

The Axolotl in its Native Habitat

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Experimental zoologists, accustomed to ready accessibility of axolotls for their studies, from numerous sources scattered worldwide, and to the relatively facile reproduction of the animals in captivity, are likely to assume that *Ambystoma mexicanum* is comfortably secure in its native habitat, where virtually everything worth knowing about its ecology and natural history has long been on record. After all, it is doubtful that any anamniote is better known in contexts pertinent to experimental study (e.g., anatomy, physiology, endocrinology, etc.).

Not so. The axolotl, *Ambystoma mexicanum* (Shaw), has suffered a severe diminution of its range in the past century, and is regarded as in danger of extinction in its native habitat (González et al., 1986:30). A permit is required for possession of wild-caught specimens—*i.e.*, not captive bred (Berger, 1981:105). Worse yet, virtually nothing is known of its ecology, natural history, and relationships with other members of the genus, at least in the detail essential for modern considerations.

At the time of Cortez' conquest of Mexico, the species is thought to have occurred throughout the large lake that occupied most of the Valley of Mexico, and that was more or less arbitrarily subdivided into at least six sectors, each named as a lake: Chalco, México, Texcoco, Xaltocán, Xochimilco, and Zumpango (fig. 1). Now the species is regarded as being restricted to the small canals that remain of Lago de Xochimilco, and to the minute remnant, Lago de Chapultepec (sometimes regarded as two lakes), of the former Lago de México. In both areas it is now reported to be rare, threatened by over-exploitation in the past, introduction of trout, and severe pollution (Lazcano et al., 1986:26-28, 37). Fossils have been reported from Cerro de Tlapacoya, bordered by Lake Chalco (Alvarez and Huerta, 1975), but separation from *A. tigrinum* is not conclusive.

There is apparently little danger of the species becoming extinct in the foreseeable future, because of its successful and abundant propagation in captivity. Not only do experimental and commercial centers maintain large stocks (see list of 31 in Axolotl Newsletter, no. 15, 1986:38-39), but as many as 12 zoos are reported to have bred them in 1982-3 (Olney et al., 1986:430), and at least 33 zoos possessed some examples in the period 1986-1988 (Slavens, 1988:162). More important, the species is so decimated in nature that even if it manages to survive there, its ecology and relationships may no longer be deciphered, and even if they can, they will inevitably reflect a very major influence of man; no known populations exist in a habitat not grossly altered by human influence.

Thus the problems of origin, relationships and unaltered (by man) ecology are probably no longer assailable by direct study. To a limited degree they can be inferred, but the laboratory of nature no longer exists where definitive answers lay.

The problems are not insignificant. If *A. mexicanum* actually did occur throughout the broadly continuous lakes of the Valley of Mexico 500 years ago, as presumed in Frost (1985), what was the status then of *A. tigrinum*, of which at least one subspecies now exists in the Valley (*A. t. velasci*, widely distributed; an unnamed cryptic subspecies sympatric with *A. mexicanum* may also exist; "*A. lacustris*" of Lago de Zumpango is now known to be inseparable from *A. t. velasci*, vide Brandon, 1989)? It would be somewhat iconoclastic to suppose that both differentiated after the various lakes to which they were later restricted became completely isolated from each other (although

selection pressures undoubtedly became very strong, and taxonomic differentiation can occur very rapidly through the "founder" principle, Mayr, 1963:529). Yet such a scenario seems highly likely, and suggests that all taxa of *Ambystoma* in the Valley of Mexico and its immediate environs are closely related, recent derivatives of *A. tigrinum*, even though that species possibly maintains its integrity in sympatry with *A. mexicanum*. However, sympatry in nature remains to be demonstrated; both species are marketed in Xochimilco (Dyer and Brandon, 1973:27-28; Brandon, 1977:437), but they may well have been collected in different areas. Sympatry means allospecificity, but does not preclude common origin; if geographic location of pre-*mexicanum* did not occur, some other isolating factor was involved, if indeed it is not in reality a subspecies of *A. tigrinum* (and is therefore not sympatric with it).

That *A. mexicanum* might ultimately be regarded as a subspecies of *A. tigrinum* (the International Commission on Zoological Nomenclature [1974:133] having decreed that *Salamandra tigrina* Green, 1825, is to have priority over *Gyrinus mexicanus* Shaw, 1798 [often erroneously cited as 1789; see Smith and Smith, 1973:221, entries 3641 and 3644, confirmed by reference to Sheborn, 1895:375] only when the two are regarded as conspecific) was anticipated by Wegner (1928:97), who adopted the onymorph *Ambystoma tigrinum mexicana* [sic] for the axolotl (nomenclaturally in error at that time, since the priority of *G. mexicanus* had not been waived in favor of *S. tigrina*). Indeed, concern for nomenclatural stability prompted the request for declaration of priority for *S. tigrina* if conspecificity with *S. tigrina* were accepted; enormous and totally unnecessary confusion would result otherwise. Although Collins et al. (1980) and Shaffer (1988) have pointed out that electrophoretically *A. tigrinum* appears to be a complex of genetically distinct species, the studies reported by Pierce and Mitton (1980) and by Jones et al. (1988) make it clear that taxonomically distinct, interbreeding populations of *A. tigrinum*, unquestionably of subspecific rank (not specific), may differ electrophoretically to such a degree that on that evidence alone they would be regarded as allospecific. Resolution of taxonomic status requires careful field studies in zones of contact of each subspecies with others.

A further complication in determination of the taxonomic status and origin of *A. mexicanum* is the fact that it is often confused with *A. tigrinum* and other taxa, even by those who might be expected to know better, including myself (Brandon, 1977:437, correcting my identification in 1970 of an *A. tigrinum* as *A. mexicanum*). However, the population of *A. tigrinum* that is usually represented in the Xochimilco market along with *A. mexicanum* does not resemble any recognized subspecies of that species; it is astonishingly similar to the axolotl in its dark appearance, whereas other subspecies in the area are light-colored, patterned or not, and commonly inhabit muddy waters. It is either a mimic or parallel of *A. mexicanum*—very likely the latter in parallel adaptation perhaps to originally clear waters (Herrera, 1891:76, 77 states that the larvae darken when exposed to light; he quite likely was dealing with *A. tigrinum* larvae, which are normally much lighter in color than those of *A. mexicanum*; Fernandez and Collins [1988] have confirmed correlation of color with substrate color and water transparency in *A. tigrinum nebulosum*; very likely both *A. mexicanum* and its sympatric subspecies of *A. tigrinum* evolved their dark coloration in adaptation to clear waters in at least parts of the original lake occupying the Valley of Mexico, before human overpopulation altered their habitat), since no known benefit is likely to have occurred from mimicry. The high altitude subspecies of *A. tigrinum (nebulosum)* in Colorado, also an inhabitant of clear waters, is similarly dark-colored.

But confusion of the two species has been frequent for many years, perhaps from the very outset of introduction of the axolotl to the scientific world in 1863 (Smith, 1989), when both species may have been represented in that first shipment of 34 animals to Paris. Certainly the specimens referred to this species by Diaz de León (1904) from Durango, Jalisco and Mt. Orizaba; by Dugès (1890) from Guanajuato; by Carr and Goin (1943) from km 224 SE of the city of Puebla; and by some current work-

ers in Mexico from various localities in the state of Puebla, are not *A. mexicanum*; most if not all are probably referable to some subspecies of *A. tigrinum*. Actual occurrence at Mixquic, D.F. (Feder et al., 1982), if the specimens were market-purchased and not field collected, and in Lake Chalco (Lazcano et al., 1986) are also suspect, since *A. tigrinum* is known from both areas, and no confirmed records exist for *A. mexicanum* there in this decade.

Not only is "*A. lacustris*" of Lakes Texcoco and Zumpango referable to *A. tigrinum velasci* (Brandon, 1989, who treats that taxon as a full species), but records of it from areas far distant, in Hidalgo (Singuilucan, Krebs, and Brandon, 1984; Laguna de Tecocomulco, 2500m, Lara, 1986) and Puebla (Rio Honey, nr. Honey, 2250m, Lara, 1986) probably also pertain to *A. t. velasci*.

Since the axolotl now occurs only where human alteration of its habitat is extreme, virtually eliminating any chance of deduction of original ecology, one might hope for some clues in the literature of past decades. Regrettably, that is not the case. In the some 4,656 works consulted dealing with *A. mexicanum*, incredibly not a single field study exists. All original works are based on laboratory observations. Four works by Mexican zoologists that come the closest are by Velasco (1879; translation by Kranz et al., 1971), Herrera (1891, 1900) and Calderón and Rodríguez (1986), but they too are basically laboratory, literature, or distributional studies. The only hope for meaningful field studies now lies in areas relatively free from human alteration, although at present none are confirmed.

Summary

Although field studies on *A. mexicanum* have never been undertaken, they are urgently needed in order to clarify its origin and relationships. Unfortunately the species is now so decimated and so besieged by habitat alteration that no meaningful field studies seem possible. The axolotl almost certainly is of common origin from what is now *A. tigrinum*, and may be a subspecies of it. Identification of populations outside of the canals of Xochimilco and Lago de Chapultepec are highly suspect and are probably misidentified *A. tigrinum*.

Acknowledgments

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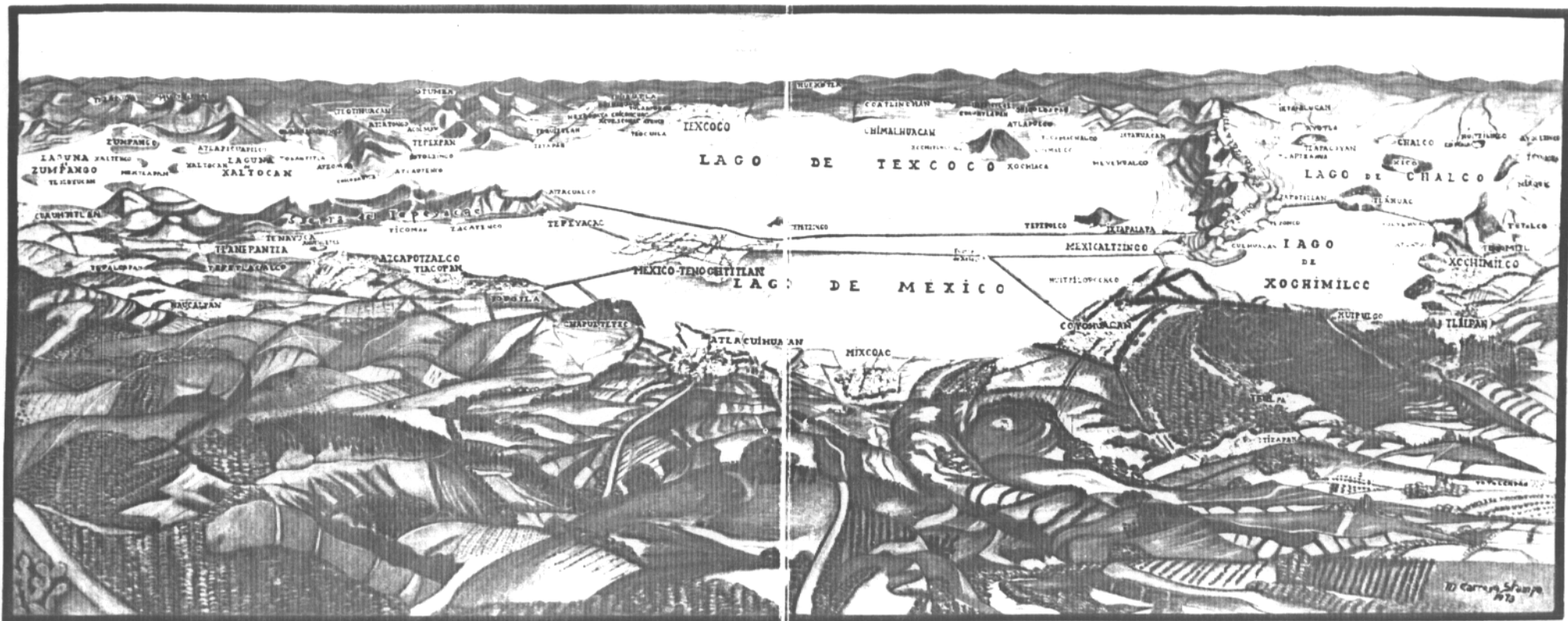
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Fig. 1. The lakes of the Valley of Mexico as depicted in 1519, looking east from its western escarpment. Modified from Rogelio (1985).



Interpretación de Manuel Carrera Stampa.
Según Cortés Díaz del Castillo, González Obregón y
los planos de A. P. Maudslayi, Ola Apenas y C. Castri.

MÉXICO-TENOCHTITLAN

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Area la cumbre del Valle de México vista desde el "Contadero" hacia el Este.