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TAXONOMIC REEVALUATION OF *THAMNOPHIS COUCHII*
(SERPENTES: COLUBRIDAE)By DOUGLAS A. ROSSMAN AND GLENN R. STEWART¹

The most recent morphological and biochemical studies of the Pacific Coast garter snakes of the *Thamnophis elegans* complex demonstrated that *T. couchii* is a species distinct from *T. elegans* (Rossman, 1979; Lawson and Dessauer, 1979). The latter paper also revealed that *T. couchii* consists of two distinct subgroups (*couchii* subgroup--*T. c. couchii*, *T. c. hammondi*; *atratus* subgroup--*T. c. aquaticus*, *T. c. atratus*, *T. c. gigas*, *T. c. hydrophilus*) whose taxonomic status is in doubt.

We examined the relationship between the two subgroups and between taxa within each subgroup. We investigated the zones of contact between *T. c. couchii* and the two members of the *atratus* subgroup with which it has been alleged to intergrade (Fitch, 1940), *T. c. hydrophilus* and *T. c. gigas*. The other member of the *couchii* subgroup, *T. c. hammondi*, was reported by Fox (1951) to be broadly sympatric with *T. c. atratus* in coastal Monterey and San Luis Obispo counties; he found no evidence of intergradation. Because of Fox's findings, the *hammondi*-*atratus* relationship was not an important focus of our study; nevertheless, some pertinent information about it was obtained.

In addition to examining the status of the two subgroups, we also investigated the zones of contact or nearest proximity between the following taxon-pairs: *couchii*-*hammondi* and *gigas*-*hydrophilus* (including *aquaticus*). The ranges of *gigas* and *atratus* appear to be allopatric (Fitch, 1940). The race *aquaticus* is weakly differentiated and appears to represent a broad zone of intergradation between *atratus* and *hydrophilus*.

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MATERIALS AND METHODS

We examined all of the available preserved specimens of the *Thamnophis couchii* complex from the areas of parapatry or geographic proximity mentioned above, including all of those cited by Fitch (1940) or Fox (1951) as being intergrades. We also obtained fresh material from each of those areas.

In addition to making notes on color pattern, the following meristic and mensural characters were recorded: numbers of ventrals, subcaudals, supralabials, infralabials, preoculars, and dorsal scale rows (at the level of V 10, at midbody, and at the level of the penultimate V); tail length/total length (T/TL); anterior genial length/posterior genial length (AG/PG); loreal dorsal margin length (to prefrontal-preocular junction)/loreal ventral margin length (LD/LV); supralabial 6 length at mid-height/supralabial 7 length (SL 6/7); muzzle length (combined length of internasal and prefrontal medial sutures)/frontal length (ML/FL); muzzle width (combined width of internasals at posterolateral corners)/muzzle length (MW/ML); prefrontal medial suture length/internasal medial suture length (Prf/In); eye diameter/frontal length (E/FL); posterior frontal width (where parietals meet supraoculars and frontal)/maximum anterior frontal width (FWP/A); frontal length/parietal length (FL/PL). Some of the mensural characters were not recorded for juveniles. All variable characters except the numbers of preoculars, infralabials, and dorsal scale rows were tested for statistical significance by means of the Student's t-test. For those characters that are sexually dimorphic, data for each sex were treated separately. Each table compares dorsal scale row numbers only for that body region (anterior or midbody) exhibiting the greatest inter-taxon differences.

The meristic features examined in this study are the ones traditionally used by herpetologists; most of the mensural characters are not. We are convinced that such measurements and the proportional data generated from them are an effective way to describe the many subtle, but often highly important, differences in head shape that can permit discrimination among groups of closely related species. The data sets produced by this method are time consuming to acquire, but we believe them to be well worth the effort.

RESULTS

Taxon-Pair Relationships

For convenience we discuss the relationship between each taxon-pair in turn, deferring our taxonomic conclusions to a later section. Also, for brevity, we will refer to each taxon by its subspecific epithet alone unless otherwise noted.

I. The *couchii-hydrophilus* Relationship

Fitch (1940) presented the only evidence to date for intergradation between *couchii* and *hydrophilus*, namely that specimens of *hydrophilus* from the northern and western sides of the Sacramento River Valley in Siskiyou (1 locality), Shasta (2 localities), Tehama (1 locality), Glenn (1 locality), Colusa (1

locality), Lake (1 locality), and Yolo (1 locality) counties resemble *couchii* in having 21 dorsal scale rows on the anterior part of the body and in having more ventrals and subcaudals. These animals were said to have a pale ground color, unlike that of *couchii*. Fox (1951) stated without documentation that snakes from the Sacramento Valley appear to be *couchii-hydrophilus* intergrades. Neither Fitch nor Fox examined any specimens of *hydrophilus* from east of the Sacramento River where *couchii* occurs.

Subsequent collecting has yielded a relatively large number of *hydrophilus* from 17 localities in the McCloud River and Pit River drainages, all of which are east of the Sacramento River in Shasta County. Although *hydrophilus* and *couchii* usually occur on either side of the Pit River, they are sympatric where Deep Creek enters the Pit River and in Rock Creek from 1.6-8 km north of the Pit River (Fig. 1). Additionally, a single *hydrophilus* (LSUMZ 39088) has been found in Roaring Creek approximately 6.4 km east of the Pit River.

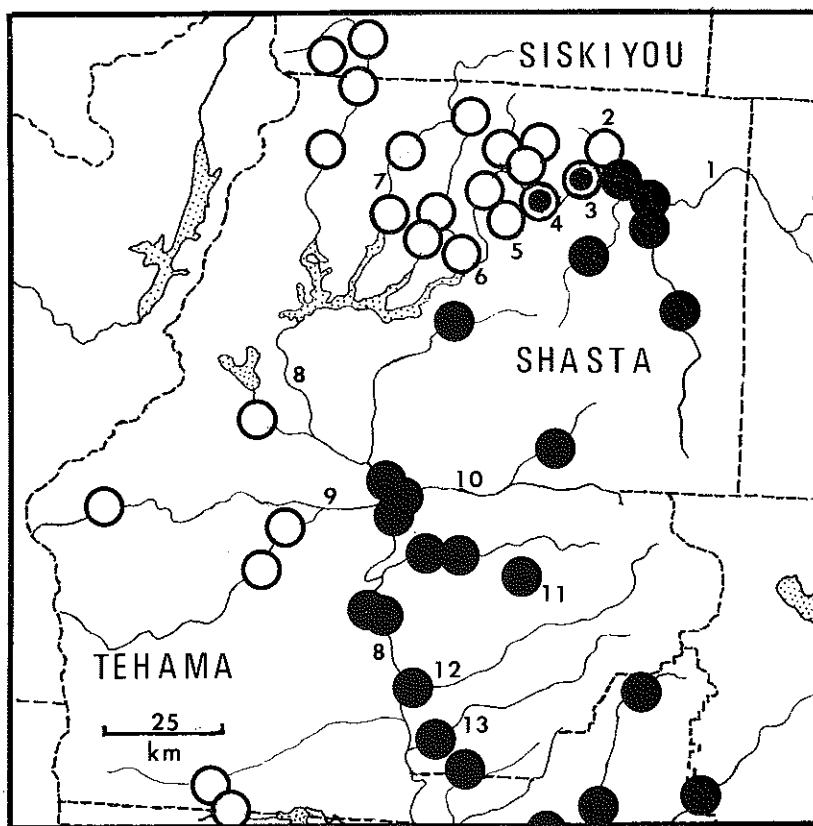


FIGURE 1. Distribution of the *Thamnophis couchii* complex in the Pit River and Sacramento River drainages in north-central California. Solid circles represent *couchii*, hollow circles represent *hydrophilus*, and dotted circles represent localities where both taxa occur. Symbols on this and all succeeding maps represent localities from which specimens were examined in this study. The numbers refer to the following sites mentioned in the text: 1. Pit River; 2. Clark Creek; 3. Rock Creek; 4. Deep Creek; 5. Roaring Creek; 6. Potem Creek; 7. McCloud River; 8. Sacramento River; 9. Cottonwood Creek; 10. Battle Creek; 11. Plum Creek; 12. Mill Creek; 13. Deer Creek.

The parapatric samples of *couchii* and *hydrophilus* differ in 12 meristic and mensural characters (Table 1) and 4 aspects of color pattern (Figs. 2-3). With regard to the latter, *couchii* can be distinguished from *hydrophilus* in usually possessing a less distinct vertebral stripe, light streaks on the anterior margin of the parietal and often extending onto the adjacent frontal (no such light streaks in *hydrophilus*), broad dark markings on the posterior supralabial sutures (narrow markings in *hydrophilus*), and the venter heavily blotched or marbled with black pigment (*hydrophilus* never having anything more than some small black flecking medially, and that rarely).

Table 1 reveals that *couchii* differs from *hydrophilus* in having more ventrals, a proportionately shorter tail, the loreal with a shorter dorsal margin (*couchii* exhibits significant sexual dimorphism in this character, *hydrophilus* does not), a narrower frontal posteriorly, the sixth supralabial longer than the seventh, the anterior genials usually slightly longer than the posterior pair, a shorter and narrower muzzle, the internasals substantially longer than the prefrontals (most of the shortening of the muzzle taking place in its posterior portion), shorter parietals, 21 dorsal scale rows at midbody (a not uncommon variant in female *hydrophilus*, though rare in males), and 11 infralabials on at least one side of the head. The difference in infralabial number is even greater than it appears, inasmuch as 3 of the 6 *hydrophilus* having more than 10 on at least one side do so because of the presence of an anomalous scale in the anterior part of the series, whereas the additional scale in *couchii* lies in the posterior part.

Five male specimens from the Pit River drainage are of particular interest. These individuals (3 from Rock Creek and one each from Clark Creek and the mouth of Deep Creek) possess apparently hybrid genotypes at one or more of the loci shown by Lawson and Dessauer (1979) to have fixed, or nearly fixed, differences between the *atratus* and *couchii* subgroups (R. Lawson, personal communication). No morphological data from these animals were included in Table 1.

The specimen from Clark Creek (LSUMZ 39099) has the *atratus* subgroup genotype at the superoxide dismutase locus but is heterozygous at the transferrin locus (aconitase-2, the other diagnostic locus, was not assayed). Morphologically this animal resembles the *hydrophilus* sample in all respects. The *couchii* subgroup genotype at the transferrin locus has been reported previously to occur at low frequency in the *atratus* subgroup (Lawson and Dessauer, 1979), so its presence in LSUMZ 39099 does not necessarily indicate that this animal is a hybrid.

The specimen from the mouth of Deep Creek (LSUMZ 40023) has the *couchii* subgroup genotype at the transferrin locus but is heterozygous at the superoxide dismutase locus (aconitase-2 was not assayed). Morphologically this animal resembles a typical *couchii* in the four characters that can be determined from the preserved skin (dorsal and ventral colors, numbers of ventrals and dorsal scale rows) as well as in having the tail only 22.7% of the total length (recorded on the tag). If this animal is a hybrid, its morphology exhibits no apparent influence from *hydrophilus*.

The three Rock Creek specimens (LSUMZ 40015, 40016, 40019) appear to be unequivocal hybrids. All three snakes are heterozygous at both superoxide dismutase and aconitase-2 loci, but LSUMZ 40015 has the *atratus* subgroup genotype at the transferrin locus (not assayed in 40016 or 40019). Morphologically all three animals have more features in common with *couchii*, but 40016 and 40019 have relatively little black pigment on the venter and a more distinct vertebral stripe than is characteristic of *couchii*, 40015 has only

Table 1. Comparison of meristic and mensural characters in population samples of *couchii* and *hydrophilus* in the Pit River drainage. Character abbreviations on this and subsequent tables are explained in the text (p. 2). For characters with two values, the upper refers to males, the lower to females.

Character	<i>couchii</i>				<i>hydrophilus</i>				Significance <i>p</i>
	\bar{x}	SD	Range	<i>n</i>	\bar{x}	SD	Range	<i>n</i>	
Ventrals	178.3±2.94	(173-187)	24		164.2±2.90	(158-168)	30		<0.001
	172.5±2.63	(169-178)	22		160.4±3.01	(156-166)	20		<0.001
Subcaudals	89.8±3.05	(84-95)	22		86.6±3.39	(79-93)	25		<0.01
	76.2±2.90	(72-80)	19		76.2±3.67	(69-81)	15		N.S.
T/TL (%)	24.0±0.93	(22.1-25.7)	18		25.6±0.89	(24.1-27.5)	25		<0.001
	22.0±0.89	(20.6-23.7)	17		24.2±0.88	(22.6-25.6)	14		<0.001
LD/LV (%)	57.1±4.92	(50.0-66.7)	15		70.6±4.86	(63.5-79.9)	22		<0.001
	48.1±5.39	(34.4-58.4)	16		68.4±4.35	(60.8-77.6)	17		<0.001
FWP/A (%)	73.4±4.79	(61.2-81.5)	29		83.4±4.40	(75.0-92.2)	37		<0.001
SL 6/7 (%)	123.8±12.58	(104.0-150.0)	23		84.9±6.30	(72.4-97.5)	41		<0.001
AG/PG (%)	104.9±8.69	(88.4-128.0)	29		83.2±8.06	(71.6-114.4)	41		<0.001
ML/FL (%)	77.7±6.22	(67.2-88.6)	22		85.1±7.29	(75.8-101.5)	30		<0.001
MW/ML (%)	88.2±5.19	(78.5-101.4)	27		98.4±7.04	(85.9-115.6)	39		<0.001
Prf/ln (%)	67.7±11.77	(40.6-83.9)	19		94.3±15.92	(60.5-125.2)	24		<0.001
E/FL (%)	65.1±3.00	(58.1-69.2)	23		63.8±3.65	(57.1-71.4)	31		N.S.
FL/PL (%)	79.7±4.15	(72.0-88.5)	23		71.2±4.70	(59.7-79.4)	30		<0.001
				<i>n</i> %					<i>n</i> %
Total Pro									
2				23(51.1)					42(84.0)
3				8(17.8)					4(8.0)
4				13(28.9)					4(8.0)
5				1(2.2)					
Total IL									
18									2(4.1)
19									5(10.2)
20				2(4.4)					36(73.5)
21				5(11.1)					5(10.2)
22				31(68.9)					1(2.0)
23				7(15.6)					
Midbody DSR									
19				1(4.2)					27(90.0)
20				1(4.2)					1(3.3)
21				22(91.7)					2(6.7)
19									12(60.0)
20									2(10.0)
21				21(100.0)					6(30.0)

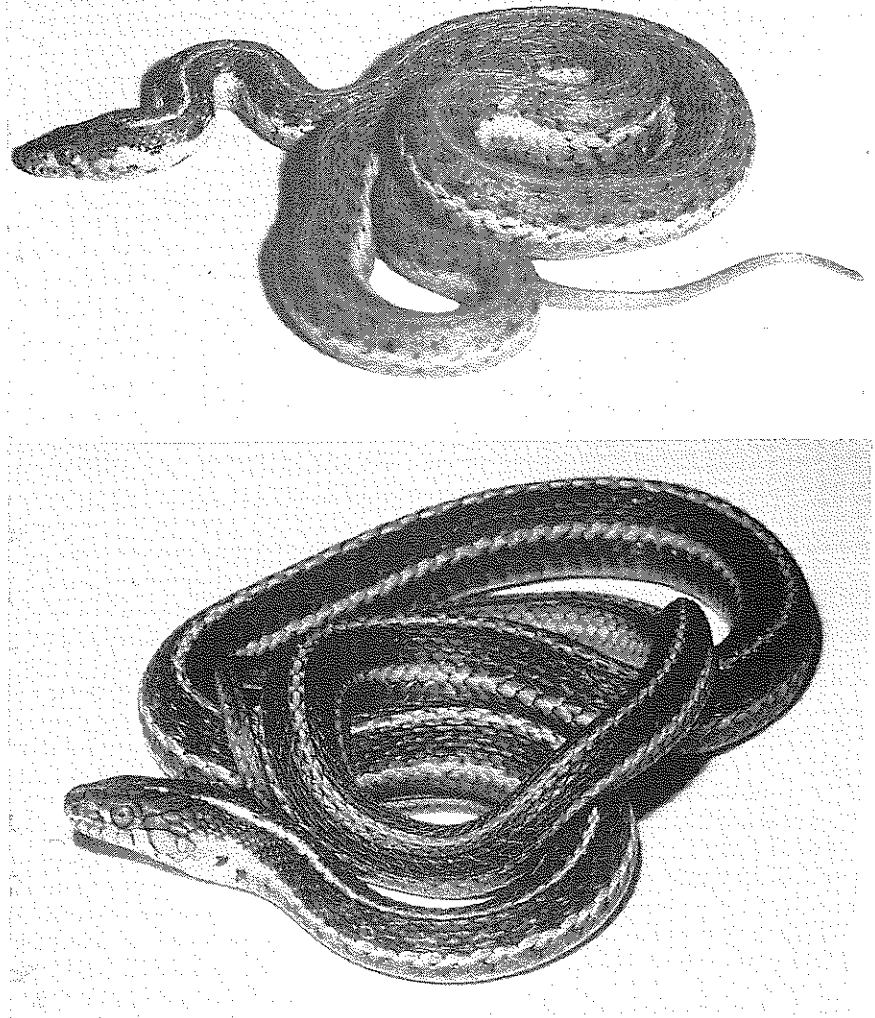


FIGURE 2. Dorsal color patterns of members of the *Thamnophis couchii* complex from the Pit River drainage, Shasta Co., California. Upper: *couchii* from the mouth of Deep Creek. Lower: *hydrophilus* from Potem Creek.

168 ventrals and the seventh supralabial longer than the sixth, 40015 and 40016 have a *hydrophilus*-shaped loreal, and 40016 has a Prf/In value of 93.5% (near the mean for *hydrophilus*). It is worth noting that four other specimens from Rock Creek (3 *hydrophilus* and a *couchii*) show no signs of intermediacy either biochemically or morphologically.

In extreme southern Shasta Co. and in Tehama Co., *couchii* and *hydrophilus* are separated by the Sacramento River (Fig. 1). The former taxon is locally abundant on the valley floor within sight of the river, but *hydrophilus* appears to be sparsely distributed in the Cottonwood Creek drainage, and the

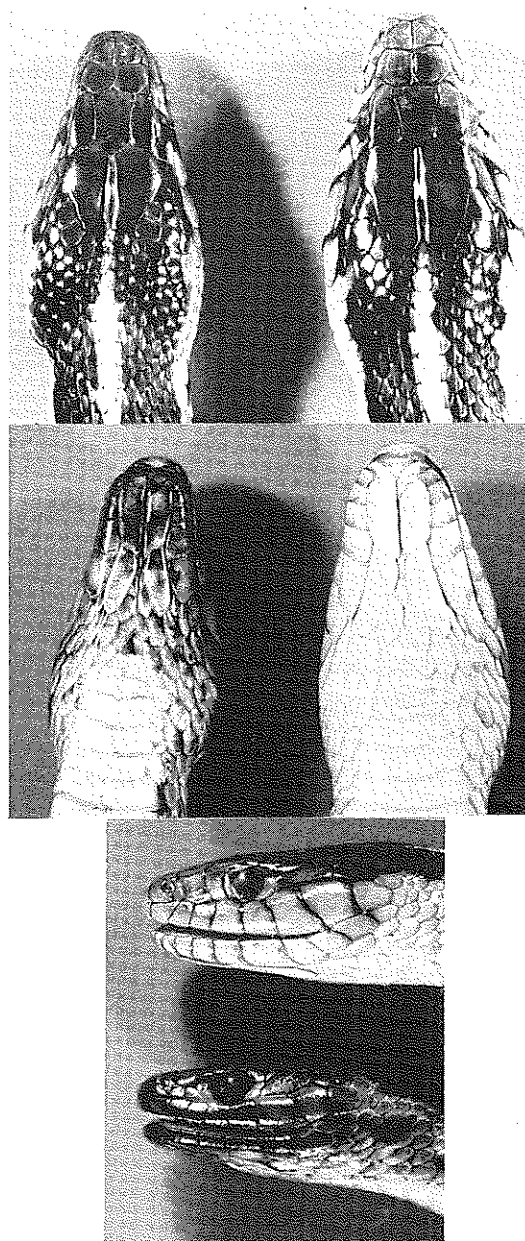


FIGURE 3. Comparisons of the heads of *couchii* (on left and below) and *hydrophilus* (on right and above) from the Pit River drainage, Shasta Co., California. The *couchii* is from the mouth of Deep Creek, the *hydrophilus* from Clark Creek. Note the differences in head shape and scale proportions as well as color pattern.

Table 2. Comparison of meristic and mensural characters in population samples of *couchii* and *gigas* in the Sacramento Valley. For characters with two values, the upper refers to males, the lower to females.

Character	<i>couchii</i>				<i>gigas</i>				Significance <i>p</i>
	\bar{x}	SD	Range	<i>n</i>	\bar{x}	SD	Range	<i>n</i>	
Ventrals	172.3±2.59	(169-178)	18		163.8±1.82	(162-168)	12		<0.001
	167.5±3.30	(161-175)	36		159.5±2.69	(156-164)	23		<0.001
Subcaudals	88.1±1.98	(85-91)	12		76.1±2.64	(73-81)	8		<0.001
	75.8±3.75	(68-82)	27		69.7±2.44	(65-73)	15		<0.001
T/TL (%)	25.3±0.97	(23.8-27.0)	12		24.2±0.91	(23.2-25.9)	8		<0.05
	22.8±0.92	(21.0-24.9)	27		21.7±0.92	(20.4-23.4)	15		<0.001
LD/LV (%)	59.4±4.56	(53.6-68.6)	14		74.7±3.43	(69.7-79.2)	11		<0.001
	51.9±5.59	(38.5-59.8)	30		73.4±4.97	(63.7-84.0)	23		<0.001
FWP/A (%)	67.7±6.47	(54.6-79.5)	43		76.4±5.90	(64.3-86.0)	32		<0.001
SL 6/7 (%)	118.5±9.35	(100.0-134.5)	31		75.6±7.24	(56.3-89.6)	30		<0.001
AG/PG (%)	96.2±9.39	(72.6-119.0)	53		88.4±6.28	(77.2-103.5)	33		<0.001
ML/FL (%)	76.9±5.77	(69.7-86.1)	13		85.0±6.82	(69.2-96.1)	11		<0.01
	80.5±4.71	(73.2-91.3)	30		95.4±6.77	(81.3-106.6)	21		<0.001
MW/ML (%)	84.9±5.20	(73.2-96.2)	45		96.0±5.93	(85.7-106.4)	32		<0.001
Prf/ln (%)	73.9±10.52	(47.6-100.0)	42		104.4±10.25	(85.4-122.7)	32		<0.001
E/FL (%)	64.4±3.48	(57.7-72.6)	42		64.0±3.99	(56.8-74.0)	32		N.S.
FL/PL (%)	76.7±5.11	(64.0-90.8)	44		66.7±4.55	(57.4-76.4)	33		<0.001
<i>n</i> %					<i>n</i> %				
Total Pro	2	37(71.2)			31(88.6)				
	3	6(11.5)			4(11.4)				
	4	9(17.3)							
Total IL	18	1(1.9)							
	19								
	20	4(7.5)			17(50.0)				
	21	7(13.2)			8(23.5)				
	22	32(60.4)			6(17.6)				
	23	6(11.3)			2(5.9)				
	24	3(5.7)			1(2.9)				
Anterior DSR									
	21	16(94.1)			5(41.7)				
	22				2(16.7)				
	23	1(5.9)			5(41.7)				
	21	27(75.0)			6(27.3)				
	22	5(13.9)			1(4.5)				
	23	4(11.1)			15(68.2)				

most proximate localities for the two taxa are nearly 24 km apart. Although *couchii* from the upper Sacramento Valley tend to be darker than those in the Pit River drainage and also differ from them in several morphological characters (compare Tables 1 and 2), these animals show no influence from *hydrophilus*.

II. The *couchii*-*gigas* Relationship

The giant garter snake was described as a subspecies by Fitch (1940), who thought that specimens from the eastern edge of the San Joaquin Valley represented intergrades between *gigas* and *couchii*. At that time Fitch was unaware of the presence of *gigas* in the Sacramento Valley, which was first reported by Fox (1951), who discussed intergradation there between *gigas* and *aquaticus* but not *couchii*. The giant garter snake once occurred as far south as Buena Vista Lake in west-central Kern Co., but *gigas* appears to have been extirpated south of Fresno (Hansen and Brode, 1980).

Figs. 4 and 5 illustrate the distribution of *gigas* and *couchii* in the Sacramento and central San Joaquin valleys, respectively. We did not study preserved *gigas* from the now-extirpated lower San Joaquin Valley deme because it appears to have been so isolated from the neighboring *couchii*-complex demes as to prevent gene flow between them. Morphological comparisons of the two taxa in each area are represented in Tables 2 and 3, respectively, and their color patterns in Figs. 6 (upper) and 7. In the upper Sacramento Valley, the dorsal color pattern of *gigas* consists of a relatively dark brown ground color with three bright stripes. Farther south, and in the central San Joaquin Valley, pattern polymorphism prevails; in addition to dark individuals with light stripes, there are others with an olive ground color and varying degrees of suppression of the stripes (Hansen, 1980). The *couchii* from the eastern side of the central San Joaquin Valley have a very dark dorsum and lack any trace of a vertebral stripe except on the neck; in contrast to the Pit River drainage sample, there is considerably less black pigment on the posterior supralabial sutures and on the ventral surface. On the eastern side of the Sacramento Valley, many *couchii* from Tehama and Butte counties are almost uniformly dark brown and virtually stripeless dorsally (a series from Plum Creek in north-central Tehama Co. are actually melanistic). The amount of black pigment on the posterior supralabial sutures and ventral surface varies considerably from specimen to specimen, even at a single locality.

Morphologically, both *gigas* and *couchii* exhibit some geographic variation between the Sacramento and central San Joaquin valleys (compare each between Tables 2 and 3). In *gigas* the only pronounced difference is in ventral number (higher in the north); Sacramento Valley *couchii* differ from upper San Joaquin Valley *couchii* in having fewer subcaudals, a relatively shorter tail, a slightly longer loreal dorsal margin, a substantially narrower frontal posteriorly, longer anterior genials, a slightly narrower muzzle, shorter prefrontals, and predominantly 11 infralabials (rather than 10) on at least one side of the head. In all of these characters except loreal proportions, Sacramento Valley *couchii* are more like Pit River drainage *couchii* (Table 1), to which the former are also closer geographically. Despite the greater amount of geographic variation present in *couchii*, when the adjacent samples of *gigas* and *couchii* are compared (Tables 2 and 3), it can be seen that the two taxa differ in 13 different characters. In both geographic regions, *couchii* has more ventrals and

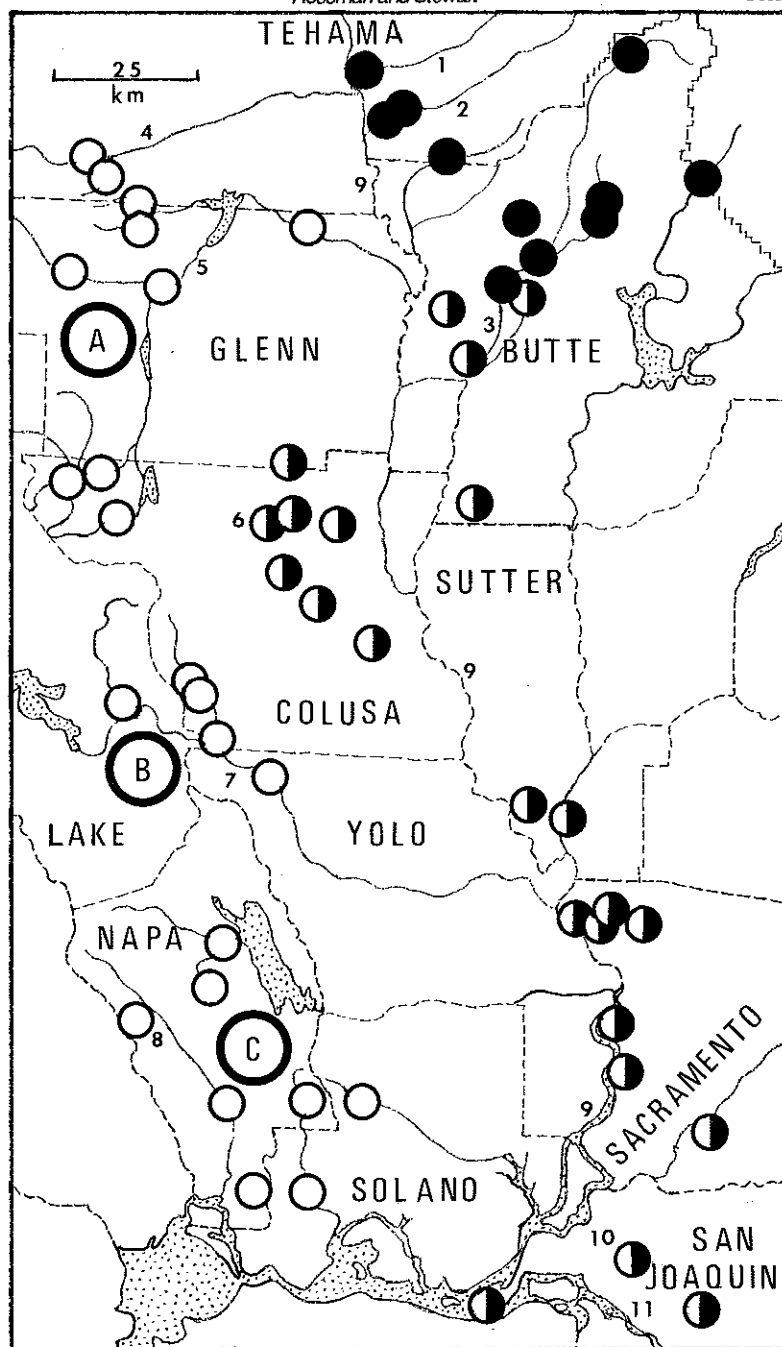


FIGURE 4. Distribution of the *Thamnophis couchii* complex in the Sacramento Valley, California, and adjacent foothills. Solid circles represent *couchii*, hollow circles represent *hydrophilus* (including "*aquaticus*"), and semi-solid circles represent *gigas*. For statistical purposes, the *hydrophilus* sample was subdivided into: A. Thomas Creek and Stony Creek drainages; B. Cache Creek drainage; C. Napa-Solano counties. The numbers refer to the following sites mentioned in the text: 1. Mill Creek; 2. Deer Creek; 3. Butte Creek; 4. Thomas Creek; 5. Stony Creek; 6. Stone Corral Creek; 7. Cache Creek; 8. Dry Creek; 9. Sacramento River; 10. White Slough; 11. San Joaquin River.

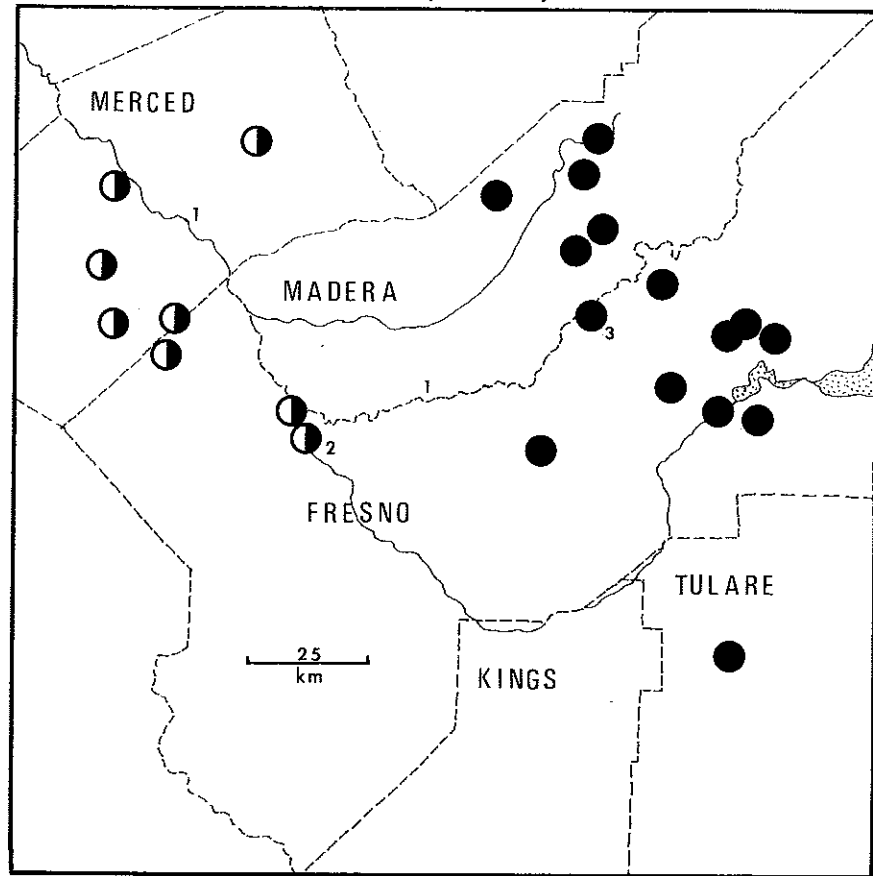


FIGURE 5. Distribution of the *Thamnophis couchii* complex in the central San Joaquin Valley, California, and adjacent foothills to the east. Solid circles represent *couchii*, semi-solid circles represent *gigas*. The numbers refer to the following sites mentioned in the text: 1. San Joaquin River; 2. Mendota Wildlife Management Area; 3. Millerton Lake.

subcaudals, a proportionately longer tail, the loreal with a shorter dorsal margin, the sixth supralabial longer than the seventh, a shorter muzzle (*gigas* also showing more pronounced sexual dimorphism in this feature than *couchii*) and a somewhat narrower muzzle, the internasals substantially longer than the prefrontals, and shorter parietals. The effects of geographic variation can be seen in three characters: Sacramento Valley *couchii* have a narrower frontal posteriorly than adjacent *gigas* (in central San Joaquin Valley *couchii* it is significantly wider than in adjacent *gigas*); Sacramento Valley *couchii* have significantly longer anterior genials than do adjacent *gigas* (central San Joaquin Valley *couchii* and *gigas* do not differ in this character); and central San Joaquin Valley *couchii* predominantly have no more than 10 infralabials on each side of the head (77% of adjacent *gigas* have 11 on at least one side; conversely, in the Sacramento Valley 91% of the *couchii* have 11 or more on at least one side in contrast to only 50% of the *gigas*). Clearly, not every character is of equal discriminatory value throughout the ranges of the taxa.

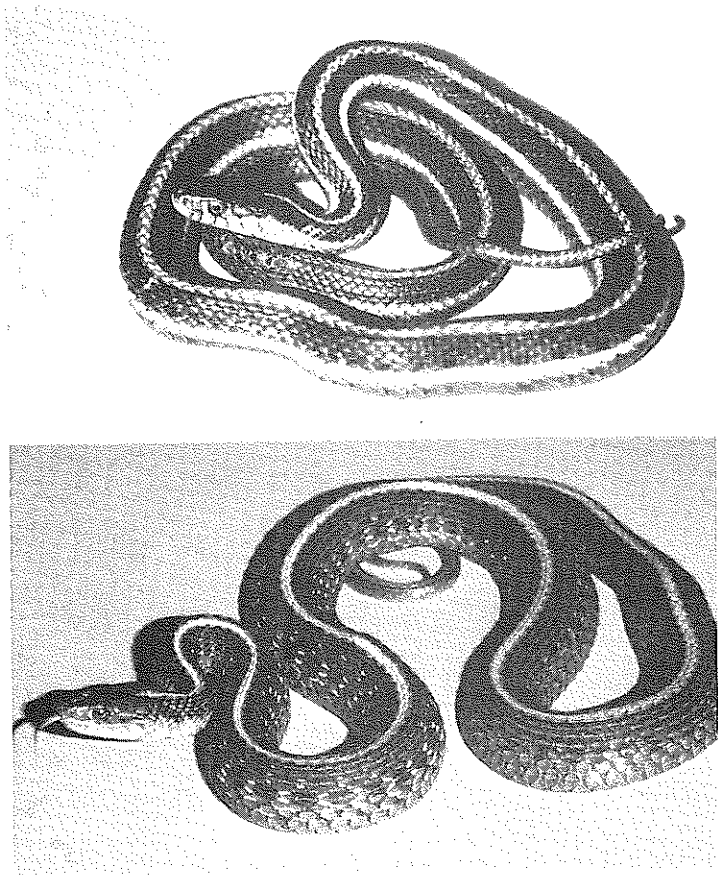


FIGURE 6. Dorsal color patterns of members of the *Thamnophis couchii* complex from central California. Upper: *gigas* from White Slough, San Joaquin Co. Lower: "*aquaticus*" from Dry Creek, Napa Co.

We have no biochemical data from the central San Joaquin Valley. Ten of 12 animals collected from Butte and Tehama counties in the Sacramento Valley had the *couchii*-subgroup genotype at the transferrin locus, but one specimen (LSUMZ 40260 from Mill Creek, Tehama Co.) had the *atratus*-subgroup genotype and another specimen (LSUMZ 40536 from Deer Creek, Tehama Co.) was heterozygous (R. Lawson, personal communication). Neither of the other discriminatory loci was assayed. The latter two specimens are typical of *couchii* from this area in both color pattern and morphology; neither shows any approach to *gigas*, the nearest occurrence of which is 40 km to the south. Lawson and Dessauer (1979) reported an apparent hybrid transferrin genotype in LSUMZ 9075, a snake with a *couchii* morphology from Battle Creek in southeastern Shasta Co. some 40 km from the nearest point where *hydrophilus* is known to occur. There is no reasonable possibility that that genotype could have resulted from a *couchii* x *hydrophilus* mating and, in the face of the morphological evidence, we doubt that the two "aberrant" Tehama Co. genotypes resulted from *couchii* x *gigas* matings. Both of the latter taxa have

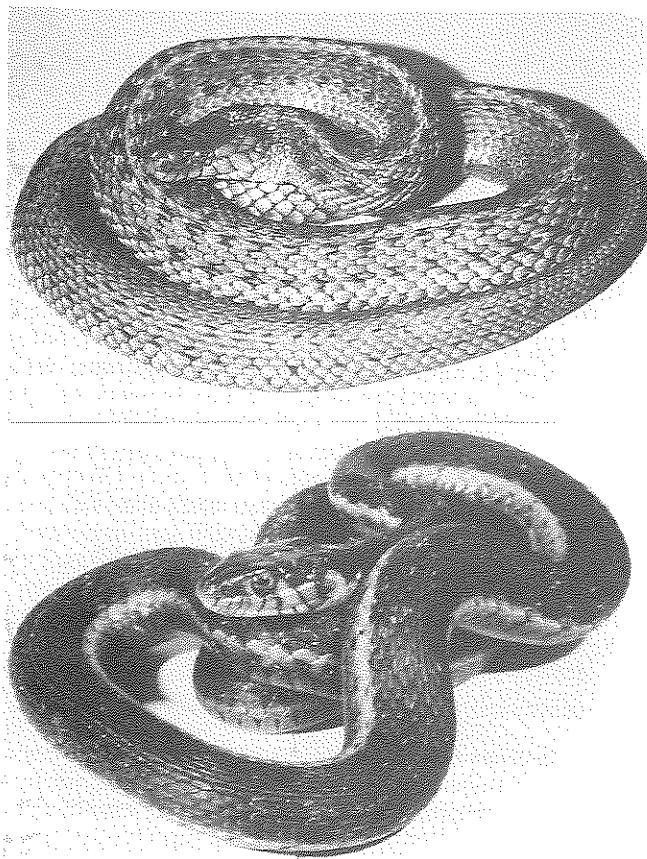


FIGURE 7. Dorsal color patterns of members of the *Thamnophis couchii* complex from the central San Joaquin Valley, California, and adjacent foothills to the east. Upper: *gigas* from Mendota Wildlife Management Area, Fresno Co. Lower: *couchii* from Millerton Lake, Fresno Co.

been found in the Butte Creek drainage at localities only 4.8 km apart, so an occasional encounter between them is by no means out of the question, but their markedly different habitat preferences (*couchii* in rocky or gravel-bottomed streams, *gigas* in tule-cattail marshes and sloughs) make it unlikely.

In the central San Joaquin Valley, the closest localities for *couchii* and *gigas* lie more than 48 km apart, apparently separated by a zone of habitat that is submarginal for both taxa. Hansen (1980) doubted if they ever came in contact except when floods might bring an occasional *couchii* down into *gigas* habitat. Neither he nor we examined any specimens exhibiting morphological intermediacy; the specimens thought to be intergrades by Fitch (1940) all proved to be typical of *couchii*.

Table 3. Comparison of meristic and mensural characters in population samples of *couchii* and *gigas* in the central San Joaquin Valley. For characters with two values, the upper refers to males, the lower to females.

Character	<i>couchii</i>				<i>gigas</i>				Significance <i>p</i>
	\bar{x}	SD	Range	<i>n</i>	\bar{x}	SD	Range	<i>n</i>	
Ventrals	172.6±1.94	(170-176)	22		158.3±1.89	(157-161)	4		<0.001
	168.0±2.52	(163-173)	17		153.1±1.60	(150-155)	10		<0.001
Subcaudals	92.8±2.71	(88-97)	8		77.0±1.00	(76-78)	3		<0.001
	80.3±1.67	(77-83)	8		70.7±1.38	(69-73)	7		<0.001
T/TL (%)	26.2±0.50	(25.2-26.8)	8		24.5±0.69	(24.1-25.3)	3		<0.01
	24.4±0.75	(23.5-25.4)	8		22.1±0.30	(21.8-22.6)	6		<0.001
LD/LV (%)	56.6±5.79	(44.6-63.4)	14		76.8±8.51	(67.2-83.4)	3		<0.001
	47.9±3.97	(40.7-56.1)	16		75.5±7.35	(65.3-88.4)	10		<0.001
FWP/A (%)	83.6±5.84	(73.7-100.0)	27		75.9±5.53	(71.7-87.3)	11		<0.001
SL 6/7 (%)	121.0±10.65	(102.7-147.0)	34		77.6±4.62	(71.1-87.0)	11		<0.001
AG/PG (%)	85.2±7.23	(70.2-100.0)	34		86.5±5.42	(82.6-97.8)	13		N.S.
ML/FL (%)	76.9±8.04	(62.2-93.2)	13		84.7±10.25	(77.4-91.9)	2		N.S.
	76.4±4.78	(68.0-90.9)	16		95.9±3.44	(89.9-101.4)	10		<0.001
MW/ML (%)	91.4±4.87	(79.4-97.8)	28		94.8±5.11	(87.4-104.3)	13		<0.05
Prf/ln (%)	84.0±10.33	(67.0-101.7)	26		107.9±10.76	(94.9-128.4)	13		<0.001
E/FL (%)	68.6±3.56	(62.7-75.1)	27		64.7±5.33	(54.4-71.7)	11		<0.02
FL/PL (%)	79.2±4.73	(68.5-87.3)	29		65.3±5.66	(57.0-76.4)	12		<0.001
<hr/>									
	<i>n</i> %				<i>n</i> %				
Total Pro	2	28	(71.8)		12	(92.3)			
	3	6	(15.4)		1	(7.7)			
	4	5	(12.8)						
Total IL	19	2	(5.1)		1	(7.7)			
	20	31	(79.5)		2	(15.4)			
	21	4	(10.3)		8	(61.5)			
	22	2	(5.1)		2	(15.4)			
Anterior DSR	21	21	(100.0)		2	(66.7)			
	22				1	(33.3)			
	21	12	(75.0)		2	(22.2)			
	22	1	(6.3)		1	(11.1)			
	23	3	(18.8)		5	(55.6)			
	24				1	(11.1)			

III. The *couchii*-*hammondii* Relationship

Although Lawson and Dessauer (1979) demonstrated that *hammondii* and *couchii* belong to the same subgroup, the nature of the relationship between them is unclear. Fitch (1940) concluded that "Although *couchii* and *hammondii* show trends toward each other in certain characters, intergradation is not complete, and their ranges are separated by a barrier, the crest of the Tehachapi Mountains, where no permanent water supply is available....The relationship between *hammondii* and other members of the *Thamnophis ordinoides* group is...best expressed by classifying *hammondii* as a distinct species." Eight years later, after having studied two specimens from Tehachapi Creek, a locality well to the south of his previously examined Kern Co. *couchii*, Fitch (1948) stated that "The head markings in these resemble *hammondii* more than do any other *couchii* examined, but in numbers of ventrals they resemble typical *couchii*. In view of the partial intergradation demonstrable and the probable occurrence of further intermediate populations, it now seems best to relegate *hammondii* to the status of a subspecies."

Since Fitch's (1948) study, many specimens of *couchii* have been collected in southern Kern Co. and *hammondii* in adjacent Ventura and Los Angeles counties that allow us to test Fitch's hypothesis. We discovered that, although it is generally true that the two taxa are separated by the Tehachapi crest, *couchii* has breached the crest at Gorman and *hammondii* just west of Frazier Park in Cuddy Canyon (Fig. 8). The latter is inferred from the presence of a biochemically and morphologically intermediate individual (LSUMZ 39081) in a deme that is otherwise unquestionably *couchii*. Except for that one snake, we found that the geographically proximate populations of *couchii* and *hammondii* are distinct from each other in a broad suite of characters.

These southernmost *couchii* have a very dark brown to black dorsum with a narrow vertebral stripe that is indistinct or nonexistent beyond the neck; the adjacent *hammondii* are brown and lack a vertebral stripe (Fig. 9). The black nuchal blotches in *couchii* are large and fused middorsally; in *hammondii* they are relatively small and separated (Fig. 10). In *couchii* there is extensive black pigment on the temporals and, at least, the seventh and eighth supralabials; in *hammondii* such pigment is essentially confined to a very narrow bar immediately preceding the supralabial sutures (Fig. 9).

Morphologically, *couchii* differs from *hammondii* (Table 4) in having slightly more ventrals in females, substantially more subcaudals in both sexes, a relatively longer tail, a shorter loreal dorsal margin, a narrower frontal posteriorly, the sixth supralabial distinctively longer than the seventh (subequal in *hammondii*), a somewhat narrower muzzle, a smaller eye, slightly shorter parietals, fewer preoculars (only 13.5% have more than one per side in contrast to 82.5% in *hammondii*), more infralabials (69.4% have 11 on at least one side compared to 10.6% in *hammondii*), and more dorsal scale rows at midbody (approximately two-thirds of the *couchii* have more than 19, whereas about the same fraction in *hammondii* have 19).

Lawson and Dessauer (1979) reported that *hammondii* possesses the *atratus*-subgroup transferrin allele despite the fact that it shares the *couchii*-subgroup alleles at several other critical loci. Of the 17 specimens Lawson subsequently examined from the area of geographic proximity, only one male (LSUMZ 39081) possessed a hybrid transferrin. Except for having a brown dorsum and no trace of a vertebral stripe beyond the nape, the specimen has a

couchii color pattern (including light streaks on the frontal). The SL 6/7 value of 121.7% is a *couchii* feature, too, but the presence of 85 subcaudals, a T/TL value of 24.8%, an LD/LV of 66.7%, and a FWP/A of 82.6% are *hammondii* characteristics.

Of historical interest is the fact that the two syntypes of *hammondii* (both catalogued as USNM 5496) from Fort Tejon, Kern Co., are actually *couchii*.

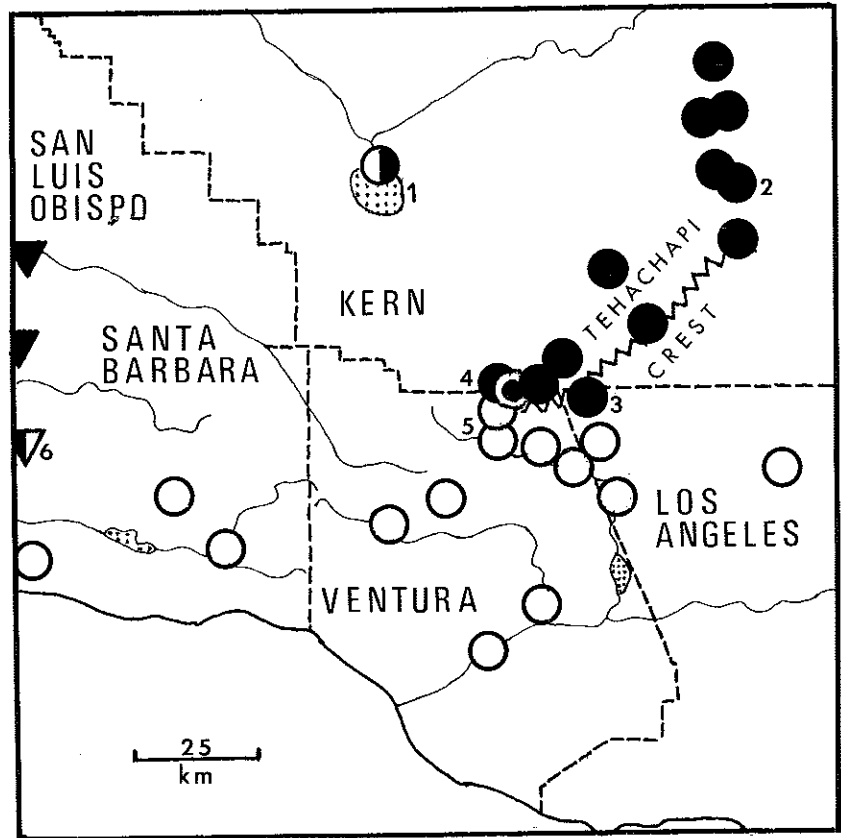


FIGURE 8. Distribution of the *Thamnophis couchii* complex at the southern end of the San Joaquin Valley, California. Solid circles represent *couchii*, hollow circles represent *hammondii*, the dotted circle represents a locality where both *couchii* and *hammondii* occur, the semi-solid circle represents *gigas*, the solid inverted triangle represents *atratus*, and the semi-solid inverted triangle represents a locality where both *atratus* and *hammondii* occur. The numbers refer to the following sites mentioned in the text: 1. Buena Vista Lake; 2. Tehachapi Creek; 3. Gorman; 4. Cuddy Valley; 5. Lockwood Valley; 6. Alamo Pintado Creek.

IV. The *gigas-hydrophilus* Relationship

We consider *aquaticus* to be a weakly differentiated subspecies, at best, and group it with *hydrophilus* for comparisons with *gigas*. Fox (1951) suggested that specimens from the vicinity of Gridley, Butte Co., may be intergrades between

aquaticus and *gigas* because they have the color pattern of the former and dorsal scale row number of the latter. The color patterns are similar (Fig. 6), but *gigas* and its adjacent sister *atratus*-subgroup taxa differ in a number of morphological characters (Table 5). We do not know if *gigas* and *hydrophilus* (in the broad sense) occur any closer than 19.2 km apart (Fig. 4). We have seen what appeared to be suitable *hydrophilus* habitat in Stone Corral Creek (Colusa Co.) no more than 8 km from the westernmost *gigas* locality (ca. 5.6 km W Maxwell, Colusa Co.), which is in the same stream. The single male (LSUMZ 44368) taken at the latter locality was in rather atypical habitat for *gigas* (an ecotonal situation in a narrow stream where short stretches of mud and cattails were interspersed with a gravel bottom and no emergent vegetation), and it is questionable how much farther upstream it would have proceeded before returning to a more favorable habitat.

Because some north-south variation occurs in *hydrophilus* west of the Sacramento Valley (see especially ventral number and relative muzzle length), we divided the specimens we examined into three seemingly natural assemblages (A--Thomes and Stony creek drainages; B--Cache Creek drainage; C--Napa and Solano counties). Morphologically, Sacramento Valley *gigas* differ from these *hydrophilus* samples in having fewer ventrals in females (in comparison only with Sample C), fewer subcaudals, a much shorter tail, a more nearly rectangular loreal, a narrower frontal posteriorly, the sixth supralabial much shorter than the seventh (rather than only a little shorter), the anterior genials a little shorter than the posterior ones (rather than much shorter), a much longer muzzle (the distinction is greatest in comparing *gigas* with all *hydrophilus* females and with Sample C males), a slightly narrower muzzle in comparison to samples A and C, the prefrontals slightly longer than the internasals (the internasals are significantly longer in Sample C), proportionately longer parietals, and 21 or more dorsal scale rows anteriorly (only 2 of the 76 *hydrophilus* have as many as 21 rows).

V. The *hammondii*-*atratus* Relationship

As noted earlier, Fox (1951) reported that *hammondii* and *atratus* occur sympatrically without interbreeding from just west of Salinas, Monterey Co. (the northernmost locality for *hammondii*), to Oceano, San Luis Obispo Co. (the southernmost locality then known for *atratus*). Subsequent fieldwork by J. F. Copp revealed that the range of *atratus* extends south to central Santa Barbara Co. (Alamo Pintado Creek, N Los Olivos), the area of overlap between the two taxa thus extending an airline distance of nearly 280 km. Specimens collected during the past 36 years have, in the main, substantiated Fox's interpretation of the relationship between *hammondii* and *atratus*. However, we can report three localities (2 in San Luis Obispo Co., 1 in Santa Barbara Co.) where limited gene exchange has taken place between the two taxa, and S. S. Sweet (personal communication) has observed apparent intermediates at an additional locality in each of these counties.

The intermediate we have examined from Santa Barbara Co. is JFC 61-7, an adult female collected in Alamo Pintado Creek, a locality from which 4 *hammondii* and 2 *atratus* were also taken. The snake resembles *hammondii* in having a brown dorsum (dark to very dark brown in *atratus*), 21-19-17 dorsal scale rows (19-19-15 in *atratus*), 161 ventrals (southern *atratus* have a

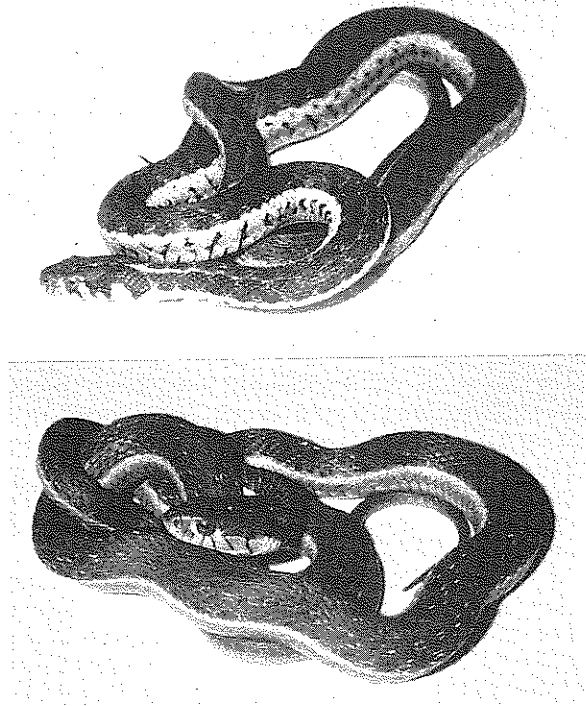


FIGURE 9. Dorsal color patterns of members of the *Thamnophis couchii* complex at the southern end of the San Joaquin Valley, California. Upper : *couchii* from Cuddy Valley, Kern Co. Lower : *hammondi* from Lockwood Valley, Ventura Co.

maximum of 157; Fox 1951), and a muzzle almost as wide as it is long (wider than long in *atratus*); it is similar to *atratus* in having a well-defined vertebral stripe (none in *hammondi*), 78 subcaudals (northern *hammondi* have a maximum of 75; Fitch 1940), a T/TL value of 24.7% (the maximum recorded for *hammondi* is 23.5%), and a relatively small eye (E/F value of 62.1% is near the mean for southern *atratus* and at lower end of range for *hammondi*). It should be noted that the vertebral stripe, although clearly distinct, is both narrower and paler than is typical of *atratus*.

Three intermediate specimens are available from San Simeon Creek, San Luis Obispo Co. (LSUMZ 37188 and two unnumbered specimens in the collection of Stewart). The latter individuals were born to a melanistic female *hammondi* (unfortunately no longer available) collected in 1968, and they presumably represent F₁ hybrids. Their features are predominantly those of *hammondi*, but the two snakes resemble *atratus* in having a distinct vertebral stripe and, in the case of the female, a relatively small eye (E/F=58.5%). LSUMZ 37188, an adult male collected in 1972, also is more similar to *hammondi* morphologically, but it agrees with *atratus* in having a vertebral

stripe (although narrow and very faint) and a SL 6/7 value of 83.3%. This animal was heterozygous at the superoxide dismutase locus (R. Lawson, personal communication). Stewart has captured and released many specimens from this locality over a ten-year period and has seen no others that appeared to be intermediates.

The only other intermediate we have examined is UCSB 13714, an adult male collected in 1982 in Alamo Creek, 0.8 km north of the Cuyama River, which forms the boundary between San Luis Obispo and Santa Barbara counties. This animal also more nearly resembles *hammondii* except for having a pale vertebral stripe and a relatively small eye (E/F=64.2%).



FIGURE 10. Comparison of the heads of *couchii* (on left) from the Tehachapi Mountains, Kern Co., and *hammondii* (on right) from Lockwood Valley, Ventura Co., California.

SYSTEMATIC CONCLUSIONS

Marked morphological differences, and minimal or no gene flow, were observed between the members of each taxon-pair where their ranges abut (or overlap). Our data reveal a very different picture than that implied by a classification in which all of these taxa are treated as subspecies of *Thamnophis couchii*. The morphological evidence is supported by starch gel electrophoretic analysis of proteins (Lawson and Dessauer, 1979; R. Lawson, personal communication), so we formally propose that *T. couchii*, *T. hammondii*, *T. gigas* (new combination), and *T. atratus* (including its subspecies *T. a. hydrophilus*--and *T. a. aquaticus*, if one wishes to recognize it) be accorded full species status. The most recent synonymy of this complex was presented by Fitch (1984). These taxa not only qualify as "evolutionary species" (Simpson, 1961; Wiley, 1981), but the incidence of hybridization in nature is so low that they seem to be behaving as good "biological species" as well. At least some members of the *couchii* complex do interbreed in the laboratory (S. J. Arnold in

Table 4. Comparison of meristic and mensural characters in population samples of *couchii* and *hammondii* in southern California. For characters with two values, the upper refers to males, the lower to females.

Character	<i>couchii</i>				<i>hammondii</i>				Significance <i>p</i>
	\bar{x}	SD	Range	<i>n</i>	\bar{x}	SD	Range	<i>n</i>	
Ventrals	170.5±2.47(166-175)13				170.4±3.60(165-177)18				N.S.
	167.8±2.44(163-173)24				163.5±3.04(159-168)21				<0.001
Subcaudals	92.3±2.42(90-97)12				79.7±3.74(74-89)17				<0.001
	78.9±2.99(72-82)22				70.4±1.91(67-75)17				<0.001
T/TL (%)	26.6±0.58(25.6-27.5)11				23.7±0.92(22.2-25.2)16				<0.001
	24.2±0.69(22.7-25.3)18				22.3±0.77(21.1-23.5)15				<0.001
LD/LV (%)	50.5±6.73(38.4-58.0)10				70.0±7.50(62.4-89.8)15				<0.001
	44.6±7.06(31.0-57.2)14				64.3±4.67(56.7-70.7)17				<0.001
FWP/A (%)	71.3±5.76(52.1-79.9)23				86.9±6.23(72.8-101.7)31				<0.001
SL 6/7 (%)	124.0±7.56(111.8-140.0)35				101.3±8.45(85.0-120.5)35				<0.001
AG/PG (%)	85.5±5.62(76.4-100.0)34				80.9±5.74(73.0-94.7)38				<0.01
ML/FL (%)	76.6±5.61(66.0-90.9)23				77.4±6.10(62.4-90.7)31				N.S.
MW/ML (%)	95.0±3.67(87.1-100.0)23				100.1±6.01(88.7-113.0)32				<0.001
Prf/In (%)	86.0±9.63(68.3-101.2)22				82.6±11.15(62.1-110.4)31				N.S.
E/FL (%)	68.3±3.99(57.7-76.9)23				73.4±4.91(60.0-86.9)31				<0.001
FL/PL (%)	78.9±4.96(67.9-88.2)23				73.5±4.39(62.8-84.8)31				<0.001
				<i>n</i> %					<i>n</i> %
Total Pro									
				2					7(17.5)
				3					8(20.0)
				4					24(60.0)
				5					1(2.5)
Total IL									
				18					1(2.6)
				19					4(10.5)
				20					28(73.7)
				21					2(5.3)
				22					2(5.3)
				23					
				24					1(2.6)
Midbody DSR									
				19					14(77.8)
				20					3(16.7)
				21					1(5.6)
				19					13(65.0)
				20					4(20.0)
				21					3(15.0)
				22					

Table 4. Comparison of meristic and mensural characters in population samples of *couchii* and *hammondi* in southern California. For characters with two values, the upper refers to males, the lower to females.

Character	<i>couchii</i>				<i>hammondi</i>				Significance <i>p</i>
	\bar{x}	SD	Range	<i>n</i>	\bar{x}	SD	Range	<i>n</i>	
Ventrals	170.5±2.47(166-175)13				170.4±3.60(165-177)18				N.S.
	167.8±2.44(163-173)24				163.5±3.04(159-168)21				<0.001
Subcaudals	92.3±2.42(90-97)12				79.7±3.74(74-89)17				<0.001
	78.9±2.99(72-82)22				70.4±1.91(67-75)17				<0.001
T/TL (%)	26.6±0.58(25.6-27.5)11				23.7±0.92(22.2-25.2)16				<0.001
	24.2±0.69(22.7-25.3)18				22.3±0.77(21.1-23.5)15				<0.001
LD/LV (%)	50.5±6.73(38.4-58.0)10				70.0±7.50(62.4-89.8)15				<0.001
	44.6±7.06(31.0-57.2)14				64.3±4.67(56.7-70.7)17				<0.001
FWP/A (%)	71.3±5.76(52.1-79.9)23				86.9±6.23(72.8-101.7)31				<0.001
SL 6/7 (%)	124.0±7.56(111.8-140.0)35				101.3±8.45(85.0-120.5)35				<0.001
AG/PG (%)	85.5±5.62(76.4-100.0)34				80.9±5.74(73.0-94.7)38				<0.01
ML/FL (%)	76.6±5.61(66.0-90.9)23				77.4±6.10(62.4-90.7)31				N.S.
MW/ML (%)	95.0±3.67(87.1-100.0)23				100.1±6.01(88.7-113.0)32				<0.001
Prf/In (%)	86.0±9.63(68.3-101.2)22				82.6±11.15(62.1-110.4)31				N.S.
E/FL (%)	68.3±3.99(57.7-76.9)23				73.4±4.91(60.0-86.9)31				<0.001
FL/PL (%)	78.9±4.96(67.9-88.2)23				73.5±4.39(62.8-84.8)31				<0.001
<hr/>									
	<i>n</i> %				<i>n</i> %				
Total Pro	2	32(86.5)			7(17.5)				
	3	2(5.4)			8(20.0)				
	4	3(8.1)			24(60.0)				
	5				1(2.5)				
Total IL	18				1(2.6)				
	19				4(10.5)				
	20	11(30.6)			28(73.7)				
	21	8(22.2)			2(5.3)				
	22	16(44.4)			2(5.3)				
	23	1(2.8)							
	24				1(2.6)				
Midbody DSR	19	4(30.8)			14(77.8)				
	20	1(7.7)			3(16.7)				
	21	8(61.5)			1(5.6)				
	19	9(37.5)			13(65.0)				
	20	5(20.8)			4(20.0)				
	21	9(37.5)			3(15.0)				
	22	1(4.2)							

Table 5. Comparison of meristic and mensural characters in population samples of *gigas* and *hydrophilus/aquaticus* in the Sacramento Valley. The geographic parameters of the three samples of the latter taxon are delimited in Fig. 4. For characters with two values, the upper refers to males, the lower to females.

Character	<i>gigas</i>				<i>hydrophilus/aquaticus</i>				Significance <i>p</i>
	\bar{x}	SD	Range	<i>n</i>	\bar{x}	SD	Range	<i>n</i>	
Ventrals	163.8 \pm 1.82(162-168)	12			(A) 164.9 \pm 3.01(161-170)	14			N.S.
					(B) 164.6 \pm 3.42(157-168)				N.S.
					(C) 160.5 \pm 3.93(156-168)				<0.02
	159.5 \pm 2.69(156-164)	23			(A) 158.3 \pm 3.04(151-162)	17			N.S.
					(B) 158.1 \pm 3.35(154-164)				N.S.
					(C) 151.9 \pm 2.31(149-157)				<0.001
Subcaudals	76.1 \pm 2.64(73-81)	8			(A) 87.2 \pm 3.04(81-92)	12			<0.001
					(B) 84.8 \pm 2.39(82-88)				<0.001
					(C) 84.5 \pm 3.67(78-91)				<0.001
	69.7 \pm 2.44(65-73)	15			(A) 77.0 \pm 2.98(72-82)	15			<0.001
					(B) 75.5 \pm 2.98(71-79)				<0.001
					(C) 75.8 \pm 2.57(71-79)				<0.001
T/TL (%)	24.2 \pm 0.91(23.2-25.9)	8			(A) 26.8 \pm 0.86(25.5-28.2)	12			<0.001
					(B) 26.8 \pm 0.61(25.7-27.1)				<0.001
					(C) 26.8 \pm 1.37(24.5-29.2)				<0.001
	21.7 \pm 0.92(20.4-23.4)	15			(A) 24.6 \pm 0.98(23.3-26.8)	15			<0.001
					(B) 25.6 \pm 0.66(24.5-26.4)				<0.001
					(C) 24.7 \pm 0.61(23.6-25.4)				<0.001
LD/LV (%)	74.7 \pm 3.43(69.7-79.2)	11			(A) 66.1 \pm 4.91(60.8-78.7)	13			<0.001
					(B) 66.0 \pm 5.52(58.5-74.0)				<0.001
					(C) 68.7 \pm 4.38(64.1-76.2)				<0.01
	73.4 \pm 4.97(63.7-84.0)	23			(A) 65.1 \pm 4.74(58.1-75.9)	12			<0.001
					(B) 63.3 \pm 4.45(53.3-68.5)				<0.001
					(C) 66.0 \pm 5.34(55.0-70.6)				<0.001
FWP/A (%)	76.4 \pm 5.90(64.3-86.0)	32			(A) 87.3 \pm 7.63(75.9-105.9)	27			<0.001
					(B) 85.4 \pm 5.21(78.0-99.3)				<0.001
					(C) 84.1 \pm 4.77(77.6-92.3)				<0.001
SL 6/7 (%)	75.6 \pm 7.24(56.3-89.6)	30			(A) 88.0 \pm 5.76(76.8-98.5)	26			<0.001
					(B) 91.0 \pm 5.78(80.9-100.0)				<0.001
					(C) 86.6 \pm 7.97(75.7-109.1)				<0.001
AG/PG (%)	88.6 \pm 6.28(77.2-103.5)	32			(A) 79.8 \pm 4.35(70.9-86.9)	27			<0.001
					(B) 79.0 \pm 5.05(68.4-87.2)				<0.001
					(C) 79.2 \pm 5.41(72.6-89.6)				<0.001
ML/FL (%)	85.0 \pm 6.82(69.2-96.1)	11			(A) 76.9 \pm 5.77(69.9-87.0)	13			<0.01
					(B) 73.1 \pm 6.13(64.5-81.7)				<0.01
					(C) 69.0 \pm 6.04(57.8-77.0)				<0.001
	95.4 \pm 6.77(81.3-106.6)	21			(A) 75.0 \pm 4.14(66.1-80.9)	12			<0.001
					(B) 72.9 \pm 5.22(67.4-83.9)				<0.001
					(C) 78.5 \pm 5.57(72.0-87.0)				<0.001
MW/ML (%)	96.0 \pm 5.93(85.7-106.4)	32			(A) 101.8 \pm 5.87(94.3-114.2)	25			<0.001
					(B) 98.3 \pm 6.62(87.3-116.1)				N.S.
					(C) 103.9 \pm 7.47(88.0-115.3)				<0.001

Table 5. Comparison of meristic and mensural characters in population samples of *gigas* and *hydrophilus/aquaticus* in the Sacramento Valley. The geographic parameters of the three samples of the latter taxon are delimited in Fig. 4. For characters with two values, the upper refers to males, the lower to females.

Character	<i>gigas</i>				<i>hydrophilus/aquaticus</i>				Significance <i>p</i>
	\bar{x}	SD	Range	<i>n</i>	\bar{x}	SD	Range	<i>n</i>	
Ventrals	163.8 \pm 1.82		(162-168)	12	(A) 164.9 \pm 3.01		(161-170)	14	N.S.
					(B) 164.6 \pm 3.42		(157-168)	8	N.S.
					(C) 160.5 \pm 3.93		(156-168)	15	<0.02
	159.5 \pm 2.69		(156-164)	23	(A) 158.3 \pm 3.04		(151-162)	17	N.S.
					(B) 158.1 \pm 3.35		(154-164)	10	N.S.
					(C) 151.9 \pm 2.31		(149-157)	14	<0.001
Subcaudals	76.1 \pm 2.64		(73-81)	8	(A) 87.2 \pm 3.04		(81-92)	12	<0.001
					(B) 84.8 \pm 2.39		(82-88)	5	<0.001
					(C) 84.5 \pm 3.67		(78-91)	13	<0.001
	69.7 \pm 2.44		(65-73)	15	(A) 77.0 \pm 2.98		(72-82)	15	<0.001
					(B) 75.5 \pm 2.98		(71-79)	12	<0.001
					(C) 75.8 \pm 2.57		(71-79)	12	<0.001
T/TL (%)	24.2 \pm 0.91		(23.2-25.9)	8	(A) 26.8 \pm 0.86		(25.5-28.2)	12	<0.001
					(B) 26.8 \pm 0.61		(25.7-27.1)	5	<0.001
					(C) 26.8 \pm 1.37		(24.5-29.2)	13	<0.001
	21.7 \pm 0.92		(20.4-23.4)	15	(A) 24.6 \pm 0.98		(23.3-26.8)	15	<0.001
					(B) 25.6 \pm 0.66		(24.5-26.4)	8	<0.001
					(C) 24.7 \pm 0.61		(23.6-25.4)	12	<0.001
LD/LV (%)	74.7 \pm 3.43		(69.7-79.2)	11	(A) 66.1 \pm 4.91		(60.8-78.7)	13	<0.001
					(B) 66.0 \pm 5.52		(58.5-74.0)	7	<0.001
					(C) 68.7 \pm 4.38		(64.1-76.2)	11	<0.01
	73.4 \pm 4.97		(63.7-84.0)	23	(A) 65.1 \pm 4.74		(58.1-75.9)	12	<0.001
					(B) 63.3 \pm 4.45		(53.3-68.5)	10	<0.001
					(C) 66.0 \pm 5.34		(55.0-70.6)	9	<0.001
FWP/A (%)	76.4 \pm 5.90		(64.3-86.0)	32	(A) 87.3 \pm 7.63		(75.9-105.9)	27	<0.001
					(B) 85.4 \pm 5.21		(78.0-99.3)	17	<0.001
					(C) 84.1 \pm 4.77		(77.6-92.3)	19	<0.001
SL 6/7 (%)	75.6 \pm 7.24		(56.3-89.6)	30	(A) 88.0 \pm 5.76		(76.8-98.5)	26	<0.001
					(B) 91.0 \pm 5.78		(80.9-100.0)	16	<0.001
					(C) 86.6 \pm 7.97		(75.7-109.1)	21	<0.001
AG/PG (%)	88.6 \pm 6.28		(77.2-103.5)	32	(A) 79.8 \pm 4.35		(70.9-86.9)	27	<0.001
					(B) 79.0 \pm 5.05		(68.4-87.2)	17	<0.001
					(C) 79.2 \pm 5.41		(72.6-89.6)	19	<0.001
ML/FL (%)	85.0 \pm 6.82		(69.2-96.1)	11	(A) 76.9 \pm 5.77		(69.9-87.0)	13	<0.01
					(B) 73.1 \pm 6.13		(64.5-81.7)	7	<0.01
					(C) 69.0 \pm 6.04		(57.8-77.0)	10	<0.001
	95.4 \pm 6.77		(81.3-106.6)	21	(A) 75.0 \pm 4.14		(66.1-80.9)	12	<0.001
					(B) 72.9 \pm 5.22		(67.4-83.9)	10	<0.001
					(C) 78.5 \pm 5.57		(72.0-87.0)	7	<0.001
MW/ML (%)	96.0 \pm 5.93		(85.7-106.4)	32	(A) 101.8 \pm 5.87		(94.3-114.2)	25	<0.001
					(B) 98.3 \pm 6.62		(87.3-116.1)	17	N.S.
					(C) 103.9 \pm 7.47		(88.0-115.3)	17	<0.001

Table 5, continued

Character	<i>gigas</i>				<i>hydrophilus/aquaticus</i>				Significance <i>p</i>
	\bar{x}	SD	Range	<i>n</i>	\bar{x}	SD	Range	<i>n</i>	
Prf/ln (%)	104.4±10.25		(85.4-122.7)	32	(A) 100.7±10.55		(84.1-123.8)	22	N.S.
					(B) 99.5±12.08		(77.5-123.8)	16	N.S.
					(C) 91.7±10.18		(79.5-117.2)	18	<0.001
E/FL (%)	64.0±3.99		(56.8-74.0)	32	(A) 66.7±4.89		(57.4-75.0)	28	<0.05
					(B) 65.5±3.15		(61.4-70.9)	17	N. S.
					(C) 63.8±3.42		(57.2-69.7)	18	N. S.
FL/PL (%)	66.7±4.55		(57.4-76.4)	33	(A) 71.3±4.20		(61.7-81.4)	28	<0.001
					(B) 74.2±3.86		(66.7-80.8)	17	<0.001
					(C) 72.8±3.73		(65.7-77.8)	20	<0.001

	<i>gigas</i>		(A)	(B)	(C)	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Total Pro						
2		31(88.6)	30(96.8)	16(94.1)	26(100.0)	
3		4(11.4)	1(3.2)	1(5.9)		
Total IL						
18					1(3.8)	
19			2(6.5)	1(5.9)	2(7.7)	
20		17(50.0)	26(83.9)	16(94.1)	20(76.9)	
21		8(23.5)			3(10.7)	
22		6(17.6)	3(9.7)			
23		2(5.9)				
24		1(2.9)				
Anterior DSR						
19			9(90.0)	8(100.0)	14(93.3)	
20			1(10.0)		1(6.7)	
21		5(41.7)				
22		2(16.7)				
23		5(41.7)				
			19(90.5)	10(100.0)	12(100.0)	
19						
20						
21		6(27.3)	2(9.5)			
22		1(4.5)				
23		15(68.2)				

Lawson and Dessauer, 1979), but as Lawson and Dessauer cautioned: "...neither the successful hybridization of organisms under laboratory conditions nor the occurrence of rare natural hybrids is sufficient justification for deciding that populations are undergoing introgression in nature." There are no "hybrid zones" *per se*, the few known hybrids (except UCSB 13714, see p. 19) occurring in the presence of one or both parent species, and there is no indication that genetic influence from one taxon penetrates the other beyond the immediate point of contact.

Recognition that the *couchii* complex consists of four separate species removes the awkwardness posed by having two sympatric "subspecies" (*atratus* and *hammondii*) sympatric over an area 280 km long, but it also eliminates one

of the classical examples of a species with a circular overlap (Fox, 1951; Mayr, 1963).

The ecological relationships among these species are complex and presumably have helped to shape their present distributions. With the exception of *Thamnophis gigas*, the geographically proximate species seem to occupy similar niches and their inability to occur sympatrically is probably enforced by competition. The broad sympatry of *T. atratus atratus* and *T. hammondi* presumably is permitted by niche partitioning, the former making greater use of the terrestrial habitat and feeding more on tadpoles and small anurans than on fish (Bellemin and Stewart, 1977).

The giant garter snake has become adapted to a geographically contiguous habitat (tule-cattail marshes and sloughs in the central valleys) that apparently is not suitable for other species in the complex, and thus it has acquired both ecological and spatial isolation from them. Hansen (1980) has suggested that the ancestor of *Thamnophis gigas* may have moved from the Coastal Range into the reemerging freshwater habitat (bordered by woodland) in the central valleys about 1-2 million years ago following the closure and draining of the San Joaquin Embayment. The subsequent warming trend would have resulted in a retreat of the woodland into the foothills, thus isolating the marshland (with its incipient *gigas* population) and providing an opportunity for relatively rapid morphological divergence and speciation. Hansen's scenario seems reasonable to us, and we would add only that the similarity in color pattern between northern *T. gigas* and adjacent *T. atratus* populations leads us to suspect that the ancestral proto-*gigas* came from the Coastal Range north of what is now San Francisco Bay and that the species subsequently spread southward into the San Joaquin Valley.

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Thamnophis atratus: Contra Costa Co., UMMZ 118977; Colusa Co., CAS 4430-31, CSUS 1020, LSUMZ 40001, 40003-10, 40035, 40243-47, 40252, 40688, MVZ 16400, 48173; Glenn Co., LSUMZ 40002, 40528-32, 40537-49, 40650, MVZ 48192; Lake Co., LSUMZ 40011-14, UMMZ 128410; Monterey Co., LSUMZ 39097; Napa Co., MVZ 42639-44, 47998-99, 48010-12, 60234-35, 78050-51, 149606-09, 149621-23, 149625; San Luis Obispo Co., LSUMZ 37191; Santa Barbara Co., JFC 61-54, 61-152, 65-199, UCSB 13707; Santa Clara Co., CAS 22953-54; Shasta Co., CAS 11910-11, DZUCD uncatalogued (2), LSUMZ 16555-59, 34417-18, 34386-87, 35177, 36685-705, 36720, 36747-53, 39088-89, 40017, 40020-22, 40029-34, 46844-45, uncatalogued (1), MVZ 17375, 43674, 43677, 85059; Solano Co., MVZ 4006-08, 48017; Stanislaus Co., LSUMZ 44370, 44390; Tehama Co., LSUMZ 36900, 40528-29, 40531-32, 40537-41; Yolo Co., MVZ 4005, 78053.

Thamnophis couchii: Amador Co., SDNHM 638; Butte Co., CSUC 586-88, 2223, 2303, CSUH 3762, uncatalogued (6), LSUMZ 40253-57; Fresno Co., CAS 1753-56, 4127, CSUF uncatalogued (1), RWH 78-001, -002, -006, -007, -009, -011, -014, -015, -016, -017, -018, -021, -025, -026, -027, -039, -045, -046, -051, -060; Kern Co., CAS 10330-35, 10337-40, 13183, GRS 1802-03, LACM 21214, 103993, LSUMZ 16549, 37179-87, 39073-74, 39080, 39092-95, 39098, MVZ 178452, RWH 1000, 1041, USNM 5496 (2); Madera Co., CSUF uncatalogued (2), MVZ 2753, 25967, 27171-72, 37118, 48193-94, 55524, 56774, 63697, UMMZ 118979; Shasta Co., CAS 8708, CSUH uncatalogued (1), LSUMZ 22938, 34415, 34589, 35178-79, 36706-18, 39072, 39075-78, 39082-87, 39096, 40018, 40024-26, 40028, 40653, 47030, uncatalogued (1), MVZ 17442, 18820-32, 22938, UMMZ 112421; Tehama Co., LSUMZ 16550, 34416, 36668-84, 40258-60, 40530, 40533-36, MVZ 9924-25, 9991-95, 10962-64; Tulare Co., SDNHM 20232.

Thamnophis gigas: Butte Co., CSUC 566-69, 576, 2326-27, LSUMZ 8069, 36667, MVZ 48174, 63682-85, 63687-88; Colusa Co., CDFG 78, CSUC 2328, LSUMZ 44368-69, 44386, 45410, 45802; Fresno Co., LSUMZ 34760, MVZ 6833, RWH 78-032, uncatalogued (1); Glenn Co., UMMZ 118981; Merced Co., CAS 13635-37, 13640, 13838, 36071, 44159-60, CDFG uncatalogued (2); Sacramento Co., CDFG 75, 76, 210, uncatalogued (2), CSUS 22-24, LSUMZ 39691, UMMZ 67407; San Joaquin Co., LSUMZ 35176, MVZ 66720; Sutter Co., CDFG uncatalogued (1), MVZ 178451.

Thamnophis hammondi: Los Angeles Co., GRS 7, LACM 21213, 21223, UCSB 13716; San Luis Obispo Co., LSUMZ 37173-78; Santa Barbara Co., JFC 472, 60-60, 60-61, 60-62, 61-3, 61-8, 61-48, 61-52, 62-66, 65-170, UCSB 13114; Ventura Co., CAS 50299, 50301, 50303-05, 50343, 50347, 50350-53, JFC 62-67, LSUMZ 39090-91, 40550-51, 40651-52, LACM 21285, 104047-48, SDNHM 2829, 4968-71, UCSB 9571-76, 11361-62, 12126, 13713, 13715.

Thamnophis atratus X *couchii*: Shasta Co., LSUMZ 39099(?), 40015-16, 40019, 40023(?).

Thamnophis atratus X *hammondi*: San Luis Obispo Co., GRS uncatalogued (2), LSUMZ 37188, UCSB 13714; Santa Barbara Co., JFC 61-7.

Thamnophis couchii X *hammondi*: Kern-Ventura Co., LSUMZ 39081.

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