



Article

Bermuda's Walsingham Caves: A Global Hotspot for Anchialine Stygobionts

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Abstract: Bermuda is an Eocene age volcanic island in the western North Atlantic, entirely capped by Pleistocene eolian limestone. The oldest and most highly karstified limestone is a 2 km² outcrop of the Walsingham Formation containing most of the island's 150+ caves. Extensive networks of submerged cave passageways, flooded by saltwater, extend under the island. In the early 1980s, cave divers initially discovered an exceptionally rich and diverse anchialine community inhabiting deeper sections of the caves. The fauna inhabiting caves in the Walsingham Tract consists of 78 described species of cave-dwelling invertebrates, including 63 stygobionts and 15 stygophiles. Thus, it represents one of the world's top hotspots of subterranean biodiversity. Of the anchialine fauna, 65 of the 78 species are endemic to Bermuda, while 66 of the 78 are crustaceans. The majority of the cave species are limited in their distribution to just one or only a few adjacent caves. Due to Bermuda's high population density, water pollution, construction, limestone quarries, and trash dumping produce severe pressures on cave fauna and groundwater health. Consequently, the IUCN Red List includes 25 of Bermuda's stygobiont species as critically endangered.



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1. Introduction

Bermuda is a small, mid-Atlantic island located 1050 km off the east coast of the United States in the Sargasso Sea, at 32°20' N, 64°45' W. It lies approximately equidistant by air from Boston, New York, and Atlanta, making Bermuda only a short flight away for all of the U.S. east coast. Due to its warm climate, clear tropical waters, coral reefs, pink sand beaches, and ease of access, Bermuda is a popular tourist destination.

Although the Spanish explorer Juan de Bermudez discovered these isolated islands in 1505, he did not try to land. Ten years later, he returned to Bermuda, leaving behind a dozen pigs and sows for any castaways who might become stranded there. In 1609, the English sailing ship *Sea Venture*, on its way to resupply the Jamestown Colony, was caught in a strong storm and wrecked on Bermuda's reefs. The survivors of the shipwreck were stranded on the previously uninhabited island for nine months until two new ships could be constructed from local timber. The settlement of Bermuda did not occur until 1612, when the town of St. George officially became Bermuda's first capital and the oldest continually inhabited English town in the New World [1].

Bermuda's caves have been long recognized and prominently mentioned in early written works on the island [2]. Shakespeare's play, *The Tempest*, was likely inspired by the Bermuda shipwreck and takes place in and around a cave. The first published reference to Bermuda caves was in 1623, when Captain John Smith (of Pocahontas fame) described, "in some places varye strange, darke, and cumbersome Caues." John Hardy's 1671 poetic description of Bermuda caves states [3]:

“The water flowing to them [Harrington Sound] underground,
Being most salt, and all along the shore
There are dark caves, of a miles length or more
Extending under ground, in which there be
Deep holes with water, though no one can see
A passage for it in . . . ”

The 1872–1876 round-the-world voyage of H.M.S. *Challenger*, which marked the beginning of modern oceanography, included a stopover in Bermuda. The expedition’s commander, Captain George Nares, took the opportunity to explore Paynter’s Vale (a.k.a. Church) Cave, accompanied by the British Governor of Bermuda, Sir John Henry Lefroy. Nares rowed the governor across a lake at the bottom of the cave, remarking on “a slight change of level with the tide, sufficient to keep the water perfectly pure” [4].

2. Anchialine

Since Bermuda is a relatively small island with no place very far from, or very high above the sea, caves that descend deep enough, end at very clear, exceptionally blue seawater pools. However, until the beginning of cave diving in the early 1980s, Bermuda’s underwater caves were unexplored and unknown, as were the animals living in them. When cave divers discovered an amazing variety of new species, new genera, and even several new orders, Bermuda’s saltwater caves clearly merited status as a unique ecosystem [5].

After examining an assortment of highly unusual caridean shrimps from tropical land-locked saltwater pools on the several Indo-West Pacific islands and from the Sinai Peninsula, Dutch carcinologist, L.B. Holthuis, recognized the significance of this habitat. He created the term “anchialine” to describe “pools with no surface connection to the sea, containing salt or brackish water, which fluctuates with the tides” [6]. At the 1984 International Symposium on the Biology of Marine Cave held in Bermuda, Holthuis’s original definition was expanded and modified to include tidal, saltwater pools inside caves: “Anchialine habitats consist of bodies of haline water, usually with a restricted exposure to open air, always with more or less extensive subterranean connections to the sea, and showing noticeable marine as well as terrestrial influences” [7]. During the 2012 Second International Symposium on Anchialine Ecosystems in Croatia, the term anchialine was more broadly defined as “a tidally-influenced subterranean estuary located within crevicular and cavernous karst and volcanic terrains that extends inland to the limit of seawater penetration” [8]. The “anchialine habitat continuum”, as described by van Hengstum et al. (2019), extends uninterrupted from as far inland as saline groundwater penetrates, to the offshore edge of the platform shelf. In the Pleistocene, sea level changes alternately exposed and flooded the caves, such that anchialine groundwater alternately regressed or flooded bedrock voids [9].

3. Bermuda Geography and Geology

The islands of Bermuda lie atop the Bermuda Seamount, a volcanic peak rising from a seafloor depth of more than 4000 m. A ring of coral reefs surround a central lagoon on the flattened summit of this long extinct volcano. The islands of Bermuda, on the southeast edge of the platform, enclose several harbors and small bays. Eolian limestone completely caps the Bermuda Seamount to form the island mass. Limestone stratigraphy shows numerous cycles of subaerial eolianite and shallow marine carbonate deposition during interglacial high sea stands alternating with red clay soil horizons, marking glacial episodes of lowered sea level. Eolianites represented as lithified sand dune ridges, constitute more than 90% of the limestone volume. The main eolianite units are separated by fossiliferous soils and, listed in order of increasing age, are the Southampton, Rocky Bay, Belmont, Lower Town Hill, Upper Town Hill, and Walsingham Formations. The Walsingham Formation, made up of highly altered and very dense eolianite, was deposited $\geq 700,000$ years ago [10].

4. Bermuda Caves

Bermuda caves are believed to have formed syngenetically by a phreatic solution of limestone during glacial low stands of sea level. When the Ice Age sea level was down, the top of the seamount was emergent, and the islands' total land mass was about 13 times as large as it is today. As a result, the sizable body of fresh groundwater necessary for cave formation was present. As post-glacial sea levels rose, large portions of the caves were drowned by the encroaching seawater as it displaced the freshwater. Continuing collapse of overlying rock into the large voids created the irregular chambers and fissure entrances characteristic of Bermuda's caves [11].

Most of Bermuda's 150+ known caves are located in the Walsingham Tract, a 4 km long by 0.5 km wide surface outcropping of the Walsingham Formation, situated between Harrington Sound and Castle Harbour (Figure 1A,B). The Walsingham Tract contains the island's longest dry caves, most notably Church, Wonderland, Admiral's, Sibley's, and Jane's Caves. Crystal, Wonderland, Walsingham, Palm Caves, and others, are isolated cave entrances, interconnected as segments of a large hydrologically linked cave system. The underwater portions of caves in the Walsingham Tract reach water depths of 24 m, but still closely resemble their dry upper levels, even to the variety of large, subaerial-formed speleothems found above and below water. Caves in the Shelly Bay area, on the opposite side of Harrington Sound, are exclusively underwater with practically no dry portions. These caves have long, nearly level, anastomosing underwater passages at 18 m depth, with entrances on Harrington Sound and passageway extending under the island. Bermuda's longest cave, the 2 km long Green Bay Cave System, is located here [9,12].

Harrington Sound is an almost totally enclosed body of saltwater, with its only connection to the sea being a narrow channel at Flatt's Inlet (Figure 1B). Due to its restricted access to the ocean, tides in Harrington Sound have only 25% the range of ocean tides and occur 3 h later. When the volume of water tidally exchanging through Flatt's Inlet is compared with the total tidal volume of Harrington Sound (area \times tidal range), only about half of the tidal volume passes out through the inlet, while the remainder moves through submerged caves [13]. Tidal exchange primarily occurs in caves around the periphery of Harrington Sound where the land is the narrowest. On the east side of the Sound, exchange occurs through caves from the Walsingham Tract (Walsingham and Palm Cave Systems) to Castle Harbor, on the west side through Shelly Bay (Green Bay and Red Bay Caves) to the North Shore, and on the south side (Devil's Hole Caves) to Bermuda's South Shore. Cave pools in the Walsingham and Palm cave systems have tide ranges that decrease, while residence times increase with their relative distance away from Castle Harbour and approaching Harrington Sound. The Crystal and Wonderland Cave sections of the Walsingham System (Figure 1C) are off the main flow channels where circulation patterns are restricted. Their residence times are much longer, with the phreatic zone consisting of very clear, slowly moving or stagnant waters with a lower surface salinity [14]. Caves with greater water transport, e.g., Palm Cave System (Figure 1D), have surface waters only slightly diluted and reach normal marine salinity (35–36 ppt) below 1 m depths. The food input into caves is primarily plankton and organic matter derived from the sea itself, although primary production in open anchialine pools may provide an additional source of food in the submerged caves (Figure 2A) [15].

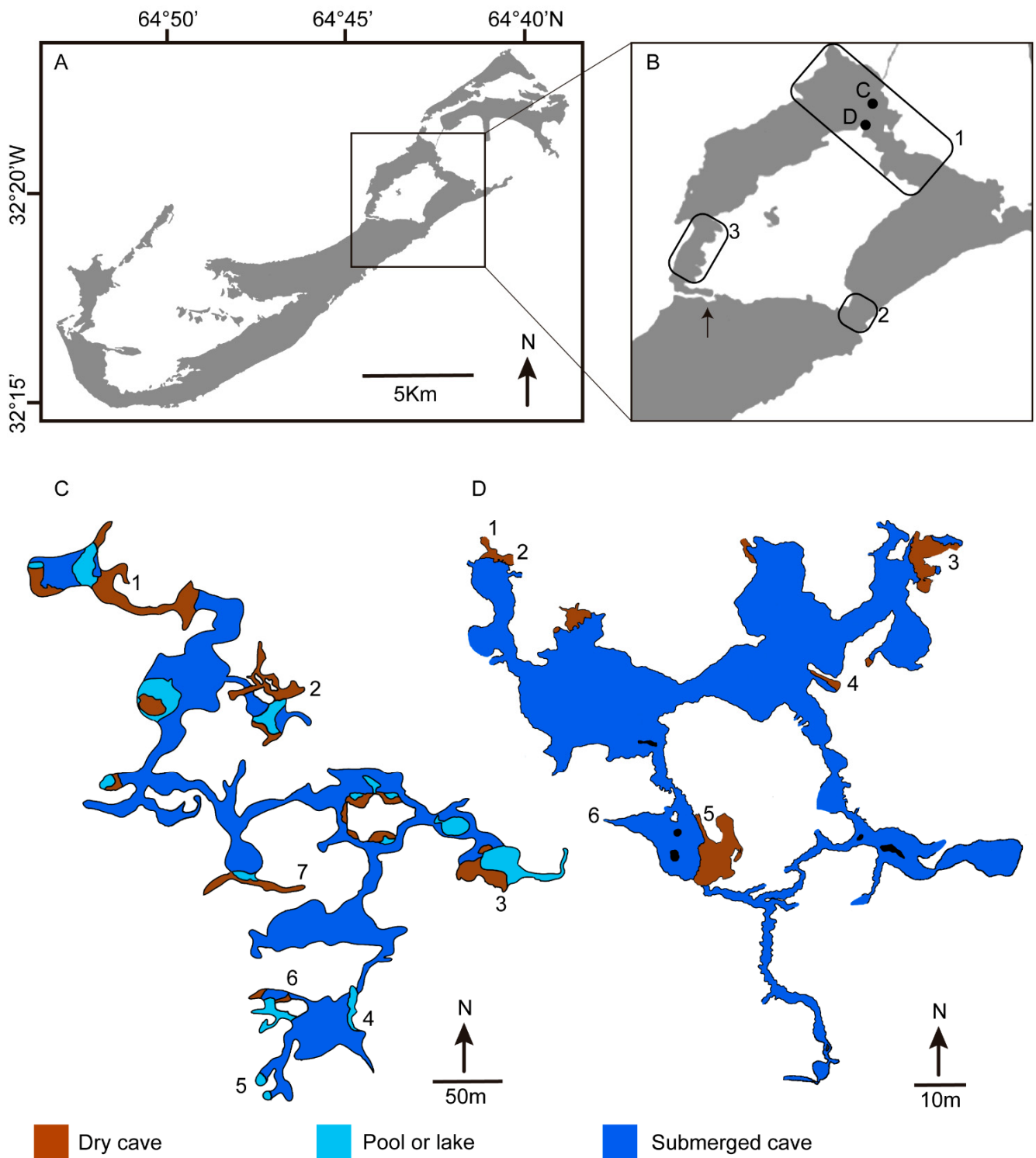


Figure 1. (A) Map of Bermuda in the North Atlantic Ocean, (B) Cave regions surrounding Harrington Sound, a large inland body of water mostly encircled by land. The arrow indicates the only opening to the sea at Flatt’s Inlet, rectangles show regions of cave and karst development in (1) the Walsingham Tract (with the letters C and D indicating the location of the two main caves), (2) Devil’s Hole, (3) Shelly Bay, (C) Walsingham Cave System with cave entrances: (1) Wonderland, (2) Crystal, (3) Walsingham, (4) Deep Blue, (5) Vine, (6) Old Horse, (7) Fern Sink (modified from map by Robert Power), (D) Palm Cave System with cave entrances: (1) Palm Slit, (2) Palm, (3) Strawmarket, (4) Sailor’s Choice, (5) Myrtle Bank, (6) Cripple Gate (modified from map by Jason Richards).

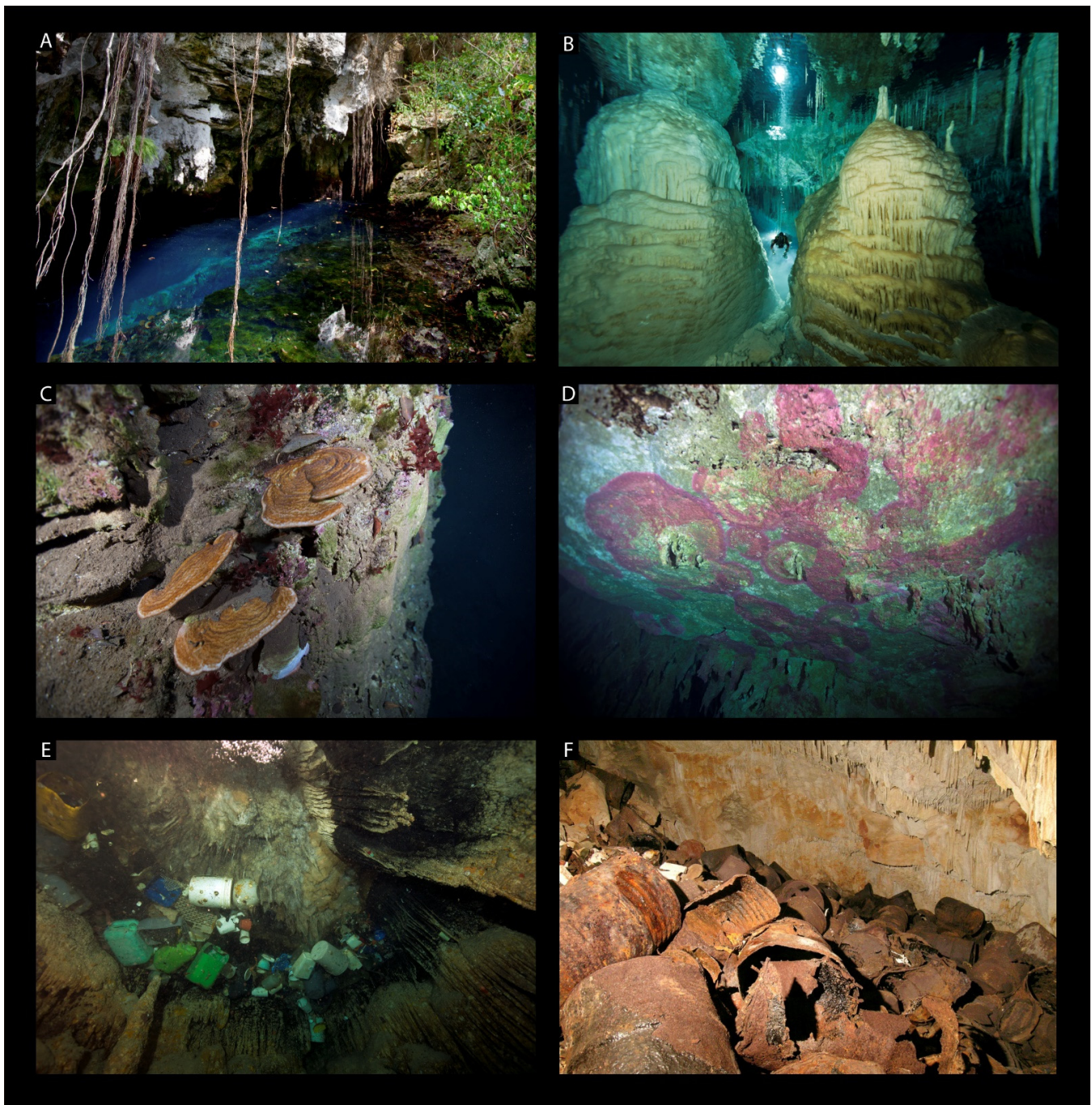


Figure 2. Caves of the Walsingham Tract. (A) Deep Blue Cave entrance pool, (B) Cave diver between underwater stalagmites near the Crystal Cave, (C) Fragile saucer coral (*Agarcia fragilis* Dana, 1848) in the cavern pool of Deep Blue, (D) Coralline algae in the cavern ceiling of Deep Blue, (E) Submerged plastic garbage floating on the ceiling in the Palm Cave System, and (F) Rusting and disintegrating bitumen barrels in Bitumen Cave (in the Walsingham Tract). Photo credits: Tamara Thomsen (A); Jill Heinerth (B,E).

5. Cave Biology

Open water marine habitats in Bermuda have been well investigated, including numerous studies focusing on lightless environments in the deep sea and interstitial. The Bermuda Biological Station for Research (now the Bermuda Institute of Ocean Sciences) has continuously conducted marine biological research since 1903. The Bermuda Aquarium, Museum and Zoo, founded in 1926, focuses on oceanic island species and the conservation, education, and research related to them. In contrast, serious biological investigations of the underwater caves did not begin until the advent of cave diving [16].

Since Bermuda's terrestrial caves contain little organic matter, there are no known endemic terrestrial species and, in general, the fauna is sparse. Cave-dwelling bats, or other animals that bring organic material into the caves, are lacking in Bermuda. However, a rich and diverse marine biota inhabits the submarine passageways and anchialine pools of Bermuda's caves. Although many marine species are accidental or occur only at coastal cave entrances, a variety of stygobiont (i.e., aquatic cave-adapted) taxa are present, with the Walsingham Cave System—containing the greatest number of Bermuda stygobionts—included as one of the original subterranean biodiversity hotspots [17].

Anchialine cave fauna have the same adaptations to caves as freshwater and terrestrial cave organisms, i.e., reduction or loss of eyes and pigmentation, elongation of appendages, and increase in nonvisual sensory receptors [18]. Recent cave colonists tend to have pigmented body and eyes, while ancient settlers of caves have lost their eyes and pigment. The eyes of Bermuda's anchialine fauna show varying degrees of adaptations to the cave environment, ranging from the depigmented and eyeless *Mictocaris halope*, intermediate *Typhlatya iliffei* with small eyes and little pigment, to *Parhippolyte sterreri* having large eyes and bright red pigmentation (Figure 3) [19–21].

Seventy-eight cave-adapted species have been recorded in caves from the Walsingham Tract, Bermuda. The great majority of these species are crustaceans, making up 85% of the fauna: 20 copepods, 19 species of ostracods, 7 amphipods, 5 cumaceans and shrimps, 4 isopods, 2 mysids and tanaidaceans, and 1 mictacean and ingolfiellid. Non-crustacean species include five mites, three polychaetes, and two ciliates and mollusks. The poor representation of taxa other than crustaceans could be due to an effort or specialist bias [22]. Ten of the recorded species are the only representative of their genus, while *Mictocaris halope* is the only known species of its order. Twenty species belong to exclusively stygobiont taxa, while eighteen species have close relatives inhabiting the deep-sea (Table 1, Figure 3).

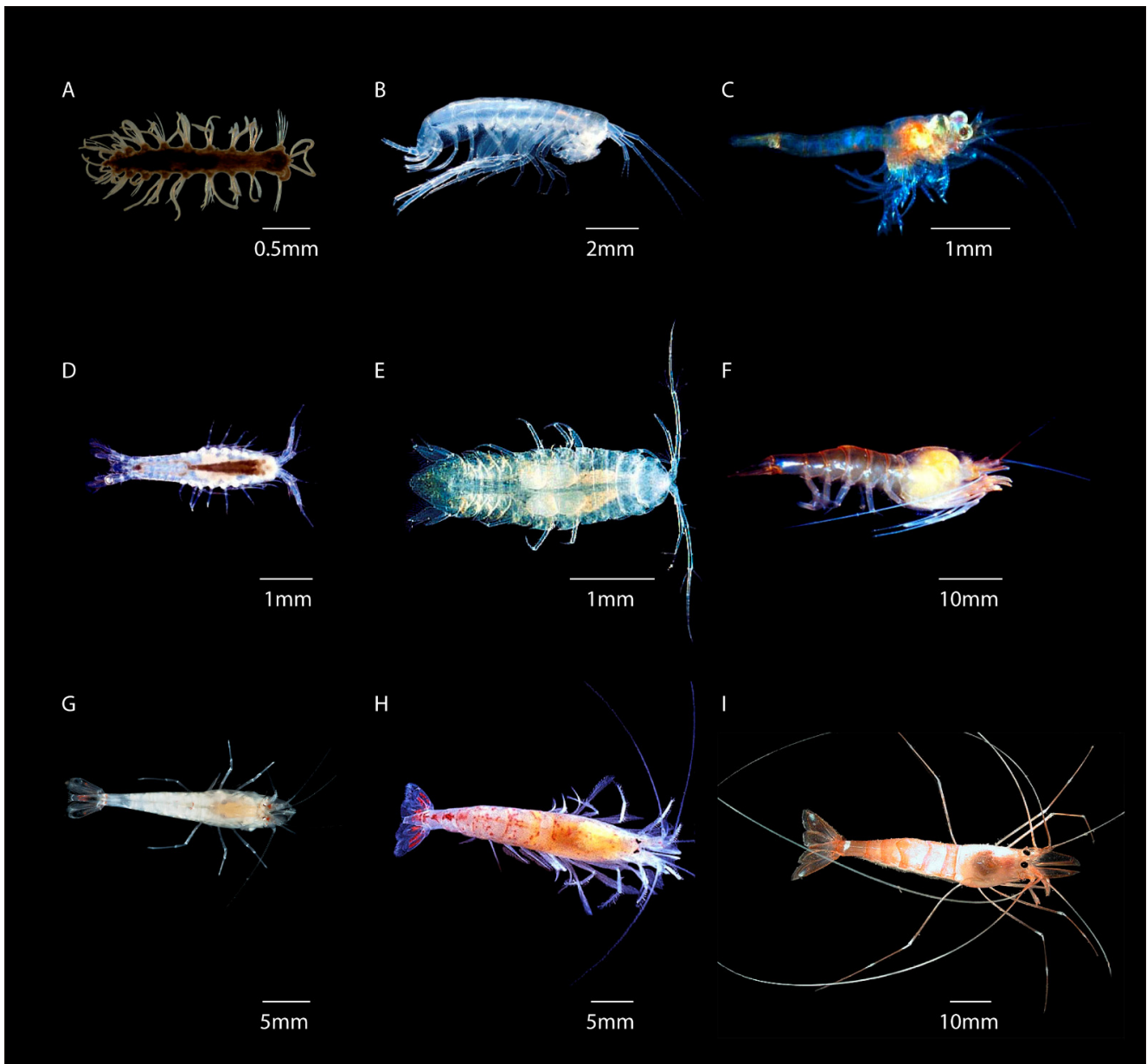


Figure 3. Examples of stygobiont species from the Walsingham cave system. (A) *Leptonerilla prospera*, (B) *Pseudoniphargus grandimanus*, (C) *Bermudamysis speluncola*, (D) *Mictocaris halope*, (E) *Arubolana aruboides*, (F) *Barbouria cubensis*, (G) *Typhlatya iliffei*, (H) *Procaris chacei*, and (I) *Parhippolyte sterreri*. Photo credits: (A) from Katrine Worsaae.

Table 1. Cave species inhabiting the Walsingham Tract in Bermuda. Ecology (B = Stygobiont, P = Stygophile, e = endemic to Bermuda). Species habitat (W = Water column, S = Sediment/interstitial). # Bermuda’s caves (from where the species has been recorded). Monospecific taxa (belong to higher taxa to which they are the only representative, O = Order, G = Genus). Habitat and Region relationships (related species in the immediate superior taxa, “+” = numerous). Conservation status (in accordance with the IUCN Red List [23], Cr = Critically Endangered). Taxonomic status was validated in WoRMS [24].

	Ecology	Species Habitat	# Bermuda Caves	Monospecific Taxa	Species in the Genus	Habitat Relationship			Region Relationship			Conservation Status	Reference
						Cave/Interstitial	Deep Sea		Caribbean	Atlantic	Other		
Chromista													
Ciliophora, Euplotidae													
<i>Euplotes iliffei</i> Hill & Small in Hill, Small & Iliffe, 1986	B,e	W	1		50				X	X	X		[25]
Ciliophora, Parauronematidae													
<i>Glaucanema bermudense</i> Small, 1986	B,e	W	4		2					X			[26]
Annelida													
Polychaeta, Nerillidae													
<i>Leptonerilla prospera</i> (Sterrer & Iliffe, 1982)	B,e	S	8		3	2				X	X	Cr	[27]
<i>Speleonerilla saltatrix</i> (Worsaae, Sterrer & Iliffe, 2004)	B,e	S	1		4	3			X	X			[28]
Oligochaeta, Tubificidae													
<i>Phallodriloides macmasterae</i> (Erséus, 1986)	B,e	S	1		5		2			X		Cr	[29]
Mollusca													
Gastropoda, Caecidae													
<i>Caecum caverna</i> Moolenbeek, Faber & Iliffe, 1988	B,e	S	2		218	1			X	X	X		[30]
<i>Caecum troglodyta</i> Moolenbeek, Faber & Iliffe, 1988	B,e	S	2		218	1			X	X	X		[30]

Table 1. Cont.

	Ecology	Species Habitat	# Bermuda Caves	Monospecific Taxa	Species in the Genus	Habitat Relationship		Region Relationship			Conservation Status	Reference
						Cave/Interstitial	Deep Sea	Caribbean	Atlantic	Other		
Arthropoda												
Arachnida												
Acari, Halacaridae												
<i>Agauopsis bermudensis</i> Bartsch & Iliffe, 1985	B,e	S	2		90	1		X	X	X		[31]
<i>Agauopsis littoralis</i> Bartsch & Iliffe, 1985	B,e	S	1		90	1		X	X	X		[31]
<i>Copidognathus bermudensis</i> Bartsch & Iliffe, 1985	B,e	S	2		380	2		X	X	X		[31]
<i>Copidognathus longispinus</i> Bartsch & Iliffe, 1985	B,e	S	1		380	2		X	X	X		[31]
<i>Copidognathus subterraneus</i> Bartsch & Iliffe, 1985	B,e	S	1		380	2		X	X	X		[31]
Crustacea												
Copepoda, Calanoida												
<i>Enantiosis bermudensis</i> Fosshagen, Boxshall & Iliffe, 2001	B,e	W	10		7	6		X		X		[32]
<i>Epacteriscus rapax</i> Fosshagen, 1973	P	W	9		3	2			X	X		[33]
<i>Erebonectes nesioticus</i> Fosshagen, in Fosshagen & Iliffe, 1985	B,e	W	4	G	1	29	1	X	X		Cr	[34]
<i>Exumella polyarthra</i> Fosshagen, 1970	P	W	X		4	2		X		X		[35]
<i>Miostephus leamingtonensis</i> Yeatman, 1980	B,e	W	1		2	1		X				[36]
<i>Paracyclops naessi</i> Fosshagen in Fosshagen & Iliffe, 1985	B,e	W	5	G	1	4					Cr	[34]
<i>Ridgewayia marki</i> (Esterly, 1911)	P	W	2		14	4		X	X	X		[37]

Table 1. Cont.

	Ecology	Species Habitat	# Bermuda Caves	Monospecific Taxa	Species in the Genus	Habitat Relationship		Region Relationship			Conservation Status	Reference
						Cave/Interstitial	Deep Sea	Caribbean	Atlantic	Other		
Copepoda, Cyclopoida												
<i>Halicyclops bowmani</i> Rocha & Iliffe, 1993	B,e	W	2		89	21		X	X	X		[38]
<i>Halicyclops herbsti</i> Rocha & Iliffe, 1993	B,e	W	1		89	21		X	X	X		
<i>Halicyclops ytororoma</i> Lotufo & Rocha, 1993	P	W	2		89	21		X	X	X		[39]
<i>Speleoithona bermudensis</i> Rocha & Iliffe, 1993	B,e	W	2		3	2		X			Cr	[38]
Copepoda, Harpacticoida												
<i>Intercrusia problematica</i> Huys, 1996	B,e	W	1		2	1				X		[40]
<i>Neoechinophora fosshageni</i> Huys, 1996	B,e	W	2		5	4		X	X	X		[40]
<i>Neoechinophora daltonae</i> Huys, 1996	B,e	W	3		5	4		X	X	X		[40]
<i>Neoechinophora jaumei</i> Huys, 1996	B,e	W	2		5	4		X	X	X		[40]
<i>Superornatiremis mysticus</i> Huys, 1996	B,e	W	3		2	1				X		[40]
Copepoda, Misophrioida												
<i>Speleophria bivexilla</i> Boxshall & Iliffe, 1986	B,e	W	1		6	5		X	X	X	Cr	[41]
<i>Speleophriopsis scottodicarloi</i> (Boxshall & Iliffe, 1990)	B,e	W	2		5	4			X	X	Cr	[42]
Copepoda, Platycopioida												
<i>Antriscopia prehensilis</i> Fosshagen in Fosshagen & Iliffe, 1985	B,e	W	1	G	1	1		X		X	Cr	[34]
<i>Nanocopia minuta</i> Fosshagen in Fosshagen & Iliffe, 1988	B,e	W	1	G	1	1		X		X	Cr	[43]

Table 1. Cont.

	Ecology	Species Habitat	# Bermuda Caves	Monospecific Taxa	Species in the Genus	Habitat Relationship			Region Relationship			Conservation Status	Reference
						Cave/Interstitial	Deep Sea		Caribbean	Atlantic	Other		
Ostracoda, Bairdiidae													
<i>Aponesidea iliffei</i> Maddocks in Maddocks & Iliffe, 1986	B,e	S	10		4						X		[44]
<i>Havanardia keiji</i> Maddocks in Maddocks & Iliffe, 1986	Pe	S	9		12				X	X			[44]
<i>Neonesidea omnivaga</i> Maddocks in Maddocks & Iliffe, 1986	Pe	S	3		99				X	X	X		[44]
<i>Paranesidea sterreri</i> Maddocks in Maddocks & Iliffe, 1986	Pe	S	2		41				X	X	X		[44]
Ostracoda, Candonidae													
<i>Dolerocypria bifurca</i> Maddocks in Maddocks & Iliffe, 1986	B,e	S	3		14	2					X		[44]
<i>Paracypris crispa</i> Maddocks in Maddocks & Iliffe, 1986	Pe	S	3		39				X	X	X		[44]
Ostracoda, Cytherellidae													
<i>Cytherella bermudensis</i> Maddocks in Maddocks & Iliffe, 1986	Pe	S	2		158		+		X	X	X		[44]
<i>Cytherella kornickeri</i> Maddocks in Maddocks & Iliffe, 1986	B,e	S	6		158		+		X	X	X		[44]
Ostracoda, Cyindroleberididae													
<i>Parasterope muelleri</i> (Skogsberg, 1920)	P		2		46					X	X		[45]
Ostracoda, Deeveyidae													
<i>Spelaeoecia bermudensis</i> Angel & Iliffe, 1987	B,e	W	11		11	10			X			Cr	[46]

Table 1. Cont.

	Ecology	Species Habitat	# Bermuda Caves	Monospecific Taxa	Species in the Genus	Habitat Relationship		Region Relationship			Conservation Status	Reference
						Cave/Interstitial	Deep Sea	Caribbean	Atlantic	Other		
Ostracoda, Halocypridae												
<i>Metapolycope duplex</i> Kornicker & Iliffe, 1989	B,e	S	12		10		4		X			[47]
<i>Micropolycope eurax</i> Kornicker & Iliffe, 1989	B,e	S	3		11	1			X	X		[47]
<i>Micropolycope styx</i> Kornicker & Iliffe, 1989	B,e	S	6		11	1			X	X		[47]
Ostracoda, Philomedidae												
<i>Pseudophilomedes kyllix</i> Kornicker & Iliffe, 1989	B,e	S	5		11				X	X		[47]
Ostracoda, Polycopidae												
<i>Polycopissa anax</i> Kornicker & Iliffe, 1989	B,e	S	8		4				X	X		[47]
Ostracoda, Pontocyprididae												
<i>Iliffeocia iliffei</i> Maddocks, 1991	B	S	2		3					X		[48]
<i>Kareloecia minacis</i> (Maddocks in Maddocks & Iliffe, 1986)	B,e	S	1		2	1				X		[44]
<i>Thomontocypris lurida</i> (Maddocks in Maddocks & Iliffe, 1986)	B,e	S	5		9		6	X	X	X		[44]
Ostracoda, Sarsiellidae												
<i>Eusarsiella styx</i> Kornicker & Iliffe, 1989	B,e	S	6		86	7	+	X	X	X		[47]
Caridea, Atyidae												
<i>Typhlatya iliffei</i> Hart & Manning, 1981	B,e	W	1		17	16		X	X	X	Cr	[19]
Caridea, Alpheidae												
<i>Bermudacaris harti</i> Anker & Iliffe, 2000	B,e	W	4		3					X		[20]

Table 1. Cont.

	Ecology	Species Habitat	# Bermuda Caves	Monospecific Taxa	Species in the Genus	Habitat Relationship		Region Relationship			Conservation Status	Reference
						Cave/Interstitial	Deep Sea	Caribbean	Atlantic	Other		
Caridea, Barbouriidae												
<i>Barbouria cubensis</i> (von Martens, 1872)	B	W	3	G	1	8		X	X	X	Cr	[22]
<i>Parhippolyte sterreri</i> (Hart & Manning, 1981)	B	W	2		6	5		X	X	X	Cr	[19]
Caridea, Procarididae												
<i>Procaris chacei</i> Hart & Manning, 1986	B,e	W	1		5	4		X	X	X	Cr	[49]
Isopoda, Atlantasellidae												
<i>Atlantasellus cavernicolus</i> Sket, 1979	B,e	S	1		2	1	1		X		Cr	[50]
Isopoda, Cirolanidae												
<i>Arubolana aruboides</i> (Bowman & Iliffe, 1983)	B,e	W	4		4	3		X		X	Cr	[51]
Isopoda, Leptanthuridae												
<i>Curassanthura bermudensis</i> Wägele & Brandt, 1985	B,e	S	1		5	4		X	X		Cr	[52]
Isopoda, Stenetriidae												
<i>Stenobermuda iliffei</i> Kensley, 1994	B,e	S	1		6			X	X	X		[53]
Amphipoda, Amphilochidae												
<i>Hourstonius petulans</i> (Karaman, 1980)	P	S	1		18		1			X		[54]
Amphipoda, Bogidiellidae												
<i>Bermudagiella bermudiensis</i> (Stock, Sket & Iliffe, 1987)	B,e	S	2	G	1	115	114	X	X	X	Cr	[55]
Amphipoda, Liljeborgiidae												
<i>Idunella sketi</i> Karaman, 1980	P	S	1		44	1		X	X	X	Cr	[56]
<i>Idunella verrilli</i> Yabut & Sawicki, 2015	B,e		1		44	1		X	X	X		[56]

Table 1. Cont.

	Ecology	Species Habitat	# Bermuda Caves	Monospecific Taxa	Species in the Genus	Habitat Relationship		Region Relationship			Conservation Status	Reference	
						Cave/Interstitial	Deep Sea	Caribbean	Atlantic	Other			
Amphipoda, Phoxocephalidae													
<i>Cocoharpinia iliffei</i> Karaman, 1980	B,e		1	G	1		+	X	X	X	Cr	[57]	
Amphipoda, Podoceridae													
<i>Podobothrus bermudensis</i> Barnard & Clark, 1985	B,e		1	G	1		+	X	X	X		[58]	
Amphipoda, Pseudoniphargidae													
<i>Pseudoniphargus grandimanus</i> Stock, Holsinger, Sket & Iliffe, 1986	B,e	W	20		72	71			X	X	Cr	[59]	
Ingolfiellida, Ingolfiellidae													
<i>Ingolfiella (Tethydiella) longipes</i> Stock, Sket & Iliffe, 1987	B,e	S	1		44		+	+	X	X	X	Cr	[55]
Tanaidacea, Apseudidae													
<i>Apseudes orghidani</i> Gutu & Iliffe, 1989	B,e	W	1		44			+	X	X	X		[60]
<i>Paradoxapseudes bermudeus</i> (Băcescu, 1980)	P	S	1		18	3		1	X		X		[61]
Mictacea, Mictocarididae													
<i>Mictocaris halope</i> Bowman & Iliffe, 1985	B,e	W	4	O	1	3		3	X		X	Cr	[21]
Cumacea, Nannastacidae													
<i>Cumella (Cumella) iliffei</i> Băcescu, 1992	B,e	S	2		102				X	X	X		[62]
<i>Cumella (Cumella) ocellata</i> Băcescu, 1992	B,e	S	1		102				X	X	X		[62]
<i>Cumella (Cumella) spinosa</i> Băcescu & Iliffe, 1991		S	1		102				X	X	X		[63]

Table 1. Cont.

	Ecology	Species Habitat	# Bermuda Caves	Monospecific Taxa	Species in the Genus	Habitat Relationship		Region Relationship			Conservation Status	Reference
						Cave/Interstitial	Deep Sea	Caribbean	Atlantic	Other		
Cumacea, Nannastacidae												
<i>Schizotrema agglutinanta</i> (Băcescu, 1971)	P	S	8		20	1		X	X	X		[64]
<i>Schizotrema wittmanni</i> Petrescu & Sterrer, 2001	P	S	1		20	1		X	X	X		[65]
Mysida, Mysidae												
<i>Bermudamysis speluncola</i> Băcescu & Iliffe, 1986	B,e	W	2	G	1	2	1		X	X	Cr	[66]
<i>Platyops sterreri</i> Băcescu & Iliffe, 1986	B,e	W	2	G	1	2	1		X	X	Cr	[66]

Sixty-three species are stygobionts, and fifteen stygophiles (i.e., aquatic animals living in and outside caves). Most of Bermuda's endemic cave species have an extremely restricted distribution, with 26 species known only from a single cave, 14 more species limited to just two caves, and 52 species in total occurring in five or fewer caves. The ostracod *Iliffeoecia iliffei* also occurs in caves from the Galápagos Islands, while the barbouriid shrimp *Barbouria cubensis* inhabits caves from Bahamas, Caicos Islands, Cayman Islands, Cuba, Jamaica, and Mexico's Yucatan Peninsula, and *Parhippolyte sterreri* is found from caves in the Bahamas and the Yucatan Peninsula, in addition to Bermuda [67,68]. The stygophile ostracods *Havanardia keiji*, *Neonesidea omnivaga*, *Paranesidea sterreri*, *Cytherella bermudensis*, and *Paracypris crispa* were described from sample specimens collected in caves but have been also found in the island's open water environments, and are endemic to Bermuda [44]. The copepods *Epacteriscus rapax*, *Exumella polyarthra*, *Halicyclops ytororoma*, and *Ridgewayia marki*, the ostracod *Parasterope muelleri*, the cumaceans *Schizotrema agglutinanta* and *S. wittmanni*, the amphipods *Hourstonius petulans* and *Idunella sketi*, and the tanaidacean *Paradoxapseudes bermudeus* are also found from open water or interstitial environments outside Bermuda [32–34,39,65,68–71].

Considering Bermuda's isolated mid-ocean location, biogeographical affinities of the cave species may provide significant clues as to their origins. While the Gulf Stream may have transported some species to the island, others may have survived on submerged or emergent seamounts near the Mid-Atlantic Ridge, originated from Tethyan relicts, or are derived from deep-sea taxa [5]. Here are a few examples: The misophrioid copepod *Speleophria bivexilla* has congeners inhabiting caves from the Balearic Islands, Croatia, northwestern and southern Australia, and the Yucatan Peninsula, suggesting possible dispersal by plate tectonic processes [72]. The atyid shrimp *Typhlatya iliffei* belongs to an exclusively cave-adapted genus with species spread around the Caribbean and Western Mediterranean, as well as the Galapagos Islands, Ascension Island, and Madagascar. Their ancestors likely inhabited the ancient Tethys Sea with both vicariance (the opening of the Atlantic) and dispersal leading to their isolation and divergence [73]. The stygobiont amphipod *Pseudoniphargus* includes species from North Africa, the Mediterranean region and its islands, the Iberian Peninsula, the Canary Islands, Madeira, and the Azores, in addition to two species in Bermuda, on the west side of the mid-Atlantic rift, but is absent from the American continent or from the Caribbean. Based on phylogenetic analyses, the estimated age of the *Pseudoniphargus* lineage on Bermuda is relatively young, only 5 Ma [74]. The ostracod *Spelaeoecia bermudensis* belongs to a stygobiont genus with seven species from the Bahamas, two from Cuba, and one each from Jamaica, the Yucatan Peninsula, and Bermuda. The cluster of this ostracod in the Bahamas suggests possible ocean dispersal via the Gulf Stream rafting adults or larvae to Bermuda [75].

While numerous cave taxa in Bermuda are significant in their presence, the absence of several globally prominent stygobiont taxa is also remarkable. The crustacean class Remipedia inhabits anchialine caves in the Bahamas (21 spp.), Yucatan Peninsula (3 spp.), the Dominican Republic (1 sp.), Cuba (1 sp.), and Belize (1 sp.), plus the Canary Islands (2 spp.) and Australia (1 sp.) but, despite many hundreds of cave dives, has never been observed in Bermuda [76,77]. The ostracod stygobiont genus *Humphreysella* has a similar distribution and ecology to Remipedia, while being absent from Bermuda. *Humphreysella* occurs in caves in the Bahamas (3 spp.), Yucatan Peninsula (1 sp.), Cuba (1 sp.), Jamaica (1 sp.), Galápagos Islands (1 sp.), and Canary Islands (1 sp.), as well as having a closely related monotypic genus in Western Australia and Christmas Island (Indian Ocean) [24,78].

Important questions arise as to the age and origins of Bermuda's endemic cave fauna. The Bermuda seamount formed from volcanic eruptions occurring approximately 35 million years ago. Due to its attachment to the North American Plate, the seamount remained at a constant distance from the North American coast, but an ever-increasing distance from Europe as the Atlantic Ocean expanded. Limestone bedrock containing all known caves is only 1–2 million years in age. The limestone capping the summit of the Bermuda seamount extends down to about 30 m below present sea level, such that during Pleistocene regressions to 130 m, all of the island's limestone and, thus, its caves, were exposed above

the ocean and were dry. The exceptionally large stalactites and stalagmites in the now underwater caves, and the level of the Pleistocene ocean, corroborate that caves must have been continuously dry for many tens thousands of years at a time (Figure 2B). It was not until about 7000 years ago that the sea level rise from the last glacial maximum (~20,000 years ago) caused Bermuda's caves to become flooded [9].

Considering the high diversity, unique ecological and taxonomic nature of the cave fauna, a relatively modern origin by cave colonization from the open ocean is highly unlikely and can be ruled out. Instead, the cave species currently found in Bermuda must have been dark-adapted organisms that moved into caves from suitable crevice or crevicular habitats in the volcanic bedrock or sides of the Bermuda seamount occurring at depths greater than where sea level was during the last glacial maximum. The presence of a highly diverse and endemic stygobiont fauna in a young (~21,000 years old) volcanic cave in the Canary Islands presents a comparable case. La Corona lava tube on Lanzarote formed during the last ice age as a dry cave that was flooded by rising sea level to a maximum water depth of 64 m [79].

6. Threats to Bermuda's Cave Fauna

Bermuda represents an extreme case of threats to marine cave fauna and a microcosm of issues facing caves around the world. The primary threats to Bermuda caves and their fauna include: (i) filling and quarrying activities, (ii) water pollution, (iii) dumping and littering, (iv) vandalism [80], and (v) climate change [81]. Since most of Bermuda's endemic stygobionts inhabit only a single cave or cave system, pollution of these habitats can threaten entire species with extinction.

Population growth and land development have adversely affected Bermuda's caves and cave fauna. The islands have a total land area of 53.3 km², of which 20% (or 10 km²) is forest and woodland [77]. As of May 2021, Bermuda's population was estimated to be 62,069, down from a high of 66,257 in 2005 [82], yielding an average population density of 1164 persons per km². In such a small, densely populated island, considerable human pressures have been brought to bear on the relatively unknown and poorly appreciated caves.

Intentional dumping of large quantities of refuse, raw sewage, and waste fuel oil into anchialine cave pools in Bermuda resulted in the depletion of dissolved oxygen and production of hydrogen sulfide in deep lakes from Government Quarry and Bassett's Caves [83]. The resulting anoxic conditions not only eliminated all typical cave invertebrates, but also formed black metal sulfide precipitates that substantially reduced water clarity. Such polluted waters can move for considerable distances underground and appear years later in distant cave pools. In addition, broken or missing speleothems, graffiti, names on cave walls, and litter are common sights in many dry caves in Bermuda, while sinkholes and cave entrances were long used for trash disposal [80] (Figure 2F). Tidal currents suck floating plastic bottles and bags into coastal caves (Figure 2E). Such negative impacts to caves reduce their esthetic value and, therefore, make it more difficult to justify protective measures.

Climate change is a medium-term to long-term threat, since warming climate causes an increased frequency and strength of hurricanes and sea level rise, which will directly affect the habitat availability. Furthermore, cave organisms are especially vulnerable to rapid environmental changes [81,84].

In an effort to protect caves, Bermuda's planning laws now afford caves the highest level of protection [85]. The Fourth Schedule of the Planning Act 1974 states: "The protection of caves shall take precedence over all other planning considerations and the Board shall refuse any development application or planning of subdivision if, in the opinion of the Board, the proposal will have detrimental impact on a cave entrance or underlying cave." The Protected Species Act 2003 and Protected Species Order 2012 list 22 cave-dwelling species for legal protection, while the 2014 "Management Plan for Bermuda's Critically Endangered Cave Fauna" seeks adequate protection for the entire cave habitat. The Man-

agement Plan is designed to protect caves through legislation and raised public awareness, comprehensive mapping of caves, identifying and managing point source pollution, monitoring cave air and water, examining the potential for hatchery breeding, facilitating ecological research, and undertaking active restoration of impacted caves [85].

Unfortunately, loopholes in the laws have allowed important caves with endangered and protected species to be destroyed. Wilkinson Quarry Cave at the northern end of the Walsingham Tract was discovered during blasting operations in 2002. The cave contained profuse and actively growing speleothems and a large network of submerged cave passages where biological collections identified four species of stygobiont crustaceans on the IUCN Red List. While biology and conservation experts pressed for protection and preservation of the cave, consultants hired by quarry management supported its destruction arguing that the cave was (1) small, (2) structurally compromised and therefore unsafe, and (3) not ecologically or esthetically significant [86]. Despite the Planning Act law and the presence of endangered species, the Bermuda Development Applications Board approved destruction of the cave and removal of all bedrock to level off the lower quarry floor.

Another way to safeguard caves is through private and government owned nature reserves that effectively protect undeveloped woodland, karst topography, extensive cave systems, saltwater ponds, and endemic cave-adapted plants, mosses, and ferns. The 400-acre (160 ha) Walsingham Tract includes four adjacent nature reserves: the 23-acre (9.3 ha) Walsingham Trust Nature Reserve, 1.25-acre (0.5 ha) Idwal Hughes Nature Reserve, 12-acre (4.9 ha) Blue Hole Hill Park, and Crystal and Fantasy Caves operated by the Wilkinson Trust as commercial tourist attractions [87]. Since the mid-20th century, sections at the northern and southern ends of the Tract have been lost to quarrying, hotel, and residential development, increasing the importance of these nature reserves as a key conservation and restoration areas.

Thus, conservation actions to protect Bermuda's anchialine cave habitat and its unique stygobiont fauna, especially caves in the Walsingham Tract, are crucial. Further research is needed to understand the biodiversity, species biology, population sizes, and carrying capacity of the ecosystem in relation to diverse human activities.

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