); methodology (equal); writing – review and editing (equal). William F Keegan: Conceptualization (lead); data curation (equal); funding acquisition (equal); investigation (equal); project administration (equal); resources (equal); supervision (equal); visualization (supporting); writing – review and editing (equal). Tanya M Simms: Data curation (equal); formal analysis (equal); methodology (equal); resources (equal); software (equal); visualization (supporting); writing – review and editing (equal). Michael P Pateman: Conceptualization (lead); data curation (equal); funding acquisition (equal); investigation (equal); project administration (equal); resources (equal); supervision (equal); visualization (lead); writing – original draft (equal); writing – review and editing (equal). L. Tinker, Director (former) of The National Museum of The Bahamas.

DATA AVAILABILITY STATEMENT

The genetic data used in this study were first reported in Fernandes et al. (2021). The aligned sequences are available through the European Nucleotide Archive under accession number PRJEB38555. Genotype data used in analysis are available at https://reich.hms.harvard.edu/datasets. The Sr isotope and radiocarbon AMS dates are available in Schulting et al. (2021), and additional AMS dates are reported in Hanna et al. (2021) and Keegan et al. (2021). Descriptions of the archeological sites from which Lucayan remains were recovered are described in Fernandes et al. (2021, S1, pp. 19–30, https://static-content.springer.com/esm/art%3A10.1038%2Fs41586-020-03053-2/MediaObjects/41586_2020_3053_MOESM1_ESM.pdf). All other relevant data are available from the corresponding authors upon reasonable request.

ORCID

Vanessa Forbes-Pateman https://orcid.org/0000-0002-5403-6821
Miguel Vilar https://orcid.org/0000-0002-8164-4064


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