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Notes on the behavior and first records of three enigmatic anchialine shrimps (Decapoda: Caridea: Barbouriidae, Palaemonidae) in the Bahamas

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ABSTRACT

Barbouria cubensis von Martens, 1872, *Parhippolyte sterreri* Hart & Manning, 1981 (Barbouriidae) and *Macrobrachium lucifugum* Holthuis, 1974 (Palaemonidae) are recorded for the first time from anchialine systems on Acklins Island, Bahamas. Seventy-two individuals of *B. cubensis*, 29 of *P. sterreri*, and nine of *M. lucifugum* were collected in July 2017 from five sites across the island. We also report on observations on behavior for all three species during collection and of *B. cubensis* monitored in a laboratory setting over a two-year period.

Key Words: anchialine systems, cenotes, coastal sink holes, Cuban cave shrimp, Sterrer's cave shrimp, tidal pools

INTRODUCTION

Anchialine systems are comprised of landlocked bodies of water with subterranean connections to the surrounding ocean that permit tidally driven water exchange (Bishop *et al.*, 2015). Members of the family Barbouriidae Christoffersen, 1987 are globally distributed along tropical latitudes and are mostly endemic to anchialine systems (De Grave *et al.*, 2014). The family consists of four genera, *Barbouria* Rathbun, 1912, *Calliasmata* Holthuis, 1973, *Janicea* Manning & Hart, 1984, and *Parhippolyte* Borradaile, 1900. *Macrobrachium* Spence Bate, 1868 is a species-rich genus of the family Palaemonidae Rafinesque, 1815 widely distributed in bodies of freshwater across tropical and subtropical latitudes (Holthuis, 1980; Vera-Silva *et al.*, 2016). Some palaemonids, such as *M. lucifugum* Holthuis, 1974, are sometimes found in anchialine systems and coastal freshwater sink holes (Hobbs, 1994; Komai & Fujita, 2005).

It is common for different species of Barbouriidae to inhabit the same locality (Hart & Manning, 1981). Such cohabitation has previously been observed in anchialine caves in Bermuda and in Exuma and San Salvador islands in the Bahamas (Hart & Manning, 1981; Botosaneanu & Iliffe, 1999; Ditter *et al.*, 2015). *Barbouria cubensis* von Martens, 1872 and *Parhippolyte sterreri* Hart & Manning, 1981 are anchialine species that lack many troglomorphic characteristics associated with cave dwelling organisms such as the absence of pigmentation, reduced or absent eyes, cuticular structural reduction, and the elongation of sensory and ambulatory appendage (Holthuis, 1963; Turk *et al.*, 1996; Lamoreux, 2004; Bishop & Iliffe, 2012; Friedrich, 2013; Pérez-Moreno *et al.*, 2017).

Barbouria cubensis has been reported from Cuba and the islands of Abaco, Exuma, Mayaguana, Grand Bahama, and San

Salvador islands in the Bahamas, Providenciales in the Caicos Islands, Bermuda, Jamaica, Cayman Brac in the Cayman Islands, and in the Yucatán Peninsula (Hobbs *et al.*, 1977; Manning & Hart, 1984; Hart *et al.*, 1985; Bishop & Iliffe, 2012; Ditter *et al.*, 2015). *Parhippolyte sterreri* is known to occur in Bermuda, the Yucatan Peninsula, and Andros, Exuma, Grand Bahama, and San Salvador islands, Bahamas (Hart & Manning, 1981; Manning *et al.*, 1984; Brooks, M., 1987; Kensley, 1988; Wicksten, 1996; Ditter *et al.*, 2015). Despite their abundance, little is known about the biology of these two species, with only anecdotal observations of their behavior reported. There is so far only one study comparing physiological differences between populations of *B. cubensis* (Bishop & Iliffe, 2012). *Macrobrachium lucifugum* has previously been reported from Bonaire, Cuba, Curaçao, the Dominican Republic, Grand Bahama, Jamaica, and Puerto Rico (Holthuis, 1974; Chace, 1975; Hobbs, 1994; De Grave & Fransen, 2011).

We report on the first occurrence of *Barbouria cubensis*, *Parhippolyte sterreri*, and *Macrobrachium lucifugum* in the anchialine pools of Acklins Island, Bahamas. In addition to these first records, we discuss observations made for these species during collection as well as the behavior of *B. cubensis* in its natural habitat and in a laboratory setting over a 2-year period.

MATERIALS AND METHODS

Collection of specimens

Seventy-two specimens of *B. cubensis*, 29 of *P. sterreri*, and nine of *M. lucifugum* were collected on Acklins Island, Bahamas (22.3658°

N, 74.0535° W) in July 2017. Specimens were collected from Big Pond, Harbour Hill Cave (“Darling’s Cave”), Harbour Hill Cenote, Flamingo Pond, Nibbles Cave, Red Lantern Cave, and Student Pond (**Fig. 1**).

Specimens were captured using a baited minnow trap deployed near the mouth of the conduit while snorkeling, or by hand. Specimens were preserved in 95–100% ethyl alcohol or RNAlater (Sigma-Aldrich, St. Louis, MO, USA) on site or kept alive until they could be properly processed. Specimens were transferred to the Florida International University Crustacean Collection (FICC) located on the Biscayne Bay campus, North Miami, FL, USA after preservation.

Barbouria cubensis was captured from Big Pond, Flamingo Pond, Nibbles Cave, Red Lantern Cave, and Student Pond (**Fig. 1**), *P. sterreri* from Flamingo Pond, and *M. lucifugum* was from Harbour Hill and Red Lantern cave, juveniles observed in a freshwater cenote (Harbour Hill Cenote) 150 m north of the cave entrances. We noted that *B. cubensis* collected alongside *M. lucifugum* were smaller in size than those found at other sites.

Behavioral observations

Ten *B. cubensis* individuals previously collected from San Salvador Island, Bahamas were used for behavioral observations made between October 2016 and December 2018. Eight individuals were paired and placed into four 19 l (5 gal.) aquaria and two were isolated in two separate aquaria to serve as the control groups. The six aquaria were placed in a light controlled environment. Each aquarium contained one limestone shelter to mimic cave substratum to recreate the natural habitat as best as possible. Each aquarium was equipped with bubble filters, and timers were utilized to control the day/night cycles as follows: 2 h of indirect light, 8 h of direct light, 2 h of indirect light, and 12 h of dark. Red LED lights were installed to observe specimens during the night cycle.

Water was changed every other day using fresh filtered seawater from Biscayne Bay. Water quality parameters were monitored daily to maintain optimal water quality. Specimens were fed frozen brine shrimp daily. Noteworthy behavior was digitally recorded using a GoPro Hero2 and any exuvia recovered were preserved in 70% ethyl alcohol.

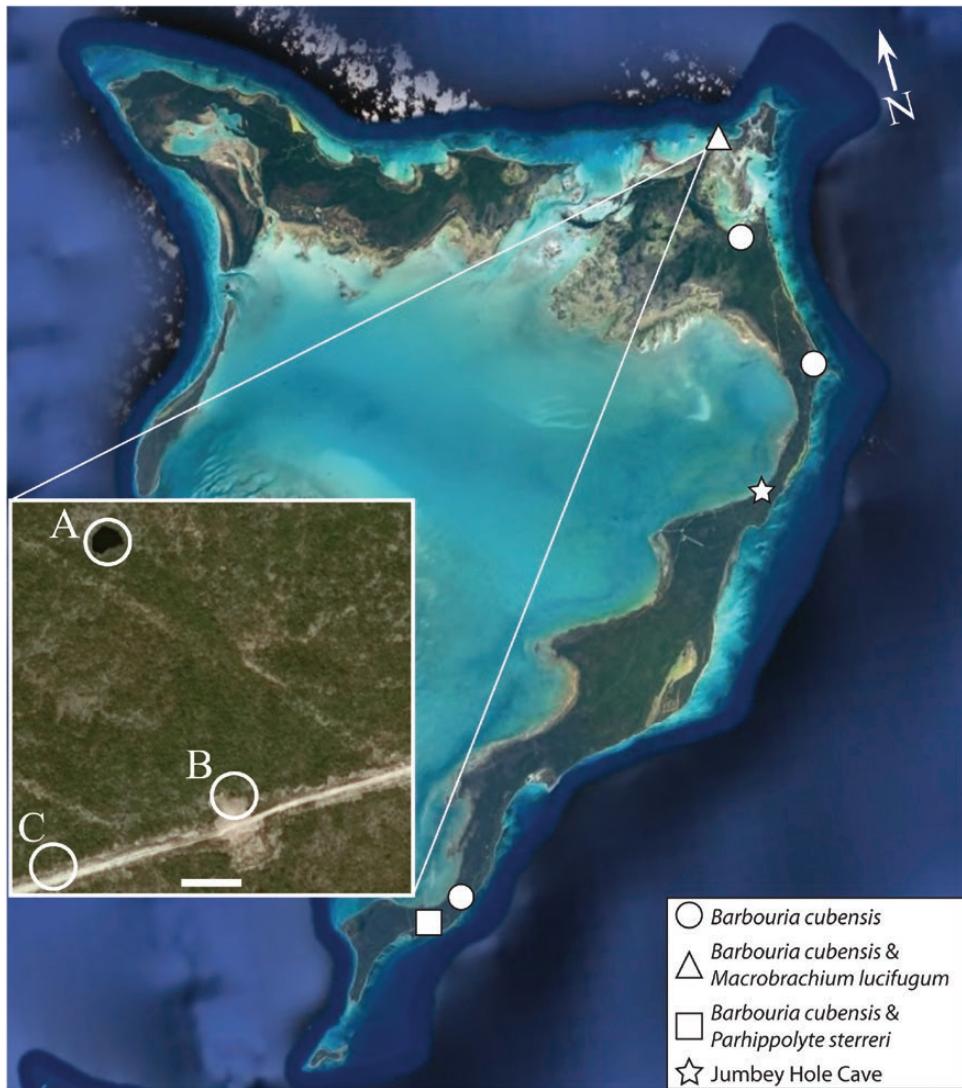


Figure 1. Map of Acklins, Bahamas adapted from Google Earth indicating the collection sites of *Barbouria cubensis*, *Parhippolyte sterreri*, and *Macrobrachium lucifugum* and the location of Jumbey Hole Cave. Magnified view of Harbour Hill Cenote (A), Harbour Hill Cave (B), and Red Lantern Cave (D). Scale bar = 50 m. This figure is available in color at *Journal of Crustacean Biology* online.

RESULTS AND DISCUSSION

The presence of *B. cubensis*, *P. sterreri*, and *M. lucifugum* on Acklins Island, Bahamas represents minor range extensions for all three species (Fig. 2). *Barbouria cubensis* has the widest distribution on Acklins, being found in all sampling sites except for Harbour Hill Cave. As in San Salvador Island, *P. sterreri* is only found on the southern portion of the island, possibly indicating that this species is a recent arrival due to its limited distribution on the island compared to *B. cubensis* (Ditter *et al.*, 2015). *Parhippolyte sterreri* is present in other anchialine pools on southern Acklins Island, but these sites were not sampled. *Macrobrachium lucifugum* is limited to the northeastern portion of the islands (Fig. 1). Juvenile *M. lucifugum*

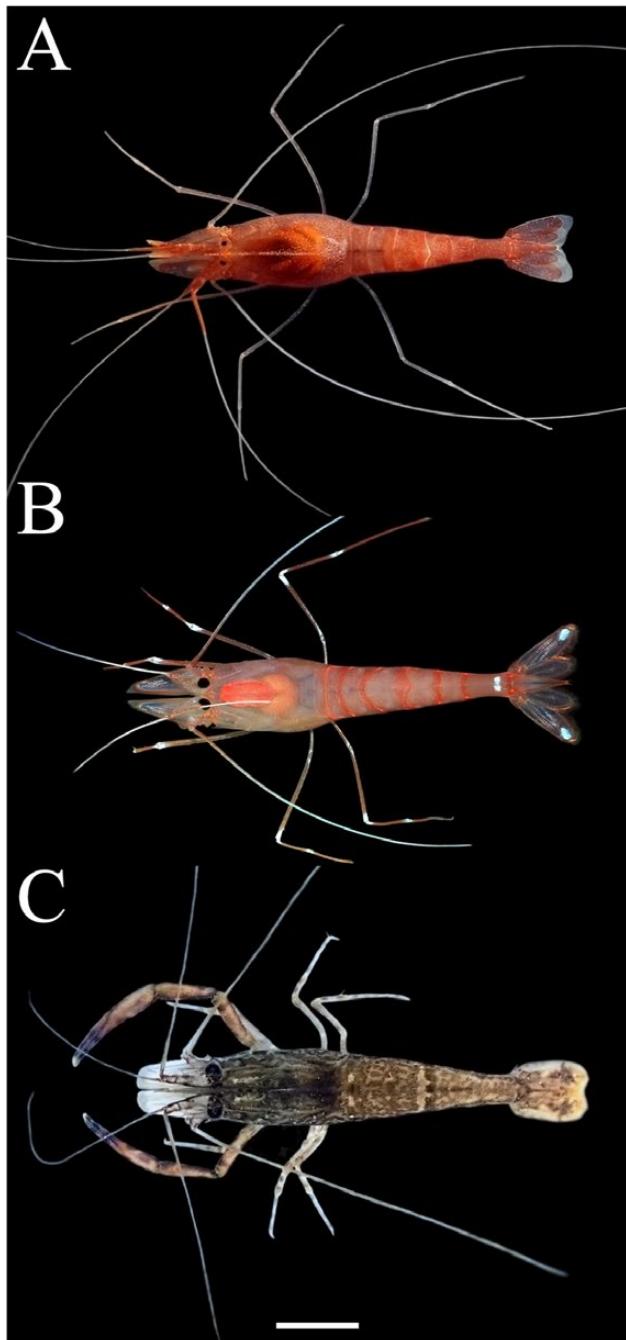


Figure 2. Dorsal views of *Barbouria cubensis* (A), *Parhippolyte sterreri* (B), and *Macrobrachium lucifugum* (C). Scale bar = 1 cm. This figure is available in color at *Journal of Crustacean Biology* online.

were only observed in one freshwater cenote (Fig. 1A), and adults were only collected in two marine caves (Fig. 1B, C). Many species of *Macrobrachium* are amphidromous, migrating between freshwater and saltwater habitats as part of their life history (Bauer & Delahoussaye, 2008). Harbour Hill and Red Lantern caves are the only localities found in close proximity to a non-ephemeral surface freshwater feature on Acklins Island. It is likely that the distribution of juvenile and adult *M. lucifugum* indicates subterranean connections between these localities because of its amphidromous life history. Alvarez *et al.* (2004) reported observing *B. cubensis* from Jumbey Hole cave; however, the cave was found to be a dry cave. There is no evidence that Jumbey Hole is or was an anchialine cave in recent history and island residents indicated that it has always been a dry cave.

Field observations

The number of shrimp in anchialine pools are most abundant during high tide and absent during low tide. The presence or absence of shrimp in surface pools appears to be tidally driven. *Barbouria cubensis*, *P. sterreri*, and *M. lucifugum* began migrating into surface waters shortly after the start of flood tides and retreating during ebb tides. Further studies are necessary to understand the possible physiological mechanisms and environmental cues underlying this behavior, which may also further the understanding of the evolution of anchialine organisms. No remarkable agonistic behaviors were detected when *B. cubensis* and *P. sterreri* were observed in the same locality or housed in the same aquarium. When housed together for an extended period of time, *B. cubensis* mirrored the coloration of *P. sterreri*. This was done by increasing the intensity of white coloration along the joints of pereiopods 3–5 and expanding the white spots on the posterior surface of the uropodal exopods and the sixth abdominal somite (Fig. 2B). When *B. cubensis* and *M. lucifugum* were observed in the same locality, *B. cubensis* avoided *M. lucifugum*. *Barbouria cubensis* and *M. lucifugum* could not be housed in the same aquarium due to the aggressive behavior of *M. lucifugum*. *Barbouria cubensis* and *M. lucifugum* also exhibited no flight response to the presence of human observers, and often boldly foraged on the observers. *Parhippolyte sterreri* stayed deeper within the conduits and retreated in the presence of observers.

Laboratory observations

Barbouria cubensis was found to exhibit phenotypic hypervariation (PhyV) defined as the presence of extensive morphological variation that far exceeds variation described in previous records (see Ditter *et al.*, 2019 for an in-depth review of PhyV in *B. cubensis*). Our initial observations showed the presence of PhyV in captive individuals of *B. cubensis*, and exuvia from each specimen were examined monthly to determine if PhyV was retained after ecdysis. If PhyV was lost after ecdysis it would possibly indicate physical trauma as a source of PhyV. This was not the case as all individuals retained identical variations over the course of two years in captivity, and no additional morphological variations were observed in any individuals. To our knowledge, the retention of extensive morphological variation has only been reported over the course of 130 d in *Palaeomon longirostris* (Béguer *et al.*, 2010).

The color of *B. cubensis* has been described to range from white and nearly transparent to deep red or crimson (Hobbs *et al.*, 1977). Prior to light exposure, individuals appear nearly translucent (Fig. 3A), turning light to dark red within 4 min after exposure to full-spectrum light (Fig. 3B). Once returned to darkness, individuals lose color within 15 min. As ecdysis neared, the degree of color change in response to light decreased. When exposed to only blue light (455 nm) individuals of *B. cubensis* exhibited a flight response of erratic swimming seeking refuge. Individuals rapidly changed

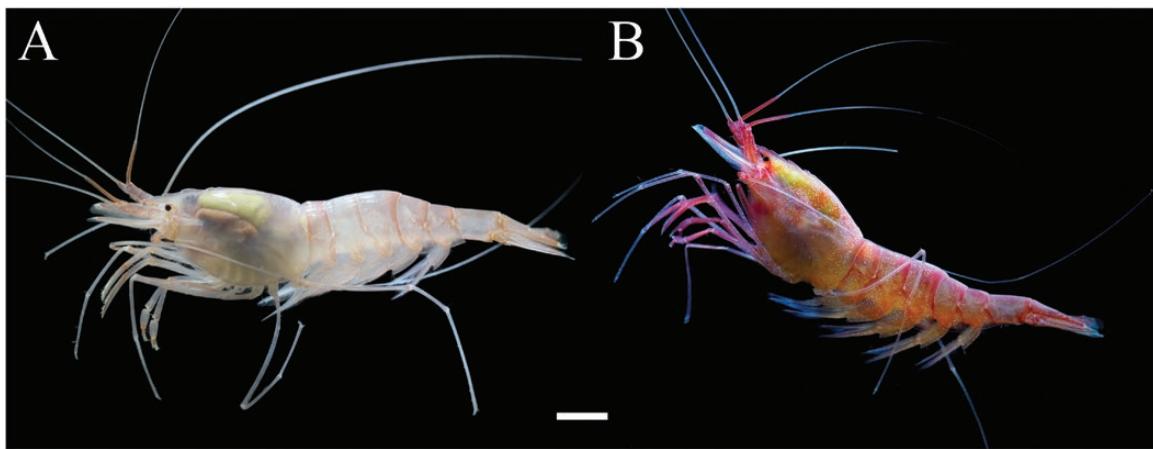


Figure 3. Left lateral view of an individual of *Barbouria cubensis* exhibiting color change before and after light exposure, being nearly translucent pale when not exposed to light, (A) and deep red/crimson after five minutes of exposure to direct light (B). Scale bar = 1 cm. This figure is available in color at *Journal of Crustacean Biology* online.



Figure 4. Dorsal view of the cephalothorax of *Barbouria cubensis* cephalothorax (40x magnification) with distinct small red and large white chromatophores visible. Scale bar = 1 mm. This figure is available in color at *Journal of Crustacean Biology* online.

color from nearly translucent to deep red in the presence of light due to the presence of two types of chromatophores: smaller red and larger white (Fig. 4). Both types of chromatophores are distributed along the body and appendages. The white chromatophores are much larger and less abundant than the red chromatophores. The contrast in color change from pale to red decreased over a 30 d period. Once color change could no longer be detected, ecdysis occurred within 48 h. The increasingly red coloration of individuals appears to be a strong indicator for ecdysis.

Paired *B. cubensis* were highly active, either swimming or walking around the substrate, and cleaning themselves. Individuals were able to locate and consume food within 1 min. This species also exhibited agonistic behavior by means of antennal fencing (Dunham, 1972). Caridean shrimps have been found to behave

aggressively to retain access to limited space, food, and potential mates (Ra'anan & Sagi, 1985; Karplus & Harpaz, 1990; Correa & Thiel, 2003). When not active, *B. cubensis* hid underneath the limestone shelters or the water filter. Isolated individuals exhibited behavior that was unlike their paired counterparts. They were less active, remaining underneath their shelters most of the time and taking 2–6 min to locate and consume their food. Lack of competition may be a possible explanation for the decreased activity and feeding response of isolated specimens.

Habitat destruction is a serious threat to the biodiversity of anchialine habitats (Culver & Sket, 2000; Iliffe & Kornicker, 2009), so it is imperative to document even minor range expansions to these species. The IUCN (2019) lists *B. cubensis* and *P. sterreri* as critically endangered, and *M. lucifugum* as least concern, but we believe reassessment of *M. lucifugum* would change its status to critically endangered (Iliffe, 1996a, 1996b; De Grave, 2013). As many caves have already been altered or destroyed by pollution and development, and it is essential to continue studying anchialine organisms to learn more about their dispersal ability, life history and basic biology.

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REFERENCES

- Alvarez, F., Villalobos, J.L. & Iliffe, T.M. 2004. A new species of Agostocaris (Caridea: Agostocarididae) from Acklins Island, Bahamas. *Proceedings of the Biological Society of Washington*, **117**: 368–376.
- Bauer, R.T. & Delahoussaye, J. 2008. Life history migrations of the amphidromous river shrimp *Macrobrachium ohione* from a continental large river system. *Journal of Crustacean Biology*, **28**: 622–632.
- Béguer, M., Feuillassier, L., Elie, P., Boët, P. & Girardin, M. 2010. Exoskeletal deformities in Palaemonidae: are they a threat to survival? *Marine Environmental Research*, **69**: 109–117.
- Bishop, R.E. & Iliffe, T.M. 2012. Ecological physiology of the anchialine shrimp *Barbouria cubensis*: a comparison of epigean and hypogean populations. *Marine Biodiversity*, **42**: 303–310.

- Bishop, R.E., Humphreys, W.F., Cukrov, N., Žic, V., Boxshall, G.A., Cukrov, M., Iliffe, T.M., Kršinić, F., Moore, W.S., Pohlman, J.W. & Sket, B. 2015. 'Anchialine' redefined as a subterranean estuary in a crevicular or cavernous geological setting. *Journal of Crustacean Biology*, **35**: 511–514.
- Borradaile, L.A. 1900. On the Stomatopoda and Macrura brought by Dr. Willey from the South Seas. In: *Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896, and 1897* by Arthur Willey, D.Sc. Lond., Hon. M.A. Cantab. (Willey, A., ed.), pp. 395–428, pls. 36–39. University Press, Cambridge, UK.
- Botosaneanu, L. & Iliffe, T.M. 1999. On four new stygobitic cirolanids (Isopoda: Cirolanidae) and several already described species from Mexico and the Bahamas. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, **69**: 93–123.
- Brooks, M. 1987. *A discussion of the shrimps (Crustacea: Decapoda) inhabiting the marine blue holes of the South Shore of Grand Bahama Island, Bahamas*. M.S. thesis, Florida Atlantic University, Boca Raton, FL, USA.
- Chace, F.A. Jr. 1975. Cave shrimps (Decapoda: Caridea) from the Dominican Republic. *Proceedings of the Biological Society of Washington*, **88**: 29–44.
- Correa, C.R. & Thiel, M.A. 2003. Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. *Revista Chilena de Historia Natural*, **76**: 187–203.
- Culver, D.C. & Sket, B. 2000. Hotspots of subterranean biodiversity in caves and wells. *Journal of Cave and Karst Studies*, **62**: 11–17.
- De Grave, S. 2013. *Macrobrachium lucifugum*. The IUCN Red List of Threatened Species: e.T198104A2512014 [http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T198104A2512014.en].
- De Grave, S. & Fransen, C.H.J.M. 2011. Carideorum Catalogus: The Recent Species of the Dendrobranchiate, Stenopodidean, Procarididean and Caridean Shrimps (Crustacea: Decapoda). *Zoologische Mededelingen*, **85**: 195–589.
- De Grave, S., Li, C.P., Tsang, L.M., Chu, K.H. & Chan, T.Y. 2014. Unweaving hippolytid systematics (Crustacea, Decapoda, Hippolytidae): resurrection of several families. *Zoologica Scripta*, **43**: 496–507.
- Ditter, R.E., Goebel, A.M. & Erdman, R.B. 2015. First record of the anchialine shrimp *Parhippolyte sterreri* (Decapoda, Barbouriidae) from San Salvador Island, Bahamas, with observations on *Barbouria cubensis*. *Marine Biodiversity Records*, **8**: e46 [doi.org/10.1017/S1755267215000196].
- Ditter, R.E., Goebel, A.M., Erdman, R.B. & Bracken-Grissom, H.D. 2019. Widespread phenotypic hypervariation in the enigmatic anchialine shrimp *Barbouria cubensis* (Decapoda: Barbouriidae). *Zootaxa* [doi.org/10.11646/zootaxa.4648.1.1].
- Dunham, P.J. 1972. Some effects of group housing upon the aggressive behavior of the lobster *Homarus americanus*. *Journal of Fisheries Research Board of Canada*, **29**: 598–601.
- Friedrich, M. 2013. Biological clocks and visual systems in cave-adapted animals at the dawn of speleogenomics. *Integrative and Comparative Biology*, **53**: 50–67.
- Hart, C.W. Jr. & Manning, R.B. 1981. The cavernicolous caridean shrimps of Bermuda (Alpheidae, Hippolytidae, and Atyidae). *Journal of Crustacean Biology*, **1**: 441–56.
- Hart, C.W. Jr., Manning, R.B. & Iliffe, T.M. 1985. The fauna of Atlantic marine caves: evidence of dispersal by sea floor spreading while maintaining ties to deep waters. *Proceedings of the Biological Society of Washington*, **98**: 288–92.
- Hobbs, H.H. III. 1994. Biogeography of subterranean decapods in North and Central America and the Caribbean region (Caridea, Astacidea, Brachyura). *Hydrobiologia*, **364**: 1–143.
- Hobbs, H.H. Jr., Hobbs, H.H. III & Daniel, M.A. 1977. A review of the troglobitic decapod crustaceans of the Americas. *Smithsonian Contribution to Zoology*, **244**: 1–183.
- Holthuis, L.B. 1963. On red coloured shrimps (Decapoda, Caridea) from tropical land-locked saltwater pools. *Zoologische Mededelingen*, **38**: 261–279.
- Holthuis, L.B. 1973. Caridean shrimps found in land-locked saltwater pools at four Indo-West Pacific localities (Sinai Peninsula, Funafuti Atoll, Maui and Hawaii Islands): with the description of one new genus and four new species. *Zoologische Verhandelingen*, **128**: 3–48.
- Holthuis, L.B. 1974. Subterranean Crustacea Decapoda Macrura collected by Mr. L. Botosaneanu during the 1973 Cuban-Roumanian Biospeleological expedition to Cuba. *International Journal of Speleology*, **6**: 231–242.
- Holthuis, L.B. 1980. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries. FAO Species Catalogue. Vol. 1. *FAO Fisheries Synopsis*, **125**: 1–271.
- Iliffe, T.M. 1996a. *Barbouria cubensis*. The IUCN Red List of Threatened Species: e.T2559A9454288 [dx.doi.org/10.2305/IUCN.UK.1996.RLTS.T2559A9454288.en].
- Iliffe, T.M. 1996b. *Somersiella sterreri*. The IUCN Red List of Threatened Species: e.T20371A9192483 [dx.doi.org/10.2305/IUCN.UK.1996.RLTS.T20371A9192483.en].
- Iliffe, T.M. & Kornicker, L.S. 2009. Worldwide diving discoveries of living fossil animals from the depths of anchialine and marine caves. *Smithsonian Contributions to the Marine Sciences*, **38**: 269–280.
- Karplus, I. & Harpaz, S. 1990. Preliminary observations on behavioral interactions and distribution patterns of freshwater prawns *Macrobrachium rosenbergii* under semi-natural conditions (Decapoda, Caridea). *Crustaceana*, **59**: 193–203.
- Kensley, B. 1988. New species and records of cave shrimps from the Yucatan Peninsula (Decapoda: Agostocarididae and Hippolytidae). *Journal of Crustacean Biology*, **8**: 688–99.
- Komai, T. & Fujita, Y. 2005. A new stygobiont species of *Macrobrachium* (Crustacea: Decapoda: Caridea: Palaemonidae) from an anchialine cave on Miyako Island, Ryukyu Islands. *Zootaxa*, **1021**: 13–27.
- Lamoreux, J. 2004. Stygobites are more wide-ranging than troglobites. *Journal of Cave and Karst Studies*, **66**: 18–19.
- Manning, R.B. & Hart, C.W. Jr. 1984. The status of the hippolytid shrimp genera *Barbouria* and *Ligur* (Crustacea: Decapoda): a reevaluation. *Proceedings of the Biological Society of Washington*, **97**: 655–665.
- Martens, E., von. 1872. Über cubanische Crustaceen nach den Sammlungen Dr. J. Gundlach's. *Archiv für Naturgeschichte*, **38**: 77–147.
- Pérez-Moreno, J.L., Baláz, G., Wilkins, B., Herczeg, G. & Bracken-Grissom, H.D. 2017. The role of isolation on contrasting phylogeographic patterns in two cave crustaceans. *BMC Evolutionary Biology*, **17**: 247.
- Ra'anan, Z. & Sagi, A. 1985. Alternative mating strategies in male morphotypes of the freshwater prawn *Macrobrachium rosenbergii* (De Man). *Biological Bulletin*, **169**: 592–601.
- Rathbun, M.J. 1912. Some Cuban Crustacea, with notes on the Astacidae by Walter Faxon, and a list of Isopoda, by Harriet Richardson. *Bulletin of the Museum of Comparative Zoology*, **54**: 451–460.
- Spence Bate, C. 1868. On a new genus, with four new species, of freshwater prawns. *Proceedings of the Zoological Society of London*, **1868**: 363–368.
- Turk, S., Sket, B. & Sarbu, S. 1996. Comparison between some epigean and hypogean populations of *Asellus aquaticus* (Crustacea: Isopoda: Asellidae). *Hydrobiologia*, **337**: 161–170.
- Wicksten, M.K. 1996. *Parhippolyte cavernicola*, new species (Decapoda: Caridea: Hippolytidae) from the tropical eastern Pacific, with taxonomic remarks on the genera *Somersiella* and *Koror*. *Journal of Crustacean Biology*, **16**: 201–207.
- Vera-Silva, A.L., Carvalho, F.L. & Mantelatto, F.L. 2016. Distribution and genetic differentiation of *Macrobrachium jelskii* (Miers, 1877) (Natantia: Palaemonidae) in Brazil reveal evidence of non-natural introduction and cryptic allopatric speciation. *Journal of Crustacean Biology*, **36**: 373–383.