

Revision of the Bahamian cave-fishes of the genus *Lucifuga* (Ophidiiformes, Bythitidae), with description of a new species from islands on the Little Bahama Bank

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Abstract

Since the description of the Bahamian cave-fish *Lucifuga spelaeotes* Cohen & Robins, 1970, which was based on two specimens from New Providence Island, the species has been observed and/ or collected several times in marine blue-holes and inland caves on various Bahamian Islands. Hitherto, all *Lucifuga* records from the Bahamas have been referred to *L. spelaeotes*, but examination of 50 specimens (42–166 mm SL) collected at 7 different islands showed that two species are represented in the Bahamas: 44 specimens from Berry, New Providence, Eleuthera, Great Exuma and Long Island belong to *L. spelaeotes*, whereas 6 specimens from Grand Bahama and Abaco Islands are referable to *L. lucayana*, new species. The new species is here described and compared to the material of *L. spelaeotes*, which includes specimens from several hitherto unpublished locations. The two species are well separated from the Cuban species in number of caudal finrays (10 vs. 8), size of eye (0.7–1.8 vs. 0.0–0.3 % SL) and number of vertebrae (50–55 vs. 45–48). The Bahamian species differ from each other mainly in head squamation, palatine dentition, number of finrays and pigmentation of the three elongated gill-rakers. *Lucifuga lucayana* is geographically separated from *L. spelaeotes* by the deep waters of the Northeast and Northwest Providence Channels.

Key words: Viviparous brotulas, Bahamas, anchialine caves, blue holes, cave-fishes

Introduction

Our knowledge about the bythitid cave-fishes of the genus *Lucifuga* Poey was summed up by Cohen & McCosker (1998) and more recently in a FAO species catalogue of ophidiiform fishes (Nielsen *et al.* 1999). The genus was formerly split in two, based on presence

(*Stygicola* Gill) or absence (*Lucifuga* Poey) of palatine teeth (Gill 1863). *Stygicola* was lowered to subgeneric rank by Cohen & Robins (1970) and has been used commonly (e.g. Cohen & Nielsen 1978; Nalbant 1981; Cohen & McCosker 1998; Romaro & Paulson 2001). Phylogenetic and biogeographic analyses by Vergara (1980, 1981) did not support this subdivision of the genus, and in Nielsen *et al.* (1999) and Nielsen (2002) it was abandoned without arguments.

Presently six species are recognised: 4 from Cuba, 1 from the Bahamas and 1 from off Galapagos. The latter, *L. inopinata* Cohen & McCosker, 1998, was included with some uncertainty due to strong affinities to *Calamopteryx* Böhlke & Cohen, 1966 (Cohen & McCosker 1998; Møller *et al.* 2004a). It is not included in the present paper, but will be treated separately in a subsequent paper.

The Bahamian species *L. spelaeotes* Cohen & Robins, 1970 was described from two specimens from a brackish water sinkhole (Mermaid's Pool) on New Providence Island. Since then it has been collected and/ or reported several times from marine blue holes and inland caves on seven additional islands so that the total list of localities includes:

Little Bahama Bank Islands:

1. Grand Bahama Island: Lucayan Caverns (Yager 1981, Yager & Williams 1988, Smith–Vaniz & Böhlke 1991); Zodiac Caverns (Palmer 1985b, Cunliffe 1985)
2. Abaco Island: Inland sink hole (Smith–Vaniz & Böhlke 1991)

Great Bahama Bank Islands:

3. Berry Islands (Proudlove 2001)
4. Andros Island: ocean blue holes (Proudlove 1984, B. Kakuk *in litt.* (in Cohen & McCosker 1998)); Uncle Charlie's Blue Hole (Farr & Palmer 1984, Proudlove 1984)
5. New Providence Island: Mermaid's Pool (Cohen & Robbins 1970); R.M. Bailey School Cave (R. Attrill web page a)
6. Eleuthera Island: Nixon's Blue Hole (B. Kakuk pers. comm., J. Dougherty pers. comm.); Sink Hole (A. Leggett pers. comm.)
7. Great Exuma Island: Angelfish Blue Hole (B. Kakuk pers. comm.)
8. Long Island: (J. Yager *in litt.* (in Cohen & McCosker 1998))

The Bahamas consist of two major banks: The Great Bahama Bank is a large, shallow water carbonate platform that also includes the major islands of New Providence, Bimini, Andros, Cat, Eleuthera, Great Exuma and Long Island. The Great Bahama Bank is separated from the Little Bahama Bank (containing the major Islands Grand Bahama and Abaco) by the Northeast (3800 to 4700 m deep) and Northwest (700 to 2800 m deep) Providence Channels. The banks are made up of limestone of shallow water origin having been deposited to a depth of at least 4500 m since the Cretaceous. Numerous caves and

solutional karst features are present on most islands. In the Bahamas, such partially or totally submerged cave systems, occurring both inland and on the seabed, are referred to as “blue holes”. On Long Island for example, more than 60 blue holes are listed on topographic maps. Most notable of these is Dean's Blue Hole—the World's deepest marine cave reaching depths of 200 m (Wilson 1994).

Lucifuga spelaeotes is often referred to as the blind Bahamian cave-fish, but actually all specimens have small, developed eyes. Because of this and the presence of palatine teeth and 10 caudal finrays, *L. spelaeotes* has been regarded the most primitive/ ancestral species of the Atlantic *Lucifuga* spp., compared to the Cuban species with even more reduced eyes, 8 caudal finrays and no palatine teeth (except present in *L. dentata* and *L. simile*) (Cohen and Robins 1970, Vergara 1980).

Despite the new records and collections, morphological data have only been published from the two type specimens and thus no information on the variability and ontogeny of the species is available. During examination of 50 specimens (42–166 mm SL) collected at seven different islands, it became obvious that at least two species are represented in the Bahamas. One new species is here described and *L. spelaeotes* is redescribed based on additional material (44 vs. 2 specimens).

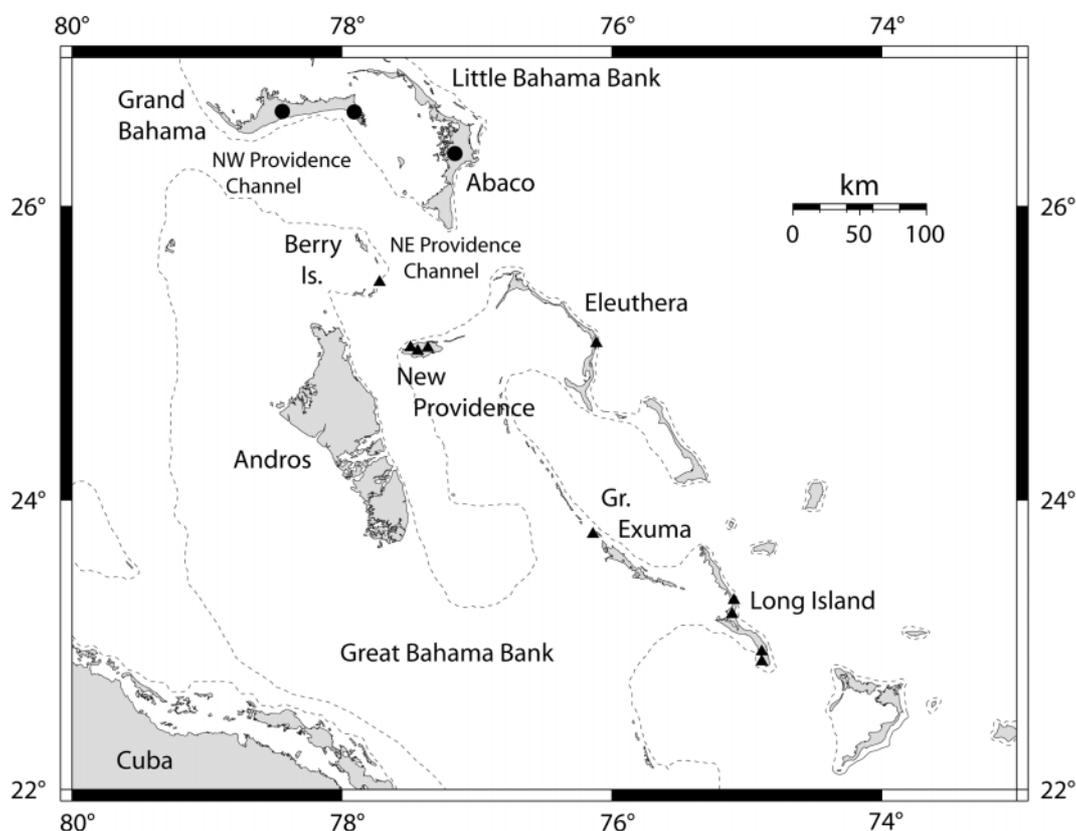


FIGURE 1. Sample sites of Bahamian *Lucifuga* spp.: ●, *Lucifuga lucayana*; ▲, *Lucifuga spelaeotes*. Depth curve 100 m.

Materials and Methods

Measurements and counts were made according to Nielsen *et al.* (1999). Standard length (SL) and head length (HL) are used throughout. Head pore nomenclature follows Møller *et al.* (2004b). In the descriptions, holotype data are given first, followed by the range of all specimens in parentheses. Institutional abbreviations follow Leviton *et al.* (1985).

In January 2005, Long Island caves were visited by Thomas Iliffe and collaborators, in an attempt to relocate known caves and find new sites for *Lucifuga* and other cave animals. Salinity in the pools was measured with a YSI Model 600XLM Multi-Parameter Water Quality Monitor.

Comparative material

Lucifuga dentata Poey, 1858: ANSP 8980, 67 mm SL, female, Cuba, near Cienfuegos; ANSP 37116, 85 and 97 mm SL, males, Cuba, Alacranes; ANSP 90770, 96 mm SL, female, Cuba, Alacranes; ZMH 18212, 89 and 114 mm SL, female and male, Cuba, Masuata, Pinar del Rio. *Lucifuga inopinata* Cohen & McCosker, 1998: CAS 86572 (holotype), 101 mm SL, female, off Galapagos Is, Seamount southeast of I. San Cristobal. *Lucifuga simile* Nalbant, 1981: ZMH 9518, 87.5 mm SL, male, Cuba. *Lucifuga subterranea* Poey, 1958: ANSP 37111, 70 mm SL, female, Cuba, Canas; USNM 204452, 40 and 72 mm SL, females, Cuba.

Systematics

Family Bythitidae

Subfamily Bythitinae

Lucifuga

Lucifuga Poey, 1858: 95 (type species: *Lucifuga subterraneus* Poey, 1858 by subsequent designation of Jordan and Evermann (1896), type locality: Caves of San Antonio, South Cuba.

Stygicola Gill, 1863: 252 (type species: *Lucifuga dentatus* (Poey, 1858) by original designation, type locality: Cave of Cajio, Cuba).

Remarks. Poey (1858) described *Lucifuga subterraneus* and *Lucifuga dentata* after the generic description in the same volume, without type species designation. The designation of a type species was done subsequently by Jordan and Evermann (1896) as stated in Cohen and McCosker (1998) and Nielsen *et al.* (1999), and not by monotypy as stated in Eschmeyer (1998) and Nielsen (2003).

Key to Atlantic species of *Lucifuga*

- 1 Caudal finrays 8; total vertebrae 45–48 (not known for *L. teresinarum*); eye diameter 0.0–0.3 % SL, Cuban *Lucifuga* spp..... 2
 - Caudal finrays 10; total vertebrae 50–55; eye diameter 0.7–1.8 % SL; Bahamian *Lucifuga* spp..... 5
- 2 Palatine teeth present..... 3
 - Palatine teeth absent..... 4
- 3 Dorsal finrays 83–95, ratio otolith length to sulcus length < 2.8..... *L. dentata*
 - Dorsal finrays 70–78, ratio otolith length to sulcus length > 3.5..... *L. simile*
- 4 Dorsal finrays 80–86; pectoral finrays 12–14..... *L. subterranea*
 - Dorsal finrays 78–80; pectoral finrays 10–11..... *L. teresinarum*
- 5 Lateral occipital area naked, palatine teeth present; long gill-rakers usually dark
 *L. spelaeotes*
 - Lateral occipital area scaled, palatine teeth absent; long gill-rakers pale
 *L. lucayana* n. sp.

***Lucifuga lucayana*, new species**

(Figs. 2–6, Tables 1–3)

Lucifuga spelaeotes (not Cohen & Robins, 1970): Yager 1981: 328; Cunliffe 1985: 108, photo; Palmer 1985a: 114, photo 51; Yager & Williams 1988: 102; Wilkens *et al.* 1989: 127 (eyes); Smith–Vaniz & Böhlke 1991: 202 (part); Cohen & McCosker 1998: 184 (part); Proudlove 2001: 207 (part).

Material examined (6 specimens, of which 3 lack the head, 44–99 mm SL, due to earlier studies of the eye development (H. Wilkens pers. comm.). Identification of headless specimens based on finray and vertebrae counts).

Holotype: ANSP 146475, 99 mm SL, female, Grand Bahama Island, Lucayan Caverns, depth 12 m, collected by Dennis Williams, 1 November 1980.

Paratypes: ANSP 148497, 44 mm SL, male, Abaco Island, inland sink hole, precise location and depth unknown, collected by Dennis Williams, date unknown; BMNH 1984.12.1.20, 80 mm SL, female, Grand Bahama Island, Pisces Cave, Zodiac Caverns, depth 15 m, collected by Robert Palmer, 4 July 1984 (see Palmer 1985a); ZMH 9517, ca. 85 mm SL, head missing, female, Abaco Island, 26°14'30"N, 77°11'25"W, collected by Dennis Williams, 7 June 1984; ZMH 9522, ca. 110 mm SL, head missing, male, Grand Bahama Island, Lucayan Caverns, other data missing; ZMH 9566, ca. 125 mm SL, head missing, male, Grand Bahama Island, Lucayan Caverns, other data missing.

Diagnosis. *Lucifuga lucayana* is distinguished from other members of the genus by the following combination of characters: Vertebrae 12–13+37–39=50–52, dorsal finrays

84–91, anal finrays 63–69, pectoral finrays 17–18, caudal finrays 10; head profile above eye strongly depressed, scales on occiput, eyes present (0.9–1.0 % SL); palatine teeth absent; color uniformly light brown, long gill-rakers 3, pale.

Similarity. *Lucifuga lucayana* resembles *L. spelaeotes* in all but a few characters listed in Tables 1–3. It differs in the lack of palatine teeth (vs. 3–56) (fig. 6), color of elongated gill-rakers (pale vs. dark) and the broadly scaled occiput (vs. occiput scaled only in central part) (fig. 4). Furthermore, *L. lucayana* in average have fewer dorsal finrays (84–91, $x=89.2$ vs. 86–109, $x=97.5$), anal finrays (63–69, $x=66.2$ vs. 66–82, $x=73.8$) (Tables 1–3) and perhaps smaller eyes (0.9–1.0, $x=1.0$ vs. 0.7–1.8, $x = 1.3$ % SL, fig. 5).

Lucifuga lucayana resembles two Cuban species *L. subterranea* and *L. teresinarum* in the lack of palatine teeth, but it differs from these and the two other Cuban species in several characters e.g. larger eye (0.9–1.0 vs. 0.0–0.3 % SL), and in the higher number of vertebrae (12–13 +37–39 = 50–52 vs. 11+34–37 = 45–48 (unknown for *L. teresinarum*) and caudal finrays (10 vs. 8) (Table 3). It further differs from the Cuban species *L. dentata* and *L. simile* by the lack of palatine teeth and number of anal finrays (63–69 vs. 69–78 and 57–60, respectively).

Description. Meristic and morphometric characters are given in Tables 1–3. Body moderately elongate, compressed. Head profile strongly depressed (figs. 2–4). Eyes relatively small, 0.9–1.0 % SL (fig. 5). Upper jaw slightly protruding. Anterior nostril tube-shaped, placed low on snout near upper lip; posterior nostril a mere hole, larger, about midway between snout and eye. Maxilla expanded posteriorly, not sheathed by skin flap. Opercular spines absent. Anterior gill arch with 3 elongate rakers and 13 (10–14) broad plates arranged in the following configuration: Upper branch with 3 (3–5) broad plates; the bend between upper and lower gill arch with one long raker, and lower gill arch with 1 (0–1) small plate, 2 elongate rakers interspersed with 1 small plate and followed by 8 (6–8) small plates. Pseudobranchial filaments 2 (1–2). Branchiostegal rays 7.

Scales on body large, oval (in HT about 1.6 mm horizontally at mid-body, and about 20 horizontal rows above anal fin origin); vertical fins and pectoral fin naked except for scales on pectoral fin peduncle. Predorsal area, operculum and top of head, including the occiput scaled. Snout, interorbital, area below eyes and narrow supraorbital and postorbital bands naked (figs. 3A, 4A–B).

Origin of dorsal fin above tip of pectoral fins. Pelvic fin with a single ray reaching about one third from its base to origin of anal fin. Pectoral fin on the middle of body, peduncle short and narrow. Caudal fin free, not fused with dorsal and anal fins.

Head sensory pores: Supraorbital pores 4, anteriormost 3 on snout and posteriormost above opercular flap; infraorbital pores 6 (3 large anteriorly and smaller 3 posteriorly); mandibular pores 6 (3 anterior and 3 posterior), the 2nd anterior very long, the posterior ones increasing in size; preopercular pores 2 (2 lower and 0 upper) (fig. 3A). Lateral line with 13 (12–13) dorsal neuromasts anteriorly and 35 (34–35) medio-lateral neuromasts posteriorly. Many small sensory papillae on head.

TABLE 1. Meristic and morphometric characters of *Lucifuga lucayana* sp. n. and *L. spelaeotes*.

	<i>L. lucayana</i>		<i>L. spelaeotes</i>	
	HT	HT and 5 PTs ¹	HT	HT, PT and 42 nontypes
	ANSP 146475	Mean and range	USNM 204603	Mean and range
SL (mm)	99	74.3(44–99)	110	106.3(42–166)
Meristic characters				
Dorsal finrays	91	89.2(84–91)	92	97.5(86–109)
Caudal finrays	10	10	10	10
Anal finrays	67	66.2(63–69)	71	73.8(66–82)
Pectoral finrays	17	17.2(17–18)	18	18.5(17–20)
Precaudal vertebrae	13	12.8(12–13)	13	13.2(13–14)
Caudal vertebrae	39	38.6(37–39)	39	39.5(38–42)
Total vertebrae	52	51.3(50–52)	52	52.7(51–55)
Rakers on anterior gill arch	16	15.3(13–17)	21	18.8(15–23)
Pseudobranchial filaments	2	1.5(1–2)	0	1.3(0–4)
Anterior dorsal fin ray above vertebra no. (D/V)	8	8.5(8–9)	9	9.0 (8–10)
Anterior anal fin ray below dorsal fin ray no. (D/A)	27	26.3(23–28)	25	27.2(24–32)
Anterior anal fin ray below vertebra no. (V/A)	19	18.8(18–20)	19	18.9(18–20)
Palatine teeth rows	0	0	5	3.7(1–7) ²
Palatine teeth number	0	0	?	22.6(3–56)
Premaxillary teeth rows	7	5–7	8	6.8(4–10)
Morphometric characters in % of SL				
Head length	28.8	28.4(27.1–29.3)	29.1	28.8(26.2–31.3)
Head width	14.2	12.3(10.5–14.2)	14.2	14.5(11.4–17.0)
Head height	16.8	15.1(13.9–16.8)	16.3	16.4(13.7–19.4)
Snout length	7.3	7.3(7.1–7.6)	7.5	7.4(6.2–8.7)
Upper jaw length	14.9	14.2(13.2–14.9)	16.2	14.7(12.4–16.8)
Maxillary height	4.3	4.1(3.9–4.3)	5.4	5.0(3.5–6.3)
Diameter of pigmented eye	1.0	1.0(0.9–1.0)	1.3	1.3(0.7–1.8)
Interorbital width	6.9	6.0(4.3–6.9)	5.5	5.6(4.1–7.6)
Postorbital length	20.9	20.5(19.3–21.3)	21.0	20.4(18.4–22.6)
Preanal length	55.6	55.0(51.7–57.6)	54.1	54.2(48.2–60.5)
Predorsal length	37.0	36.4(35.5–37.0)	39.3	38.1(34.7–41.1)
Body depth at origin of anal fin	14.6	13.4(9.9–15.8)	14.3	13.5(10.9–15.4)
Pectoral fin length	13.3	12.6(11.3–13.3)	12.5	12.7(11.1–14.4)
Pelvic fin length	11.8	10.6(9.4–11.8)	14.7	14.0(8.0–20.0)
Base of pelvic fin to anal fin origin	34.9	33.7(29.4–36.9)	31.3	31.2(27.0–36.9)
Caudal fin length	9.6	10.9(9.6–12.2)	?	9.5(6.4–12.3)

1 Head missing in three paratypes.

2 Bony projection without teeth on left palatine and damaged palatine teeth on right palatine in one specimen (USNM 274737).

TABLE 2. Meristic frequency.

	Number of dorsal finrays																			n							
	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102		103	104	105	106	107	108	109
<i>L. lucayana</i> n. sp.																											
Grand Bahama Island	1				1		2																				4
Abaco Island							1																				1
<i>L. spelaeotes</i>																											
Berry Islands								1																			1
New Providence Island		1			1		1	2	1		6	2	3	2	4		6	1	1	1	1	0	1				34
Eleuthera Island															1												1
Great Exuma Island																			1								1
Long Island															1	1							2				1 5
Number of anal finrays																											
	Number of anal finrays														n												
	63	64	65	66	67	68	69	70	71	72	73	74	75	76		77	78	79	80	81	82						
<i>L. lucayana</i> n. sp.																											
Grand Bahama Island	1			1	1		1																				4
Abaco Island				1																							1
<i>L. spelaeotes</i>																											
Berry Islands						1																					1
New Providence Island			1	1		1	2	7	5	3	3	2	2	2	2	1	1	1									34
Eleuthera Island										1																	1
Great Exuma Island																	1										1
Long Island										1	1					2				1							5
Number of pectoral finrays Number of total vertebrae																											
	Number of pectoral finrays					n	Number of total vertebrae					n															
	17	18	19	20	21		50	51	52	53	54		55														
<i>L. lucayana</i> n. sp.																											
Grand Bahama Island	3	1				4										1		2									3
Abaco Island						2												1									1
<i>L. spelaeotes</i>																											
Berry Islands				1			1											1									1
New Providence Island	1	16	15	2			34											12	17	4	1					34	
Eleuthera Island				1			1													1							1
Great Exuma Island				1			1													1							1
Long Island		1	2	2			5													4	1						5

TABLE 3. Selected characters of all species of *Lucifuga*.

	n. examined	Vertebrae	Dorsal/ Anal finrays	Pectoral finrays	Caudal finrays	Palatine teeth	Lateral line neuromasts	Total Gill-rakers	Long gill-raker pigmentation	Occiput squamation	Eye size (% SL)
Bahamas											
<i>L. lucayana</i> sp. n.	6	12–13+37–39 =50–52	84–91/ 63–69	17–18	10	Absent	12–13/ 34–35	13–17	Pale	Dense	0.9–1.0
<i>L. spelaeotes</i>	44	13–14+38–42 =51–55	86–109/ 66–82	17–20	10	Present 3–56	12–19/ 30–47	15–23	Dark	Weak	0.7–1.8
Cuba											
<i>L. dentata</i> ^{1,2}	6	11+36–37 =46–48	83–95/ 69–78	15–17	8	Present 23–24	13/35	15–21	Pale	Absent	0.0
<i>L. simile</i> ^{2,3}	1	11+34–35 =45–46	70–78/ 57–64	11–16	8	Present 25	12/ 20–24	18	Pale	Absent	0.0
<i>L. subterranea</i> ^{1,2}	3	11+36–37 =46–48	80–86/ 61–66	12–14	8	Absent	?	14–15	Pale	Weak	0.0–0.3
<i>L. teresinarum</i> ^{2,4}	0	?	78–80/ 61–64	10–11	8	Absent	?	13–14	Pale	Weak	0.0

1 Data from Cohen and Robins (1970) included.

2 Data from Cohen and McCosker (1998) included.

3 Data from Nalbant (1981) included.

4 Data from Diaz Perez (1988) included.

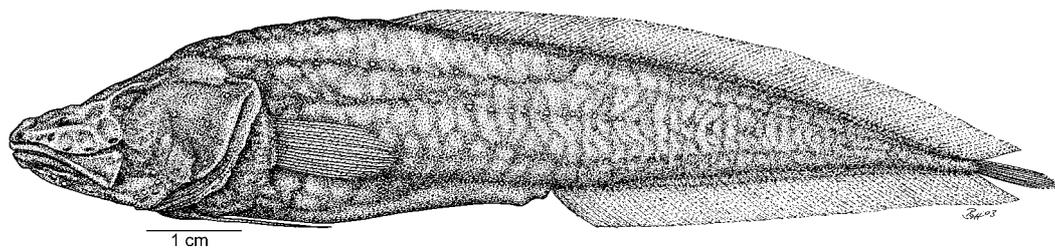


FIGURE 2. *Lucifuga lucayana*. Holotype, ANSP 146475, female, 99 mm SL, Grand Bahama Island. Drawn by Birgitte Rubæk, ZMUC.

Dentition: Premaxilla with 6 (5–7) rows of granular teeth, slightly larger in inner row. Vomer horseshoe-shaped, with 3 (2–3) teeth rows and a total of 31 (24–43) teeth. Palatines without teeth (fig. 6). Dentary with 6 (3–6) outer rows of granular teeth and an inner row of long, pointed teeth.

First neural spine less than half the length of second spine; spine 2–4 slightly longer and more slender than spines 5–10; spines 4–9 slightly depressed. Parapophyses present

from vertebra 7–13, increasing in length. Pleural and epipleural ribs on vertebrae 2–13. Last precaudal vertebra without ribs.

Male copulatory organ completely integrated in the fleshy genital hood, similar to the configuration in *L. spelaeotes* (fig. 8C–D; Cohen & Robins 1970). Penis not easily visible underneath oval accessory organ. Soft lateral lips covering over accessory organ, distally with fleshy wing-shaped expansion not unlike the outer pseudoclasper in *Dinematichthyini*, but clearly attached to the hood and thus not homologous.

Otolith thin, elongate, with pointed anterior and posterior tips in smaller specimens (ANSP 146475) and strongly expanded broad anterior region and broad postdorsal concavity in large specimens (ZMH 9566, fig. 3B–C). Otolith length to height ratio 2.2 to 2.4. Sulcus very short, with single fused colliculum, between 28% and 35% of otolith length and located nearly at centre of inner face. Ventral furrow on inner face indistinct, dorsal depression very feeble or absent.

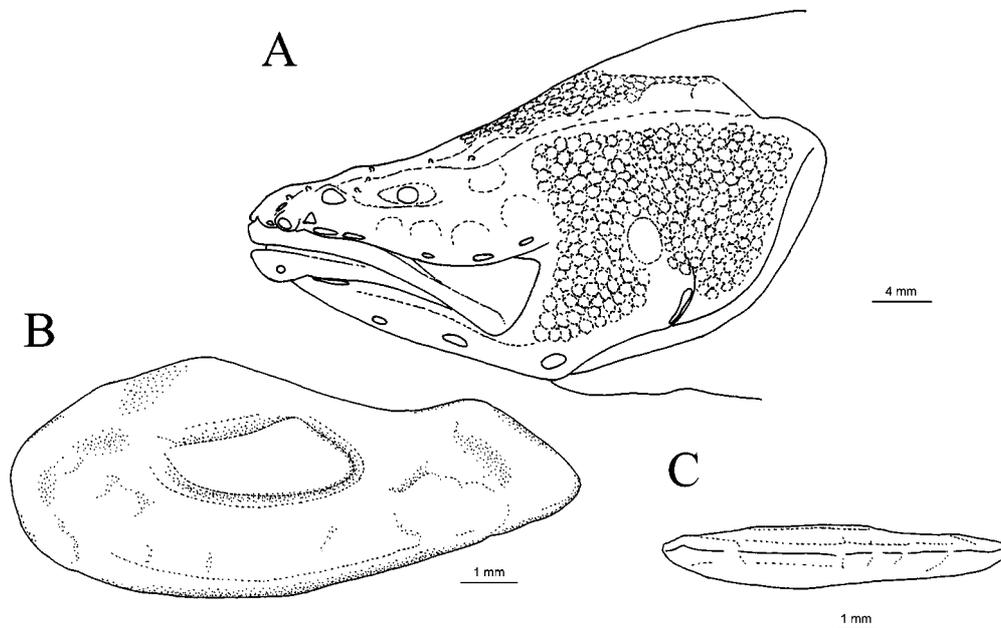


FIGURE 3. *Lucifuga lucayana*. (A) Lateral view of head, Holotype, ANSP 146475, female, 99 mm SL, Grand Bahama Island; (B) Median view of right otolith, ZMH 9566, male, ca. 125 mm SL, Grand Bahama Island; (C) Ventral view of same otolith, ZMH 9566.

Coloration. Live color uniformly pale brown (Palmer 1985a, fig. 51). Preserved color light brown, with lighter fins (figs. 2, 4A–B). No pigment on vertical fin bases or elongated gill-rakers.

Etymology. The specific epithet *lucayana*—is in honor of the Lucayan Indians, who inhabited the Bahamas for more than 2000 years, before they were eliminated by European invaders. They gave name to the type-locality, Lucayan Caverns, which they used as a graveyard (Palmer, 1985a)

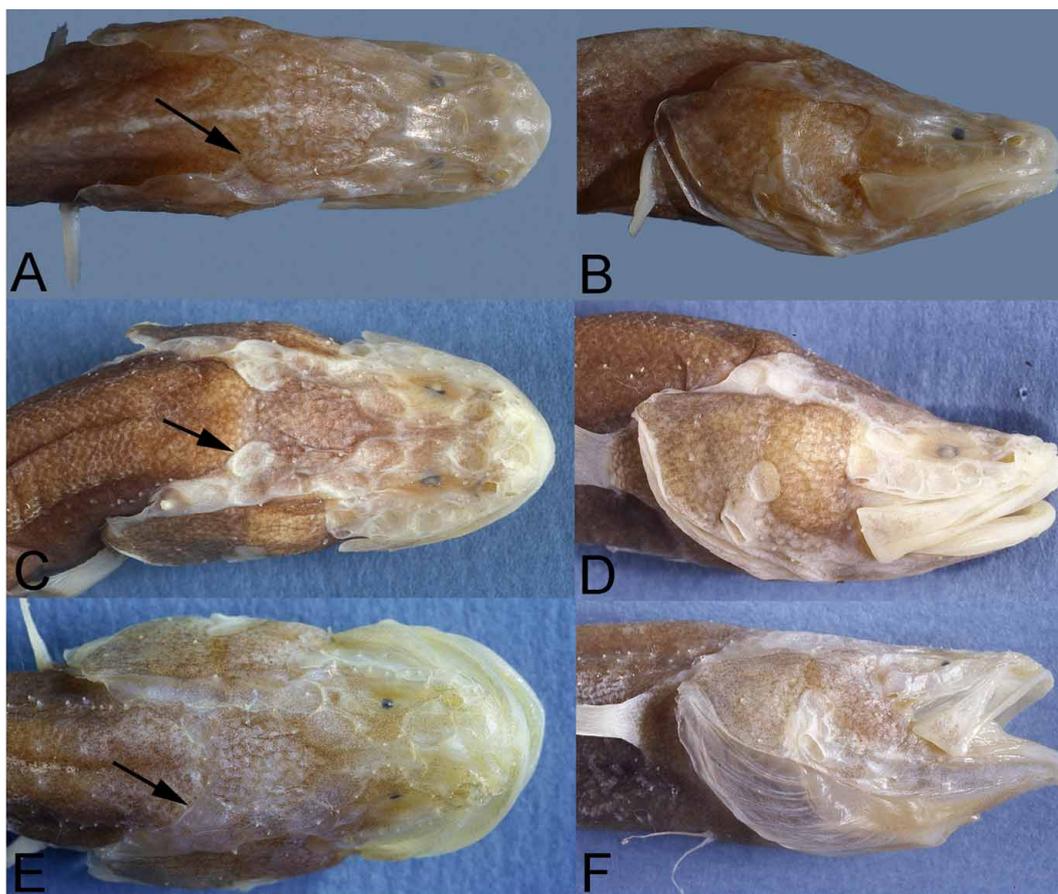


FIGURE 4. Head squamation of Bahamian *Lucifuga* spp. (A–B) *Lucifuga lucayana*, Paratype, BMNH 1984.12.1.20, 80 mm SL female, Grand Bahama Island, Pisces Cave, Zodiac Caverns; (C–D) *Lucifuga spelaotes*, ZMUC P771363, 90 mm SL, female, Great Exuma Island; (E–F) *L. spelaotes*, AMNH 57448, 96 mm SL, male, Bahamas, southern Long Island, Hard Bargain, Alphonso Dean's Blue Hole. Note the difference in squamation on the lateral occipital parts (indicated by arrows).

Distribution and habitat. Known from at least three inland cave systems on Grand Bahama and Abaco Islands, located on the Little Bahama Bank, northern Bahamas (fig. 1): 1. Lucayan caverns, an anchialine cave located on the central southern part of Grand Bahama Island, about 1 km from the ocean. The cave is connected to the sea via a submerged passage which opens into a tidal saltwater creek. The upper about 14 m in the cave consists of freshwater (22 °C), separated from a lower, slightly warmer (23–25 °C), salty layer by a distinct halocline (Yager 1981). According to the ANSP museum label, the holotype was caught in a depth of 12 m, which must then most likely have been in fresh water. The Lucayan Caverns is the type-locality of the crustacean class Remipedia (Yager 1981) and several other cave-dwelling crustaceans (see e.g. Carpenter 1994; Pesce & Iliffe 2002). 2. Zodiac Caverns, north of Sweetings Cay Settlement, eastern Grand Bahama. The cave system was described by Palmer (1985a, b) and seems to have connections to the Sea via Zodiac Creek (see maps in Palmer (1985a, b)). One specimen of *L. lucayana* was col-

lected in the cave Pisces at 15 m and more specimens have been observed in the caves Aquarius and Sagittarius in depths down to about 20 m in salty water (Cunliffe 1985; Palmer 1985b). 3. Abaco Island. Collected from one or two inland sink holes, but the physical conditions are unknown.

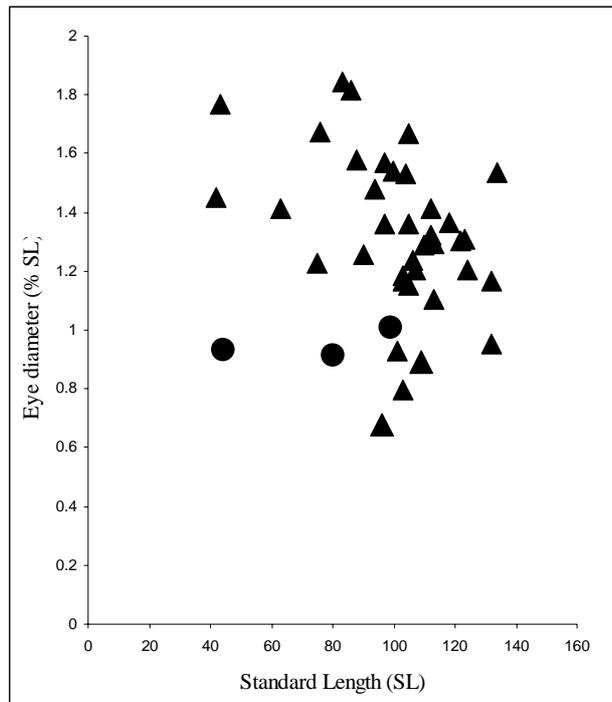


FIGURE 5. Diameter of pigmented eye and standard length. ●, *Lucifuga lucayana*; ▲, *Lucifuga spelaeotes*.

***Lucifuga spelaeotes* Cohen & Robins, 1970**

(Figs. 4-9, Tables 1-3)

Lucifuga spelaeotes Cohen & Robins, 1970: 133, fig. 1; Barton & Wilmhoff 1996: 9; Cohen & McCosker 1998: 184 (part); J. Yager (part) *in litt.* in Cohen & McCosker 1998: 185; Nielsen *et al.* 1999: 122 (part); Proudlove 2001: 207 (part); Romero & Paulson 2001: 32.

Material examined (44 specimens, 42–166 mm SL).

Holotype: USNM 204603, 110 mm SL, male, Bahamas, New Providence, Mermaid's Pool, 25°01'N, 77°22'W, 0–5 m depth, collected by C. Ray, 24 Oct. 1967.

Paratype: USNM 204604, 75 mm SL, female, same data as for holotype.

Additional specimens: AMNH 53011 (5 specimens), 94–132 mm SL, New Providence, Ocean Blue Hole (precise location and collection data unknown); AMNH 53012 (4 specimens), 103–113 mm SL, New Providence, ocean blue hole (precise location and collection data unknown); AMNH 53011 (5 specimens), 101–124 mm SL, New Providence,

ocean blue hole (precise location and collection data unknown); AMNH 57448, 96 mm SL, male, Bahamas, southern Long Island, Hard Bargain, Alphonso Dean's Blue Hole, most likely at 23°1.071'N, 74°54.085'W, depth unknown, collected by Dennis Williams, 2 August 1985; ANSP 147575, sex unknown, 121 mm SL, New Providence Island, south-western side of island, sinkhole adjacent to 15th hole, South Ocean Golf Club, 25°00'N, 77°32'W, depth 0–0.5 m, collected by J.E. and M.W. Böhlke with hand net, 21 Aug. 1972; ANSP 148055, sex unknown, 138.5 mm SL, New Providence, small ocean hole northwest of Robertson Road east-west highway junction, 25°02'N, 77°20'W, 3–4 m depth, collected by J.E. Böhlke with hand net, 24 Aug. 1972; ANSP 148058 (8 specimens), 42–134 mm SL, same data as for ANSP 148055; ANSP 148059 (10 specimens), 88–123 mm SL, New Providence, south-western side of island, sinkhole adjacent to 15th hole, South Ocean Golf Club, 25°00'N, 77°32'W, 3 m depth, 31 Oct. 1973; UMMZ 213989, 148 mm SL, male, Berry Islands, Holmes Key, Blue Hole, 25°37'N, 77°44'25"W, depth unknown, collected by D.L. Schultz, 25 February 1982; USNM 274737, 109 mm SL, male, Bahamas, southern Long Island, Twin Pillars Cave System, Miley, 23°3.841'N, 74°55.503'W, depth 0–2 m, collected by Dennis Williams, 29 July 1985; ZMUC P771363, 90 mm SL, female, Stocking Island, near Great Exuma, Angelfish Blue Hole, approximately 23°31.5'N, 75°45.6'W, collected by hand net, about 57 m inside the cave, at depth of 28 m, by B. Kakuk and T. Iliffe, 1 March 2003; ZMUC P771365, 132 mm SL, male, Eleuthera Island, Nixon's Blue Hole, approximately 24°05'N, 76°00'W, collected at the cave entrance by hand net, at depth of 12 m, by B. Kakuk, 24 Feb. 2003; ZMUC P771452, 136 mm SL, female, central Long Island, Silent Hole, (circular blue hole 30 m diameter with an undercut lip and a 3 m drop to water level) in Gray's settlement, 23°13.361'N, 75°05.862'W, maximum water depth 15 m, with a halocline and associated hydrogen sulfide layer at 8 m, collected with dip net by T. Iliffe and collaborators, 8 January 2005; ZMUC P771453, 166 mm SL (182 mm TL before preservation), male, central Long Island, Grotto, behind the ruins of the old Spanish Church in Pratts Hill settlement, 23°16.590'N, 75°5.995'W, depth 2.5 m, temperature 24°C, pH 7.33 and dissolved oxygen 5.5 mg/l, collected with a dip net by T. Iliffe and collaborators, 7 January 2005; ZMUC P771454, 155 mm SL, female, central Long Island, Grotto, 23°16.590'N, 75°5.995'W, collected with a dip net by T. Iliffe and collaborators, 12 January 2005.

Diagnosis. *Lucifuga spelaotes* is distinguished from other members of the genus by the following combination of characters: Vertebrae 13–14+38–42=51–55, dorsal finrays 86–109, anal finrays 66–82, pectoral finrays 17–20, caudal finrays 10; head profile above eye strongly depressed, eyes 0.7–1.8 % SL; palatine teeth present, in 1–7 short irregular rows, with 3–56 teeth totally; long gill-rakers 3, dark pigmented.

Similarity. *Lucifuga spelaotes* is most similar to *L. lucayana* (Tables 1–3). It differs mainly in the reduced squamation on the occiput (vs. densely scaled in *L. lucayana*) (fig. 4), the presence of palatine teeth, except absent in one side of a single specimen, USNM 274737 (vs. absent in *L. lucayana*) (fig. 6), and in having dark pigmentation on the three

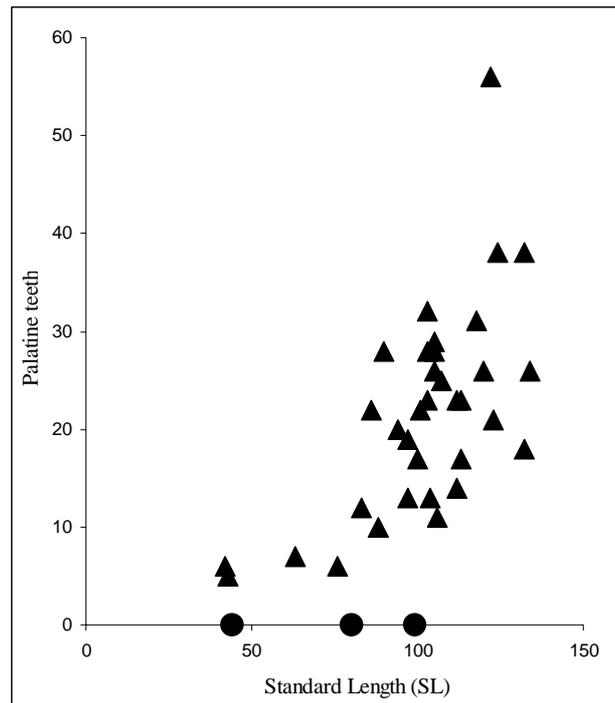


FIGURE 6. Number of palatine teeth and standard length. ●, *Lucifuga lucayana*; ▲, *Lucifuga spelaeotes*.



FIGURE 7. Color variability in *Lucifuga spelaeotes* (A) ANSP 148059, 97 mm SL, female, New Providence Island; (B) ANSP 148059, 104 mm SL, male, New Providence Island; (C) ZMUC P771365, 132 mm SL, male, Eleuthera Island.

elongated gill-rakers, except absent in 3 specimens: AMNH 57448, USNM 274737 and ZMUC P771363 (vs. pale in *L. lucayana*). Also, the number of finrays and vertebrae tend to be higher in *L. spelaeotes* than in *L. lucayana* (Tables 1–3).

Differences to the four Cuban species are shown in Table 3. *Lucifuga spelaeotes* resemble the Cuban species *L. dentata* and *L. simile* in the presence of palatine teeth, but the teeth bearing area of the palatine is broader, shorter and with more teeth rows in *L. spelaeotes* than in *L. dentata* and *L. simile* (see Nalbant 1981), when comparing specimens of similar sizes.

Description. Meristic and morphometric characters are given in Tables 1–3. Body moderately elongate, compressed. Head profile strongly depressed (figs. 4, 7–9). Eyes usually relatively large ($> 1\%$ SL), except for a few specimens (AMNH 53011, 132 mm SL, New Providence; AMNH 53013, 101 and 103 mm SL, New Providence; AMNH 57448, 96 mm SL, Long Island (fig. 4E–F); USNM 274737, 109 mm SL, Long Island and ZMUC P771452, 136 mm SL, Long Island) with eyes from 0.7 to 1.0 % SL (fig. 5). Upper jaw slightly protruding. Anterior nostril tube-shaped, low on snout near upper lip; posterior nostril larger, a mere hole, closer to lip than to eye. Maxilla expanded posteriorly, not sheathed by a skin flap. Opercular spines absent. Anterior gill arch with 3 elongated rakers and 17 (12–20) broad plates arranged in the following configuration: upper branch of anterior gill arch with 4 (2–5) broad plates, the bend between upper and lower arch with 1 elongate raker and lower branch with 1 small plate, 2 elongate rakers interspersed with 1 small plate and followed by 12 (7–12) small plates. Pseudobranchial filaments 0 (0–4). Branchiostegal rays 7.

Scales on body relatively small, oval (horizontal diameter about 1.3 mm at mid-body and about 25 horizontal rows above anal fin origin in a 132 mm SL male); vertical fins and pectoral fins naked except for scales on pectoral fin peduncle. Predorsal area, operculum and top of head, including a narrow central part of the occiput scaled. Interorbital, snout and at the course of the head pore channels, including the lateral parts of the occipital area naked (figs. 4C–F, 8A–B).

Origin of dorsal fin above tip of pectoral fins. Pelvic fins with a single ray reaching about $1/2$ ($1/3$ – $1/2$) from its base to anal fin origin. Pectoral fins on the middle of body, peduncle short and narrow. Caudal fin free, not fused with dorsal or anal fins.

Head sensory pores: Supraorbital pores 4, anteriormost 3 on snout and posteriormost above opercular flap; infraorbital pores 6 (3 large anteriorly and smaller 3 posteriorly); mandibular pores 6 (3 anterior and 3 posterior), the 2nd anterior very long, the posterior ones increasing in size; preopercular pores 2 (2 lower and 0 upper) (fig. 8A–B). Lateral line with 14 (12–19) dorsal neuromasts anteriorly and 38 (30–47) medio-lateral neuromasts posteriorly. Many small sensory papillae on head.

Dentition: Premaxilla with 7 (3–9) rows of granular teeth and 1 inner row of small pointed teeth. Vomer horseshoe-shaped, with 2–6 rows and a total of 6–114 teeth, larger in inner row. Palatines with 5 (1–7) rows and 3–56 teeth totally, except for absent on one side

in one specimen (USNM 274737). The number increasing with the size of the fish (fig. 6). Dentary with 3–14 outer rows of granular teeth and an inner row of longer pointed teeth.

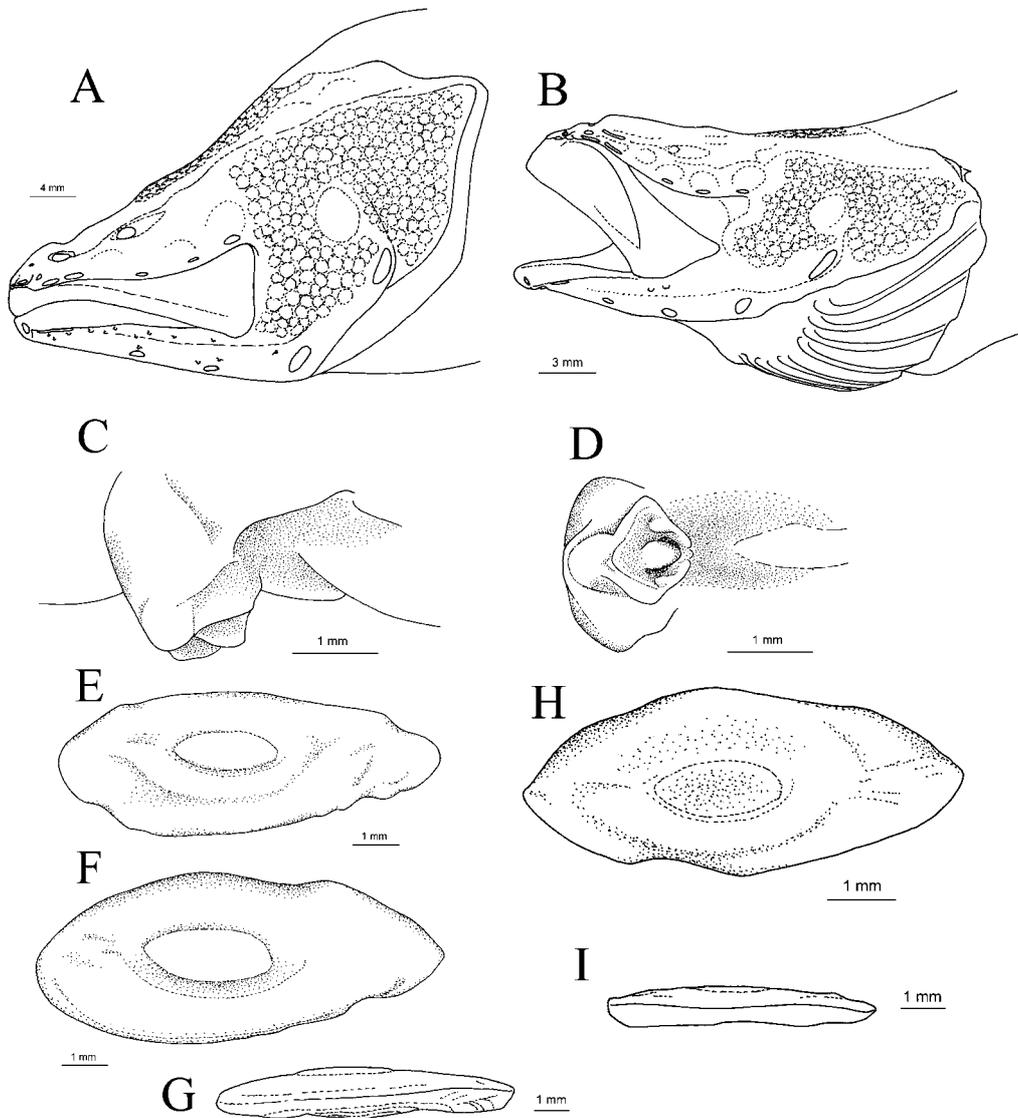


FIGURE 8. *Lucifuga spelaotes*. (A) Lateral view of head, ANSP 148059(4), 112 mm SL, female, New Providence Island; (B) Lateral view of head, USNM 274737, 109 mm SL, male, Bahamas, Long Island, Twin Pillars Cave System, Miley; (C) Lateral view of copulatory organ, USNM 274737; (D) Ventral view of copulatory organ, USNM 274737; (E) Median view of right otolith, ANSP 147575, 121 mm SL, New Providence Island; (F) Median view of right otolith, ANSP 148055, 138.5 mm SL, New Providence Island; (G) Ventral view of right otolith, ANSP 148055; (H) Median view of right otolith, USNM 274737, 109 mm SL; (I) Ventral view of right otolith, USNM 274737.

First neural spine less than half the length of second spine; spine 2–4 longer and more slender than spines 5–9; spines 4–9 slightly depressed. Parapophyses present from vertebra 8–13, increasing in length. Pleural and epipleural ribs on vertebrae 2–12. Last precaudal vertebra without ribs.

Male copulatory organ completely integrated in the fleshy genital hood (fig. 8C–D; Cohen & Robins 1970), similar to the configuration in *L. lucayana*.

Otolith thin, elongate to very elongate (length to height ratio 2.2 to 2.7), with rounded (fig. 8E–F) or pointed (fig. 8H) anterior tip. Posterior tips pointed. Postdorsal and to a lesser degree also postventral region irregularly concave. Sulcus very short, with fused colliculum, between 27 % and 32 % of otolith length and located slightly anterior of centre of inner face. Ventral furrow on inner face indistinct or absent (figs. 8E–F, New Providence Island specimens) or broad (fig. 8H, Long Island specimen).

Coloration. Very variable from uniformly pale to dark brown (figs. 7, 9). Dark specimens either with completely light vertical fins or with dark fin bases and light margins. A recently caught dark specimen, ZMUC P771365, 132 mm, from Eleuthera Island is unique by having dark head and body, except for a light predorsal area (fig. 7C). Elongate gill-rakers dark in all specimens, except in three specimens from Great Exuma Island (ZMUC P771363) and Long Island (AMNH 57448, USNM 274737).

Distribution and habitat. Known from the Great Bahama Bank area, with confirmed localities on five islands (Berry, New Providence, Great Exuma, Eleuthera and Long Islands (figs. 1, 10) (see Material examined). Unconfirmed records of *L. spelaotes* from Andros Island (Farr & Palmer 1984, Proudlove 1984, B. Kakuk *in litt.* (in Cohen & McCosker 1998) and Long Island, Grand Canyon, 22°57.423'N, 74°51.238'W, east of Berrys settlement (T. Iliffe January 2005, personal observation).

Twin Pillars Cave in Miley, southern Long Island (23°03.841'N, 74°55.503'W) was rediscovered in 2005 and is situated within a few meters of the east side of the main road. It consists of an air-filled cave with a 30 to 150 cm deep saltwater (34 ppt) pool covering most of the floor. At least 10 skylight entrances, only one of which is climbable, provide access to the cave. While many parts of the cave are well illuminated during the day, various recesses are only dimly lit. At least 24 *Lucifuga* were observed but not collected in 2005. Other stygobitic species from this cave include the hippolytid shrimp *Barbouria cubensis*, the polynoid polychaete *Pelagomacellicephala iliffei*, the halocyprid ostracod *Spelaeoecia capax*, several species of copepods and a parasitic gnathiid isopod. About 10 specimens of the latter were removed from the gill-cavity of a 109 mm SL *L. spelaotes* collected in 1985 (USNM 274737).

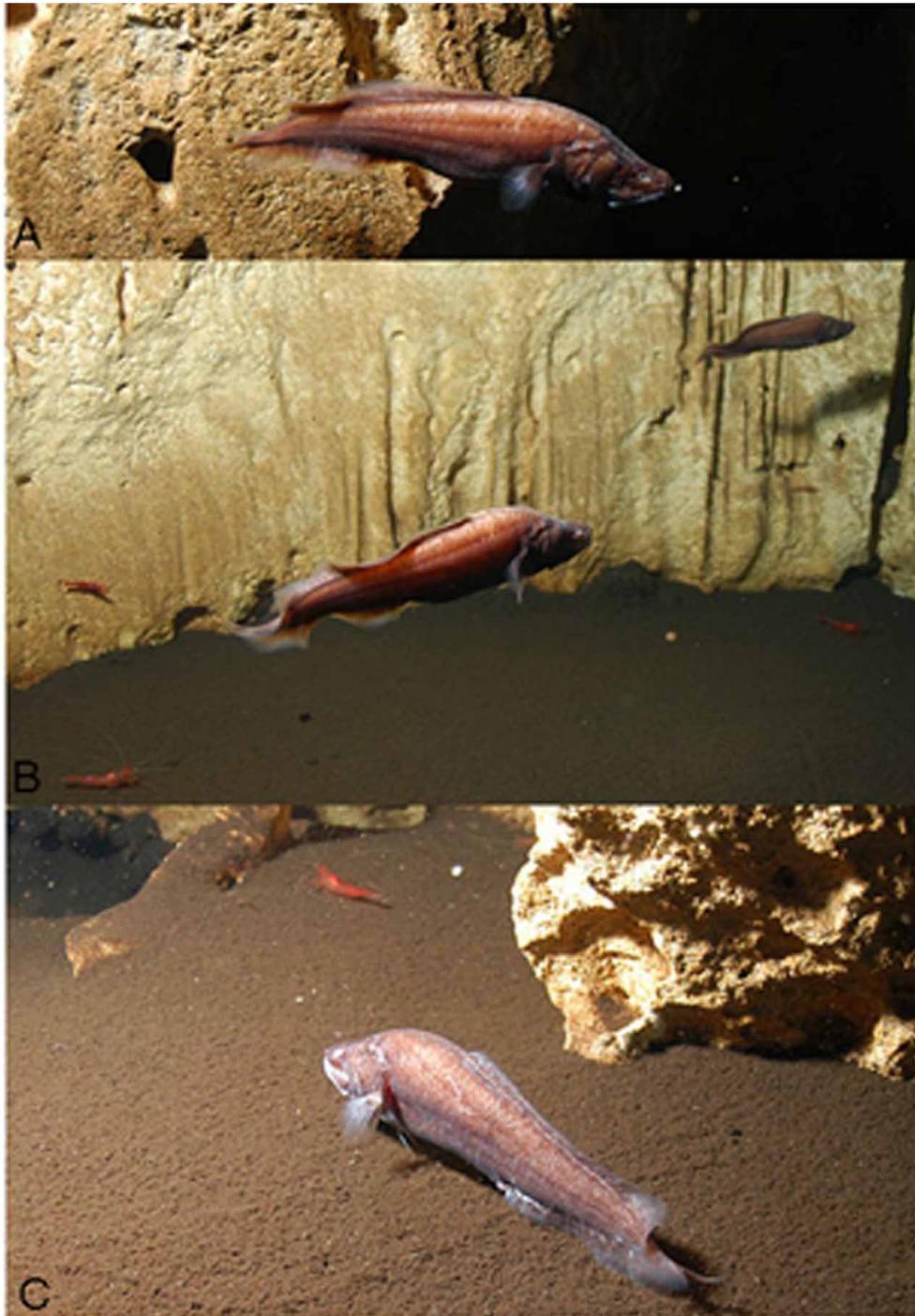


FIGURE 9. *Lucifuga spelaeotes* in Grotto, central Long Island, 23°16.590'N, 75°5.995'W, 6 January 2005. (A) Lateral view; (B) Two specimens swimming; (C) Specimen resting on the bottom with the hippolytid shrimp *Barbouria cubensis*. Photos by Tamara Thomsen, Wisconsin, were taken immediately prior to collection of ZMUC P771453, but may not necessarily include this specimen.

Alphonso Dean's Blue Hole on southern Long Island was searched for during the January 2005 trip to Long Island and it was confirmed that this locality is not the same as Dean's Blue Hole described in details by Wilson (1994). Alphonso Dean's Blue Hole (perhaps at 23°01.071'N, 74°54.085'W) in Hard Bargain could not be relocated with certainty, although a 50 m diameter, circular blue hole located between the main road and the abandoned Diamond Salt airstrip was tentatively identified by several locals as Alphonso Dean's Blue Hole. At 6 m depth, a small cave extends off the east side of this open blue hole and contains the shrimp *B. cubensis*, but no fish were observed. Unfortunately, a large amount of rusted metal, broken bottles, old tires and other debris have been dumped on the bank of the blue hole and may be adversely impacting the water quality.

Salinity data from the various records indicate that *L. spelaeotes* is a truly euryhaline species.

Specimens from New Providence Island have been collected within the upper 3–4 meter of the holes, apparently preferring the upper, warmer, brackish layer to the lower, colder, more saline water in the holes (Cohen & McCosker 1998). Recently caught specimens from Eleuthera and Great Exuma Islands, however, were captured at depths of more than 10 meters, indicating a tolerance to more saline waters. This is also the case in the two new localities on central Long Island.

In Grotto, central Long Island (fig. 10), which is a partially flooded cave, salinity was measured at 33.8 ppt. In addition to the main collapsed entrance, several smaller, skylight entrances also help to illuminate the 20 m long by 8 m wide and 2.5 m deep pool. Most of the 8–10 fish in the pool were observed in a dark alcove at the rear of the cave. Large numbers (many hundreds to thousands) of the shrimp *B. cubensis* were present in all parts of the pool during the day but were absent when the cave was visited after dark. This suggests that the known parts of the cave are only a small segment of a much larger and well integrated system.

In Silent Hole salinity increased from 8.4 ppt at the surface to 26 ppt at 12 m, temperature likewise rose from 23 to 26 °C, pH dropped from 8.2 to 7.3 and dissolved oxygen plummeted from 7.5 to less than 1 mg/l. Several *Lucifuga* were observed and one collected in the more saline water near the bottom, under a ledge, where a few *B. cubensis* shrimp were also found.

Remarks. Sexual dimorphism is not observed in any of the described characters. The morphology of the few specimens from Berry, Eleuthera, Great Exuma and Long Island are generally well within the ranges of the numerous specimens from New Providence Island (Table 2).

The few exceptions, such as unique coloration and longer pelvic finrays (20.0 vs. 8.0–18.9 % SL) of the specimen from Eleuthera; weak palatine dentition and unusually small eyes of the two specimens from southern Long Island; and pale, elongated gill-rakes in the specimen from Great Exuma Island, are not enough difference to warrant status as separate species. More material is needed in order to further study the morphological and genetic plasticity of the populations on the various Islands.

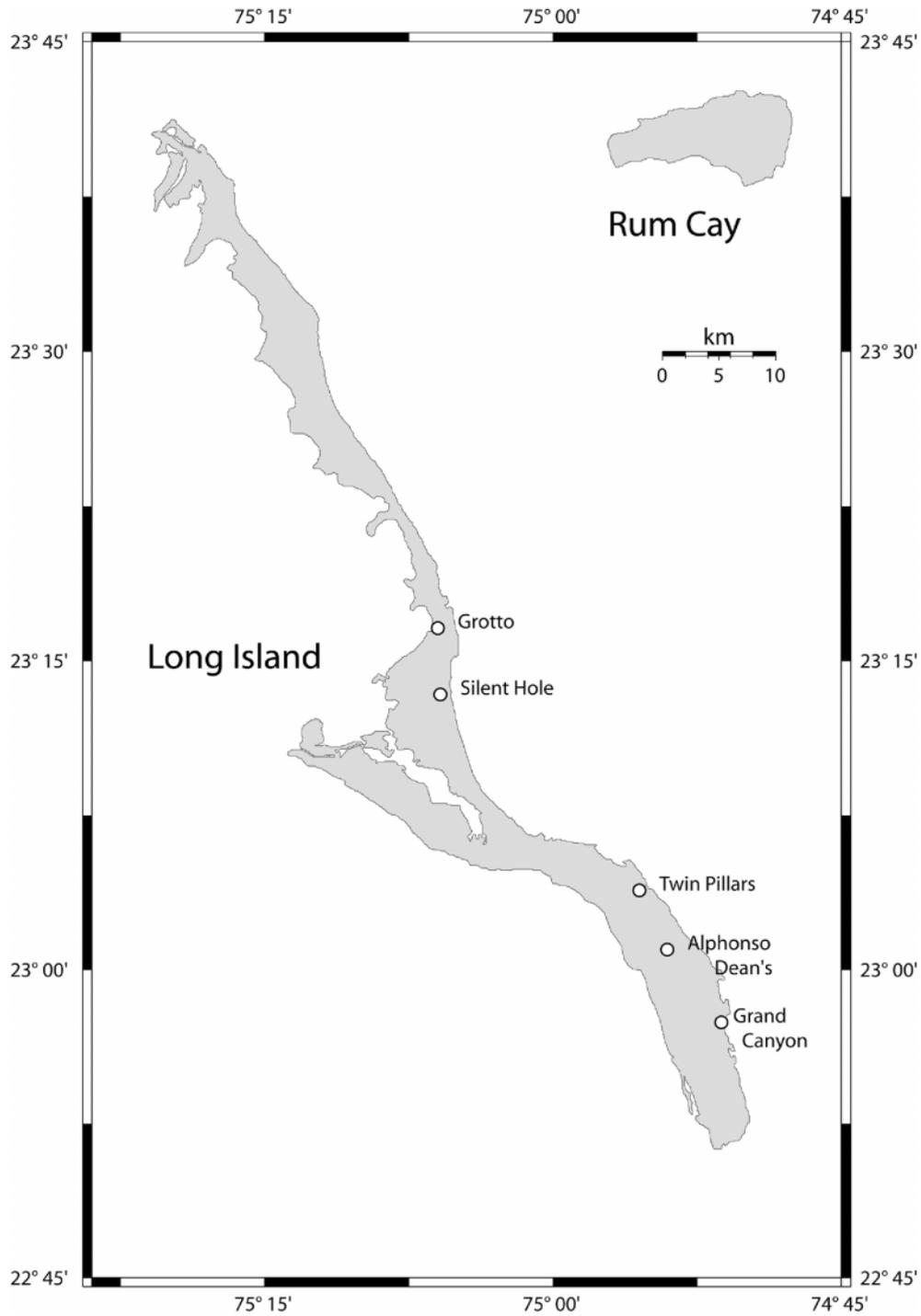


FIGURE 10. Locations of caves and blue holes on Long Island, Bahamas from which *L. spelaeotes* have been collected or observed.

Discussion

With the data presented above, it has become obvious that the diversity of Bahamian *Lucifuga* is larger than hitherto assumed, i.e., that at least two species (*L. lucayana* and *L. spelaeotes*) are present. The Bahamian species seem to be closely related, differing from the four Cuban species by having more caudal finrays (10 vs. 8), larger eyes (0.7–1.8 vs. 0.0–0.3 % SL), more vertebrae (50–55 vs. 45–48) (not known for *L. teresinarum*) and more pectoral finrays (17–20 vs. 10–17) (Table 3). The new Bahamian species supports and extends the results of Vergara (1980), who hypothesized that the Bahamas and Cuba are inhabited by two lineages of *Lucifuga* evolution, with the Bahamian species being more plesiomorphic in the above mentioned characters. Based on this hypothesis, the reduction of palatine dentition and head squamation must have occurred independently in both lineages (see Romaro 2001).

Given the homoplasious nature of this character, the presence or absence of palatine teeth is not useful for supporting generic (Gill 1863) or subgeneric (Cohen & Robins 1970) ranking in *Lucifuga*. It is, however, a useful character in defining the cave-dwelling bythitid genus, *Grammonus* Gill (Nielsen *et al.* 1999) and in the separation of *Lucifuga* species, although the number of teeth are here shown to be rather variable and to increase with increased specimen size in *L. spelaeotes* (fig. 6).

Another controversial character is the degree of eye-reduction. Cohen and McCosker (1998) and Nielsen *et al.* (1999) argued that the degree of eye development is not a good taxonomic character and should be avoided in keys for *Lucifuga*, because it has been reported to vary and to be less well developed in older specimens of *L. dentata* and *L. subterranea* (Eigenmann 1909, Wilkens *et al.* 1989). Great variability and a tendency to negative allometric growth is here shown for *L. spelaeotes* as well (fig. 5), but this does not mean that the size of the eye-ball cannot be used in *Lucifuga* taxonomy. It is useful for separating Bahamian from Cuban *Lucifuga* spp. and in the systematics of many other bythitid fishes, of course with due consideration of allometric change.

We agree with Nielsen *et al.* (1999) that the amount of pigmentation is not a good taxonomic character in *Lucifuga*, since it varies considerably even among fish from the same cave (fig. 7A–B).

The distribution pattern of *Lucifuga* in the Bahamas shows endemic species from the Little Bahama Bank area and the Grand Bahama Bank area, separated by the Northeast (3800 to 4700 m deep) and Northwest (700 to 2800 m deep) Providence Channels (fig. 1). A similar distribution pattern has been reported for other anchialine cave animals as well. Among the 13 stygobitic species of the crustacean class Remipedia known from the Bahamas archipelago, five are recognized from Grand Bahama Island and the same five also inhabit Abaco Island. Although one remipede, *Speleonectes lucayensis*, occurs on both the Great Bahama Bank (Andros and Cat) and the Little Bahama Bank (Grand Bahama and Abaco), the remaining species are known from a single platform, Great Bahama Bank (Great Exuma), San Salvador Bank and Caicos Bank (Koenemann *et al.* 2003; 2004).

Thus, *Lucifuga* seems at least to some extent to show a similar pattern of endemism as some of its potential food items.

It is possible that the deep Northeast and Northwest Providence Channels form a barrier for most marine shallow-water bythitid fishes as well. Six species (*Ogilbia boehlkei* Møller *et al.*, 2005; *Ogilbia sabaji* Møller *et al.*, 2005; *Ogilbia suarezae* Møller *et al.*, 2005; *Ogilbichthys kakuki* Møller *et al.*, 2004b; *Ogilbichthys longimanus* Møller *et al.*, 2004b and *Stygnobrotula latebricola* Böhlke, 1957) are found only south of the Channels, whereas only one species (*Calamopteryx goslinei* Böhlke & Cohen, 1966) occurs both to the north and south of the deep Channels.

Conservation. *Lucifuga spelaeotes* is on the Red List of threatened species of International Union for Conservation of Nature and Natural Resources (IUCN), 2003. It is listed as vulnerable (VU (A1ce, B1+2bc, D2)), based on decline in area, quality of habitat and pollution. For instance, it has not been observed in recent years in the type-locality, Mermaid's Pool (Proudlove 2001). The D2 criterion requires an estimated population size of less than 1000, or that the area of occupancy is less than 100 km², or that the number of recorded locations is fewer than 5. Proudlove (2001) suggested a lower degree of protection (least concern, LC), based on the reported wide distribution in relatively unspoiled nature, and well separated from the polluted type locality. Because of the present separation of the new species, *L. spelaeotes* is now known from six locations (islands) of which only 5 could be confirmed by examination of specimens. We therefore strongly recommend that the D2 status is maintained until we have a more detailed picture of the diversity and distribution of the Bahamian species and populations. Since *L. lucayana* is known from very few specimens, and fewer than five localities, it is obvious that it should be given at least the same rank of protection as *L. spelaeotes*.

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