Investigations on the Skin Toxin of the Adult Rough-Skinned Newt, *Taricha granulosa*

EDMUND D. BRODIE, JR.

Thirty species of potential predators on *Taricha granulosa* were tested by injection or force-feeding to determine their susceptibility to adult *T. granulosa* skin toxin. All species tested were found to be susceptible to *Taricha* skin toxin. The action of adult *T. granulosa* skin toxin is identical to that described for tetrodotoxin from the eggs of *T. torosa* and the puffer fish. Mammals and birds are susceptible to similar relative amounts of toxin; 0.0002 cc of back skin of *T. granulosa* killed white mice in 10 min. Snakes other than garter snakes were about 200 times more resistant, and garter snakes were 2000 times more resistant than white mice. *T. granulosa* was self-susceptible to large doses. Garter snakes, *Thamnophis sirtalis concinnus*, were able to eat adult newts, even though they were killed by injections. *Taricha* toxin was very stable and did not lose potency over an 11-month period.

INTRODUCTION

THE defense mechanisms of salamanders have long been of interest to scientists. The most obvious of these mechanisms, the presence of skin toxins, has been studied in several species of European salamanders, *Salamandra* and *Triturus* (Phisalix, 1922).

Hubbard (1903), in an early study of defense mechanisms of North American salamanders, reported on the distastefulness of salamanders to snake predators. *Taricha torosa* was refused by all snakes tested. Stuhr (1936) observed the effect of the integumental toxin of *T. granulosa* on the heart rate of frogs. These two reports comprise the available knowledge on adult *Taricha* skin toxins.

The toxicity of *T. torosa* embryos has, however, been extensively studied. Twitty and Johnson (1934) discovered their toxic properties and further work by Twitty (1935, 1937), Horsburgh *et al.* (1940), van Wagtendonk *et al.* (1942), Fuhrman and Field (1941), Davenport and Smith (1942), and Turner and Fuhrman (1947) established the physiological effects of the toxin. Brown and Mosher (1963), Kao and Fuhrman (1963), and Fuhrman *et al.* (1963) isolated and purified this toxin in crystalline form and described it as a nonproteinaceous neurotoxin, "tarichatoxin." The empirical formula of "tarichatoxin" was established as C_{11} H_{17} N_3 O_8 (Buchwald *et al.*, 1964) and found to be identical in makeup and structure to tetrodotoxin, previously isolated from the ovaries and liver of *Sphoeroides rubripes*, the Japanese fugu or puffer fish. Mosher *et al.*, (1964) and Fuhrman (1967) reviewed the available knowledge concerning tetrodotoxin and determined the toxin of the eggs of *T. rivularis* and *T. torosa* to be identical. They also found that the eggs of *T. granulosa* are toxic but did not isolate or identify the toxin. Wakely *et al.* (1966) have shown that adult *T. torosa* and *T. rivularis* contain a toxin which cannot be distinguished from tetrodotoxin by analytical thin-layer chromatography.

The primary aim of this study was to determine if toxin was present in the skin of adult *T. granulosa*, to compare its action with that described for tetrodotoxin, and to link the toxin with possible protection from predation. To this end, 30 vertebrate species, many of them potential predators, were tested for susceptibility to *Taricha* skin toxin.

MATERIALS AND MATERIALS

Susceptibility of animals to *Taricha* toxin was tested by two methods: feeding and injection. In this study, most of the submammalian forms were tested by feeding, either voluntarily or by force, usually the latter. A newt or a section of newt's tail was placed into the test animal's mouth, which was then held closed until the animal swallowed.

Mammals were tested by injection in order to have a precise measurement of the amount of toxin given. Toxin was administered orally, by means of a blunt needle, and

TABLE 1. SUSCEPTIBILITY OF VARIOUS VERTEBRATES TO INTRAPERITONEAL INJECTIONS OF *Taricha* TOXIN. (NL = non-lethal.)

Species	Wt (g)	Dose (cc of Skin)	Time to Death	Remarks
Mus musculus	21.5	0.0002	10.25 min	$\bar{x}$; 26 animals
	22.8	0.0004	5.5 min	$\bar{x}$; 2 animals
	21.5	0.0005	4.5 min	$\bar{x}$; 12 animals
	19.9	0.001	2.0 min	$\bar{x}$; 2 animals
	23.9	0.0015	2.0 min	
	21.3	0.002	2.0 min	
	25.3	0.004	2.0 min	
Rattus rattus	181	0.001	NL	$\bar{x}$; 2 animals
	152	0.001	NL	hind leg coordination affected
	146	0.001	15.0 min	$\bar{x}$; 3 animals
	152	0.002	6.5 min	$\bar{x}$; 7 animals
	155.7	0.0035	5.0 min	
	184.2	0.005	2.5 min	
	180	0.02	1.5 min	
Felis catus	290	0.001	NL	
	350	0.002	NL	
	413	0.005	17.0 min	$\bar{x}$; 3 animals
	440	0.01	6.0 min	
Zapus sp.	21	0.0002	17.0 min	
Mustela erminea	57.5	0.002	2.5 min	
Scapanus townsendi	—	0.005	2.5 min	
Neotoma lepida	81.8	0.002	8.5 min	
Ondatra zibethica	670	0.002	32.0 min	
Citellus beecheyi	669	0.005	NL	
	727	0.02	19.0 min	
Myocastor coypus	3085	0.1	12.0 min	
Lynx rufus	8000	0.15	13.0 min	
Sturnus vulgaris	—	0.0002	NL	$\bar{x}$; 2 animals
	77	0.0005	7.0 min	$\bar{x}$; 3 animals
Taricha granulosa	16.5	0.2	17.5 hr	
	16.3	0.4	20.0 hr	$\bar{x}$; 2 animals
Coluber constrictor mormon	42.6	0.002	10.0 min	
	52	0.002	NL	affected for several hr
	54.6	0.004	NL	not affected
	48.3	0.03	NL	complete recovery after 6 days
	49.7	0.1	45.0 min	
	93.9	0.2	24.0 min	
	45.9	0.4	65.0 min	
Pituophis melanoleucus catenifer	90.1	0.002	NL	complete recovery after 5 days
	86.8	0.02	3.0 days	
	265	0.2	30.0 hr	
	285	0.4	30.0 hr	
Crotalus viridis	110	0.002	NL	complete recovery after 5 days

TABLE 1. (*Continued.*)

Species	Wt (g)	Dose (cc of Skin)	Time to Death	Remarks
Masticophis taeniatus	110.4	0.2	17.0 min	
Charina bottae	48.8	0.1	42.0 min	
Contia tenuis	4.4	0.02	15.0 min	
Thamnophis elegans vagrans	14.6	0.2	59.0 min	
	58.5	0.4	2.5 days	
	70.8	0.4	380.0 min	
T. ordinoides	32.5	0.001	NL	complete recovery after 12 hr
	11.1	0.002	NL	complete recovery after 12 hr
	11.7	0.05	8.0 hr	
	25.9	0.1	50.0 min	
	12.3	0.2	29.0 min	
	18	0.2	38.0 min	
	25.5	0.2	68.0 min	
	27.5	0.2	36.0 hr	
	32.2	0.4	44.0 min	
T. sirtalis fitchi	79.3	0.2	NL	complete recovery after 4 days
	46	0.4	80.0 min	
	55.7	0.4	36.0 hr	
	129	0.4	68.0 hr	
	27.4	0.5	100.0 min	
	47.4	0.5	2.0 hr	
T. s. concinnus	6.7	0.2	86.0 min	
	37.9	0.4	36.0 hr	
	38.8	0.4	25.0 hr	
	105	0.5	2.5 days	
T. s. concinnus × *T. s. fitchi* (intergrade)	64	0.5	2.5 days	
T. marciana	65.5	0.4	62.0 min	

intraperitoneally, by injection. Intraperitoneal injections yielded more consistent results and were used more extensively. For injection, a stock solution of *T. granulosa* skin was prepared by blending a known volume of skin with a known volume of Holtfreter's solution. Using a Waring blender, the mixture was macerated until no color was apparent in the skin remnants. Unless otherwise indicated, all tests were made with skin from the back of terrestrial adult *T. granulosa*. All newts used were collected in Benton Co., Oregon.

One and 10% homogenates of skin were made and diluted as required; volumes of 1, 0.4, and 0.2 cc were injected. From the percentage and volume administered it was possible to compute the actual amount of skin volume in each dose.

Whenever possible, experimental controls were run; these were of two types: injections of Holtfreter's solution or macerated portions of subintegumental muscle. Twenty-three white mice were injected with Holtfreter's solution and 10 were injected with 0.1 cc each of muscle; none of these was noticeably ill affected.

In all susceptibility tests, the time, amount, and method of administration of toxin were recorded. Any visible change in the test animal was recorded; in case the injection or feeding was lethal, the time to death was noted to the nearest 30 sec.

RESULTS

Effects on vertebrates.—All animals tested with *Taricha* skin toxin, either by injection

or feeding, displayed similar symptoms. Generally these symptoms were, in order: 1) muscular weakness, especially prevalent in the hind limbs, causing splayed gait; 2) loss of righting reflex; 3) convulsions; 4) gasping, gaping, and regurgitation, accompanied by violent contractions of the thoracic muscles; 5) flaccid paralysis; 6) fall in blood pressure. Five white rats were anesthetized, connected to a tambour-manometer apparatus, and injected with lethal doses of *Taricha* toxin. There was a decrease in blood pressure (the rapidity of which was directly correlated with the amount of toxin injected), accompanied by vasodilation as seen in the blood capillaries of frog webs and mice ears; and 7) continuous heart beat after cessation of respiration. These symptoms were observed primarily in white mice but also appeared in the other vertebrates tested.

Mammals were tested only by injection since all newts offered as food to mammals were refused (I have, accidentally, while handling newts, touched my fingers to my tongue and mouth and experienced a severe burning sensation; when cats were forced to bite newts they reacted by pawing at their mouths). White mice were consistently killed by as little as 0.0002 cc of back skin of *T. granulosa*. Ten other species of mammals, many of them possible predators, were found to be susceptible to the same degree, relative to weight, as white mice (Table 1).

Peromyscus maniculatus were administered toxin orally as well as intraperitoneally. It took 16 times as much toxin given orally to kill a mouse in two hr as to kill a mouse in ½ hr when given intraperitoneally.

Birds were easily force-fed and this was, therefore, the primary method used in testing bird susceptibility. A robin (*Turdus migratorius*) (65.9 g) was force-fed 20 mm of newt tail. After 1.5 hr the bird showed a lack of coordination and an inability to stand erect. After 24 hr, in addition to these symptoms, it did not attempt to fly or break its fall when dropped, or close its eyes when the eyeball was touched, and it reacted to vibration and touch by jumping. The robin made no attempt to escape and could not perch or grip with its feet. At 25 hr, it suddenly stiffened, flapped its wings, and died. It was dissected and the remains of the newt, as evidenced by a slight orange color, were found in the large intestine.

Two of the birds tested, a belted kingfisher (*Megaceryle alcyon*) and a great blue heron (*Ardea herodias*), are potential avian predators on *T. granulosa*. The kingfisher (120 g) was force-fed 30 mm of newt tail and was dead two min after the tail was placed in its mouth. A 50 mm section of newt tail was placed in the mouth of the heron (1260 g) and was promptly spit out. The tail was then placed in the rear of the bird's mouth and the bill was tied loosely shut. One and one-half min later the bird was unable to stand upright and in two min it was dead. Both the kingfisher and the great blue heron were dissected and found not to have been injured by the force-feeding; in both cases the tail was found in the proventriculus.

Starlings (*Sturnus vulgaris*) were tested by intraperitoneal injections in order to determine more accurately the susceptibility level for birds (Table 1).

Reptiles, particularly snakes, are also potential predators on *T. granulosa*; several species were tested for susceptibility to *Taricha* toxin by intraperitoneal injections (Table 1). Those affected by *Taricha* toxin injections reacted within a few hr by losing muscle coordination, as evidenced by an inability to crawl, elevate the head, or extend the tongue. These symptoms were usually followed by loss of righting reflex and cessation of breathing. Nine snakes were moribund for several days; four of these recovered after four–six days (Table 1).

Snakes were not force-fed, but all those injected were first offered *T. granulosa* as food. The only snake which ate newts was *Thamnophis sirtalis concinnus*; several of these ate adult *T. granulosa* in the laboratory with no apparent ill effects. One snake, 965 mm in total length, devoured eight adult newts (15–18 g) in two weeks. These snakes have also been observed to take newts from drop traps along a drift fence (Thomas Darrow, pers. comm.).

Gerrhonotus multicarinatus were tested for susceptibility by forcing them to bite the tail of *T. granulosa*. Two lizards, whose mouths were held closed on the tail as it was pulled from their mouth, died in five and 15 min. Another bit solidly on the newt but did not chew; it died in one hr. The symptoms exhibited by this lizard were also typical of the other lizards tested; immediately—rubbed its open mouth in the gravel of the terrarium; one min—regurgitated; three min—gaped;

TABLE 2. SUSCEPTIBILITY OF FISH TO FORCE-FEEDINGS OF ADULT NEWTS.

Fish	Wt (g)	Amt of newt fed	Time to death (min)
Bluegill	108	entire	13
(*Lepomis macrochirus*)	75	20 mm tail	14
Largemouth bass	145	20 mm tail	30
(*Micropterus salmoides*)	180	20 mm tail	30
Channel catfish	414	entire	19
(*Ictalurus punctatus*)	750	entire	20

4½ min—voided cloaca; 6–13 min—lay motionless with eyes closed, yet was able to right itself rapidly; 14 min—writhed and rolled, no righting reflex was evident; 19 min—violent convulsions (two of the lizards shed their tails during convulsions, but this one did not); 20–57 min—heart beat was present but there were no other signs of life; 60 min—heart had ceased to beat.

Two *G. multicarinatus* survived after biting the tail of *T. granulosa*. One of these bit the newt tail but immediately released it; the lizard subsequently exhibited the same symptoms as the others and, after 90 min showed only a faint heart beat. After 24 hr in this condition, the lizard was able to right itself slowly; it had completely recovered after 40 hr. The other lizard bit very lightly on the newt tail and showed none of the symptoms except the immediate response of rubbing its mouth on the floor of the terrarium.

One potential amphibian predator, *Rana catesbeiana*, was tested for susceptibility by force-feeding. Three min after swallowing a newt, a frog was unable to right itself and could not control its hind legs, and after 10 min the frog was dead; the frog indicated no distaste. Five min after the frog's death, the newt emerged under its own power from the frog's mouth, unharmed, but covered with a heavy coating of what was apparently its own skin secretion. On 12 April 1967, Hobart L. Landreth found a dead bullfrog at the edge of a pond while collecting newts; upon cutting the frog open, he found an intact adult *T. granulosa* in the frog's stomach.

Susceptibility of fish was tested by force-feeding (Table 2). The three entire newts fed to fish were recovered alive after the fish had died; in each case the newt was left in the fish's mouth until the fish was dead and then removed, alive and seemingly unhurt, but covered with secretion.

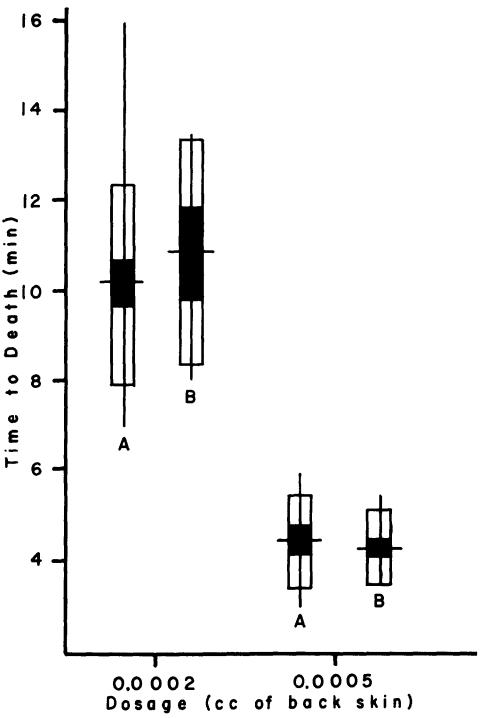

Fig. 1. Stability of *Taricha* toxin. A. Tests made with fresh toxin; 38 mice averaged 21.5 g; B. Tests made with toxin after 11 months; 14 mice averaged 23.0 g. Symbols: vertical line, range; horizontal line, mean; open rectangle, 1 standard deviation ± mean; closed rectangle, 1 standard error ± mean.

Self-susceptibility.—*T. granulosa* was tested for self-susceptibility by intraperitoneal injections (Table 1). Many newts were injected with 0.0002–0.04 cc of skin but exhibited no symptoms of susceptibility. Three newts tested with 0.1 and 0.2 cc of skin exhibited reactions similar to those observed in white mice. They were, however, able to swim well after they had lost ability to coordinate their movements on land.

Toxin stability.—Of the several mixtures of *Taricha* toxin used in this study, one was used over a period of 11 months, from 28 July 1965 to 28 June 1966. The relative potency of the toxin homogenate during this time is shown in Fig. 1. The toxin was kept at 4° C, but allowed to reach room temperature, 22° C, for each test.

DISCUSSION

Mosher, *et al.* (1964) and Fuhrman (1967) have suggested that the toxin of *T. torosa*

eggs, tetrodotoxin, is probably identical with the skin toxin of that species and with both the egg and skin toxins of *T. rivularis* and *T. granulosa*; toxins found in adult *T. rivularis* and *T. torosa* cannot be distinguished from tetrodotoxin by analytical thin-layer chromatography (Wakely *et al.*, 1966). Twitty (1937, 1966) maintained that the egg and skin toxins of *T. torosa* are not the same. The action of *T. granulosa* skin toxin appears to be identical with the action of *T. torosa* egg toxin (tetrodotoxin) as described by Horsburgh, *et al.* (1940) and Mosher, *et al.* (1964), indicating the two are probably identical or at least quite similar. The homogenate of *T. granulosa* skin toxin did not lose potency over an 11 month period.

Wakely, *et al.* (1966) reported the average total toxin content for a 10 g *Taricha* to be 250 μg; Kao and Fuhrman (1967) set the minimal lethal dose for white mice at 8 μg/kg. The isolated toxin from one adult *T. torosa* would therefore kill 1500–1600 white mice. According to my findings it would require less than 0.33 cc of *T. granulosa* skin to kill this many white mice. Possible explanations for this are that *T. granulosa* is more toxic than *T. torosa*, there are other toxins than tetrodotoxin involved, or the isolation techniques lose much of the toxin.

Taricha toxin was lethal when introduced into the esophagus of mice, indicating either that the toxin is not neutralized in the digestive system or absorption of the toxin by the oral and esophageal surfaces is sufficient to be lethal.

All fish tested were found to be susceptible. Susceptibility of catfish is confirmed by a report of a dead catfish with the tail of a *T. granulosa* protruding from its mouth (Lynn Goodwin, pers. comm.). Mosher *et al.* (1964) have reported "numerous dead catfish" in the ponds from which they collected *T. torosa* eggs but did not make it clear whether they believed adult newts or their eggs were responsible for the deaths of the catfish. There are reports of rainbow trout caught with *T. granulosa* in their stomachs (Vincent, 1947; Pimentel, 1952). The trout reported by Pimentel is known to have been alive when collected (R. M. Storm, pers. comm.). These conflicting reports may indicate differences in susceptibility for different fish.

The bullfrog, which has been introduced into Oregon, is large enough to eat an adult newt and is the most likely amphibian predator. The one known case of a bullfrog's natural predation on a newt occurred shortly after the frogs had been introduced into a pond (the frog was found dead).

It was found that adult newts are susceptible to injections of their own toxin, but only to massive doses. The times to death using 0.1 cc (17.5 hr) and 0.2 cc of skin (18 and 22 hr) indicate the great resistance newts have to their own toxin. *T. torosa* and *T. granulosa* are also approximately 3000–30,000 times more resistant than frogs to tetrodotoxin (Kao and Fuhrman, 1963, 1967; Buchwald *et al.*, 1964; Mosher *et al.*, 1964). Taylor (1934) stated that *T. granulosa* "are highly sensitive to even small quantities of their own poison, I found that often the inserting of the needle through the skin in the course of suturing the wounds made by the operation was sufficient to bring about the death of the animal." Taylor was thyroidectomizing the newts in question and the "extreme nervous sensibility" he describes as a symptom is not typical of animals affected by the skin toxin of *T. granulosa*. The death of these newts was probably due to some other cause.

Reptiles are the most likely predators on newts and are often abundant near newt ponds. Alligator lizards were found to be highly susceptible to *Taricha* toxin and were the only animals to die after biting a newt. Susceptibility of snakes is sharply divided into two groups, garter snakes and other snakes. Six genera of snakes, other than garter snakes, were found to be approximately 200 times more resistant to *Taricha* toxin than white mice. The toxin needed to kill a 110.4 g *Masticophis*, a 265 g *Pituophis*, and 93.9 *Coluber*, in each case, was equal to 0.2 cc of newt back skin.

The integumental toxin of *Taricha* has been regarded by several writers as effective protection against predation by snakes, including garter snakes (Hubbard, 1903; Fitch, 1941; Pimentel, 1952; Mosher *et al.*, 1964; and Wakely, *et al.*, 1966). In the cases reported the snakes either refused the newts, reacted by gaping after biting a newt, or died after eating a newt. However, garter snakes are susceptible only to large amounts of injected *Taricha* toxin (they are about 2000 times more resistant than white mice).

Wakely *et al.* (1966) assumed the same level of susceptibility for snakes as for mammals, fish, and frogs when they calculated that a 500 g snake would be killed by eating a 10 g *Taricha*. Many garter snakes less than 200 g have successfully eaten one, two or even three adult *T. granulosa*, larger than 10 g, at once without any visible ill effects. Too few tests were made to determine if resistance to *Taricha* toxin is confined to those garter snakes sympatric with *Taricha*. *Thamnophis sirtalis* was the only animal tested which could be an actual predator on *T. granulosa*.

Birds exhibited the same level of susceptibility as white mice. Storm (1948) reported a mallard dead with a *T. granulosa* in its crop, and many turkeys and chickens were reported dead after eating newts (Pimentel, 1952).

Mammals were tested only by injection and all were similarly susceptible to *Taricha* toxin; there was no apparent resistance in potential predators. *T. granulosa* possess a potent skin toxin, yet it is unlikely that the toxic property of the skin secretion would be selected for if it killed each predator which ate a newt. The toxin is probably selected for due to its distastefulness. Predators may be able to recognize newts as distasteful by their bright ventral coloration as displayed by the unken reflex, which is easily elicited in *T. granulosa*.

Acknowledgments

This study was carried out under the direction of Dr. Robert M. Storm and was submitted in partial fulfillment of the requirements for the degree of Master of Science in the graduate school of Oregon State University, Corvallis, Oregon. I wish to thank Dr. Kenneth M. Walker for stimulating my interest in this project and Dr. John A. Wiens for reviewing the manuscript.

Literature Cited

Brown, M. S. and H. S. Mosher. 1963. Tarichatoxin: isolation and purification. Science 140:295–296.

Buchwald, H. D., L. Durham, H. G. Fischer, R. Harada, H. S. Mosher, C. Y. Kao, and F. A. Fuhrman. 1964. Identity of tarichatoxin and tetrodotoxin. Science 143:474–475.

Davenport, D. and J. W. Smith. 1942. Action of triturustoxin on the heart of the frog. Proc. Soc. Exp. Biol. Med. 51:81–82.

Fitch, H. S. 1941. Feeding habits of California garter snakes. Calif. Fish Game 27(2):2–32.

Fuhrman, F. A. 1967. Tetrodotoxin. Sci. Am. 217(2):60–71.

——— and J. Field, II. 1941. Effect of triturustoxin in respiration of rat tissues *in vitro*. Proc. Soc. Exp. Biol. Med. 48:423.

———, C. Y. Kao, H. S. Mosher, and M. S. Brown. 1963. Tarichatoxin—a potent neurotoxin from the California newt. Proc. West. Pharm. Soc. 6:31–2.

Horsburgh, D. B., E. L. Tatum, and V. E. Hall. 1940. Chemical properties and physiological actions of *Triturus* embryonic toxin. J. Pharm. Exp. Therap. 68:284–291.

Hubbard, M. E. 1903. Correlated protective devices in some California salamanders. Univ. Calif. Pub. Zool. 1(4):157–170.

Kao, C. Y. and F. A. Fuhrman. 1963. Pharmacological studies on tarichatoxin, a potent neurotoxin. J. Pharm. Exp. Therap. 104:31–40.

——— and ———. 1967. Differentiation of the actions of tetrodotoxin and saxitoxin. Toxicon 5:25–34.

Mosher, H. S., F. A. Fuhrman, H. D. Buchwald, and H. G. Fischer. 1964. Tarichatoxin-tetrodotoxin: a potent neurotoxin. Science 144:1100–1110.

Phisalix, M. 1922. Animaux venimeux et venines. Vol. 2. Masson, Paris.

Pimentel, R. A. 1952. Studies on the biology of *Triturus granulosus skilton*. Ph. D. thesis. Ore. St. Univ., Corvallis, Oregon.

Storm, R. M. 1948. The herpetology of Benton County, Oregon. Ph. D. thesis, Ore. St. Univ., Corvallis, Oregon.

Stuhr, E. T. 1936. A toxicological study of the cutaneous secretions of the salamander *Triturus torosus* (Rathke). J. Am. Pharm. Assoc. 25:117–119.

Taylor, A. 1934. The susceptibility of the newt *Triturus torosus* to its own poison. Copeia 1934(4):183.

Turner, R. S. and F. A. Fuhrman. 1947. Modification of the action potential of amphibian nerves by *Triturus* embryonic toxin. Am. J. Physiol., 150:325–328.

Twitty, V. C. 1935. Nature of paralysis produced in *Amblystoma* by *Triturus* transplants. Proc. Soc. Exp. Biol. Med. 32:1283–1284.

———. 1937. Experiments on the phenomenon of paralysis produced by a toxin occurring in *Triturus* embryos. J. Exp. Zool. 76:67–104.

———. 1966. Of scientists and salamanders. W. H. Freeman Co., San Francisco.

——— and H. H. Johnson. 1934. Motor inhibitions in *Amblystoma* produced by *Triturus* transplants. Science 80:78.

van Wagtendonk, W. J., F. A. Fuhrman, E. L. Tatum, and J. Field. 1942. Triturustoxin; chemical nature and effects on tissue respiration and glycolysis. Biol. Bull. 83:137–144.

Vincent, W. S. 1947. A checklist of amphibians and reptiles of Crater Lake National Park. Crater Lake Nat. Park Nat. Notes 13:19–22.

Wakely, J. F., G. J. Fuhrman, F. A. Fuhrman, H. G. Fischer, and H. S. Mosher. 1966. The occurrence of tetrodotoxin (tarichatoxin) in amphibia and the distribution of the toxin in the organs of newts (*Taricha*). Toxicon 3:195–203.

Department of Zoology, Oregon State University, Corvallis, Oregon 97331.