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Replacement of the Troglomorphic Population of *Rhamdia quelen* (Pisces: Pimelodidae) by an Epigean Population of the Same Species in the Cumaca Cave, Trinidad, West Indies

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In 1926, Norman described the cave fish population in the Cumaca Cave of Trinidad, West Indies, as a new troglomorphic (blind/depigmented) genus and species, *Caecorhamdia urichi*, based on its reduction in eye size and pigmentation. Later studies indicated that this was just a cave population of the widely distributed epigean (surface, eyed/pigmented) catfish *Rhamdia quelen*. Beginning in the 1950s, a number of specimens were collected in the cave showing variability in eye size and pigmentation. In 2000 and 2001, we conducted field studies that included direct observation of individuals using infrared visual equipment (video cameras and night-vision goggles) and echo-sounders and also collected some individuals for behavioral research. We also examined all available specimens of the cave population that have been deposited in museums. Our results strongly suggest that the troglomorphic population has been completely replaced by the epigean one of the same species in as little as 50 years. We hypothesize that the most important reason for this replacement was the reinvasion of epigean individuals of *R. quelen* prompted by changes in precipitation regimes. Epigean individuals, because of their morphology, behavior, and ecological requirements, were well suited to outcompete troglomorphic individuals.

THE phenomenon of ecological replacement, particularly among living organisms, has received little attention. Most of the work pertains to native species being replaced by species introduced by humans (e.g., Harris et al., 1991; Lockwood et al., 2000). This lack of information is particularly evident in the case of both fishes and cave organisms. That may be a result of the fact that this phenomenon is difficult to demonstrate in nature (Long, 1996 and references therein).

Norman (1926) described *Caecorhamdia urichi* as the first troglomorphic (blind/depigmented) fish species in Trinidad, West Indies (W.I). This new genus and species was erected in the typological-essentialist philosophical framework of the 1920s and 1930s when every new cave species of fish was assigned a new generic status based solely on its troglomorphic features (blindness and/or depigmentation; Romero, 2001). Norman himself had pointed out the fact that "apart from the absence of eyes, this fish appears to be almost identical with *Rhamdia queleni*" [sic] (Norman, 1929:325). Mees (1974) considered this cave fish population as a subspecies of *Rhamdia quelen* and Silfvergrip (1996) just as a cave population of that species.

In 2000 and 2001, we conducted field observations of this fish in its natural environment which suggested that the original troglomorphic population had vanished, having been replaced by individuals of the epigean population of *R. quelen* (Romero and Creswell, 2000; Romero et al., 2001). Here we report what we believe is the first case of replacement of a troglomorphic fish population by its epigean ancestor.

Materials and Methods

The only cave in Trinidad inhabited by *R. quelen* is known by several names: Guacharo (Norman, 1926) and Oropouche or Urumaca (Darlington, 1995; Romero and Creswell, 2000), but based on our conversations with the inhabitants of the area during our last expedition, we concluded that locally it is now better known as the Cumaca Cave. The Cumaca Cave is located in the Northern Range of Trinidad, W.I., at 10°42'53" N, 61°10'29" W at an altitude of 185–215 m above sea level. It is a linear limestone cave with an emergent stream running its full length. During the day, fish are found only in the dark portion of the cave, that is, from about 15 m from the entrance all the way to where human penetration is possible. These fish feed, among other things, on the droppings of oil birds, *Steatornis caripensis* (Romero and Paulson, 2001), which provide a steady and abundant source of food. In the deepest part of the cave, the ceiling is occupied not by oil birds but by bats (Darlington, 1985). Bat guano has been found as a large proportion of the stomach contents of other cave fishes (Breder, 1942). Yet, it is known that epigean *R. quelen* are omnivorous but show preference to feed on other fish (Carvalho Gomes et al., 2000). This cave is located in a private property, and access is only possible through a special permit by the owner who also requires that appropriate government collecting permits be obtained. The fact that these fish are difficult to collect (as noted in Mees, 1974) suggests that with the exception of few scientific collecting efforts, this is a fish population that has been largely, if not almost entirely, undisturbed by humans.

We visited the cave once in January 2000 and twice in March 2001. Because preliminary observations suggested that all fish in the cave were strongly scotophilic (tendency to stay away from light, Romero and Creswell, 2000), for the 2001 visits we used infrared ("night vision") goggles (DIPOL-2MB) and a video camera (SONY HandyCam Vision CCD-TRV99) with infrared capabilities. We also used a fish echo-sounder (EAGLE Strata 128) to make sure that no fish in the cave escaped visual observation. All the fish detected by the fish echo-sounder were also observed using the night vision goggles, which lead us to believe that we were able to observe all individuals present in the cave at that time. Using infrared illumination, we not only observed the fish but also were able to determine that all of them were fully eyed, because of the strong reflectance of the infrared illumination from their tapetum lucidum. We explored the entire length of the cave using these devices and videotaped the fish. On 13 and 20 March 2001, we collected two and nine fish, respectively, using seine and dip nets.

All fish were carried back to a laboratory at the University of the West Indies in St. Augustine, Trinidad, where they were observed in an aquarium and photographed. They were measured to the nearest 0.1 mm using a digital caliper (Fowler NSK Pro-Max). None of the fish were sacrificed, and they are maintained in aquaria at the University of West Indies at St. Augustine. All the individuals captured by us were photographed using a regular 35-mm photographic camera and those from museum collections with a NIKON digital camera (DXM 1200) installed on a NIKON SMZ 1500 dissecting microscope at the Environmental Studies lab in Macalester College to carry out comparative analysis of their eye and pigment conditions.

We examined and photographed all known specimens of *R. quelen* from that cave that have been deposited at museums around the world (see Comparative Material Examined). We also included descriptions from unpublished sources such as J. Kenny (pers. comm.), descriptions of two specimens from Mees (1974), and observations of 20 individuals in the wild (Romero and Creswell, 2000), because no specimens of these samples have been deposited in museum collections. We classified eye condition as follows: (1) fully eyed: eyes externally visible; and (2) eyeless: the eyes were either sunken in the eye orbit socket or not visible at all. Pigment condition was classified as follows: (1) "normally" pigmented: pigmentation was not different in intensity from what could be observed in epigean *R. quelen*; (2) partially pigmented: pigmentation was somewhat intermediate between fully pigmented individuals and depigmented ones; and (3) depigmented: melanophores were totally or almost totally absent in these specimens. Then, we grouped these specimens into six morphs: eyed/pigmented, eyed/partially pigmented, eyed/depigmented, eyeless/pigmented, eyeless/partially pigmented, eyeless/depigmented.

To have a more quantitative approach to phenotypic differences among specimens collected, we measured every specimen following Silfvergrip's (1996) notation. We then divided the diameter of the orbit of the left eye (ORBL; there is some variation in orbit diameters between both eyes for the same specimens) by the SL of each individual and multiplied it by 1000. We tested the null hypotheses that the 2001 collections did not differ from earlier ones in terms of phenotypic characteristics (eyes and pigmentation) and that there had not been changes in the average of both SL and SL/ORBL through time. Finally, we analyzed all rainfall data from 1862 until 2000 (the last available data) to test the null hypothesis that no changes of precipitation had occurred through time.

Results

All individuals of *R. quelen* found in 2000 and 2001 at the Cumaca Cave are identical to the epigean form in terms of eye and pigment condition and do not show any troglomorphic feature (Fig. 1). This was further confirmed by the fact that ORBL/SL ratio increased over time (t-test, $P < 0.05$, Fig. 2), being very similar for all 2001 individuals. SL of individuals also increased over time (t-test, $P < 0.05$, Fig. 3), being very similar among all 2001 individuals. Rainfall changed through time (Spearman's correlation coefficient, $P < 0.05$) supporting the assump-

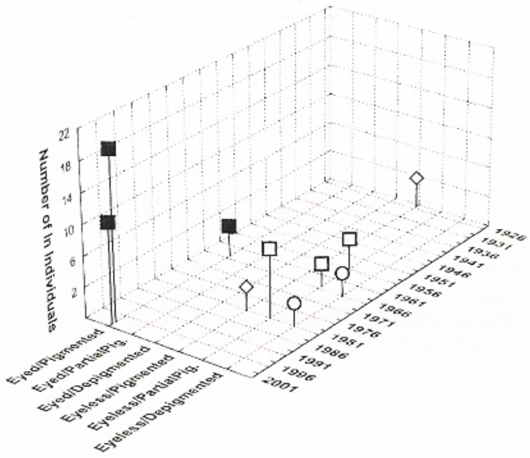

Fig. 1. Changes in cave *Rhamdia quelen* morphs through time. Solid squares = eyed/pigmented individuals, open diamonds = eyeless/pigmented, open squares = eyeless/partially pigmented, open circles = eyeless/depigmented.

tion that there had been a significant increase in rainfall over time (Fig. 4).

Discussion

Changes in phenotypic features among hypogean (cave, artesian) fishes are usually described as an increase in troglomorphism or the tendency to reduce or lose eyes and pigmentation (Romero and Paulson, 2001). Instances of increasing eye size and pigmentation among troglomorphic fishes under natural conditions have been reported only twice, in both cases for the characid *Astyanax fasciatus*, and they were the result of introgressive hybridization (Romero, 1983; Langecker et al., 1991).

Data represented in Figures 1 and 2, which show variability of both eye pigment condition and ORBL/SL ratio, suggest that hybridization between troglomorphic and epigean forms of *R. quelen* may have taken place at least between the 1950s and the 1980s. Similar patterns have been described for the *A. fasciatus* introgressed population at La Cueva Chica in Mexico (Romero, 1983). However, and unlike the La Cueva Chica population, no phenotypically intermediate individuals of *R. quelen* can be found at the Cumaca Cave today, which supports our contention that even if some hybridization occurred in the past, the 2001 cave population is largely (if not entirely) the result of replacement, not hybridization. Despite the fact that intraspecific variation of orbital width and eye diameter as well as pigmentation in *R. quelen* has been reported (Silfvergrip, 1996), the 11 individuals we collected in 2001 were very much uniform in eye and pigment condition as well as in their ORBL/SL ratio (Fig. 2).

Given that the epigean *R. quelen* as well as individuals of the current population in the cave

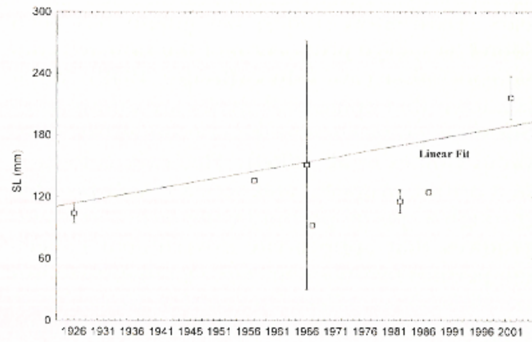

Fig. 3. Changes in SL length among cave specimens of *Rhamdia quelen*. The squares represent the average and the vertical lines the standard deviation.

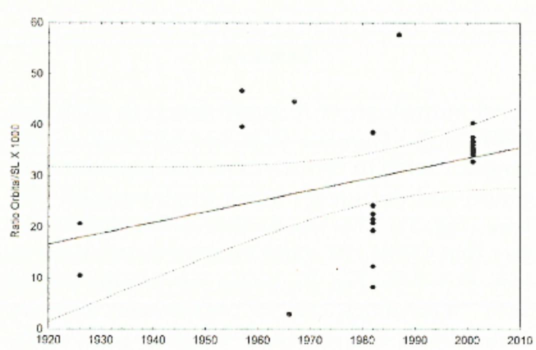

Fig. 2. Scatterplot of ORBL/SL ratios for all available specimens. The solid line represents the linear fit and the broken one the 95% confidence limit.

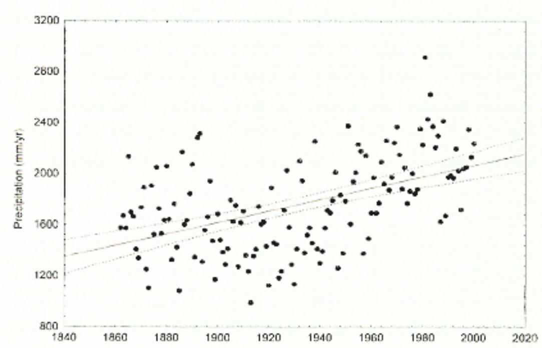

Fig. 4. Scatterplot of precipitation in Trinidad between 1862 and 2000. Solid line is the linear fit; broken lines are the 95% confidence limit (data extrapolated until 1952 from Wehekind and Smith, 1955, and since 1952 from unpublished data by the Trinidad and Tobago Meteorological Service).

are on average larger than the troglomorphic ones (Fig. 3), we hypothesize that the former out-competed the original troglomorphic population. Epigean *R. quelen* are nocturnal, have long barbels, can spawn several times per year, develop very fast (achieving sexual maturity within a year), and are omnivorous, with preference to eat fish (Carvalho Gomes et al., 2000). Therefore, it is not surprising that they have successfully colonized the cave environment and even replaced the smaller, troglomorphic *R. quelen*.

Obviously the cave was initially populated by epigean individuals of *R. quelen* that later developed into a troglomorphic population. A rapid evolution from an epigean population into a troglomorphic one is possible. Rasquin (1947) reported changes leading to troglomorphic features (particularly depigmentation) in epigean fishes when raised under conditions of total darkness. Experimental work with other fishes, has shown similar results (Rasquin, 1949). Reverse changes in pigmentation have also been observed among depigmented *R. quelen* collected at the Cumaca Cave once they are placed under conditions of light (J. Kenny, pers. comm.). To what extent those changes are genetically fixed among troglomorphic fishes is not known, but we do know that many troglomorphic fish populations achieved dramatic phenotypic transformations with very little genetic variation (affecting mostly a few regulatory genes; for some examples, see Romero and Paulson, 2001). If that is the case, then we should not be surprised that phenotypic plasticity plays a major role in the morphologies usually associated with life in dark environments, nor that *R. quelen* is an example of that. Silfvergrip (1996) found a great deal of intraspecific variation in *R. quelen* throughout its range, which he assigned to environmental factors. Variation in meristic characteristics as a result of environmental factors in fish has been well documented (e.g., temperature affecting meristic counts or Jordan's rule) and has been found to have a genetic basis (Billerbeck et al., 1997). How those changes become genetically fixed has yet to be ascertained for cave animals, but genetic assimilation has been proposed for explaining phenotypic changes in many organisms (for examples and full discussion on this subject, see Pigliucci, 2001).

On the question of what triggered ecological replacement, we believe that changes in climatological (rainfall) conditions were ultimately responsible for the morphological changes observed. According to the correspondence written by F. W. Urich, which accompanied the cave fish specimens he sent to the British Museum of Natural History, "It rarely happens but at times of heavy rains the pool can be connected with a rivulet running out of the cave" (unpubl.). If that was the case, the isolation of the pools inside the cave early in this century may explain the origin of the troglomorphic population. During our visit in March 2001, at the height of the dry season, the connection between the pools inside the cave and the outside rivulet was constant, with a flow of water of about 50 cm in depth, thus, permitting the movement of epigean fish into the cave. Our statistical analysis of rainfall (see Results) are consistent with our premise that after a prolonged drought early in this century, there has been a steady and significant increase in rainfall from 1862 until 2000 (Fig. 4), which is also consistent with the differences in the level of water connection described by F. W. Urich and the one we found. That increase in rainfall probably reestablished or reinforced the connection between the water inside and outside the cave. This, in turn, would have led to hybridization with the generation of intermediate morphs between troglomorphic and epigean *R. quelen* and later to the final replacement by epigean fish, which still today can freely enter the cave.

Future work should look into three areas to better understand the phenomenon reported here: (1) studies on fish movement into and out of the cave using both mark-recapture methods as well as long-term video recording devices; (2) experimental work to document phenotypic changes of epigean *R. quelen* when raised under total darkness; and (3) DNA analysis to discern sequence changes among samples collected at different points of time. This is feasible since most museum specimens have been kept in alcohol.

Comparative Material Examined

BMNH 1926.7.28:1, BMNH 1926.7.28:2, BMNH 1982.9.11:30, BMHN 1982.9.11:31, BMHN 1982.9.11:32, BMHN 1982.9.11:33, BMHN 1982.9.11:34, BMHN 1982.9.11:35, BMHN 1982.9.11:36, BMHN 1982.9.11:37, BMHN 1982.9.11:38, RMNH 26733:A, ROM 45113:A, ROM 45113:B, UWI.47, UWI.487, UWI 2001:1, UWI 2001:2, UWI 2001:3, UWI 2001:4, UWI 2001:5, UWI 2001:6, UWI 2001:7, UWI 2001:8, UWI 2001:9, UWI 2001:10, UWI 2001: 11. All these fish had been collected at the Cumaca cave. Institutional abbreviations are as listed in Leviton et al. (1985) except for the University of West Indies at San Augustine for which we used UWI.

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