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Observations on Garter Snakes of the *Thamnophis eques* Complex in the Lakes of Mexico's Transvolcanic Belt, with Descriptions of New Taxa

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This report is dedicated to my late wife, Isabelle Hunt Conant, who was my constant companion during our full year of peregrinations throughout Mexico. Her presence has caused me to use the plural pronouns “our” and “we” many times in my text. She shared our hardships, hazards, and triumphs. She ran the camp, tended to our culinary needs, photographed habitats and living examples of our catch, including all the photographs that appear in this publication, and helped in too many ways to list. This analysis of the garter snakes of the *Thamnophis eques* complex across Mexico’s transvolcanic belt would not have been possible without her constant and enthusiastic support. We were pair-bonded and always acted as one. I deeply regret that she did not live to see this opus, the result of our joint efforts.

ABSTRACT

There are many isolated endorheic lakes in the transvolcanic belt of Mexico, which are the result of volcanism or extreme flooding. Organisms living in the lakes have had ample time to differentiate, and endemism is well known and documented, especially among the fishes. Other organisms also show endemism, including salamanders, crayfish, and even birds and mammals. The same is true for the garter snake, *Thamnophis eques* (Reuss). Seven new subspecies are described in this paper, each from a different lake or from the remnants of a former large lake. Based on morphological differences in coloration and pattern, they are *Thamnophis eques cuitzeoensis* from El Lago de Cuitzeo, *Thamnophis eques patzcuaroensis* from El Lago de Pátzcuaro, *Thamnophis eques insperatus* from La Laguna de Zacapu, *Thamnophis eques obscurus* from El Lago de Chapala, *Thamnophis eques diluvialis* from Las Lagunas Atotonilco and Cajititlán and several isolated localities, *Thamnophis eques scotti* from El Lago de Magdalena, and *Thamnophis eques carmenensis* from La Lagunilla del Carmen. Among six of these, series of specimens were collected and studied in detail. The seventh (*insperatus*) is known only from a single imperfect individual.

RESUMEN

Hay muchos lagos endorhéicos en el cinturón transvolcánico de México, que son el resultado de vulcanismo e inundaciones extremas. Los organismos que viven en los lagos han tenido un tiempo amplio para diferenciarse, y el endemismo ha sido bien documentado, especialmente para los peces. Otros organismos también exhiben endemismo, entre ellos, salamandras, langostinos, e incluso aves y mamíferos. Lo mismo es cierto de la culebra ranera, *Thamnophis eques* (Reuss). Siete nuevas subespecies se describen en este papel, cada una de un lago distinto o de los remanentes de lo que fue un gran lago. Basado en diferencias morfológicas de coloración y patrón, estas son *Thamnophis eques cuitzeoensis* de El Lago de Cuitzeo, *Thamnophis eques patzcuaroensis* de El Lago de Pátzcuaro, *Thamnophis eques insperatus* de La Laguna de Zacapu, *Thamnophis eques obscurus* de El Lago de Chapala, *Thamnophis eques diluvialis* de Las Lagunas de Atotonilco y Cajititlán y varias localidades aisladas, *Thamnophis eques scotti* de El Lago de Magdalena, y *Thamnophis eques carmenensis* de La Lagunilla del Carmen. De cada una de seis de estas subespecies, una serie de ejemplares fue colectada y estudiada en detalle. La séptima (*insperatus*) es conocida de un solo ejemplar en mal estado.

INTRODUCTION

In essence, this is a historic review of some of my work on natricine snakes in Mexico. Beginning in 1949 and continuing through 1965, my late wife, Isabelle Hunt Conant, and I undertook fieldwork with the objective of studying geographical distribution and speciation among the water and garter snakes of the genera *Natrix* (= *Nerodia*) and *Thamnophis* inhabiting Mexico. Our 10 trips were mostly lengthy, but they varied in duration from a few days to more than two months; in all, we spent a full year in the field in Mexico. We visited all 31 states and the Federal District, and amassed a large representative collection of both genera that was deposited in the herpetological collection of the American Museum of Natural History.

During our peregrinations in Mexico we

did fieldwork, chiefly in the early 1960s, at a number of lakes in or close to the transvolcanic belt, including Alchichica, Atotonilco, Cajititlán, Chapala, Cuitzeo, Pátzcuaro, Yuriria, and remnants of Magdalena and Toltcingo. We also briefly explored the highly saline and nonproductive Laguna Sayula, but we failed to reach the lagunas San Marcos and Zirahuén because their access roads were choked by deep mud. We visited what was left of Texcoco and Xochimilco, and planned to return to all those areas and as many other lakes as possible. After our 1965 expedition, however, my administrative duties at the Philadelphia Zoo increased so enormously that we were unable to visit Mexico again, except for a brief vacation excursion to Creel and the Barranca del Cobre in the state of Chihuahua.

A number of papers based on our activities

in Mexico have been published, as well as those listed in the References. The most thorough was a monographic review of the water snakes (Conant, 1969). Similar lengthy contributions on *Thamnophis eques*, *T. melanogaster*, and *T. rufipunctatus*, three species of garter snakes that occupy the water snake niche over wide areas of Mexico, were contemplated, but I was forced eventually to abandon them because of lack of time. The extraordinary variations in coloration and pattern of the populations of *T. eques* in the lakes of Mexico's transvolcanic belt have continued to intrigue me, however, and I herewith summarize many facts about those snakes and their environments, the lakes that vary greatly from one another.

Because our fieldwork in the many isolated lakes, or remnants thereof, was terminated in the 1960s, I am nearly 40 years in arrears. It would be helpful to return to Mexico, but current restrictions concerning collecting and personal physical handicaps preclude any resumption of the activities that Isabelle and I endured and enjoyed so many years ago. Further, the lakes are under severe anthropogenic pressure. More water is being diverted for human use from many; others suffer from pollution, including the inflow of raw sewage, silting, the development of eutrophic conditions, and the introduction of exotic species of fish. Alterations in the environment were evident to us in the 1960s, but they are continuing with increased velocity (Chacón, 1993; León and Escalante, 1993; Lyons et al., 1998; Flores-Villela, personal commun.).

From the above circumstances, it became apparent that I should prepare this paper as though it were written a few years following our fieldwork, and in a style then prevalent. After much thought and consultation with several colleagues, I decided to compile the following text, in part, as a historic record based almost exclusively on our own abundant material and other specimens in the American Museum collection. I have chosen to consider the new taxa described below as subspecies, even though I can demonstrate morphological intergradation in some instances but not in others. They are obviously closely related (see The Species Model). The use of subspecific names for the taxa I de-

scribe herein was widely accepted three decades ago. Several herpetologists have eschewed subspecies in recent years, but the status of that category has been restored by a blue-ribbon "Standard Names" committee sanctioned by the Society for the Study of Amphibians and Reptiles, the American Society of Ichthyologists and Herpetologists, and the Herpetologists' League (Moriarty, 2001).

Descriptions of the lakes and their environments where we collected reflect conditions as they were during the early 1960s, although I have added some recent information.

PROCEDURES

It was our practice, while in the field, to preserve most material in formalin for later transfer to alcohol. The largest and most photogenic snakes and all gravid females, however, were transported alive to our bases at the Philadelphia Zoological Garden and the spacious study in our residence. At the latter, portrait photography could be done under studio conditions. Both at home and in my office at the zoo, I maintained series of cages where the snakes were observed and where young were born. Neonates were weighed and measured as soon as possible. Many also were photographed, and pertinent details, including coloration and pattern, were recorded. Incidentally, live captives, whenever possible, were preserved immediately after shedding their skins in an effort to reduce shedding in the bottle and loss of scales, when the snakes needed to be handled at later dates.

INSTRUMENTS USED FOR RECORDING DATA

We recorded temperatures of air, water, and snakes, as well as the relative alkalinity of the lakes and other bodies of water where we worked. Because I briefly summarized our methods and procedures previously for water snakes, *Natrix* = *Nerodia* (Conant, 1969: 127–128), I quote as follows:

Temperatures were obtained through the use of quick-recording thermometers distributed by the Schultheis Corporation of Brooklyn, New York. Water temperatures were usually noted at a depth of one or two inches beneath the surface. Air temperatures were taken within one foot of the surface and shaded, if necessary, by my own shadow. Most were recorded

at night, and care was taken to make sure the instrument was perfectly dry so the reading would not be affected by evaporation. Temperature of a snake was made by inserting the bulb in the cloaca and keeping the fingers as far removed as possible in order to negate heat transfer from them to the body wall of the live snake and secondarily to the thermometer.

Power of hydrogen readings were obtained through the use of a pHydron paper dispenser (AB pH 1-11) manufactured by the Micro Essential Laboratory, Inc., Brooklyn, New York.

All snake temperatures were taken as quickly as possible after capture. Because garter snakes are chiefly diurnal, air and water readings were made virtually simultaneously during daylight hours.

Unless otherwise stated, lengths of specimens are total lengths. In those with incomplete tails the numeral is followed by +.

ILLUSTRATIONS

Isabelle took many black-and-white field pictures and studio close-ups of snakes and other amphibians and reptiles we collected. We had experimented in depth with color film while working on our field guides during the 1950s and 1960s, but found it unsatisfactory. Pictures or slides returned to us from commercial developers were invariably off-color. The enormous recent improvements in film, lenses, cameras, and especially the skill of developers were not available to us at the time we were working in Mexico. Isabelle executed the color plate that accompanies this report by using the same technique of applying watercolor dyes to toned black-and-white prints that she employed in our field guides (Conant, 1958, 1975). All illustrations herein, unless otherwise credited, are by Isabelle Hunt Conant.

Colors were recorded from live snakes, or more frequently from specimens that had just been euthanized but before they were preserved. Care was taken to avoid snakes approaching ecdysis. I recorded the colors in my notes or wrote them on photographic matte prints of the animals involved. Specific color names are from the 1115 swatches published by Ridgway (1912).

Illustrations of each taxon are noted below the appropriate new names. Also included for quick orientation are references to pertinent maps or habitat pictures. An exception involves the Laguna Yuriria in which there is

an intergrading population, and the reference to figure 4 follows the name of the lake.

PROBLEMS

It was our practice to photograph samples of each population of *Thamnophis eques* as soon as possible after our return from Mexico. It could be done quickly and easily in our home studio. I often preserved such specimens as soon as we knew we had good pictures. Sometimes the AMNH numbered tags did not arrive for weeks, and because we always had series of adult specimens and cage space was at a premium, I could not always be sure which number was assigned to the animal portrayed. That proved embarrassing when it came time to prepare the figures to accompany this report. In an effort to remedy the situation I examined dozens of preserved specimens, usually in vain because of look-alikes and postmortem changes. As a result, the AMNH numbers are missing from several specimens shown on the illustrations. Sex, locality, and live lengths are included for all, however, inasmuch as those data were typed on the negative holders.

Another problem arose because we took all gravid females back alive with us. These gave birth to their litters and several adults were kept alive for observation, often with live males, and they bore young again in subsequent years. As a result, we eventually had a plethora of neonates of a few taxa (207 of the population named herein as *Thamnophis eques diluvialis*, for example). It was futile to tag and make scale counts on all of them. So there are a number of untagged neonates in the AMNH collection, but most of them bear locality data and dates.

My unexpected major chore of having to take over the management of the Philadelphia Zoological Garden as acting director immediately after our return from Mexico in 1965 prevented my close attention, as in previous years, to the snakes I kept alive. Inevitably, some data were lost, as well as a female that had given birth to young.

Whenever we stopped in Mexico near villages we invariably were joined by small boys who seemed to be drawn to us as though we were magnets. Some, especially along the highways, were looking for *pro-*

pinas (tips) in exchange for favors—helping to change a tire, for example. Farther away, they sensed adventure and stayed with us for hours. Sometimes we could put them to work doing minor chores, but when they joined us at night while we were snake hunting they could be unmitigated nuisances. That was the case when two boys spoiled my once-in-a-lifetime chance to study a ball of snakes near Magdalena, Jalisco.

USE OF THE NAME *THAMNOPHIS EQUES*

The taxonomy of the garter snakes was long confused, partly because many of the species are similar in appearance and scutellation, and partly because many of the early museum specimens were in such poor or faded condition that it was difficult to study them. Some early workers, including G.A. Boulenger, according to Smith (1951), even lumped together several closely related species and subspecies from the southwestern United States and Mexico.

Hobart M. Smith, long a leading authority on Mexican herpetology, validated *eques* as the proper specific name by resurrecting *Coluber eques* Reuss, described in 1834. Smith's (1951) conclusion was accompanied by a reproduction of a photograph of the type specimen labeled, in part, "Senckenberg Museum, No. 7209a". That number has since been changed, as I discovered while on a tour of European zoos. I spent November 8, 1967, examining natricine snakes at the Senckenberg Museum in Frankfurt am Main, Germany. The type, an adult female, is now SMF 17179. In the bottle with it was a loose tag bearing the following: "F.A. Dillenburg, d. 1832 (Bttgr. Kat. 7209a)". There were also two male paratypes (SMF 17180, 17181) with the same accession data as the holotype.

Konrad Klemmer, custodian of the Senckenberg collection, stated that determining the provenance of the type is impossible. Dillenburg was a casual (commercial?) collector. The best guess is that, at the early date of 1832, the snakes may have come from Mexico City or were shipped from there after being obtained elsewhere.

My notes on the three type specimens of

eques are summarized briefly as follows: Holotype soft and end of tail missing (head-body length 639 mm). Body shriveled in SMF 17180. In both males, the tail tip had been desiccated in life and subcaudals were uncountable (head-body lengths 509 and 539 mm, respectively). Maximum number of dorsal scale rows 21 in all three snakes. Ventrals 153 in the female holotype, and 164 and 167 in the males, respectively. Pale lateral stripe on third and fourth scale rows, only third row posteriorly. Pale middorsal row occupying vertebral and most of the paravertebral rows on both sides of the body.

Rossman et al. (1996: 171, 175) reviewed the synonymy and commented on the variety of names that were applied over the years to the species of garter snake now known as *Thamnophis eques*.

If time had permitted, I had intended to search for color and pattern characteristics among our live and freshly preserved material to assist in separating *T. eques eques* from *T. eques megalops*. They are now recognized as two subspecific forms solely on the basis of ventral and subcaudal counts that widely overlap (Smith, 1942: 115). Smith discussed them under *Thamnophis m. macrostemma*, now a synonym of *eques*.

THE SPECIES MODEL

Thamnophis eques is a relatively large garter snake that attains a known maximum length of 1216 mm (a female from the Lago de Chapala). It is widespread in Mexico, ranging from the vicinity of the Pico de Orizaba northwestward to and through Sonora and Chihuahua to Arizona and New Mexico. Rossman et al. (1996: 173) mapped the range and showed disjunct colonies in Oaxaca and Nuevo León.

Rossman et al. also indicated the ranges of the subspecies heretofore recognized. *Thamnophis eques eques* occurred to the south and southwest, and *T. e. megalops* throughout most of the rest of the range. The third subspecies, *T. e. virgatenuis*, was described by Conant (1963: 490) as a dark snake with an exceptionally narrow middorsal stripe; apparently it is confined to the highlands of Durango and Chihuahua.

As the title implies, we are concerned in

this paper with *Thamnophis eques* and its relationships to the lakes of Mexico's transvolcanic belt, lakes that because of volcanic activity, extraordinary flooding, and isolation under endorheic conditions for millions of years offer a wide variety of habitats. Speciation has been widespread. My studies, based on scale counts of more than 600 specimens and copious notes on coloration and pattern, reveal that scutellation is more or less constant, whereas the snakes, even in lakes that are fairly close together, look very different. I have seven new taxa to describe.

To avoid repetition in the descriptive matter below, a hypothetical *Thamnophis eques* is herewith created based on specimens from Mexico's transvolcanic belt, but none of which is associated with any of the lakes, endorheic or otherwise. This should be considered as the "model" of a typical *Thamnophis eques* of the region. Describing its scalation and pattern characteristics will serve to avoid writing details over and over again that are applicable to all members of the species. The composite description follows.

SCUTELLATION: Nine crown scutes (paired internasals, prefrontals, supraoculars, and parietals, and a single frontal). Rostral wider than high and barely visible from above. Two nasals, the anterior bearing the nostril entirely within it. Loreal subtrapezoidal, about as wide as high. One preocular; 3 postoculars. One temporal anteriorly; 2 posteriorly. Supralabials 8, sixth and seventh largest, fourth and fifth entering orbit. Infralabials 10, sixth the largest, and first pair meeting on the mid-ventral line; first five on each side in contact with the corresponding chin shield. Two pairs of chin shields, the posterior longer than the anterior.

Dorsal scales carinate throughout the length of the body and most of the tail; keels weak on the first row of scales on each side of body. Apical pits, if present, are most apt to be found in the nuchal region. Scale rows most frequently 21–19–17. Anal plate single (undivided). Ventrals variable, subcaudals variable, and total and tail lengths variable.

Whereas the scutellation is relatively similar in the separate populations, coloration and pattern vary distinctly from one lake to

another. They are described in detail for each taxon.

PATTERN: A few more or less constant pattern details are as follows: When three pale longitudinal stripes are present, the central one occupies the middorsal row of scales and parts of adjacent rows depending on the subspecies involved. The lateral stripes occupy scale rows 3 and 4 anteriorly and rows 2 and 3 or row 3 only posteriorly. Small paired yellowish parietal spots. Labials whitish or yellowish, the sutures of the labials black. A yellowish crescent two scales wide posterior to the temporals, followed posteriorly by a black semicrescent two scales wide. When markings are present between the light stripes they are usually black or dark brown, paired but variable in size and position. Venter often gray. A black crossline at the base of each ventral, but hidden or not by the overlapping preceding scute. Underside of tail, chin, and throat whitish or yellowish and unmarked. Anal plate similar in coloration or same color as venter in general.

In the descriptions of holotypes in the text below all scutellation features are the same as those in the hypothetical specimen, except as indicated. Patterns and coloration are described in full.

MEXICO'S TRANSVOLCANIC BELT

A high mountainous volcanic belt crosses southern Mexico from the Pacific Ocean to the coastal plain of the Gulf of Mexico. On the north it is bordered by the *altiplano* (high plain) and on the south by the Balsas–Tepalcatepec Depression. It approximates 900 km in extent from east to west, and is 130 km wide in the vicinity of Tepic, Nayarit. It swings southward to include the Nevado and Volcán de Colima, then narrows and extends eastward roughly near the 19th parallel of north latitude. The belt is highly irregular in shape, however, and has a northward extension that includes the towering Popocatepetl and Iztaccíhuatl southeast of Mexico City. The belt terminates in the east at Citlaltépetl (Orizaba), the highest mountain in Mexico, but with an extension north to the Cofre de Perote. East of those two peaks is a Gulf Coastal Plain of variable width.

The transvolcanic belt, designated as the

Cordillera Neo-Volcánica by Tamayo (1949, I: 368), is a rugged region, the highest in Mexico, with snow persisting on the tallest peaks during and after the rainy season and sometimes year round. In an accompanying infolded page, credited to Ramiro Robles Ramos, Tamayo showed a profile of the Cordillera, a cross-section giving elevations of the highest volcanos and also indicating a few cities and high-level lakes. (This profile was reproduced on page 29 of the *Atlas Goodrich Euzkadi*, Caminos de México, 1964, 1966.)

There are fertile valleys occupying many parts of the transvolcanic belt, but volcanos of various sizes dominate much of the region. The Volcán Parícutin erupted in a farmer's field in 1943. At one point on the east-west highway across Michoacán there is an overlook called Mirador de Mil Cumbres (a thousand peaks). Volcanism created many lakes with interior drainage, and it was to them that we directed a large part of our field studies on *Thamnophis eques*.

I could be spared from my duties at the Philadelphia Zoo chiefly in late summer. That coincided with the rainy season in the transvolcanic belt when amphibians and reptiles were most frequently in evidence. Often it meant, however, that we and they were exposed to intermittent cold rains, especially at high elevations, such as at the Lago de Pátzcuaro at 2035 m.

INTERNATIONAL INTEREST

The transvolcanic belt of Mexico has long been an important topic for scientists of many disciplines both in North America and Europe. A considerable number of their papers are cited in the following text, particularly those originating on this continent. European interest is reflected by the two contributions of Alcocer et al. (1997, 1998), of which one was printed in the Netherlands and the other in Stuttgart, Germany. The paper by Metcalfe et al. (1994) came from the United Kingdom, and that by Tricart (1985) from Strasbourg, France.

During the 1940s and thereabouts it was fashionable to create biotic provinces based on genera, families, or groups of animals or plants. To cite two examples, Moore (1945)

proposed six biotic provinces for Mexico, one of which he named the "Transverse Volcanic". Smith (1940), as an offshoot of his extensive studies on the lizards of the genus *Sceloporus*, with 85 forms then known to occur in Mexico, proposed 23 regions, subregions, and provinces, of which several fell within the transvolcanic belt.

Biotic provinces are now seldom used. Differences of opinion caused confusion, and the usefulness of such designations gradually diminished.

TRANSVOLCANIC BELT ENDEMISM

Tamayo with West (1964: fig. 4) published an excellent map showing a series of lentic basins that existed circa A.D. 1500, shortly before the arrival of the conquistadors. Those authors indicated that a large series of isolated basins, all lying within the transvolcanic belt, were formed when normal drainage was disrupted by volcanic activity. As an example, they included an aerial photograph (their fig. 6) showing how a lava flow cut off a portion of the Lago de Pátzcuaro to form the Laguna de Zirahuén. Figure 1 of the current paper was adapted from the Tamayo with West map.

Robert R. Miller, a noted authority on Mexican fishes, stated (personal commun.) that the Río Lerma "wandered all over the map." The Río Lerma formerly flowed northeastward across Michoacán, but today, some millions of years later, it rises in marshes and lakes east and southeast of Toluca and flows essentially westward. A probable scenario was that its course was blocked by volcanic upheaval, a lake formed that eventually found another outlet, and the Río Lerma followed a different course, often leaving the lake isolated. The process was repeated at successively lower elevations.

Organisms living in the lakes have had ample time to differentiate, and endemism is well known and documented, especially among the fishes. Barbour (1973b: 533) analyzed the evolution of the 18 species and 6 subspecies of fishes of the genus *Chirostoma* in the southern part of the Mexican Plateau. He wrote, "The Mesa Central has a long history of geological instability. Tectonic movements associated with the Laramide Orogeny, mid-Tertiary and

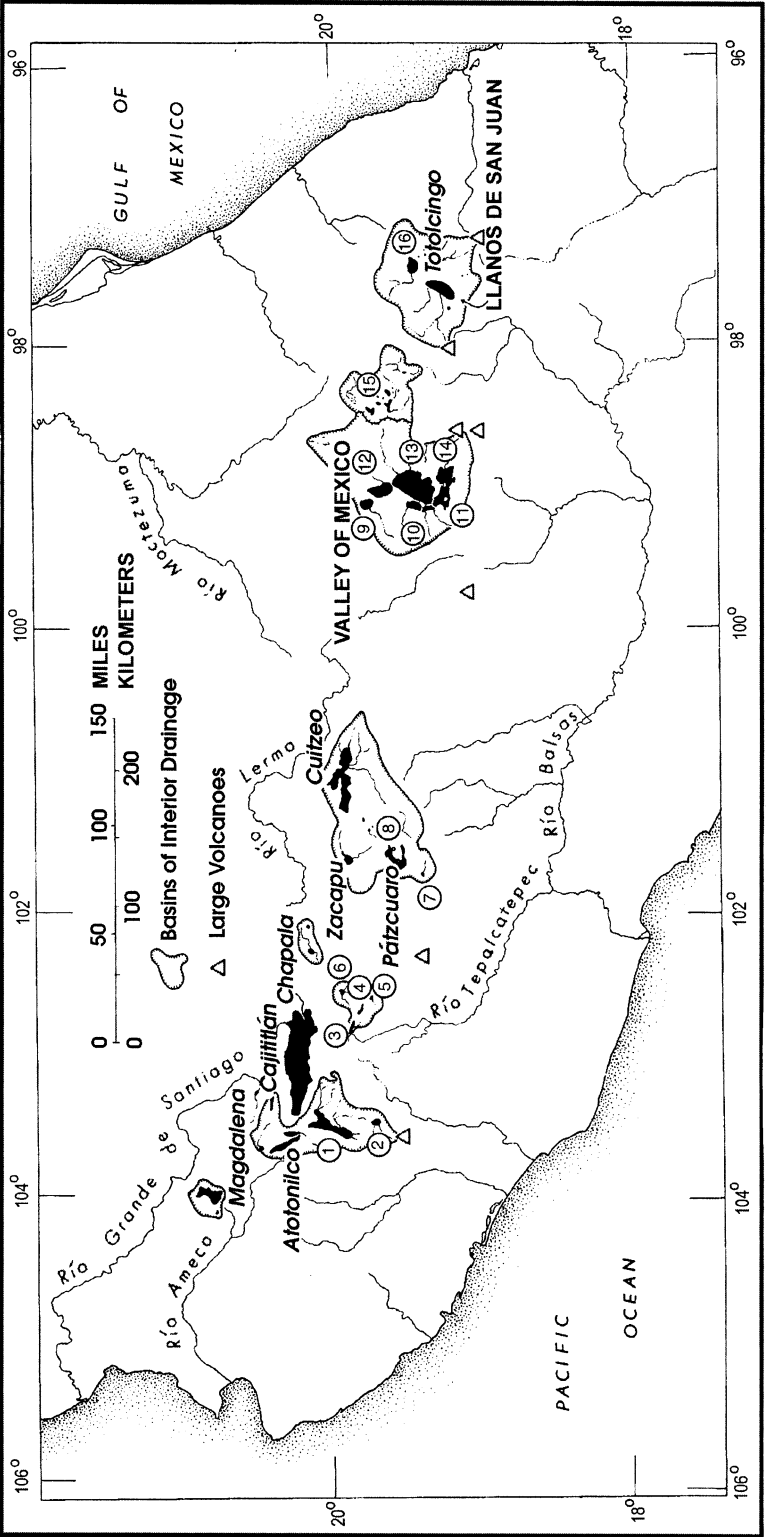


Fig. 1. Areas of lakes and interior drainage of the transvolcanic belt (axis) of Mexico as they existed before the coming of the conquistadors circa A.D. 1500. Adapted from the excellent map serving as figure 4 (p. 108) in the first volume of the *Handbook of Middle American Indians*, Robert Wauchope, general editor, in a section on hydrography by Jorge L. Tamayo in collaboration with Robert C. West, and published by the University of Texas Press in 1964. The eight lakes from which samples of *Thamnophis eques* are available for this study are shown in boldface type. Other lakes and two ancient capitals are indicated by circles containing numerals as follows: 1 Sayula, 2 Zapatlán, 3 Guadalupe, 4 Magdalena, 5 Tacumbo, 6 Jariepo, 7 Zirahuén, 8 Tzintzuntzan the Tarascan capital, 9 Zumpango, 10 Tenochtitlán the Aztec capital, 11 Xochimilco, 12 Xaltocan, 13 Texcoco, 14 Chalco, 15 Apam, and 16 Tepeyahualco.

Plio-Pleistocene vulcanism and mid-Pleistocene uplift and associated vulcanism have resulted in continuously changing drainage patterns. During the Tertiary and early Pleistocene, the ancestral Río Lerma probably flowed westward, perhaps through a series of lakes, to the Pacific Ocean." Barbour (1973a: 98) also stated, "... in the westward flowing Lerma-Santiago river system and contiguous fluvial and lacustrine basins, endemism reaches generic and familial levels."

Robert R. Miller, in a letter to me dated November 11, 1958, wrote, "The Río Lerma system, which rises above Toluca and once included such lakes as Pátzcuaro and Cuitzeo ... contains a fascinating fish fauna. It is the home of an endemic family of viviparous fishes, the Goodeidae, and also of the endemic silverside genus *Chirostoma*, belonging to an otherwise largely maritime family. Both groups have flowered in what was once a relatively unsaturated environment."

Other kinds of organisms inhabiting the transvolcanic belt also show endemism. The late James D. Anderson, our companion in the field twice in Mexico, suspected that salamanders of the genus *Ambystoma* would vary from lake to lake and also occur in some habitats that were unsuitable for garter snakes. His ambitious plans to investigate were thwarted by his early death, but one of his students, Salome Litwin Krebs, armed with Anderson's notes, data, and a partially written manuscript, joined with Ronald A. Brandon (Krebs and Brandon, 1984) in describing *Ambystoma andersoni* as a new species. The type locality was the Laguna de Zacapu, Michoacán. Brandon was already aware of the new species and had previously begun studies in depth on the general topic and continued to do so. In his *Natural History of the Axolotl and Its Relationships to Other Ambystomatid Salamanders*, Brandon (1989: 18) listed 19 then-recognized species of *Ambystoma* in Central Mexico. The status of some was in question, and a number were known only from their type localities. It was obvious, however, that they collectively exhibited endemism.

Robert W. Dickerman (1963) reported on endemism among the song sparrows, *Melospiza melodia*, indigenous to the region. He recognized seven subspecies from the trans-

volcanic belt, three of which he personally described as new, and two others in collaboration with a colleague. A population from the marshes at the east end of the Lago de Chapala may now be extinct. Dickerman (1965, 1970) also showed that endemism as a result of splitting occurs in at least two other birds of the transvolcanic belt. In the first of two papers he described a new race of the red-winged blackbird, *Agelaius phoeniceus*; in the second a new subspecies of the black-pollled yellowthroat, *Geothlypis speciosa*. He also called my attention to two small mammals, of the genera *Neotomodon* and *Reithrodontomys*, listed and mapped by Hall (1981), that have similarly split into two separate subspecies in parts of their wide ranges in the transvolcanic belt.

Crayfish of the genus *Cambarellus* also vary from lake to lake. Two leading astacologists, Horton H. Hobbs, Jr., of the U.S. National Museum, and Alejandro Villalobos Figueroa, of Mexico's Instituto de Biología, agreed, but they differed on whether they were species or subspecies. Villalobos Figueroa (1943) preferred subspecies, as when he described a new race from the Lago de Pátzcuaro. Hobbs (1971), in listing the hosts of ostracods from the lakes, also used subspecies for the crayfish, but in later papers (Hobbs, 1972, 1974) he elevated them all to full species.

Hobbs succinctly summarized the situation in a letter to me dated November 12, 1965, in which he wrote, "Present data indicate very much the same thing that you have found with your *Thamnophis eques*, for at least many of the lakes have their own peculiar form of the crayfish that we are calling *Cambarellus montezumae*."

Other organisms, including additional invertebrates and vegetation, doubtless show splitting into two or more closely related taxa within the transvolcanic belt.

Flores-Villela (1993), in writing about the distribution and endemism of the herpetofauna of Mexico, stated:

Mexico's rugged topography has resulted in a great variety of habitats and microhabitats that are subject to variable environmental conditions. Consequently, there are different ecological conditions that allow the establishment of distinct animal populations isolated in small areas. Amphibians and reptiles are organisms of low vagility with a few exceptions [sea snakes and sea turtles]; their tolerance levels of climatic and eco-



Fig. 2. Lago de Cuitzeo, Michoacán. South shore and southern end of the 19th-century causeway across the lake.

logical factors are generally low, and they are susceptible to environmental changes. The rugged topography and the varied environments have contributed to the differentiation and radiation of these isolated populations into species, making Mexico exceptionally rich in amphibians and reptiles.

Based on morphological differentiations in coloration and pattern, there is marked variation among the populations of *T. eques* we encountered. These are discussed below, following descriptions of the environments in which they were living during the 1960s.

EL LAGO DE CUITZEO

This once large natural lake, second in size in Mexico only to the Lago de Chapala, apparently is now almost entirely in Michoacán. It formerly extended well into southern Guanajuato and its widest east-west length was once in excess of 35 km (Comisión Intersecretarial, maps, sheets 31 and 36, 1:500,000). Its size and volume have been severely reduced because its chief tributaries have long been utilized to supply the state capital of Morelia and nearby agriculture. The remaining southern and deepest part of the lake is 32 km north of Morelia, and a 19th-century causeway crosses it from south to north. It is now paved and wide enough to accommodate two-

way traffic. On its east side rocks may protrude above the surface of the water. Rainfall during the summer season affects the depth of the water. During our four visits to the lake, all in August, it probably was near its maximum. The water was low on two occasions, only partially covering the rocks. During the early morning of August 20, 1961, after a cool night, we saw hundreds of garter snakes (*Thamnophis eques* and *T. melanogaster*) all out in the open at the same time warming themselves in the early morning sun on the exposed rocks on the east side of the causeway. On August 5, 1964, the rocks were mostly under water (fig. 2). I was able to wade out, clad in hipboots, for a considerable distance, and a *campesino* who lived nearby informed me that it was up to his neck at the deepest point. The Lago de Cuitzeo must, indeed, have been a large lake before it shrank drastically in size following the European occupation of Mexico. According to Ceballos and Guzmán-Villa (1991), Cuitzeo was $1820 \pm$ m above sea level.

We were amazed at the extraordinary abundance of garter snakes in and around the edges of the lake. The small fishes on which they fed were also present in enormous num-

bers and they supported a small industry. A few men seined in the shallow turbid water, caught large numbers of small fishes of three sizes, and spread them on the paving of the causeway to dry in the sun. They told us they were readily salable in Morelia for making tacos and enchiladas.

We noted that *Thamnophis melanogaster* occurred with *T. eques* in all habitats we investigated at the Lago de Cuitzeo—in the water, along the lake shore, on the rocks along the causeway, and in isolated rock-piles. Invariably, *melanogaster* was the more abundant. The catch during 1960 was 42 *melanogaster* and only 10 *eques*; in 1961, 15 and 13; in 1964, 30 and 15; and in 1965, 19 and 7. These figures include a few DOR (dead on the road) specimens.

Ceballos and Guzmán-Villa (1991) attested to the continued abundance of the snakes at Cuitzeo. They wrote that, at the end of the 1970s and through the decade of the 1980s, the level of the lake fluctuated greatly. The basin west of the causeway was completely dry coincidental with the installation of a gas pipeline paralleling the highway. Great numbers of snakes remained present, however, and an appeal was made to the authorities for permission to kill them for their skins, but the application was denied.

Our air temperature readings taken in the early morning varied from 16.8 to 22.7°C; one afternoon reading was 32.2°. Morning water temperatures at the same times were 26.6–31.7°. Cloacal temperatures for the few *T. eques* tested matched or were very close to that of the water in which they were caught. A large male, found in the open, had a cloacal reading of 24.4° when the nearby air and water temperatures were 22.3° and 26.6°, respectively. Temperatures of three snakes found hiding in rockpiles were 28.2°, 28.3°, and 28.5°. The very similar recordings indicate they probably had sought shelter just before capture; temperatures under adjacent rocks were 24.3°, 29.2°, and 30.7°, respectively. The pH of the open lake and on the west side of the causeway was 8, but it was 7.5 on the east side where there were evidences of pollution, including rotting dead fishes. Several of the garter snakes of both species showed injuries, some severe. They had evidently been hit by rocks thrown down

at them from the causeway. We witnessed two such attempts to kill them.

In a footnote (Tamayo, 1949, I: 330), the following appears: “Cuitzeo, Tar. Lugar de zorillos”, which translates as, “In the Tarascan Indian language Cuitzeo means place of the skunks.” Martín del Campo (personal commun.) stated that the Tarascan word for garter snakes is “Akuitze”. Does the lake (Cuitzeo) get its name from the pungent musk of *Thamnophis*? (Notice the similarity of “Akuitze” and “Cuitzeo” when pronounced.)

The population of *T. eques* inhabiting the Lago de Cuitzeo is unique and for it I propose a new name.

Thamnophis eques cuitzeoensis,
new subspecies

Figures 2, 3

HOLOTYPE: AMNH 93915, a large gravid female from ~100 m east of the southern end of the south–north causeway across the Lago de Cuitzeo, Michoacán, Mexico, collected August 5, 1964, by Roger Conant. Total length 1020 mm, tail length 229 mm, tail/total length = 0.225.

PARATOPOTYPES: AMNH 85141–85146, 87530–87542, 88710, 88711, 93901–93914, 93916–93933 (young born to the holotype in captivity on September 13, 1964), 93934, and 96846–96851, all from near the south end of the causeway, and taken, collectively, on August 16, 1960, August 20, 1961, August 5–6, 1964, and August 3–4, 1965. The nearest settlement, Cato del Porvenir, is 5 km south of the causeway.

ETYMOLOGY: Derived from Cuitzeo + the adjectival-forming suffix *-ensis* (belonging to a place).

DIAGNOSIS: A race of *Thamnophis eques* characterized by its virtually uniform, intense black pigmentation. Traces of a striped and spotted pattern may appear in the young, especially on or near the head, and the pattern is sometimes faintly discernible in adults that have just shed their skins or in specimens that have been preserved for many years; in essence, however, the dorsum of virtually all individuals is jet black (fig. 3). The venter is also black and dark gray, with the exception of the chin and throat and the underside of the tail, which are white or cream-colored

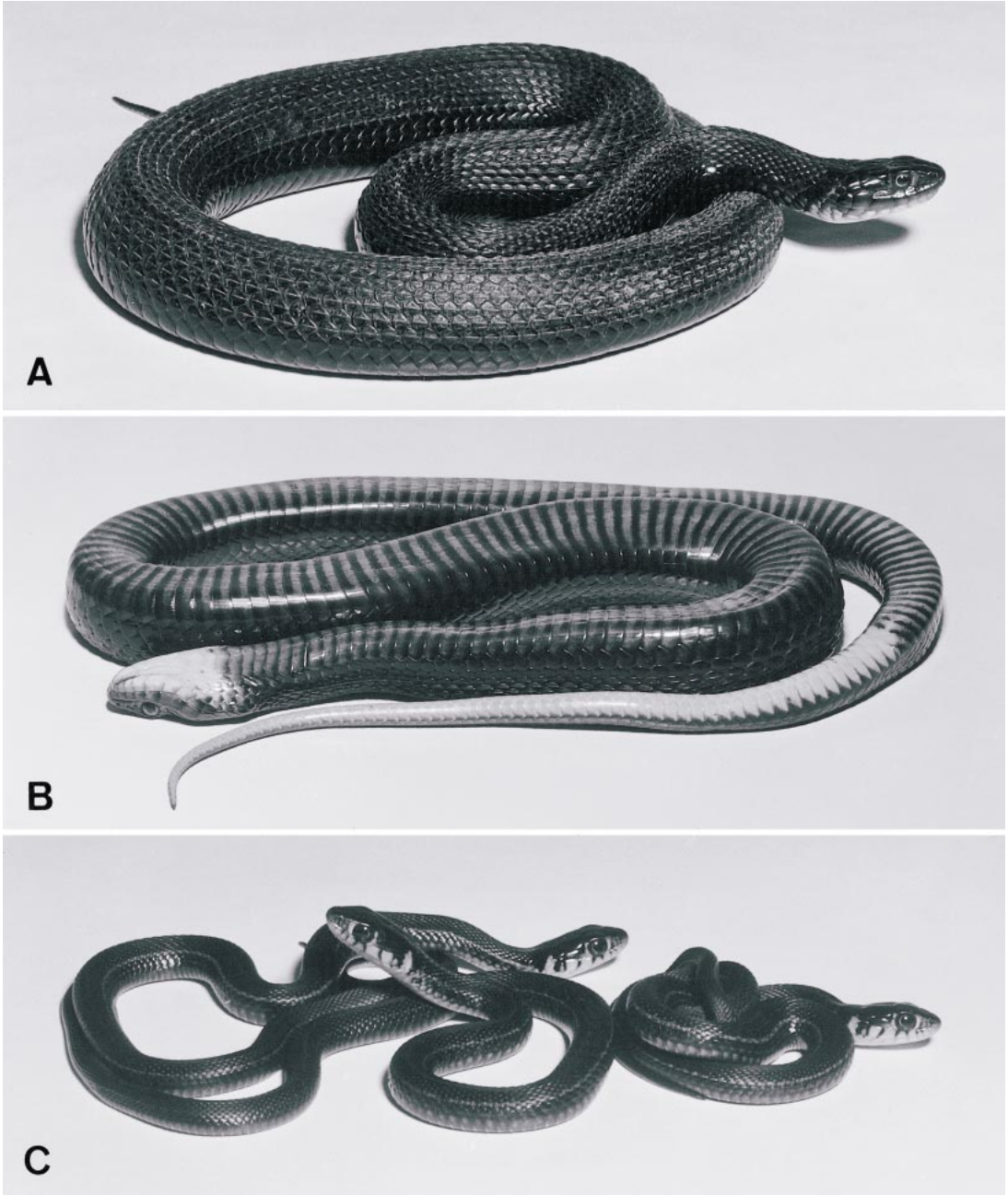


Fig. 3. **A.** Dorsal view of the gravid holotype of *Thamnophis eques cuitzeoensis* (AMNH 93915), 1020 mm in total length, collected August 5, 1964, near the causeway. **B.** Venter of the holotype. **C.** Three of 18 young born September 13, 1964, to the holotype.

TABLE 1
Variation in Scutellation and Tail Length Proportions in *Thamnophis eques cuitzeoensis*, New Subspecies

	Wild-caught males (23) ^a	Captive-born males (10)	Wild-caught females (20)	Captive-born females (8)
Scale rows	21-19-17 (20) 19-21-19-17 (3)	21-19-17 (10)	21-19-17 (17) 21-23-21-19-17 (1) 19-21-19-17 (2)	21-19-17 (8)
Ventrals	157–167 (23) \bar{x} = 162.2	163–168 (10) \bar{x} = 164.8	144–158 (20) \bar{x} = 154.4	154–161 (8) \bar{x} = 157.0
Subcaudals	71–83 (20) \bar{x} = 76.0	74–82 (10) \bar{x} = 77.5	61–72 (16) \bar{x} = 66.1	63–69 (8) \bar{x} = 66.8
Supralabials	8 (45) 9 (1)	8 (20)	7 (1) 8 (38) 9 (1)	8 (16)
Infralabials	10 (44) 11 (2)	9 (1) 10 (19)	10 (32) 11 (6) 12 (2)	10 (16)
Preoculars	1 (46)	1 (20)	1 (40)	1 (16)
Postoculars	3 (35) 4 (11)	3 (20)	2 (1) 3 (28) 4 (11)	2 (1) 3 (15)
Temporals, 1st row	1 (46)	1 (20)	1 (40)	1 (16)
Temporals, 2nd row	1 (5) 2 (25) 3 (16)	1 (4) 2 (15) 3 (1)	1 (4) 2 (21) 3 (15)	1 (1) 2 (14) 3 (1)
Tail/total length	22% (4) 23% (9) 24% (6) 25% (1)	23% (5) 24% (4) 25% (1)	20% (2) 21% (4) 22% (8) 23% (2)	22% (6) 23% (2)

^a Figures in parentheses indicate sizes of samples.

without dark markings, and are strikingly in contrast with the remainder of the under surface. The anal plate may be light or dark or partly both. Most populations of the *T. eques* complex from other localities bear pale longitudinal stripes or paired dark lateral spots or both. Neonates and the other young specimens of *cuitzeoensis* have pale upper labials with dark lines on the sutures. Dorsal scale rows normally 21-19-17, ventrals 144–168, subcaudals 61–83, anal plate usually single (divided in AMNH 85145, a female 561 mm long). Apical pits present.

DESCRIPTION OF THE HOLOTYPE: In its scutellation this specimen agrees with The Species Model, except as follows: There are four postoculars on the left side of the head instead of the normal three. On both sides the lowermost postocular extends slightly for-

ward beneath the eye. A small scale is wedged between the anterior temporal and the parietal on both sides of the head. The rostral is damaged as the result of abrasion while the snake was held in captivity for nearly four years.

Scale rows 21-19-17, the first reduction resulting from the loss of row 5 at the level of ventral 75 on the left and ventral 72 on the right. Reduction to 17 rows occurs through the loss of row 4 at the level of ventral 93 on the left and ventral 87 on the right. Total ventrals 154, plus a single anal plate that bears a longitudinal groove across its left side; subcaudals 71 pairs. Tip of tail sharply pointed. Total length 1020 mm, tail length 229 mm, tail/total length = 0.225. A summary of scale counts for the entire sample from the Lago de Cuitzeo is in table 1. Sev-

eral wild-caught specimens have incomplete tails.

The presence of apical pits was amply demonstrated by an examination of a skin (the stratum corneum) that was shed by the holotype on January 28, 1965, while it was alive in captivity. A large part of the skin was preserved by affixing it in a spread-out position to a white parchmentlike sheet of paper shortly after it was cast. From this it was readily apparent that paired apical pits were present throughout the length of the body; they also extended onto the tail. They apparently occurred on all scales except those of the two lowermost rows on each side of the body, and were faint on scales of the third row. These observations were made within a day or two after the skin was shed. In July 2000 the pits had nearly disappeared when viewed with the naked eye. This was not surprising in view of the difficulty of finding apical pits in long-preserved specimens (Conant, 1961).

Dorsum virtually uniform black, even after more than 35 years of preservation. Keels of the dorsal scales faintly marked with dark brownish black except on the two or three lowermost rows where they and the anterior portions of the scales of the lowermost row are marked with a slightly paler gray that was not visible in life (fig. 3A). Anterior half of each ventral scute black, posterior half dark gray flecked with darker gray to black; pale halves of ventrals more conspicuous toward posterior part of the body. The chin, throat, and infralabials are cream-colored; some black pigment encroaching on the upper edges of the infralabials, especially the 6th–10th. A few small black spots on the posterior part of throat; cream-colored area terminating rather abruptly at the level of the first enlarged scale anterior to where the ventral count starts. Ventral side of tail uniformly cream-colored, except that dark pigment encroaches slightly from the sides of the tail onto the posterolateral edges of the first 13 or 14 subcaudals, less so on the more posterior subcaudals. Most of the anal plate cream-colored, but with dark pigment at its lateral edges.

VARIATION AMONG THE NEONATES: Total lengths of 18 neonates born in captivity to the holotype on September 13, 1964, varied

from 244 to 264 mm, mean 252.1—10 males 244–264 mm, mean 255.8; eight females 244–253 mm, mean 247.5. Tail/total length in males 0.229–0.246, mean 0.236; in females 0.216–0.225, mean 0.221. Weights recorded on date of birth varied from 4.0 to 4.9 g, mean 4.55. A summary of scale counts for all the neonates is included separately in table 1.

The general appearance at birth was black, but the head markings common to all races of *Thamnophis eques* were in evidence, including dark downward streaks on the sutures of otherwise cream-colored supralabials, pale preoculars and postoculars, and a pale crescent at the angle of the jaw (fig. 3). A trace of pale lateral stripes, but none of a middorsal stripe except for a short distance on the nape. Ventrals black along the anterior edges of the ventrals. Posterior halves of ventrals very dark bluish gray. The lower labials, chin, throat, underside of the tail, and the anal plate were cream-colored and unmarked.

When the neonates were examined recently, after being preserved for over 35 years, faint traces of a pale middorsal stripe were evident as well as faint indications of dark lateral spots.

VARIATION AMONG THE OTHER PARATOPOYPES: This series of specimens varied in size from that of the larger neonates to adults approaching the length of the holotype. In life all adults were black except for whitish or cream-colored undersides of heads and tails. Juveniles were similar but they had pale supralabials with dark vertical sutures, a pale crescent at the angle of the jaw, and occasional traces of lateral stripes. In contrast, all adults had black supralabials. Several large adults also had small blackish spots on their throats, and black encroached from the dorsal surfaces of the tails onto the lateral edges of the anterior subcaudals. Keels on the dorsal scales in a few snakes were very dark brown instead of black. Tongue red or reddish, ranging from Vinaceous-Pink and Coral Red to Dragon's-blood Red; tips black. Eye: pupil black narrowly ringed by yellow in juveniles, darker shades in adults; iris dark brown or black. (All capitalized color names from Ridgway, 1912.)

The two following paragraphs are con-

densed from detailed notes made after the snakes were at our home base for observation.

Total length 633 mm. Jet black above; chin, throat, infralabials, and lower parts of supralabials Pale Olive-Buff, suffused subcutaneously with pinkish; underside of tail Pale Smoke Gray, purplish toward tip; dark markings on supralabials black with a bluish cast; belly Delft Blue, same color extending onto infralabials and lower part of angle of jaw.

Total length ~300 mm. A very narrow and faint Brownish Olive (dark) middorsal stripe, expanding on nape and changing to Reed Yellow; faint lateral stripe bluish-gray; dorsum black; keels on dorsal scales dark brown; top of head black; faint pair of parietal spots dull olive-yellow; supralabials bluish-green on dull yellow, sutures black; infralabials, chin, and throat Massicot Yellow; belly between Delft Blue and Deep Delft Blue; anal plate Vinaceous-Pink; underside of tail grayish-white.

When reexamined after more than three decades of preservation, many of the large specimens that had been uniformly black in life showed traces of pattern, some rather strongly, especially those involving the upper labials and the crescent at the angle of the jaw.

FOOD: Small fishes were so abundant in the Lago de Cuitzeo that the snakes never lacked for food. At least five species were involved (Robert R. Miller, personal commun.), viz.: *Allophorus robustus*, *Chiostoma jordani*, *Goodea atripinnis*, *Xenotoca variata*, and an unidentified member of the genus *Skiffia*. Examples of the first four were all palpated and removed from live snakes that had recently fed. The small *Skiffia* was partially decayed and wedged between rocks.

At home we seined for small fishes in Taunton Lake in the New Jersey Pine Barrens and caught darters (*Etheostoma fusiforme*), small suckers (*Erimyzon oblongus*), and small sunfish (*Lepomis gibbosus*). Our captive *Thamnophis eques cuitzeoensis* caught the fishes as they were swimming in shallow glass dishes. Other snakes from Mexico's transvolcanic belt fed on the same three species of fish at our home base.

A large male (AMNH 85141), 833 mm in length, had swallowed a hard, almost round, rubbery object that was revealed by dissection to be lodged in the stomach at the pylorus. The inedible object was dull yellow and measured 20 × 18 mm. When caught,

the snake was as active as others collected on August 16, 1960.

BEHAVIOR: Richard M. Blaney (personal commun.) visited Lake Cuitzeo in 1966 and 1979 and, as we had in earlier years, he found both *Thamnophis eques* and *T. melanogaster* and the small fishes on which they fed extraordinarily abundant. He made his field notes available to me. From them and subsequent conversations, I summarize the following: Several pregnant *T. eques* were observed sunning with the posterior loops of their bodies exposed, presumably warming the developing young. Both species of *Thamnophis* were seen hanging from holes between the rocks along the causeway, head in the water and catching fish as they swam by. Numerous *T. eques* were observed in open water floating in a single looped position, head submerged near the tail. Close observation revealed that the snakes slowly twitched and wiggled their tails as a lure to attract fish. Two were seen successfully catching small fish in this manner. Blaney was standing in water a foot or more in depth, and he remained motionless as he watched. The turbidity made visibility difficult, but he was close enough to be sure of what he was seeing. His field notes from Lake Cuitzeo concluded with, "While being photographed, specimens continued to display the tail in a manner similar to the behavior observed at the lake."

Blaney's findings explain the propensity of snakes of the *eques* complex to curl their tails. During our own photographic sessions, even in the studio, tail curling was frequent (see fig. 12), and we saw it in living *eques* from a number of far distant parts of the species' range. Pictures in the Conant collection include tails curled or partly so in snakes of the *eques* complex from the Mexican states of Chihuahua, Durango, Guanajuato, Jalisco, México, Michoacán, Nayarit, Tlaxcala, and Zacatecas. This suggests that using the tail as a lure for prey is widespread. Probably nowhere is it better perfected than at Lake Cuitzeo where the snakes are black, dorsally and ventrally, except for the whitish undersides of the head and tail. The contrast is the greatest in them. Blaney was apparently the first to observe the tail being used as a lure in this species.

Similar use of the tail occurs in many kinds of snakes, notably the viperids. Juvenile members of the genus *Agkistrodon*, for example, have yellow tail tips that are raised and wiggled in imitation of an insect. Included is the cantil, *Agkistrodon bilineatus*, of Mexico and other parts of Middle America (Gloyd and Conant, 1990: 78).

Our photo collection of the *Thamnophis eques* complex includes pictures of venters as well as snakes in normal positions. Curled tails are far more prevalent among the snakes lying upside down, suggesting another serpentine behavior, that is, moving the tail in the presence of a predator, ostensibly to distract attention from the more vulnerable head.

A female *eques*, length 915 mm, from Chihuahua remained rigidly supine while being photographed except that every few seconds the tail was coiled in a different position. For a short time the anal opening was expanded and part of the cloaca exposed.

LA LAGUNA DE YURIRIA

Figure 4

About 30 km north of the Lago de Cuitzeo is a much smaller body of water, the Laguna de Yuriria, that is roughly oval and ~15 km wide in its east-west long dimension. It was artificially created as a reservoir in the 16th century (Tamayo, 1949, II: 318). The nearby bifurcation of the Río Lerma permitted a manmade diversion into a low area. During the general period when we visited the area, the level of the Laguna de Yuriria varied greatly and was dependent on precipitation. Dickerman (1963: fig. 13) showed it at low level, and he wrote, "In May 1958, the lake was nearly dry. Aquatic vegetation along the shore was desiccated and the lake bottom was cracked to a depth of 30 centimeters. By December 1958, heavy summer rains had caused the lake to overflow its shores and flood surrounding pastures and fields."

Our visit was from August 3 to 6, 1965, and Yuriria was lower than normal, but collecting was marred by almost continuous rain and the water was rising. On the afternoon of August 5 the air temperature was 23.5°; water 27.0°; pH 6. Cloacal temperatures of five *eques* taken under rocks were the same

as or fairly close to the temperatures of the damp muddy substrate on which they were lying. The snake temperatures ranged from 24.2 to 26.5°.

MATERIAL: Near the town of Yuriria (AMNH 96852–96863); 10 km west-northwest of Yuriria (AMNH 96864–96868, 118723, 118724); both localities in Guanajuato.

Among these 19 snakes, all collected near the west and south sides of the lake, most were hidden beneath stones near the water's edge or in stone piles. Others were on the road near Yuriria, one alive and two dead. The majority were small (237–300 mm in length) and patterned with three well-defined pale longitudinal stripes, as in *Thamnophis eques eques*. They also bore dark lateral spots that varied in size and intensity, but were more prominent and darkest in larger specimens. In comparison, small snakes from the Lago de Cuitzeo were all strongly melanistic with body patterns suppressed and difficult to see. There were variations. AMNH 96864 (435 mm in length) was still well patterned, whereas AMNH 96866 (330 mm) was very dark and the stripes were obscure. For variation in specimens of comparable size see figure 4.

The largest snake from Yuriria (AMNH 96852, DOR and 670+ mm in length) was jet black and unpatterned both dorsally and ventrally except for the underside of the head and tail, which were whitish and unmarked; it matched adults of *cuitzeoensis*. In addition to the specimens listed, we found an almost complete shed skin (AMNH 148804) in reeds along a small stream ~10 km east of Yuriria. It was nearly a meter in length and was preserved by spreading it flat on a sheet of heavy paper. When compared with a similarly prepared shed skin from the type specimen of *cuitzeoensis*, the Yuriria skin was paler and almost patternless except for faint indications of three pale longitudinal stripes.

Only a few of the snakes from Yuriria show dark ventral crosslines narrower but comparable with those exhibited by specimens of *cuitzeoensis*. In the latter melanistic serpents, the anterior half or less of each ventral scute is black, with the posterior portion very dark gray (see fig. 9A). In most snakes taken near



Fig. 4. Laguna de Yuriria, Guanajuato. Young intergrading snakes (*Thamnophis eques eques* X *T. e. cuitzeoensis*). **Left.** Strongly patterned (270 mm) as in *Thamnophis e. eques*. **Right.** Dark and pattern obscure (335 mm), resembling *T. e. cuitzeoensis*.

Yuriria the dark ventral areas are narrow and confined to the bases of the ventrals.

The samples we obtained of the *eques* complex at the Laguna de Yuriria had elements of the patterns and coloration of both the widespread *Thamnophis eques eques* and the geographically restricted *T. e. cuitzeoensis*, and they are considered as intergrades between the two subspecies.

EL LAGO DE PATZCUARO

Among the many endorheic lakes that existed five centuries ago (fig. 1), Pátzcuaro remains similar in size and appearance. It is shaped roughly like the letter "C", its greatest length is almost 20 km, its greatest width 10.9 km, and it lies ~40 km southwest of the Lago de Cuitzeo. It is surrounded in large part by steep hills and contains eight islands, some inhabited by Indians. Chacón (1993) reviewed many features of the present-day Lago de Pátzcuaro. According to him, the lake's surface occupies 130 km² and is 2035 m above sea level. Its maximum depth is 12.2 m, mean depth 4.9 m. There is no outlet and it is fed by intermittent surface streams during the July–September rainy season. Annual evaporation exceeds rainfall; the deficit is partially mediated by seepage. Chacón wrote that "during the first quarter of the century seepage contributed at least 12% of the hydrological influx to the lake. It is estimated that watershed seepage has been reduced by watershed deforestation and erosion to 8%."

The elevation of the lake varies by mod-

erate amounts. De Buen (1944) published lists indicating the levels recorded at the Estación Limnológica de Pátzcuaro every 15 days over a period in excess of four years (1939–1943), during which the elevation decreased only by approximately three-fourths of a meter. Many other endorheic lakes, such as Cuitzeo, have much greater fluctuations and their surface elevations, unless dated, should have \pm following the figures quoted.

The Lago de Pátzcuaro has been subject to severe anthropogenic pressure. Chacón (1993), in his account of that lake, discussed the problem in detail, including siltation, dumping of raw sewage, and a marked deterioration in the catch of *pescado blanco*, a highly prized whitefish. The large butterfly nets formerly used extensively are now seldom seen except when tourists pay to film them in use.

According to Tamayo (1949, II: 124), three lakes—Zirahuén, Pátzcuaro, and Cuitzeo—were formed by the Río Lerma. The small Laguna Zirahuén is about 13 km south-southwest of the Lago de Pátzcuaro, and it was created when (Tamayo with West, 1964: fig. 6) "a lava flow . . . blocked normal drainage to help form this deep lake." The Río Lerma originally flowed onward to Pátzcuaro and eventually to the Lago de Cuitzeo. Goldman (1951), in writing about his 1892 and 1904 visits to the Lago de Pátzcuaro, noted, "There is no outlet at present, but low elevation of the southeastern shore indicates former drainage toward the Lago de Cuitzeo."

The respective levels of the three lakes

support the route postulated for the Río Lerma. The elevations are: Zirahuén 2120 m (de Buen, 1943), Pátzcuaro 2035 m (Chacón, 1993), and Cuitzeo $1820 \pm$ m (Ceballos and Guzmán-Villa, 1991). Tamayo (1949, II: 422) wrote that the *cuenca* (basin) of Pátzcuaro and Zirahuén is in the highest part of the Cordillera Neo-Volcánica. Zirahuén has a maximum depth of 46 m according to de Buen (1943).

In August of both 1960 and 1961, when we were at Pátzcuaro, we made abortive attempts to visit the Laguna de Zirahuén. Heavy showers fell daily. We were able to reach Santa Clara del Cobre, partly over difficult roads, but from there onward deep mud blocked us. Ceballos and Guzmán-Villa (1991) thought *Thamnophis eques* probably occurred around Zirahuén.

Chacón (1993), under the heading of "Vegetation", wrote, "Emergent macrophyte communities consist of tules (*Scirpus americanus*, *Typha latifolia*, *Sagittaria graminea*, and *Cyperus niger*)."

Much of the perimeter of the Lago de Pátzcuaro, at least when we approached it from Quiroga in August 1964, consisted of a solid impenetrable wall of tules up to 3 m high. Apparently, only where openings had been cleared or maintained through them was it possible to reach the lake. We found a marina under construction, obtained permission to collect, to pull our camper under a vehicular ramada to shelter us from the intermittent showers, and to stay as long as we liked. After dark I searched the shoreline and the water up to the limit of my hipboots, but I saw nothing herpetological other than *Rana dunni* and members of the *Rana pipiens* complex.

The following morning, the Tarascan caretaker stated that "water snakes" are diurnal. It was too cold for them at night. We passed through a cut in the wall of tules in his rowboat. Beyond them were great floating mats of dead tules. After briefly exploring the open lake, we returned to see several large *T. eques* lying on the mats, apparently warming themselves and their developing embryos even though the sky was overcast. The moment our boat touched the floating mats the snakes retreated downward. They also vanished, we observed later, when the sun came out strongly between showers.

The caretaker, who had watched me preserving specimens during the previous rainy afternoon, realized I did not need live snakes. He said he had a way of getting some. He summoned his teenaged son, who proved to be a crack shot with a muzzle-loading carbine. He used bird shot that gave the effect of a miniature shotgun. The dead snakes were retrieved chiefly with poles from the mats. He shot 15 basking ones, all of which proved to be gravid females.

In the straight-sided water tank at the marina three small male *eques* were found in 1960 and two more in 1961. In 1960 we discovered an inlet (fig. 5) used by Indians who arrived by dugout canoe with their handicrafts to sell on market days at the town of Pátzcuaro. Near the opening a few other snakes were caught by hand on a clear morning, including three *Thamnophis melanogaster*, the only members of that species we saw at the lake. The difficult collecting at Pátzcuaro was in sharp contrast to the ease with which we acquired both species at Cuitzeo. We saw many snakes swimming at Pátzcuaro, but they were far beyond our reach.

Temperatures recorded at the marina were air 15.5° and water 18.0° at 8:30 AM, and air 16.6° and water 22.2° at 7:00 PM. The pH was nearly neutral, probably because of the abundance of rain. Chacón (1993) recorded 8.8 in the north basin of the lake and 7.8 near sewage inlets. Yet both he and Ceballos and Guzmán-Villa (1991), in their charts on water quality for the Lago de Pátzcuaro, gave the pH as 9.3.

The population of *T. eques* inhabiting the Lago de Pátzcuaro differs sufficiently to warrant a new name, which I propose below.

Thamnophis eques patzcuaroensis,
new subspecies

Figures 5–7, 9B

HOLOTYPE: AMNH 93937, a large gravid female from the lakeshore north of the town of Pátzcuaro, Michoacán, Mexico, collected August 7, 1964, by Roger Conant. Total length 1025 mm, tail length 242 mm, tail/total length = 0.236.

PARATYPES: AMNH 93936 same data as holotype; AMNH 93935 ~11 km north of Pátzcuaro; AMNH 85123–85140, 87548,



Fig. 5. Lago de Pátzcuaro, Michoacán. An inlet from the open lake north of the town of Pátzcuaro. Here Indians arrived in their dugout canoes with their handicrafts for market day. An impenetrable wall of tules is visible at the extreme right. August 15, 1960.

87549, 88713 ~5 km southwest of Quiroga; AMNH 93938–93957 (young born to holotype on August 29, 1964); AMNH 58230; LSUMZ 38558, 38559, 40864; UMMZ 93938, all from the Lago de Pátzcuaro.

[Note: Virtually all material on which this review is based is from the AMNH collection, but information from a few adult male specimens from the Louisiana State University Museum of Natural Science (LSUMZ) and the University of Michigan Museum of Zoology (UMMZ) is included for two reasons: (1) my material is skewed in favor of females because all 15 snakes shot on mats of tules were of that sex, and (2) the male depicted in figure 7 has an aberrant ventral pattern. See caption for it.]

ETYMOLOGY: Derived from Pátzcuaro + adjectival-forming suffix *-ensis* (belonging to a place).

DIAGNOSIS: A large three-striped garter snake with the dorsal coloration often subdued and stripes frequently inconspicuous. Lateral stripes on rows 3 and 4 anteriorly; row 3 only posteriorly. Paired dark spots on

each side of body between stripes that are best developed in young specimens, becoming less so with age; spots may virtually disappear in large females.

The best diagnostic characters are on the ventral surfaces. The underside of the head and tail are yellow, often brilliant in life. Dark, often black, lines cross the anterior edge of each ventral. These may vary with age. They are usually narrowest in juveniles, but gradually increase posteriorly in width, darkness, and intensity. They collectively produce a series of dark and lighter cross-bands throughout the length of the belly (see fig. 9B).

DESCRIPTION OF THE HOLOTYPE: The scutellation agrees with that of *The Species Model*, with the following exceptions: The preoculars extend upward to and slightly involve the weakly developed canthus rostralis on both sides of the head. Three posterior temporals on right, the normal two on left. A small scale wedged between parietal and upper secondary temporal, much larger on right side of head than on left.

TABLE 2
Variation in Scutellation and Tail Length Proportions in *Thamnophis eques patzcuaroensis*, New Subspecies

	Wild-caught males (12) ^a	Captive-born males (10)	Wild-caught females (17)	Captive-born females (10)
Scale rows	21-19-17 (3) 21-23-21-19-17 (6) 23-21-19 (1) 23-21-19-17 (2)	21-19-17 (4) 21-23-21-19-17 (1) 23-21-19 (1) 21-23-21-19 (3) 23-21-19-17 (1)	21-19-17 (10) 21-23-21-19-17 (4) 21-23-21-19 (1) 23-21-19-17 (2)	21-19-17 (5) 21-23-21-19-17 (3) 23-21-19 (1) 21-23-21-19 (1)
Ventrals	157–170 (12) \bar{x} = 161.9	156–162 (10) \bar{x} = 159.6	150–159 (17) \bar{x} = 154.1	150–158 (10) \bar{x} = 153.6
Subcaudals	70–80 (9) \bar{x} = 75.7	77–83 (10) \bar{x} = 79.7	64–73 (9) \bar{x} = 66.7	67–73 (9) \bar{x} = 69.3
Supralabials	8 (22) 9 (2)	8 (20)	8 (28) 9 (6)	8 (18) 9 (2)
Infralabials	10 (21) 11 (2)	9 (1) 10 (16) 11 (2) 12 (1)	10 (30) 11 (4)	10 (18) 11 (2)
Preoculars	1 (24)	1 (20)	1 (34)	1 (20)
Postoculars	1 (3) 3 (19) 4 (2)	1 (2) 2 (18)	2 (1) 3 (31) 4 (2)	2 (14) 3 (6)
Temporals, 1st row	1 (24)	1 (20)	1 (33)	1 (20)
Temporals, 2nd row	1 (3) 2 (10) 3 (11)	1 (1) 2 (19)	1 (1) 2 (21) 3 (11)	2 (16) 3 (4)
Tail/total length	22% (1) 23% (4) 24% (3) 25% (1)	24% (2) 25% (8)	20% (4) 21% (5)	22% (2) 23% (6) 24% (1) 25% (1)

^a Figures in parentheses indicate sizes of samples.

Scale rows 21-(23)-21-19. The short increase to 23 results from the addition of a fifth row of scales from the level of ventrals 26–38 on the left and ventrals 34–39 on the right. The decrease from 21 to 19 results from the dropping of row 5 at the level of ventral 83 on the left and of row 4 at the level of ventral 81 on the right. Total ventrals 150; subcaudals 73 pairs. Tip of tail sharply pointed. Total length 1025 mm, tail length 242 mm, tail/total length = 0.236. A summary of scale counts for the entire sample from the Lago de Patzcuaro is in table 2. Also see the commentary on the number of dorsal scale rows in the Discussion. In *patzcuaroensis* there are 23 rows, chiefly for short distances, in 55% of the population

sample. Note: many wild-caught specimens have incomplete tails. Aberrations: anal plate grooved (not divided) in AMNH 85134 (female, 1010 mm) and 93943 (male, 243 mm, born in captivity). Anal partially divided in AMNH 85126 (female, 1013+ mm) and 93940 (female, 249 mm, born in captivity).

In life, the holotype was dark, with the three pale stripes relatively inconspicuous, the paired dark spots between the stripes almost indiscernible (fig. 6). When it was examined 35 years later, considerable fading had occurred, and pattern features were clearly visible. The description of them is from the snake as it appeared in 1999. Coloration in life was recorded on January 9, 1965, as quoted below from my notes.

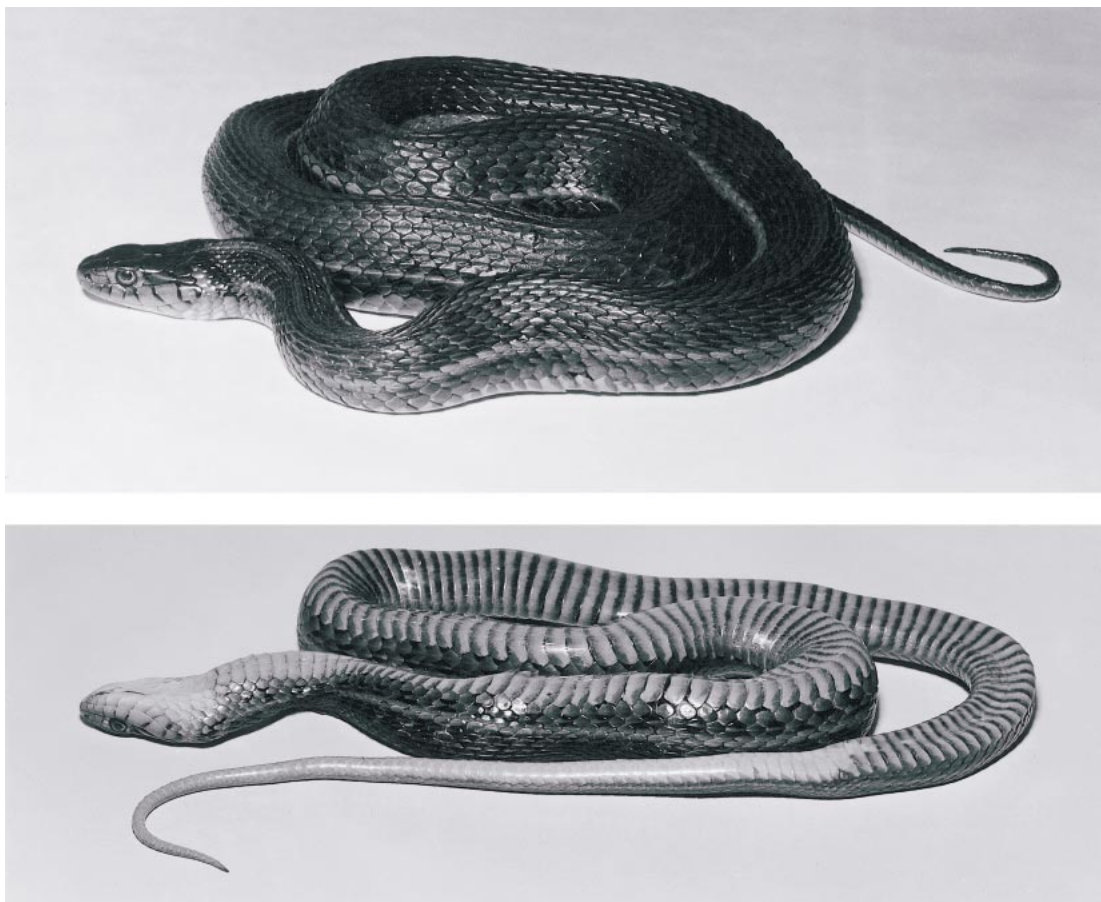


Fig 6. **Upper.** Dorsal view of the gravid holotype of *Thamnophis eques patzcuaroensis* (AMNH 93937), 1025 mm in total length, collected August 7, 1964, 3 km north of the town of Pátzcuaro, Michoacán. **Lower.** Venter of the holotype, after the birth of her young, showing the characteristic broad black crossbands, one on each ventral scute.

The middorsal stripe involves the vertebral row of scales and most of the paravertebral rows. In the nuchal region all three rows are included in full. Farther posteriorly the outer edges of the paravertebrals are invaded by the dark lateral spots as far as the keels. The middorsal stripe narrows to a single row of scales on the head and terminates where it meets the parietal scutes. The lateral stripes are on scale rows 3 and 4 anteriorly, but row 3 only posterior to midbody. The small yellowish parietal spots are slightly elongated, and narrowly edged with black. A yellowish crescent two scales wide posterior to the temporals is followed posteriorly by a black semicrescent two or three

scales wide. Two pairs of black spots are present on each side of body between the light stripes; the spots are relatively small, chiefly alternating with each other but variable in size and position.

The ventral crosslines are faint for about the first 20 ventrals. They then become dark gray, almost black, and extend to the last two ventrals that are invaded in their centers by yellow matching the underside of the tail. The anal plate is mostly yellow, and a short groove is present anteriorly on the right side. The dark crosslines are stippled where they first begin, becoming solid afterward, and occupying the anterior third and more of each ventral. The posterior

part of the ventrals are greenish gray and unmarked.

The following paragraphs on coloration of the holotype are from my notes. Capitalized names are from Ridgway (1912).

Middorsal stripe Deep Olive, lateral stripe Deep Grape Green, area between stripes Brownish Olive, two lowermost rows of scales Medial Bronze.

Throat, chin, and lower labials Mustard Yellow but Naples Yellow over most of the central area. Underside of tail Warm Buff but becoming pinkish toward the tip. Pale part of anal plate Ochraceous-Buff. Belly Mytho Green at lateral edges, *Corydalis* Green in lighter areas between black crosslines on ventrals.

Top of head Brownish Olive, upper labials Serpentine Green, parietal spots Olive-Yellow.

Eye—pupil black narrowly surrounded by yellow; iris Yellowish Olive to Brownish Olive.

Tongue—tips and distal end of base black; base Dragon's-blood Red.

NEONATES: Born August 29, 1964, in a snakebag containing the holotype (AMNH 93937) in transit while returning from Mexico. Eighteen were alive; two others seemingly in perfect condition were dead (crushed under the weight of mother and siblings?). There were also five fairly well-developed embryos, one hard, the others in an advanced state of putrefaction.

Measurements and color notes were made en route on the 20 young on September 3, 1964. Lengths of the 10 males varied from 217 to 268 mm, mean 250.9; of the 10 females 208–252 mm, mean 239.8. Tail/total length in males 0.237–0.253, mean 0.247; in females 0.221–0.245, mean 0.230. In the absence of a sensitive balance, no record of weights was made.

Like very young *T. eques* from most parts of the wide range of the species, the neonates in this litter were marked with pale longitudinal stripes and a double row of dark spots between the stripes on each side of the body. The stripes, however, were subdued, even obscure in some members of the brood. Anteriorly they occupied scale rows 3 and 4; posteriorly row 3 only. Small dark spots on row 2 helped obscure lighter pigment if the lateral stripes actually occurred on row 2. The dark spots were conspicuous and some ran together. Dark transverse lines near the sutures of the ventral scales were present in all, but their intensity and the general darkness of the venter varied. The following

notes on coloration of the neonates (without benefit of Ridgway's 1912 color charts) are from my fieldbook:

Middorsal light stripe khaki-colored; lateral stripes yellowish tan. Dorsal ground color between stripes slightly darker than middorsal stripe, but becoming browner near the lateral stripes. First two rows of scales medium brown with a slightly orange tone. Tops of heads variable—light olive-brown to dark olive, sometimes almost black. Paired parietal spots bright yellow [small, faint, or even lacking in some]. Nuchal blotches black. Labials, oculars, nuchal "crescent," chin, and throat yellow. Venter quite variable from snake to snake, especially insofar as dark pigment is concerned. Ground color of venter in most is green; in one it is pale "tan." Dark areas across the ventrals medium to dark olive. Anal plate and underside of tail yellowish to flesh color and in contrast with the ventral part of body. Tongue: pink with black tips. Eye: pupil black narrowly ringed with gold; iris dark olive-brown in some to brown in others.

After being in preservative for more than 35 years the pattern features in this brood are now more sharply defined than when they were born.

VARIATION AMONG THE OTHER PARATYPES: Pattern notes were made on the 15 large females collected by shooting in 1960 (AMNH 85123–85137) as soon as they were preserved. All but one were dark. The dorsal stripes and spots could be made out only with difficulty. Ventrally, all but one were well marked. Dark crosslines occupied approximately the anterior third to half of each ventral. Most were solid black, but in a few snakes the crosslines consisted of dark stippling that slightly invaded the otherwise unmarked posterior pale green two-thirds or less of each ventral. The undersides of the tail and head were bright yellow. When re-examined in 1999, the preserved snakes looked much the same except for a small amount of fading. The pale snake (AMNH 85130, almost a meter in length) apparently lacked black pigment and it thus resembles the two males discussed below.

Three adults of *patzcuaroensis* lacked conspicuous ventral crosslines in life, viz.:

(1) AMNH 88713, a male 721 mm in length, collected August 15, 1960, hemipenes everted. The venter in life is depicted in figure 7. When examined in 1999, dark crosslines had appeared across approximately the anterior fourth of each ventral, a cu-

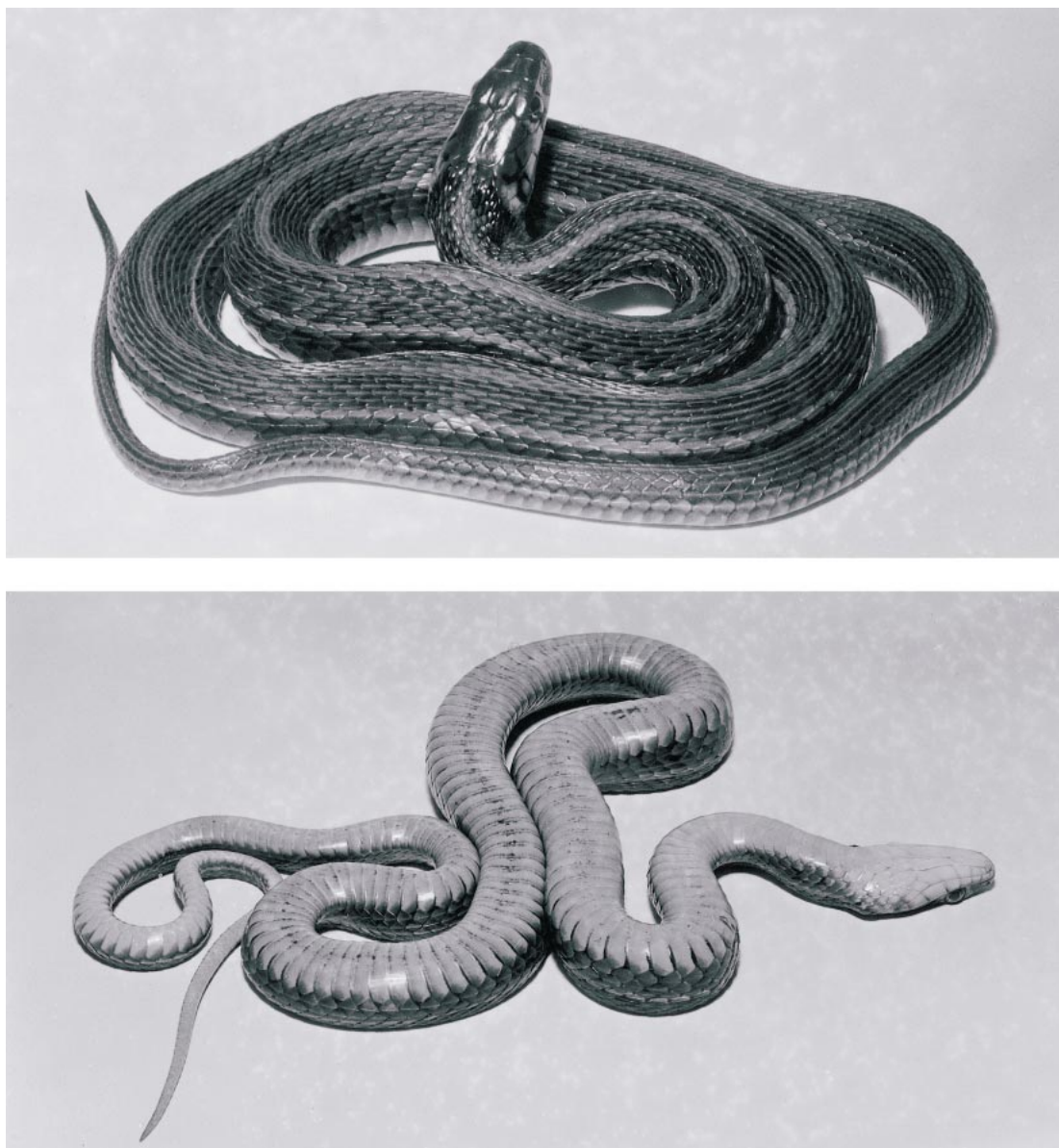


Fig. 7. **Upper.** Adult male of *Thamnophis eques patzcuaroensis* (AMNH 88713), 721 mm in total length, collected August 15, 1960, near the shore of the Lago de Pátzcuaro, 5 km southwest of Quiroga, Michoacán. The intensity of the pale longitudinal stripes is variable in this subspecies, regardless of sex. **Lower.** Venter of snake above, which had an aberrant pattern in life. After long preservation dark crossbands appeared matching those on the venter of the female holotype.

rious postmortem change. The faint dark longitudinal streaks on the midline of the belly were still visible. The following colors (capitalized colors from Ridgway, 1912) recorded from this snake in life are from my notes: "Middorsal stripe Dull Citrine. Lateral

stripes Light Elm Green. Dorsal ground color Brussel's Brown. Below lateral stripe Sudan Brown. Belly Light Hellebore Green. Chin Mustard Yellow. Top of head dark olive-brown. Anal plate and underside of tail Straw Yellow."

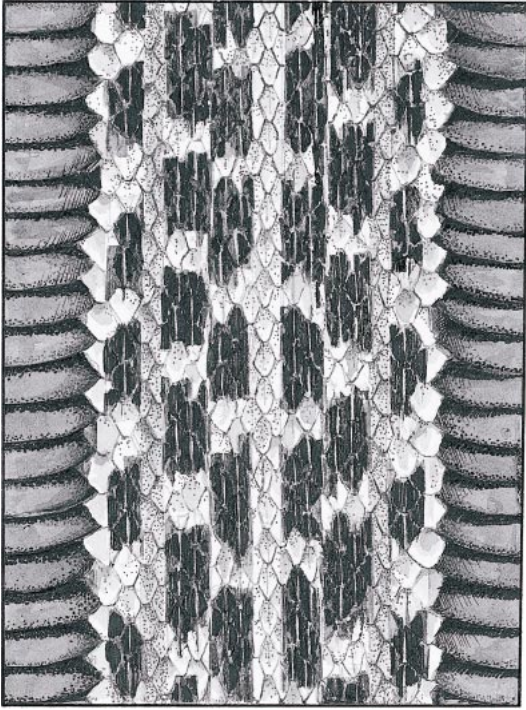


Fig. 8. Dorsal pattern of *Thamnophis eques insperatus* (AMNH 87550), 600+ mm in original length, from near Zacapu, Michoacán, found dead on the road and not in the best of condition, August 22, 1961. Drawing represents a section of skin from anterior third of body as though belly had been slit down its center, the skin loosened, and then stretched out flat. Head end toward top. Delineated by W.H. Brandenburg. (Unfortunately, this is the only available specimen from the Lago de Zacapu and its huge plexus of irrigation canals.)

(2) AMNH 58230, a male 896+ mm, collected at the lake by Rodolfo Ruibal on August 14, 1953. Despite its long period of preservation there apparently has been no change in pattern. The venter is still unmarked except for slight suggestions of crosslines.

(3) AMNH 85130, a female, 996+ mm, shot August 15, 1960. This snake lacks black pigment and the undersurfaces have no dark markings.

OTHER PARATYPES: Most of the remaining specimens are small and they resemble the neonates in general. They are chiefly dark but with patterns readily visible in some, obscure in others. In several, the lowermost row

of scales bears a continuous row of pale spots. The markings are best seen when the snakes are immersed in fluid. A female (AMNH 93936), 775 mm long, has all the pattern features strongly evident; like the holotype, fading in preservative apparently helped to bring them into sharp focus.

FOOD: Snakes of this subspecies eat fishes, salamanders, and doubtless other aquatic organisms. I palpated two fishes from snakes that had eaten them and sent them to Robert R. Miller for identification. Under date of November 23, 1960, he wrote, "The two specimens for Pátzcuaro are a viviparous goodeid, *Goodea luitpoldi*, and one of the pescados blancos, *Chirostoma estor*. These two families (Goodeidae and Atherinidae) have undergone explosive speciation in the 'Lerma System' of lakes and streams; the genus *Chirostoma* and virtually all of the numerous goodeids are confined to that basin."

Chacón (1993) stated that the "fish fauna [of the Lago de Pátzcuaro] consists of 10 native and 4 introduced species . . .". Smaller fishes and the young of all others are probably consumed by *Thamnophis eques patzcuaroensis* regardless of species.

LA LAGUNA DE ZACAPU

This body of water is a giant spring that forms a small lake and then flows rapidly outward to sustain a large network of irrigation canals to the east, northeast, and southeast (INEGI, Zacapu sheet, 1:50,000, 1998). According to Julio A. Lemos-Espinal (personal commun.), "The area around Zacapu is well known as an important crop field."

We passed through the town of Zacapu only once, on August 22, 1961. We were unaware of the lake's existence at the time. It did not appear on the road map we were using, and it did not come into focus for us until 1964 when the *Atlas Goodrich Euzkadi*, Caminos de México, was published. During the same year, the first volume of the *Handbook of Middle American Indians* (Tamayo with West, 1964) appeared with its map of the endorheic lakes as they were circa A.D. 1500. We planned to visit the Laguna de Zacapu later, but our fieldwork terminated abruptly when we returned from our 1965 trip to Mexico and I had to take over the

management of the Philadelphia Zoological Garden.

We were fortunate, however, in finding a DOR snake about 6 km southeast of Zacapu where a small branch canal passed under Mexico Highway 15 midway between Naranja de Tapia and Tirindaro. The specimen was doubtless a member of the Zacapu population of *Thamnophis eques*. It represents another new taxon, for which I propose the name below.

Thamnophis eques insperatus,
new subspecies
Figures 8, 9C

HOLOTYPE: AMNH 87550, a female found run over on the highway 6 km southeast of Zacapu, Michoacán, Mexico, on August 22, 1961, by Roger Conant. A torrential rainstorm was in progress at the time, but it had been hot and sunny all morning. The snake was slightly decayed. The epidermis sloughed off when it was injected and preserved in formalin. The head and forepart of the body are flattened and burst open in two places. The posterior half of the tail is almost severed from the rest of the snake. The snout-vent length is 467 mm; the estimated total length 605 mm. There are no paratypes.

ETYMOLOGY: From the Latin *insperatus*, meaning "unhoped for; unexpected".

DIAGNOSIS: A strongly checkerboarded garter snake with lateral spots black and alternated with pale grayish areas. Middorsal stripe present; lateral light stripes vaguely visible. The ventrals are black anteriorly, gray posteriorly (fig. 8).

DESCRIPTION OF THE HOLOTYPE: The scutellation agrees with that of The Species Model, with the following exceptions: Four postoculars on right side of head, lowermost extending slightly forward beneath eye. Some cephalic scutes distorted or slightly displaced as a result of being pressed against the pavement by a passing vehicle. An example: a movement of the third supralabial on the left that seemingly makes it enter the orbit.

No discernible apical pits; all apparently were sloughed off with the epidermis. Scales carinate throughout length of body and extending onto tail; keels weak on three lowermost rows of scales, possibly as a result of

sloughing. Scale rows 21-19-17, reducing to 19 by the loss of the fourth row at the level of ventral 83 on both sides of the body. Reducing again to 17 by the loss of the fourth row at the level of ventral 109 on left and ventral 110 on right. Ventrals 155 plus a single anal plate. Subcaudals uncountable; posterior half of tail badly mashed. Tip of tail sharply pointed.

Dorsum strongly checkerboarded with black "rectangles" conspicuous against a pale grayish background (fig. 8). Over a large part of the body each black rectangle involves three transverse dorsal scales and the length of a scale or a scale and a half longitudinally. There is frequent variation and there are no sharp 90° angles. The general effect is as though the dark spots commonly present between the pale longitudinal stripes in various species of *Thamnophis* had greatly increased in size and intensity at the expense of the stripes. The central stripe occupies the middorsal row of scales and the adjacent halves of the paravertebrals, but it is less conspicuous than in most other forms of garter snakes. Its pale scales are "dusted" with flecks of pale gray. Labials yellow and matching the yellow of the chin and throat. Black lines extend downward, chiefly anterior to the sutures between the labials, but they reach the commissure only on labials 7 and 8. The eighth supralabial is mostly black posteriorly. A partial yellow crescent marked with a few tiny black stipplings curves forward and upward behind the angle of the mouth. It is followed by a black area two scales wide that extends upward to the pale middorsal stripe. There are three rows of black rectangles on each side of the body. A narrow, more or less continuous black line extends along scale row 7 and then row 6 on the posterior half of the body.

The undersurfaces match snakes from other lakes in the Cuenca de Michoacán. Anteriorly, each ventral is black but the dark pigment is not as wide as in *patzcuaroensis*. Posteriorly, the ventrals are gray but not as dark as in *cuitzeoensis* (fig. 9C). The underside of the tail in the holotype is yellowish cream.

A close look at figure 8 reveals the pale middorsal stripe common to most populations of the *Thamnophis eques* complex.

Less conspicuous are faint indications on scale rows 3 and 4 of lateral stripes. The many black markings appear to represent the dark spots between and beneath the stripes. The resultant drawing bears an almost uncanny resemblance to many of the nine faded, century-old AMNH specimens from Guadalajara. See the discussion about them at the end of the section on *diluvialis*. The snake depicted lost its epidermis through sloughing as the result of minor decay. Of all the forms of *Thamnophis eques* examined in this study of variation of *Thamnophis eques* in Mexico's transvolcanic belt, this is the only one not seen both in life as well as preserved. How regrettable that no other specimens of *insperatus* were obtained, and even more regrettable was my inability to return to Zacapu after 1965.

LA CUENCA DE MICHOACAN

Tamayo with West (1964: fig. 4) delineated the basins of interior drainage in the transvolcanic belt of Mexico, and the *cuenca* (basin) of Michoacán occupies the center of their map. Four lakes of various sizes are indicated within it.

Much of the preceding text is concerned with snakes we obtained in the basin. Good study samples are available from the Lagos de Cuitzeo and Pátzcuaro, but we have no specimens from the Laguna de Zirahuén, and only the single one found DOR and slightly decayed from the vicinity of Zacapu. Incomplete though the material may be, it is sufficient to permit the following generalizations:

(1) The snakes from any one of the endorheic lakes in the basin are different in coloration and pattern from those of the other lakes. Their isolation, over possibly millions of years, has enabled them to evolve into distinguishable populations. In the two lakes, Cuitzeo and Pátzcuaro, from which ample study material is available, they are so different from each other and from the widespread *Thamnophis eques eques* that they warrant new subspecific names. The single imperfect specimen from near Zacapu represents another new taxon. In brief, the chief differences are as follows: at Cuitzeo all snakes, even the newborn, are strongly mel-

anistic except for the undersurfaces of the heads and tails, which are white; at Pátzcuaro pale middorsal and lateral stripes are present, as well as paired dark lateral spots, although such pattern features are variable—the undersides of the heads and tails are yellow; and near Zacapu the dorsal pattern is checkerboarded. The assumption that snakes from Zirahuén are also different remains to be demonstrated. If the species occurs there it may resemble the population from nearby Pátzcuaro.

(2) After reviewing all our material from the Michoacán basin of interior drainage, it is apparent that a significant pattern feature is the presence, in all specimens, of a long series of conspicuous, usually black, crosslines on the venter.

In the widespread *Thamnophis eques eques* and *T. e. megalops* there usually is a narrow dark line across the anterior edge of each ventral, but it may be hidden by the imbrication of the ventral preceding it, and the venter may appear to be unmarked. When we photographed such specimens in a supine position, however, the narrow black line was often visible at bends of the body, as delineated in figure 9D.

In some specimens from other lakes of the transvolcanic belt, notably the very large free-flowing Lago de Chapala and its nearby lakes, dark crosslines may be clearly visible, but they are not nearly so wide in comparison with those occurring in *cuitzeoensis*, *patzcuaroensis*, and *insperatus*. Wide ventral crosslines may occur in other populations of the *Thamnophis eques* complex, but in all the hundreds of snakes I have examined from throughout the extensive range of the species the crosslines are not as broad and conspicuous as in the Michoacán basin. Semidiagrammatic renderings are in figure 9.

Scale counts are comparable in *cuitzeoensis* with those of *patzcuaroensis* and *insperatus*, and they also fall within the counts of the wide-ranging *eques* complex (Rossman et al., 1996: 174).

In summary, three new taxa are described from Michoacán. Their main points of difference are as follows:

(1) *Thamnophis eques cuitzeoensis* from the Lago de Cuitzeo. This is a strongly melanistic snake. Adults are jet-black dorsally.

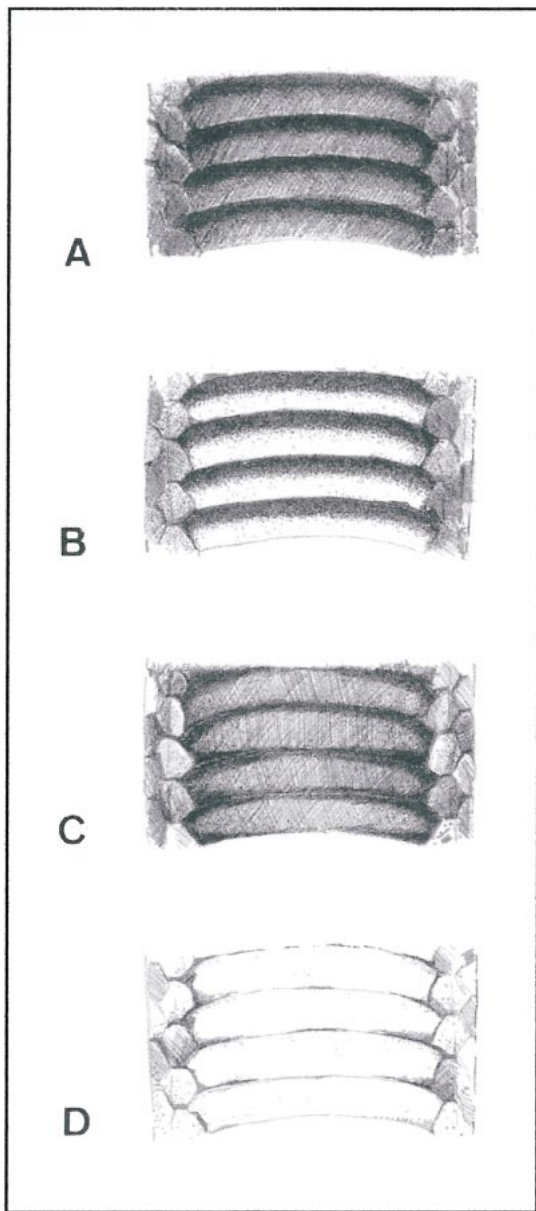


Fig. 9. Semidiagrammatic drawings of individual ventral scutes of snakes from the Cuenca de Michoacán. (Delineated by W.H. Brandenburg.) **A.** *Thamnophis eques cuitzeoensis*. Anterior edge (upper) black; posterior very dark gray. **B.** *Thamnophis eques patzcuaroensis*. Broad anterior dark, usually black; posterior portion light and in strong contrast with remainder of scute. **C.** *Thamnophis eques insperatus*. Anterior black but not as wide as in *cuitzeoensis*; posterior medium gray. **D.** *Thamnophis eques* ssp. Not from the Cuenca de Michoacán but included for contrast.

In the very young the labials are yellowish with black lines on the sutures between the individual scales; sometimes there are also pale longitudinal stripes near the head. As they grow, the markings turn black. Ventrally, the tail, chin, and throat are unmarked and whitish. The remainder of the venter consists of broad black anteriors on each ventral; posteriorly, each ventral is dark dray. Intergradation with *Thamnophis eques eques* occurs in the Lago de Yuriria, a small manmade lake about 30 km north of the Lago de Cuitzeo.

(2) *Thamnophis eques patzcuaroensis* from the Lago de Pátzcuaro. Members of this taxon are striped and spotted. A pale mid-dorsal stripe occupies the middorsal row of scales and adjacent halves of the paravertebral stripes, and there is a lateral stripe on each side of the body on scale rows 3 and 4 anteriorly and row 3 posteriorly. Between the stripes are two rows of dark spots on each side of the body. Juveniles are usually well patterned, but there is a tendency dorsally toward melanism among larger individuals, females especially. Ventrally, dark crosslines are conspicuous. The anterior third to a half of each ventral scale is very dark, usually black. The remaining posterior part of each scute is pale. The underside of the tail, chin, and throat are yellow, often brilliant, but paler in young specimens. Darker adults of *patzcuaroensis* bear a slight resemblance to individuals of *cuitzeoensis*, but when they are turned upside down the difference is striking. The dark ventral crosslines are conspicuous and unlike the dark bellies in *cuitzeoensis*.

(3) *Thamnophis eques insperatus* from near the Laguna de Zacapu. With only one imperfect specimen available, no general description of this taxon is possible. It apparently is heavily checkerboarded dorsally and lacks conspicuous lateral light stripes. In its ventral pattern, however, it shows a strong affinity with other taxa inhabiting the Cuenca de Michoacán.

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In most populations of *Thamnophis eques* the black pigment consists of a narrow dark line at the extreme anterior edge of each ventral and is more or less hidden by the imbrication of the preceding ventral.

With no material from the Laguna de Zirahuén, if the species actually occurs there, comment about it is futile.

EL LAGO DE CHAPALA

This, the largest lake in Mexico, measuring 80 km east–west and 20 km in width, lies chiefly in the southwestern state of Jalisco, except for a short southeastern extension into Michoacán. Unlike its small lacustrine neighbors, it has a major affluent, the Río Lerma, flowing in from the east. Almost due north, near Ocotlán, the water exits as the Río Grande de Santiago that flows onward to the Pacific Ocean. In essence, there is only a single river, the longest in Mexico, despite the two designations. More or less midway in its course, it supports an enormous body of shallow water, El Lago de Chapala.

De Buen (1945) conducted hydrologic studies at the lake in April 1943 and reported the depth as 9.8 m at the west end and 8.0 m at the east end. His party recorded pH readings at various depths, averaging about 9. The Lago de Chapala occupies an east–west-trending graben, the time of origin of which is in dispute. Palmer (1926) suggested the Pleistocene or late Pliocene, but admitted that his conclusion was partly speculative. Clements (1963), whose paper was on the Pleistocene of the region and his personal observations on the geology of the basin and the surrounding hills and highlands, reached a similar but firmer conclusion. In contrast, Urrutia-Fucugauchi and Rosas-Elguera (1994), based on paleomagnetic studies, suggested that the Chapala graben developed early in the Miocene.

The normal elevation of the lake during the 1960s was about 1525 m. Geological evidence, however, indicates that during the Pleistocene the Lago de Chapala shrank to virtually nothing at times and contrariwise increased vastly in size depending on tectonics, climatics, local wet and dry cycles, and increment from the Río Lerma and its vast catchment basin. According to Clements (1963), the lake rose as high as almost 200 m above its current level on one occasion and at other times to approximately 150 and 100 m above, spilling over into neighboring

areas. Remnants of the latest flooding are represented by a series of small lakes west, northwest, and southwest of the big one (see fig. 10). For a long time the outlet from the Lago de Chapala was at its western end.

The members of the *Thamnophis eques* complex discussed previously in this paper occupy a basin of interior drainage, the Cuenca de Michoacán, within which there are four lakes, all isolated from one another by volcanism probably for millions of years. There was ample time for differentiation of their respective but related aquatic and semi-aquatic organisms.

The free-flowing Lago de Chapala with its satellite lakes to the west obviously has had a vastly different physiographic history.

Thamnophis eques was abundant at the Lago de Chapala when we worked there during the period from 1959 to 1965. Not only was it encountered along or near the shoreline, but it also swam freely far out in the open lake.

Because of the suppression or complete loss of the pale striped pattern so common to most other populations of *Thamnophis eques*, I propose for the members of the complex inhabiting the Lago de Chapala the name below.

Thamnophis eques obscurus, new subspecies

Figures 10, 11

HOLOTYPE: AMNH 87543, a moderately large male from the town of Chapala, Jalisco, Mexico, collected August 29, 1961, by Roger and Isabelle Hunt Conant. Total length 762 mm, tail length 179 mm, tail/total length = 0.235.

PARATYPES: All from or near settlements bordering the Lago de Chapala. Chapala AMNH 82032–82046, 87544, 87545, 91693–91695; Jamay AMNH 19544, 19545; Jocotepec AMNH 87546, 87547, 96841–96845; 10 km northeast of Sahuayo AMNH 93958.

ETYMOLOGY: From the Latin *obscurus* in reference to the faintness to complete absence of pale longitudinal stripes.

DIAGNOSIS: A virtually stripeless race of *Thamnophis eques*. Adults in life lacked pale longitudinal dorsal stripes (fig. 11). A few

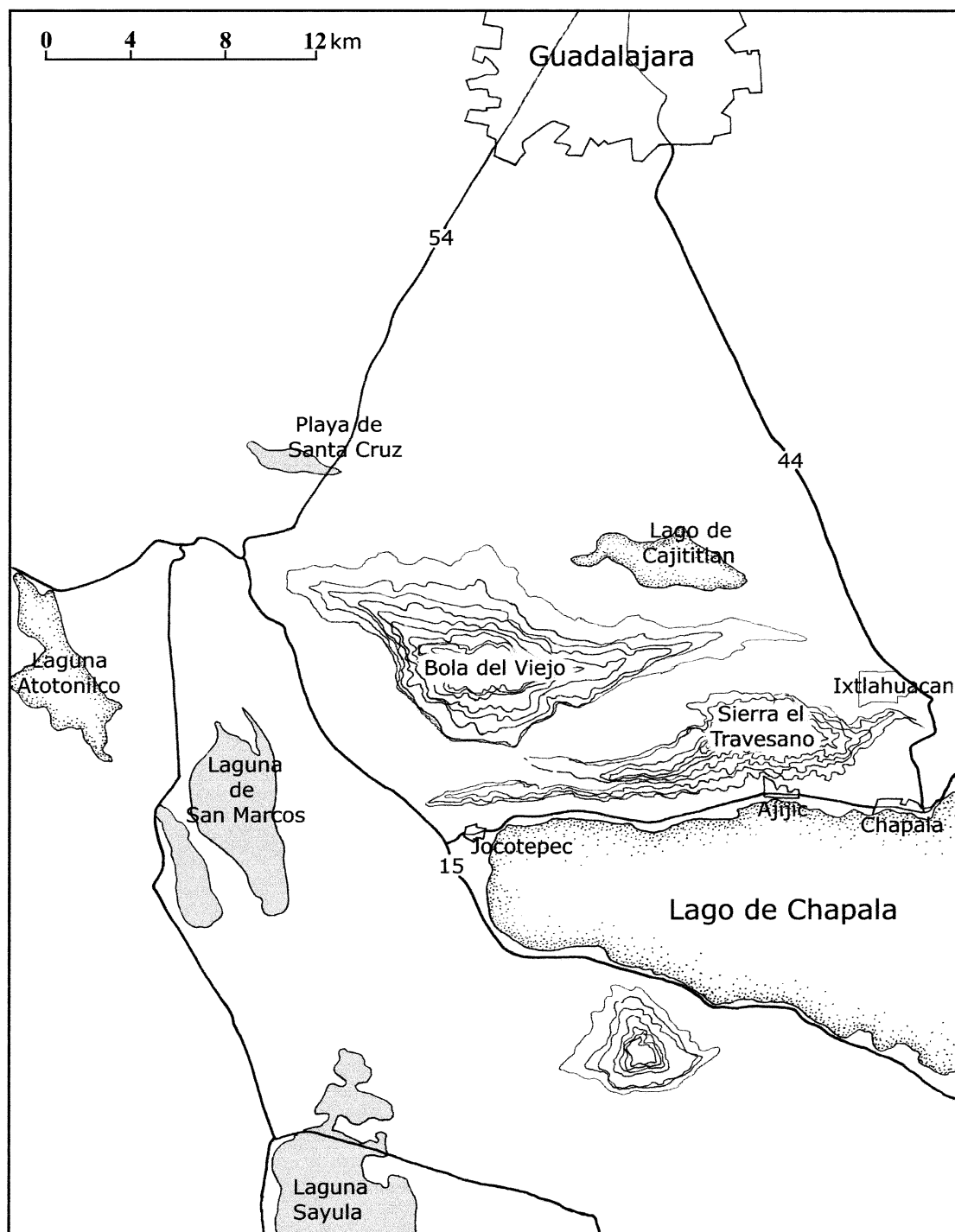


Fig. 10. Map of the western end of the Lago de Chapala and several small satellite lakes, all in Jalisco. Delineated by W.H. Brandenburg.



Fig. 11. **Upper.** Adult female of *Thamnophis eques obscurus* (AMNH 91693), 834 mm in total length, from the Lago de Chapala, collected July 15, 1959, at the town of Chapala, Jalisco. Note the complete absence of pale longitudinal stripes. **Lower.** Venter of same snake. The anterior of each ventral scute is dark but not nearly as wide as in the snakes from the Cuenca de Michoacán.

preserved for many years show faint traces of lateral stripes that now appear bluish. There is no indication of a middorsal stripe in any adult of the sample available. In the young, arbitrarily considered as all specimens less than 300 mm in total length, there may be traces in life of pale stripes immediately posterior to the head.

The venter is grayish and the anterior edge of each ventral scute is black or dark gray (fig. 11). The resultant crossbanding is prominent, but the components are narrower than those on the venters of snakes from the Cuenca de Michoacán. The chin, throat, and underside of the tail are white and more or less unmarked. The anal plate is undivided and usually white in color, but it is dark in a few specimens.

DESCRIPTION OF THE HOLOTYPE: Scutellation the same as that of The Species Model, with the following exceptions: Postoculars 4 on left side of the head instead of 3. Three

temporals in second row (on left); 2 on right, but with a small scale about as large as the lower secondary temporal wedged between the anterior temporal and the parietal. Scale rows 21-19-17, reducing to 19 by the loss of the fifth row at the level of ventral 81 on the left and the loss of the fifth row at the level of ventral 77 on the right. Reducing again to 17 by the loss of the fourth row at the level of ventral 94 on the left and ventral 98 on the right. Total ventrals 158; subcaudals 73. Both hemipenes everted and of similar shape and appearance as in figure B in Rossman et al. (1996: 32). A summary of scale counts and other data for the entire sample from the Lago de Chapala is in table 3 (also see the Discussion). One of the 31 specimens, AMNH 93958 from near Sahuayo, was found DOR and was so badly damaged that few data could be recorded from it. Some of the others had incomplete tails.

The holotype was preserved in the field,

TABLE 3
Variation in Scutellation and Tail Length Proportions in *Thamnophis eques obscurus*, New Subspecies

	Males (7) ^a	Juvenile males <300 mm (4)	Females (12 or 13)	Juvenile females <300 mm (7)
Scale rows	21-19-17 (7)	21-19-17 (4)	21-19-17 (5) 21-23-21-19-17 (6) 23-21-19-17 (1)	21-19-17 (5) 21-23-21-19-17 (2)
Ventrals	158–166 (7) \bar{x} = 161.7	161–165 (4) \bar{x} = 162.8	150–159 (13) ^b \bar{x} = 155.2	153–160 (7) \bar{x} = 157.0
Subcaudals	69–89 (5) \bar{x} = 76.8	77–80 (3) \bar{x} = 78.7	62–73 (11) \bar{x} = 66.3	63–74 (7) \bar{x} = 66.7
Supralabials	8 (10) 9 (4)	8 (8)	8 (22) 9 (2)	8 (14)
Infralabials	10 (12) 11 (2)	10 (8)	9 (2) 10 (16) 11 (6)	10 (13) 11 (1)
Preoculars	1 (14)	1 (8)	1 (24)	1 (14)
Postoculars	3 (10) 4 (4)	3 (7) 4 (1)	3 (18) 4 (6)	3 (11) 4 (3)
Temporals, 1st row	1 (14)	1 (8)	1 (24)	1 (14)
Temporals, 2nd row	2 (2) 3 (12)	2 (4) 2 (4)	1 (1) 2 (9) 3 (14)	2 (9) 3 (5)
Tail/total length	22% (1) 23% (1) 24% (2) 25% (1)	23% (1) 24% (2)	20% (2) 21% (3) 22% (5) 23% (1)	21% (1) 22% (3) 23% (3)

^aFigures in parentheses indicate sizes of samples.

^bIncluding DOR samples.

unfortunately just before unsuspected ecdysis. I had selected a large male as the type, but when I reexamined it in 2000 two soft spots had developed, probably because formaldehyde had not been injected evenly by the person who preserved it. Although the holotype had shed its scales (the stratum corneum) in part, many of the dorsal scales remaining in situ show evidences of apical pits.

This is a dark brown snake that, in life, showed no signs of a striped pattern but, as in other long-preserved adults, there is a faint bluish gray line on each side of the body on scale rows 3 and 4 anteriorly and 2 and 3 posteriorly, where a prominent pale lateral stripe would have appeared in a living specimen of *Thamnophis eques eques*, for example. The top and sides of the head are dark brown, and the upper labials are dark gray and virtually unmarked. The two lowermost

rows of scales have light centers, but these markings are weak in comparison with several other preserved adults.

The anterior edge of each ventral is dark gray, almost black, and collectively is part of a long series of crosslines that show clearly through the overlapping part of the preceding scale. The unmarked posterior part of each scale is medium gray in coloration.

The chin, throat, and infralabials are pale yellow, but the throat is invaded by dark pigment on the two scales preceding the first ventral. There are small black markings on about half of the infralabials. The underside of the tail is also pale yellow, but the outer edges of the first 25 subcaudals are slightly marked with pale brown.

The anal plate is mostly pale yellow, but the dark pigment of the belly scales intrudes slightly on the right side of the body.

VARIATION AMONG THE PARATYPES: This subject is discussed in part under the diagnosis of *obscurus*, but there have been a few notable postmortem changes. Most conspicuous is the development of a row of light spots on each of the two lowermost rows of scales in all of the large- and medium-sized snakes collected during the 1959–1965 period when we visited the Lago de Chapala. The edges of the scales in the two lower rows are dark, whereas the centers are pale, even white. The two light rows of spots are conspicuous in some specimens, less so in others. In the case of AMNH 91693, the two rows of light spots barely showed in life (fig. 11). When examined in 2000, after being preserved in 1959, the light spots were prominent throughout the length of the body, especially on the lowermost row.

The two oldest specimens (AMNH 19544, 19545), preserved in 1919, have faded to dull gray. Most of their dorsal scales are edged with dark pigment, but the centers are pale. A faint suggestion of lateral stripes is gray rather than bluish.

Juveniles in life were pale to medium brown dorsally and grayish ventrally. Faint markings appeared dorsally in the form of light stripes near the head. After a long period of preservation most of them now show evidences of both striping and spotting. A particularly well-patterned juvenile female (AMNH 91694), collected at the town of Chapala on July 15, 1959, has faint middorsal and lateral stripes extending rearward to the tail. There are also small brown spots in two longitudinal rows occupying the areas between the faint stripes, and measuring about one scale in width and two scales in depth. There is also a smaller row of brown spots below each lateral stripe. The chin, throat, anal plate, and underside of the tail are unmarked yellow.

The coloration in life of three snakes from Jocotepec (AMNH 96842, 96844, 96845) was recorded, one soon after our return to base in 1965 and the others after they had been held in captivity for about a year. The following is a condensation of longer descriptions (capitalized color names are from Ridgway, 1912): Dorsal ground color olive. Lateral ground color Light Brownish Olive. Top of head olive. Labials Pistachio Yellow,

sutures black. Belly Deep Bluish Gray-Green. Lines across ventrals black. Under-side of tail Olive-Buff. Chin and throat pale greenish yellow. Eye: Pupil black ringed by bright yellow, iris olive. Tongue: Dragon's-blood red, tips black.

Brumwell (1939) published a paper on variation in *Thamnophis macrostemma* (= *T. eques*) which included material from Chapala, lake or town not stated. The specimens he examined were from the Edward H. Taylor–Hobart M. Smith collection preserved in earlier years, and his descriptions of them matched those of mine after my snakes had been preserved for decades. According to Brumwell, all juveniles were strongly patterned and the adults had developed pale lateral lines. Neither was true when my snakes were alive. What an advantage I had in being able to study the snakes in life and again after there had been strong postmortem changes.

REPRODUCTION: At each of the other lakes in Mexico's transvolcanic belt where we collected series of specimens, gravid females were included. We kept them alive until the birth of their young, which were measured and weighed. No such females were found at the Lago de Chapala and thus no data are available on dates of parturition or number of young in *obscurus*. Several small specimens were obtained during July 1959 at the town of Chapala, some of them in storm sewers. The smallest was 244 mm in total length and another, with much of its tail missing, was 219+ mm. Based on measurements of newborn snakes from other lakes of the region, virtually all the juveniles we and others caught at Chapala were probably recent neonates. The largest specimen, a female also from Chapala, measured 1216 mm in length soon after it was preserved in 1959.

BEHAVIOR: We made pertinent observations on behavior, some of which did not come into focus until the end of July 1965, when we left the Lago de Chapala for the last time. Others, notably Allen G. Brown, had watched the snakes for hours and he permitted me to record many of his observations in my notebook. In the company of the late Charles M. Bogert, Brown and two other students spent a few weeks during 1959 doing

fieldwork in the area. We joined them for a few days.

The town of Chapala is a resort on the lake roughly 40 km southeast of the large city of Guadalajara. A pier with benches and a ramada extended into the lake, and on weekends it was frequented by many people. Both observation and collecting were possible, the first by day, the second by night. I caught the holotype and two other *eques* by leaning over the edge of the pier at night and using my headlamp. The water was too low for me to reach it, but my wife, Isabelle, clung to my ankles, which gave me enough extra distance "to accomplish the impossible", as she recorded in her diary.

Brown (personal commun.) stated that it was normal to see the snakes swimming in the open water from the pier, sometimes far from shore, and even quite small ones moved about on the surface. He also said he watched several of the snakes swim toward the pier across wide stretches of open water. They would advance leisurely until they neared the pier, when they apparently detected motion and possible danger. They came right up to the pier at night. Brown and another student caught AMNH 82037, a female 654 mm in length, swimming far out in the open lake during daytime roughly midway between Chapala and the relatively distant Isla de Alacranes.

The available sample from the Lago de Chapala of 31 *obscurus* contains 11 males and 20 females ranging from neonates to large adults, including a heavy-bodied female 1216 mm (almost 4 feet) in length. This is a small number in view of the fact that we visited the lake during the summers of 1959, 1961, and 1964, and were in residence at Jocotepec at its western end for almost the full month of July in 1965. We rented a cottage for a headquarters from which we visited the Lagunas de Atotonilco and Cajititlán and the remnants of the Lago de Magdalena, and we collected almost all the way to the Pacific coast near Tepic. While we were in Jocotepec, I obtained much useful information about the behavior of *Thamnophis eques obscurus*, almost all of it negative. During the early evening of each of the many nights we were in residence I waded in the shallow water at the edge of the lake looking for snakes.

The relatively small *Thamnophis melanogaster* was abundant and found during every foray, 11 in one evening. It was also available by day, chiefly hidden among rocks or under clumps of vegetation near the water's edge. *Thamnophis eques* was conspicuous by its absence. I failed to obtain any of that species until the very end of the month when the level of the lake began to rise (about 15 cm in 24 hours on July 27–28). Meantime, a strong east wind drove water into areas that had remained dry all month. On the evenings of July 29–31 I found five *obscurus*, two of which were gorging themselves on small fishes that had ascended new channels into formerly dry territory. The following paragraph is condensed from my fieldnotes.

A pattern has emerged. While the lake was low *melanogaster* was conspicuous, *eques* totally absent. Apparently, *melanogaster* is adapted to a riparian habitat that it exploits year round. Contrariwise, *eques* remains quiescent during the dry season. I had explored the landward side near Jocotepec to where there were weed-choked fields through which a machete would have been necessary to penetrate. The four *eques* I found nearby were along a narrow ditch where many fishes, which had worked their way upstream when the wind and waves propelled water inland, were trapped when it receded. Does the *eques* population go through some form of estivation during dry weather? At least at the western end of the Lago de Chapala?

According to word received from Joseph Jordan of Jocotepec, our landlord for the cottage we occupied, Lake Chapala rose to a very high level after our departure on August 2, 1965. In a letter dated December 16, 1965, he admonished me, "When you make your next visit, do it in August or September, as the lake is real high and there are thousands of large snakes swimming wherever you look, and every little wash has several snakes in it. The lake, by the way, is at its highest level in twenty-one years, and my lower property is under five feet of water. It crossed the road in several places, but it is receding a little now."

The Jordans were a middle-aged couple and members of the large American colony in the towns of Ajijic, Chapala, and Jocotepec on the shore of the lake. They owned

considerable property, including the weed-choked fields I could not penetrate. I had indoctrinated them soon after we first met in 1964 and had shown them several living examples of the two "water" snakes. I feel confident that Jordan's "thousands" of large snakes were *Thamnophis eques obscurus*.

When the water was rising, Paul Ruthling collected two *eques* along the edges of flooded fields near Jamay at the eastern end of the lake on August 19, 1919. These are AMNH 19544 and 19545, about the first of which Ruthling wrote (personal commun.), "It was very large and fat and 42 inches long." Snakes approaching or exceeding a meter in length from the Lago de Chapala were all large in girth and heavy bodied, as indeed are large snakes from other lakes of the general region.

It is obvious that *obscurus* is a common snake in the Lago de Chapala despite the small size of our sample. Our experiences confirmed once again that "the collector must be in the right place at the right time."

A unique feature of the Lago de Chapala in 1959 was the presence of huge masses of water hyacinths of giant size covering the western half of the lake and completely halting all navigation. Manatees, *Trichechus manatus*, were introduced to eat the hyacinths and by 1965 the pestiferous plants were no longer a menace.

FOOD: The following is quoted from correspondence with Robert R. Miller: "The tiny fish trapped by receding waters of Lake Chapala include 12 juveniles of *Goodea atripinnis*, 2 young of *Chapalichthys encaustus*, one young of *Allophorus robustus*, and 6 young of *Poeciliopsis infans*. The first 3 belong to the family Goodeidae, the last to the Poeciliidae." I sent the fishes to him in October 1965. Probably any fish small enough to swallow would be eaten. No evidence is available about other food such as frogs, salamanders, and invertebrates. Captives fed on frogs.

WHAT OF THE FUTURE?: There have been many changes at the Lago de Chapala since we worked there in the 1960s. It is the principal water source for Guadalajara, Mexico's second largest city. Water also is drawn for the production of electricity. Pollution is acute. León and Escalante (1993) stated that

the inflow stream, the Río Lerma, "drains a basin of almost 52,500 km² receiving urban, agricultural, and industrial untreated waters." The inflow to the shallow Lago de Chapala is highly polluted. Many native fishes have been locally extirpated and exotic species now constitute a large part of the catch. What effect are all these problems having on the population of *Thamnophis eques obscurus*?

LAS LAGUNAS DE ATOTONILCO Y CAJITITLÁN

Northwest of the Lago de Chapala are two small lakes, from each of which we obtained series of specimens of the *Thamnophis eques* complex that proved to be of exceptional interest because they are markedly different from those of the nearby big lake.

The Laguna de Atotonilco, highly irregular in shape, lies south of the settlement of Villa Corona, which has an elevation of 1350 m above sea level. The lake's longest dimension, roughly northwest-southeast, is 13 km and its widest, toward the south, is about 6 km. Collecting both in 1964 and 1965 was exclusively at night at the north end of the lake. Fishermen cleaned their catches along the shore; flies and other insects congregated and they, in turn, attracted anurans. Some of the snakes were in shallow water actively swimming; others were secreted beneath an old boat. Using my headlamp, I stalked one, well in excess of a meter in length, until I was close enough to grab it even as it bit me savagely. It was the most continuously aggressive of the many *T. eques* I kept in captivity. The pH of the lake was 9 and the temperature of the water was 30° at 9:30 PM when tested in 1964; both figures were exceptionally high.

The Laguna de Cajititlán lies about 30 km almost due east of Atotonilco and its eastern extremity is 12 km north of Ajijic on the shore of the large Lago de Chapala. It has an east-west orientation and is 10 km in length, including a narrow neck of about 2 km at its western end. Its greatest width is approximately 4 km. During our visits in 1965 (July 15 and July 28) the part of the Laguna de Cajititlán adjacent to the village of the same name (elevation 1560 m) was clear and open, but its western end was a jungle of tules and

smaller emergent vegetation. Boats of several sizes, including a large one with an outboard motor, were available. We tried several, but the prows of all were so high and sharply pointed that it was awkward to try standing with a long-handled dipnet hoping to lift a swimming snake. The ubiquitous boys who appear like magic whenever a gringo stops to do anything in Mexico and a lad whose father owned the powerboat came to our rescue. They stripped to their shorts, went overboard, grabbed snakes, and tossed them into my boat where I could catch them. We obtained 11 large *Thamnophis eques*, most from near the tules, some of which had broken horizontal reeds that were good perches for basking snakes. Another specimen was caught at night eating a small fish discarded by a fisherman, and identified as *Chapalichthys encaustus* by Robert R. Miller. The cloacal temperature was 24.2°; the water nearby was 24.7°. We made no attempt to record data for the snakes pursued by the boys and thrown into the boat.

We took samples of tules home with us. They were identified by Alfred E. Schuyler of the Academy of Natural Sciences of Philadelphia as *Scirpus californicus* which, despite its name, we were told is fairly common throughout northern and central Mexico.

The Cajititlán snakes matched those from Atotonilco in pattern and coloration. All had three longitudinal stripes. The middorsal one was wide and conspicuous. It involved three rows of scales, the vertebral and paravertebrals and, in a few cases, it even extended onto the edges of the adjacent scale rows so that the width of the dorsal stripe could be scored as 3+ instead of 3.

Clements (1963), based on his carefully researched "Pleistocene history of Lake Chapala" and the hills and mountains surrounding it for a considerable distance away, showed that during the Pleistocene Chapala "rose to a level almost 200 meters (656 feet) above the present lake level, spilling over into neighboring basins to the north and west and extending several kilometers farther into the state of Michoacan than now." Clements also pointed out that presumably during the Wisconsin glacial age the water rose to "a level approximately 150 meters (492 feet) above the present lake level." The high lev-

els of the Lago de Chapala in times past must have created vast habitats for aquatic and semiaquatic organisms.

During our month's residence in 1965 at Jocotepec at the west end of the big lake, and after we learned there was a population of *Thamnophis eques* at Cajititlán, we became curious about whether that snake occurred elsewhere in the vicinity. Both our resident American and Mexican friends were skeptical. They said the area was very dry and not suitable for "water" snakes. We went exploring, however, chiefly driving along roads, and the vegetation of the region confirmed the semi-aridity. Someone mentioned a pond near Estipac west of the Laguna de Atotonilco. We drove to that settlement and, with the aid of a local resident, hiked ~2 km to a small pond where I caught a young snake (AMNH 94964). Subsequently, I found two adults at Acatlán de Juárez (AMNH 94924, 94925) along ditches through a small swampy area. After our return to home base, a review of the snakes collected by the Bogert party in 1959 revealed another taken approximately 8 km west of Ixtahuacán de los Membrillos, which is south of Cajititlán and only 6 or 7 km north of the Lago de Chapala, but separated from it by the Sierra el Travesano. That snake (AMNH 91692) is strongly striped (see fig. 13, lower) and very different from the stripeless ones inhabiting Lago de Chapala. These scattered localities suggested that the snakes of the Atotonilco-Cajititlán complex once ranged widely across a former large lake, as Tamayo (1949, II: 416-417) wrote (translation): "It is possible to suppose that the Lagunas Atotonilco and Cajititlán constitute the residue of an old large lake."

Douglas A. Rossman (personal commun.) reported that he and his students found another locality. They were driving southwest from Guadalajara on May 29, 1969. The highway passed over a pond on which they saw swimming snakes. Investigation revealed that *Thamnophis eques* was numerous. Seven *eques* and four *T. melanogaster* were collected and are now at Louisiana State University (LSUMZ). The environs of the small body of water were extremely dry and some of the snakes had taken shelter under thorn bushes. The locality was the east-

ern tip of the Playa de Santa Cruz, an intermittent lake 5 km long that probably remained dry except after periods of heavy rain. There must have been a place, however, where the snakes could retreat (estivate?) during long dry periods.

In both 1964 and 1965, we attempted to explore some of the other small lakes south of Atotonilco, but we were blocked by deep mud at the Laguna San Marcos, and the Laguna Sayula was too saline at the time to support snakes and their food animals. The lower lakes apparently are gradually drying up. On a map published in 1973 (DETENAL, Guadalajara sheet, 1:250,000), the Laguna Sayula is marked with hatching, indicating it is intermittent, containing water at times but dry at others. On a more recent map dated 1998 (INEGI, Guadalajara sheet, same scale), Sayula, San Marcos, and Zacualco, which parallels San Marcos in part, are now all intermittent. Atotonilco and Cajititlán appear to remain much as we had found them. With only rains, a few springs, and small, mainly intermittent streams for increment, the entire area continues to desiccate.

Guerrero (1964), in his "Esquema geográfico de México", included a map showing the wet and dry zones of his country. Except for a small area adjacent to Nayarit, he designated all of Jalisco as semiarid.

Lago Cajititlán, a large and well-illustrated paperback written by Ramón Rubín and published in Guadalajara in 1960, reviewed the history of the lake in both Spanish and English. Rubín stated that the lake was 25 km due south of Guadalajara and that its surface occupied 16 million square meters. Following the Spanish Conquest, five small towns were established around the lake and remnants of their churches and other structures survived, some in excellent condition. In early times, fishing and agriculture along the lake's perimeter were the principal activities. In the late 1940s, there was a strong movement in official Mexico to drain lakes to provide more farmland. Cajititlán was emptied, but trying to cultivate the slimy, muddy lake bottom was a dismal failure. Concurrently, there was a bitter battle to save the huge Lago de Chapala from a similar fate. In time, Cajititlán was refilled and re-

stocked, largely with exotic fishes. The snakes, presumably from small relict habitats nearby, eventually returned.

In all individual populations of *Thamnophis eques* summarized thus far the samples at hand were from separate lakes that are isolated in one way or another from other lakes of the transvolcanic belt. In the case of the Atotonilco-Cajititlán population, its range has been fragmented into two lakes and several isolated localities, all being remnants of a former large body of water that apparently is shrinking as aridity increases. For this unusual group of snakes with an unorthodox distribution I propose the name below.

Thamnophis eques diluvialis,
new subspecies
Figures 10, 12, 13

HOLOTYPE: AMNH 93966, a medium-large male from near Villa Corona at the north end of the Laguna de Atotonilco, Jalisco, Mexico, collected August 16, 1964, by Roger Conant. Total length 756 mm, tail length 175 mm, tail/total length = 0.231.

PARATYPES: Several gravid *diluvialis* gave birth to young after our return from Mexico. Each mother's number below is followed in parentheses by the numbers of her offspring. One female from Atotonilco and one from Cajititlán bore two litters, the second, in each case, about a year after the first. All localities are from the Mexican state of Jalisco.

Laguna de Atotonilco: AMNH 93959–93978, 93979 (brood 93980–93984), 93985 (brood 93986–94005), 94006 (brood 94007–94029), 94030 (brood 94031–94047), 96806 (brood 96807–96816), 96817, 94006 (2nd brood 96818–96835).

Laguna de Cajititlán: AMNH 96727–96734, 96736, 96737 (brood 96738–96773), 96774 (brood 96775–96805), 96736 (2 broods not numbered—18 slightly premature, 29 normal).

Acatlán de Juárez: AMNH 94924, 94925.
Near Estipac: AMNH 94964.

Approximately 8 km west of Ixtahuacán de Los Membrillos: AMNH 91692.

Playa de Santa Cruz: LSUMZ 23578, 23579, 24554–24558.

ETYMOLOGY: From the Latin *diluvialis*, in reference to the overflowing of the land by

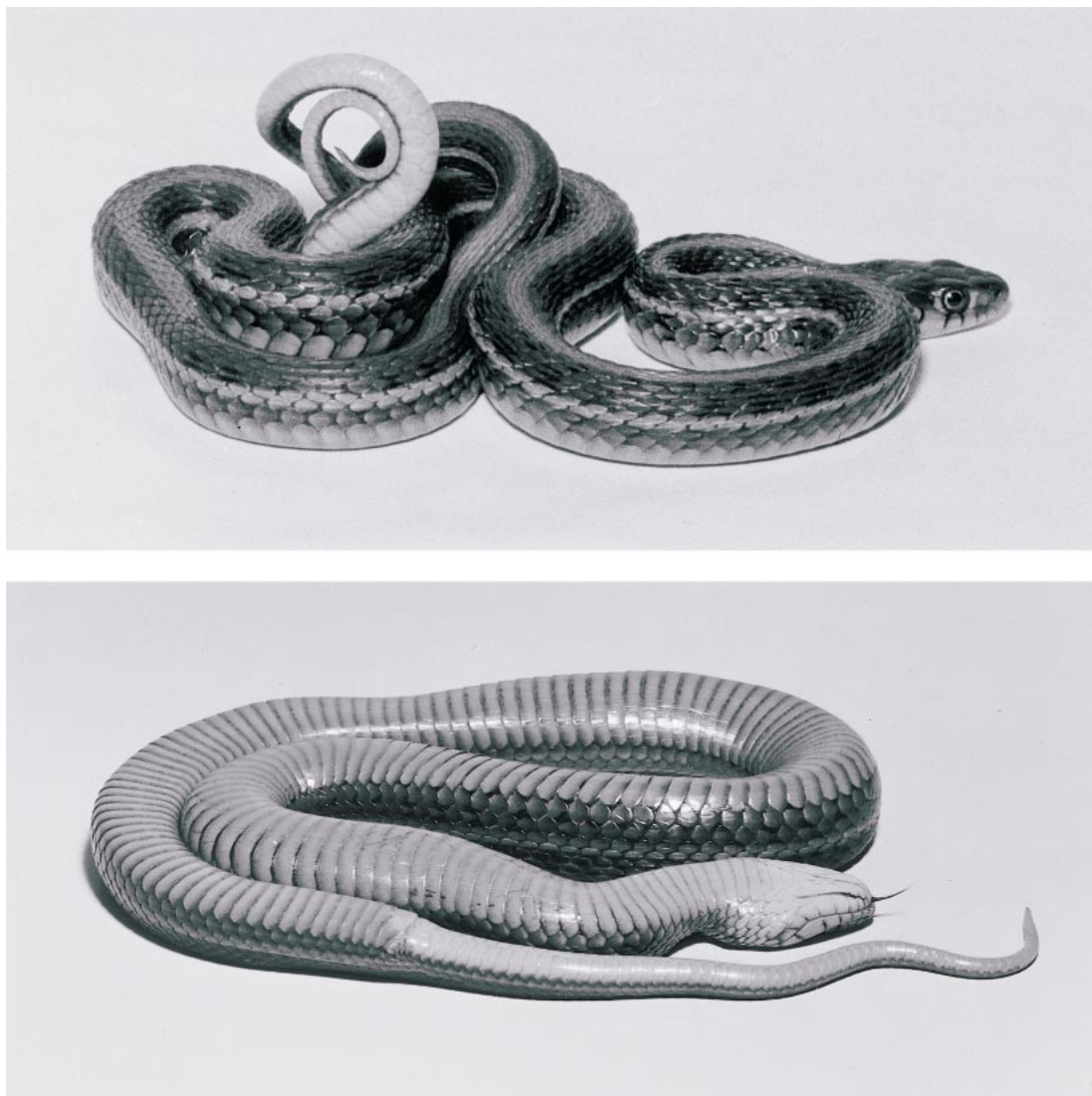


Fig. 12. From the Laguna de Atotonilco. **Upper.** A male *Thamnophis eques diluvialis*, 730 mm in length, collected August 16, 1964, near Villa Corona, Jalisco. The curling of the tail occurs frequently when a snake of the *T. eques* complex is captured or handled. **Lower.** Venter of a gravid female, 855 mm in length, same date and locality. Belly relatively dark.

water when the habitat was created by the huge rises in level of the Lago de Chapala.

DIAGNOSIS: A large, conspicuously pale-striped snake in which the longitudinal mid-dorsal stripe is a full three scales wide, involving the vertebral and paravertebral rows of scales and frequently small portions of the adjacent scales. Lateral stripes normally on rows 3 and 4 anteriorly, and rows 2 and 3 posteriorly. General dorsal coloration various

shades of dark brown. Venter grayish, with a dark line across the anterior edge of each ventral scute. Chin, throat, and underside of tail yellow.

DESCRIPTION OF THE HOLOTYPE: The scutellation agrees with The Species Model, with the following exceptions: The postoculars are 4 instead of 3, and the lowermost extends slightly beneath the orbit. On the right side of the head a small scale is wedged

TABLE 4
Variation in Scutellation and Tail Length Proportions in *Thamnophis eques diluvialis*, New Subspecies

	Wild-caught males (25) ^a	Captive-born males (74)	Wild-caught females (16)	Captive-born females (86)
Scale rows	21-19-17 (22) 19-21-19-17 (3)	21-19-17 (66) 19-21-19-17 (5) 21-19-17-15 (3)	21-19-17 (15) 19-21-19-17 (1)	21-19-17 (71) 19-21-19-17 (15)
Ventrals	159–170 (25) \bar{x} = 165.0	159–176 (74) \bar{x} = 167.6	153–161 (16) \bar{x} = 157.7	149–172 (86) \bar{x} = 159.0
Subcaudals	71–81 (17) \bar{x} = 76.5	71–91 (74) \bar{x} = 78.5	61–71 (10) \bar{x} = 65.6	56–80 (86) \bar{x} = 66.6
Supralabials	7 (2) 8 (48)	7 (1) 8 (145) 9 (2)	8 (29) 9 (3)	7 (2) 8 (155) 9 (15)
Infralabials	9 (1) 10 (48) 11 (1)	9 (3) 10 (137) 11 (8)	10 (29) 11 (3)	9 (5) 10 (138) 11 (23) 12 (6)
Preoculars	1 (50)	1 (147) 2 (1)	1 (32)	1 (171) 2 (1)
Postoculars	3 (43) 4 (7)	2 (1) 3 (122) 4 (25)	3 (27) 4 (5)	2 (3) 3 (141) 4 (28)
Temporals, 1st row	1 (50)	1 (146)	1 (32)	1 (172)
Temporals, 2nd row	1 (4) 2 (39) 3 (6) 4 (1)	1 (11) 2 (104) 3 (32) 4 (1)	2 (19) 3 (13)	1 (1) 2 (108) 3 (63)
Tail/total length	22% (2) 23% (6) 24% (8) 25% (1)	21% (7) 22% (25) 23% (26) 24% (13)	19% (1) 20% (3) 21% (3) 22% (2)	18% (1) 19% (2) 20% (23) 21% (17) 22% (20) 23% (16) 24% (4)

^aFigures in parentheses indicate sizes of samples.

between the anterior temporal and the parietal.

Scale rows 21-19-17, reducing to 19 by the loss of row 5 at the level of ventral 90 on the left and the level of ventral 87 on the right. Reducing again to 17 by the loss of row 4 at the level of ventral 116 on the left and ventral 117 on the right. Total ventrals 166; subcaudals 75. Tip of tail sharply pointed. Apical pits present, but difficult to find in this long-preserved specimen. Hemipenes not everted. Total length 756 mm, tail length 175 mm, tail/total length = 0.231. A summary of scale counts for the entire numbered

sample from the Lagunas Atotonilco and Cajititlán and vicinity is in table 4. Many wild-caught specimens had incomplete tails.

Dorsally, this is a dark brown snake strongly patterned at midbody by a wide longitudinal stripe of medium or orange brown. Lateral stripes normally on scale rows 3 and 4 anteriorly; rows 2 and 3 posteriorly. In life, the lateral rows were greenish, but during long preservation they have changed to bluish. A double row of dark brown spots between the stripes on each side of the body that are inconspicuous against the general dorsal ground color of the dorsum. A row of

similar dark spots below each lateral stripe. Top of head dark brown and unmarked, except for a faint, very small pair of parietal spots.

The anterior edge of each ventral is dark gray, approaching black, and collectively is part of a long series of crosslines that show clearly through the overlapping part of the preceding scale. The unmarked posterior portion of each scale is medium gray in coloration.

The chin, throat, and lower labials are yellow, but the throat is invaded by dark pigment on the scale preceding the first ventral. Most of the sutures between the infralabials are black, but in a few cases the dark pigment is lacking. The underside of the tail is brighter yellow than the chin and throat. The single (undivided) anal plate is colored the same, except for its lateral edges. It bears slight traces of the coloration and pattern of the ventral scutes.

VARIATION AMONG THE PARATYPES: In life, these were brown snakes, varying from pale to dark brown in general appearance, except for the three pale longitudinal stripes that were usually in strong contrast with the more somber hues of the rest of the dorsum. With the snake in hand, paired and alternating dark spots between the pale stripes were evident, but in photographs (figs. 12, 13) they were scarcely noticeable.

After being in preservatives for more than a third of a century, there have been many changes in color pattern, drastic in some specimens, minor in others. The broad (three scales wide) middorsal stripes may be in weaker or stronger contrast with the adjacent dark dorsum. The dark spots are visible in all specimens and they stand out in striking fashion in a few. The two lowermost rows of dorsal scales may show dark spots or pale rounded ones. The top of the head is dark brown, unmarked except for tiny parietal spots.

Dark lines across the anterior edge of each ventral. Remainder of belly usually grayish yellow; greenish or bluish in others. Undersides of chin, throat, and tail unmarked pale yellow. Anal plate similar, but dark pigment may encroach slightly from the sides.

Neonates in life were more or less replicas of the adults, except that they were paler. Af-

ter long preservation there were changes, notably fading and a concomitant strengthening of patterns. The paired dark spots between the lateral stripes became conspicuous. Pattern and color descriptions of two specimens are as follows:

(1) AMNH 94004, 228 mm in total length, a member of a litter of 20 born November 9, 1964; female parent (AMNH 93985) collected at the Laguna de Atotonilco on August 16, 1964. The paired dark spots are prominent and some of them are conjoined with their neighbors. Similar but smaller dark spots are continuous below each lateral stripe. A series of narrow dark lines is present where the dorsal and ventral scales meet and these form a continuous dark line in part. The dorsal stripe widens from a width of 3 scales to 5 on the nape and then narrows to a single scale where it meets the parietals. The result is a heart shape posterior to the almost black head. The belly is similar to that of adults. The chin, throat, and underside of the tail are pale yellow.

(2) AMNH 96800, total length 244 mm, from a litter of 31 born November 21, 1965, to a female (AMNH 96774) from the Laguna de Cajititlán collected July 28, 1965. Similar to the juvenile from Atotonilco, but the dorsal stripe widens only slightly on the nape. An intermittent dark line at the juncture of the dorsal and ventral scales forms part of the lowermost row of dark spots.

REPRODUCTION: Unlike our experience with *obscurus* at the Lago de Chapala where we found no gravid females, eight *diluvialis* in that condition were collected, five at Atotonilco and three at Cajititlán.

Dates of collection ranged from July 14 to August 16. Dates of birth of young were from September 7 to November 26. Late dates probably reflect the interruption of normal development of the offspring. The gravid females were kept inert in bags all through the long drive from the lakes to our home bases in and near Philadelphia.

The number of young in a brood varied from 5 to 36. The total lengths of the offspring were 171–244 mm, and the weights immediately after birth 2.0–4.7 g. One female from each of the two lakes, and which had been caged with one or more males, bore a second litter about a year later. In all, there



Fig. 13. From the Laguna de Cajititlán, Jalisco. **Upper.** A female *Thamnophis eques diluvialis*, 1055 mm in length, collected July 29, 1965. **Lower.** A male, AMNH 91692, 900 mm in length, from an isolated locality west of Ixtlahuacán de los Membrillos, Jalisco, collected July 10, 1959. Because of the angle at which the photographs of the two snakes were taken, the pale middorsal stripe is less conspicuous than it was in life.

were 207 young in a total of 10 litters, one litter slightly abnormal. Scale counts are available for most of these and are summarized separately in table 4.

A large female (AMNH 96736), 1015 mm in length, collected July 28, 1965, at the Laguna de Cajititlán, gave birth to two litters of young in captivity. The first, born September 5, 1965, and numbering 18, was slightly premature. The yolk sacs in all were completely free from the bodies, except for a narrow cord. None of the young showed any

indication of crawling, but they extended their tongues, flattened their bodies, and even struck defensively. All hemipenes were inverted, with none visible externally. They were all flabby and did not preserve well. The same snake, caged for a while with a male, bore a normal litter of 29 young on July 26, 1966. Only the adult female was numbered. No scale counts were made on the young. The abundance of data available from neonates born to other females from Cajititlán was more than adequate.

To analyze all 10 broods would occupy an inordinate amount of space, but details are given below for the components of the largest brood, with information on sizes and weights.

A gravid female (AMNH 96737) measured 1031 mm in length and weighed 276.5 g immediately after the birth of her 36 young on November 17, 1965. She was collected on July 28, 1965, in the Laguna de Cajititlán. She was confined in a cloth bag on a pile of foam rubber in a storage space beneath the bed in our camper with a number of other gravid snakes. There she remained as we zig-zagged across Mexico and then home, where we arrived 17 days and almost 4000 miles later. I inspected our live collection almost daily and each snake was given a chance to drink every few days. The mother ate sporadically at our home base, chiefly on small *Rana pipiens*. My notes, written on the day the young were born, state, "She is thin and spent but still vigorous, pugnacious, and fairly heavy."

Among the 36 young (AMNH 96738–96773), 20 were males and 16 females. The males, after they were preserved and sexed by dissection, measured 214–233 mm in length, mean 224; the females 203–236 mm, mean 219. The live neonates were weighed but not sexed on November 19, 1965. Individual weights varied from 3.4 to 4.7 g, mean 4.0. Several of the tails of both sexes were slightly curled at birth. Two infertile ova were passed with the young.

Color notes were made after the young were euthanized and before they were preserved. Capitalized color names are from Ridgway (1912). The dorsal ground color was dark brown (Mummy Brown); the lateral coloration was paler (Dresden Brown). The middorsal stripe was an orange-brown (Buckthorn Brown) anteriorly, but it changed to a dark reddish brown (Prout's Brown) for most of its length. The lateral stripes were light green (Deep Lichen Green). Top of head darker than ground color. Chin and throat pale yellow (Straw Yellow); underside of tail similar. Eye: pupil black bordered by yellow; iris Olive-Brown. Tongue: Dragon's-blood Red at base, but becoming Brick Red anteriorly; tip black.

OCCURRENCE AT GUADALAJARA: Despite a

search for one, no map is at hand to show the maximum extent of the lake or lakes that came into existence when the Lago de Chapala rose almost 200 m above its present level and spilled over (Clements, 1963). How far north did it go? Did it reach the area of the present city of Guadalajara, which is now only about 25 km north of the Laguna de Cajititlán? The *Atlas Goodrich Euzkadi* (1964) shows changes in altitude in color throughout Mexico, and its map 17 indicates that low areas are currently present from Cajititlán all the way to Guadalajara so, presumably, it was possible for the flood waters to extend that far northward even though it was a very long time ago and may have been influenced by tectonic events.

There is some evidence that it may have extended at least that far. In the herpetological collection of the American Museum of Natural History there are nine specimens from Guadalajara (AMNH 3199–3202, 3206, 3207, and 3438–3440) that were collected a century ago (1899–1901) by L. Diguët, the Duke of Loubat, when the city was much smaller than it is today. All of these snakes are still in good condition, but they have faded and only the black pigment, chiefly that which composes the dark spots between the pale stripes, is conspicuous. The dark spots, which scarcely show in the accompanying illustrations (figs. 12, 13), were visible when the live snakes I collected were in hand during 1964 and 1965. After more than 35 years of preservation, some have changed rather slightly, whereas others have faded, two of them so much that they somewhat resemble the century-old snakes.

An examination of the nine Guadalajara snakes reveals that the middorsal stripe is three scales wide as in specimens of *diluvialis*, but occasional small amounts of darker adjacent pigment invade the paravertebral scales. In six specimens, the dark spots are prominent; they are less so in the other three. All are of relatively large size, ranging in length from 539 to more than 800 mm. Tentatively, I place these nine old snakes in *diluvialis*.

EL LAGO DE MAGDALENA

This large body of water, about 65 km west-northwest of Guadalajara, was the west-



Fig. 14. The Lago de Magdalena, Jalisco, as it looked when it still existed during the first half of the 20th century. Adapted from a map in the *Atlas Geográfico de los Estados Unidos*, published in 1946. Redrawn by W.H. Brandenburg.

ernmost of the endorheic lakes of the transvolcanic belt (fig. 1). Goldman (1951), in writing about the extensive peregrinations he and Edward A. Nelson made from 1892 to 1906 while collecting mammals and birds in almost all parts of Mexico, was in Etzatlán, Jalisco, in June 1892. He wrote that the town “is located at the southern end of the Laguna de la Magdalena, which is a body of water several miles wide and about 20 miles long, occupying a basin without outlet.”

Two thousand and more years ago, the Lago de Magdalena was an important cultural center. About the time of the birth of Christ some of the Indian residents moved northward to found a new center in the Cañon de Bolaños (Cabrero G., 1991).

The lake had several towns along its eastern shore (fig. 14), the largest and northernmost of which was Magdalena. According to Tamayo with West (1964: 109–110), “in 1900 it was still supplying large quantities of *pescado blanco* to the Guadalajara area . . .”. By about the middle of the 20th cen-

tury, however, the lake had lost its water and ceased to exist.

How was the lake emptied? Where did its waters go? Tamayo (1949, II: 417) explained it by manmade sluiceways that discharged into La Colorada lake, which lies 13 km almost due south of the town of Magdalena (INEGI, Guadalajara sheet, 1:250,000, 1998).

Smith and Miller (1980: 416) hypothesized that the “Laguna de Santa Magdalena” was once drained to the Pacific Ocean by the Río Ameca, possibly when that river served as the outlet for the Río Lerma basin a very long time ago.

Our discovery of the remnants of the Lago de Magdalena was accidental. For reasons unknown, there was a customs checkpoint at Magdalena, far from any alien border. On July 12, 1959, we were stopped and required to produce our car and tourist permits. We were driving a station wagon and the rack of wooden drawers at its rear containing snakes in bags we had caught near Tepic, Nayarit, invited inspection. My collecting permit validated them, but it triggered a long conversation. The customs men stated that in a low area due south of their station snakes were numerous. A tight schedule prevented an investigation at the time, but when we returned on August 30, 1961, the abundance of *Thamnophis eques* was quickly confirmed. Details are given in my memoirs (Conant, 1997: 217), the highlight being our discovery by headlamp at night of a slowly roiling ball of snakes perhaps “two feet wide and half as high”, and composed of about 50 large snakes. I wanted to observe and study them, but two Mexican boys who had attached themselves to us rushed in to grab all they could. The serpents scattered and the boys spoiled a once-in-a-lifetime opportunity for me.

We were back at the remains of the Lago de Magdalena on August 18, 1964, and we did a little exploring along the gravel and mud roads. The “lake” was far from empty. It contained numerous ponds, swales, and marshes, as well as the straight-sided ditch on a ledge of which (fig. 15) we found the ball of snakes in 1961. The water in it flowed slowly. It was fairly shallow, scarcely above my booted knees. Other ditches drained wa-



Fig. 15. The ledge near Magdalena, Jalisco, where we observed about 50 large *Thamnophis eques scotti* assembled in a ball-like mass at night. Water flowed across the ledge after heavy rains and a crude bridge passed over it.

ter away. Obviously, at least some of the sources that kept the lake full for centuries were still functioning. Water birds such as wood storks, egrets, gallinules, coots, and cormorants were much in evidence.

Our last visit was on July 7, 1965, accompanied by herpetologist James D. Anderson and his student, Robert Giacosisie. We arrived in advance of and witnessed the first heavy rain of the season. Frogs and toads of many species emerged from estivation in large numbers, and snakes were gorging themselves on the sudden bonanza. Mostly, the predators were *Thamnophis eques*, but a few *T. melanogaster* also participated.

In summary, *T. eques* was abundant during all three of our visits. We refrained from catching all we saw, but, even so, including

the many young born to gravid females, our voucher sample numbered 136.

The lake does not appear on modern maps, but the detailed sheet of the state of Jalisco in the *Atlas Geográfico de los Estados Unidos Mexicanos* (1946) shows the Lago de Magdalena southwest of the town of the same name. Artist W.H. Brandenburg developed a facsimile that appears as figure 14. He further, based on maps (CETENAL, Etzatlán and Tequila sheets, 1:50,000, 1973), created a hypothetical map involving all the flat land that once was occupied by a larger Lago de Magdalena and its environs (fig. 16) extending northwestward to the village of La Quemada. Brumwell (1939) produced evidence that snakes designated by him as *Thamnophis macrostemma* (= *T. eques*)

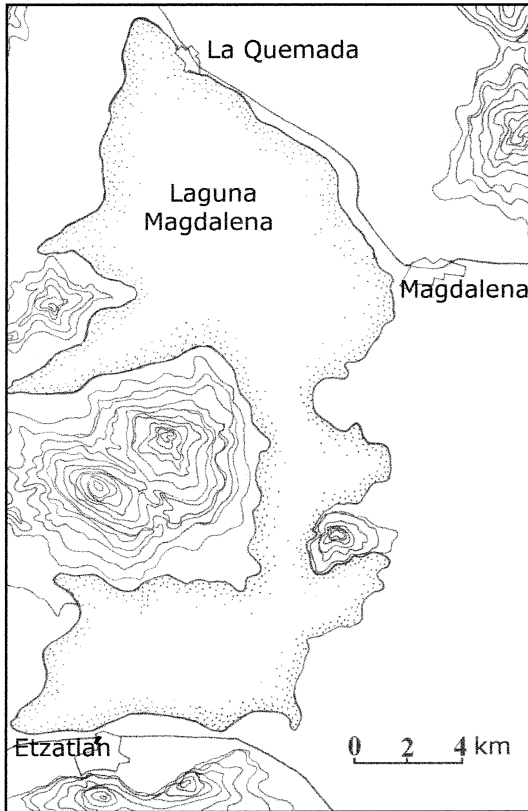


Fig. 16. The Lago de Magdalena, Jalisco, when it was considerably larger and extended to La Quemada. Adapted by W.H. Brandenburg from Mexican CETENAL topographic maps of 1973 showing low flat areas that at one time were presumably occupied by the lake.

from La Quemada exhibited the same wide variation in pattern that is evident in the available sample from the recent remnants of the Lago de Magdalena. Apparently, there had been widespread desiccation similar to that exhibited west and north of the not-too-distant Lago de Chapala, as indicated under the text for *Thamnophis eques diluvialis*. Presumably, the Lago de Magdalena formerly was once much larger than it was early during the 20th century. The elevation of the town of Magdalena is 1380 m above sea level.

Variations in dorsal pattern and coloration are the chief characteristics of the population of *Thamnophis eques* that inhabited the remnants of the Lago de Magdalena in the 1960s

and probably still does. We found it expedient to camp, during each of our three visits, near the small bridge (fig. 15) over the ledge where we found so many snakes engaged in what, in all probability, was a sexual orgy. All of our material was collected within a half kilometer, virtually a single locality, but from which the amount of variation is extraordinary.

The dorsal coloration may be light or dark, with the paler specimens predominating. In them, the lateral ground color between the dark side spots is only slightly darker than the coloration of the middorsal stripe, and the two similar colors are not separated by dark pigment (fig. 17, upper). In the dark snakes the lateral coloration is in strong contrast with the stripe (color plate, fig. 18, upper).

The width of the middorsal stripe varies from zero to seven scales. In most specimens three to five scales are involved, but in AMNH 94904 there are seven. A middorsal stripe is lacking in several, including AMNH 94050, 94906, and 94910.

For this unique population of garter snakes I propose the name below.

Thamnophis eques scotti, new subspecies

Figures 14–18

HOLOTYPE: AMNH 96691, a female from near Magdalena, Lago de Magdalena, Jalisco, collected July 7, 1965, by James D. Anderson, Robert Giacosis, and Roger Conant. Total length 819 mm, tail length 191 mm, tail/total length = 0.233. The holotype gave birth to 18 young on July 31, 1965.

PARATYPES: Several gravid *scotti*, in addition to the holotype, bore young after our return to base. Each mother's number listed below is followed in parentheses by the numbers of her offspring; other numbers are of individual specimens: AMNH 87496–87529, 94048, 94049, 94050 (brood 94051–94058), 94059 (brood 94060–94077), 94078 (brood 94079–94091 removed by dissection), 94902–94923, 96691 (brood 96692–96709), 96710 (brood 96711–96726).

ETYMOLOGY: Named for Norman J. Scott, Jr., who might have been a coauthor of this paper if his superiors had permitted him to remain in Albuquerque. A few years ago, he visited several of the lakes of Mexico's trans-

volcanic belt and confirmed for me that the snakes were still actively present.

DIAGNOSIS: A large, usually three-striped garter snake, but subject to wide variation. A majority, in life, were relatively pale in coloration, with the ground color between the lateral spots only slightly darker than that of the middorsal stripe. Others were dark, with the body color in strong contrast with the central stripe. The latter normally involves three to five rows of scales, but it may vary from zero to seven scales wide. Pale parietal spots are tiny or absent. No dark line paralleling each side of the pale middorsal stripe as in *T. e. carmenensis*. The tail spine is usually short and not part of a long scale as in many forms of *T. eques*.

DESCRIPTION OF THE HOLOTYPE: In its scutellation this specimen agrees with The Species Model, except as follows: The postoculars are 4 instead of 3, with the lowermost on each side extending slightly beneath the eye. A small scale is wedged between the temporals and the parietal, larger on the left than on the right.

Scale rows 21-19-17, reducing to 19 by the loss of row 5 at the level of ventral 82 on the left and ventral 78 on the right. Reducing again to 17 by the loss of row 4 at the level of ventral 105 on the left and ventral 103 on the right. Total ventrals 150; subcaudals 73. Tip of tail bluntly pointed. Apical pits present, but difficult to find in this long-preserved specimen. Total length 819 mm, tail length 191 mm, tail/total length = 0.233. A summary of scale counts for the entire cataloged sample from the Lago de Magdalena is in table 5. An exceptionally large number of wild-caught specimens have incomplete tails.

This is a "blonde" snake and a good example of the way I remember a majority of the specimens of *scotti* in life. It may be described as follows: Dorsal coloration yellowish brown, middorsal stripe 3 scales wide and a little paler than ground color between stripes. Lateral stripes pale greenish gray on scale rows 3 and 4 anteriorly, rows 2 and 3 posteriorly. An irregular, relatively inconspicuous double row of black spots between the dorsal and lateral stripes; a similar row on scales of first row. Top of head medium brown with several slightly darker, scarcely

visible, more or less longitudinal streaks. Pale parietal spots lacking.

Anterior edge of each ventral scute marked with stippled pale gray; posterior part of each ventral pale greenish gray. Posterior three-fourths of the ventrals bear pale yellow spots or streaks at the center of their anterior edges that collectively suggest a narrow intermittent yellow midventral line.

Supralabials pale gray. Infralabials, except along or near sutures, yellow. Chin, throat, anal plate, and underside of tail also yellow, unmarked.

VARIATION AMONG THE NEONATES: Total lengths of 18 neonates born in captivity to the holotype (AMNH 96691) on July 31, 1965, varied from 193 to 232 mm, mean 220.6—12 males 216–232 mm, mean 225.6; 6 females 193–222 mm, mean 210.8. Tail/total length in males 0.244–0.255, mean 0.248; in females 0.229–0.243, mean 0.235.

A careful inspection of the 18 neonates revealed that they collectively bridged almost the entire range of color and pattern variation in the large adult sample of *scotti* available. In the latter, the width of the middorsal stripe normally varies from one to five scales (a few have no stripe and one has such a broad stripe that it measures almost seven scales wide). In the neonates the central stripe varies from one to five scales wide regardless of sex. The paired yellowish parietal spots are tiny or missing, as in the adults. Most of the neonates tended to be pale, whereas in others, where the dark spots between the pale lateral stripes are large and dark, they probably would have grown into the dark morph of *scotti* illustrated in the upper half of the color plate (fig. 18).

The head markings of the neonates differ from those of the adults. The posterior half of the preocular and the anterior half of the postocular are whitish. Immediately posterior to the angle of the jaw the whitish color of the throat extends upward for the height of three scales to form a pale, more or less triangular marking at the rear of the head on each side. Posterior to that marking is a dark bar about three scales wide extending diagonally forward to meet the parietals. Top of head dark brown. A few of the neonates have slight variations from the pattern described.

Among the many snakes collected at the

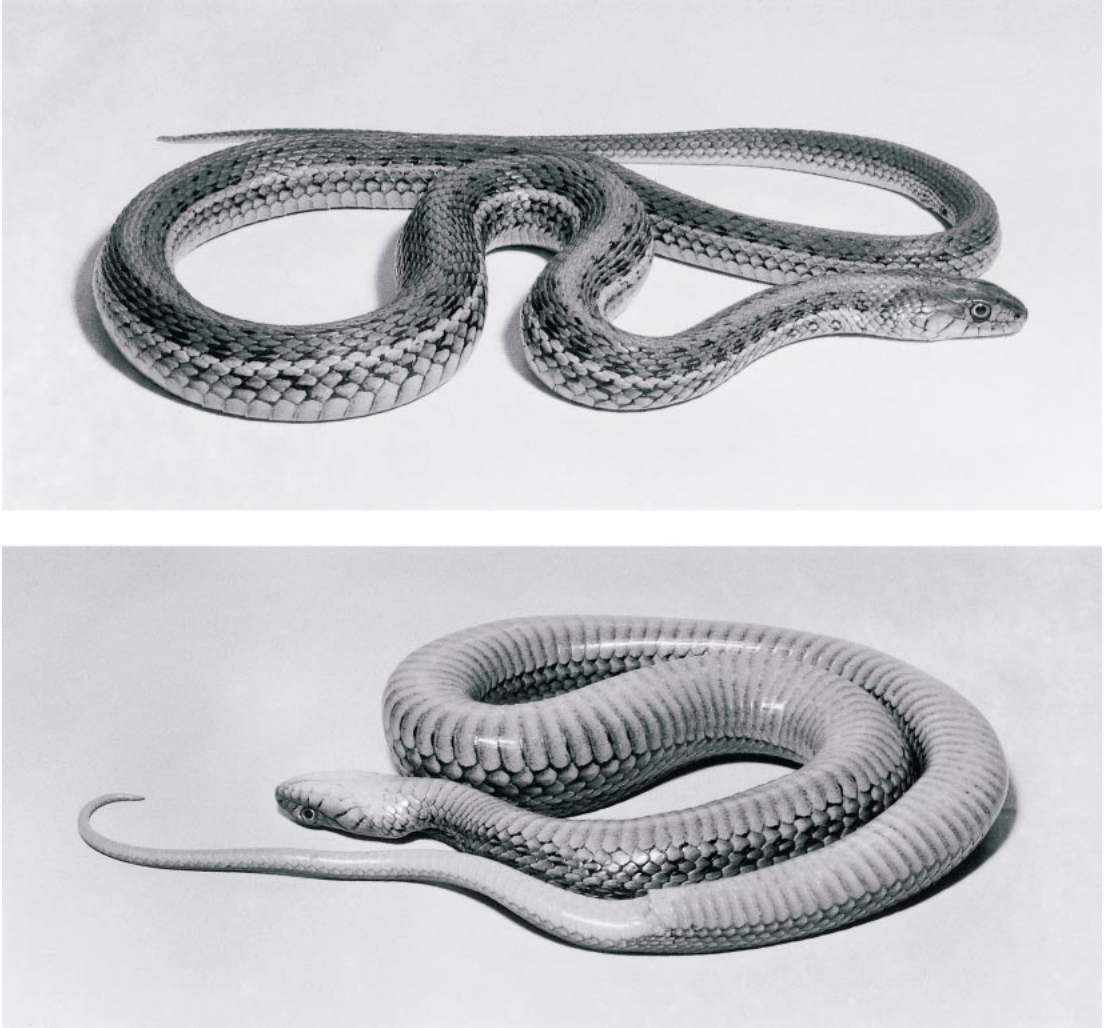


Fig. 17. From the former Lago de Magdalena, Jalisco. **Upper.** A male of *Thamnophis eques scotti*, 953 mm in length, collected August 30, 1961. The middorsal stripe is variable in width but not sharply defined from the ground color between the lateral dark spots. **Lower.** Venter of gravid female, same locality and date, length 1009 mm. Belly pale.

Lago de Magdalena, two of similar size, taken July 7, 1965, and stored in isopropanol rather than ethanol, have retained their coloration and pattern so that they look much as they did in life. They are the holotype (AMNH 96691) and AMNH 96710. They both still agree rather closely with detailed color notes I made on them late in 1965, using the color swatches of Ridgway (1912). The differences involving the two types of preservatives are pronounced. AMNH 96710 would have been chosen as the type, except

that a large part of its tail is missing, probably bitten or broken off by a turtle, heron, or other predator. She bore a litter of 16 young on October 11, 1965, and detailed data from that litter, including weights and color notes recorded shortly after birth, are condensed herewith.

The 16 young of AMNH 96710 include 7 males and 9 females measuring, collectively, 193–217 mm in total length, mean 207.7; weights 2.8–4.0 g, mean 3.4. The head patterns among snakes of this brood are slightly

TABLE 5
Variation in Scutellation and Tail Length Proportions in *Thamnophis eques scotti*, New Subspecies

	Wild-caught males (28) ^a	Captive-born males (38)	Wild-caught females (34)	Captive-born females (36)
Scale rows	21-19-17 (24) 21-23-21-19-17 (4)	21-19-17 (38)	21-19-17 (27) 21-23-21-19-17 (7)	21-19-17 (34) 21-23-21-19-17 (2)
Ventrals	154-165 (28) \bar{x} = 159.4	155-163 (37) \bar{x} = 158.5	145-156 (34) \bar{x} = 150.4	147-153 (35) \bar{x} = 150.7
Subcaudals	73-84 (16) \bar{x} = 78.2	73-89 (37) \bar{x} = 82.1	61-73 (21) \bar{x} = 68.4	63-78 (36) \bar{x} = 69.8
Supralabials	8 (53) 9 (3)	6 (1) 8 (75)	8 (66) 7 (2)	8 (69) 9 (3)
Infralabials	9 (2) 10 (55) 11 (1)	8 (2) 9 (7) 10 (65) 11 (2)	8 (1) 9 (2) 10 (64) 11 (1)	9 (8) 10 (63) 11 (1)
Preoculars	1 (56)	1 (76)	1 (67) 2 (1)	1 (71) 2 (1)
Postoculars	2 (1) 3 (48) 4 (7)	3 (69) 4 (5)	2 (1) 3 (53) 4 (13) 5 (1)	3 (67) 4 (5)
Temporals, 1st row	1 (56)	1 (74)	1 (68)	1 (72)
Temporals, 2nd row	1 (6) 2 (39) 3 (11)	1 (13) 2 (52) 3 (11)	1 (1) 2 (57) 3 (10)	1 (1) 2 (56) 3 (15)
Tail/total length	22% (1) 23% (3) 24% (6) 25% (5)	23% (3) 24% (12) 25% (19) 26% (3)	20% (1) 21% (5) 22% (9) 23% (5) 24% (1)	22% (8) 23% (20) 24% (7) 25% (1)

^aFigures in parentheses indicate sizes of samples.

different from those of the young born to the holotype (AMNH 96691). The small dark bars immediately posterior to the head run crosswise and are separated from the parietals instead of extending diagonally forward to meet those large scales. Pale parietal spots present, but faint and tiny.

The dorsal ground color in life was medium dark brown (Dresden Brown), and the lateral ground color was yellowish brown (Buckthorn Brown). In some of the young snakes the middorsal stripe matched the darker shade of brown; in others they matched the paler one. Top of head dark brown. Supralabials, preoculars, and lower postoculars bright yellow (Wax Yellow). Chin and throat paler (Massicot Yellow). Un-

derside of tail even paler (Olive Buff). Venter yellow with a slight greenish tinge (Reed Yellow). Eye: pupil black ringed by orange-yellow; iris brownish olive. Tongue: Coral Red; tips black. Capitalized color names from Ridgway (1912).

VARIATION AMONG THE PARATYPES: In life, most specimens were relatively pale and the middorsal stripe was more or less similar in hue with the coloration between the dark spots on the sides of the body. In essence, they more or less matched the snake portrayed in the upper half of figure 17. Other specimens were dark, with the middorsal stripe in sharp contrast with the adjacent parts of the body as in the upper figure on the color plate (fig. 18).



Fig. 18. **Upper.** A dark morph of *Thamnophis eques scotti*, a female 1009 mm in length from the Lago de Magdalena, Jalisco, collected August 30, 1961. **Lower.** A female *Thamnophis eques carmenensis* 700 mm in length and collected southeast of El Carmen, Tlaxcala, July 8, 1964. Note the solid black line bordering the pale middorsal stripe.

A recent examination of all the snakes from the Lago de Magdalena revealed many postmortem changes. In a great many there was a darkening, mostly on the sides of the body, but also frequently involving the mid-dorsal stripe. Especially noticeable was a change in the upper labials from a pale gray in some to black in others. In life, the supralabials were usually pale gray to yellowish (figs. 17, 18). Other postmortem changes involved the lower sides of the body. The lateral stripes had become bluish and the two

lowermost rows of scales had light centers in dark scales, some black, resulting in continuous rows of light spots. In some that had lost many scales (the stratum corneum), the sides of the body were pale in color.

Both in the field and when snakes were euthanized after periods of captivity they were thoroughly injected with formalin for hardening. Almost all were then transferred to ethanol, in which preservative they darkened, some of them considerably.

REPRODUCTION: The gravid females we

took home with us gave birth to their young, and some of the mothers that were retained alive with captive males had additional offspring a year or more later.

Five broods of young were born in captivity from females collected at Magdalena. Dates of collection were July 7 and August 18. Dates of birth ranged from July 31 to November 10. In the case of the latter date, the apparently full-term young were removed by dissection when the mother, held captive in my office at the Philadelphia Zoo, was euthanized after she strained for several hours but was unable to extrude her young.

The number of young in a brood varied from 8 to 18. The total lengths of the offspring were from 186 to 251 mm. Not all the young were weighed, but those that were varied from 2.3 to 5.5 g. Scale counts for most of these are summarized separately in table 5.

One large heavy-bodied female, AMNH 94050, collected August 18, 1964, near Magdalena had an unusual record. From her impregnation in the wild she had eight young (AMNH 94051–94058) on September 1, 1964. She was caged with a male and she bore 14 additional young on July 18, 1967. Because so many other neonates were available, the 14 were not tagged, but they were preserved with their dam. She bore another litter on July 26, 1968, that was discarded. The male died during June 1968. On October 17, 1969, the female passed three young, one alive and two full term but dead, probably a case of delayed fertilization, at one time called *amphigonia retardata*. The female died on October 24, 1971, after living in excess of seven years in captivity. More than half of her tail was missing and she bore a large, well-healed, protuberant rounded scar 30 mm in diameter and 13 mm in depth on the right side of her neck, less than a head length posterior to the angle of the jaws.

REMARKS

Synchronization in time was absent. The thought often occurred to me, however, about what an ideal place the half hectare or so where *scotti* was so abundant in the early 1960s would have been for present-day sophisticated studies. They might have includ-

ed the implantation of high-tech devices capable of recording a variety of data.

EL VALLE DE MEXICO

As is clearly depicted on the map showing the natural lakes as they existed prior to A.D. 1500 (fig. 1), the Valley of Mexico was largely covered by water. The Aztec capital of Tenochtitlán was situated on an island reached by a trio of causeways. Brandon (1989), in a review of the axolotl and other ambystomatid salamanders, succinctly described the region and the many changes it has undergone.

Originally, there were several shallow lakes in the valley that, during exceptionally rainy summers, might coalesce to form a huge body of water called the Lake of the Moon by the Aztecs. The Lago de Texcoco at the lowermost part of the basin was highly saline and was blocked off from the smaller freshwater Lagos de Xochimilco and Chalco to the south by the great Aztec dike just to the east of Tenochtitlán. Brandon included a map showing the Basin of Mexico before the Spanish Conquest, and superimposed on which he indicated the extent of modern Mexico City (as of 1961), the small remnant lakes and wetlands, and the location of the Aztec dike. In contrast, the endpapers in the book *Aztecs of Mexico*, by Vaillant (1962), show details of the lakes and their environs as they existed at the time of the arrival of the conquistadors.

Historically, water has been a major problem for centuries and great efforts were made to reduce it. Canals and a tunnel beneath the highlands at the north end of the Valley (Secretaría de Fomento, 1888) carried off large quantities of water to drain into the Ríos Tula and Moctezuma and onward to the Gulf of Mexico. Today, a very large part of the area is occupied by Mexico City, the world's second largest and still growing metropolis. Only Tokyo, Japan, exceeds it in population (*World Almanac and Book of Facts*, 2000).

Thamnophis eques undoubtedly once occurred widely through the Valley of Mexico, but the mass disturbance of habitats for centuries has made it impossible to determine whether there was any isolation or speciation evident long ago. For that reason, we avoided

fieldwork within its boundaries, although we did briefly visit some of the remnants of the former lakes.

LA LAGUNILLA DEL CARMEN

A sizable Lago Totolcingo in the far eastern part of Mexico's transvolcanic belt appears in figure 1 as occupying a portion of the Llanos (plains) de San Juan circa A.D. 1500. As of today, most of the lake has disappeared, but we had heard there was still water near the village of El Carmen. So we decided to investigate, inasmuch as we planned to work in eastern Mexico during the early part of our 1964 expedition. Unexpectedly, we discovered large colonies of *Thamnophis eques* and of a small frog of the *Rana pipiens* complex, later described as *Rana spectabilis*, a new species, by Hillis and Frost (1985). The snakes and frogs were in and near small pools of water kept flooded by the overflow from a freshwater spring.

After camping in a secluded arroyo, we drove in the late morning of July 7, 1964, to the Entronque (junction) Zacatepec and turned right onto a paved road to El Carmen. Eventually, we could see a low hill running perpendicular to the highway and, when we were about 3 km from it, shallow water that gradually deepened appeared on both sides of the road. Farther ahead, women were washing clothes at an *ojo de agua* (spring). Nearby, during late morning, I found a live garter snake and a dead one. Exploration revealed a second *ojo* somewhat farther southwest, but garter snake habitat was lacking.

We returned the following morning before 8:30 AM. I was joined by two boys, and within less than an hour I had caught 22 *eques*, all considerably smaller than members of the same species from larger lakes (see Size in text below). I also learned that the habitat supported hundreds of frogs. Just as early on July 9 we were back again, but I devoted most of my time to taking temperatures, recording alkalinities, and studying the habitat. The shallow pools of water alternated with sizable dry areas (fig. 19). Both were utilized by *ganado* (e.g., burros, horses, sheep) that kept the vegetation well cropped. Footprints of the animals left depressions in the mud, some dry and some partially filled with wa-

ter, that served as shelters for both snakes and frogs from the fierce winds that blew almost constantly. It was at gale force on July 7, but less so on July 8 and 9. The most popular shelters, as expected, were those on which the sun shone.

The vegetation in and around the *lagunilla* was mostly low thanks to the *ganado*. We took a few samples home and they were identified by Alfred E. Schuyler, of the Academy of Natural Sciences of Philadelphia, as the rush, *Juncus balticus*, and a nut sedge, *Eleocharis* sp.

The water being utilized for the washing of clothes was badly polluted by soap (and detergents?), but farther away from the spring the pH was 6. That reading gradually increased to 7, 8, 9, and 10 at the more distant parts of the *lagunilla*. Near its extreme end were several large, parallel rectangular pools, each bordered by a low mud dike. The basins were about 30 cm deep and roughly 60 cm across. They were lengthy, however, each about 25 m in extent, arranged three across, and separated by narrow shallow ditches containing low vegetation apparently kept cropped by wandering *ganado*. In answer to my query, the boy who had joined me at that time said the basins were for the gathering of liquid to make *jabón* (soap) and the alkalinity (pH 10) was thus their equivalent of lye. The snakes crawled across the miniature impoundments and along the ditches, but I saw only one frog in the strongly alkaline water. I did find another, however, hopping through liquid measuring pH 9. Voles were abundant and their trails were clearly visible.

Snakes lying in pools had temperatures the same as that of the water, 18° at 9:52 AM, but others that were active were warmer, 26.1°, for example, when the water had risen to 19.5°. A curious observation was that all activity on the part of the snakes seemed confined to the mornings. They had all disappeared by noon. We stopped back during the afternoon on two occasions, once in 1964 and again in 1965, during which latter year the level of the water had risen considerably, probably because of heavy rains which we also encountered in several other parts of Mexico. Although I prowled through the habitat for considerable time and distance, I saw



Fig. 19. Part of the Lagunilla del Carmen looking southeastward on July 8, 1964. The various pools and puddles were kept filled by the overflow from a large spring on a hillside near El Carmen, Tlaxcala. Domestic stock wandered about freely. *Thamnophis eques carmenensis* and a frog of the *Rana pipiens* complex were abundant in many parts of the watery landscape.

no snakes. Were the fierce winds responsible? A wet snake would chill rapidly from evaporation. We were back on the morning of August 10, 1965, when there were periods of gentle rain interspersed with bright sunshine. A small “army” of boys accompanied me, and their sharp eyes helped in finding neonates of *T. eques*. I wanted to compare them with young born in captivity the previous year. Apparently, there had been a sizable parturition before our arrival. Altogether I collected 36 snakes, but in the interest of conservation I refrained from taking most of the larger ones. In view of the disaster that apparently overtook the colony several years later, I should have collected all we saw.

Alcocer et al. (1997: 271) reported that the two freshwater springs near El Carmen have been channelized all the way to the town as

a source of drinking water. The *lagunilla* has doubtless been reduced in volume or vanished altogether except during especially rainy seasons. Does the colony of garter snakes still exist? On a map published in 2000 (INEGI, Guadalupe Victoria sheet, 1:50,000) the former fairly extensive habitat is now represented solely by two very small blue ovals that are hatched, suggesting that water is present in them only after heavy rains.

For this relatively small-sized garter snake I propose the name below.

Thamnophis eques carmenensis,
new subspecies

Figures 18–20

HOLOTYPE: AMNH 93842, a female from near El Carmen, Tlaxcala, collected July 8,

1964, by Roger Conant. Total length 691 mm, tail length 142 mm, tail/total length = 0.205. The holotype gave birth to 14 young on July 20, 1964.

PARATYPES: Several gravid *carmenensis*, in addition to the holotype, bore young in captivity. Each mother's number listed below is followed in parentheses by the numbers of her offspring; other numbers refer to individual specimens: AMNH 93818–93841, 93842 (brood 93843–93856), 93857 (brood 93858–93875), 93876 (brood 93877–93887), 93888 (brood 93889–93900), 94926–94959.

ETYMOLOGY: Derived from El Carmen + the adjectival-forming suffix *-ensis* (belonging to a place).

DIAGNOSIS: A garter snake of medium size characterized by a narrow pale middorsal stripe. It involves the vertebral and paravertebral scales, but black pigment normally encroaches from the sides to include the keels on the paravertebral scales or even beyond them. The pale central stripe is bordered by a continuous black line a scale or two in width. The paired dark lateral spots are discernible and their upper edges are fused with the black line bordering the middorsal stripe. Many specimens exhibit a tendency toward melanism; others, probably those that had recently passed through ecdysis, have the pale stripes vividly evident against the darker parts of the body. The pale lateral stripes occupy scale rows 3 and 4 anteriorly and 2 and 3 posteriorly, but small black flecks invade the edges so broadly as to reduce the thickness of the stripes. The lowermost rows of scales are punctuated with black spots.

The portions of both the preoculars and postoculars closest to the orbit are conspicuously whitish or yellowish. A black crescentic mark about two scales wide across the angle of the jaws is preceded by a pale crescent one or two scales wide extending upward for the length of three or four scales. Belly pale bluish or greenish, the black line at the anterior end of the ventrals faint in some, conspicuous in others.

DESCRIPTION OF HOLOTYPE: In its scutellation this snake agrees with The Species Model, except that the postoculars on the right are two instead of three. The two lower ones are fused into one long vertical scale.

Scale rows 21–19–17, reducing to 19 by

the loss of row 5 at the level of ventral 82 on the left and the level of ventral 76 on the right. Reducing again to 17 by the loss of row 4 at the level of ventral 111 on the left and ventral 110 on the right. Total ventrals 155; subcaudals 68. Tip of tail sharply pointed. No apical pits found in it or other long-preserved specimens. Total length 691 mm, tail length 142 mm, tail/total length = 0.205. A summary of scale counts from the entire numbered sample from La Lagunilla del Carmen is in table 6. Only four wild-caught specimens had incomplete tails. Other than humans, there apparently were few predators.

General appearance, both in coloration and pattern, very similar to the snake shown in color in the lower part of figure 18. The dorsal surface consists of a variety of longitudinal areas that differ in coloration. Most prominent is the bright yellow middorsal stripe. It is narrow, involving the vertebral row of scales, but only a small portion of the paravertebral ones. Black pigment extends upward to encompass the keels on the paravertebrals. The black line paralleling the yellow middorsal line is virtually two scales wide because it truncates the tops of the lateral dark spots, although less conspicuously toward the rear of the body. In comparison with other races of *Thamnophis eques*, the lateral dark spots are small and concentrated largely against the longitudinal stripes. They leave a patternless area between them that is dark olive-green. Lateral stripes olive-yellow, occupying scale rows 3 and 4 anteriorly and rows 2 and 3 posteriorly. Lateral stripes flecked with black, especially along their lower edges.

Top of head brownish olive. Middorsal stripe widens to three scales on the nape and then reduces to a single scale. Pale parietal spots, each surrounded by black. Both preocular and postocular scales with pale pigment. Upper labials pale olive-yellow, sutures black. Chin and throat, including infralabials, yellow, extending to about the fifth ventral and then becoming greenish gray that darkens slightly toward the tail and continues onto the first 10 or 12 subcaudals. It then changes to dull yellow.

VARIATION AMONG NEONATES: Total lengths of 14 neonates born in captivity to the holotype (AMNH 93842) on July 20,

TABLE 6

Variation in Scutellation and Tail Length Proportions in *Thamnophis eques carmenensis*, New Subspecies

	Wild-caught males (31) ^a	Captive-born males (29)	Wild-caught females (31)	Captive-born females (36)
Scale rows	21-19-17 (8) 19-21-19-17 (18) 19-17 (5)	21-19-17 (15) 19-21-19-17 (12) 19-17 (2)	21-19-17 (15) 19-21-19-17 (13) 19-17 (3)	21-19-17 (26) 19-21-19-17 (10)
Ventrals	152-163 (31) \bar{x} = 159.0	155-163 (29) \bar{x} = 159.4	144-157 (31) \bar{x} = 151.5	147-156 (36) \bar{x} = 151.8
Subcaudals	60-75 (30) \bar{x} = 69.8	65-77 (29) \bar{x} = 70.8	57-68 (28) \bar{x} = 61.6	56-68 (36) \bar{x} = 61.4
Supralabials	7 (2) 8 (60)	7 (3) 8 (54) 9 (1)	7 (2) 8 (56) 9 (4)	7 (1) 8 (68) 9 (3)
Infralabials	9 (1) 10 (61)	9 (5) 10 (52) 11 (1)	10 (60) 11 (2)	9 (2) 10 (62) 11 (8)
Preoculars	1 (62)	1 (58)	1 (62)	1 (72)
Postoculars	2 (1) 3 (57) 4 (4)	2 (6) 3 (50) 4 (2)	2 (2) 3 (45) 4 (15)	2 (3) 3 (60) 4 (8) 5 (1)
Temporals, 1st row	1 (62)	1 (58)	1 (62)	1 (72)
Temporals, 2nd row	2 (26) 3 (36)	2 (37) 3 (21)	2 (26) 3 (34)	2 (45) 3 (27)
Tail/total length	19% (1) 20% (1) 21% (10) 22% (13) 23% (5)	20% (5) 21% (9) 22% (6) 23% (8) 24% (1)	18% (1) 19% (3) 20% (12) 21% (9) 22% (2)	18% (1) 19% (6) 20% (21) 21% (6) 22% (2)

^aFigures in parentheses indicate sizes of samples.

1964, varied from 207 to 227 mm, mean 218.3—8 males 215–227 mm, mean 221.1; 6 females 207–220 mm, mean 214.5. Tail/total length in males 0.223–0.236, mean 0.229; in females 0.203–0.216, mean 0.212. The young were born in Mexico and I euthanized and preserved them the following day in the field.

In these young the three longitudinal stripes are conspicuous and so are the pairs of dark spots between them. A black line borders the pale middorsal stripe and the upper lateral spots are fused with it. The lower dark spots border the upper edge of each pale lateral stripe. The lowermost rows of scales are flecked, spotted, or vertically barred with black. The venter is whitish to dull gray, with crosslines visible. The chin, throat, and most

of the underside of the posterior part of the tail are yellow. The oculars are chiefly white. All have very small yellow, paired parietal spots.

Four other litters of *carmenensis* were born in captivity on dates ranging from June 24 to September 19. The numbers of young in the litters were 11, 11, 12, and 18; the shortest individual (a female) measured 163 mm in length, the longest (a male) 218 mm. The second litter of 11 was born presumably on July 24, 1965, while we were in Mexico. The female parent was the holotype of *carmenensis*, which was caged with a male in my office at the Philadelphia Zoo. The reptile keeper who made the daily inspection found the litter dead and not in prime condition. He froze the juvenile snakes pending my return.

They are now AMNH 96836–96840 and 148799–148803. One was so poor that it was discarded.

The 12 young of AMNH 93888 were weighed soon after birth. They varied from 1.2 to 1.6 g, mean 1.4. They weighed considerably less than neonates from other populations of the complex.

On August 10, 1965, we collected 36 *carmenensis* (34 preserved, 2 small ones escaped), among which the great majority were presumably neonates. The largest born in captivity was 227 mm long. Among the wild-caught specimens, 24 were 227 mm or less. The shortest, a male, was 172 mm.

In coloration and pattern, all captive-born and wild-caught neonates were similar to those born to the holotype and described in some detail above. Ample allowance had to be made, however, for ecdysis. The baby snakes apparently grew gradually duller until they once again shed their skins (the stratum corneum).

VARIATION AMONG OTHER PARATYPES: Neonates constitute a majority of the paratypes. Fifty-five were born in captivity and 24 of those collected are of neonate size. Thus, about 65% of the material from the *lagunilla* has already been reviewed in the section above.

The remaining paratypes in general are similar. The smaller specimens are darker, the larger ones more conspicuously marked. The dark lateral spots vary in intensity. In many, the upper row is virtually fused with the black stripe paralleling the yellow middorsal stripe. Pale parietal spots, small to tiny, are present as in the neonates, but they are narrowly margined with black in the larger snakes. AMNH 93818, a female 646 mm in length, has the dorsal surface of the head, including the supralabials, dark and unmarked; on its venter the dark crosslines are strongly evident. These lines vary. They are visible in some specimens, but scarcely show in others.

The dorsal ground color in life was olive (Buffy Citrine to Sepia). Middorsal stripe Amber Yellow or Wax Yellow. Top of head dark olive. Lateral stripes Strontian Yellow to Yellowish Citrine. Venter greenish (Veronese Green, Kildare Green, or Rainette Green). Chin, throat, and underside of tail

Barium Yellow to almost Light Dull Green-Yellow. Eye: pupil black ringed by orange-yellow; iris brownish olive. Tongue: Coral Red, tips black. Capitalized colors are from Ridgway (1912).

SIZE: *Thamnophis eques* is a large garter snake. In every sample examined from single localities and which was sufficiently abundant to provide a good cross-section of size, coloration, and pattern, one or more individuals exceeded a meter in length. AMNH 82039, a female from the Lago de Chapala, the largest specimen on record, is 1216 mm long.

The population from the Lagunilla del Carmen, on the contrary, is dwarfed. Among the 66 specimens collected from that small body of water, the largest female was only 724 mm long; the largest male 693 mm. From all Mexican localities examined, including those beyond the transvolcanic belt, the largest specimens are females. The longest males fall within the 900 mm bracket and many, especially from the Lago de Magdalena, approach a meter in length. One from the Lago de Pátzcuaro, UMMZ 98938 (from the Museum of Zoology of the University of Michigan), measures 980+ mm. It has only 48 subcaudals and, if the missing scales were present, it would have surpassed a meter.

The small size of specimens of *carmenensis* creates the illusion that their heads are exceptionally small. To test that possibility, I measured numerous heads of it and other *eques* subspecies using the Rossman formula (Rossman et al., 1996: 24). Under that system, the head length from the anterior tip of the rostral to the angle of the jaws is divided by the snout-vent length. The results demonstrated that the heads in *carmenensis* are proportionately the same length as in the other races of *Thamnophis eques*.

BEHAVIOR: The young exhibit a strong tendency to arrange themselves in coils, even immediately after birth. The snakes in one litter, when removed from the terrarium in which they were born, were coiled in all cases—on the flat bottom, between their water dish and the side of the terrarium, and on the cork bark provided for their shelter. The head often would be hidden either toward the center or under a loop of the body (fig. 20). Many retained this attribute throughout the

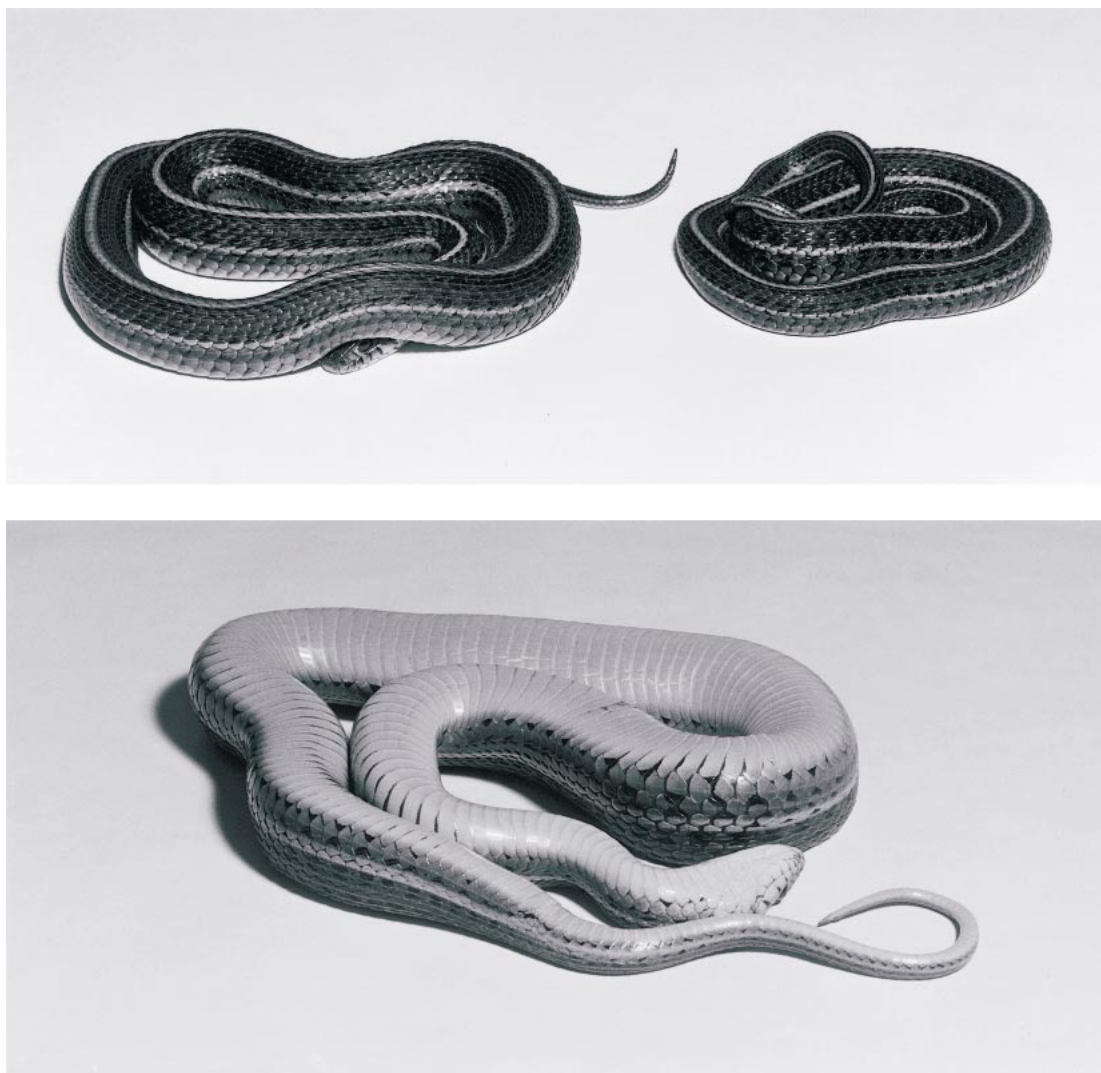


Fig. 20. **Upper.** Two young dark examples of *Thamnophis eques carmenensis* from near El Carmen, Tlaxcala. Lengths 686 mm left, 562 mm right. Smaller members of this taxon frequently hid their heads beneath their bodies. **Lower.** Nearly white venter of a female 700 mm in length from the same locality. All collected July 8, 1964.

length of their captivity and regardless of size.

When picked up to be photographed, they might be lying in more or less a straight line, but when on the posing table they soon coiled. The photo of the venter (fig. 20, lower), as in the cases of all pictures of under-surfaces, was obtained by restraining the snake inert in an upside-down position.

Neonates were placed in small safety match boxes to be weighed; afterward, when

the box was overturned to free the animal, the coil was retained whether right side up or not.

The habit of coiling may have survival value. Young in such positions were noted three or four times as we wandered over the shallow habitat, and small boys found two I failed to see. Would a predator overlook an inert coil?

Only one snake, an adult female, among several of various sizes tested, coiled its tail

the way specimens of other subspecies did as, for example, the male *diluvialis* depicted in figure 12.

FOOD: *Rana spectabilis* was surely the principal food of adult *Thamnophis eques carmenensis*, and the tadpoles and metamorphs for the young snakes. I collected four voucher frog specimens in 1964 (AMNH A-73392–73395), measuring 33.9–43.9 mm in snout–vent length. I also obtained a transforming one (AMNH A-75255) in 1965 that was being eaten by a snake (AMNH 94931) only 299 mm long. It had begun at the frog's snout and engulfed the left front leg, but it was unable to advance any further. The frog retained a long tail, 40 mm measured ventrally.

The frogs were abundant in the *lagunilla*, except in the highly alkaline portions of its lower ends. Two other potential food animals also were present. During our 1965 visit, I did some seining and caught a few small goldfish, *Carassius auratus*, that I preserved and which were confirmed by Robert R. Miller. They doubtless had been introduced.

Alcocer et al. (1997: 271) wrote that ambystomatid salamanders are absent in the springs. I failed to find salamanders, but one of the snakes (AMNH 94926) did, not far from the actual *ojo*. It had half swallowed a salamander when I caught it on August 10, 1965. Because I feared I might damage them, I did not separate the two animals, but permitted the snake to finish engulfing its prey. Several hours later, I euthanized the snake and used a long narrow-gauge needle to inject reptile-strength formalin into its body cavity and also that of the salamander. Back at my home base, I removed the amphibian by dissection and stored it in weaker formalin. Eventually, it was deposited in the American Museum of Natural History where it was cataloged as *Ambystoma velasci* (A-135815). Total length, measured in April 2001, 114 mm; snout to rear of anal slit 68.7 mm. No indication of external gills. Costal grooves 12, including an axillary and inguinal. Many ill-defined grayish spots on a pale gray background. See Shaffer and McKnight (1996: 419) for a map showing the distribution of *Ambystoma velasci*.

ORIENTATION: Alcocer et al. (1997) published a review of the large endorheic basin

at the eastern end of the Mexican plateau. They referred to it as the “Oriental”, but it is the equivalent of the Llanos de San Juan indicated on figure 1 of this paper. Much of the area was once occupied by lakes, one of which bears the name of Totolcingo or El Carmen. They have been gradually drying up because of overextraction and channelization of springs for human use. In May 1933, rain water persisted for only one month, and since then “Totolcingo Lake has remained dry.”

Alcocer et al. (1998) quoted from a government document (Anonymous, 1982, translation) which stated that “the Oriental basin is located almost 100 m above Mexico City, so its extensive ground-water resources are being gravity-transported to satisfy Mexico City's requirements.” The altitude for El Carmen is given as 2340 m above sea level.

Javier Alcocer, the authority on the “Oriental”, wrote (personal commun.), “Fortunately there are other loci that could serve to preserve aquatic fauna in the area. Not long ago I visited the railway station named Mantantales [‘springs’] where there is at least one large spring left. Also, there are small scattered veneers throughout the lower portion of the basin where El Carmen playa intermittently formed. El Carmen is not an ephemeral lake yet . . .”. Unhappily, the map published in 2000, as mentioned above, indicates that there is no longer water in the *lagunilla* where I obtained a large series of snakes during the 1960s.

REMARKS

Snow-capped Orizaba was visible to the southeast from the *lagunilla* when the weather was clear, especially in the early mornings. Incidentally, we confirmed that the area where we worked was in Tlaxcala and not the closely adjacent Puebla, first by word of mouth and later by a badly battered roadside sign. A minor correction should be noted. On the tags attached to the snakes and elsewhere the locality was given as “east of El Carmen” when it actually should have been “southeast”. I have used *lagunilla* for this tiny lake at the suggestion of Jonathan A. Campbell, even though my notes refer to it as *lagunita*. That was how I interpreted what the boys I met called it. The town of El Car-

TABLE 7
Characteristics of New Races of *Thamnophis eques* (in same order as they appear in the text)

Name	Lake(s)	Characteristics
<i>cuitzeoensis</i>	Cuitzeo	Strongly melanistic
<i>patzcuaroensis</i>	Pátzcuaro	Venter with broad black crosslines; undersides of head and tail bright yellow in life; pale longitudinal stripes may not be well developed
<i>insperatus</i>	Zacapu	Checkerboarded
<i>obscurus</i>	Chapala	Pale longitudinal stripes lacking except in the very young and long-preserved specimens
<i>diluvialis</i>	Atotonilco, Cajititlán, and nearby isolated localities	Pale middorsal stripe conspicuous; 3 scales wide
<i>scotti</i>	Magdalena	Pale middorsal stripe variable, 1–7 scales wide or none and not bordered by dark pigment
<i>carmenensis</i>	Del Carmen	Pale middorsal stripe narrow and bordered by a black line 1 or 2 scales wide; a dwarfed race

men is designated on a recent map as El Carmen Tequexquitla (INEGI, Guadalupe Victoria sheet, 1:50,000, 2000).

LA LAGUNA ALCHICHICA

This unusual body of water, the largest and deepest of six in the *llanos* (plains) of eastern Puebla, is a crater lake. Water accumulated in the extinct volcanoes, and salamanders of the genus *Ambystoma* are known to occur in several of them (Brandon et al., 1981). The geographical locations of the crater lakes are shown in figure 1B of Alcocer et al. (1998). According to those authors, both Alchichica and Axtcac to the southwest are saline; the others are fresh.

Although we did not expect that the Laguna Alchichica would provide habitat suitable for garter snakes, we decided to visit it on July 8, 1964, while we were in the general vicinity. Our expectations were confirmed. At least it gave us the opportunity to see what, for us, was a different type of lake in Mexico's transvolcanic belt.

DISCUSSION

The isolation of individual lakes as a result of volcanism or severe flooding, probably a million or more years ago, has given *Thamnophis eques* time to differentiate from one

locality to another. During personal fieldwork in the transvolcanic belt of Mexico, seven new subspecies were found. They are named herein and studied in detail. All are associated with lakes, most of them endorheic. The snakes parallel the endemism previously reported among salamanders, crayfish, birds, mammals, and especially fishes. Series of specimens of *Thamnophis* were obtained for six of the seven new subspecies. The seventh is represented by a single damaged snake found by accident.

Explanations follow about some of the methods and devices used while studying this material. More than 600 specimens were examined in detail, a large percentage of them neonates born in captivity. All gravid females were transported to our home base at the Philadelphia Zoo, except for two litters that were born en route.

IDENTIFICATION

Table 7 is included in lieu of a dichotomous key. The differences in coloration and pattern in the various races of *Thamnophis eques* in Mexico's transvolcanic belt are so readily distinguishable that they can be quickly identified. Note should be taken of the presence or absence of a pale longitudinal middorsal stripe, its width, and its edges,

whether strong or weak (or black-bordered). Also, are the ventral crosslines conspicuous? One race is plain black dorsally. All are easily recognizable, and with the backup of geography, the lakes and their environs to which they are confined, a complicated key is superfluous. Reference also can be made to the figures, most of them depicting the various subspecies from life.

TABLES OF SCUTELLATION

To save space, scale counts are summarized (in tables 1–6) using the style developed in an earlier paper (Conant, 1961). In general, counts were made only on perfect specimens, but on rare occasions individual or small groups of head scales were found to be sufficiently damaged as to be uncountable. They were omitted. They are the reason for a few discrepancies among the scale counts in the tables. Also, tails are incomplete in many wild-caught specimens, presumably as the result of injury by predators. Counts of subcaudal scales and tail/total length proportions are thus affected. Statistics for them in the tables are fewer than for scale counts on the heads and ventrals. Several neonates were omitted because of their poor condition.

A comparison of the tables with one another reveals several items of interest. The normal maximum number of scale rows is 21, but 23 were recorded in a single individual of *cuitzeoensis*, in 10% of the sample of *scotti*, 29% of *obscurus*, and 55% of *patzcuaroensis*. Thus, *patzcuaroensis* has a greater number of dorsal scale rows than in any other population of *Thamnophis eques* studied, although the increase to 23 was only for a short distance in almost all cases. The lowest maximum number is also usually 21, but in *carmenensis*, which is dwarfed in total length when compared with any of the other races, 10 snakes (~8% of the total of 127 in the sample) have only a maximum of 19 scale rows.

By comparing the means for the numbers of ventral scales, the lowest counts occur in *scotti* and *carmenensis*, which are from the two extremes of the geographical range of *eques* in the transvolcanic belt—*scotti* at the westernmost and *carmenensis* at the easternmost locality, respectively.

Comparison of the means for subcaudals shows that the dwarf race (*carmenensis*) has the fewest number.

I have not attempted to analyze the variations statistically, but have merely shown that there are at least some differences, usually minor, in scale counts among the material examined.

FUTURE EXPLORATION

There are a number of small endorheic lakes (see fig. 1) that were not accessible by road during the early 1960s when our fieldwork was conducted in the transvolcanic belt of Mexico. Both my wife, my constant companion, and I were middle-aged at the time, and trying to use horses and/or a packtrain to reach the isolated lakes was beyond our ability. Additional races of *Thamnophis eques* may eventually be discovered in lakes we were unable to reach. Two unvisited basins of interior drainage are shown in figure 1, one due east of the large Lago de Chapala, the other southeast of it. Within these are several small lakes which would be worth exploring for possible additional isolated races of *Thamnophis eques*. Visits to the Laguna Zirahuén might also be productive, and to the Laguna de Zacapu and vicinity to obtain good specimens of *T. e. insperatus* to support the single damaged one we found.

ACKNOWLEDGMENTS

Because my work on the variations of *Thamnophis eques* in Mexico's transvolcanic belt was unexpectedly long delayed, this paper is based on two disjunct time periods. The first was from 1959 through 1965 when my late wife, Isabelle Hunt Conant, and I were actively doing fieldwork in the region. The second began in the late 1990s after I cleared my agenda and gave the completion of this report top priority. Because Isabelle and I worked chiefly alone at the lakes in the transvolcanic belt, this list of acknowledgments is relatively short, but I have included the names of persons at the various supportive institutions who helped so importantly, and those few who devoted endless hours in specialized ways.

Radcliffe Cheston, Jr., late President of the Zoological Society of Philadelphia, was en-

thusiastic about my fieldwork in Mexico, and he encouraged me to apply for grants from the National Science Foundation. He also permitted me to be away from my responsibilities at the Philadelphia Zoological Garden for a summer month in each of six years. That, in addition to my annual month's vacation, gave us ample time to drive to Mexico and pursue our activities there. Philadelphia Zoo keepers Sarah Cunius, Edward T. Endy, and Ray Hance alternated in caring for study specimens I kept alive after our many expeditions. Ruth G. Endy (now Jerdan), my secretary, typed many of my voluminous notes on the adult snakes and the birth of their young.

The members of the Department of Herpetology at the American Museum of Natural History were so friendly and helpful that I frequently thought I was almost a part of the department. I visited there often from my headquarters at the Philadelphia Zoo. It started with Charles M. Bogert, who was my mentor for several years and who made me a Research Associate in 1948, a privilege I still enjoy. He kindled my interest in Mexican herpetology, and we even visited Jalisco, Oaxaca, and Sonora together. Others from the department assisted in innumerable ways, but in the interest of saving space, it is best to list them alphabetically. Curators and Chairmen: The very helpful Charles J. Cole, Darrel R. Frost, Charles W. Myers, Christopher J. Raxworthy, and Richard G. Zweifel. Staff members: Iris Calderon, George W. Foley, Brenda Jones, Irene Palser, and Margaret Shaw. Linda S. Ford, Curatorial Assistant and manager of the collection, helped in many ways as I queried her about the specimens of *Thamnophis eques*, the great bulk of which my late wife and I collected in Mexico and which I gave to the Museum 30- to 40-odd years ago.

At the University of New Mexico, Donald W. Duszynski, both during his long tenure as Chair of the Department of Biology and subsequently, offered constant encouragement. At the Centennial Science and Engineering Library, Diana Northup was helpful, and especially Bruce D. Neville, who found many references for me, even one from another university, photocopied pertinent pages, and then mailed them to me. He was so adept

with his computer that he sometimes located the book I needed before I finished describing it over the telephone. Mary Terese Wyant, map librarian (Map and Geographic Information Center—acronym MAGIC), ferretted out localities I needed and carefully determined the approximate elevations above sea level of many of the lakes from which *Thamnophis eques* material was available. Her chief source of reference was the *Nomenclátor de Jalisco* and similar volumes on other Mexican states published in Mexico by the SSP (Secretaría de Programación y Presupuesto). She was able to find names of towns bordering the lakes, which were higher than the water surface but close enough for practical purposes. All the lakes, especially the endorheic ones, varied with wet and dry seasons.

Several persons associated with the Museum of Southwestern Biology, at the University of New Mexico, have been kind and helpful. Alexandra M. Snyder, a professional collections manager, kept my American Museum material in excellent condition, shipped and received specimens for me, and frequently took my arm to keep me from falling in my old age. Steven P. Platania ferried large numbers of gallon jars full of specimens to my home for study and then back to the Museum. My two handicapped parking permits were mere hunting licenses amid the superabundance of student automobiles, and it was fruitless to try working regularly at the University. Sara J. Gottlieb, through her skill with her computer, adjusted figure 1 to conform with AMNH requirements. W. Howard Brandenburg drew several maps and portions of snakes for me. Jacek Tomas Giermakowski helped with moving the collection to new and modern quarters in the old bookstore.

I am deeply indebted to two colleagues who served as outside reviewers and who recommended that this opus be published by the American Museum of Natural History. They are: Jonathan A. Campbell of the University of Texas at Arlington and a recognized authority on the herpetology of Mexico; and Douglas A. Rossman, Professor Emeritus of Louisiana State University and an outstanding student of the garter snakes. As each section of the manuscript was completed, I sent them copies and they made sev-

eral useful suggestions that I incorporated. Jonathan A. Campbell also very kindly translated my abstract into Spanish to serve as the Resumen. There were also two unnamed reviewers, and Robert G. Webb of the University of Texas at El Paso. Several of Webb's suggestions have been incorporated in this manuscript.

My profound thanks are extended to the Mexican officials who issued collecting permits for me during the years when we were actively working in their country. They were the Directors General Luis Macias Arellano and Rodolfo Hernandez Corzo, Departamento de Conservación de la Fauna Silvestre. My fieldwork in Mexico was supported by the National Science Foundation (grants G-9040, G-22657, and GB-2177).

I am especially pleased to use a map adapted from figure 4 in the *Handbook of Middle American Indians* (vol. I, p. 108), edited by Robert Wauchope, in the chapter on the "Hydrography of Middle America" written by Jorge L. Tamayo in collaboration with Robert C. West (1964) and published by the University of Texas Press. That illustration succinctly delineates areas of interior drainage and lakes of the central plateau of Mexico circa A.D. 1500 before the coming of the conquistadors. It clearly indicates the areas where endemism is abundantly evident among a wide variety of aquatic or semi-aquatic organisms or those dependent on a hydric environment. I have referred to it repeatedly as I worked on this manuscript.

Robert Rush Miller, long the leading authority on the fishes of Mexico, helped me in a variety of ways, suggesting localities where I might search for garter and water snakes, how to seek help in the field, and also by identifying a great many fishes for me. Some I caught by hand or with a seine or tea strainer. Whenever palpation revealed the presence of recently swallowed food, I forced the snakes to regurgitate, preserved any fishes involved, and sent them to Miller for identification. He quickly responded and I have recorded his determinations under the heading of Food for most of the snake populations I studied. I regret that we never were in the field together. His activities were during the winter months, when the weather was best in Mexico. We had to wait for the am-

phibians and reptiles to emerge from estivation, and we tried to be in the field at the onset of the rainy season, usually in July. At least we were pen pals and I owe Bob Miller much for his enthusiastic help.

M. Norma Feinberg did almost all of the scale counting. She was accurate and dependable and, although I spot-checked her work, I almost never found an error. Occasionally, we disagreed on interpretations in those very few cases when the scutellation was not clearly evident. We then would re-examine the specimen together and determine whether it should be retained or eliminated from the scale count summarizations because of injury or gross variation from the normal, at least among neonates. A large percentage of the material I gave her consisted of newly born specimens and, even though she used a dissecting microscope, counting the ventrals, and especially the subcaudals, on such miniscule snakes was a tedious and exacting chore. I was very fortunate to have her help during the early 1960s when we were bringing back much material annually from Mexico.

Candice R. Corley, my faithful part-time secretary, doubtless was glad she had a word-processing program on her computer, as she frequently prepared new versions of the manuscript. New information surfaced, reviewers offered helpful suggestions, and I developed ways to improve the diction. She caught mistakes and repetitions and, because she was accustomed to typing theses and dissertations for students from the University of Arizona, she was adept at turning phrases to make them read better. Her skillful typing was a major and indispensable asset. I am particularly grateful for her thorough and time-consuming task of preparing the final manuscript to be transferred to computer disk after the copyediting had been completed.

My wife, Kathryn J. Gloyd, was plagued with all the problems that accompany research in the home; for example, dead silence for hours, cross-reading sections of the manuscript for accuracy, and cleaning up after I fell with a gallon bottle filled with snakes and isopropanol in my makeshift laboratory in our utility room. She also listened to my explaining what I was doing and pronouncing Mexican place names that were

completely foreign to her ears. She had visited Sonora, chiefly Nogales, but she and her late husband, Howard K. Gloyd, had never ventured far south into Mexico. Through it all, she was patient, supportive, and anxious for me to complete a lengthy herpetological project on which, long ago, I had worked for many years.

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SOURCES OF MAPS AND ATLASES

Mexico has been abundantly mapped but, until recently, finding some of the reported localities was a matter of hard work or even luck. Names like La Gloria and Villa Nueva were repeated even in the same state, and names of long-established settlements were changed to honor some local hero. The town of Carmen on the Río del Carmen in northern Chihuahua became Ricardo Flores Magón, for example.

During our fieldwork in Mexico we used many maps, mostly published in that country, but others in the United States. Those we consulted in conjunction with this study, both atlases and map series, are listed below in alphabetical order with appropriate personal comments. In the text, I refer to sheet names or numbers or other means of identification. To avoid confusion, referral should be made to the maps listed below rather than to the References section.

In an excellent book, *World Mapping Today* (1987), there is a review of the history of official mapping in Mexico that serves to clarify the confusion of the many different official agencies involved. The preparation of maps was centralized in 1968 in the Comisión de Estudios del Territorio

Nacional (CETENAL), but it soon degenerated into more than six "acronyms", including DETENAL. The present title for the coordinating body for statistical and geographic information is the Instituto Nacional de Estadística, Geografía e Informática (INEGI).

While driving in Mexico, we normally used the Texaco and/or Enco road maps. I also had the 47 topographic sheets of the Comisión Intersecretarial bound into a large flat book that fitted on end in the clothes closet of our camper. It was useful in finding streams or other aquatic features that might be out of sight of the road.

Atlas Geográfico de los Estados Unidos Mexicanos. 1946. Secretaría de Agricultura y Fomento, Dirección e Hidrología, República Mexicana. General maps of the individual states; topographic with political overlays (1:200,000 to 1:1,000,000).

Atlas Goodrich Euzkadi. 1964, 1966. Caminos de México. Excellent road maps showing highways and secondary routes as they existed during the period when we were active in Mexico.

CETENAL. 1968 [first date]. Comisión de Estudios del Territorio Nacional. Subject to name changes and "acronyms". Topographic.

Comisión Intersecretarial. 1958. La Carta Geográfica de la República Mexicana. 47 topographic sheets (1:500,000).

DETENAL. Various dates. An "acronym" of CETENAL. Topographic.

INEGI. Various dates. Instituto Nacional Estadística, Geografía e Informática. Topographic.

SSP. 1982. Secretaría de Programación y Presupuesto. Derived from INEGI.

World Mapping Today. 1987. London: Butterworths (Mexico).

REFERENCES

- Alcocer, J., A. Lugo, E. Escobar, and M. Sánchez. 1997. The macrobenthic fauna of a former perennial and now episodically filled Mexican saline lake. *International Journal of Salt Lake Research* 5: 261–274.
- Alcocer, J., A. Lugo, M.R. Sánchez, M. Chávez, and E. Escobar. 1998. Threats to the saline lakes of the Oriental Basin, Mexico, by human activities. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* (Stuttgart) 26: 1383–1386.
- Anonymous. 1982. Sistema hidráulico del Distrito Federal. Dirección General de Construcción y Operación Hidráulica, Secretaría de Obras y Servicios del D.D.F. México.
- Barbour, C.D. 1973a. The systematics and evolution of the genus *Chirostoma* Swainson (Pi-

- scas, Atherinidae). *Tulane Studies in Zoology and Botany* 18(3): 97–141.
- Barbour, C.D. 1973b. A biogeographical history of *Chirostoma* (Pisces: Atherinidae): a species flock from the Mexican Plateau. *Copeia* 1973(3): 533–556.
- Brandon, R.A. 1989. Natural history of the axolotl and its relationships to other ambystomatid salamanders. In J.B. Armstrong and G.M. Malacinski (editors), *Developmental biology of the Axolotl*: 13–21. New York: Oxford University Press.
- Brandon, R.A., E.J. Maruska, and W.T. Rumph. 1981. A new species of neotenic *Ambystoma* (Amphibia, Caudata) endemic to Laguna Alchichica, Puebla, Mexico. *Bulletin of the Southern California Academy of Sciences* 80(3): 112–125.
- Brumwell, M.J. 1939. Variation in the snake, *Thamnophis macrostemma* Kennicott. *Transactions of the Kansas Academy of Science* 42: 423–429.
- Cabrero G., M.T. 1991. Cultura arqueológica de Bolaños (Zacatecas y Jalisco). Una frontera cultural. *Ancient Mesoamerica* 2: 193–203.
- Ceballos, C.-J.G., and U. Guzmán-Villa. 1991. Guía limnológica del estado de Michoacán. Laboratorio de Biología Acuática, Escuela de Biología Coordinación de la Investigación Científica, Morelia, Michoacán, 30 pp.
- Chacón, T.A. 1993. Lake Patzcuaro, Mexico: watershed and water quality deterioration in a tropical high-altitude Latin American lake. *Lake and Reservoir Management* 8(1): 37–47.
- Clements, T. 1963. Pleistocene history of Lake Chapala, Jalisco, Mexico. In *Essays in marine geology in honor of K.O. Emery*: 35–49. Los Angeles: University of Southern California Press.
- Conant, R. 1958. A field guide to reptiles and amphibians of the United States and Canada east of the 100th meridian. Boston: Houghton Mifflin, 366 pp. + 40 plates, 248 maps.
- Conant, R. 1961. A new water snake from Mexico, with notes on anal plates and apical pits in *Natrix* and *Thamnophis*. *American Museum Novitates* 2060: 1–22.
- Conant, R. 1963. Semiaquatic snakes of the genus *Thamnophis* from the isolated drainage system of the Río Nazas and adjacent areas in Mexico. *Copeia* 1963(3): 473–499.
- Conant, R. 1969. A review of the water snakes of the genus *Natrix* in Mexico. *Bulletin of the American Museum of Natural History* 142(1): 1–140.
- Conant, R. 1975. A field guide to reptiles and amphibians of eastern and central North America. Boston: Houghton Mifflin, 429 pp. + 48 plates, 311 maps.
- Conant, R. 1997. A field guide to the life and times of Roger Conant. Provo, UT: Canyonlands Publishing Group, 498 pp. + 8 color plates.
- de Buen, F. 1943. Los lagos Michoacanos: I. Caracteres generales. El lago de Zirahuén. *Revista de la Sociedad Mexicana de Historia Natural* IV(3–4): 211–232.
- de Buen, F. 1944. Los lagos Michoacanos: II. Pátzcuaro. *Revista de la Sociedad Mexicana de Historia Natural* V(1–2): 99–125.
- de Buen, F. 1945. Resultados de una campaña limnológica en Chapala y observaciones sobre otra aguas exploradas. *Revista de la Sociedad Mexicana de Historia Natural* VI(3–4): 129–144.
- Dickerman, R.W. 1963. The song sparrows of the Mexican Plateau. *Occasional Papers of the Minnesota Museum of Natural History* 9: 1–79.
- Dickerman, R.W. 1965. The nomenclature of the red-winged blackbird (*Agelaius phoeniceus*) of south-central Mexico. *Occasional Papers of the Museum of Zoology Louisiana State University (Baton Rouge)* 31: 1–6.
- Dickerman, R.W. 1970. A systematic revision of *Geothlypis speciosa*, the black-pollled yellowthroat. *Condor* 72(1): 95–98.
- Flores-Villela, O. “1992” [1993]. Herpetofauna of Mexico: distribution and endemism. In T.P. Ramamoorthy, R. Bye, A. Lot, and J. Fa (editors): 253–280. New York: Oxford University Press.
- Gloyd, H.K., and R. Conant. 1990. Snakes of the *Agkistrodon* complex; a monographic review. *Society for the Study of Amphibians and Reptiles Contributions to Herpetology* 6: 614 pp. + 33 color plates.
- Goldman, E.A. 1951. Biological investigations in México. *Smithsonian Miscellaneous Collections* 115: 476 pp.
- Guerrero, R.A. 1964. Esquema geográfico de México. In *Caminos de México*, Atlas Goodrich Euzkadi: 1–8.
- Hall, E.R. 1981. The mammals of North America, 2nd ed., vol. 2.: 601–1181 + 1–90 (index). New York: John Wiley.
- Hillis, D.M., and J.S. Frost. 1985. Three new species of leopard frogs (*Rana pipiens* complex) from the Mexican plateau. *Occasional Papers of the Museum of Natural History University of Kansas* 117: 1–14.
- Hobbs, H.H., Jr. 1971. The entocytherid ostracods of Mexico and Cuba. *Smithsonian Contributions to Zoology* 81: 1–55.
- Hobbs, H.H., Jr. 1972. Crayfishes (Astacidae) of North and Middle America. *Environmental Protection Agency, Biota of Freshwater Eco-*

- systems Identification Manual 9: 173 pp. + 115 figs.
- Hobbs, H.H., Jr. 1974. A checklist of the North and Middle American crayfishes (Decapoda: Astacidae and Cambaridae). *Smithsonian Contributions to Zoology* 166: 1–161.
- Krebs, S.L., and R.A. Brandon. 1984. A new species of salamander (family Ambystomatidae) from Michoacan, Mexico. *Herpetologica* 40(3): 238–245.
- León, L.F., and M. Escalante. 1993. Flow and pollutant transport in Lake Chapala, Mexico. In C.A. Brebbia and L.C. Wrobel (editors), *Water pollution II: modelling, measuring, and prediction*: 279–286. Second International Conference, Milan, Italy. Boston: Computational Mechanics Publications.
- Lyons, J., G. González-Hernández, E. Soto-Galera, and M. Guzmán-Arroyo. 1998. Decline of freshwater fishes and fisheries in selected drainages of west-central Mexico. *Fisheries Management* 23(4): 10–18.
- Metcalfe, S.E., F.A. Street-Perrott, S.L. O'Hara, P.E. Hales, and R.A. Perrott. 1994. The palaeolimnological record of environmental change: examples from the arid frontier of Mesoamerica. In A.C. Millington and K. Pye (editors), *Environmental change in drylands*: 131–145. London: John Wiley.
- Moore, R.T. 1945. The transverse volcanic biotic province of Central Mexico and its relationship to adjacent provinces. *Transactions of the San Diego Society of Natural History* 10(12): 219–235 + map.
- Moriarty, J.J. (editor). "2000" [2001]. Scientific and standard English names of amphibians and reptiles of North America. . . . B.I. Crother, chair. *Society for the Study of Amphibians and Reptiles, Herpetological Circular* 29: 1–82.
- Palmer, R.H. 1926. Tectonic setting of Lago de Chapala. *Pan-American Geologist* 45: 125–134.
- Reuss, A. 1834. *Zoologische miscellen, reptilien, ophidier. Abhandlungen von der Senckenbergischen Museum*: 130–162, pls. 7–9.
- Ridgway, R. 1912. *Color standards and color nomenclature*. Privately printed, 44 pp. + 53 pls.
- Rossman, D.A., N.B. Ford, and R.A. Seigel. 1996. *The garter snakes: evolution and ecology*. Animal Natural History Series, vol. 2. Norman: University of Oklahoma Press.
- Rubín, R. 1960. *Lago Cajititlán. Jalisco en el arte. Planeación y Promoción*, S.A., Guadalajara: 60 pp.
- Secretaría de Fomento. 1888. *Desagüe del Valle de México*, documentos relativos al proyecto en ejecución: 145 pp., map.
- Shaffer, H.B., and M.L. McKnight. 1996. The polytypic species revisited: differentiation and molecular phylogenetics of the tiger salamander *Ambystoma tigrinum* (Amphibia: Caudata) complex. *Evolution* 50(1): 417–433.
- Smith, H.M. 1940. An analysis of the biotic provinces of Mexico, as indicated by the distribution of the lizards of the genus *Sceloporus*. *Anales de la Escuela Nacional de Ciencias Biológicas de México* 2(1): 95–110 + map. [in English and Spanish]
- Smith, H.M. 1942. The synonymy of the garter snakes (*Thamnophis*), with notes on Mexican and Central American species. *Zoologica* 27(17): 97–123.
- Smith, H.M. 1951. The identity of the ophidian name *Coluber eques* Reuss. *Copeia* 1951(2): 138–140.
- Smith, M.L., and R.R. Miller. 1980. *Allotoca maculata*, a new species of goodeid fish from western México, with comments on *Allotoca dugesi*. *Copeia* 1980(3): 408–417.
- Tamayo, J.L. 1949. *Geografía general de México*. Talleres Gráficos de la Nación, México, D.F. Tomos I, II: 628; 580 pp.
- Tamayo, J.L., in collaboration with R.C. West. 1964. The hydrography of Middle America. In R. Wauchope (editor), *Handbook of Middle American Indians I*: 84–121. Austin: University of Texas Press.
- Tricart, J. 1985. Pro-lagos. Los lagos del eje neovolcánico de México. Université Louis Pasteur-Strasbourg I. Consejo Nacional de Ciencia y Tecnología Centre National de la Recherche Scientifique Instituto de Geografía. Universidad Nacional Autónoma de México: 58 pp.
- Urrutia-Fucugauchi, J., and J. Rosas-Elguera. 1994. Paleomagnetic study of the eastern sector of Chapala Lake and implications for the tectonics of west-central Mexico. *Tectonophysics* 239(1–4): 61–71.
- Vaillant, G.C. 1962. *Aztecs of Mexico*. Garden City, NY: Doubleday.
- Villalobos Figueroa, A. 1943. Estudios de los cambarinos Mexicanos I. Observaciones sobre *Cambarellus Montezumae* (Saussure) y algunos de sus formas con descripción de una subespecie nueva. *Anales del Instituto de Universidad Nacional Autónoma de México* 14(2): 587–611.
- World almanac and book of facts. 2000. New York: New York Times.