

The Crayfish Snakes of North America

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Introduction

One of the greatest feats of evolutionary innovation, the amniotic egg, allowed vertebrate organisms more freedom from the aquatic environment by being able to place their eggs on land. Amniotes became a diverse group occupying a myriad of habitats around the globe. Over time, there have been multiple independent invasions of aquatic systems by terrestrial amniotes from a variety of taxa. Reptiles (the historically recognized group) are a diverse group of organisms with aquatic representative taxa on every continent except Antarctica. Within reptiles, the ophidia (snakes) are found all across the globe and in most aquatic habitats. There have been multiple invasions of both freshwater and marine systems by snakes in several families, and members of the subfamily Natricinae are found in many freshwater systems in North America.

The Natricinae is a group of snakes within the family Colubridae, and various species of natricines are found from Canada to Panama and from the Atlantic to Pacific coasts of North America. The terrestrial/aquatic habits within natricines vary from terrestrial to fully aquatic, and these snakes occur in virtually every habitat within their large range. The genera *Thamnophis* and *Nerodia* are particularly diverse, and among the most well studied snakes (for overviews of biology see Rossman et. al., 1996; and Gibbons and Dorcas, 2004). Members of the genus *Thamnophis* can be terrestrial, semi-aquatic, or primarily aquatic, whereas species of *Nerodia* are semi-aquatic to fully aquatic. The literature on these natricines is fairly vast and covers multiple aspects of their evolution and ecology. This research has increased our understanding of thermoregulation, chemical ecology and predator-prey interactions in aquatic systems.

Among aquatic snakes, one group has received relatively little attention by researchers and continues to provide interesting questions for future research. Crayfish snakes are a highly

specialized group of snakes that created controversy among systematists, intrigued biologists interested in chemical ecology, and provide an excellent opportunity for studying predator-prey dynamics for a highly specialized predator. Their almost exclusive diet of crayfish intimately ties these snakes to the health and integrity of aquatic systems. Here I present a brief review of the biology of crayfish snakes with an emphasis on their natural history and role as predators in aquatic systems. In this review, I also elucidate gaps in the knowledge of crayfish snakes and suggest some areas for future research.

Taxonomy and systematics

The genus *Regina* was erected by Baird and Girard (1853), and includes four species that are very similar in general morphology (e.g. dark dorsum and light venter, medium size, short robust skulls). In fact, distinguishing between these species in the field requires knowledge of distributions and habitat preferences and the few distinct morphological features. *Regina grahamii* (Graham's Crayfish Snake) has a lower head to body length ratio, and three rows of white scales on the lateral side of the body (Fig. 1), although the latter trait may vary. The Queen snake (*R. septemvittata*) is the only aquatic snake in North America with four brown stripes on the ventral scales. Unlike *R. grahamii*, *R. septemvittata* has two rows of white scales on the lateral side of the body (Fig. 2). *Regina rigida* (Glossy Crayfish Snake) has two rows of black triangular markings on the ventral scales (Fig. 3). There are two subspecies of *R. rigida*; the Delta Crayfish Snake (*R. r. deltae*) and the Gulf Crayfish Snake (*R. r. sinicola*). *Regina alleni* (Allen's Crayfish Snake) is the only member of the genus that has smooth dorsal scales (Fig. 4), and a quick examination for keels can distinguish this snake from the other species.

The obvious morphological similarities of the four species of *Regina* led to the conclusion that they were closely related. This relationship has been called into question with the advancement of molecular techniques for resolving phylogenies. Analysis of allozyme data (Lawson, 1985) was the first to indicate that the genus was potentially polyphyletic. This was further supported by the work of Alfonso and Arnold (2001), which used mitochondrial DNA to reassess the phylogenetic relationships of natricines. The most parsimonious tree recovered from an analyses of 28 species indicates that only *R. septemvittata* and *R. grahamii* are sister taxa while *R. rigida* is nested within a distinct lineage, and *R. alleni* is a sister group of nearly all natricines (Fig. 5). There is growing acceptance for the phylogeny recovered by Alfonso and Arnold, and it is almost certain that the genus *Regina* will be split, and two new genera of natricines will be erected.

Ecology and behavior

While all species of *Regina* are highly aquatic, there are slight differences in habitat use throughout the collective range (Conant and Collins, 1998; Gibbons and Dorcas, 2004), and areas of sympatry are restricted to small areas within the range of the genus (Fig. 6). The range maps for each species may reflect the ability (or lack thereof) to disperse through river drainage systems. Queen snakes are often associated with clear rocky streams and seem to prefer basking in trees over the water (personal observation). As do Northern Watersnakes (*Nerodia sipedon*), Queen snakes dive into the water when disturbed and often seek refuge under rocks in the stream. Glossy Crayfish snakes are often found in bottomland wetlands, and are occasionally seen in brackish water (Conant and Collins, 1998). It is possible that Allen's Crayfish snake has benefited from the introduction and spread of the invasive water hyacinth, which these snakes

often hide in (Gibbons and Dorcas, 2004). Graham's Crayfish snake is fairly restricted to permanent wetlands and slow moving streams (Conant and Collins, 1998).

As their name implies, all crayfish snakes feed on crayfish and vary somewhat in degree of specialization. *Regina septemvittata* and *R. grahamii* feed almost exclusively on softer bodied crayfish that have recently molted. In contrast, *R. rigida* and *R. alleni* are capable of feeding on hard and soft shelled crayfish, and it has been speculated that this is a consequence of differences in skull morphology (Gibbons and Dorcas, 2004). Crayfish snakes undergo an ontogenetic shift in prey selection with young snakes feeding on smaller macroinvertebrates such as grass shrimp and odonate larvae. These prey items are small enough for the younger snakes to ingest and provide more nutrition gram for gram than crayfish. As adults, the snakes switch to a diet consisting almost exclusively of crayfish.

Foraging on crayfish presents a couple of problems for crayfish snakes. All predators must locate their prey, and crayfish may often be in microhabitats that leave them less detectable and accessible. While snakes can use visual cues in prey detection, the use of chemical cues by snakes is well established and thought to be the primary mechanism for locating prey (Burghardt, 1970). It is likely that the chemosensory network of crayfish snakes is the primary sensory feature used in prey detection and location of crayfish. The species inhabiting aquatic systems with higher turbidity may not be able to see their prey very well, and crayfish hiding in burrows cannot be seen at all. Even for species inhabiting clear streams, crayfish are often concealed beneath rocks. Queen snakes can often be observed tongue flicking underwater and probing rock crevices. Neonate *R. grahamii* and *septemvittata* also exhibit stronger tongue flick responses to chemical stimuli of freshly molted crayfish than toward chemical cues of hard bodied crayfish and other macroinvertebrates (Waters and Burghardt, 2005).

In addition to finding prey, predators must subdue and consume their prey. Snakes have posteriorly curved teeth located in multiple rows in the upper jaw. These are well suited for securing a prey item once it is within the snakes mouth, however, crayfish are not readily swallowed head first. Snakes typically ingest prey head first, although some prey items can be swallowed in the opposite direction with relative ease. Crayfish however must be oriented in the opposite direction (Fig. 7), which could increase handling time leaving the snakes potentially vulnerable to predators. Herons, large fish, bull-frogs, and other snakes all prey on crayfish snakes and it is possible that selection has favored a mechanism for detecting the posterior end of prey that reduces handling time. Alternatively, prey might be carried to and ingested under some form of cover or refuge.

Physiology and reproduction

Few physiological studies have been conducted on crayfish snakes, and most of the available information concerns thermoregulation and feeding. Studies of *R. alleni* revealed that active foraging may be limited by suitability of water temperatures, and juvenile snakes feeding on odonate naiads had shorter digestion times than adults feeding on crayfish at a given body temperature (Godley, 1980). Other studies have demonstrated that higher body temperature is associated with increased locomotive performance (Finkler and Claussen, 1999) and metabolic rate (Butler, 1978) in *R. septemvittata*. Flight initiation distance, often used as a measure of anti-predator behavior, increased with increasing air temperatures as well (Layne and Ford, 1984). These thermal biology studies combined with observations of basking snakes indicate that *R. septemvittata* may be a more precise thermoregulator than some other species of *Regina*. For example, *R. rigida* is often reported to be a fossorial burrower that rarely basks, and this species

may conform to substrate temperatures rather than actively regulate its body temperature within a more narrow range.

Like other natricines, crayfish snakes are viviparous and give birth to live young contained within the soft amniotic sac. The young are born precocial, and receive no protection from the mother. It appears that each species of *Regina* breeds in the spring and parturition occurs in the fall (Gibbons and Dorcas, 2004). Clutch size for the genus ranges from 4-39, and average clutch size is highest for *R. grahamii* and lowest for *R. alleni* (Gibbons and Dorcas, 2004). Little information is available regarding courtship behavior, however, Tennant (1997) reported that some species of *Regina* exhibit mate balling behavior and that mating occurs in the water. In the laboratory, male *R. septemvittata* tapped females on the back of the neck as a form of courtship behavior (Ford, 1982).

Conclusions

The historical assignment of four species to the genus *Regina* does not reflect the actual evolutionary relationships of the members of this group and other natricine snakes. It appears that the genus is polyphyletic and should be split into three separate genera. The similarities in morphology observed among these species are a classic example of convergent evolution. This leads to an interesting question that would not arise under the old taxonomic assignment. Why has convergence in morphology (even in coloration) occurred in these snakes? Some of the similarities in skull morphology may be more easily attributed to the diet, but it is possible that these snakes have evolved under similar selective regimes with respect to predation. Perhaps natural selection via predation has led to convergence in color patterns that reduce conspicuousness.

Examination of the distribution maps for the four species of *Regina* reveals that some species have likely dispersed through river drainages following glacial retreat. No study has looked at the link between habitat use and dispersal ability of these snakes. Dam building and the creation of reservoirs may interfere with dispersal and gene flow, as well as taking away suitable habitat for the species requiring clear flowing streams. Another interesting observation is that there are no species of *Regina* in western Tennessee and Kentucky between the Mississippi, Tennessee, and Ohio Rivers. The use of GIS and surveys in this area could provide insights as to why this pattern is observed. It is possible that suitable habitat is not available in this region, however, there are many streams in this geographic area and many historically had crayfish.

Finally, the fact that *Regina* spp. feed exclusively on crayfish makes them more vulnerable to environmental perturbations. Environmental degradation that causes large declines in crayfish populations will surely lead to large declines in the number of crayfish snakes. Because many populations are localized and some species may have limited dispersal abilities, re-colonization may not be possible after extirpations occur. Local extirpations have already been observed for some species of *Regina* and more information about reproduction, habitat use, and population dynamics is needed to aid in conservation efforts. Studies that examine the anthropogenic impacts on streams and suitable prey (odonate larvae and crayfish) might provide insights into the absence of crayfish snakes in some regions. In addition, radio telemetry is a very useful tool in gathering basic natural history data and other information that is important for improving conservation practices. Long-term population studies would also be useful in understanding the population dynamics of crayfish snakes and their prey.

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Figures



Figure 1. The ventral and dorsal scales of *R. grahamii* are separated by a zig-zag pattern of black, and three rows of white scale extend up the lateral side of the body. (Google image search)



Figure 2. Queen snakes (*R. septemvittata*) are often observed basking in trees above clear rocky streams. Four brown stripes are present on the ventral surface, and two rows of white scales are present on the lateral side of the body. (Google image search)



Figure 3. The Glossy Crayfish Snake (*R. rigida*) has two rows of dark triangles on the ventral scales. This feature is sufficient to distinguish *R. rigida* from other species of *Regina*. (Google image search)



Figure 4. *Regina alleni* is the only species in the genus with smooth dorsal scales. (Google image search)

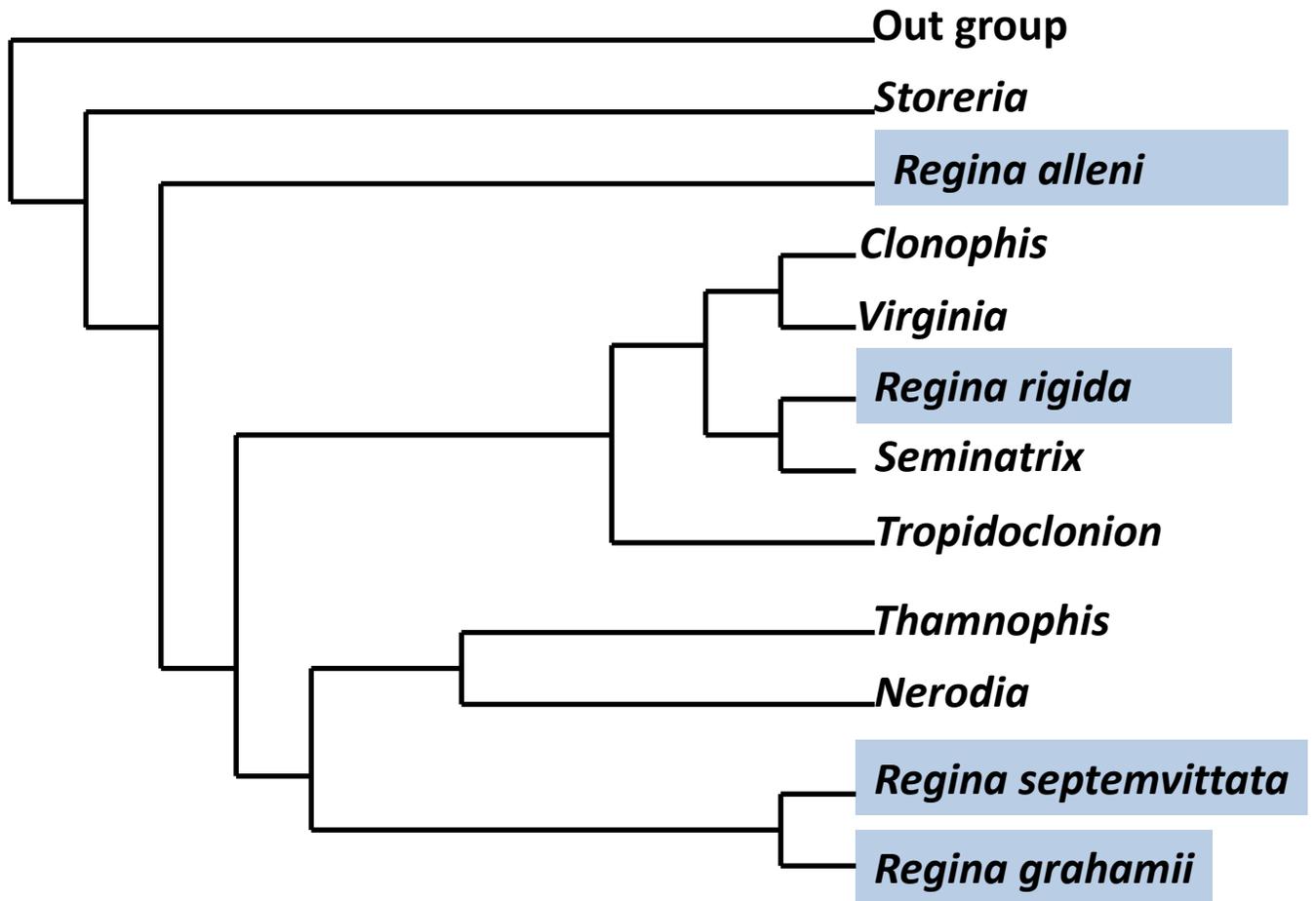


Figure 5. A highly simplified version of the most parsimonious tree recovered by Alfonso and Arnold, 2001 showing relationships among North American snakes in the sub-family Natricinae. The tree was constructed using mitochondrial DNA under topological constraints of the allozyme tree published by Lawson, 1985. Note the positions of the four members *Regina* which appears to be a polyphyletic genus.

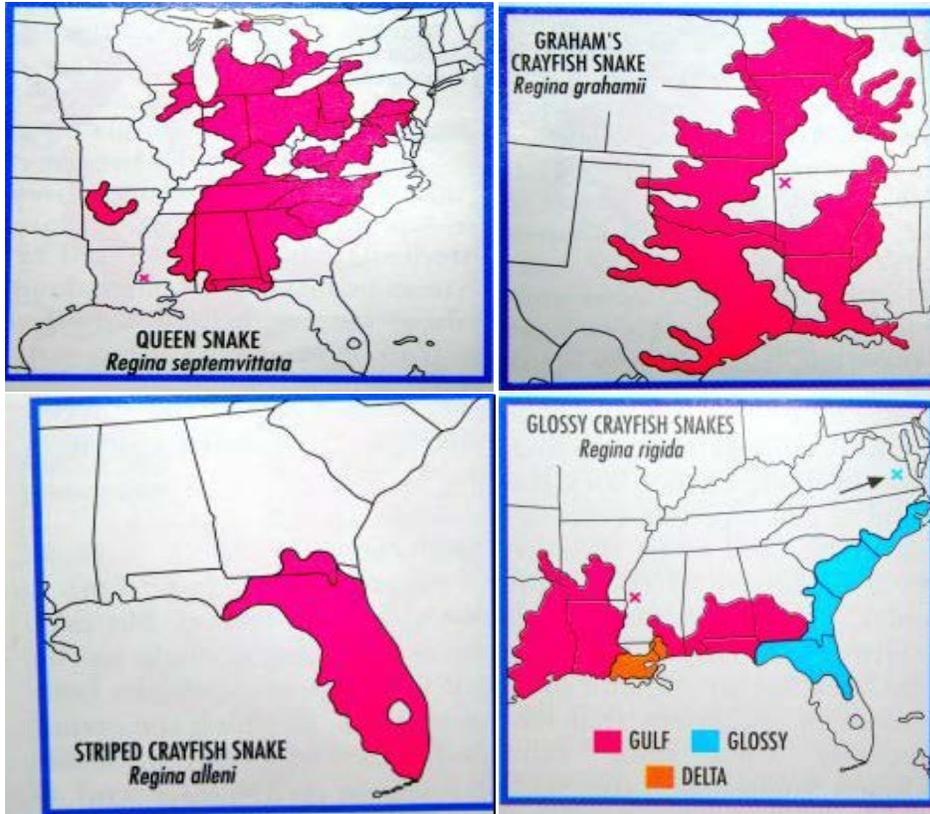


Figure 6. The four species (and associated subspecies) of *Regina* are distributed across most of the eastern United States. (Taken from Conant and Collins, 1998)



Figure 7. A Queen Snake devouring its prey tail first instead of the head first ingestion typically exhibited by snakes. (Google image search)