

TWITTY, VICTOR C. 1964. *Taricha rivularis*, p. 9. In W. J. Riemer (ed.), Catalogue of American Amphibians and Reptiles. American Society of Ichthyologists and Herpetologists, Kensington, Maryland.

*Taricha rivularis* (Twitty)  
Red-bellied newt

*Triturus rivularis* Twitty, 1935:73. Type-locality, "Gibson Creek, about one mile west of Ukiah, [Mendocino County], California." Holotype, Mus. Vertebr. Zool. 18131, collected by V. C. Twitty, 22 February 1935.

*Taricha rivularis*: Schmidt, 1953:27. New combination.

• CONTENT. No subspecies are recognized.

• DEFINITION. Adults are about 150 to 185 mm in total length (see DESCRIPTIONS). The eyes are prominent, the iris dark brown (black to casual examination); the dorsum is black or very dark brown; the venter is tomato red, except for extensive invasion by dark dorsal pigment onto the lower surfaces of fore- and hind-limbs and usually as a band across the cloacal lips.

• DESCRIPTIONS. Adults: Descriptions of adults are found in Twitty, 1935:73, 1942:65; Bishop, 1943; Stebbins, 1951; and Riemer, 1958:301. Riemer's account gives the most detailed and complete information available on body proportions, and pigmentary characteristics and variations. The largest series measured (Gilbert Church, unpublished), 1035 adult males from Pepperwood Creek, Sonoma County, California, averages 167.5 mm in total length, with extremes of 142-193 mm (94.5% of the series ranges between 154 and 184 mm); and they average 68.2 mm in snout-vent length, with extremes of 60-76 mm.

Eggs: Eggs are laid during March and April (mostly from mid-March to mid-April) in flat packets on the undersurfaces of stones (sometimes on submerged roots) in the clear, rapid water of mountain brooks. The average number of eggs per cluster is 10, with extremes of 6 and 16, in 45 clusters counted. Egg size averages 2.58 mm, with extremes of 2.40 and 2.70 mm in 42 eggs measured, as compared with averages of 2.10 and 1.77 mm in *T. torosa torosa* and *T. granulosa*, respectively. In 14 mature females dissected there was an average of 63 ova per ovary, the ova being 2.5 mm in diameter.

Larvae: The larvae are characterized by uniform dispersal of melanophores over the back and sides, by reduction in size of the dorsal fin (it extends less far forward on the trunk than in other species of *Taricha*), and by complete absence (in 59% of 1948 larvae scored) or marked reduction in the size of the balancer. Larvae at hatching average 11.8 mm with extremes of 10.5 and 12.7 mm in 47 larvae measured. Larvae were abundant in a tributary of Pepperwood Creek, Sonoma County, 4 September 1963: 85 of them averaged 44 mm in total body length with extremes of 31 and 55 mm. On 14 October the same stream yielded few larvae, and all of these were in the process of transformation. Metamorphosis normally occurs during late summer or early fall at about 45-55 mm total length. As in other urodeles some shrinkage in body length accompanies metamorphosis. Of larvae reared in the laboratory, 32 on the verge of metamorphosis averaged 53 mm in total body length with extremes of 45 and 61 mm; 21 of the same series having completed transformation at the same date averaged 48 mm with extremes of 46 and 52 mm. There is no indication that the larvae ever overwinter before metamorphosing, as has been observed in several instances in *T. granulosa*, *T. torosa torosa*, and *T. t. sierrae*.

The large egg size, reduced dorsal fin, and loss of a balancer in *T. rivularis* possibly reflect the commitment of this species to a mountain-brook habitat.

• ILLUSTRATIONS. Color drawings of adults are available in Twitty, 1942:65, and photographs in Bishop, 1943. Photographs of egg clusters and larvae appear in Twitty, 1942:65. See COMMENT for information on the spermatophore.

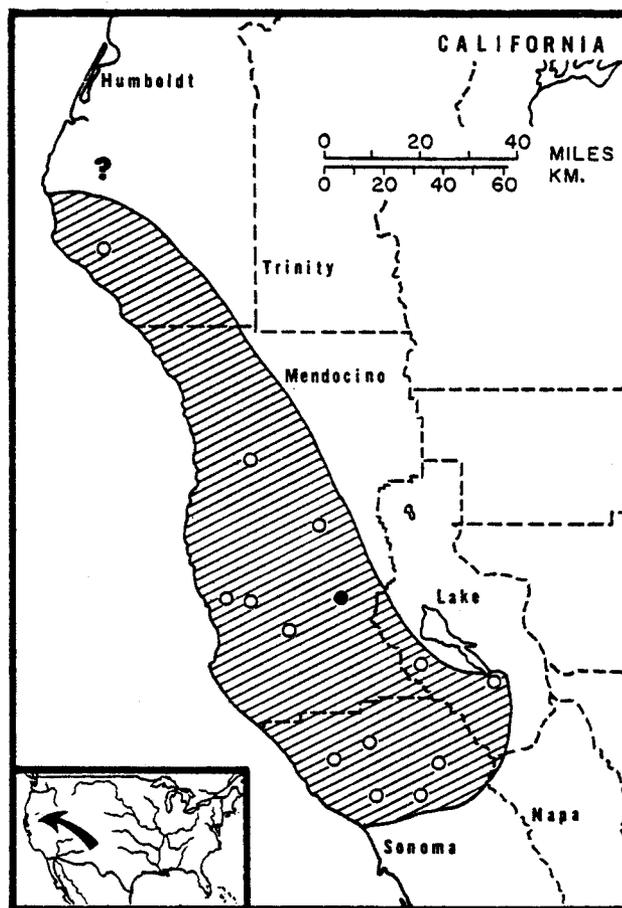
• DISTRIBUTION. Known only from coastal California north of San Francisco Bay in Sonoma, Lake, Mendocino, and Humboldt Counties, this species occupies the same general area as the coast redwood (*Sequoia sempervirens*). With rare exceptions adults are aquatic only during the breeding season (also see REMARKS).

• FOSSIL RECORD. None.

• PERTINENT LITERATURE. The most complete account of adult variation and systematic relationships of *T. rivularis* and other western forms is in Riemer, 1958:301. Other general accounts of this species are in Twitty, 1935:73, and 1942:65; Bishop, 1943; and Stebbins, 1951.

• REMARKS. Little is known about feeding or other activities during the period of underground concealment, or the precise locations and depths of hiding places, except that numerous animals have been captured in traps built around the partly hollow bases of trees with old root channels that presumably lead to depths necessary to assure sufficient moisture during the long dry season (Packer, 1960:509). Animals are also often seen during the winter and spring just within the apertures of root channels opening on the eroded faces of vertical or overhanging stream banks, and the deeper parts of these recesses are probably used for summer estivation.

Emergence from underground begins with the first substantial autumn rain and continues at times of rainfall until midwinter. Movements during migration are stimulated primarily by rain, but rain in heavy amounts inhibits movement toward the stream. In the absence of rainfall the magnitude of the breeding migration is correlated with daily changes in the mean evening temperature and the minimum relative humidity (Packer, 1960:509).



MAP. The solid circle marks the type-locality; open circles show most other localities. The question mark indicates an unknown distributional boundary.

Males are usually present in abundance in the breeding stream before the first females enter. In years when the weather and stream conditions are favorable, male entry may begin as early as the first or second week in February; substantial numbers were recorded in Pepperwood Creek, Sonoma County, on 12 February 1953. Daily records of the number of males and females entering the water throughout the breeding season are given by Twitty (1961b:figs. 2-3). Records for one stream for the years 1956-1961 show that by mid-point in the breeding season an average of about 60 percent of the males have entered the water compared to only 25 percent of the females. Males locate females by chemical sex attractants released from the female into the water (Twitty, 1955:129).

Because of the remarkably small number of juveniles observed, or captured in land traps during the rainy season when large numbers of adults are in evidence, *T. rivularis* is thought to remain almost continuously underground during the long period (estimated at 5 years or longer) between metamorphosis and maturity. This inference is strengthened by the fact that although the population of adult *T. granulosa* in the same area (Pepperwood Creek, Sonoma County) is much smaller than that of *T. rivularis*, juvenile *T. granulosa* are captured in conspicuously larger numbers than are juvenile *T. rivularis*.

Marking studies show that terrestrial migrations by adults may carry them a mile or more from the breeding stream, but a well-developed homing ability enables them to relocate the same restricted segment of the stream for successive breeding entries (Twitty, 1959, 1961b). Packer (1963:378) found that most animals return to within approximately 50 feet of the same point previously occupied in the stream. The homing migration of animals transferred major distances is executed mostly on land and is usually postponed until the next breeding season or even longer (Twitty, Grant, & Anderson, 1964), but aquatic homing is reported by Packer (1962) for animals displaced for very short distances. The presumed effect of homing is to restrict greatly gene flow within the population of a given stream, and it appears that there is virtually no breeding interchange between the populations of neighboring streams. Of thousands of adults marked during the past 10 years in the upper reaches of Pepperwood Creek, Sonoma County, not one has subsequently been found in the two nearest streams, Jim and Danfield Creeks. The homing habit also protects against gametic wastage, for almost no adults enter portions of streams that appear to be suitable for egg laying during the breeding season but regularly dry up during the summer months before larvae could successfully metamorphose. The limited evidence thus far available (Twitty, 1961a:1461, and unpublished) indicates that association with a particular stream segment is fixed early in life, possibly when the larvae transform and first emerge on land.

Vision is not essential to homing, as has been shown by displacement of blinded animals for various distances, even to another stream (Twitty, 1959:1735, 1961b, and unpublished). Animals with sectioned olfactory nerves have not homed, but studies on olfaction are still in progress and permit no final conclusions.

Success in homing in *T. rivularis* is not dependent on prior acquaintance with the displacement site. Captures of marked adults in land traps show that terrestrial excursions are mostly confined to relatively limited segments of hillside overlooking the parts of the stream in which the animals breed. Experiments using these traps also indicate that animals detect the direction of the home area and move toward it with a minimum of preliminary random search, even after displacement for long distances.

Of series of animals marked in 1953, more than ¼ of the individuals were still being recaptured in 1964, indicating that the life span is relatively long and the mortality rate low in adults of this species. These and other similar marking experiments also reveal that whereas a large percentage of males (probably over half) breed in immediately successive years, females rarely breed except at two- or three-year intervals or

even longer (Twitty, unpublished). Of 1273 breeding females marked in Pepperwood Creek during 1960, 9 were recaptured in the stream in 1961, 179 in 1962, and 242 in 1963. A series first marked in 1961 and another in 1962 have followed similar patterns of return.

Packer (1961) reports that *T. rivularis* does not feed while in the water for breeding.

Although *T. rivularis* is sympatric with *T. granulosa*, natural hybridization seems to be extremely rare; only 2 hybrids were encountered during extensive field experience with both species. However, artificially produced hybrids between *T. rivularis* and the other species and subspecies of *Taricha*, including *T. granulosa*, are both viable and fertile (Twitty, 1955, 1961a, 1964). Speciation in *Taricha* thus does not seem to have led to the differentiation of basically incompatible genomes, and it is accordingly assumed that the reproductive barriers isolating the species and subspecies of *Taricha* are primarily geographical or ethological. Also see COMMENT.

• ETYMOLOGY. The name *rivularis* (from Latin *rivulus*, "brook" or "small stream") was chosen because this species, unlike other forms of *Taricha*, breeds exclusively in streams and exhibits larval features apparently reflecting its commitment to this habitat.

#### COMMENT

A detailed account of courtship behavior in *T. rivularis*, and a discussion of the basis of reproductive isolation, is now in press by William Davis & V. C. Twitty. This paper also contains descriptions and drawings of the spermatophore.

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