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Ambystoma maculatum.
Photo: J.D. Willson

Overview of the Genus

Ambystoma



This article is an overview of the species and subspecies of the genus *Ambystoma*, the mole salamanders. For a clearer picture they are arranged into a number of groups — primarily based on genetics according to SHAFFER (1984a, b), SHAFFER et al. (1991), JONES et al. (1993), SHAFFER and MCKNIGHT (1996), HIGHTON (2000), SAMUELS et al. (2005), WEISROCK et al. (2006), and PAULY et al. (2007); and then based on morphology. Unless otherwise stated, descriptions are of metamorphosed adult forms.

Today, all species of *Ambystoma* are more or less threatened — mainly by habitat destruction including the draining of breeding ponds or introduction of predatory fish. Species that are especially threatened will be mentioned again as such in their respective descriptions.

The most popular group of *Ambystoma* species are the tiger salamanders — the *Ambystoma mexicanum* and *Ambystoma tigrinum* complexes — including all of

the species of the genus found in Mexico. Typical of tiger salamanders is a large and massive body, an especially broad head with small eyes, and a tail about the same length as the body. Within this group is the species of *Ambystoma* that is by far the best known among both researchers and private keepers, *Ambystoma mexicanum*, the axolotl.

Ambystoma mexicanum complex (Group A)

Ambystoma mexicanum (Shaw and Nodder, 1789). The common name for this species, axolotl, comes from the Aztec Nahuatl dialect. One of the most popular translations associates the axolotl with the Aztec god of the underworld, Xolotl. But the most widely accepted translation is “water dog” from *atl* (= water) and *xolotl* (= dog).

As early as 1804, Alexander von Humboldt brought the first specimens (females) of this species to the Paris Natural History Museum. The most interesting feature of the axolotl is its lifelong neoteny (reaching sexual

maturity while retaining its aquatic larval form), and its ability to regenerate limbs and even internal organs, including parts of its brain. Neoteny is also found in populations of many other species of *Ambystoma*, such as some subspecies of *A. mavortium*, but these species also have populations that undergo metamorphosis to become terrestrial adults. *Ambystoma mexicanum* and the genetically very closely related *A. andersoni*, *A. dumerilii*, *A. lermaense*, and *A. taylori*, are among very few species that, whether in the wild or in captivity, extremely seldom metamorphose into adult forms. Interestingly, neoteny in *Ambystoma* populations increases with elevation (the axolotl occupies one of the highest distributions of the genus), and is associated with an iodine deficiency, which causes reduced function of the thyroid gland. If an axolotl is injected with thyroid hormone (e.g., thyroxin), the animal metamorphoses into a terrestrial adult form. This is a delicate procedure and should be done only by a qualified specialist. Risk of death is high, and animals that metamorphose successfully are then rather short-lived — with a life span of only 1–5 years, whereas neotenic axolotls that do not metamorphose and are well cared for can live for 10–25 years. Another method said to induce metamorphosis is reducing the water depth, but this is not scientifically proven, and often leads to death of the animal.

Axolotls in the aquatic larval form reach 15–45 centimeters in total length (usually about 23 centimeters) — if they metamorphose, the terrestrial adult length is about 20 centimeters. There are 11–13 rib grooves along the flanks.

The natural wild coloration of the axolotl is dark to light grayish brown with small black and light brown or golden spots. There are also specimens that are melanistic (entirely black or dark gray), albino (entirely white with red eyes), golden albino (yellow with red eyes), leucistic (white or yellowish with dark eyes), and harlequin (white or yellow with highly contrasting black and greenish markings), as well as other variants. None of the golden albinos are pure *A. mexicanum*, but rather trace back to a cross between a female albino *A. mavortium* and a male *A. mexicanum* (HUMPHREY, 1967). Many experts believe that practically all the axolotls in captivity today are hybrids to a certain degree, and true pure axolotls are rare. This is true at least for the popular albino axolotls. Specimens with wild coloration that metamorphose become blackish with yellowish spots or flecks of variable size — they are quite similar in appearance to the terrestrial forms of either *A. velasci* or *A. granulosum*.

Ambystoma mexicanum is native to Lake Chalco and Lake Xochimilco, at an elevation of more than 2,270 meters above sea level in the central highlands of Mexico, not far from Mexico City. Unfortunately, wild populations are gravely threatened because of draining and pollution of the water, and consumption by local residents. With the growth of Mexico City's metropolitan area, Lake Chalco has disappeared completely and Lake Xochimilco has been reduced to little more than a few canals. The survival of the species in captivity is guaranteed. It is kept and bred in great numbers by scientists and private keepers.

Ambystoma tigrinum. Photo: J.D. Willson



***Ambystoma amblycephalum* Taylor, 1940.** The skin is finely wrinkled. Total length reaches 16.1 centimeters. Coloration is black with cream-colored spots on the ventral surface and lower flanks and light markings on the chin. Neoteny is rare in this species.

Ambystoma amblycephalum is found in meadows and pine/oak woodland of the province of Morelia in the northwestern state of Michoacán, Mexico.

***Ambystoma andersoni* Krebs and Brandon, 1984.** This species has a massive body with a relatively short tail, and grows to a total length of 21.4 centimeters. Coloration is reddish brown with numerous black spots, which are often fused to form larger black areas. In the wild, only neotenic populations are known. Genetically closely related to *A. mexicanum* (SAMUELS et al., 2005).

Ambystoma mexicanum "Humphrey Form." Photo: B. Love



This species is native to Lake Zacapu at an elevation of 2,000 meters above sea level, and the river between Lake Zacapu and Lake Patzcuaro in the state of Michoacán, Mexico.

***Ambystoma ordinarium* Taylor, 1939.** The head is long and broad. The species grows to 16.2 centimeters in length. Dorsal coloration is blackish, often with small dark gray spots. Ventral coloration is grayish. The limbs are blackish brown.

According to HEIGHTON (2000) there are two genetically distinct forms requiring further morphological research — one of these forms may be conspecific with *A. dumerilii*. According to WEISROCK et al. (2006) there are as many as four genetically distinct forms, of which one is seen as a hybrid between *A. ordinarium* and *A. dumerilli*. Neotenic populations are known and are not rare.

Ambystoma ordinarium is found in conifer forests in areas with abundant streams at elevations of 2,200–3,000 meters above sea level. There are two isolated ranges of genetically distinct forms: one in Puerto Hondo, Michoacán; and one (genetically similar to *A. dumerilii*) in Lake Patzcuaro east to Tianguistenco, Mexico.

***Ambystoma taylori* Brandon, Maruska, and Rumph, 1981.** This species grows to 11.5 centimeters in length. Coloration is a yellow to chestnut brown ground color with darker spots. *Ambystoma taylori* is purely neotenic in the wild. Artificially induced metamorphosis in the laboratory produces terrestrial adults that look nothing like the terrestrial adults of *A. subsalsum*, found in the same natural distribution area.

This species is restricted to the salty Lake Alchichica, in eastern Puebla, Mexico.

***Ambystoma mexicanum* complex (Group B)**

***Ambystoma altamirani* Dugès, 1895.** Synonymous with *A. zempoalaensis* Taylor and Smith, 1945, from the Lagunas of Zempoala, Morelos, Mexico. This species grows to 20 centimeters in length. Dorsolateral coloration is grayish brown with fine dark-brown dots. Larvae have medium-sized yellow spots. The belly is light brown. Neotenic populations are common.

Ambystoma altamirani is found in pine forest with small streams and high plains at elevations of 2,700–3,200 meters above sea level, west and southwest of Mexico City in the Lagunas of Zempoala, Monte Ajusco, and Los Leones desert in northern Morelos, and in the southern Distrito Federal.

***Ambystoma dumerilii* (Dugès, 1870).** Short, thick-set, flattened body and very robust flattened head, growing to 24 centimeters in length. Dorsolateral coloration is creamy yellow with a violet vertebral stripe. Ventral coloration is light brown. Purely neotenic.



Ambystoma andersoni male. Photo: J. Fleck



Ambystoma taylori. Photo: T. Burkhardt

Genetic studies (SAMUELS et al., 2005) show that *A. dumerilii* is closely related to the *A.-mexicanum/A.-andersoni* clade. According to HIGHTON (2000), citing data from SHAFFER and MC-KNIGHT (1996), *A. dumerilii* may be the same as one form of *A. ordinarium*.

Ambystoma dumerilii is found in Lake Patzcuaro at 1,920 meters above sea level, and in the Cuitzeo-Patzcuaro canal system of Michoacán, Mexico. Due to habitat destruction, introduction of predacious fish, and local consumption, this species is seriously threatened.

***Ambystoma granulatum* Taylor, 1944.** This species grows to 17 centimeters in length and is similar in appearance to *A. bombypellum*, but with a shorter tail and a shorter but wider head. It also resembles metamorphosed *A. mexicanum*. Dorsal coloration is brown with small yellow, black, and greenish spots. Ventral coloration is olive brown without spots.

Ambystoma granulatum is found in grassland around Mexico City and Toluca, at 3,000 meters above sea level. Because it is often confused with other *Ambystoma* species in the region, the distribution is not clear and needs further research.

***Ambystoma lermaense* (Taylor, 1940).** This species grows to 16–26.1 centimeters. Coloration is black with a purplish shimmer and gray legs. Metamorphosed specimens are dark gray with light claws, but the species is primarily neotenic.

Ambystoma lermaense is found in the Lerma and Santiago rivers and Lake Lerma, east of Toluca in Mexico's central highlands, at elevations of 2,800–3,000 meters above sea level. The species is in grave danger of extinction due to pollution, habitat loss (draining of Lake Lerma), and consumption by the local residents.

***Ambystoma rivulare* (Taylor, 1940).** According to WEISROCK et al. (2006), this species is genetically related to *A. granulatum* and not to the similar species *A. altamirani*. It differs from the latter in having a longer, flattened, and stockier body. It grows to 17.2 centimeters in length. Coloration is blackish with dark



Lake Alchichica, at 2,345 meters above sea level in Puebla, Mexico, is habitat for the endemic *Ambystoma taylori*. Photo: J. Fleck



The Lagunas of Zempoala in the central highlands of Mexico are home to *Ambystoma altamirani*. Photo: H. Werning



Ambystoma ordinarium larva. The metamorphosed adult forms continue to live a partly aquatic lifestyle. Photo: J. Fleck



Variety of *Ambystoma m. mavortium* from habitat in Crosby County, Texas.
Photo: T. Dimmler



Male *Ambystoma m. mavortium*. Photo: T. Blanck



Ambystoma mavortium diaboli male. Photo: T. Blanck

brown spots, gray with small black spots on the belly. Neoteny is common. Hybrids of *A. rivulare* and *A. altamirani* have been produced in the laboratory.

Ambystoma rivulare lives at elevations of more than 2,800 meters above sea level. It is found in pine forests with rocky streams near Ajusco (Distrito Federal), west of Mexico City, and in northeastern Guerrero between Taxco and Tetipac. It may also live on the volcano Nevado de Toluca, but the specimens here may be *A. altamirani*.

***Ambystoma tigrinum* complex**

The *Ambystoma tigrinum* complex has been keeping scientists busy for 150 years. It is by far the most complex group of forms in the genus, both genetically and phenotypically (in appearance), and is very closely related to the *Ambystoma mexicanum* complex. Currently eight species are classified in the *Ambystoma tigrinum* complex, and they are the largest terrestrial salamanders on Earth. The largest *A. mavortium* on record was 35 centimeters long, until the recent discovery of a specimen in North Dakota measuring a record-breaking 44 centimeters. Thus the subspecies *A. mavortium diaboli* is the largest of all known terrestrial salamander forms, even larger than *Dicamptodon tenebrosus*, which has a documented record length of 35.1 centimeters.

Members of the *Ambystoma tigrinum* complex include forms that metamorphose into terrestrial adults, and others that are completely neotenic — and both include distinct forms that are specialized for cannibalism, having flatter, wider heads with a wider bite and an extra row of prevomerine teeth.

All eight species have long, massive, plump bodies with 11–14 (usually 12) rib grooves. The skull is wide and massive; the eyes, relatively small.

The species of the *Ambystoma tigrinum* complex are quite adaptable, and can be found in habitats ranging from marshes and meadows to steppe, pine forest, and alpine regions. Like all salamanders, they depend on the proximity of suitable breeding waters, so their distributions are irregular, with gaps where none are found.

The *Ambystoma tigrinum* complex has the most extensive overall distribution of any *Ambystoma* form — from southern Canada through most of the United States and south to central Mexico. *Ambystoma mavortium*, with its various subspecies, has the largest range.

***Ambystoma mavortium mavortium* Baird, 1850.** This is the largest subspecies, growing to 25–33 centimeters in length, rarely 35 centimeters, and the neotenic form can grow to 40 centimeters. It has 11–14 rib grooves. Coloration consists of black with olive to yellow bars, stripes, and large spots of variable sizes and thickness. The black color is usually predominant. Neotenic populations are rare.



Ambystoma mavortium diaboli male. Photo: T. Blanck

Ambystoma mavortium mavortium is found from southeastern Texas and adjacent Mexico (with a gap in south central Texas) west into central New Mexico to the eastern edge of the *A. mavortium nebulosum* range. It has presumably been introduced in southwestern Arizona where it is found to the edge of the *A. mavortium stebbinsi* range. The range extends north into southwestern Colorado — to the edge of the *A. mavortium utahense* range in the west and to the edge of the *A. mavortium melanostictum* in the east — and across Oklahoma and Kansas into extreme southern Nebraska to the edges of the ranges of *A. mavortium melanostictum* and *A. tigrinum*.

The taxon *A. proserpine* (Baird and Girard, 1852) is probably synonymous with this subspecies. Populations on the edges of the range are known to mix with populations of adjacent subspecies producing a great variety of colorations. The larvae are sold throughout the United States for fishing bait, increasing the chances of hybridization.

Ambystoma mavortium mavortium has been successfully bred in captivity in France, Germany, Austria, and Japan.

***Ambystoma mavortium diaboli* Dunn, 1940.** Terrestrial forms of this subspecies grow to 25–30 centimeters in length, rarely to 43.5 centimeters; neotenic forms grow to 43.5 centimeters. Coloration is dark olive green, olive brown, or olive yellow on the back and flanks, and yellow on the belly. The entire body is covered with black dots of variable size that can be fused into larger markings. Neotenic populations are common in this subspecies.

Ambystoma mavortium diaboli is found from southern Saskatchewan and Manitoba into North Dakota, South Dakota, and extreme western Minnesota. In North Dakota, the subspecies meets and hybridizes with *A. mavortium melanostictum* and *A. tigrinum*, resulting in an unusually great variety of forms of tiger salamanders in this state.

***Ambystoma mavortium melanostictum* (Baird, 1860).** This subspecies exists in two distinct forms, here A and



Ambystoma mavortium diaboli male. Photo: T. Blanck



Ambystoma mavortium diaboli male. Photo: T. Blanck

B, which do not seem to have originated from hybridization. The head is relatively small and never wider than the body, unlike any other form or subspecies of *A. mavortium*. It is also the smallest subspecies, with the terrestrial forms growing to 15–20 centimeters, seldom to 25 centimeters. The neotenic form grows to 30 centimeters.

Form A is light gray to brownish gray on the back and flanks and creamy white on the belly, with a fine black reticulate pattern that separates the ground color into large patches forming a tigerlike pattern. Form B has a fine black marbled pattern with reticulation and smaller spots. The belly is dark gray with lighter blotches. Melanism is more common in this subspecies than in the others.

In my observation, metamorphosed adults are more aquatic than in the other subspecies, spending long periods of each day in the water. Neotenic populations are not uncommon.

Form A is found from southern Alberta and southwestern Saskatchewan south to northern Idaho, Wyoming, and South Dakota. An isolated population is found from extreme southern central British Columbia south into Washington state and across into eastern Idaho.

Form B is found from South Dakota to southern Nebraska and west across southeastern Wyoming into extreme northwestern Colorado.

***Ambystoma mavortium nebulosum* Hallowell, 1852.** This subspecies grows to 20–30 centimeters; the neotenic form, to 35 centimeters. Coloration is dark



Ambystoma tigrinum. Photo: D. M. Dennis

brown to black on the back and flanks and yellowish or black on the belly. There are variable small to medium-sized yellow to yellowish brown spots on the back and yellow spots on the belly. Neotenic populations of this subspecies are very common at high elevations.

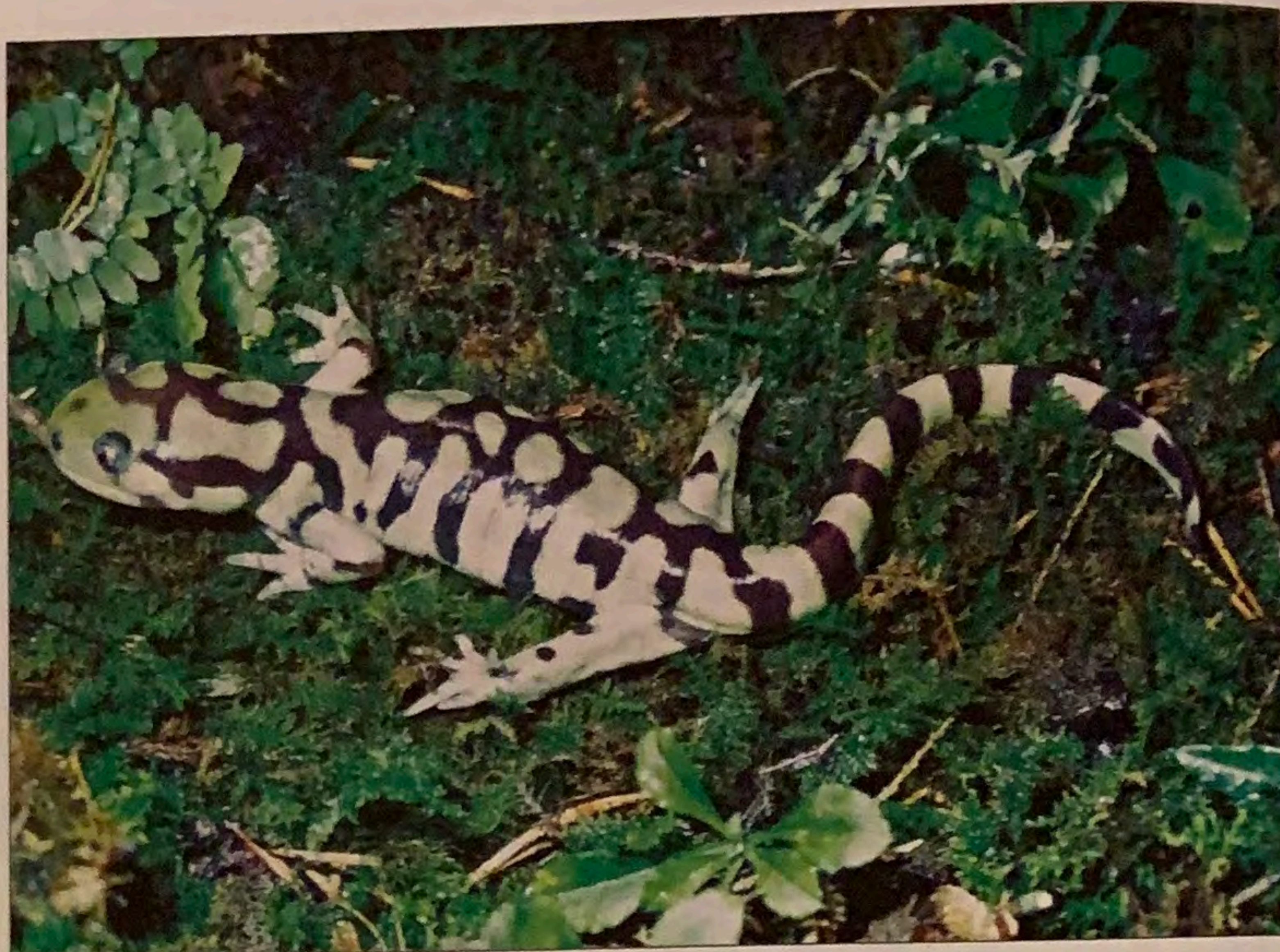
Ambystoma mavortium nebulosum is found from central Colorado through western New Mexico and into eastern Arizona where it inhabits higher elevations. *Ambystoma mavortium mavortium* inhabits the lower elevations farther west. *Ambystoma mavortium nebulosum* seems not to be present south of the Gila River in Arizona (LOWE, 1995).

Ambystoma mavortium stebbinsi Lowe, 1954. This subspecies seems to have originated from hybridization between *A. mavortium mavortium* and *A. mavortium nebulosum*, or through a genetic bottleneck from an earlier *A. mavortium mavortium* (JONES et al. 1988, 1995). It grows to 15–25 centimeters in length. Coloration is a black ground color marbled or reticulated with a more or less equal amount of yellow. Juveniles are black with yellow spots (JONES et al., 1988). The belly is dark gray. No neotenic populations are known.

Ambystoma mavortium stebbinsi is found only in the flats between the Huachara and Patagonia mountains in southeastern Arizona in Santa Cruz County, mainly in the San Rafael Valley. It has been found only in artificial ponds (for livestock). It is the only strictly protected form.

Ambystoma mavortium utahense Lowe, 1955. This subspecies grows to 20–30 centimeters. It has an olive green back and flanks, sometimes with a few small black, brown, or yellow spots, but usually of uniform color.

Ambystoma mavortium utahense is found from extreme southwestern Wyoming through Utah and the Colorado Plateau into northern New Mexico and Arizona. An isolated population seems to exist in Siskiyou County, northern California.



Ambystoma tigrinum. Photo: B. Love

Ambystoma tigrinum (Green, 1825). The terrestrial form of this species grows to 15–21 centimeters, rarely to 30 centimeters; the neotenic form, to 33 centimeters. There are 11–13 rib grooves. The species looks much like *A. mavortium nebulosum*. In fact, until recent studies (COLLINS et al., 1980; PIERCE and MITTON, 1980; SHAFFER and MCKNIGHT, 1996), most authors included *A. mavortium* as a subspecies of *A. tigrinum*. A dorsolateral black ground color is covered with a variable number of medium-sized yellowish-brown spots or dots, which may be fused to form larger blotches. Ventral coloration is yellow. Rarely a specimen is seen with the dorsal and ventral coloration reversed. According to SHAFFER and MCKNIGHT (1996) there are three genetically distinct forms: an eastern form, a western form, and a third form in western Florida. According to CHURCH et al. (2003) there are two genetically distinct groups, one being the populations in the western Apalachicola delta (Florida), which have been isolated since the ice age about 2 million years ago. Neotenic populations are known only in Michigan.

Ambystoma tigrinum is widely distributed from southern Ontario along the northern shores of the Great Lakes, around the lakes into Minnesota, Wisconsin, Michigan, and western Ohio. The range continues as far as northeastern Nebraska where it meets *A. mavortium diaboli*, *A. mavortium melanostictum*, and *A. mavortium mavortium*, with which it hybridizes to varying degrees. The species is present in Iowa, Illinois, and Indiana, and south through western Kentucky and Tennessee, across Alabama and part of Mississippi to Louisiana in the west, and east into Florida, from which it extends up the Atlantic coast all the way to New York, where the most northern locality is Long Island. *Ambystoma tigrinum* is not found in the high elevations of the Appalachian Mountains. Reports of the species in eastern Texas are probably misidentified *A. mavortium*.

Ambystoma californiense Gray, 1853. This species grows to 15–20 centimeters in length, rarely to 22

centimeters. The back and flanks are black and the belly is a creamy grayish yellow. The ground color is marked with round and oval yellow spots, similar to, but normally larger and fewer than the spots of *A. tigrinum* and *A. mavortium nebulosum*. Some specimens of *A. californiense* have a uniform black dorsal coloration with no yellow spots. Noticeable are the pure creamy yellow claws that stand out from the black legs of *A. californiense* — the claws of *A. tigrinum* and *A. mavortium nebulosum* always have black on them. According to SHAFFER et al. (2004) there are six genetically distinct forms of this species, one of which (Sonoma/Santa Barbara) is quite different from the others and most likely represents a subspecies. There are no known neotenic populations.

Ambystoma californiense is restricted to the central and western lowlands of California at elevations from sea level to 1,054 meters. It is found in Sonoma, Santa Barbara, Central Valley, Colusa, San Francisco, and Kern counties. The species is gravely threatened by habitat loss and mixing with introduced *A. mavortium*.

Ambystoma flavipiperatum Dixon, 1963. This species grows to 17.5–20 centimeters. There are 13 rib grooves compared to 11 in *A. amblycephalum*, with which it is often considered synonymous. WEBB (2004) believes there is a relationship between this species and *A. subsalsum*; perhaps they are the same. According to brief mention in the original species description and in WEBB (2004), this species has a dorsal gray-black ground color with numerous bright yellow spots, a bright yellow stripe along the lower flank, and a gray belly with two yellow stripes.

Ambystoma flavipiperatum is found in dry rocky regions at elevations of 2,000–2,100 meters above sea level near Santa Cruz in southwestern Guadalajara, south to Jalisco and west to the central high plateau of Mexico.

Ambystoma rosaceum Taylor, 1941. Similar to *A. velasci*, this species grows to 14–15.5 centimeters in length. There are 11–13 rib grooves. Coloration is a brown to blackish background with few pinkish-white to cream-colored spots, which are especially clear on the flanks and tail. Specimens with no spots are common. According to SHAFFER (1983, 1984) and SHAFFER and MCKNIGHT (1996) there are two genetically distinct forms; according to HIGHTON (2000) there are three. Subspecies have been described (SHANNON, 1951), but their validity is unclear (ANDERSON, 1961). Neoteny is not uncommon.

Ambystoma rosaceum is found in pine and oak forest with clear streams at elevations of 1,675–3,100 meters above sea level in the Sierra Madre Occidental (Mexico) — in northeastern Sonora into western Chihuahua, south into Durango, eastern Sinaloa, and southwestern Zacatecas.

Ambystoma silvensis Webb, 2004. Interestingly this species is very similar to *A. mavortium diaboli* and *A.*

mavortium utahense. It grows to 15–16 centimeters in length; larvae, to 20 centimeters. There are 11 rib grooves. Dorsal coloration is a light olive brown ground color that becomes lighter on the flanks toward the venter. The back and flanks usually bear small black dots in varying number.

Ambystoma silvensis is found in pine-oak highland forests of the Sierra Madre Occidental in Durango, at elevations of 2,400–2,500 meters above sea level. It is sympatric with *A. rosaceum* in eastern Durango.

Ambystoma subsalsum Taylor, 1943. This species also resembles *A. mavortium nebulosum* and other members of the genus that are black with yellow markings. It grows to 15–20 centimeters and has 10–11 rib grooves. Unlike *A. californiense*, *A. tigrinum*, and *A. mavortium nebulosum*, however, the ground color of *A. subsalsum* has a grayish brown reticulation. Also, *A. subsalsum* has significantly fewer cream to yellowish spots than *A. tigrinum* and *A. mavortium nebulosum*, and its spots are significantly smaller than those of *A. californiense*. There are some specimens that are entirely black on the back and sides. Ventral coloration is yellowish white to yellow or dark gray with light spots in varying number. Neotenic populations are not uncommon at high elevations.



Ambystoma rosaceum. Photo: T. Burkhardt



Lake Chapala in the central highlands of Mexico is the home of *Ambystoma flavipiperatum*. Photo: H. Werning



Ambystoma velasci. Photo: T. Burkhardt



Lake Tecuitlapa, at 2,300 meters above sea level in Puebla, Mexico; is habitat for *Ambystoma velasci*. Photo: J. Fleck

Ambystoma subsalsum is found in the low regions of the Sierra Madre Oriental, Hidalgo, Tlaxcala, Zacatecas, Guanajuato, and Puebla in the east, and in Durango in the northern Mexican highlands.

Ambystoma velasci (Dugès, 1888). This species grows to 20–25 centimeters; neotenic specimens, to 30 centimeters. It is distinguishable from *A. californiense*, *A. tigrinum*, and *A. mavortium nebulosum* by its gray to olive-brown ground color with fine reticulation — it has significantly fewer yellow spots than *A. tigrinum* and *A. mavortium nebulosum*, and the spots it has are smaller than those of *A. californiense*. Some specimens have entirely blackish dorsolateral coloration. Ventral coloration is yellowish white or yellow. Neotenic populations are not uncommon, especially at elevations over 1,800 meters above sea level.

Once considered a subspecies of *A. tigrinum*, recent studies (SHAFFER and MCKNIGHT, 1996; IRSCHICK and SHAFFER, 1997; HIGHTON, 2000) demonstrate the validity of full species status for *A. velasci*. Four genetically distinct forms have been described (SHAFFER and MCKNIGHT, 1996; WEISROCK et al., 2006), although further research is needed. *Ambystoma velasci* is now taken to include *A. lacustris* (Taylor and Smith, 1945) from Tescoco, Zumpango, Nopaltepe, and Xochimilco lakes, Distrito

Federal (BRANDON, 1988). The specimens used to describe *A. lacustris* were olive brown with small black spots, especially on the head. BRANDON (1988) shows photos of brown specimens with yellow spots.

Ambystoma velasci is found from the Mexican state of Chihuahua, not far from the U.S. New Mexican border, south to Michoacán and Puebla.

Note: Classification of the species in the following groups is unclear due to insufficient data.

Group 1

Ambystoma bombypellum Taylor, 1940. The validity of this taxon is unclear as it has not been closely studied. It grows to 14.2 centimeters in length and is similar in appearance to *A. granulatum*. The head is flattened. Coloration is a brownish ground color with a dark dorsal stripe from head to tail. The flanks are light gray and the belly is brownish gray.

Ambystoma bombypellum is found in grassland and light pine and oak woodland at elevations of about 2,500 meters above sea level. It occurs in central Mexico east to San Martín (Asunción) and northwest to the state of Mexico. The species is threatened by habitat loss due to pollution and introduction of predacious fish.

Ambystoma leorae (Taylor, 1943). This species grows to 20.7 centimeters in length. The head is shorter and wider than the head of the similar *A. rivulare*. Dorsal coloration is greenish with dark brown spots on the flanks. Ventral coloration is cream colored. Mostly neotenic, only rarely metamorphosing to a terrestrial form.

Ambystoma leorae is found in mountain streams in pine forest at elevations of 3,000 meters above sea level, in the vicinity of Río Frío in the state of Mexico, near the Puebla border.

Group 2

This group constitutes the subgenus *Linguaelapsus*, which was described by COPE (1887) from skull form and external gill structures. Recent studies have both disproved (SHAFFER et al., 1991) and supported (JONES et al., 1993) the validity of the classification.

Compared to other species of *Ambystoma*, the species of this group all have a very long, cylindrical, slender body form, and a smallish head with a rounded snout. Females usually grow larger than males.

Ambystoma annulatum Cope, 1886. This species grows to 14–23.5 centimeters in length and has 15 rib grooves. Dorsal coloration is a black ground color with 10–20 whitish to yellow thin bands, which are sometimes broken. A longitudinal stripe runs between the eyes. Ventral coloration is gray or creamy yellow.

Ambystoma annulatum occurs in mixed woodlands of the Ozark Plateau and Ouachita Mountains of Arkansas, Missouri, and Oklahoma, U.S.A.

Ambystoma barbouri Kraus and Petranks, 1989. Growing to 11–17 centimeters in length with 14–15 rib grooves, this species is similar to *A. texanum*, but differs in breeding habitat, larval morphology, and dentition. Whereas *A. texanum* deposits eggs in ponds, *A. barbouri* deposits eggs in streams — despite this difference, hybrids of the two species have been found in nature. Dorsal coloration is grayish brown to grayish black with a fine gray reticulation. Ventral coloration is dark gray to black.

Ambystoma barbouri is found in mixed woodland with plenty of streams in the limestone highlands of central Tennessee, central and western Kentucky, southeastern Indiana, southwestern Ohio, and extreme western West Virginia, U.S.A.



Ambystoma jeffersonianum. Photo: D. M. Dennis

Ambystoma bishopi Goin, 1950. First considered a subspecies of *A. cingulatum*, *A. bishopi* was raised to full species status as a result of recent genetic studies (PAULY et al., 2007). It grows to 8–11 centimeters in length. Dorsal coloration is dark gray with grayish brown reticulation. Ventral coloration is dark gray with brownish dots and spots.

Ambystoma bishopi is found in pine forests and pine savanna in Georgia, Florida, and Alabama, U.S.A. The species is very rare because of habitat loss — it is probably already extinct in Alabama, and only two remaining breeding ponds are known in southwestern Georgia. A few populations that are more stable are found in Western Florida.



Ambystoma cingulatum. Photo: B. Love

Ambystoma cingulatum Cope, 1867. This species grows to 8.9–13.5 centimeters in length, and has 15 rib grooves. Dorsal coloration is dark gray with light gray to blue-gray reticulation. Ventral coloration is dark gray with light gray dots and spots.

Ambystoma cingulatum is found in pine forest and pine savanna in South Carolina, Georgia, northern Florida, and southern Alabama, U.S.A. This species is rare due to



Ambystoma mabeei. Foto: D.M. Dennis

habitat loss, and presumably already extinct in Alabama. Its original habitat of longleaf pine (*Pinus palustris*) was practically entirely destroyed by the first European colonists.

***Ambystoma mabeei* Bishop, 1928.** This species grows to 7.5–12 centimeters in length with 13 rib grooves, and is similar in coloration to *A. texanum*, but smaller, and has a significantly shorter tail (less than 40 percent of the total length). Dorsal coloration is grayish brown to black with numerous light-gray to whitish spots, especially on the flanks. Ventral coloration is gray to grayish brown with a few light spots.

Ambystoma mabeei is found in sandy pine woodland along the Atlantic coast from southeastern Virginia to southern South Carolina.

***Ambystoma texanum* (Matthes, 1855).** This species grows to 10–19 centimeters with a proportionally very small head and small mouth. Dorsal coloration is grayish brown to grayish black with a light gray or blue-gray marbled pattern, especially on the flanks. Ventral coloration is similar to dorsal coloration but with less marbling. Populations in Texas and Oklahoma have the most intense colorations. Hybrids of *A. texanum* with the closely related *A. barbouri* and *A. laterale* are fairly common.

Ambystoma texanum is found in lowland forest near suitable wet areas from Ohio to eastern Kansas and south to Texas Louisiana, Mississippi, and Alabama. Hybrids with *A. laterale* are found especially in northwestern Ohio, southeastern Michigan, and Pelee Island, Kelleys Island, and the Bass Islands, in Lake Erie. Hybrids with *A. barbouri* are possibly found in southeastern Ohio.

Group 3

This group includes the smallest species of the genus *Ambystoma*. They typically have relatively large eyes and long powerful tails.

***Ambystoma jeffersonianum* (Green, 1827).** Long and slender in build, this species grows to 11–21 centimeters in length, with a relatively broad mouth, and 12–13 rib grooves. The tail is nearly the same length as the body. Dorsal coloration is dark gray to brownish gray with a large number of blue-gray to silver-gray spots of varying sizes, especially on the flanks and legs. Ventral coloration is grayish. The male often has a yellow stripe on the top of the tail. There are a variety of hybrids with *A. laterale*, *A. texanum*, and *A. tigrinum*.

Ambystoma jeffersonianum is found in deciduous forests at relatively high elevations from southern Quebec and perhaps Ontario, Canada, through New England, New York, Pennsylvania, and Ohio into Indiana, Kentucky, West Virginia, and Virginia, U.S.A. As with most species of the genus, its distribution is quite scattered because of its reliance on suitable breeding waters. It was once quite common, but with habitat destruction has become scarce.

***Ambystoma laterale* Hallowell, 1856.** This species grows to 7.5–14 centimeters with 13 rib grooves. The male remains smaller than the female and has a proportionally longer tail. It resembles the closely related *A. jeffersonianum*, but is smaller, with a narrower mouth, and darker in coloration with a greater number of light spots. Dorsal coloration is grayish black to blue-black with many light gray and blue-gray spots of varying sizes and shapes, especially on the flanks. Ventral coloration is black.



Ambystoma cingulatum. Photo: B. Love



Ambystoma gracile gracile male. Photo: T. Blanck

Ambystoma laterale is found in mixed forest with sandy soil from southeastern Canada (Newfoundland to Quebec, and Ontario along the Great Lakes) into the United States in Maine, New Hampshire, Vermont, Massachusetts, Connecticut, New York, New Jersey, Ohio, Michigan, Indiana, Illinois, Wisconsin, Minnesota, and Iowa.

Ambystoma macrodactylum macrodactylum Baird, 1850. All five subspecies of this species are small and long with long legs, growing to 10–17 centimeters (usually 13 centimeters), and having 12–13 rib grooves. The male remains a little smaller than the female, but has a proportionally longer tail. They are found between the Rocky Mountains and the Pacific coast of northwestern North America, inhabiting evergreen forest, shrub plains, and alpine meadows and lakes to elevations of 2,700.

The nominate form has a gray dorsal ground color with a greenish yellow dorsal stripe of variable width, and sometimes small yellow dots on the flanks and head. The flanks and belly are speckled with light gray. Southeastern populations



Ambystoma opacum. Photo: D. M. Dennis



Juvenile *Ambystoma gracile gracile*. Photo: T. Blanck



Ambystoma macrodactylum. Photo: D. M. Dennis

hybridize with *A. macrodactylum columbianum*, and southern populations hybridize with *A. macrodactylum sigillatum*.

Ambystoma macrodactylum macrodactylum is found from western Oregon through western Washington into extreme western British Columbia, along the Pacific coast. According to RAFFAELLI (2007), this species has been successfully bred in captivity in England.

Ambystoma macrodactylum columbianum Ferguson, 1961. This subspecies has a grayish brown ground color with a completely golden yellow head, a golden yellow dorsal stripe, and golden yellow marbling on the legs and tail. The lower flanks and ventral surface are grayish with small white dots.

Ambystoma macrodactylum columbianum is found in western Idaho, northeastern Oregon, and eastern Washington north into British Columbia to southeastern Alaska.

Ambystoma macrodactylum croceum Russell and Anderson, 1956. This subspecies has a black ground color with irregular medium-sized yellow-orange to orange spots that may fuse into longitudinal bands.

Isolated from the other subspecies, *Ambystoma macrodactylum croceum* is found only in a small region of central California, along the Pacific coast between Monterey and Santa Cruz.

Ambystoma macrodactylum krausei Peters, 1882. This subspecies has a dark gray ground color with irregular intense yellow dorsal stripes from head to tail. On the flanks, the stripes break into spots. Ventral coloration is gray with small lighter spots.

Ambystoma macrodactylum krausei is found from northeastern Idaho and western Montana north to central eastern British Columbia and central western Alberta.

Ambystoma macrodactylum sigillatum Ferguson, 1961. This subspecies is blackish with yellow-orange dorsolateral stripes that are marked with black spots, especially on the head and tail. Ventral coloration is a lighter ground color with light dots.

Ambystoma macrodactylum sigillatum is found in northwestern California and southwestern Oregon.

Ambystoma opacum (Gravenhorst, 1807). This short, stocky species grows to 7.5–13 centimeters in length. It has a short tail and relatively large eyes. Dorsal coloration is black with whitish to silver-gray or blue-gray crossbands that fuse with longitudinal stripes. Ventral coloration is black. The male is usually lighter (more silver-gray) with a more pronounced pattern than the female. According to RAFFAELLI (2007) this species has been successfully bred in captivity in the Netherlands and Germany.

Ambystoma opacum is found in mixed forest, especially with oak, sandy soil, and marshy areas. It ranges

through much of the eastern United States from southern New Hampshire, Massachusetts and extreme southern New York, west and southwest in a sporadic distribution through central Pennsylvania, Ohio, Indiana, southern Illinois, southern Missouri, Arkansas, southeastern Oklahoma, and eastern Texas; and more abundantly south to the Gulf Coast and east to the Atlantic Coast, including the Florida panhandle.

Group 4

The species in this group are medium-sized and stocky with large skulls and short to medium-length tails.

Ambystoma gracile gracile (Baird, 1859). This species grows to 14–22 centimeters in length; neotenic specimens, to 26 centimeters. There are 11 very prominent rib grooves. Dorsal coloration is light brown, grayish brown, or dark brown, and sometimes almost black. The belly is a slightly lighter brown, and the head sometimes has orangish tones. Neotenic specimens are olive to brownish black. Males become darker during the breeding season. Neoteny is common, increasing with elevation. This species has been successfully bred in captivity in England.

Ambystoma gracile gracile is found in wet forests and grassland at elevations of up to 3,110 meters above sea level along the Pacific coast from the Gualala River of northern California (Sonoma County) north through Oregon and Washington into British Columbia.

Ambystoma gracile decoraticum (Cope, 1886). This subspecies grows to 14–20 centimeters in length, and, unlike the nominate form, is a uniform brown color with small white to yellowish spots on the back. There are also internal differences, one being that the toes of this subspecies have only three instead of four bones. The status of the taxon is disputed — the distinguishing

features are not constant, and genetic studies carried out by TITUS (1990) do not support subspecies status.

Ambystoma gracile decoraticum is found in British Columbia and southeastern Alaska. The dividing line between the two subspecies is considered to be 51 degrees north latitude, with *A. gracile decoraticum* north, and the nominate subspecies south of this line.

Ambystoma maculatum (Shaw, 1802). This species grows to 13–25 centimeters (usually to 15 centimeters). It has 11–13 rib grooves. According to PHILLIPS (1994) and ZAMUDIO and SAVAGE (2003) there are two genetically distinct forms that need further investigation. Dorsal coloration is black or dark gray with irregular yellow and yellow-orange spots from the head to the tip of the tail. Specimens in certain populations have bright orange spots on the head. Ventral coloration is gray, often with small white dots. Melanistic specimens

are known, as are brownish specimens — both rare. According to RAFFAELLI (2007), this species has been successfully bred in captivity in the Netherlands.

Ambystoma maculatum is found in old deciduous, evergreen, and mixed lowland forests. Form 1, the coast form, is found in Canada from Nova Scotia through southern Quebec east along the Great Lakes, and in the United States from Maine and New York south along the Atlantic coast all the way to central Georgia, around the Gulf Coast from southern Alabama to eastern Texas and eastern Oklahoma, and north to Missouri. Form 2, the inland form, is found in Canada from southern Ontario west along the Great Lakes, and in the United States in Wisconsin, Illinois, Indiana, Ohio, and south through Kentucky and Tennessee into northern Alabama.

Ambystoma talpoideum (Holbrook, 1838). Short and stocky, this species grows to 8–12 centimeters in



Ambystoma maculatum. Photo: J. D. Willson

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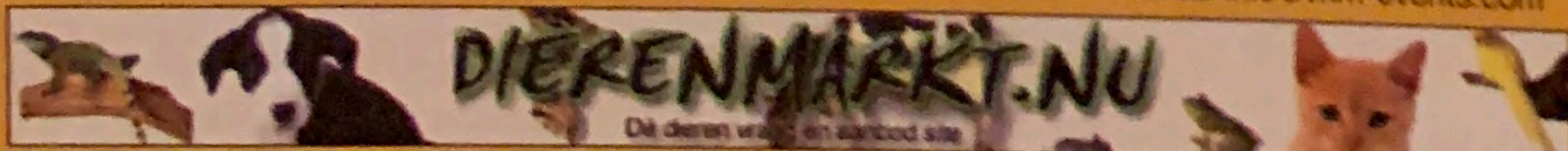
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length, with a short tail, a proportionally large head, and long limbs. Due to differences in behavior and egg clutch sizes populations on the Atlantic coast and those on the coast of the Gulf of Mexico are seen as separate forms, but further study is needed. Dorsal coloration is light brown to blue-gray, dark gray, or almost black, usually with small, irregular light-gray spots, especially on the flanks. Ventral coloration is gray. Neotenic forms are known. According to RAFFAELLI (2007) this species has been successfully bred in captivity in France.

Ambystoma talpoideum is found in lowland coastal regions and flood plains including cypress forests. It is distributed from Virginia to northern Florida and west through Kentucky and extreme southern Illinois to southeastern Missouri, and through Tennessee and the Gulf States to eastern Texas and southern Oklahoma. ■

Bibliography

ANDERSON, J. D. 1961. The life history and systematics of *Ambystoma rosaceum*. *Copeia* 1961(4): 371-377.

BAIRD, S. F. 1860. *Siredon lichenoides*. In: COOPER (ed.): *Rep. Expl. Surv. R.R. Route Mississippi-Pacific Ocean, 36th Cong. 1st Sess., House Ex. Doc. 56, Vol. 12, P. 306, Plate, 31.*

BRANDON, R. A. 1988. Nomenclatural and taxonomic status of *Ambystoma lucustris*. *Herpetologica* 44(4): 427-430.

CHURCH, S. A., J. M. KRAUS, J. C. MITCHELL, D. R. CHURCH, and D. R. TAYLOR. 2003. Evidence for multiple pleistocene refugia in the postglacial expansion of the eastern tiger salamander, *Ambystoma tigrinum tigrinum*. *Evolution* 57: 372-383.

COLLINS, J. P., J. B. MITTON, and B. A. PIERCE. 1980. *Ambystoma tigrinum*: a multispecies conglomerate? *Copeia* 1980: 938-941.

COPE, E. D. 1867. A review of the species of the Amblystomidae. *Proc. Acad. Nat. Sci. Philadelphia* 19: 166-211.

DUNN, E. R. 1940. The races of *Ambystoma tigrinum*. *Copeia* 1940: 154-162.

FROST, D., and AMNH. 2007. Amphibian Species of the World Version 5.0 (1 February 2007). <http://research.amnh.org/herpetology/amphibia/index.php>.

GEHLBACH, F. R. 1967. *Ambystoma tigrinum* (Green). Tiger salamander. *Catalogue of American Amphibians and Reptiles* 52: 1-4.



Ambystoma talpoideum. Photo: B. Love

- HIGHTON, R. 2000. Detecting cryptic species using allozyme data. In: R. C. BRUCE, R. G. JAEGER, and L. D. HOUCK (eds.). *The Biology of Plethodontid Salamanders*. Kluwer Academic/Plenum Publishers, New York.
- HUMPHREY, R. R. 1967. Albino axolotls from an albino tiger salamander through hybridization. *Journal of Heredity* 58: 95–101.
- IRSCHICK, D. J., and H. B. SHAFFER. 1997. The polytypic species revisited: morphological differentiation among tiger salamanders (*Ambystoma tigrinum*) (Amphibia: Caudata). *Herpetologica* 53(1): 30–49.
- JONES, T. R., J. P. COLLINS, T. D. KOCHER, and J. B. MITTON. 1988. Systematic status and distribution of *Ambystoma tigrinum stebbinsi* Lowe (Amphibia: Caudata). *Copeia* 1988: 621–635.
- JONES, T. R., A. G. KLUGE, and A. J. WOLF. 1993. When theories and methodologies clash: a phylogenetic reanalysis of the North American ambystomatid salamanders (Caudata: Ambystomatidae). *Systematic Biology* 42: 92–102.
- JONES, T. R., E. J. ROUTMAN, D. J. BEGUN, and J. P. COLLINS. 1995. Ancestry of an isolated subspecies of salamander, *Ambystoma tigrinum stebbinsi* Lowe: the evolutionary significance of hybridization. *Molecular Phylogenetics and Evolution* 4: 194–202.
- LOWE, C. H. 1955. The salamanders of Arizona. *Transactions of the Kansas Academy of Science* 58: 237–251.
- PAULY, G. B., O. PISKUREK, and H. B. SHAFFER. 2007. Phylogeographic concordance in the southwestern United States: the flatwoods salamander, *Ambystoma cingulatum*, as a test case. *Molecular Ecology* 16: 415–429.
- PETRANKA, J. W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, D.C.
- PHILLIPS, C. A. 1994. Geographic distribution of mtDNA variants and the historical biogeography of the spotted salamander, *Ambystoma maculatum*. *Evolution* 48: 597–607.
- PIERCE, B. A., and J. B. MITTON. 1980. Patterns of allozyme variation in *Ambystoma tigrinum mavortium* and *A. t. nebulosum*. *Copeia* 1980: 594–605.
- RAFFAELLI, J. 2007. *Les Urodeles du Monde*. Penclen éd.
- REILLY, S. M., and R. A. BRANDON. 1994. Partial paedomorphosis in the Mexican stream ambystomatids and the taxonomic status of the genus *Rhyacosiredon* Dunn. *Copeia* 1994(3): 656–662.
- SAMUELS A. K., D. W. WEISROCK, J. J. SMITH, K. J. FRANCE, J. A. WALKER, S. PUTTA, and S. R. VOSS. 2005. Transcriptional and phylogenetic analysis of five complete ambystomatid salamander mitochondrial genomes. *Gene* 349: 43–53.
- SHAFFER, H. B. 1983. Biosystematics of *Ambystoma rosaceum* and *A. tigrinum* in northwestern Mexico. *Copeia* 1983: 67–78.
- SHAFFER, H. B. 1984a. Evolution in a paedomorphic lineage. I. An electrophoretic analysis of the Mexican ambystomatid salamanders. *Evolution* 38: 1194–1206.
- SHAFFER, H. B. 1984b. Evolution in a paedomorphic lineage. II. Allometry and form in the Mexican ambystomatid salamanders. *Evolution* 38: 1207–1218.
- SHAFFER, H. B., J. M. CLARK, and F. KRAUS. 1991. When molecules and morphology clash: a phylogenetic analysis of the North American ambystomatid salamanders (Caudata: Ambystomatidae). *Systematic Zoology* 40: 284–303.
- SHAFFER, H. B., and M. L. MCKNIGHT. 1996. The polytypic species revisited: genetic differentiation and molecular phylogenetics of the tiger salamander (*Ambystoma tigrinum*) (Amphibia: Caudata) complex. *Evolution* 50: 417–433.
- SHANNON, F. A. 1951. Notes on a herpetological collection from Oaxaca and other localities in Mexico. *Proc. U.S. Natl. Mus.* 101: 465–484.
- TITUS, T. A. 1990. Genetic variation in two subspecies of *Ambystoma gracile* Baird (Caudata: Ambystomatidae). *Journal of Herpetology* 24: 107–111.
- WEBB, R. G. 2004. Observations on tiger salamanders (*Ambystoma tigrinum* complex, Family Ambystomatidae) in Mexico with description of a new species. *Bulletin of the Maryland Herpetological Society* 40: 122–143.
- WEISROCK, D. W., H. B. SHAFFER, B. L. STORZ, S. R. STORZ, and S. R. VOSS. 2006. Multiple nuclear gene sequences identify phylogenetic species boundaries in the rapidly radiating clade of Mexican ambystomatid salamanders. *Molecular Ecology* 15: 2489–2503.
- ZAMUDIO, K. R., and W. K. SAVAGE. 2003. Historical isolation, range expansion, and secondary contact of two highly divergent mitochondrial lineages in spotted salamanders (*Ambystoma maculatum*). *Evolution* 57(7): 1631–1652.

Internet:

<http://amphibiaweb.org/>
www.livingunderworld.org/caudata/database/ambystomatidae/
www.caudata.org
www.ag-urodela.de/