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## Predatory behavior of the cave shrimp *Creaseria morleyi* (Creaser, 1936) (Caridea: Palaemonidae), the blind hunter of the Yucatán cenotes, Mexico

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### ABSTRACT

Recent studies of the trophic structure of the underwater cave ecosystems in the Yucatán Peninsula have regarded the largest crustacean inhabitant, the blind palaemonid shrimp *Creaseria morleyi* (Creaser, 1936), as a scavenger and predator without any evidence on the behavior of the shrimp. The predatory behavior of *C. morleyi* is here described for the first time, verifying its classification as a predator. A variety of prey targets, including the atyid shrimp *Typhlatya* sp., were used to demonstrate predation and saprophagous feeding behavior in *C. morleyi* using *in vitro* and *in situ* observations. Scanning electron microscope images show the structures of the antennules and antennae that could be responsible for prey detection. Findings show that *C. morleyi* is capable of hunting a variety of prey, most likely depending on their relative size. Observations on the feeding strategy of *C. morleyi* suggest any animal within a particular size range is a potential prey, including its own species, which suggests the hypothesis that growth may be favored in early stages of life in order to reach a size refuge from predation. These observations provide information of some of the adaptations necessary for a predator to thrive in an aphotic and oligotrophic environment.

**Key Words:** anchialine environment, cave adaptations, decapods, feeding strategies, stygofauna

### INTRODUCTION

The diversity and biomass of the Yucatán Peninsula underwater, cave-restricted fauna (stygofauna) is dominated by 47 crustacean species out of a total of 49 freshwater and anchialine species currently described (Álvarez & Iliffe, 2008; Álvarez *et al.*, 2015; Mejía-Ortiz *et al.*, 2017). These numbers exclude some exceptional caves in Cozumel island that host a number of echinoderm, polychaete stygofauna and other marine stygofauna species (Trujillo Pisanty *et al.*, 2010; Frontana-Urbe & Solis-Weiss, 2011; Bribiesca-Contreras *et al.*, 2013). The top stygobiont predators in the freshwater portion of the anchialine ecosystems are the palaemonid shrimp *Creaseria morleyi* (Creaser, 1936) and two species of fishes, *Typhliasina pearsei* (Hubbs, 1938) and *Ophisternon infernale* Hubbs, 1938 (Pohlman *et al.*, 2000). The

shrimp is widely distributed in Yucatán caves (Pérez Aranda, 1983; Botello, 2007). Although the trophic level of *C. morleyi* has been assessed through indirect measurements (Pohlman *et al.*, 1997), no prior visual evidence of its predatory behavior had been previously reported.

The trophic structure of anchialine ecosystems is relatively simple and composed of a small number of levels with fewer species than most epigean habitats. Pohlman *et al.* (2011) suggested only three trophic levels: producers (photosynthetic and chemosynthetic), primary and detrital consumers, and generalist or opportunistic predators and scavengers. Nutrients and organic matter (e.g., plant or animal detritus and feces) can reach anchialine systems by several processes: lixiviation or filtration of the surrounding soil into the natural sinkhole, or cenote, and aquifer

(Pohlman *et al.*, 2000), carried by other animals (bats, birds, humans), or produced within the cenotes or caves. Primary production is limited in the anchialine ecosystems and is generated mainly by chemosynthetic prokaryotes in the aphotic areas of the caves (Pohlman, 2011). The great majority of cave systems in the Yucatán Peninsula are flooded. The well or sinkhole that is formed by the collapse of the surface limestone that exposes the aquifer is regionally called *cenote*, a word derived from the Mayan *dzonot* (Schmitter-Soto *et al.*, 2002). The morphology of each cenote governs the amount of light that reaches the water surface, which is the only place, in the otherwise underground system, where photosynthesis may occur.

Primary consumer stygofauna in Yucatán is mainly composed of crustaceans having specialized filtering or scavenging feeding strategies (Mejía-Ortiz *et al.*, 2013), either on the benthos or the water column. Some anchialine isopods (family Cirolanidae) tend to be omnivores, display cannibalism, and feed on carcasses and other organic material deposited on the sediment (Pohlman *et al.*, 1997). Others, like the mysid *Antromysis* (*Antromysis*) *cenotensis* Creaser, 1936 and the thermosbaenacean *Tulumella unidens* Bowman & Iliffe, 1988, filter organic matter and microbes suspended in the water column. Attyd shrimps (such as *Typhlatya*) display water-column filtering as well as sediment-scraping strategies (Pohlman *et al.*, 1997; Mejía-Ortiz *et al.*, 2006). Under the halocline, the marine cave systems are inhabited by other predators such as remipedes (*Xibalbanus* spp.), which feed on other anchialine crustaceans that may also live in the marine portion of these caves.

The stygofauna has adapted to different cave conditions, which result in convergent traits. The stygofauna generally has high tolerance to long starvation periods through reduction of metabolic rate (Hervant *et al.*, 1999, 2001; Bishop *et al.*, 2004), increased longevity (Vogt, 2012), delay of reproduction, reduction in the number of eggs (Culver & Pipan, 2009), changes in behavioral traits (Abele & Felgenhauer, 1985; Carpenter, 1999; Friedrich, 2013), loss of pigmentation and eye structures, and the development of other sensory organs and structures (Mejía-Ortiz & Hartnoll, 2006; Mejía-Ortiz *et al.*, 2013). Feeding behavior and strategies of stygobiont predators like *C. morleyi* have hardly been investigated, although feeding (or fasting) is one of the most powerful drivers of evolution (Sket, 1996).

In the extensive groundwater habitats of Yucatán Peninsula, which have an overall constant environment with only subtle seasonal changes in most abiotic variables, simplified trophic chains with low biological diversity, and biomass with reduced numbers of small individuals, the probability of encounters between prey and predator could be one of the crucial aspects of feeding success. Optimal foraging theory predicts an optimization of the energy input for the energy spent searching, chasing, capturing, and ingesting prey (Charnov, 1976; Pyke *et al.*, 1977).

We demonstrate that *C. morleyi* is an effective predator that can anticipate prey movement and is capable of precise and efficient attack on their prey, either starting from a still or a moving position. We present scanning electron microscopy (SEM) images of structures on the antennules (A1) and antennae (A2) that could be involved in prey detection as well as video recordings of *in vitro* and *in situ* predation showing the prey-capture behavior of *C. morleyi*.

## METHODS

### In vitro observations

Six individuals of *C. morleyi* and 18 of *Typhlatya* sp. were collected from the Nayah cenote (20.646513°N, -89.404690°W) following Mexican regulations (NOM126; collection permit SEMARNAT,

no. SGPA/DGVS: 05263/14) during several night dives on 17 March 2014 at depths of 18 to 33 m using cave-diving techniques.

A system of five 12 l glass aquaria was built to keep experimental shrimps under observation at Unidad Académica de Yucatán, Universidad Nacional Autónoma de México (UNAM), Sisal, Yucatán (Fig. 1): one experimental aquarium with both species, three holding aquaria to only keep *C. morleyi* individuals, and one to keep *Typhlatya* sp. Each aquarium contained approximately 200 g of sediment from the cenote, a small karst rock, and a continuous water flow from a 150 l reservoir of water collected from cenote Yaal Utsil (20.623889°N, -89.606667°W). Central aeration was provided in the 150 l reservoir. Room temperature was kept at 27 °C in accordance to temperature recorded at the site. The room was permanently kept in total darkness. Four closed-circuit surveillance infra-red cameras (CCTV-131, Steren Electronics, China) and two commercial infra-red lights (Steren CCTV-450) (Fig. 1) were installed to record the experimental aquarium at different angles.

Individuals of *Typhlatya* sp. were placed together in an aquarium, whereas those of *C. morleyi* were distributed among three aquaria, each separated by a dividing mesh. Shrimps were fed with commercial Purina® (Camarónina Agribrands, Ciudad Obregón, México) penaeid-shrimp pellets once a day.

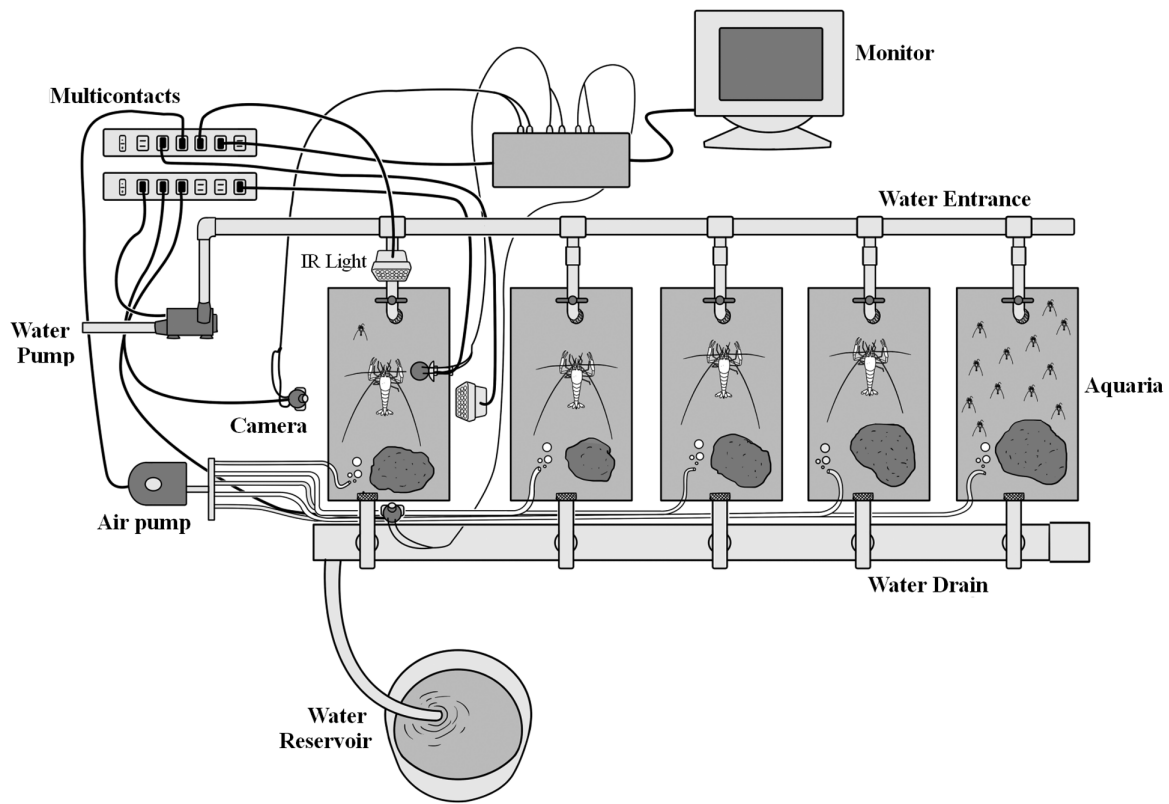
Experimental observations began 48 h after relocation of shrimps to the laboratory: one individual of *C. morleyi* and one of *Typhlatya* sp. were transferred into the experimental aquarium for continuous 24 h filming. The process was repeated with other individuals of the two species for the following two days. Aquaria were examined each day and the remaining individuals returned to their respective holding tanks. A total of 120 h (5 d) from the three infra-red cameras were reviewed: 24 h of film every time we transferred a *Typhlatya* individual into the experimental aquarium, with a total of five replicates. Three replicates were with complete, unharmed *C. morleyi* individuals and two with individuals that lost one or both of their second pair of pereopods during capture and handling.

### In situ observations

*In situ* videos were filmed using GoPro Hero 4 silver at 1080 pixels, narrow view, at 60 frames per second, mounted on two underwater SolaDive2000 film lights. The first two predatory interactions were filmed in cenote San Juan, Homún, Yucatán (20.734056°N, -89.288500°W) at 18 m and 22 m depth, respectively, on 2 November 2016, whereas the third filmed interaction was recorded in cenote Kankirixché, Abalá, Yucatán (20.637235°N, -89.632969°W) at a depth of 24 m on 6 April 2016. All video recordings shown in the supplementary material (see below) were made in the twilight zone of the cavern. The films were made during over 70 dives and a total of 90 h from 20 different cenotes in Yucatán Peninsula. When feeding bouts were recorded, the video clips were cut and edited using GoPro Studio® software ([www.gopro.com](http://www.gopro.com)) and sent for post-production editing to VisualMates ([www.visualmates.mx](http://www.visualmates.mx)).

### Scanning electron microscopy

Two individuals of *C. morleyi* were captured from Cueva Pamul, Playa del Carmen, Quintana Roo, México for observation. Preparations used protocols modified from Felgenhauer (1987) and viewed under a Hitachi Scan Electron 2460 microscope (Hitachi, Tokyo) at Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City. The antennular (A1) and antennal (A2) flagella (as defined by Garm, 2004) were selected for imaging considering them the main chemical and mechanical receptors as described for other cave crustaceans (Mejía-Ortiz *et al.* 2006, 2013).



**Figure 1.** Aquaria, infrared cameras, lights, recorder, and monitor set-up used for recording behavior of *Creaseria morleyi* (large crustacean) and *Typhlatya* sp. (small crustacean).

## RESULTS

Individuals of *C. morleyi* were observed constantly moving during field observations, both on the cave bottom and in the water column. When on the bottom, they moved mostly in a straight line in an apparent random direction, beating their pleopods with the abdomen slightly lifted as they walked touching the ground with the third to fifth pereopods (Fig. 2A, B). The second pereopods were held parallel to the ground and the chelae were always open. The second pereopods were laterally extended (Fig. 2A) resulting in the pereopods being at right angles, or slightly bent forward (Fig. 2B). Individuals observed swimming in the water column also exhibited rapid, rhythmic movement of the pleopods but retracted their pereopods under the cephalothorax, except for the first and second, which were extended forward with chelae opened (Fig. 2C).

Several predatory interactions were observed in the laboratory, but only one event was filmed (Supplementary material Video S1). Other predation events were not recorded but the prey was confirmed as individuals of *Typhlatya* sp. No body parts of the latter were found in aquaria.

Individuals of the two species moved frequently after being relocated to the observation aquarium but reduced the swimming efforts after 20–60 min. Activity was observed periodically in *Typhlatya* sp., with individuals spending most of the time settled on the aquarium wall and bottom or swimming short distances in the water column. Individuals of *C. morleyi* showed greater activity than *Typhlatya* sp. individuals, and although the aquaria were covered and the room was kept in complete darkness, *C. morleyi* individuals increased their activity after sundown by continually moving across the aquaria.

The *in vitro* observation involved an individual of *C. morleyi* (total length (TL) 61 mm) and an individual of *Typhlatya* sp. (TL 16 mm;

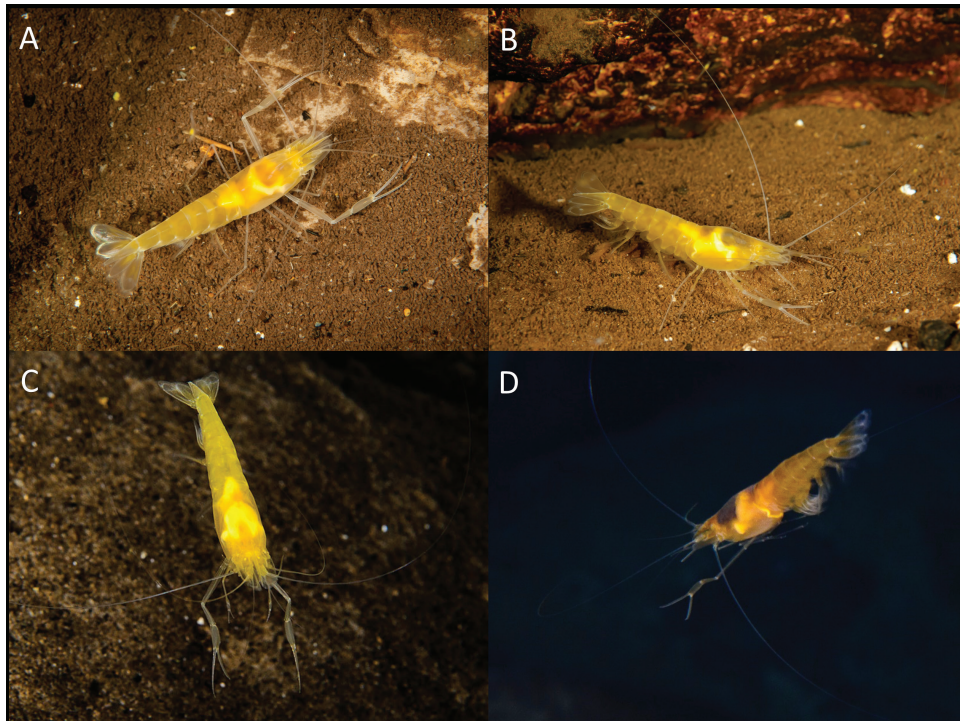
the “prey”) (Supplementary material Video S1). Before the attack, around dawn, both individuals increased their movements and started to swim around the aquarium. Their movements included “rest” stops of a few seconds between bouts of swimming. During several times, the individual of *C. morleyi* stopped at exactly the same location where the prey individual had rested. Before the final approach, both shrimps stopped about 10 cm apart, then the prey began to swim until it sharply changed direction after apparently being touched by the antennal (A2) flagella of *C. morleyi* at a distance of approximately 6 cm. Only a fraction of a second after the sharp change in direction of the prey, *C. morleyi* began the attack from a stationary position. It quickly turned its body towards the contact direction and leaped up and forward from the bottom using its third to fifth pereopods. Once in the water column, it swam towards the prey using its pleopods, tail, and abdomen until finally it captured the prey in its extended left second pereopod chela (Supplementary material Video S1).

Once captured, the prey was held with the chelae of the second pereopod and ripped apart with the chelae of the first pair of pereopods, which transferred the food to the mouth. The predator sank to the bottom and continued feeding. These events took place in less than one second and the total distance covered by the predator was approximately 8 cm from the beginning of the attack until the predator settled on the bottom.

Other individuals of *C. morleyi* that had lost their second pair of pereopods, showed a similar attack behavior when placed under the same conditions, but in all their attempts the *Typhlatya* sp. individuals escaped. Although such predatory behavior had been observed several times in the wild, we only video recorded three capture events (Supplementary material Video S2–4).

The predation event filmed in cenote San Juan, Homun (Supplementary material Video S2) shows an individual of *C. morleyi* walking on the cenote bottom when it suddenly stretched the





**Figure 2.** *Creaseria morleyi* in the wild: **A)** standing still in cenote Tza Itza at a depth of 12 m deep (31 August 2015); **B)** walking on the sediment in cenote Tza Itza at a depth of 18 m at the far end of the cavern (31 August 2015); **C)** swimming close to a rock in cenote Dzombakal at a depth of 14 m at the entrance of the cave passage (7 October 2014); **D)** swimming in the water column at a depth of 14 m, with pleopods 3–5 close to the body and the second pair of pleopods extended forward, cenote Kanun (4 June 2016). This figure is available in color at *Journal of Crustacean Biology* online.

chela of its right second pereopod and caught a smaller crustacean that had passed in front of it. The prey was most likely the mysid *Antromysis cenotensis* or an unidentified crustacean larva. The slow-motion sequence shows the prey struggling unsuccessfully to get free with a series of tail flips, with the predator continuing to move while eating its prey.

A second video from cenote San Juan (Supplementary material video S3) shows another *C. morleyi* individual holding a captured *Typhlatya* sp. with the chelae of its first and second pereopods while swimming. The capture process was not observed, but on-site observations revealed the individual of *Typhlatya* sp. was still alive during the filming.

Video from cenote Kankirixche (Supplementary material video S4) shows an individual of *C. morleyi* capturing and feeding on a small crustacean, most likely *A. cenotensis* or a crustacean larva. The attack began with the predator walking on the bottom when suddenly it stopped at about 2.5 body lengths from its prey, turned, and advanced directly towards it. Once it reached its prey, the predator caught the smaller crustacean with the chelae of its second pair of pereopods. The prey tried to free itself with a series of approximately nine tail flips in a fraction of a second, but failed. The *C. morleyi* individual then moved backwards with three consecutive tail flips and placed the prey into position in front of its mouthparts, holding it with the chelae of both pereopods, then continued walking towards its original direction.

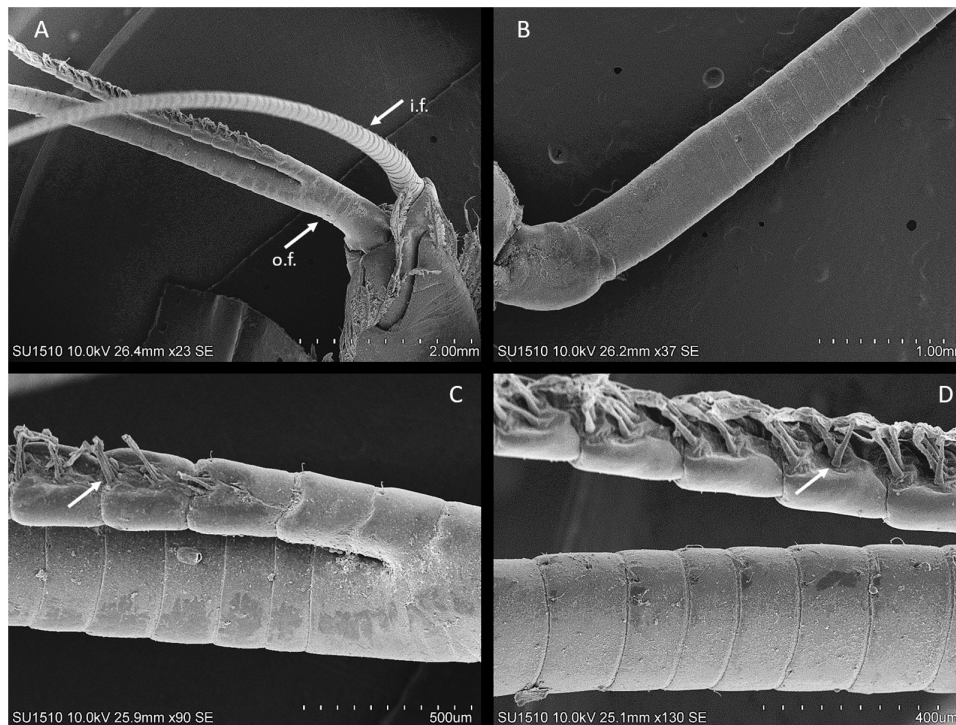
Scanning electron microscopy (SEM) of the antennae (A2) of *C. morleyi* (Fig. 3A, B) shows the absence of setae on the first articles. The outer antennular (A1) ramus, however, has two rows of four well-defined, short aesthetascs with flattened ends from the third to the fourth article (Fig. 3C, D). *Creaseria morleyi* has no setae or pores on the eyes that could function as aids for sensing movement as reported for other cave crustacean species (Mejía-Ortiz & Hartnoll, 2006; Mejía-Ortiz *et al.*, 2013).

## DISCUSSION

Anchialine ecosystems are considered oligotrophic environments (Schmitter-Soto *et al.*, 2002; Pohlman, 2011; Torres-Talamante *et al.*, 2011; Derrien *et al.*, 2015) except for cave entrances and cenotes, which are exposed to sunlight where photosynthetic primary production occurs. The light-less portions of these caves typically support low population densities, resulting in very low probabilities for predators to encounter prey. The stygofauna have a variety of adaptations for survival in the anchialine environment (Bishop *et al.*, 2004; Bishop & Iliffe, 2012; Culver & Pipan, 2013; Mejía-Ortiz *et al.*, 2013), with food scarcity being one of the most crucial evolutionary pressures (Sket, 1996). We confirm that *C. morleyi* is a generalist top predator that has evolved feeding strategies adapted to live in an anchialine environments.

The most common prey in Yucatán anchialine systems are typically mysids, thermosbaenaceans, and small caridean shrimps such as *Typhlatya* sp. These species are pelagic, benthic, or benthopelagic consumers that feed on organic matter and microbes (Pohlman *et al.*, 2000). Predation in *C. morleyi* begins with individuals resting at the bottom, suggesting that it is an ambush predator. The *in situ* recordings nevertheless show the opposite, with *C. morleyi* moving around continuously searching and capturing prey. The attack strategy starts with ambulatory search behavior showing that the shrimp is capable of capturing prey while swimming.

Swimming behavior suggests that *C. morleyi* invests a considerable amount of energy to encounter prey. The area covered when moving forward is increased by spreading the second pereopods laterally. Swimming through the water column increases the possibility of encounters with pelagic prey such as *A. cenotensis*, and it is more likely to encounter benthic or benthopelagic species, such as *Typhlatya* sp., when moving on the substrate. This constant motion could also be the result of avoidance of the diver's presence with the associated impact of air bubbles and light. We were nevertheless able to capture successful feeding behavior on film,



**Figure 3.** Scanning electron micrographs of *Creaseria morleyi*: **A**) antennule (A1), inner flagellum (i.f.) and outer flagellum (o.f.); **B**) antennal (A2) flagellum; **C**) base of antennular (A1) outer flagellum; **D**) antennule (A1) with eight setae per article on the outer flagellum. Arrows in **C** and **D** indicate aesthetascs.

indicating some tolerance to such disturbances. The linear trajectories described in the wild could not be observed in the aquarium due to the obvious size limitations. *In vitro* behavior was that of a “lie in wait” predator, which could be an alternative strategy to find prey in the stable and quiet cave environment.

SEM analysis showed a low density of setae on the antennae of *C. morleyi* (Fig. 3) compared to other freshwater decapods (see Mejía-Ortiz & Hartmoll, 2005; Mejía-Ortiz *et al.*, 2006, 2013). Perhaps this is compensated with a high density of short, flat-ended aesthetascs on the articles of the antennules similar to those reported from other anchialine species belonging to several families (Mejía-Ortiz *et al.*, 2013). The main function of the antennae and antennule complex are to increase sensitivity to vibrations and chemical signals (Mejía-Ortiz *et al.*, 2006). Epigean crustaceans rely on both vision and olfactory cues for intraspecific interactions, feeding, and reproduction (Delgado-Morales *et al.*, 2004). Stygobionts rely only on mechanical and chemical inputs in the aphotic environment. Evidence from cenote Kankirixche shows *C. morleyi* sharply changing direction towards its prey at a distance greater than twice its body length, which is usually the length of the antennal flagellum (Creaser, 1936). We propose that the antennae and antennules are paramount for effectively sensing the prey and making the final precise approach to capture the prey.

*Creaseria morleyi* has been reported to exhibit cannibalism (Creaser, 1936; Hobbs & Hobbs, 1976; Iliffe, 1993), a behavior confirmed during our collections, when large individuals were observed eating smaller ones. Cannibalism could indicate a selection pressure in favor of rapid growth to a large size at the expense of a delay in reproduction, as reported in other cave crustaceans that reproduce at a larger size and older age (Cooper, 1975; references in Vogt, 2012). *Creaseria morleyi* could be an example for the size-refuge hypothesis (Paine, 1976). When small, the shrimp could be preyed on by its larger conspecifics or fish predators (in this case *Typhlosina pearsei* (Hubbs, 1938), *Ophisternon infernale* Hubbs, 1938, or *Rhamdia guatemalensis* (Günther, 1864)), but after it reaches a certain size it might lack any natural predators, thus becoming a top predator.

*Creaseria morleyi* has been observed feeding on bat and bird excrement, is known to be attracted to baited traps, and even feed on the cave fish *T. pearsei* (E. Sosa, pers. com.), although it is not clear if the fish was captured alive. There is therefore evidence the shrimp is a generalist that could act as an opportunistic scavenger. Our observations suggest that it can choose its prey depending on the relative predator-prey size; as the predator grows the targeted prey gets bigger as well. Multiple feeding strategies could therefore allow the shrimp to feed on a variety of prey and exhibit both predatory and saprophagous feeding as stated by E. Racovitza (in Culver & Pipan, 2013: 51), “many subterranean organisms are carnivores by predilection but saprophagous by necessity.”

Feeding behavior, previous reports of *C. morleyi* as a generalist predator (Pohlman *et al.*, 1997), and seemingly sensitive antennae and antennules could explain that this species is one of the largest crustacean anchialine predators. The low probabilities of prey encounters in most oligotrophic cave environments could have resulted in *C. morleyi* evolving behaviors that improve the likelihood of prey encounters, the ability to feed on a variety of prey species, an effective capture behavior, and possibly saprophagy.

Although our observations demonstrate that *C. morleyi* can attack, capture, and eat *Typhlatya* sp. and *A. cenotensis*, still the frequency of the predatory, saprophagy, and cannibalistic behaviors as well as the factors that trigger each remain unknown.

Future studies of stomach content, using genomic analysis or stable isotope food-web tracing, together with chemosensory experiments, underwater field observations using rebreathers or infrared cameras and lighting to avoid perturbation, will help elucidate how prey is captured and which types are most commonly captured and ingested by *C. morleyi*.

## SUPPLEMENTARY MATERIAL

Supplementary material is available in *Journal of Crustacean Biology* online and dryad.org (doi:10.5061/dryad.rv801).



S1 Video (first video sequence). *In vitro* experimentation, *C. morleyi* captures and feeds on a *Typhlatya* sp. individual in an aquarium (0:00 to 01:22).

S2 Video (second video sequence). *In situ* observation of *C. morleyi* capturing a small crustacean (possibly *A. cenotensis*) in the cavern area of cenote San Juan (1:24 to 2:27).

S3 Video (third video sequence). *In situ* observation of *C. morleyi* swimming with a captured *Typhlatya* sp. individual in its second pereopod chelae in the cavern area of cenote San Juan (2:28 to 2:53).

S4 Video (fourth video sequence). *In situ* observation of *C. morleyi* capturing a small crustacean (possibly *A. cenotensis*) in cenote Kankirixche (2:54 to 4:41).

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