Monsters in the dark

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Monsters in the dark: systematics and biogeography of the stygobitic genus *Godzillius* (Crustacea: Remipedia) from the Lucayan Archipelago

Lauren BALLOU 1,*, Thomas M. ILIFFE 2, Brian KAKUK 3, Brett C. GONZALEZ 4, Karen J. OSBORN 5, Katrine WORSAAE 6, Kenneth MELAND 7, Kenneth BROAD 8, Heather BRACKEN-GRISSOM 9 & Jørgen OLESEN 10

1,2 Department of Marine Biology, Texas A&M University at Galveston, USA.
2,3,8 Bahamas Caves Research Foundation, Marsh Harbor, Abaco Island, The Bahamas.
2,4,5 Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.
6 Department of Biology, University of Copenhagen, Denmark.
7 Department of Biological Sciences, University of Bergen, Norway.
8 Department of Environmental Science and Policy, Rosenstiel School of Marine and Atmospheric Science & Abess Center, University of Miami, USA.
9 Institute of Environment and Department of Biology, Florida International University – Biscayne Bay Campus, USA.
10 Natural History Museum of Denmark, University of Copenhagen, Denmark.

*Corresponding author: balloul@tamu.edu

1 Email: iliffet@tamug.edu
2 Email: bahamacave@aol.com
3 Email: GonzalezB@si.edu
4 Email: osbornk@si.edu
5 Email: kworsaae@bio.ku.dk
6 Email: Kenneth.Meland@uib.no
7 Email: kbroad@rsmas.miami.edu
8 Email: hbracken@fiu.edu
9 Email: jolesen@snm.ku.dk
10 Email: jolesen@snm.ku.dk
Abstract. Remipedia is a stygobitic group commonly associated with coastal anchialine caves. This class consists of 12 genera, ten of which are found within the Lucayan Archipelago. Herein, we describe a new species within the genus Godzillius from Conch Sound Blue Hole, North Andros Island, Bahamas. Godzillius louriei sp. nov. is the third known remipede observed from a subseafloor marine cave, and the first from the Godzilliidae. Remipedes dwell within notoriously difficult to access cave habitats and thus integrative and comprehensive systematic studies at family or genus level are often absent in the literature. In this study, all species of Godzillius are compared using morphological and molecular approaches. Specifically, the feeding appendages of G. louriei sp. nov., G. fuchsi Gonzalez, Singpiel & Schlagner, 2013 and G. robustus Schram, Yager & Emerson, 1986 were examined using scanning electron microscopy (SEM). Species of Godzillius are identified based on the spines of maxilla 1 segment 4 and by the denticles on the lacinia mobilis of the left mandible. A molecular phylogeny using the mitochondrial 16S rRNA and nuclear histone 3 genes recovered G. louriei sp. nov. within the Godzillius clade and 16S genetic distances revealed a 13–15% difference between species of Godzillius.

Keywords. Anchialine, cave, new species, phylogeny.


Introduction

The crustacean class Remipedia is an enigmatic stygobitic group consisting of 29 species, 12 genera and eight families. Remipedes predominantly dwell within anchialine cave habitats (i.e., subterranean estuaries) (Bishop et al. 2015; Brankovits et al. 2017; van Hengstum et al. 2019). Like most anchialine fauna, remipedes exhibit a globally disjunct distribution, inhabiting submerged cave systems in the Caribbean, West Atlantic Ocean, Canary Islands and Western Australia (Koenemann & Iliffe 2014). A majority of remipedes (20 of 29 species) are reported from the Lucayan Archipelago (Bahamas and Turks and Caicos), suggesting a potential biodiversity hotspot for the group (Reid 1998). The karst dominated landscapes of these islands, as well as the presence of freshwater/saltwater mixing layers, provide optimal conditions for rapid dissolution and cave formation (Mylroie & Carew 1990; Mylroie & Mylroie 2011).

The clade Godzilliidae is one of four families endemic to the Lucayan Archipelago. Godzilliidae currently consists of two genera, Godzilliognomus Yager, 1989 and Godzillius Schram, Yager & Emerson, 1986. The family’s name is attributed to the great size (43.2 mm) of the type species, Godzillius robustus Schram, Yager & Emerson, 1986, which is the largest observed remipede species to date (Schram et al. 1986). There are two previously described species within Godzillius: G. robustus and G. fuchsi Gonzalez, Singpiel & Schlagner, 2013. All members of Godzillius are found within the Lucayan Archipelago and are known to inhabit anchialine cave systems. Godzillius robustus occurs exclusively in Cottage Pond, North Caicos Island, Turks and Caicos Islands, while G. fuchsi inhabits the Dan’s Cave and Ralph’s Sink sections of the Dan’s Cave System, Abaco Island, Bahamas (Fig. 1). Recent exploration of a subseafloor marine cave off Andros Island, Bahamas, revealed an unknown member of the genus Godzillius, described here.

Cryptic speciation can create taxonomic concerns for stygobitic fauna; thus, integration of morphological and molecular approaches (DNA barcoding) are useful in distinguishing species (Juan et al. 2010; Canovas et al. 2016). Within Remipedea alone, Xibalbanus fuchscockburni (Neiber et al., 2012), and X. cozumelensis Olesen et al., 2017, were recognized as cryptic/pseudocryptic when compared to other members of their genus using mitochondrial genes (Neiber et al. 2012; Olesen et al. 2017). Since the use
of highly specialized technical cave diving technology is essential to access underwater cave systems, comprehensive comparisons across taxa are challenging and often absent from studies of Remipedia. Of the 29 previous remipede species descriptions, only four have included genetic data for species level identifications. Herein, we describe Godzillius louriei sp. nov. based on morphological (LM, SEM) and molecular techniques (16SrRNA and histone 3). Furthermore, we provide a morphological overview and molecular phylogenetic analysis of Godzillius with remarks on the biogeographic distribution of the genus.

**Material and methods**

**Sampling and localities**

A single remipede specimen (holotype) of Godzillius louriei sp. nov. was collected on 4 September 2017 in a 50 ml plastic Falcon tube from Conch Sound Blue Hole (25°07′ N, 78°00′ W), a subseafloor marine cave located 20–30 m offshore from North Andros Island, Bahamas. Conch Sound Blue Hole is the longest known subseafloor marine cave, consisting of a predominantly linear, southward trending conduit found just offshore from the northeastern coast of North Andros (Fig. 2) (Palmer 1997; Daenekas et al. 2009). The holotype was collected in the ‘Collapse Room’ at a water depth of 30–32 m and approximately 1600 m from the cave’s only entrance. The remipede was collected in the saltwater

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**Fig. 1.** Distribution of the genus *Godzillius* Schram, Yager & Emerson, 1986 within the Lucayan Archipelago. Type localities of *Godzillius fuchsi* Gonzalez, Singpiel & Schlagner, 2013, *G. louriei* sp. nov. and *G. robustus* Schram, Yager & Emerson, 1986 are indicated. Map constructed using the open source QGIS ver. 3.12 software (QGIS Development Team 2020) and metadata from Natural Earth (2020).
zone just above a hydrogen sulfide layer. The holotype was preserved in 80% ethanol and stored in the refrigerator prior to morphological and molecular work. Additional specimens used for comparative investigations were collected from Dan’s Cave, Abaco Island, Bahamas in March 2017 (LB, TMI, BK, KM, JO) and in Cottage Pond, North Caicos Island, Turks and Caicos Islands (LB, TMI, BCG, KW, JO) in January 2019. Specimen details are provided below in ‘Comparative material’.

Photography, specimens and morphology

The single specimen of *G. louriei* sp. nov. was used for both morphological and molecular studies. Ten limbs were removed for molecular work (see below) prior to photographing the habitus of the specimen. All specimens were photographed using a Canon EOS 5D Mark IV fitted with a Canon Macro Twin Lite MT-24EX flash and a Canon MP-E 65mm f2.8 macro lens tethered to a PC and operated using standard EOS software. Depth of field in the final images of *G. louriei* sp. nov. was enhanced by shooting and combining z-stacks later blended using Zerene Stacker ver. 1.04. Left side mouthparts (maxilla 1, maxilla 2, maxilliped, both mandibles) and one trunk limb were removed and prepared for SEM. Additionally, the mouthparts (maxilla 1, maxilla 2, maxilliped) of two individuals of *G. fuchsi* and one individual of *G. robustus* were prepared for comparison. All dissected appendages for SEM were dehydrated in a graded ethanol series (80%, 90%, 95%, 100%), critical point dried, mounted on aluminum stubs and sputter coated with platinum/palladium. Morphological observations and micrographs were made using a JEOL JSM-6335-F (FE) field emission SEM at the Natural History Museum of Denmark (University of Copenhagen). Selected appendages (left antenna 1, left antenna 2, trunk limbs 1, 2, 7, 28 and 29) were additionally prepared on permanent slides. Slides were photographed using an inverted Olympus microscope (IX83) with automatized stacking and stitching capabilities. Terminology follows Gonzalez et al. (2013), Koenemann & Iliffe (2014) and Schram et al. (1986). Material of the new species is deposited at the Natural History Museum of Denmark (NHMD), University of Copenhagen.

Comparative material

The following material of *Godzillius fuchsi* and *G. robustus* from NHMD and the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM) were included for comparison:

Fig. 2. Cave profile of Conch Sound Blue Hole, North Andros Island, the type locality of *Godzillius louriei* sp. nov. Sampling of *G. louriei* sp. nov. occurred in the “Collapse Room” at approximately 1600 m. Abbreviations: x = chambers too small for diver entry; ? = undescribed/unexplored passage; ← m = penetration distance from cave entrance; ‡ = depth of cave passage. Cave map illustrated by authors Brian Kakuk and Lauren Ballou; cave passages ranging from the entrance to 1153 m within the system were based off of previous illustrations and descriptions (Farr & Palmer 1984; Farr 2017).
Godzillius fuchsi Gonzalez, Singpiel & Schlagger, 2013  
BAHAMAS • 4 specs; Abaco Island, Dan’s Cave; 10 Mar. 2017; T. Iliffe and B. Kakuk leg.; GenBank: MW760694–MW760696, MW768707–MW768709; NHMD 165814, 165841, 165850, 165860.

Godzillius robustus Schram, Yager & Emerson, 1986  

Taxon selection for molecular phylogeny

In order to systematically evaluate our new material, we compared it with all other species within Godzillius and Godzilliognomus (Table 1). A total of six individuals across three species were newly sequenced: three Godzillius fuchsi, two G. robustus and one G. louriei sp. nov. Additionally, eight individuals across four species were obtained from GenBank (Benson et al. 1998) for this study: one G. robustus, two Godzilliognomus schrami Iliffe, Otten & Koenemann, 2010, four Godzilliognomus frondosus Yager, 1989 and one Cryptocorynetes haptodiscus Yager, 1987. Cryptocorynetes haptodiscus (Cryptocorynetidae) was selected as the outgroup as it was shown to be one of the closest relatives to Godzilliidae that has data available in GenBank (Hoenemann et al. 2013).

DNA extraction, amplification, sequencing, molecular analyses

Trunk limb tissue was dissected from our new material, three individuals of G. fuchsi and two individuals of G. robustus. DNA extraction was performed using the Qiagen DNeasy Tissue and Blood Kit following the manufacturer’s protocol. 16S rRNA and histone 3 (H3) were selected for amplification by polymerase chain reaction (PCR) using primers sets 16S arL/brH (5′ CGCCTGTTTATCAAAAACAT 3′) (5′ CCGGTCTGAACTCAGATCACGT 3′) and H3 AF/AR (5′ ATGGCTCGTACCAAGCAGACVGC 3′) (5′ ATATCCTTRGGCATRATRGTGAC 3′) with M-13 F/R tails, respectively (Colgan et al. 1998; Palumbi et al. 2002). While mitochondrial genes are typically selected for species level differentiation, the nuclear gene H3 was also selected, as significant variation can be observed at the species level within Remipedia (Hoenemann et al. 2013). PCR reaction mixtures totaled 25 μl and included GoTaq polymerase (12.5 μl), forward and reverse primers (1 μl each), RNAfree water (8.5 μl) and DNA template (2 μl). All PCR reactions began using the following temperature profiles: denaturation at 94°C for 3:30 min; 35–40 annealing cycles, 30 seconds each between 40–50°C for 16S and 50°C for H3; an extension period at 72°C for 1:00 min; and a final extension at 72°C for 7:00 min. PCR reactions were visualized on 1–2% agarose gels stained with GelRed. Successful PCR productions (20 μl) were sent to GENEWIZ (South Plainfield, NJ) for sequencing.

Sequences (16S rRNA and H3) of G. louriei sp. nov. (n = 2), G. fuchsi (n = 6) and G. robustus (n = 4) were visually inspected, trimmed and cleaned using Geneious Prime ver. 2019.2.3 (Kearse et al. 2012). All sequences were checked for potential contamination by running a nucleotide BLAST similarity search (Altschul et al. 1990). Protein-coding H3 gene sequences were inspected for stop codons and point mutations using Geneious Prime to reduce the risk of including pseudogenes (Song et al. 2008). All sequence data were submitted to GenBank under accession numbers MW760694–MW760699 and MW768707–MW768712. The GenBank H3 gene sequence of G. robustus (KC989960) was excluded due to probable contamination, as the sequence genetically resembled that of Godzilliognomus. Sequences from multiple individuals previously identified as Godzilliognomus schrami and Godzilliognomus frondosus were concatenated from available GenBank data for H3 and 16S rRNA sequences to avoid excessive gaps in the phylogeny. These included KC989961 + KC989998, KC989983 + KC989999 and KC989962 + KC990013. As these sequences were not from the same individuals, individual gene trees for H3 and 16S rRNA were constructed using maximum likelihood to identify potential issues from concatenation, and are provided in the supplementary material (Supplementary File 1 and Supplementary File 2).
Table 1. Taxon and voucher information for all sequence data included in phylogenetic and pairwise distance analyses. GenBank accession numbers provided for each gene used; bolded individuals indicate sequence data novel to this study (HBG = Florida International University Crustacean Collection).

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Sequences were aligned using the MAFFT ver. 7 auto-iterative alignment program (Katoh et al. 2019). MAFFT was selected due to its greater accuracy relative to other alignment programs (Pais et al. 2014). Gene alignments were subsequently concatenated within Geneious Prime (H3: 327bp, 16S: 543bp). Both Maximum Likelihood (ML) and Bayesian Inference (BI) were utilized. ML substitution models for each gene were selected based on the Akaike Information Criterion (AIC) in ModelFinder within IQ-Tree ver. 1.6.11 (Nguyen et al. 2014; Kalyaanamoorthy et al. 2017). The most optimal DNA substitution models for ML analyses of 16S rRNA and H3 alignments were GTR + F + R2 and TN + F + G4, respectively. The optimal AIC model for BI analyses of both 16S rRNA and H3 alignments was GTR + G. Individual gene trees and the concatenated gene tree were constructed using the program IQ-TREE for Maximum Likelihood (ML) analyses (Nguyen et al. 2014). IQ-TREE was selected for this analysis as it was shown to outperform other ML programs in increased likelihood values when analyzing concatenated species trees (Zhou et al. 2017). Nodal support was quantified using ultrafast bootstrapping methods (UFBoot) with 1000 replicates (Hoang et al. 2018). jModelTest ver. 2.1.10 (Guindon & Gascuel 2003; Darriba et al. 2012) was used to find the optimal BI substitution models based on AIC and the alignment was subsequently run in MrBayes ver. 3.2.6 (Ronquist et al. 2012) on XSEDE within the Cipres Science Gateway (Miller et al. 2010). Four Markov Chain Monte Carlo (MCMC) chains were run twice for 30000000 generations with a burn-in of 10000000. Convergence was evaluated using trace plots and effective sample size (ESS > 200) within the program Tracer ver. 1.7.1 (Rambaut et al. 2018).

Molecular variation in Godzillius relative to that in other genera within Remipedia was compared using 16S rRNA sequence pairwise distances calculated using p-distance and pairwise deletion of gaps in MEGA ver. 7 (Kumar et al. 2016). All GenBank 16S rRNA material was used, with the exception of a potentially contaminated sequence of Pleomothra apletocheles Yager, 1989 KC990006 (Table 1).

Abbreviations

a1 = antenna 1
a2 = antenna 2
md = mandible
mx1 = maxilla 1
mx2 = maxilla 2
mxp = maxilliped

Results

Systematics

Subphylum Crustacea Brünnich, 1772
Class Remipedia Yager, 1981
Order Nectiopoda Schram, 1986
Family Godzilliidae Schram, Yager & Emerson, 1986
Genus Godzillius Schram, Yager & Emerson, 1986

Godzillius louriei Ballou, Bracken-Grissom & Olesen sp. nov.
urn:lsid:zoobank.org:act:F0D0FD57-4ACF-4BC3-B8D2-CBCF00E16026
Figs 3–8

Diagnosis

25 mm in length with 29 trunk segments. Cephalic shield subtrapezoidal. Pleurotergite lateral margins pointed posteriorly. Sternal bars isomorphic. A1 bifurcated, dorsal branch with 11 articles. Right and left md gnathal edges crescentiform, asymmetrical; left lacinia mobilis with 5 denticulae. Mx1 with
7 segments; segment 1 with 10 large and 3 small spines; segment 4 endite digitiform, anterior margin lined with 10 conical denticulae. Mx2 with 6 segments; distal segment unguiform, bearing seven denticulae. Mxp with 9 segments; terminal claw with conical, laminate spines. Caudal rami short and distally covered with plumose setae.

Etymology
Named for Robert Lourie whose financial support of the Bahamas Caves Research Foundation contributes to furthering cave and blue hole related research in the Bahamas. The taxonomic description and underlying molecular justification for Godzillius louriei sp. nov. was prepared by LB, HBG, and JO, who are thus responsible for making the specific name louriei available.

Material examined
Holotype
BAHAMAS • holotype; North Andros Island, Conch Sound Blue Hole, The Collapse Room; 25°07′ N, 78°00′ W; depth 30–32 m, approximately 1600 m horizontal distance from single cave entrance; 4 Sep. 2017; B. Kakuk leg.; specimen dissected and distributed on four light microscopy slides, six SEM stubs and one alcohol voucher; GenBank: MW760699, MW768712; NHMD 669698.

Description
Cephalon (Fig. 3). Cephalic shield subtrapezoidal, posterior margins wider than anterior. Posterolateral margins rounded; sutures absent. Anterior margin folds ventrally, covering a1 aesthetascs and bifurcated frontal filaments.

Body (Fig. 3). Body length 25 mm; 29 trunk segments. Pleurotergite lateral margins pointed posteriorly. Sternal bars isomorphic. Trunk limbs bifurcated with endopods and exopods consisting of three and four segments respectively. Trunk limbs 1 and 18–29 reduced in size (Figs 3–4). Trunk limb 14 protopod with large lobate protrusion and ventrally with slender genital flap (Fig. 3F).

Antenna 1 (Fig. 4A). Biramous, located posterior to frontal filaments. Peduncle with two articles; proximal article bearing numerous aesthetascs. Distal peduncle article bifurcated, acts as base of dorsal and ventral rami. Dorsal ramus (i.e., dorsal branch) with 11 articles; girth decreasing distally through articles. Article 1 with single anteriodistal setal cluster; article 2 with one medial seta, one distal cluster; article 3 with two medial setae; article 4 with two medial setae, one distal seta, fine marginal setae; article 5 with one medial seta, one distal cluster; article 6 with three medial setae, one distal seta; article 7 possessing two to three medial setae, one distal seta; article 8 bearing one fine medial seta; articles 9 and 10 lacking setae; article 11 with terminal tuft of setae. Ventral ramus (i.e., ventral branch) with ambiguous articulation, treated as three articles (Fig. 4A). Proximal article shorter than article 2, no setae, partly fused with peduncle. Article 2 length ~2× that of proximal article. Article 3 length ~3× that of article 2, with one filiform medial seta and a distal setal tuft.

Antenna 2 (Fig. 4B). Protopod with two articles (i.e., coxa and basis). Basis with exopod unarticulate and endopod of three articles. Exopod ovoid, lateral margin with ~50 long, plumose setae. Endopod proximal article distomedial margin bearing two long setae. Article 2 median margin with 10–20 long setae; lateral margin with 3–4 short setae. Article 3 entire margin with 55–65 setae.

Mandible (Fig. 5). Gnathal edge comprised of lacinia mobilis, incisor and molar process. Molar processes crescentiform, with slight invagination along midline. Molar process wider ventrally than dorsally, covered in setae. Left and right md asymmetrical; right incisor with three slightly serrated denticulae extending medially towards atrium oris; left with three distinctly serrated denticulae and small fourth tooth on posterior margin. Right lacinia mobilis with three slightly serrated denticulae; left with five smooth, uneven denticulae.
Maxilla 1 (Fig. 6). Comprised of seven segments, posterior to a2. Segment 1 with medially-extending endite bearing ten conical spines and three small spines (Fig. 6D–E). Segment 2 with dorso-ventrally flattened, broad, spatulate endite; oblong distal edge of endite with 4–5 short conical spines and 25–30 moderate to long simple setae. Segment 3 with no setae nor endites. Segment 4 robust with single digitiform endite extending medially; medial anterior margin bearing ten conical denticles, decreasing in

Fig. 3. Godzillius louriei sp. nov., holotype (NHMD 669698), light microscopy. A. Entire animal, ventral view. B. Entire animal, dorsal view. C. Cephalon, ventral view. D. Cephalon, dorsal view. E. Frontal filament, left side. F. Sternal bars and trunk segments (Ts), ventral view. G. Telson, lateral view.
size distally, and endite disto-medial edge with ~19–20 long, simple setae (Fig. 6F). Segment 4 antero-medial face with setal cluster of 11 moderate, simple setae. Segment 5 robust, with proximal cluster of simple setae. Segment 6 narrow, ventral margin with a long, simple setal cluster (at least 23 setae); anterior and posterior faces with two long, simple clusters. Segment 7 with long, simple setal cluster

Fig. 4. *Godzillius louriei* sp. nov., holotype (NHMD 669698), light microscopy. **A.** Antenna 1 (a1), dorsal view. **B.** Antenna 2 (a2), dorsal view. **C.** Trunk limb 1. **D.** Trunk limb 2. **E.** Trunk limb 7. **F.** Trunk limb 28. **G.** Trunk limb 29. Small numbers represent segments of the dorsal and ventral branches of a1 and the exopod of a2.
underneath elongate, robust, talon-like claw. Claw distally curved towards atrium oris; duct opening at distal tip.

**Fig. 5.** *Godzillius louriei* sp. nov., holotype (NHMD 669698), scanning electron microscopy. **A.** Left mandible (md), anterior view. **B.** Left md, apical view of the lacinia mobilis and incisor. **C.** Left md, posterior view. **D.** Left md, apical view of the setae within the molar process. **E.** Right md, posterior view; incisor unintentionally removed in dissection. **F.** Right md, ventral view of the gnathal edge without the incisor. **G.** Right md, ventral view of the incisor.
Maxilla 2 (Fig. 7). Comprised of six segments, posterior to mx1. Segment 1 with three digitiform endites (a–c on Fig. 7K–L) angled antero-medially; each endite distal margin with one conical spine, pore cluster and a variable number of short, simple setae (endite a, 5 setae; endite b, 14; endite c, 15). Each endite anterior margin with long, simple setae (endite a, 1 seta; endite b, 2; endite c, 2). Segment 1 posterior maxillary gland comprised of large tubular conduit opening toward cephalic shield (Fig. 7J). Segment 2 with one conical endite extending postero-medially; bearing distal cluster of short, simple setae (Fig. 7G–I). Segment 3 (lacertus) somewhat triangular, longer than segments 1 and 2 combined. Lacertus ventral margin extending beyond dorsal margin; with ~four rows of moderate-to-long, vertically striated setae. Brachium (segments 4–6) extending length of lacertus; terminal claw spines extend beyond lacertus. Segment 4 extending ~5/5 length of brachium; fine setae throughout segment, with 1–3 short, simple setae at ventral distal end. Segment 5 1/5 length of brachium; distal margins with four short, simple setal clusters (5–6 setae in each). Segment 6 with distal arrangement of seven conical spines decreasing in length distally; curved downward over setal pad in a grappling hook arrangement (terminal claw complex) (Fig. 7D–F). Setal pad with long, simple setae; proximal edge conical, lacking setae, directed towards lacertus.

Fig. 6. Godzillius louriei sp. nov., holotype (NHMD 669698), left maxilla 1 (mx1), scanning electron microscopy. A. Anterior face of mx1. B. Posterior face of mx1. C. Apical view of mx1. D–E. Endite of segment 1, unintentionally removed during dissection. F. Conical spines along the surface of the digitiform endite on segment 4, posterior view. G. Spatulate endite of segment 2, apical view. Small numbers represent segments of mx1.
Maxilliped (Fig. 8). Comprised of nine distinct segments, with flexion point between segments 5 and 6. Segment 1 with one medial setal cluster of five small, vertically striated setae. Segment 2 anterior face proximal medial margin with eight vertically striated setae; posterior face medial margin with six short, vertically striated setae. Segment 3 triangular along posterior face; proximal margin three times wider than distal margin. Distal margin of segments 3 and 4 align, reaching proximal margin of segment 5.

**Fig. 7.** *Godzillius louriei* sp. nov., holotype (NHMD 669698), left maxilla 2 (mx2), scanning electron microscopy. A. Anterior face of mx2; endites of segment 1 indicated as lowercase letters a–c. B. Apical view of mx2. C. Posterior face of mx2. D. Terminal claw, apical view. E. Terminal claw, posterior face. F. Terminal claw, anterior face. G. Endite of segment 2, median view. H. Endite of segment 2, posterior face. I. Hollowed conical tip of the endite of segment 2. J. Maxillary gland opening of mx2. K. Triplet endites of segment 1 (a–c) and singular endite of segment 2, posterior face. L. Triplet endites of segment 1 (a–c) and singular endite of segment 2, apical view. M. Conical spine on the third endite of segment 1, apical view. N. Conical spine on the second endite of segment 1, apical view. O. Conical spine on the first endite of segment 1, apical view. Small numbers represent segments of mx2.
Segment 3 anterior face rectangular and narrower than segment 2; proximal medial margin bearing four small setae (2 grooved, 1 simple, 1 conical). Segment 4 exhibiting different shapes along anterior and posterior faces. Segment 4 posterior face triangular, with proximal margin narrower than distal margin; proximal margin with one vertically-striated seta and 2–3 simple setae. Segment 4 anterior face rectangular, small suture along its length; with two small, vertically striated setae. Segment 5 similar

Fig. 8. Godzillius louriei sp. nov., holotype (NHMD 669698), left maxilliped (mxp) scanning electron microscopy. A. Anterior face of mxp. B. Posterior face of mxp. C. Apical view of mxp. D. Vertical striations of setae along the surface of the lacertus. E. Terminal claw, anterior face. F. Terminal claw, posterior face. G. Posterior segments and telson, ventral view. H. Telson, lateral view; caudal rami separated by invagination of the telson. Small numbers represent segments of mxp.
in shape to lacertus of mx2; width decreasing proximally to distally. Lacertus with rows of vertically striated setae along ventral margin (Fig. 8D). Segments 6–9 (brachium) extending beyond length of lacertus. Brachium with short setae along surface, subsiding at terminal claw complex. Segment 6 nearing length of lacertus; distal margin with setal cluster of three simple setae. Segment 7 ~\frac{1}{8} length of segment 6; extends beyond lacertus with distal cluster of three simple setae. Segment 8 longer than segment 7, with one setal cluster (5 simple setae, moderate length) above terminal claw, one posterior cluster (5 simple setae, moderate length) and two clusters (several simple setae, moderate length) oriented towards lacertus. Segment 9 with terminal claw complex (Fig. 8E–F); at least seven curved spines extending over setal pad (difficult to give exact number due to position of appendage). Six most proximal spines conical, robust; distal spine(s) small, laminate. Setal pad covered by terminal claw, protrudes downward, with long simple setae.

**Telson, Caudal Rami** (Figs 3, 8). Telson subrectangular, slightly longer than wide; ventral surface medial axis with deep invagination. Caudal rami short, extending distally past edge of telson; surface bearing short, scattered, simple setae. Each ramus distal margin with single cluster of ~10 long, plumose setae.

**Remarks**

Species of Godzillius can be distinguished by several morphological characters, most notably relating to the md and the three pairs of prehensile/raptorial post-mandibular mouthparts (Figs 9–10, Table 2). On the left md, the lacinia mobilis of both G. louriei sp. nov. and G. fuchsi have five denticulae, whereas G. robustus has six. One of the most striking distinctions between species of Godzillius is the number of conical denticles on the mx1 endite segment 4 anteriodistal margin (Fig. 9B, F, J). While G. fuchsi and G. robustus have been observed or described as having between 6 and 8 denticles along its margin, G. louriei sp. nov. has 10. Furthermore, the mx1 endite first segment has a unique spination, with 10 large spines and 3 small (Fig. 9D), contrasting with those of G. robustus (11 large, 4 small) and G. fuchsi (10 large, 2 small).

The terminal claw of mx2 in G. robustus is reported to have 10 free spines, whereas that of G. fuchsi and G. louriei sp. nov. have 7 (Fig. 9O, R, U). The mxp terminal claw in G. fuchsi has an elongate protrusion of the setal pad that is not covered by its spines (Fig. 10F); in contrast, the spines of G. louriei sp. nov. and G. robustus cover the setal pad (Fig. 10B, D). The mxp terminal claw of G. robustus has been described as a “grappling hook” with ten spines wrapping around a setal pad (Schram et al. 1986). Godzillius louriei sp. nov. has a similar arrangement, with at least 7 spines in the grappling hook arrangement (Fig. 10B). Godzillius fuchsi differs from the aforementioned species, having shorter, denticle-like spines with narrow spaces between them and not covering a distinctly protruding setal pad (Fig. 10F). We found the mxp of all three species to be composed of 9 segments (Fig. 10), modifying the previous descriptions of G. robustus and G. fuchsi, where fewer proximal segments were identified. It should be noted that this number of mxp segments coincides with what is reported for all other remipede species (Koenemann & Iliffe 2014).

**Key to Godzillius**

1. Mx1 segment 4 without digitiform endite .................................................................Godzilliognomus Yager, 1989
   - Mx1 segment 4 with digitiform endite ........................................................................2

2. Mx1 endite segment 4 with ten conical denticulae ...........................................Godzillius louriei sp. nov.
   - Mx1 endite segment 4 with six to eight conical denticulae ........................................3

3. Left md lacinia mobilis with five denticulae ..............................................................
   - Left md lacinia mobilis with six denticulae ...Godzillius robustus Schram, Yager & Emerson, 1986
Phylogeny and pairwise distances

The same topology was recovered in both Bayesian and maximum likelihood analyses of the concatenated dataset (Fig. 11). Within the Godzilliidae, two clades were recovered with full support across analyses (UFBoot = 100, BPP = 1.0), corresponding to the genera Godzilliognomus and Godzillius. Godzilliognomus formed a fully supported clade, and included the species G. frondosus and G. schrami.

(UFBoot = 100, BPP = 1.0). Similarly, *Godzillius* also formed a fully supported clade (UFBoot = 100; BPP = 1.0), and contained representatives of *G. fuchsi*, *G. louriei* sp. nov. and *G. robustus*, which formed a polytomy.

16S rRNA pairwise distances revealed *Godzillius louriei* sp. nov. has a genetic distance of 15% when compared to all individuals of *G. fuchsi* and *G. robustus* whereas the distance between individuals of *G. fuchsi* and *G. robustus* is 13–14% (Table 3). Within *Godzilliognomus*, the sister genus to *Godzillius* (see Fig. 11), the distance between the two known species, *Godzilliognomus frondosus* and *G. schrami*, is slightly lower at 12–13%.

**Discussion**

**Molecular distinction of Godzillius louriei sp. nov.**

The present study describes a third remipede species of the genus *Godzillius*. Both morphological and molecular approaches provide support for the recovery of *G. louriei* sp. nov. within *Godzillius*, being distinct from the two other species of the genus. There is some indication within the phylogeny that *G. louriei* sp. nov. may be sister to *G. robustus* (Fig. 11); however, further data is needed to clarify
the relationships within *Godzillius*. We compared 16S rRNA pairwise distances within *Godzillius* and found them to be equal to or greater than what is observed within *Godzilliognomus*. In general, the 16S rRNA disparity observed within genera of Remipedia is notably high relative to other crustacean groups (Lefébure et al. 2006), which may suggest greater divergence times between remipede species.

**Morphological distinction of *Godzillius louriei* sp. nov.**

The shape of the cephalic shield, articulation of the ventral ramus of antenna 1 and the digitiform maxilla 1 endite fourth segment are key characteristics of the genus *Godzillius* (Schram et al. 1986; Gonzalez et al. 2013) which are shared by *G. louriei* sp. nov. *Godzillius louriei* sp. nov. can be distinguished from other species of *Godzillius* by several minute morphological characters on the prehensile/raptorial cephalic limbs, maxilla 1, maxilla 2 and maxilliped (Table 2, Figs 9–10). These limbs exhibit notable variation and often harbor specific diagnostic characters, as Koenemann et al. (2007) concluded in their detailed morphological phylogeny. The differences between *G. louriei* sp. nov. and its two congers relate to details such as the number of spines, denticles and setae on the endites of segments 1–3 of maxilla 1, and the number of spines on the terminal claws of maxilla 2 and the maxilliped (see Remarks above and Table 2, Figs 9–10). Based on new SEM examination, we identified several discrepancies between the original descriptions of *G. robustus* (see Schram et al. 1986) and *G. fuchsi* (see Gonzalez et al. 2013) relative to our newly collected topotypic material, specifically with regards to the spination and setation of maxilla 1 endites (see Table 2). These variations may be due to the use of different microscopy techniques; SEM provides alternative viewpoints of a singular structure at high magnification, capturing spines and setae that may be difficult to view in light microscopy. For instance, neither description of *G. fuchsi* or *G. robustus* report the presence of small proximal spines on the endite of segment 1, nor the presence of spines along the spatulate endite of segment 2 within maxilla 1; yet they are both observed in our SEM analyses. Based on our 16S rRNA data, the material of *G. robustus* is conspecific with similarly named material in GenBank (Fig. 11). A detailed examination of type material is needed to clarify whether the morphological differences are instances of intraspecific variation, or whether the original descriptions lack details in these respects.

**Table 2.** Morphological comparison of the species of *Godzillius* Schram, Yager & Emerson, 1986: *G. louriei* sp. nov., *G. robustus* Schram, Yager & Emerson, 2013 and *G. fuchsi* Gonzalez, Singpiel & Schlagner, 1986. All characters denoted with an asterisk (*) are from observations in this study. All other characters are from their respective species descriptions (1= Gonzalez et al. 2013; 2 = Schram et al. 1986).

<table>
<thead>
<tr>
<th></th>
<th><em>G. louriei</em> sp. nov.</th>
<th><em>G. robustus</em></th>
<th><em>G. fuchsi</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Left mandible, lacinia mobilis, number of denticles</td>
<td>5 denticles *</td>
<td>6 denticles 2</td>
<td>5 denticles *</td>
</tr>
<tr>
<td>Antenna 2, protopod, segment 2</td>
<td>1 seta *</td>
<td>17 setae 2</td>
<td>10 setae 1</td>
</tr>
<tr>
<td>Maxilla 1, segment 4, endite, setae and denticles</td>
<td>10 denticles, 19–20 setae *</td>
<td>6–8 denticles, 20–25 setae *</td>
<td>6 denticles, 11–12 setae *</td>
</tr>
<tr>
<td>Maxilla 1, segment 1, endite, spines</td>
<td>10 large and 3 small spines *</td>
<td>11 large and 4 small spines *</td>
<td>10 large and 2 small spines *</td>
</tr>
<tr>
<td>Maxilla 1, segment 2, spatulate endite</td>
<td>25–30 setae, 4–5 spines *</td>
<td>25–30 setae, 5 spines *</td>
<td>15–16 setae, 3–4 spines *</td>
</tr>
<tr>
<td>Maxilla 2, segment 6, terminal claw</td>
<td>7 denticles *</td>
<td>10 denticles 2</td>
<td>7 denticles 1</td>
</tr>
<tr>
<td>Maxilliped, segment 9, terminal claw</td>
<td>reduced setal pad *</td>
<td>reduced setal pad *</td>
<td>protruding setal pad *</td>
</tr>
</tbody>
</table>

(1) not reported
Distribution of the genus *Godzillius* within anchialine habitats

*Godzillius louriei* sp. nov. marks the first of its genus to be found on the Great Bahama Bank, considerably expanding the known distribution of *Godzillius* throughout the Lucayan Archipelago (Fig 1). The presence of a potential *G. louriei* sp. nov. – *G. robustus* clade is not readily explainable zoogeographically, as the two species occur further from each other (Andros and North Caicos: 700 km) than *G. louriei* sp. nov. and *G. fuchsi* (Andros and Abaco: 135 km) (Fig. 1). All three species are found within the Lucayan Archipelago, but each occurs on separate shallow-water platforms (banks) and are isolated by deep ocean channels. The species of *Godzillius* are only known from their type localities. This may either suggest that they are truly endemic, possibly representing remnants of an earlier broader distribution, or that their distribution spans unexplored or unknown crevicular systems.

While most remipede species have been collected within inland anchialine cave environments (n = 26), a few have been observed in offshore subseafloor marine caves. *Godzillius louriei* sp. nov. marks only the third known remipede species to inhabit subseafloor marine caves, the others being *Xibalbanus cokei* (Yager, 2013), from Caye Chapel Cave, Belize and *Speleonectes kakuki* Daenekas et al., 2009, which also inhabits Conch Sound Blue Hole (Daenekas et al. 2009; Yager 2013). Interestingly, *S. kakuki* was collected in the same section of the cave as *G. louriei* sp. nov. (Daenekas et al. 2009). Both *X. cokei*

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**Fig. 11.** Maximum likelihood analyses and Bayesian Inference of concatenated gene data (16S rRNA and H3) for Godzilliidae. Bootstrap support values and posterior probabilities provided above branches (ML/BI). Any bootstrap value or posterior probability at 100 or 1.0, respectively, is indicated with an asterisk (*). For the concatenated gene analyses, different individuals identified (not this study) as the same species were concatenated together using GenBank sequence data: KC989961 + KC989998, KC989983 + KC989999 and KC989962 + KC990013. Photos of species of Godzilliidae by Jørgen Olesen. All except *Godzillius louriei* sp. nov. are of live specimens. Photos are not to the same scale.
Table 3. Pairwise distances comparing 16S rRNA genes across Remipedia (this table is also available as Supplementary File 3).

|   | 3   | 4   | 5   | 6   | 7   | 8   | 9   | 10  | 11  | 12  | 13  | 14  | 15  | 16  | 17  | 18  | 19  | 20  | 21  | 22  | 23  | 24  | 25  | 26  | 27  | 28  | 29  | 30  | 31  | 32  | 33  | 34  | 35  | 36  | 37  |
|---|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 |
| 2 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 |
| 3 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 |
| 4 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 |
| 5 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 |
| 6 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 |
| 7 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 | 65.9 | 52.9 | 50.3 | 68.9 |

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and *G. louriei* sp. nov. are only known from their type localities, whereas *S. kakuki* has been observed within both inland anchialine cave systems and subsafloor marine caves (Daenekas *et al.* 2009; Yager 2013). The summarized occurrence of remipeds in both types of cave systems, with one species (*S. kakuki*) spanning both, suggests that a close relationship between these habitats exists, either currently or historically. van Hengstum *et al.* (2019) proposed that anchialine and marine caves may be linked through allogenic succession and should be considered parts of the “anchialine habitat continuum”.

The idea of a continuous or crevicular “spelean corridor” has been shown as a means for anchialine fauna to disperse throughout subterranean systems (Hart *et al.* 1985; Hunter *et al.* 2008; Gonzalez *et al.* 2017). Historic sea level fluctuation may also have contributed to the present day distribution of *Godzillius*. Anchialine habitats are shown to shift with sea level change, resulting in different community compositions within cave environments (van Hengstum *et al.* 2019). The type localities of *G. louriei* sp. nov., *G. fuchsi* and *G. robustus* (Conch Sound, Dan’s Cave, Ralph’s Sink, Cottage Pond) all contain large speleothems within their passages, which only form in air by dripping water (BG, BK, TI, pers. obs.; Koenemann *et al.* 2004; Surić *et al.* 2005), indicating that the caves were dry during glacial periods of low sea level. Because of these historic complexities, caution must be applied when assessing anchialine fauna distribution patterns, as we are likely only seeing a snapshot of a dynamic transgression and regression of anchialine habitats along karstic coastlines.

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**References**


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Supplemental File 1.
Maximum likelihood analyses of 16S rRNA for Godzilliidae. Bootstrap support values provided above branches.
https://doi.org/10.5852/ejt.2021.751.1383.4351

Supplemental File 2.
Maximum likelihood analyses of H3 for Godzilliidae. Bootstrap support values provided above branches.
https://doi.org/10.5852/ejt.2021.751.1383.4353

Supplemental File 3.
Pairwise distances comparing 16S rRNA genes across Remipedia (identical to Table 3 in text above).
https://doi.org/10.5852/ejt.2021.751.1383.4355