NUMBER 55 OCTOBER 15, 1979

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY

LOUISIANA STATE UNIVERSITY

BATON ROUGE, LOUISIANA

MORPHOLOGICAL EVIDENCE FOR TAXONOMIC PARTITIONING OF THE *THAMNOPHIS ELEGANS* COMPLEX (SERPENTES, COLUBRIDAE)

By DOUGLAS A. ROSSMAN

The typological approach to taxonomy predominant through much of the 19th century produced a myriad of taxa in the garter snake genus *Thamnophis*. At the turn of the century, in his posthumously published revision of North American squamates and crocodilians, Cope (1900) recognized 25 species (46 total taxa) of garter snakes and noted that "The species of the Pacific coast present the greatest difficulties to the systematist." In addition to the widespread common garter snake, *T. sirtalis*, he recognized 4 other Pacific Coast species of *Thamnophis*, one of which (*T. elegans*) was comprised of 8 subspecies.

At the onset of the 20th century, the growing awareness of geographic, sexual, and individual variation in diagnostic characters produced a reaction to what was perceived as the "splitting" taxonomy of the previous generation of herpetologists. Ruthven (1908), in his classic monograph of the genus, recognized only 12 species (19 total taxa) of *Thamnophis*, and reduced the Pacific Coast members of his Elegans group to only 2 species—*T. hammondii* and *T. ordinoides* (the latter with 2 subspecies). A decade later Van Denburgh and Slevin (1918) synonymized *T. hammondii* with *T. ordinoides*, but they did recognize 7 subspecies.

The most thorough treatment of the group to date has been Fitch's (1940) exhaustive study based on an analysis of more than 2800 specimens. Fitch concluded that the *ordinoides* artenkreis, as he called it, consisted of three groups of taxa—the Elegans group, the Hydrophila group,

and the Ordinoides group. With the exception of *hammondii* and *digueti* (from lower Baja California), which he treated as species, Fitch considered the other 9 taxa to be subspecies of *T. ordinoides*. For the most part these subspecies were perceived to be interconnected by intergrading populations, but this interpretation also produced a situation in which there were several areas where two or even three subspecies occurred in sympatry. This unusual circumstance was criticized on theoretical grounds by Mayr (1942), who suggested that each of Fitch's groups ought to be recognized as a distinct species and that the instances of interbreeding between members of different groups could be attributed to hybridization rather than intergradation. Mayr's proposal was subsequently supported by Johnson (1947), but it drew a vigorous rebuttal from Fox (1948) and from Fitch (1948). Fox (1948) demonstrated conclusively that *T. ordinoides* does not interbreed with other members of the artenkreis, which eliminated one of the areas of subspecific sympatry. Fitch (1948) reemphasized the existence of smooth intergradation between *biscutatus* (Elegans group) and *hydrophila* (Hydrophila group), and between *atratus* (Ordinoides group) and *elegans* (Elegans group), to support his original interpretation. He also cited evidence that suggested intergradation between *couchii* and *hammondii*, and he incorporated the latter in the reconstituted species *T. elegans*.

Fox (1951) demonstrated that many of the populations he and Fitch had previously referred to *atratus* were, in fact, an undescribed subpecies, *T. e. terrestris*, which intergrades freely with *T. e. elegans* and is broadly sympatric with *T. e. atratus* and, to a lesser extent, with *T. e. hammondii*. He also described as a new subspecies (*T. e. aquaticus*) the *atratus*-like populations north of San Francisco Bay. Fox arranged the 13 subspecies of *T. elegans* into two groups on the basis of their morphology and ecology—a terrestrial group and an aquatic group. The two groups were thought to be tied together in northern California by intergradation between *elegans* and *biscutatus* in southern Modoc and northern Lassen counties, and between *biscutatus* and *hydrophila* in the Klamath and Shasta river drainages in Siskiyou Co., a situation Fox verified by reexamining the preserved specimens on which Fitch had based his original conclusions.

Savage (1960), without presenting any evidence, treated the terrestrial group and aquatic group as separate species (*T. elegans* and *T. couchii*, respectively), and Mayr (1963) reiterated his earlier arguments to support such an action. In the summer of 1963 two field parties from Louisiana State University, each financed by a grant from the American Philosophical Society, collected intensively in the alleged zone of intergradation between

biscutatus and *hydrophila*,[1] as well as in adjacent areas. The party from the LSU Medical Center (Fox and Dessauer) was primarily interested in analyzing the blood proteins of the specimens we collected, whereas my primary interest was focused on the dentition and the external morphology. In my grant report to the American Philosophical Society (Rossman, 1964), I stressed that although we had collected nearly 3 dozen specimens from 12 localities in the "zone of intergradation," none of the animals appeared to be intermediate in terms of their external morphology. In their grant report, Fox and Dessauer (1965) stated that each specimen collected in the critical area possessed the plasma protein transferrin characteristic of the group to which it appeared to belong on the basis of external morphology, and that no animal possessed the transferrins of both groups. They concluded that the terrestrial and aquatic groups should be recognized as separate species, *T. elegans* and *T. couchii* (the terminal "*i*" of *couchii* was omitted, perhaps inadvertently). This arrangement was followed by Stebbins (1966) in his field guide to western amphibians and reptiles, and by all subsequent authors although no supporting evidence other than that given in the two grant reports has yet been published. The presentation of that evidence is the purpose of this paper and one by Lawson and Dessauer (1979).

Materials and Methods

I examined all of the preserved specimens of the *Thamnophis elegans* complex from Siskiyou County, California, that were available to Fitch (1940) and Fox (1951), as well as the material collected in northern California and adjacent Oregon by the two Louisiana State University field parties in 1963. Most of the latter specimens were skeletonized, but color notes in life were recorded for each snake and color transparencies made for many of them. I also examined supplementary preserved material from Jackson County, Oregon, and from the eastern slope of the Sierra Nevada and western Great Basin in California and Nevada.

I extracted and cleaned a maxilla from each of the preserved specimens as well as making notes on color pattern and recording certain meristic data (ventrals and subcaudals) and measurements. For adults (>345 mm snout-vent) the mensural data were used to generate a series of proportional characters (tail/total length, head/body, eye/head, muzzle/head, frontal/head, parietal/head, internasorostral contact/head, nasorostral con-

[1] The correct spelling of the subspecific epithet of the Oregon Garter Snake is actually *hydrophilus* (Collins *et al.*, 1978), which will be used hereinafter.

tact/head, anterior genial/posterior genial, antepenultimate supralabial height/length) that have proved to be useful in thamnophiine systematics. Tooth counts for each of the dentigerous bones included empty sockets.

Results and Conclusions

Color pattern.—As characterized by Fitch (1940), *T. e. elegans* typically has a velvety black dorsum with a bright yellow vertebral stripe and distinct lateral stripes (Fig. 1, Upper), *T. e. biscutatus* a dark to very dark brown dorsum with a duller yellow vertebral stripe and less distinct lateral stripes (Fig. 1, Lower), and *T. e. hydrophilus* a gray or gray-brown, checkerboard-spotted dorsum with a dull yellow vertebral stripe (sometimes absent) and

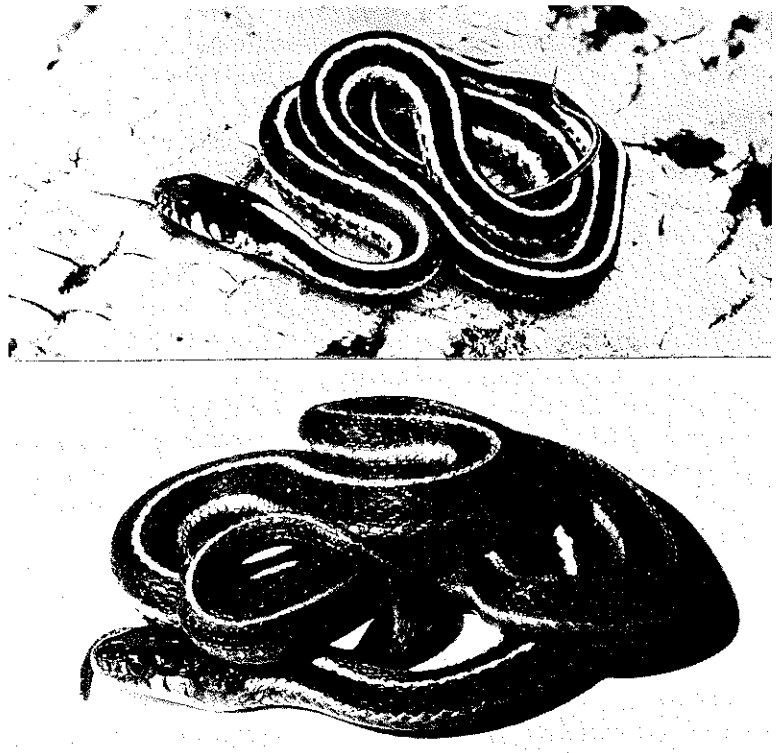

Figure 1. *Upper*: Dorsal color pattern of *Thamnophis e. elegans* (OREGON: Lane Co., NE Alma). *Lower*: Dorsal color pattern of *T. e. biscutatus* (OREGON: Klamath Co., 4 mi. S Keno).

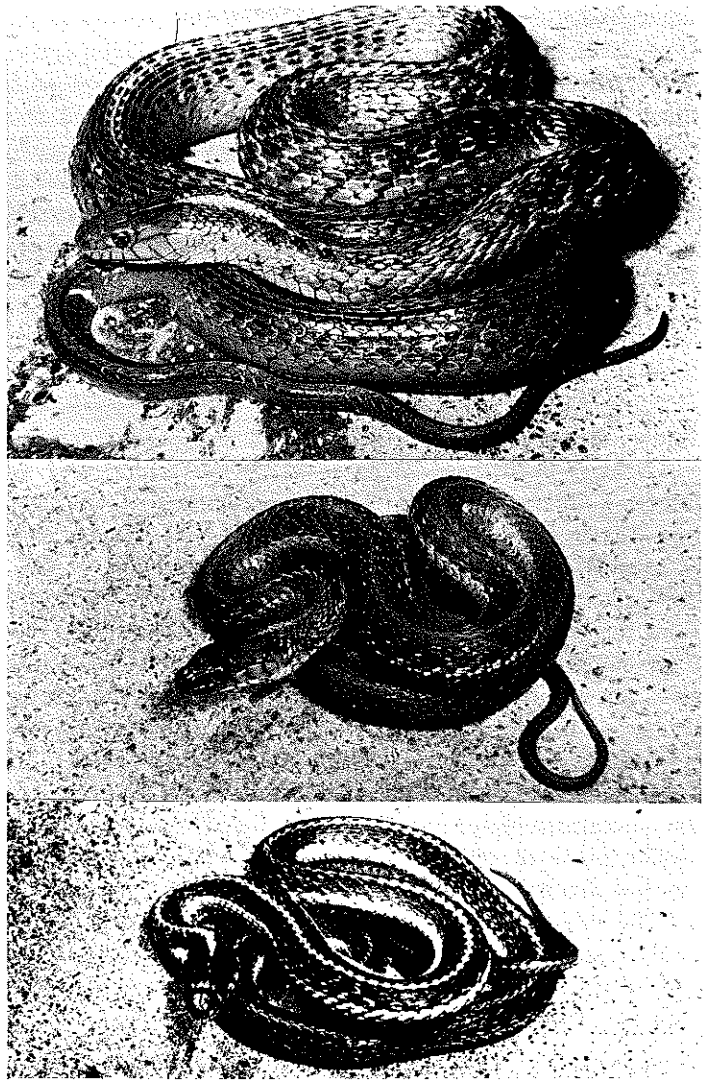

Figure 2. Variation in dorsal color pattern of *Thamnophis couchii hydrophilus* in Siskiyou Co., California. *Upper*: "Typical" pattern characterized by prominent spotting and suppression of the lateral stripes (Klamath River, 4 mi. S Hornbrook). *Middle*: Pattern in which the spotting and the vertebral stripe are less distinct, but the lateral stripes more distinct (Beaver Creek, 1 mi. N Beaver Creek Campground). *Lower*: Pattern in which the dorsum is very dark and both sets of stripes are bright (junction of the Shasta and Klamath rivers). Specimens such as the latter bear a strong superficial resemblance to *T. elegans biscutatus*.

indistinct or absent lateral stripes (Fig. 2, Upper). A number of specimens (Fig. 2, Middle and Lower) from the Klamath River drainage between Horse Creek and Hornbrook in Siskiyou County do appear to be intermediate in appearance between the color patterns described above for *biscutatus* and *hydrophilus*, so it is not surprising that both Fitch (1940) and Fox (1951) concluded that intergradation was taking place between those two taxa (Fig. 3, Upper). Both of these workers were aware, however, of a dark, brightly striped color phase of *hydrophilus* that occurs in eastern Humboldt, eastern Mendocino, and Trinity counties (and, I can add, in much of Shasta County, as well). Nevertheless, they attributed the occurrence of a similar color pattern in the middle Klamath and Shasta River basin to intergradation with *biscutatus* rather than relating it to the southern populations of *hydrophilus*. I would have to disagree with their interpretation for the following reasons: 1) all of the preserved specimens they considered to be *hydrophilus* X *biscutatus* intergrades are identifiable as *hydrophilus* on the basis of the other morphological characters considered in this study, and 2) the Louisiana State University field teams collected animals having an *elegans*, not a *biscutatus*, color pattern along the Klamath River upstream (at Copco and 5 miles N California-Oregon line) from the easternmost locality at which *hydrophilus* was taken (2.7 miles S Hornbrook). Thus the taxa *hydrophilus* and *biscutatus* cannot possibly intergrade because their ranges do not meet or even closely approach each other (Fig. 3, Lower), *biscutatus* being replaced by *elegans* with which it merges both in color pattern and dentitional characteristics (see Table 3) along the Klamath River west of Keno, Oregon. The alleged *hydrophilus* X *biscutatus* intergrades represent examples of the widespread dark, brightly striped color phase of the polymorphic *hydrophilus*, a phase that even occurs in low frequency at the type-locality near Trail, Jackson County, Oregon. The evidence that *hydrophilus* and *biscutatus* do not intergrade removes the last impediment to considering Fox's aquatic and terrestrial groups to be separate species, *Thamnophis couchii* and *T. elegans*, respectively, and they will be so treated hereinafter.

The color pattern of *Thamnophis e. biscutatus* grades from that of *T. e. elegans* into that of *T. e. vagrans* along a west-to-east cline, and it resembles that of *elegans* X *vagrans* intergrades from the Sierra Nevada-Great Basin interface in eastern California and western Nevada. In addition to its intermediate coloration, *T. e. biscutatus* was characterized by Fitch (1940) as having a high incidence of divided preoculars (hence the subspecific epithet) and frequent possession of a maximum of 23 dorsal scale

rows, but both features occur in fewer than half of the specimens he examined and two other populations have a higher incidence of divided preoculars. Fitch also considered *biscutatus* to be a larger snake than either *elegans* or *vagrans*, but size in garter snakes apparently reflects to some degree the local environmental conditions and I have seen an *elegans* from the Central Valley (where *T. couchii gigas* occurs and *T. sirtalis fitchi* reaches it maximum size) that would rival any *biscutatus* I have examined. Accordingly, I can see no justification for considering *biscutatus* to be anything more than a population of *T. e. elegans* X *vagrans* intergrades and I recommend that it no longer be given taxonomic recognition.

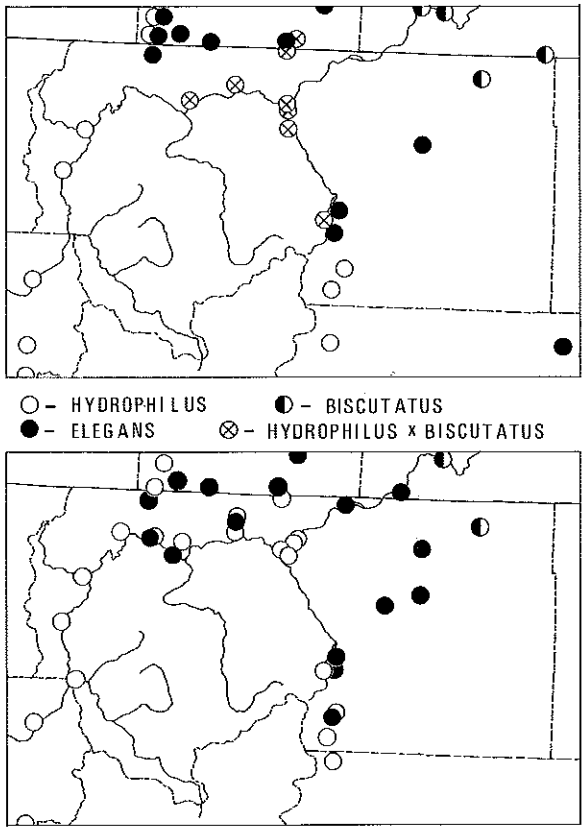

FIGURE 3. Distribution of the *Thamnophis elegans* complex in Siskiyou Co., California, and adjacent Oregon. *Upper*: Previous interpretation (adapted from Fox, 1951, Fig. 13). *Lower*: Present interpretation.

Scutellation and Proportions.—A morphological comparison of adult *Thamnophis e. elegans* with adult *T. couchii hydrophilus* from Siskiyou County, California, was hampered by the extremely small sample size of the former, so to them I added another small sample from adjacent Jackson County, Oregon (the number of males remains inadequate). The data are summarized in Table 1. In the area under discussion, *T. e. elegans* appears to have greater numbers of ventrals and subcaudals than does *T. c. hydrophilus*, although there is overlap in the ranges of both characters. There appear to be no significant differences between the two species in relative tail length, head length, parietal length, nasorostral contact, and height of the antepenultimate supralabial. *T. e. elegans* has a slightly larger eye, shorter muzzle, and ~~shorter~~ longer frontal than *T. c. hydrophilus*. The biggest differences in mensural characters (and those that are most useful in field identification) are in relative length of the genials and relative breadth of the internasorostral contact. In *T. c. hydrophilus* the posterior genials are considerably longer than the anterior genials; in *T. e. elegans* the two sets of genials are of almost equal length. In the broad-muzzled *T. e. elegans* the internasorostral contact exceeds the nasorostral contact; in the narrow-muzzled *T. c. hydrophilus* the reverse is true.

Table 1. Sexual dimorphism and interspecific variation of selected characters in sympatric populations of **Thamnophis couchii hydrophilus** and **T. e. elegans** from Siskoyou County, California[1]

Character		Thamnophis couchii hydrophilus	Thamnophis elegans elegans
Ventrals	♂♂	161.5(151-167)23[2]	170.0(167-172)4
	♀♀	158.5(148-167)22	163.4(160-170)10
Subcaudals	♂♂	85.3(77-95)18	87.0(86-88)2
	♀♀	76.5(71-79)16	81.1(77-85)9
Tail as % of Total length	♂♂	26.7(24.7-28.4)18	27.0(26.5-27.4)2
	♀♀	25.2(24.3-27.0)16	24.5(23.7-25.6)5
Head as % of Body length[3]	♂♂	4.9(4.6-5.2)10	4.9(4.8-5.0)3
	♀♀	5.2(4.9-5.6)10	4.9(4.6-5.1)7
Eye as % of Head length[3]	♂♂	15.4(14.3-16.4)10	16.6(15.9-17.5)3
	♀♀	13.7(12.7-15.0)10	15.9(14.5-16.8)7
Muzzle as % of Head length[3]	♂♂	19.8(18.3-20.9)10	18.5(18.3-18.9)3
	♀♀	19.6(18.3-21.3)10	18.5(17.8-19.6)7
Frontal as % of Head length[3]	♂♂	22.9(21.1-25.6)10	23.7(22.1-25.5)3
	♀♀	21.2(19.4-24.9)9	23.9(22.9-25.4)7
Parietal as % of Head length[3]	♂♂	31.9(30.0-34.7)10	31.7(31.0-32.5)3
	♀♀	29.7(26.8-31.9)10	30.8(28.9-32.7)7
Internasorostral contact as % of Head length[3]	♂♂	6.9(4.9-7.8)10	10.3(10.1-10.6)3
	♀♀	5.7(4.0-7.3)9	8.6(6.3-9.6)7
Nasorostral contact as % of Head length[3]	♂♂	8.1(7.4-8.8)10	7.9(7.1-8.3)3
	♀♀	8.1(6.9-8.9)9	7.7(7.2-8.4)7
Antepenultimate supralabial Height as % of length[3]	♂♂	97.7(90.3-105.3)3	103.2(95.8-111.3)3
	♀♀	95.6(87.0-104.2)6	96.6(85.1-110.5)7
Anterior genial as % of Posterior genial	♂♂	80.3(67.1-103.7)10	97.9(84.2-115.5)4
	♀♀	81.1(72.3-88.5)11	95.5(87.8-106.3)7

[1]The very small Siskiyou Co. **T. e. elegans** sample has been supplemented by a series from adjacent Jackson Co., Oregon.
[2]Mean (range of variation) number of specimens.
[3]Because of marked ontogenetic changes in cephalic proportions, no data from specimens less than 345 mm in snout-vent length are included.

Dentition.—As can be observed in Table 2, the number of teeth on each of the dentigerous bones provides the most reliable means of distinguishing *Thamnophis e. elegans* from *T. c. hydrophilus* where they occur sympatrically. There is total nonoverlap in the ranges of variation for each of the bones, with *T. c. hydrophilus* averaging about 7 more teeth on each maxilla, 4 or 5 more on each palatine, 7 more on each pterygoid, and 10 more on each dentary. The differences in tooth number probably reflect the dietary differences between the two taxa, *T. c. hydrophilus* feeding primarily on fish and *T. e. elegans* almost entirely on terrestrial prey (Fitch, 1940). *Thamnophis e. vagrans*, a feeding generalist, exhibits marked geographic variation in tooth number. Scattered samples from the southern part of its range (Arizona, New Mexico, Colorado, Utah, southern Nevada, east-central California) have tooth counts similar to, or only slightly higher than, those of *T. e. elegans*—the modal number of maxillary teeth ranges from 17 to 19 (the Mexican *T. e. errans* agrees in this respect). In the northern part of its range (northern Nevada, eastern Oregon, Idaho, Washington), *T. e. vagrans* has a substantially greater number of teeth—the maxillary tooth mode is 21 or 22.

The intergrade populations of *T. e. elegans* X *vagrans* exhibit the same pattern of geographic variation described for *T. e. vagrans*. Scattered samples from Mono and Tulare counties, California, and southern Washoe Co., Nevada, have the low counts typical of *T. e. elegans* and southern *T. e.*

Table 2. Sexual dimorphism and interspecific variation in tooth counts of sympatric populations of **Thamnophis couchii hydrophilus** and **T. e. elegans** from Siskiyou Co., California[1]

Dentigerous Bone		Thamnophis couchii hydrophilus	Thamnophis elegans elegans
Maxilla	♂♂	24.1(22-27)45[2]	16.8(16-17)4
	♀♀	23.2(21-25)77	16.0(14-17)17
Palatine	♂♂	14.5(13-16)23	9.8(9-10)4
	♀♀	13.3(12-15)54	9.5(9-11)8
Pterygoid	♂♂	26.1(23-29)22	18.7(17-21)3
	♀♀	24.6(21-30)54	17.6(17-19)8
Dentary	♂♂	27.9(26-30)23	17.3(16-18)4
	♀♀	27.1(24-29)56	17.3(16-18)7

[1]The very small Siskiyou Co. **T. e. elegans** sample has been supplemented by a series from adjacent Jackson Co., Oregon.
[2]Mean (range of variation) number of counts.

Table 3. Tooth-count variation in populations of **Thamnophis elegans** from Northeastern California and adjacent areas

Population	Sex	Maxilla	Palatine	Pterygoid	Dentary
T. e. elegans					
CALIF.: western Siskiyou Co.; ORE.: Jackson Co.	♂♂	16.8(16-17)4	9.8(9-10)4	18.7(17-21)3	17.3(16-18)7
	♀♀	16.0(14-17)17	9.5(9-11)8	17.6(17-19)8	17.3(16-18)7
CALIF.: Siskiyou Co., Copco, Klamath R.	♂♂	17.2(17-18)5	10.8(10-11)5	20.8(19-22)6	22.0(21-23)5
	♀♀				
ORE.: Klamath Co., 7 mi. ENE Beswick, Klamath R.	♂♂	19.0(19)2	11.0(11)2	25.5(25-26)2	24.0(24)2
	♀♀	17.8(17-18)12	11.2(10-12)12	20.5(19-23)12	22.1(20-24)12
T. e. elegans X vagrans					
ORE.: Klamath Co., NW Keno, Klamath R.	♂♂	20.8(19-23)16	13.0(12-15)16	24.2(18-28)15	25.3(22-28)16
	♀♀	20.6(18-22)20	12.3(11-13)20	22.7(21-26)19	24.3(23-27)19
ORE.: Klamath Co., vicin. Upper Klamath Lake	♂♂	21.1(20-23)17	12.9(12-15)18	25.4(22-28)18	25.5(23-28)16
	♀♀	20.7(19-23)23	12.1(11-14)24	24.2(21-27)23	24.9(22-27)22
ORE.: Lake Co., W Warner Mts.	♂♂	21.5(20-22)8	14.0(12-15)8	25.3(22-28)8	24.9(24-26)8
	♀♀	21.1(20-23)10	12.1(11-14)9	23.6(20-26)10	24.6(24-27)9
ORE.: Lake Co., E Warner Mts.	♂♂	22.1(20-24)20	14.8(13-17)16	25.6(22-28)20	25.6(24-27)20
	♀♀	21.5(20-24)20	13.1(12-14)19	25.0(22-27)21	25.2(23-27)20
NEV.: northwestern Washoe Co.	♂♂	22.3(21-23)8	————	————	————
	♀♀	22.2(21-23)6	————	————	————
CALIF.: Modoc Co., W Warner Mts.	♂♂	20.8(19-22)16	12.9(11-15)12	24.6(22-30)16	25.5(24-27)15
	♀♀	20.2(18-22)12	11.8(9-14)12	22.7(18-25)12	24.1(23-25)12
CALIF.: Lassen Co., E Cascade Range	♂♂	20.4(20-21)7	13.5(12-14)4	24.5(23-27)4	23.3(21-25)4
	♀♀	19.7(17-23)6	11.5(11-13)6	22.3(19-26)6	21.7(17-26)6
T. e. elegans					
CALIF.: Lassen Co., vicin. Westwood	♂♂	17.8(17-19)6	11.3(11-13)6	19.8(19-21)6	18.3(18-19)6
	♀♀	17.2(16-19)10	10.7(9-13)10	19.2(17-22)10	19.2(17-23)10

vagrans. Extensive samples from the intergrade population formerly known as *T. e. biscutatus* in south-central Oregon, northeastern California, and adjacent Nevada have higher counts comparable to those found in northern *T. e. vagrans*. As can readily be seen from Table 3, the transition from the high tooth counts of the intergrades to the low tooth counts of *T. e. elegans* takes place over a relatively short distance at the eastern front of the Cascade Range. Fitch (1940) has reported that "*biscutatus*" and the northwestern Washoe Co., Nevada, intergrades are more aquatic and feed on fish to a greater extent than any other populations of *T. elegans*; that observation may be correlated with the presence of greater numbers of teeth in this population, but whether or not it is applicable to the northern populations of *T. e. vagrans* remains to be determined.

The ecological position of the *elegans* X *vagrans* intergrades that have high tooth counts leads me to believe that competition with this population of *T. elegans* may be the principal factor preventing *T. couchii hydrophilus* and *T. c. couchii* from extending their ranges east of the Cascade Range to any significant extent. Farther south, in west-central Nevada and adjacent California, *T. c. couchii* is sympatric with those populations of *elegans* X *vagrans* (and to some extent *T. e. vagrans*) that have fewer teeth and presumably would be more divergent from *T. couchii* ecologically. Interspecific competition has undoubtedly promoted a narrowing of the ecological niches of sympatric *T. elegans* and *T. couchii*, a phenomenon to which the presence of a third species of garter snake, the habitat-and-feeding generalist *T. sirtalis*, undoubtedly contributes.

Acknowledgments

I am grateful to Robert C. Stebbins, David B. Wake, and Harry W. Greene (Museum of Vertebrate Zoology, Berkeley) for the loan of material in their care; to the late Wade Fox, Herbert C. Dessauer, and Nita J. Rossman for assistance and companionship in the field; to Larry D. Wilson for assistance in the laboratory; to Ted L. Brown and Robin Lawson for providing color transparencies of *Thamnophis e. elegans* and *T. e. "biscutatus,"* respectively; and to Herbert C. Dessauer, Henry S. Fitch, Robin Lawson, Glenn R. Stewart, and Randy H. Vaeth for critical reading of the manuscript. My fieldwork was made possible by grant 3220 (Penrose Fund) from the American Philosophical Society, and the laboratory phase of this study was supported by National Science Foundation grant GE-3111.

Literature Cited

Collins, J. T., J. E. Huheey, J. L. Knight, and H. M. Smith
1978. Standard common and current scientific names for North American amphibians and reptiles. Herpetological Circulars (7):1-36.

Cope, E. D.
1900. The crocodilians, lizards, and snakes of North America. Rept. U.S. Natl. Mus. for 1898:153-1270.

Fitch, H. S.
1940. A biogeographical study of the *ordinoides* artenkreis of garter snakes (genus *Thamnophis*). Univ. California Publ. Zool. 44:1-150.
1948. Further remarks concerning *Thamnophis ordinoides* and its relatives. Copeia 1948:121-126.

Fox, W.
1948. The relationships of the garter snake *Thamnophis ordinoides*. Copeia 1948: 113-120.
1951. Relationships among the garter snakes of the *Thamnophis elegans* rassenkreis. Univ. California Publ. Zool. 50:485-530.

Fox, W., and H. C. Dessauer
1965. Collection of garter snakes for blood studies. Yr. Bk. Amer. Philos. Soc. for 1964:263-266.

Johnson, L.
1947. The status of the *elegans* subspecies of *Thamnophis*, with description of a new subspecies from Washington state. Herpetologica 3:159-165.

Lawson, R., and H. C. Dessauer
1979. Biochemical genetics and systematics of garter snakes of the *Thamnophis-elegans-couchii-ordinoides* complex. Occas. Papers Mus. Zool. Louisiana State Univ. (56):1-24.

Mayr, E.
1942. *Systematics and the Origin of Species*. Columbia Univ. Press, New York. xiv + 334 pp.
1963. *Animal Species and Evolution*. Harvard Univ. Press, Cambridge. xvi + 797 pp.

Rossman, D. A.
1964. Relationships of the *elegans* complex of the garter snakes, genus *Thamnophis*. Yr. Bk. Amer. Philos. Soc. for 1963:347-348.

Ruthven, A. G.
1908. Variations and genetic relationships of the garter-snakes. Bull. U.S. Natl. Mus. (61):1-201.

Savage, J. M.
1960. Evolution of a peninsular herpetofauna. Systematic Zoology 9:184-212.

Stebbins, R. C.
1966. *A Field Guide to Western Reptiles and Amphibians*. Houghton Mifflin Co., Boston. xvi + 279 pp.

Van Denburgh, J., and R. Slevin
1918. The garter-snakes of western North America. Proc. California Acad. Sci. (4th Ser.) 8:181-270.