# Lungless salamanders
## *(Plethodontidae)*

**Class** Amphibia
**Order** Caudata
**Suborder** Salamandroidea
**Family** Plethodontidae

**Thumbnail description**
Small to medium-sized salamanders with generalized body form including four limbs with four fingers and four or five toes and a medium to long tail

**Size**
1–13 in (2.5–25 cm)

**Number of genera, species**
28 genera; 346 species

**Habitat**
Forest, woodlands, streams, springs, and caves

**Conservation status**
Critically Endangered: 1 species; Endangered: 4 species; Vulnerable: 11 species; Lower Risk/Near Threatened: 7 species; Data Deficient: 2 species

**Distribution**
North, Middle, and South America; Central Mediterranean Europe

## Evolution and systematics

The Plethodontidae was long thought to include the most derived salamanders, because of the terrestrial nature of so many of the species. However, studies of phylogenetic relationships using molecular markers have led biologists to question this assumption, and it is now generally recognized that the family is likely relatively old and derived near the base of the clade that constitutes the suborder Salamandroidea. There are few fossils earlier than the Pliocene and Pleistocene; the oldest are vertebrae from the Lower Miocene that are assigned to the living genera *Aneides* and *Plethodon*, thus showing that these close relatives were already differentiated by that time. Using estimates obtained from molecular evolutionary clocks, the family may be more than 100 million years old.

Plethodontids are thought to have arisen in what is present-day Appalachia, the ancient mountainous region of the southeastern United States. Lunglessness is thought to have evolved as an adaptation for life in flowing water. Larvae are small, and lungs would tend to act as air sacs that might make the animal float in the water column. This would dislodge them and threaten their survival. In well-aerated water such as a stream, respiration can take place readily through the skin, and so there would be little countervailing selection to retain lungs. While there are other hypotheses concerning lung loss, the flowing-water hypothesis is strengthened by similarities between plethodontids and other families: lungless salamanders in other families have larvae that live in flowing water, and usually the adults also live in or near streams.

At present two subfamilies are recognized.

### Desmognathinae

This subfamily includes two genera, *Desmognathus* (with 17 species) and *Phaeognathus* (with only a single species). These salamanders have highly specialized heads and necks used for burrowing, for wedging under rocks and in stream beds, and for courtship, but they retain some ancestral traits as well. The desmognathines are restricted to eastern North America, where they extend as far west as Texas. Most of the species have an aquatic larval stage that varies in length from a few months to three years. However, at least three species have abandoned the larval stage and have direct development, with miniatures of the adult hatching from eggs laid in moist terrestrial to semiaquatic habitats. It long was assumed that larvae were an ancestral retention in the desmognathines, but

Female ensatina (*Ensatina eschscholtzii*) on her nest with eggs in Jefferson County, Washington, USA. (Photo by Suzanne L. Collins/Photo Researchers, Inc. Reproduced by permission.)

now it appears that larvae may have been re-evolved within the subfamily because the species with terrestrial development include the most basal members of the clade. Either direct development evolved independently several times, or larvae reappeared.

**Plethodontinae**

This subfamily is a large and heterogeneous group that is not so well characterized as the Desmognathinae. Some molecular data suggest that the Plethodontinae may not be monophyletic, but it does contain some well-defined clades, notably a large assemblage of salamanders from the American tropics, the west coastal region of North America, and some small parts of central Mediterranean Europe that are collectively placed in the tribe Bolitoglossini and termed bolitoglossines. Two other tribes are recognized: the Plethodonini, which includes fully terrestrial species that occur in North America, and the Hemidactyliini, which includes species that have an aquatic larval stage and occur mainly in eastern North America. Whereas the monophyletic status of the Bolitoglossini is well established, the other two have only weak support.

Hemidactyliines were long thought to be most similar to ancestors of the Plethodontidae in structure and general biology. Many of them live in or near streams and have larvae that live in streams, springs, or seeps. However, there are also a few hemidactyliines that have pond larvae and more that have larvae and adults that are restricted to caves. *Hemidactylium scutatum* differs in many ways from other hemidactyliines in that it is terrestrial as an adult and has an ephemeral pond-dwelling larva. Most fully metamorphosed hemidactyliines have a projectile tongue that can be fired rapidly and for a relatively great distance, but *Hemidactylium* has a much less specialized tongue. It may represent an entirely separate clade from the other hemidactyliines. The remainder of the Hemidactyliini seems to form a clade. All of them have aquatic larvae, many of which live in streams. The rest live in springs, seeps, or caves, with the exception of two species that have pond larvae: *Stereochilus marginatus* and *Eurycea quadridigitata* (which appears to be a complex of species, not yet clearly diagnosable), both of which live on the coastal plain. *Stereochilus* lacks a highly specialized tongue and may be relatively basal in the clade. Among the members of this clade are large spring salamanders (*Gyrinophilus*, with 4 species) and mud salamanders (*Pseudotriton*, with 2 species), but most of the species are relatively small. The dominant genus is *Eurycea*, a large and complicated group of 23 species, including a number of species that fail to metamorphose and spend their entire lives as larval forms that become sexually





mature (these are termed perennibranchiate, referring to the retention of gills throughout life). These permanent larvae are surprisingly species rich, especially in and near the Edwards Plateau region of central Texas, where some of them have become restricted to underground waters. The cave species lack eyes and most pigment and may have bizarrely formed limbs and snouts. Cave-restricted permanently larval species have also evolved in the genera *Gyrinophilus* and *Haideotriton*. The genus *Typhlotriton* starts life as an *Eurycea*-like larva, but as it metamorphoses its eyes degenerate, its eyelids fuse, and it loses pigment. The adult is restricted to terrestrial habitats in caves. Both *Haideotriton* (1 species) and *Typhlotriton* (1 species) are closely related to *Eurycea*, which may be paraphyletic.

The Plethodontini includes species that have a relatively unspecialized tongue and are strictly terrestrial, with no larval stage and having direct development. They have long been considered to be close relatives, and some have even recommended that they be placed in the same genus. While *Plethodon* and *Aneides* are close relatives, *Ensatina* now appears to be only distantly related to the others. *Plethodon* is a very large genus (54 species in at least 3 and probably more major clades); *Aneides* is smaller (6 species) and appears on the basis of molecular evidence to be nested within the paraphyletic *Plethodon*. Exact relationships are uncertain, but eventually there may be taxonomic changes in this assemblage. Many of the species of *Plethodon* are cryptic and can only be distinguished from other members of the genus by molecular evidence. However, geographic distribution is distinctive for every species, and thus locality information aids immeasurably in their identification. The species of *Aneides* are generally well differentiated in morphology, but one pair of species (*A. ferreus, A. vagrans*) is virtually identical in morphology; they, too, have distinct geographic distributions. At present it appears that *Ensatina* is the sister taxon of *Plethodon* and *Aneides*; this may change as more molecular data become available.

The tribe Bolitoglossini is the only group of plethodontids that does not occur in the presumptive ancestral home, eastern North America. Instead, this tribe is widely dispersed, with many species in tropical America, a number in western North America, and a few in restricted parts of central Mediterranean Europe. All members of this group are terrestrial, with no larval stage and direct terrestrial development. There are three well supported clades recognized as supergenera:

Supergenus (SG) *Hydromantes*. This genus contains two distinct lineages, treated as genera or subgenera by different authors. SG *Hydromantes* has three species in California, and SG *Speleomantes* has five species, three on the island of Sardinia and two on the Italian mainland, also extending into extreme southeastern France.

Supergenus *Batrachoseps*. There are 20 species in this supergenus, placed in a single genus *Batrachoseps*, which in turn is divided into two subgenera that are biochemically distinct.

Supergenus *Bolitoglossa*. All tropical plethodontids are placed in this genus, which includes about 200 species. This is by far the largest salamander taxon. One genus, *Bolitoglossa*,

A spring salamander (*Gyrinophilus porphyriticus*) eats a dusky salamander (*Desmognathus fuscus*). (Photo by Gary Meszaros/Photo Researchers, Inc. Reproduced by permission.)

includes more than 80 species and has an enormous geographic range, from northeastern Mexico to central Bolivia and Brazil. Other genera contain fewer species and have smaller ranges. *Pseudoeurycea* includes about 40 species and ranges from northwestern and northeastern Mexico into southern Guatemala. *Lineatriton* includes three extremely elongate, slender species from eastern Mexico, and it is a close relative of *Pseudoeurycea*.

Also closely related to *Pseudoeurycea* are two small genera from eastern Mexico (*Parvimolge*, with one species) and southern Mexico (*Ixalotriton*, with two species). The former is a diminutive species, among the smallest of terrestrial vertebrates at about 1.5 in (3.8 cm) total length, while the latter includes one species (*I. niger*) that is an active, scansorial, leaping animal with a long whiplike tail and long legs and digits. *Chiropterotriton* includes about 14 species of diverse habitats, from cave-dwelling and arboreal to terrestrial, all from eastern and southern Mexico. *Thorius*, the minute salamanders, include 22 species from eastern and southern Mexico. All are very small and some are even smaller than *Parvimolge*, achieving sexual maturity at less than 1 in (2.5 cm) total length.

*Dendrotriton* (6 species), *Bradytriton* (1 species), *Cryptotriton* (6 species), *Nototriton* (12 species), and *Nyctanolis* (1 species) all occur in Middle America, with some entering southern Mexico and one, *Nototriton*, reaching central Costa Rica. Most of these are small, inconspicuous salamanders that are rarely seen; many of them occur in arboreal bromeliads and moss mats. *Nyctanolis* contrasts sharply in being relatively large, long-limbed, and spectacularly colored (a kind of harlequin pattern of red, yellow, and cream spots on a shiny black ground color). The final genus, *Oedipina* (21 species), differs dramatically from all other genera in having 18 to more than 20 rather than 14 trunk vertebrae and in being extremely slender and elongate, with tails of some species being more than twice head plus body size. These mainly fossorial animals occur from southern Mexico to Ecuador and are most numerous in Costa Rica.

## Physical characteristics

These are diverse organisms that include the smallest and nearly the largest terrestrial salamanders. All are lungless and breathe through their skin. All have four limbs and a tail, but some are permanently larval and some of these are blind. The vast majority develop directly with no larval stage. Many are fully terrestrial, but a number are semiaquatic and some have become secondarily aquatic as adults. There are many fossorial as well as arboreal species.

## Distribution

With the exception of six species in the middle western Mediterranean region of Europe, these are New World salamanders that occur from southern Canada throughout much of the United States and Mexico (except the north-central parts of these countries), through Central America and into southern South America (central Bolivia and Brazil). Species are most numerous in the eastern United States and Middle America.

## Habitat

These are salamanders that thrive in wooded montane areas, but they occur in many other kinds of habitats. Some terrestrial species occur in desert areas that receive far less than 10 in (25 cm) of rainfall yearly, whereas others occur in rainforests, both temperate and tropical. Many species are semiarboreal to fully arboreal.





## Behavior

Plethodontids are typically secretive by day and active by night. They have small home ranges, and seasonal migrations are limited to a few species that use aquatic breeding sites. Stream salamanders are more active than terrestrial species, but most species are capable of moving quickly when disturbed, and they are good at escaping capture. The more terrestrial species and especially the tropical species rely more on stealth to avoid detection and capture, and do not move as quickly as aquatic and semiaquatic species. Social behavior has been studied in only a few species, and in these groups, individuals display territoriality and aggression. All species have complex courtship and mating behavior, and courtship can take many hours.

## Feeding ecology and diet

These salamanders typically feed on small arthropods but occasionally take worms, and the large species can eat members of smaller species. Prey is captured by very rapid movements of the tongue.

## Reproductive biology

More generalized species lay eggs in or near shallow water, typically moving water, and eggs hatch into aquatic larvae that remain as larvae for a few months to as long as three years. Metamorphosis is somewhat more profound than in other families. A handful of species have larvae that live in standing water. More than half the species are strictly terrestrial and lay large yolky eggs that are hidden in cavities under rocks or logs, or deposited in moss mats, balls of moss hanging in vegetation, or arboreal plants including bromeliads. Hatching typically takes many weeks, and miniatures of the adult are produced.

## Conservation status

Most plethodontids are secretive animals, and their conservation depends on maintenance of habitat. However, in recent years populations of many species have dramatically declined for unknown reasons, even in protected habitats. The 2002 IUCN Red List includes 25 plethodontid species.

## Significance to humans

These are inconspicuous organisms that are not very often seen. However, they commonly occur in high density and typically are the most numerous vertebrates in a given region.




1. Talamancan web-footed salamander (*Bolitoglossa pesrubra*); 2. Mt. Lyell salamander (*Hydromantes platycephalus*); 3. Two-lined salamander (*Eurycea bislineata*); 4. Bell's salamander (*Pseudoeurycea bellii*); 5. Female ensatina (*Ensatina eschscholtzii*); 6. Red Hills salamander (*Phaeognathus hubrichti*); 7. Red-backed salamander (*Plethodon cinereus*); 8. Dusky salamander (*Desmognathus fuscus*). (Illustration by Gillian Harris)


1. Italian cave salamander (*Hydromantes italicus*); 2. Arboreal salamander (*Aneides lugubris*); 3. Costa Rican worm salamander (*Oedipina uniformis*); 4. Four-toed salamander (*Hemidactylium scutatum*); 5. Texas blind salamander (*Eurycea rathbuni*); 6. Golden thorius (*Thorius aureus*); 7. Inyo Mountains salamander (*Batrachoseps campi*). (Illustration by Gillian Harris)





# Species accounts

## Dusky salamander
*Desmognathus fuscus*

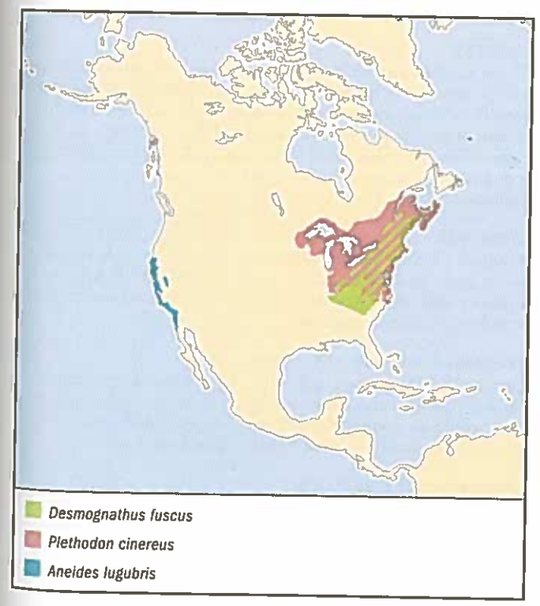
**SUBFAMILY**
Desmognathinae

**TAXONOMY**
*Desmognathus fuscus* Green, 1818, type locality not given but thought to be near Princeton, New Jersey, United States.

**OTHER COMMON NAMES**
English: Northern dusky salamander; French: Salamandre sombre du nord; German: Brauner Bachsalamander.

**PHYSICAL CHARACTERISTICS**
This is a medium-sized salamander (to about 5.5 in or 14 cm total length) with short limbs and stocky proportions. The hind limbs are much larger than the forelimbs. The head is wedge-shaped and has prominent, protruding eyes. Jaw and neck muscles are well developed, and there is no discernable neck. The tail has a low fin and terminates in a sharp point, but often it is at least partially regenerated and then is blunt-tipped. Coloration is variable, but in general the upper surfaces are darker than the cream-colored lower surfaces, and the trunk may be mottled gray and black, striped with various shades of tan to yellow-brown to brown. A black stripe extends from the eye diagonally back to the angle of the jaw.

**DISTRIBUTION**
The species ranges from Quebec and New Brunswick in eastern Canada south and west as far as Indiana and South Carolina; a related form currently treated as a subspecies extends further south and west to peninsular Florida and Louisiana.




**HABITAT**
Larvae live in seeps, springs, and small streams. Adults are more terrestrial but spend most of their time in seeps or on the margins of springs and small streams, where they are found in rocky streambanks or under logs or other cover objects.

**BEHAVIOR**
Dusky salamanders are active animals, and when one attempts to capture them they move very rapidly and are elusive. Most of their normal surface activity occurs in the early evening, but when conditions are warm and moist they may be active throughout the night. By day they typically are found only under cover objects. They defend themselves from predators either by remaining motionless or in some instances by biting. They lack effective chemical defenses.

**FEEDING ECOLOGY AND DIET**
Larvae eat small invertebrates such as larvae of aquatic insects but also copepods and tiny clams. Adults eat more terrestrial prey, principally small arthropods, but they also feed on aquatic insects when in more aquatic sites. Larger individuals eat increasingly larger prey but they continue to eat small prey. Occasional cannibalism occurs, especially on larvae. Adults capture their prey by rapidly flicking their tongues and then snapping their jaws.

**REPRODUCTIVE BIOLOGY**
Courtship behavior is well studied and takes place on land. Following extensive behavioral interactions between the male and female, a spermatophore is deposited by the male and taken up by the female. The female stores sperm internally. Eggs are deposited in mid- to late summer in moist, hidden sites in seeps or at the edges of springs and small streams. Eggs are laid in clusters of from five to six to as many as 30 or more, and they are guarded by the female, typically until hatching, which occurs after 45 days or more. Larvae hatch with a good yolk supply and do not feed immediately. Larvae grow slowly in the fall and winter but rapidly in the spring and metamorphose in about nine months.

**CONSERVATION STATUS**
This is one of the most common and widely encountered salamanders in eastern North America, and it adapts well to habitat modification so long as appropriate microhabitats remain.

**SIGNIFICANCE TO HUMANS**
None known. ◆

## Red Hills salamander
*Phaeognathus hubrichti*

**SUBFAMILY**
Desmognathinae

**TAXONOMY**
*Phaeognathus hubrichti* Highton, 1961, 3 mi (4.8 km) northwest of McKenzie on US Route 31, Butler County, Alabama, United States.


OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
This large, dark, elongate animal has a large head with protrusive eyes, short legs, a very long trunk, and a relatively short, round tail. They exceed 10 in (25 cm) in length and are the longest desmognathine.

DISTRIBUTION
This species is known only from a small part (Red Hills region) of southern Alabama.

HABITAT
The Red Hills salamander occurs in ravines in mature forests with closed canopies. These are fossorial salamanders that construct burrows in rich, friable soil.

BEHAVIOR
The species stays underground by day but partly emerges from its retreats at night to forage.

FEEDING ECOLOGY AND DIET
This salamander feeds mainly on small arthropods and snails.

REPRODUCTIVE BIOLOGY
This is a strictly terrestrial species and it lays large, yolky eggs.

CONSERVATION STATUS
The Red Hills salamander is classified as Endangered and is protected by federal law. It occupies a special habitat that is very limited in extent, and the greatest threat is deforestation and associated disturbances.

SIGNIFICANCE TO HUMANS
None known. ◆

## Arboreal salamander
*Aneides lugubris*

SUBFAMILY
Plethodontinae

TAXONOMY
*Aneides lugubris* Hallowell, 1849, Monterey, California, United States.

OTHER COMMON NAMES
Spanish: Salamandra arbórea.

PHYSICAL CHARACTERISTICS
Arboreal salamanders are large (to a little over 7 in or 17.8 cm total length), muscular animals with long limbs that overlap when adpressed to the trunk and a relatively long, strongly prehensile tail. Large adults have a formidable appearance, with a heavily muscularized head and body and long limbs and digits. The very long, prehensile digits have expanded, somewhat recurved tips. The large eyes bulge from the head in front of greatly enlarged jaw muscles. The head is nearly triangular in appearance, with the long snout having skin that is coossified to the underlying bone. The upper and lower jaws bear large, saberlike teeth with recurved tips that are capable of inflicting a serious wound. These salamanders are gray-brown to brown in coloration, with lighter ventral surfaces. Yellow spots are always present, but they may be small and scattered or large and rather densely arranged.

DISTRIBUTION
Arboreal salamanders occur mainly in California, where they are found in the coastal mountains and valleys from the northwestern part of the state continuously to the extreme northwestern part of Baja California Norte, Mexico. They are found on some off-shore islands in the Pacific Ocean. They have a disjunct distribution, with another group of populations in the foothills of the Sierra Nevada.

HABITAT
These salamanders are mainly found in oak woodland habitats, where they utilize holes in the trees for nesting sites and escape from unfavorably dry conditions. They are also found in sycamore woodlands near creeks in the southern parts of their range. They are commonly found under the bark of fallen oak logs and in rocky areas under rocks and in underground cavities.

BEHAVIOR
Arboreal salamanders are aggressive. Both sexes have enlarged jaw muscles and teeth that are used in territorial disputes and against predators. They are adept climbers but are most often found in terrestrial situations.

FEEDING ECOLOGY AND DIET
Despite their large jaws and teeth, these salamanders mainly eat arthropods, although generally an array somewhat larger than would be predicted for related less specialized species of similar size. Rarely they eat slender salamanders.

REPRODUCTIVE BIOLOGY
These fully terrestrial animals lay grape-like clusters of large, yolky eggs that are suspended from roofs of cavities, underground, in large decaying logs, or in holes in trees. Hatching takes place just before fall rains, three to four months after laying.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

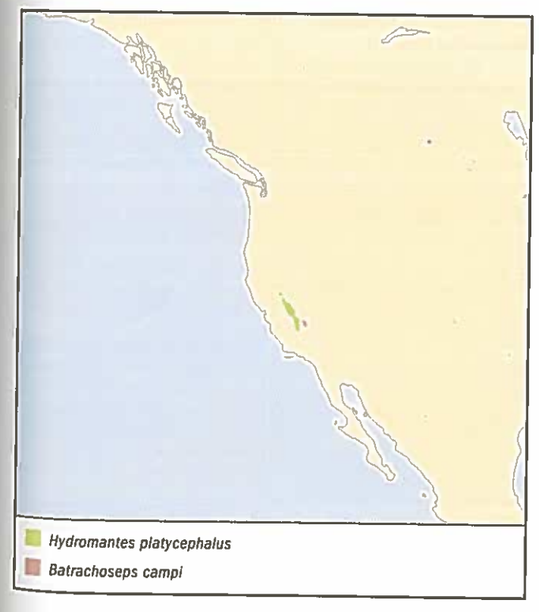
## Inyo Mountains salamander
*Batrachoseps campi*

SUBFAMILY
Plethodontinae

TAXONOMY
*Batrachoseps campi* Marlow Brode, and Wake, 1979, Long John Canyon, NE Lone Pine, Inyo County, California, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
This species differs greatly from most other members of this genus in being relatively robust, long-legged, and broad headed, with a tail that is shorter than head plus body length. Maximum size is about 4.25 in (10.8 cm). The long legs fail to overlap by two to five costal folds when adpressed to the sides of the trunk. As with other members of this genus, there are only four toes. The eyes are prominent and protrude from the flattened head. Ground color is black, both above and below, but typically there are silvery or greenish gray patches on the head and the front part of the back, especially over the forelimbs. However, there is much individual and geographic variation, and in some individuals there is a general suffusion of the light pigment over most dorsal surfaces, giving the impression of a silvery gray coloration.




DISTRIBUTION
This species has a remarkable distribution in strict desert environment throughout the Inyo Mountains in eastern California. It is found both on western facing slopes descending into the Owens Valley, and on eastern facing slopes descending into the Saline Valley, and occurs at elevations ranging from about 1,800 to 8,500 ft (550–2,590 m).

HABITAT
This species is most commonly found in moist soil near permanent streams, but it is also known from mossy limestone crevices beneath large rocks on open desert slopes. This species never enters water voluntarily but can be found in very wet soil. However, it appears not to be dependent on flowing water. It has been found in willow patches.

BEHAVIOR
Almost nothing is known concerning the biology of this remarkable species.

FEEDING ECOLOGY AND DIET
Nothing is known concerning diet, but the salamanders most likely resemble other members of the genus in eating primarily small arthropods, especially insects.

REPRODUCTIVE BIOLOGY
Large yolky eggs are produced and development is direct with no larval stage.

CONSERVATION STATUS
Classified as Endangered because of its apparent limited habitat and the fact that it is a narrow endemic, but the species is strongly differentiated genetically throughout its small range, indicating that the populations may be large and certainly that the populations are old.

SIGNIFICANCE TO HUMANS
None known. ◆

## Talamancan web-footed salamander
*Bolitoglossa pesrubra*

SUBFAMILY
Plethodontinae

TAXONOMY
*Bolitoglossa pesrubra* Taylor, 1952, Cerro de la Muerte (at crossing with the Pan American Highway), Costa Rica.

Until recently this species was known as *Bolitoglossa subpalmata*, but molecular studies demonstrated that two species were inappropriately placed in the same taxon.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
These relatively stocky salamanders reach a size of about 4.5 in (11.4 cm) total length and have a tail about the same length as the head plus body. The tail is strongly constricted at its base. Limbs fail to overlap when adpressed to the side of the trunk and bear hands and feet that are moderately webbed, with all digits having one to three phalanges extending beyond the web and bearing subdigital pads. Color pattern is extremely variable but is basically dark brown with mottled, striped, or marbled coloration, often contrasting gray and black, or it may be uni-


formly brown. The lower surfaces are lighter, but usually the belly is relatively dark gray and the throat region is much lighter and often bears yellowish pigment. The basal parts of the limbs are usually dark red to red-orange.

**DISTRIBUTION**
This species is known only from the Cordillera de Talamanca in central and eastern Costa Rica, generally at elevations above 7,500 ft (2,286 m). It is the best known of the many tropical salamanders because it has been observed by generations of students in the classes organized by the Organization for Tropical Studies.

**HABITAT**
This species is found under the bark of logs and under surface debris in oak forests, but it also has survived in many areas where habitats have been destroyed. It can be locally abundant in rubbish heaps. It has also been found in arboreal bromeliads and in moss mats on trees and roadside banks. It was once common at very high elevations (around 10,000 ft or 3,050 m), even in completely open areas where it was found under rocks, slabs of disused concrete, and other surface objects, but in recent years it has become scarce.

**BEHAVIOR**
Little is known concerning the behavior of this species. It is nocturnal and forages and mates by night.

**FEEDING ECOLOGY AND DIET**
The vast majority of prey are small terrestrial insects that are caught with a very fast, highly projectile tongue that is fired with great accuracy.

**REPRODUCTIVE BIOLOGY**
Like all tropical plethodontids, this is a direct-developing species. Eggs have been found throughout the year. They are laid in small clusters of 13–38 eggs (average 22.5). The eggs are large and yolky, and take a very long time to develop, partly because of the cool temperatures typical of the montane habitat. Females guard the eggs, which hatch after many months into tiny miniatures of the adult, well supplied with yolk.

**CONSERVATION STATUS**
Not threatened. Once this species was thought to be extremely tolerant of human activities and thrived even along heavily disturbed roadsides, but in recent years it has disappeared from much of its previous range. It is still found in deep forests.

**SIGNIFICANCE TO HUMANS**
None known. ◆

## Ensatina
*Ensatina eschscholtzii*

**SUBFAMILY**
Plethodontinae

**TAXONOMY**
*Ensatina eschscholtzii* Gray, 1850, Monterey, California, United States.

This is the celebrated "ring-species" of western North America, a polytypic species comprised of seven subspecies that are distributed in a ringlike manner surrounding the inhospitable Central Valley of California. Coastal populations are generally mottled to unmarked whereas inland populations are spotted, blotched, or banded. Coastal and inland populations either hybridize or live in sympatry as distinct species, but continuous interactions around the ring suggest that one species, in various stages of species formation, is represented. Some researchers recommend breaking the complex up into 2, 4, or 11 or more species, and the taxon is under active study.

**OTHER COMMON NAMES**
English: Large-blotched salamander, Monterey ensatina, Oregon ensatina, painted salamander, Sierra Nevada ensatina, yellow-blotched salamander, yellow-eyed ensatina; Spanish: Salamandra ensatina.








**PHYSICAL CHARACTERISTICS**
These salamanders are relatively large and stout with long legs, a large head, and a long, well-developed tail. The tail has a marked constriction at its base and is sexually dimorphic, long and thin in males and relative short and stout in females. Males in courtship season have greatly swollen upper lips and nasolabial projections. Color varies geographically. Oregon salamanders are dull brown or yellow-brown with some highlights of lighter pigment. Painted salamanders are complexly mottled with different colors, from black to yellow and orange. Yellow-eyed salamanders have reddish brown heads and backs and bright orange lower surfaces; they have a bright yellow spot in the upper eye and often have yellow-orange eyelids. Monterey salamanders are similar in color but are less vivid and more pinkish and have black eyes. Sierra Nevada salamanders are dark brown above with numerous small to moderate sized spots or blotches of red-orange to dull red. Yellow-blotched salamanders are black with lemon yellow blotches, typically larger and less numerous than those of Sierra Nevada salamanders. Large-blotched salamanders are black with a few yellow to dull orange to flesh-colored bold blotches or bands.

**DISTRIBUTION**
This group occurs from Vancouver Island and the mainland of southwestern British Columbia, Canada, southward west of the Cascade-Sierra Nevada crest, to the Sierra San Pedro Mártir in northern Baja California, Mexico. It is not present in the Central Valley of California.

**HABITAT**
These salamanders usually occur in woodlands, but the coastal forms occur in coastal sage scrub and chaparral as well. Blotched forms usually occur in mixed conifer forests with closed canopies. The species has an enormous ecological scope and occurs in areas that receive well over 150 in (381 cm) of rainfall per year to areas in southern California and northern Mexico that receive less than 10 in (25 cm) of rain per year. The species is typically found with rotting or decaying wood but also under rocks and other cover.

**BEHAVIOR**
This is a nocturnal species, but the blotched forms can be found by day during periods of rain. The species is aggressive toward conspecifics and bites and eats the tail tip of adversaries. The tail is richly supplied with poison glands and exudes a milky substance that many predators find repulsive. The tail is strongly constricted at the base, and when seized by a predator it can be autotomized (separated from the body by reflex), but autotomy is rarely observed. Nevertheless, about 20% of adults have regenerated tails.

**FEEDING ECOLOGY AND DIET**
This species generally feeds on small terrestrial arthropods, which it consumes by modulated use of a highly projectile tongue.

**REPRODUCTIVE BIOLOGY**
Courtship behavior is poorly known but involves deposition of a spermatophore following an elaborate series of maneuvers by both members. Eggs are laid in grape-like clusters (generally 12–25 eggs each) in underground cavities and are guarded by the female. Eggs are especially large and yolky, and females turn onto their backs and aid oviposition with leg movements.

**CONSERVATION STATUS**
Not threatened.

**SIGNIFICANCE TO HUMANS**
None known. ◆





## Two-lined salamander
*Eurycea bislineata*

**SUBFAMILY**
Plethodontinae

**TAXONOMY**
*Eurycea bislineata* Green, 1818, probably Princeton, New Jersey, United States.

**OTHER COMMON NAMES**
French: Salamandre á deux linges; German: Zweistreifiger Gelbsalamander.

**PHYSICAL CHARACTERISTICS**
Two-lined salamanders are small (5–5.5 in or 12.7–14 cm total length), slender salamanders with long, tapered, laterally compressed tails and limbs of moderate length. The eyes are prominent. Coloration ranges from greenish yellow to yellow or orange-brown. A broad band extends from behind the eye along the trunk to near the tip of the tail. This band is marked with dark brown or black speckles and spots in no apparent pattern, and it is bound on either side by a prominent brown or black stripe that extends from the eye well onto the tail, above the limb insertions. The lateral flanks are light with dark spots, and the venter is typically bright yellow with scattered dark spots.

**DISTRIBUTION**
This species ranges from northeastern Canada southwest through northeastern United States to Ohio, West Virginia, and Virginia. Closely related species sometimes combined with this species extend to the Gulf coastal plain, from Louisiana to Florida.

**HABITAT**
Larvae live mainly in small springs and seeps and in some places in ponds, where they are benthic (occurring near the bottom of the lake or stream). Metamorphosed young and adults generally stay near streams in forested areas but move out into the forest and can be found some distance from water. As adults they are often fully terrestrial for much of the year.

**BEHAVIOR**
Two-lined salamanders are nocturnal and forage in the forest at night. There is some evidence that they are territorial, but the species has not been intensively studied by behavioral ecologists.

**FEEDING ECOLOGY AND DIET**
Larvae feed on small aquatic insect larvae but also eat other small arthropods. Adults feed mainly on small arthropods but will also eat snails.

**REPRODUCTIVE BIOLOGY**
Courtship is thought to occur on land, and females store sperm until eggs are laid, singly, beneath rocks in small streams. Nests are formed but are not guarded. Nests can contain over 100 eggs, but clutches generally are around 50. Eggs take up to 10 weeks to hatch. Length of the larval period varies geographically but generally is two years (one year in southern parts of the range).

**CONSERVATION STATUS**
Not threatened.

**SIGNIFICANCE TO HUMANS**
None known. ◆

## Texas blind salamander
*Eurycea rathbuni*

**SUBFAMILY**
Plethodontinae

**TAXONOMY**
*Eurycea rathbuni* Stejneger, 1896, subterranean waters near San Marcos, Texas, United States.

Until recently this extraordinary salamander was placed in the genus *Typhlomolge*, but molecular systematic analyses have shown that it is a highly derived member of *Eurycea*. When first discovered it was placed in the family Proteidae, but it was soon recognized as a bizarrely specialized plethodontid.

**OTHER COMMON NAMES**
English: San Marcos salamander, white salamander; German: Rathbunscher Brunnenmolch.

**PHYSICAL CHARACTERISTICS**
This blind and pigmentless salamander is strictly subterranean, where it lives in aquifers and can be observed in waters in caves and sinkholes. It is gilled and shiny white, with long, extraordinarily slender legs that strongly overlap when adpressed to the trunk. It is large for a larval member of this genus, reaching a total length of about 5–5.5 in (12.7–14 cm). Eyes are absent and the large head is strongly depressed with a broad, blunt snout.

**DISTRIBUTION**
This species is restricted to a small area on the edge of the Edwards Plateau, near San Marcos in south-central Texas.

**HABITAT**
The species is known only from underground streams and pools that are in sinkholes, caves, and recesses.

**BEHAVIOR**
Little is known, but individuals are active and have been observed swimming in the water column of recesses and using their long limbs to grab and cling to the rocky sides of the cavity containing the water column.

**FEEDING ECOLOGY AND DIET**
Known food items include snails, amphipods, and cave-adapted shrimp.

**REPRODUCTIVE BIOLOGY**
Nothing has been reported concerning the reproductive biology of this species.

**CONSERVATION STATUS**
This species is listed as Vulnerable by the IUCN. One of the first species named to the federal endangered species list, this salamander is threatened by human withdrawals of water from the aquifers it occupies and by pollution from surface sources.

**SIGNIFICANCE TO HUMANS**
None known. ◆

## Four-toed salamander
*Hemidactylium scutatum*

**SUBFAMILY**
Plethodontinae

**TAXONOMY**
*Hemidactylium scutatum* Temminck and Schlegel, 1838, Nashville, Tennessee, United States.





**OTHER COMMON NAMES**
French: Salamandre á quatre doigts; German: Vierzehensalamander.

**PHYSICAL CHARACTERISTICS**
This small (maximum total size about 4 in or 10 cm) terrestrial species is immediately identified by having only four toes on its hind feet, having a strong constriction at the base of its tail, and in having lower surfaces that are white with conspicuous black marks, usually round spots.

**DISTRIBUTION**
This species is found all over eastern North America from southern Canada to Oklahoma, Louisiana, and Florida.

**HABITAT**
This salamander is most commonly found in forested areas near bogs, swamps, and vernal pools. The species has a wide tolerance of environmental temperatures and occurs in seasonally very cold areas of southern Canada and northern Minnesota, Wisconsin, and Michigan, to very hot parts of Louisiana, Mississippi, Alabama, Florida, and Georgia. In the southern parts of its range its distribution is highly fragmented and discontinuous, and adults are rarely seen outside the spring breeding season.

**BEHAVIOR**
There have been extensive studies of nesting behavior. Females may lay eggs in communal nests, in isolated nests that are guarded, or abandon the eggs. They occasionally form dense aggregations as winter approaches and overwinter in subterranean sites. When attacked this salamander coils tightly and hides its head, exposing the tail, which is well supplied with glands that produce a noxious secretion. The tail can be autotomized, and it then whips rapidly back and forth.

**FEEDING ECOLOGY AND DIET**
Only small arthropods have been recorded as food items.

**REPRODUCTIVE BIOLOGY**
Raised moss mats in boggy or swampy ground are favored nesting sites. More than 1,000 eggs have been found in communal nests in such habitats. Eggs hatch after about five weeks, and larvae are small and inconspicuous, metamorphosing after a brief period of as little as two and as much as six weeks, with geographic variation.

**CONSERVATION STATUS**
Not threatened, although specialized breeding habits make this species vulnerable to human disturbance, such as forestry and wetland drainage and conversion.

**SIGNIFICANCE TO HUMANS**
None known. ◆

## Italian cave salamander
*Hydromantes italicus*

**SUBFAMILY**
Plethodontinae

**TAXONOMY**
*Hydromantes italicus* Dunn, 1923, Apuan Alps and Appenines, Italy.

European members of this genus are frequently placed in the genus *Speleomantes*. European and American species are each other's closest phylogenetic relatives. All of the species involved are very similar in general morphology, which is highly specialized and distinguishes them instantly from all members of all other genera.





**OTHER COMMON NAMES**
German: Italienischer Höhlensalamander; Italian: Salamandra cavernicola italiana.

**PHYSICAL CHARACTERISTICS**
This is a stocky, short-bodied salamander with long, partly webbed hands and feet and a relatively short tail. It grows to about 4.5 in (11.4 cm) in total length. Arms and legs overlap when adpressed, and the arms are nearly the same length as the legs. The fingers and toes are relatively long and blunt-tipped. The color pattern is a rather dull gray-brown but with highlights of reddish or yellow-brown. The ventral surfaces are dark.

**DISTRIBUTION**
This species is endemic to the Appenine Alps of central and northern Italy, including San Marino.

**HABITAT**
This completely terrestrial species is associated with limestone and is most commonly found in caves. However, it also is found outside of caves, especially on wet, rocky slopes where it is active on cool, rainy nights.

**BEHAVIOR**
The Italian cave salamander is an agile climber, using its long limbs, large webbed hands and feet, and short tail to maneuver on the vertical walls of caves and on rock faces.

**FEEDING ECOLOGY AND DIET**
This salamander has a spectacular tongue that is especially long and fast and that it uses to feed on active terrestrial arthropods.

**REPRODUCTIVE BIOLOGY**
Small clusters of large yolky eggs are laid in crevices and underground cavities; these hatch after several months into miniatures of the adults. Egg-laying is so secretive that for many years the species was thought to give birth to living young.

**CONSERVATION STATUS**
Not threatened. Because the species is rarely observed, it is often thought to be rare, but in fact it is locally abundant and is very widespread. It does not appear to be in any danger but could be harmed locally by overcollection.

**SIGNIFICANCE TO HUMANS**
Italian cave salamanders are collected as pets. ◆

## Mt. Lyell salamander
*Hydromantes platycephalus*

**SUBFAMILY**
Plethodontinae

**TAXONOMY**
*Hydromantes platycephalus* Camp, 1916, head of Lyell Canyon, 10,800 ft (3,291 m) altitude, Yosemite National Park, California, United States.

**OTHER COMMON NAMES**
None known.

**PHYSICAL CHARACTERISTICS**
These salamanders have broad, relatively flattened heads and bodies and short tails. The limbs are relatively long and the





digits are extensively webbed, although all of the digits are free of the webbing for much of their length. The breadth of the body is partly the result of the generally flattened nature of the organism but is enhanced by the elongate epibranchials that lie above the shoulders lateral to the main trunk. These epibranchials extend to the middle of the trunk and are the main structural elements of the tongue, the longest of any salamander.

**DISTRIBUTION**
This species occurs in the Sierra Nevada of California, from the southern end of Sequoia National Park to the Sierra Buttes in the north, above about 3,000 ft (910 m) in elevation, ranging upward to about 12,000 ft (3,660 m).

**HABITAT**
Most species belonging to this genus are associated with limestone, but this species is a granite specialist that occurs exclusively in the high Sierra Nevada. It is very cold-tolerant and is found near melting snow, where it hides under flat pieces of granite. Much of its habitat is above tree line, and it is most frequently found in moist areas, near seeps or small streams or near snow-melt, in areas dominated by low shrubs with some scrubby trees.

**BEHAVIOR**
Locomotion is exceptional in these salamanders. They move along moist, slick rocks at steep angles and use their short, blunt-tipped tails as a fifth appendage, bracing themselves with it as they move. When exposed by day they roll up into a ball that often rolls downhill, away from a potential predator.

**FEEDING ECOLOGY AND DIET**
Very little is known concerning its diet except that it feeds using its extraordinarily long tongue and concentrates on arthropods, mainly insects.

**REPRODUCTIVE BIOLOGY**
Little is known, but these are direct-developing species that lay large, yolky terrestrial eggs.

**CONSERVATION STATUS**
Much of the range of this species is in large national parks—Yosemite, Kings Canyon, and Sequoia—as well as in wilderness areas, and the species is not threatened.

**SIGNIFICANCE TO HUMANS**
None known. ◆

## Costa Rican worm salamander
*Oedipina uniformis*

**SUBFAMILY**
Plethodontinae

**TAXONOMY**
*Oedipina uniformis* Keferstein, 1868, Costa Rica. Several other species are now included in this taxon, although recently two sets of lowland populations were separated on biochemical grounds and recognized as separate species, *O. pacificensis* and *O. gracilis* (the latter is the common species at La Selva Biological Station in northeastern Costa Rica).

**OTHER COMMON NAMES**
None known.

PHYSICAL CHARACTERISTICS
The extraordinarily slender form and tiny limbs and digits characterize this and related species. The species reaches 6–6.5 in (15.2–16.5 cm) in total length, two-thirds of which may be its tail. The head, body, and tail are of roughly equivalent width, and the tail does not taper until near its tip. Eyes are small and inconspicuous and the head is small. Typically the species is completely black with inconspicuous white speckles and occasionally light spots behind the eyes.

DISTRIBUTION
This species is known only from the region surrounding the Meseta Central of Costa Rica, generally above 4,000 ft (1,219 m) elevation.

HABITAT
This species is fossorial, found most commonly in well rotted logs and under moss mats on roadside banks, usually in forested areas.

BEHAVIOR
This salamander lives in the interstices between soil, rotting logs, leaf litter, and mats of moss and other plants covering soil and fallen logs. When uncovered the salamanders whip their tails back and forth violently in attempting to escape, and will readily autotomize any length of the tail if it is grabbed.

FEEDING ECOLOGY AND DIET
These salamanders feed on small arthropods.

REPRODUCTIVE BIOLOGY
The species lays large yolky eggs in cavities in the soil.

CONSERVATION STATUS
Not threatened. This species was once common but now is rarely seen, in part because of extensive conversion of original habitat for agriculture and urbanization.

SIGNIFICANCE TO HUMANS
None known. ◆

## Red-backed salamander
*Plethodon cinereus*

SUBFAMILY
Plethodontinae

TAXONOMY
*Plethodon cinereus* Green, 1818, New Jersey, United States.

OTHER COMMON NAMES
English: Lead-backed salamander; French: Salamandre rayée; German: Rotrücken-Waldsalamander.

PHYSICAL CHARACTERISTICS
This is a small species (3.5–5 in or 9–13 cm total length) with a small head, short limbs, and an elongate, narrow trunk and tail. It occurs in two morphs, a striped or red-backed phase that features a long, even-sided dull tan to an orange or reddish stripe extending nearly the full length of the trunk and tail, and a lead-back phase in which the dull gray-black ground color of the sides extends all over the upper surfaces. Lower surfaces are light gray with numerous black speckles.

DISTRIBUTION
This species ranges from eastern Canada to western Ontario and eastern Minnesota in the North, to North Carolina and





eastern Tennessee in the South, and eastern Illinois in the West.

HABITAT
This is a woodland salamander, and it is often extremely common. It is found under cover objects by day, usually wood debris but also rocks and leaf litter. It forages actively in the early evening hours and is common when conditions are moist and cool.

BEHAVIOR
Red-backed salamanders have been the subject of extensive behavioral ecological studies by Robert Jaeger and associates. They have a rich social life and are very aggressive toward conspecifics (members of their own species) as well as other species, actively protecting feeding territories and retreats. They modulate their behavior depending on familiarity, and they select mates according to diverse criteria including quality of the food eaten by potential mates. They are active foragers, and they are capable of modulating their tongue projection mechanisms depending on the size, distance, and other characteristics of the prey.

FEEDING ECOLOGY AND DIET
Food is basically small terrestrial arthropods, but occasionally they eat snails, slugs, and even small earthworms.

REPRODUCTIVE BIOLOGY
Courtship is terrestrial, and following acceptance of a spermatophore by a female, eggs are laid in secretive sites, typically underground cavities or crevices in logs or rocks. The grape-like clusters of three to 14 eggs are guarded by the female and hatch in about six weeks.

CONSERVATION STATUS
Not threatened. This is a highly adaptable species, but it does require wooded environments and does best in closed canopy forests.

SIGNIFICANCE TO HUMANS
None known. ◆

## Bell's salamander
*Pseudoeurycea bellii*

SUBFAMILY
Plethodontinae

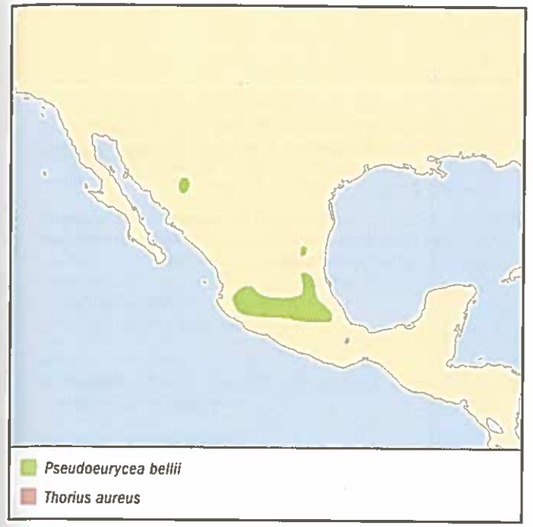
TAXONOMY
*Pseudoeurycea bellii* Gray, 1850, Mexico.

OTHER COMMON NAMES
English: Bell's false brook salamander.

PHYSICAL CHARACTERISTICS
This is a spectacular species that is the largest lungless salamander and close to the largest terrestrial salamander (it reaches nearly 14 in or 36 cm total length). It is shiny dark black with a pair of red to red-orange spots on the back of its head and paired rows of similarly colored spots along the back to the base of the tail. There is usually a chevron-shaped mark at the beginning of the paired rows. The tail is long and large and is basally contricted. The limbs are long and well developed and the overall appearance of the animal is massive.








DISTRIBUTION
Bell's salamander is widely distributed from northwestern and northeastern Mexico into central Mexico, usually at relatively high elevations (above 4,000 ft or 1,220 m).

HABITAT
This is a strictly terrestrial species that is found under large surface objects such as logs and rocks in relatively moist woods. It utilizes terrestrial burrows and can be found in holes in road banks.

BEHAVIOR
Almost nothing is known of the behavior of this species, except that it is nocturnal.

FEEDING ECOLOGY AND DIET
No information is available. It most likely feeds mainly on insects, which are caught with its freely projectile-tongue.

REPRODUCTIVE BIOLOGY
Almost nothing is known except that it lays clutches (more than 20) of large, yolky eggs.

CONSERVATION STATUS
This species is widespread and was once common in many parts of Mexico. Not threatened, although in recent years it has become scarce.

SIGNIFICANCE TO HUMANS
None known. ◆





## Golden thorius
*Thorius aureus*

SUBFAMILY
Plethodontinae

TAXONOMY
*Thorius aureus* Hanken and Wake, 1994, 0.7 mi (1.1 km) east of Cerro Pelon, Oaxáca, Mexico.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
This tiny salamander is one of the largest species of a group known as the minute salamanders, among the smallest known tetrapods. In comparison to other members of the large genus *Thorius*, this is a robust and colorful species that reaches a size of about 2.25 in (5.7 cm) total length. The legs are slender and short, separated by six to eight costal interspaces when adpressed to the sides of the body. Digits are joined to neighboring digits for most of their short length but are free at the tips. Nostrils of many members of this genus are very large, but in this species they are relatively small. This species has teeth on its upper jaw, but these are missing in most members of this genus. The bones of this species, as in other members of the genus, are weak and poorly articulated, and there is a large fontanelle in the back of the head, over the brain. Eyes are large and well developed. This is a colorful species, with a golden band or broad stripe on its back and tail and with relatively light ventral surfaces.

DISTRIBUTION
This species is known only from high elevations, from 7,500 to 10,000 ft (2,286–3,048 m) in the Sierra de Juarez, northern Oaxaca, Mexico, where a rich diversity of species of *Thorius* is found.

HABITAT
This species is found in high cloud forest under rocks, logs, and surface debris, and can be found under the bark of fallen logs and in moss on road banks.

BEHAVIOR
When uncovered these animals make a tight coil that hides the head. They have a constriction at the base of the tail and are capable of autotomy at this site, or at any point along the length of the tail.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Eggs have never been observed, but it is known that the species practices direct development.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

## Resources

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