Natural History, Ecology, and Evolution of the Mexican "Axolotls"

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The Mexican members of the family Ambystomatidae (the axolotl and its relatives) have had a long, schizophrenic association with laboratory and field biologists. On the one hand, a large number of developmental biologists, geneticists, and endocrinologists utilize *Ambystoma mexicanum* as a convenient source of experimental material. On the other, a small group of field-oriented evolutionary biologists and ecologists share a fascination with the axolotl and its relatives as a keystone group for the study of developmental variation and its consequences for evolutionary biology. My goal in this contribution is to briefly summarize the current state of knowledge on the ecology and natural history of the axolotl and its relatives in Mexico. In so doing, I will briefly discuss the phylogenetic relationships of the Mexican ambystomatids, since this information is a necessary framework for many of the recent inferences that have been made on the ecology and evolution of metamorphosis in this group. At the end of the paper, I'll also briefly discuss what I feel are some of the major problems in the evolution of the group, with the clear "hidden" agenda of trying to stimulate more potential research interactions between the two rather separate groups of biologists working with axolotls.

Distribution of ambystomatid salamanders in Mexico

The Mexican ambystomatid salamanders comprise a group of about 17 currently recognized species confined to mid to high altitude regions of northern and central Mexico. The distribution of these taxa is reviewed in Shaffer (1983, 1984a); additional information and citations to original descriptions can be found in Smith and Taylor (1948), Brandon (1988), Brandon et al, (1981), and in several contributions to the Catalogue of American Amphibians and Reptiles.

Briefly, the mountains of Mexico form three distinct chains. In the west, the Sierra Madre Occidental is a large, continuous range extending from the U.S. border south to roughly Guadalajara in the state of Jalisco. There, the mountains merge with the Transverse Volcanic range, an east-west oriented group that extends to western Veracruz, at which point the mountains plunge off into the Atlantic lowlands. A third chain, the Sierra Madre Oriental, extends north along the eastern flank of Mexico to about Monterrey, at which point the mountains become a discontinuous series of basins and ranges that ultimately end in the Big Bend region of southern Texas.

Ambystomatid salamanders are found in all of these mountains above roughly 1600 m elevation. In the western Sierras, there are two currently recognized species. *Ambystoma rosaceum* is an endemic whose range is completely restricted to these mountains (Shaffer, 1983; Anderson, 1978). In addition, the wide-ranging tiger salamander, *A. tigrinum*, is found in this region, although its precise limits are still unknown (Shaffer, 1983, Van Devender, 1973). The eastern Sierras contain only the tiger salamander; its range apparently extends from the Transverse Volcanic range north to the vicinity of Saltillo in the state of Coahuila.

The Transverse Volcanic range is where things get interesting. In this region, all of the other 15 or so recognized species of ambystomatids from Mexico exist, and all of them (with the exception of the ever-present tiger salamander) are restricted to these mountains. The obligatorily non-transforming species are found here, and virtually all of them are further restricted to single lakes that dot the Mexican Plateau in the states of Michoacan, Mexico, the Distrito Federal (Mexico City), and Puebla. Thus, the Transverse Volcanic range, and the southern edge of the Mexican Plateau just north of these mountains, is the key area to study the diversity and ecology of ambystomatids.

Ecologically, this region is an amazing conglomerate of plant communities and micro-environmental situations. The southern Plateau is dry, semi-arid oak-scrub forest with occasional pines. This area, including the Valley of Mexico and Mexico City, also contains some of the most densely populated regions on earth, and necessarily brings humans and axolotls into intimate contact. Most of the region is under intensive agriculture, and apparently has been for a long time. Further up the mountains, there is a rapid transition to pine forest, with large lakes replaced by small, fast-flowing streams. These areas are less intensively used by humans, although their impact is still severe, especially in the mountains surrounding Mexico City.

Distribution and natural history of non-transforming ambystomatids

The distribution of non-transforming ambystomatids in Mexico is discussed in Shaffer (1984a, b). First, I should emphasize that the precise taxonomic distribution of metamorphic failure is not known for many of these species. In fact, it is probably the case that *all* of the Mexican ambystomatids (and in all likelihood, all members of the family closely related to the tiger salamander) at least occasionally fail to metamorphose and instead undergo larval reproduction. However, the following taxa routinely reproduce in the larval condition, and metamorphosis appears to be a relatively rare phenomenon:

SPECIES	DISTRIBUTION
A. andersoni	Lake Zacapu, Michoacan
A. dumerilii	Lake Patzcuaro, Michoacan
A. mexicanum	Valley of Mexico, Lake Xochimilco area
A. taylori	Lake Alchichica, Puebla
A. "tigrinum"	Several lakes in eastern Puebla

These lakes share a number of features in common. First, they are all large, relatively permanent bodies of water (or at least they used to be before the intervention of man). Second, they are situated in dry areas, and in many cases are the only permanent, aquatic environment in the region. And third, they all historically lacked large, predatory fishes (although this too has changed recently).

In general, the explanation that has gained widest acceptance for the high levels of metamorphic failure in this region has been that the lakes represent a stable, benign, aquatic habitat in the midst of a relatively harsh terrestrial environment. For ambystomatids, it appears that the simplest way to exploit these habitats is to avoid metamorphosis altogether, and to reproduce simply as axolotls. Apparently, this strategy requires a both stable and predator-free aquatic environment for long-term success (Shaffer and Breden, 1989; Sprules, 1974), making the Mexican lake system an absolutely unique natural "laboratory" in which to study the evolution and ecology of variation in metamorphosis. It is also an extremely fragile environment, and one that is under incredible pressure from an enormous and growing human population.

We unfortunately know very little about the ecology and natural history of these various non-transforming axolotls. My own observations, based on nearly a year of field work in Mexico over the past decade, suggests that the axolotls are generally the top predator in any given lake; ecologically, they are similar to a predatory fish. They appear to eat virtually any animal prey that they can capture, ranging from small, minnow-sized fishes to snails, crayfish, various small invertebrates, and conspecifics and other ambystomatids. If left undisturbed, they can reach incredible densities; in lake Atexcac in eastern Puebla, I have estimated adult axolotls to be at a density of roughly one per square foot of lake bottom, based on underwater SCUBA work.

The breeding biology and development times of most Mexican ambystomatids are not well known. Brandon's (1970) analysis of *A. dumerilii* from Lake Patzcuaro suggests a winter breeding season, and this is probably true for most taxa. My own quantitative genetics work on a population of *A. tigrinum* from Lake La Preciosa, Puebla also points to a December-January breeding season (Shaffer, 1986). In addition, several of the transforming taxa that I have maintained in my lab generally come into breeding condition in November or December.

Water chemistry and temperatures

The water chemistry and temperature requirements of these animals may be important both in understanding the conditions under which metamorphic failure has evolved, and for maintaining various species under laboratory conditions. Between 1978 and 1988, I have surveyed all of the known habitats of non-transforming ambystomatids in Mexico, and representative habitats of all of the transforming species. The following table provides the temperature, pH, and conductivity measures I have accumulated. Temperatures were measured several centimeters below the surface of the water, at least several meters from shore. pH and conductivity were measured with portable meters originally provided by the Axolotl Colony.

SPECIES	TEMPERATURE (C)	pH	CONDUCTIVITY
A. andersoni	15 - 20	7.8 - 7.9	91 - 225
A. amblycephalum	16 - 29	6.8 - 7.7	156 - 220
A. dumerilii	14 - 25	8.1 - 8.8	275 - 760
A. flavipiperatum	18 - 23	7.1 - 7.9	76 - 93
A. granulosum	16 - 18	6.5 - 7.3	200
A. lermaensis	28	———	———
A. mexicanum	16 - 20	7.4 - 8.2	975 - 1650
A. ordinarium	13 - 17	5.8 - 7.7	25 - 120
A. rosaceum	13 - 30	8.0 - 8.6	20 - 210
A. taylori	15	9.2	10,950
A. tigrinum	10 - 26	5.4 - 9.8	9 - 4050
Rhyacosiredon altimirani	14	———	———
R. rivularis	11	7.6	128

These values range from a single observation in one season to five values for a single body of water covering all seasons in multiple years, and from one locality for the non-transforming taxa to 21 localities for *A. tigrinum*. A few noteworthy points—the conductivity value for *taylori* is correct, reflecting the fact that Lake Alchichica is the saltiest lake in Mexico. In this case at least, the animals appear to require a high salt concentration, and do poorly in the lab in fresh water. The other values generally point to relatively broad tolerances for the transforming taxa, which makes sense given that their ponds are generally ephemeral and undergo tremendous changes as the season progresses and they dry out. The large lakes are generally more stable, although they too can fluctuate seasonally, at least close to the surface where I sampled them. The axolotls inhabiting these lakes move up and down the water column a great deal, so they probably experience the variation reported here as they feed, mate, etc. The relatively high pH of most of these bodies of water reflects the fact that most are internal drainage basins. Whether the salamanders *require* such basic water, or simply tolerate it, is an open question. However, it certainly may be that these high pH habitats buffer the water against the onslaught of acidification from air pollution, and have thus far protected the ambystomatid fauna from destruction due to acid rain.

Phylogeny of the Mexican ambystomatids

One of the major issues in the evolution of the Mexican ambystomatids has been the evolutionary consequences of variation in metamorphosis in the group. In particular, I have been interested in the importance of metamorphosis in mediating gene flow and rates of speciation. The results of these investigations are presented in Shaffer, 1984a, b; I will briefly summarize a few points of general interest.

The relationships of the Mexican ambystomatids, based on an analysis of 32 electrophoretically detectable allozyme loci, is presented in Figure 1. The phylogeny shows a number of points, including the questionable taxonomic status of several of the included taxa. Since this is ongoing research, I will not discuss it here.

One of the major conclusions to be drawn from this phylogeny concerns the evolution of metamorphic failure (which I term larval reproduction) among the Mexican ambystomatids. Basically, the analysis clearly demonstrates that *not all of the larval reproducing taxa are each others closest relatives.* Instead, non-transforming species are most closely related to geographically proximate transforming or polymorphic taxa. Using the phylogeny as a framework, I have been able to estimate the *minimum* number of times that larval reproduction must have evolved in this group. The answer is, at least four. In fact, a very reasonable scenario is that *every* instance of larval reproduction has been *independently* derived from a transforming or polymorphic relative. If this is true, it means that we have an amazing system in which to evaluate the ways that metamorphic failure has evolved by taking a comparative approach to the study of metamorphosis in these animals. It also means that each is unique—if one goes extinct, we cannot replicate it with another species.

One other point is of particular interest to those working with the laboratory axolotl. To establish the identity of the lab axolotl, I included one Wistar White animal from the Axolotl Colony in my analysis. If our understanding of the origins of this species is correct, it should cluster with the wild-caught sample from the vicinity of Mexico City. This is in fact the case; the lab axolotl is properly assignable to *A. mexicanum.*

Axolotls and man

As I mentioned earlier, humans and axolotls have had a long history of interacting with each other on the Mexican Plateau. Right now, many of the Mexican ambystomatids, and especially the non-transforming ones, are in serious jeopardy of going extinct in the wild. The precarious position of several species stems primarily from three main problems; draining or filling of lakes, pollution, and introduced predators. In addition, human collecting efforts for food is clearly putting pressure on the remaining populations. I will briefly summarize what I know of these issues, although a much more detailed research effort is clearly needed if we are to avoid losing some or all of these species in the very near future.

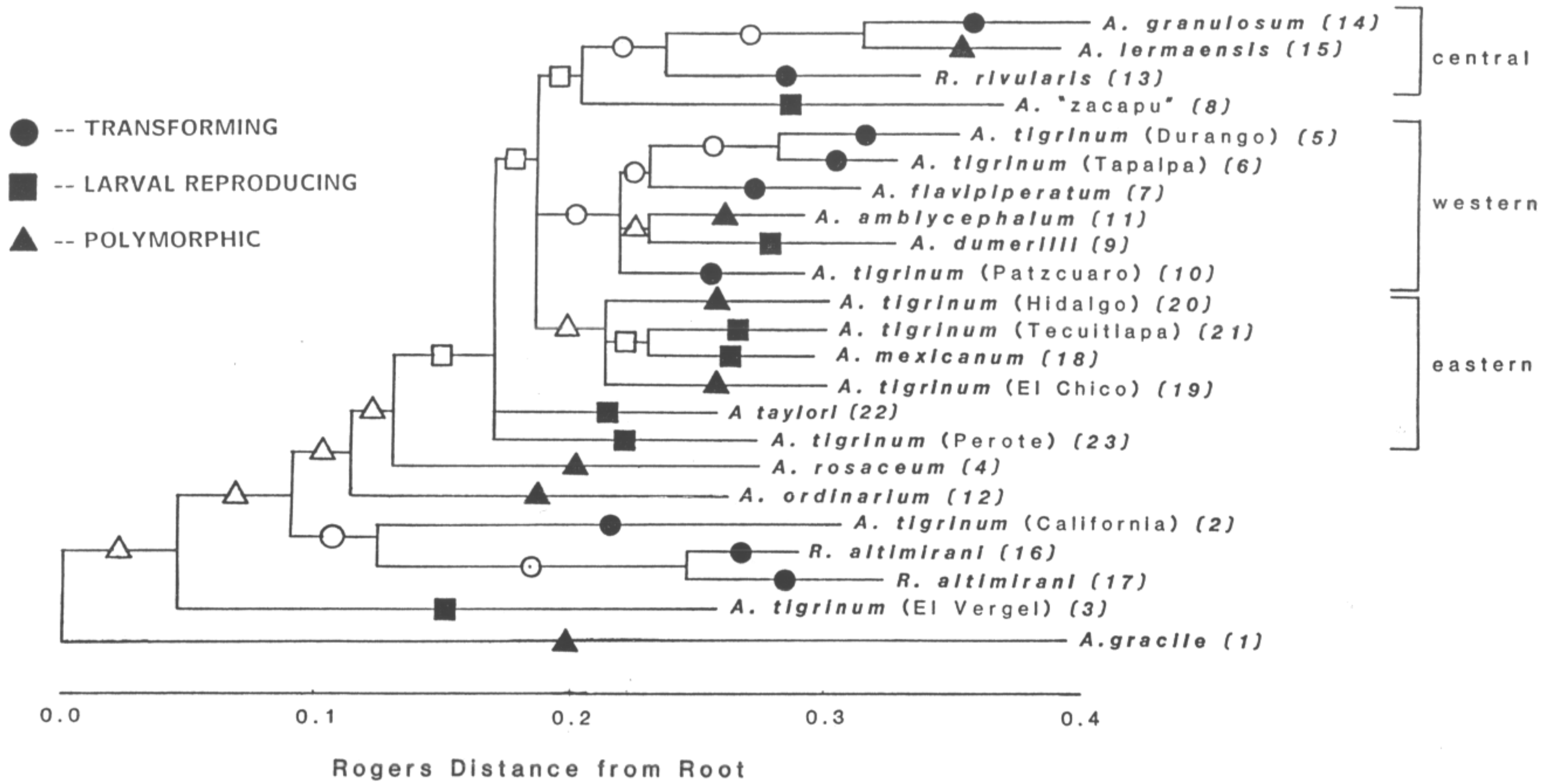

Figure 1. Phylogenetic relationships of the Mexican ambystomatid salamanders, based on a Distance Wagner analysis of 32 allozyme loci. The solid symbols reflect the metamorphic condition of populations, as measured in the field; open symbols are reconstructed conditions for ancestral populations. For details and additional references, see Shaffer (1984a).

Draining and filling lakes

This is certainly one of the major problems for all of the non-transforming species in Mexico. Lakes are drained for drinking water for Mexico City (Xochimilco, Zumpango, and Lerma are virtually gone), and the problem will only get worse as the human population of the Valley increases. Right now, *A. mexicanum* appears to persist in a few large ponds and in the canals that drain certain parts of Mexico City. These habitats are very polluted—if you work in them, it's a mystery how the animals can survive at all. However, given that they have made the transitions to these highly modified habitats, they may be able to hang on as long as they do not become too polluted. Lake Zumpango, previously home to *A. lacustris*, is now completely filled in and used for agriculture; presumably the species is extinct. Lake Lerma, just west of the Valley of Mexico, is a small remnant, but *A. lermaensis* still persists in it and the surrounding canals south of Toluca.

Other lakes that appear to be in reasonably healthy shape may not be. I have been told that Lake Patzcuaro is rapidly filling in due to erosion from agriculture—apparently the average lake depth is less than half of its former value. If this continues, *A. dumerilii* could be in very serious trouble.

Pollution

This is much harder for me to analyze, although it certainly appears to be a major issue over virtually all of the Valley of Mexico, the associated mountains, and many lakes to the west of Mexico City. Acidification has been shown to be a major source of mortality and developmental abnormalities in North American ambystomatids, and it eventually must start influencing the animals in Mexico. My very preliminary data suggest that the water is still quite basic, although I have no idea what the historical trends have been, or how this may have changed in the last few years. It is definitely a problem to contend with.

Introduced predators

In many lakes, humans have introduced game fish, either to encourage the tourist industry or as a source of food. This has been true in Lakes Patzcuaro, Aljojuca, and Quechulac, and in all cases, the consequences for the salamanders have been disastrous. According to locals, the Aljojuca axolotls are now extinct, although I have not confirmed this personally. The Quechulac animals are definitely quite rare, although the salamanders in Patzcuaro appear to be holding their own. While the precise dynamics of predatory fishes and ambystomatid salamanders is not clear (both can probably eat each other over certain size ranges), it seems that ultimately the salamanders probably lose out.

Research prospectus, and final remarks

Obviously, we have just scratched the surface of the Mexican ambystomatids as a research system. Numerous questions remain concerning the basics of the ecology and life history of the various species, their systematic status, metamorphic condition, etc. One area that I am particularly excited by is the opportunity to examine the molecular basis of metamorphic failure in the different taxa. Since the phylogenetic analyses suggest that metamorphosis has been lost independently several times, the question remains as to the molecular basis of this convergent life history pattern. Has the same point in the metamorphic pathway been blocked several times, or is each a new, novel genetic mechanism that gives a convergent result at the whole organism level? I am planning on pursuing this question in my lab in the near future.

Sadly, the future of the axolotls of Mexico is a grim prospect. The areas where they occur are under severe pressure from human exploitation, and the Mexican economy does not appear to be in a position to allow the luxury of major conservation programs aimed at protecting the animals and their habitats. Several of the species have been listed as protected, and there is an honest, intense effort by Mexican biologists to try to save the animals and their habitats, but it is a precarious situation. One partial solution may be to establish breeding colonies similar to the Axolotl Colony for other species, although this is clearly vastly inferior to protecting them in nature. All we can say at this point is that the future is unclear for many of these species, and that intervention and protection are needed, and needed soon.

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