

COMPARATIVE VISCERAL TOPOGRAPHY OF THE
NEW WORLD SNAKE TRIBE
THAMNOPHIINI (COLUBRIDAE, NATRICINAE)

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ABSTRACT

The positions and lengths of a variety of visceral organs in 631 preserved adult thamnophiine snakes were determined in terms of ventral scute number and converted into a per cent of total ventral number; a mean was calculated for each taxon to allow comparison with other taxa. Dice-Leraas diagrams were then constructed for the following organ positions and lengths: posterior end of heart, anterior and posterior ends of liver, posterior end of pancreas, anterior and posterior ends of right and left kidney, liver length, right and left kidney lengths, heart-liver interspace, and kidney overlap. Sexual dimorphism is apparent in many of the characters examined. Apparently correlated with their need for space to accommodate developing young, females tend to have their anterior and midbody organs placed more anteriorly and their kidneys more posteriorly than those in males.

Stepwise discriminant analysis was performed on the following four variables in male thamnophiine snakes: posterior end of heart, anterior end of right kidney, posterior end of left kidney, and kidney overlap. The 294 specimens represented 11 groups — 7 genera plus Ruthven's four species groups of *Thamnophis*. Two of four linear discriminant functions were retained as they explain 83.21% of the relative variation. Function 1 is generally an anterior end of right kidney dimension, and function 2 is a kidney overlap and posterior end of heart dimension. More than 66% of the specimens were correctly classified by use of the model. All groups except *Clonophis* could be classified with greater success than the 21% prior probability obtained by placing them all in the

Elegans group of *Thamnophis*, the numerically largest sample. The discriminant analysis was able to distinguish among the seven genera (as well as among Ruthven's four species groups of *Thamnophis*) at the 0.05 level except that *Clonophis* and *Tropidoclonion* could not be distinguished from each other.

Although visceral topographic data alone do not clearly delimit thamnophiine genera nor establish inter- or intrageneric relationships, some trends are apparent that serve to support taxonomic conclusions based on other kinds of characters. *Clonophis* and *Regina* can be distinguished from *Nerodia*, in which genus they were formerly included. *Thamnophis* (less *proximus* and *sauritus*) can also be distinguished from *Nerodia* (less *erythrogaster* and *valida*). The *Sauritus* group of *Thamnophis* differs markedly from the other three species groups established by Ruthven in most visceral topographic features. The ribbon snakes (*Sauritus* group) frequently tend to have a posterior displacement of organs, a condition often occurring also in the short, semifossorial genera (*Clonophis*, *Seminatrix*, *Storeria*, *Tropidoclonion*, *Virginia*). One unique feature shared by all of the semifossorial genera is the possession of a relatively long liver.

INTRODUCTION

The technique of determining snake visceral topography using ventral scutes as reference points has received little attention since its introduction by Thompson seventy years ago. Although a moderate amount of descriptive anatomical work has appeared in print, very little has

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been done of a comparative nature that might be of taxonomic value, and none using discriminant analysis. The present study was undertaken to investigate the possible taxonomic significance of visceral topography in the tribe *Thamnophiini* of the colubrid subfamily *Natricinae*.

Beddard (1908, 1909) characterized the position of visceral organs in three genera of boid snakes in terms of the distance from the snout to the organ. He also measured organ length and the distance between organs. Beddard was convinced that the position of viscera within the body of snakes generally had systematic importance. Subsequent authors who also used distance measurements were Atwood (1916, 1918), Bergman (1941 *et seq.*), and Brongersma (1951, 1957 a & b). Bergman expressed the organ positions and lengths as a per cent of snout-vent length, and both he and Brongersma also presented their data diagrammatically.

Thompson (1913a & b, 1914) was the first to relate the position of the various visceral organs to the ventral scutes in an attempt to provide a simple, yet objective, technique for stating the location of the organs. The position of an organ was expressed as a percentage of the total number of ventrals in order to compensate for individual, sexual, and geographic variation in ventral number. This technique has been utilized subsequently only by Thorpe (1975), Underwood (1976), and Rasmussen (1979). Thorpe determined the midpoint of an organ rather than the anterior and posterior ends, so his data are not comparable to ours or to those of other authors. Inasmuch as one has to ascertain the anterior and posterior ends in order to determine the midpoint, the latter would appear to be an unnecessary complication and if used alone it also results in a loss of information.

Garrigues (1962), Bogert (1968), Collins and Carpenter (1970), and Frenkel and Kochva (1970) also gave organ positions and lengths in terms of ventral number, but they did not express their data as a per cent of total ventrals. Also, by lumping his

samples for each species, Garrigues failed to take sexual dimorphism into account.

Valle (1944-45), Bragdon (1953), and Camazine et al. (1981) used ventral number to pinpoint the location of various posterior organs so that surgical procedures could be carried out using the smallest incisions possible. In each case, the investigator counted ventral scutes from the vent forward.

MATERIALS AND METHODS

We examined 631 preserved adult specimens, representing 8 *thamnophiine* genera (only *Adelophis* was omitted because of its rarity) and 35 species (4 being represented by two subspecies or populations). Large subadults were used only if their data fitted into the range of variation for the taxon under consideration. Juveniles were rejected because their values tend to lie outside the normal range of variation in adults (see Bergman, 1958a, 1961b).

Only nongravid females or those with undeveloped eggs were used because of the distortion caused by developing embryos (also noted by Bergman, 1961a; Collins and Carpenter, 1970; Thorpe, 1975). Because females tend to have their anterior organs situated more anteriorly and their kidneys more posteriorly than those of males, each sex was considered separately (see the Sexual Dimorphism section for further discussion).

Using the Dowling method for counting ventral scutes, we inserted insect pins in the 20th scute and in every 15th scute thereafter. Several midventral slits were made to expose the organs being studied. The ventral scute numbers at the anterior and posterior ends of each organ were recorded; to facilitate inter- and intraspecific comparisons, a percentage was calculated by dividing the scute number by the total number of ventrals. The following organs were considered where possible: heart, liver, gall bladder, pancreas, right and left kidneys. Lungs, thyroid, spleen, and adrenals were not considered because they were difficult to locate in many specimens. Testes and ovaries were not considered

because of the varying size depending on whether the specimens were in a breeding or non-breeding state (see Matthews and Marshall, 1956; Manna and Sircar, 1978). Organ lengths, expressed as the total number of ventral scales covered, were also recorded and treated as a percentage of total number of ventrals. The following distances were measured and expressed in the same manner: posterior end of heart to anterior end of liver, posterior end of liver to anterior end of gall bladder, distance between or overlap of the right and left kidneys. On museum material other than that in the Louisiana State University Museum of Zoology (LSUMZ), only the heart, anterior end of liver, and kidneys were examined in order to minimize the number of incisions. Preliminary data on LSUMZ specimens had indicated that these organs were the most relevant to the study.

The statistics used in the Inter- and Intrageneric Comparisons section consisted of calculating the mean, standard deviation, and standard error of the mean for each sex of each taxon, then constructing graphs by the Dice-Leraas method as discussed in Simpson et al. (1960). This method presents a graphic representation of differences between populations, and the results appear in Figs. 1-19. The 95% confidence interval of the mean was determined by dividing the standard deviation by the square root of the sample size and multiplying this figure by a value from the Student's t-test table using $n-1$ degrees of freedom (Runyon and Harber, 1968). Because of the very large confidence interval generated by a sample of two specimens, we constructed a Dice-Leraas diagram only in those cases where we had a minimum sample of three specimens of the same sex. The confidence interval results in a plus or minus figure relative to the mean. Where a determination of the statistical significance of the differences between means could not be obtained from this graphic representation (using the three general rules on p. 353 in Simpson et al., 1960), then a Student's t-test was used. When data are stated as

being significantly different in this paper, it refers to the fact that the differences are significant at the $p \leq .05$ level.

To minimize the possible effects of geographic variation, we attempted to sample populations from as restricted an area as possible. In four instances (*Thamnophis couchii*, *T. elegans*, *T. sirtalis*, *Tropidoclonion lineatum*) we treated different subspecies or geographically distant populations as separate taxon samples. Because enough male and female *Thamnophis eques* could not be obtained from one geographic area, we used females of *T. e. megalops* and males of *T. e. virgatenius*.

Due to the existence of sexual dimorphism, data for males and females could not be combined for discriminant analysis. We chose to restrict the discriminant analysis to the data for males; only a relatively few confidence intervals could be shown for females on the Dice-Leraas diagrams because many of the confidence intervals exceeded the ranges of variation. Only those specimens that had data available for all characters were used. Six variables (posterior end of heart, anterior and posterior ends of right kidney, anterior and posterior ends of left kidney, and kidney overlap) were first run after the values were standardized at the mean to allow for comparisons. Because the posterior end of the right kidney and the anterior end of the left kidney were significantly correlated, those characters were eliminated to obtain a four-variable explanatory and predictive model. The posterior end of the right kidney and anterior end of the left kidney values are reflected in the kidney overlap figures.

Because of the relatively small number of specimens in each sample, the 294 specimens were placed in the following eleven groups to achieve greater statistical significance of the discriminant values:

1. *Clonophis kirtlandii* — 6 specimens
2. *Nerodia* (*cyclopion*, *erythrogaster*, *fasciata*, *rhombifera*, *sipedon*, *valida*) — 51
3. *Regina* (*alleni*, *grahamii*, *rigida*, *septemvittata*) — 24

4. *Seminatrix pygaea* — 8
5. *Storeria* (*dekayi*, *occipitomaculata*) — 15
Thamnophis (groups from Ruthven, 1908)
6. *Sauritus* group (*proximus*, *sauritus*) — 14
7. *Radix* group [*brachystoma*,² *butleri*, *eques* (= *megalops* in Ruthven), *marcianus*, *radix*] — 44
8. *Elegans* group [*couchii couchii*,² *c. hydrophilus*,¹ *elegans terrestris*,¹ *e. vagrans*,² *melanogaster*, *nigronuchalis*,¹ *ordinoides*, *rufipunctatus* (= *angustirostris* in Ruthven), *scalaris*] — 63
9. *Sirtalis* group [*chrysocephalus*,² *cyrtopsis* (= *eques* in Ruthven), *godmani*,² *sirtalis fitchi*,¹ *s. sirtalis*] — 47
10. *Tropidoclonion lineatum* (Nebraska, New Mexico, Texas) — 5
11. *Virginia* (*valeriae*, *striatula*) — 17

Prior probabilities of group membership were calculated by dividing the number in any group by the total number in the study. These prior probabilities are used in classifying the specimens with the discriminant model.

SEXUAL DIMORPHISM

Details on sexual dimorphism in this study appear in Tables I and II and in Figs. 1-19. A comparison of sexual dimorphism data from this study with other studies appear in Table III.

Anterior organ positions

The posterior end of the heart and the anterior end of the liver in males are located posteriorly to those positions in females in 77% and 81% of the taxa, respectively. Male *Clonophis*, *Seminatrix*, *Storeria*, *Tropidoclonion* (for heart only), and *Virginia* have the posterior end of the heart and the anterior end of the liver located posteriorly to those positions in females in all species. In *Nerodia*, *Regina*, and *Thamnophis* there is interspecific variability in both features. Male *Thamnophis*

have the posterior end of the heart situated posteriorly to that of females in 74% of the taxa; male *Nerodia* in 67%; male *Regina* in 67%. The anterior end of the liver in males lies posteriorly to that of females in 80% of the species of *Nerodia*, 73% of the taxa of *Thamnophis*, and in the only species of *Regina* for which data are available.

Midbody organ positions

Sexual dimorphism of the midbody organ positions is not pronounced. Males have the posterior end of the liver located posteriorly to that of females in 50% of the taxa, the posterior end of the gall bladder posteriorly to that of females in 69%. The posterior end of the liver is more posteriorly placed in males in 60% of the species of *Nerodia*, both species of *Storeria*, and in the one species of *Virginia* examined. Males have the posterior end of the gall bladder located more posteriorly than do females in 60% of the species of *Nerodia*, 70% of the taxa of *Thamnophis*, and in the one species of *Storeria* examined.

Posterior organ positions

In contrast to most of the preceding characters, the kidneys exhibit marked sexual dimorphism in many of their features. The anterior ends of the right and left kidneys in males are anterior to those of females in all taxa, as are the posterior ends of the right and left kidneys in 86% and 73% of the taxa, respectively. The posterior end of the right kidney in males is situated anteriorly to that of females in all species of *Regina*, *Seminatrix*, *Tropidoclonion*, and *Virginia*, and 95% of the taxa of *Thamnophis*. In *Nerodia* the posterior end of the right kidney of males is situated posteriorly to that of females in 67% of the species. In both species of *Storeria* and in half the species of *Nerodia*, the posterior end of the left kidney of males is situated posteriorly to that of females. The posterior end of the left kidney of males is anterior to that of females in 95% of the taxa of *Thamnophis*, 67% of the species of *Regina*, one population of *Tropidoclonion*, and in both species of *Virginia*.

¹taxon described since Ruthven (1908)

²taxon not recognized by Ruthven (1908)

Table 1. Sexual dimorphism in certain thamnophiine snakes.

Character	n	Position in ♂ posterior to that in ♀ (or ♂ organ longer)	Position in ♀ posterior to that in ♂ (or ♀ organ longer)	♂=♀	♂ significantly different (p≤.05) from ♀
post. heart ¹	35	77%	17%	6%	27%
ant. liver	27	81%	15%	4%	41%
post. liver	18	50%	44%	6%	22%
post. gall bladder	16	69%	31%	0%	25%
ant. r. kidney	37	0%	100%	0%	81%
post. r. kidney	37	14%	86%	0%	49%
ant. l. kidney	37	0%	100%	0%	86%
post. l. kidney	37	24%	73%	3%	32%
liver length	17	18%	76%	6%	18%
gall bladder length	16	31%	69%	0%	6%
r. kidney length	37	92%	5%	3%	46%
l. kidney length	37	100%	0%	0%	73%
post. heart-ant. liver interspace	26	73%	27%	0%	12%
kidney overlap	37	84%	13%	3%	22%

¹ means of the taxa were used in computing the figures in this table

Organ lengths and interspaces

The liver and gall bladder of females are longer than those of males in 76% and 69% of the taxa, respectively. However, the right and left kidneys of males are longer than those of females in 92% and 100% of the taxa, respectively, probably due to the presence of a hypertrophied sexual segment in males (Matthews and Marshall, 1956; Prasad and Reddy, 1972). The male heart-liver interspace is longer than that of females in 73% of the taxa, as is the male kidney overlap in 84% of the taxa. In 80% of the taxa of both *Nerodia* and *Thamnophis*, males have a shorter liver than do females; the liver is also shorter in male *Storeria dekayi* (in *S. occipitomaculata* the liver shows no sexual dimorphism). Data were available for both sexes in only one species of *Regina* and one of *Virginia*. Males have a shorter gall bladder than do females in 80% of the species of *Nerodia*, in 70% of the taxa of *Thamnophis*, and in *Storeria dekayi*. Males of *Clonophis*, *Nerodia*, *Regina*, *Seminatrix*, *Storeria*, *Tropidoclonion*, and *Virginia* have longer right and left kidneys than do females. In all taxa of *Thamnophis*, males have a longer left kidney than do females; in 86% of those taxa, males also have a longer right kidney. In all species of

Clonophis, *Regina*, *Seminatrix*, *Storeria*, and *Virginia*, males have a longer heart-liver interspace than do females, as is the case for 60% of the species of *Nerodia* and 64% of the taxa of *Thamnophis*. In all species of *Clonophis*, *Nerodia*, *Regina*, *Seminatrix*, *Tropidoclonion*, and *Virginia*, males have a more extensive kidney overlap than do females, as is the case for 76% of the taxa of *Thamnophis*.

Asymmetry of kidney lengths

In 76% of the taxa, females have the right kidney longer than the left (24% differ significantly). On the other hand, males have the left kidney longer than the right in 55% of the taxa (5% differ significantly). In all species of *Nerodia*, the right kidney is the longer one in both sexes.

Summary and conclusions

In general, the anterior and midbody organs are placed more posteriorly in males than in females, whereas the kidneys of males are positioned more anteriorly than those of females. This more anterior positioning of the anterior organs and more posterior positioning of the posterior organs in females would allow greater space for the developing young.

INTER- AND INTRAGENERIC COMPARISONS

To facilitate comparisons, each set of

Table II. Sexual dimorphism in certain thamnophine snakes as reflected by a comparison of male and female means for each taxon.

Character		post. heart	ant. liver	post. liver	post. bl.	ant. kidney	post. kidney	ant. kidney	post. kidney	liver	gall bl.	r. kidney length	l. kidney length	heart-interspace	kidney overlap
Taxon															
<i>Clonophis kirtlandii</i> <i>Merodia evelynae</i> <i>erythrogaster</i> <i>fasciata</i> <i>rhombifera</i> <i>sipedon</i> <i>valida</i>	post. heart	♂ NS	♂ .01 ³	♂ NS	---	NS	NS	NS	NS	NS	---	♂ .02	♂ .02	10 NS	NS
	♂ .05	♂ NS	♂ .001	♂ NS	♂ NS	♂ NS	♂ .001	♂ NS	♂ NS	♂ NS	♂ NS	♂ .02	♂ .02	♂ NS	♂ .05
	♂ .01	♂ NS	♂ NS	♂ NS	♂ NS	♂ NS	♂ .01	♂ .01	♂ NS	♂ NS	♂ NS	♂ .01	♂ .01	♂ NS	♂ .05
	♂ NS	♂ NS	♂ NS	♂ NS	♂ NS	♂ NS	♂ NS	♂ NS	♂ NS	♂ NS	♂ NS	♂ .01	♂ .01	♂ NS	♂ NS
	♂ .001	♂ NS	♂ .02	♂ NS	♂ NS	♂ NS	♂ .02	♂ NS	♂ NS	♂ NS	♂ NS	♂ .05	♂ .05	10 NS	♂ .01
<i>Regina alleni</i> <i>grahami</i> <i>rigida</i>	♂ NS	♂ NS	♂ .02	---	---	♂ .05	♂ NS	♂ .01	♂ NS	---	---	♂ NS	♂ .05	♂ NS	♂ NS
	♂ NS	♂ NS	---	---	---	♂ NS	♂ NS	♂ NS	♂ NS	---	---	♂ NS	♂ .01	---	♂ .001
	♂ NS	---	---	---	---	♂ NS	♂ NS	♂ NS	♂ NS	---	---	♂ NS	♂ NS	---	♂ NS
<i>Seminatrix pygaea</i> <i>Storeria dekayi</i> <i>oceiptomaculata</i>	♂ .01	♂	♂ .01	---	---	♂ .02	♂ NS	♂ .01	♂ NS	---	---	♂ NS	♂ NS	♂ NS	♂ NS
	♂ .001	♂ NS	♂ .001	♂ .001	♂ .05	♂ NS	♂ .01	♂ NS	♂ NS	♂ NS	♂ NS	♂ .01	♂ .01	♂ NS	♂ NS
<i>Thamnophis brachystoma</i> <i>butleri</i> <i>chrysocephalus</i> <i>couchii</i> A4 <i>couchii</i> B5 <i>curtipetris</i> <i>elegans</i> A6 <i>elegans</i> B7 <i>eques</i> <i>godmani</i> <i>melanogaster</i> <i>nigropunctatus</i> <i>ordinoides</i> <i>proximus</i> <i>radix</i> <i>rufigipunctatus</i> <i>sauritus</i> <i>scalaris</i> <i>sirtalis</i> A8 <i>sirtalis</i> B9	♂ NS	---	---	---	---	♂ .001	♂ .01	♂ .01	♂ .01	♂ NS	---	♂ NS	♂ .001	---	♂ NS
	♂ NS	---	---	---	---	♂ .001	♂ .01	♂ .01	♂ .01	♂ NS	---	♂ NS	♂ .001	---	♂ NS
	♂ NS	---	---	---	---	♂ .001	♂ .01	♂ .01	♂ .01	♂ NS	---	♂ NS	♂ .01	---	♂ NS
	♂ NS	---	---	---	---	♂ .001	♂ .01	♂ .01	♂ .01	♂ NS	---	♂ NS	♂ .01	---	♂ NS
	♂ NS	---	---	---	---	♂ .001	♂ .01	♂ .01	♂ .01	♂ NS	---	♂ NS	♂ .01	---	♂ NS
	♂ NS	---	---	---	---	♂ .001	♂ .01	♂ .01	♂ .01	♂ NS	---	♂ NS	♂ .01	---	♂ NS
	♂ NS	---	---	---	---	♂ .001	♂ .01	♂ .01	♂ .01	♂ NS	---	♂ NS	♂ .01	---	♂ NS
	♂ NS	---	---	---	---	♂ .001	♂ .01	♂ .01	♂ .01	♂ NS	---	♂ NS	♂ .01	---	♂ NS
	♂ NS	---	---	---	---	♂ .001	♂ .01	♂ .01	♂ .01	♂ NS	---	♂ NS	♂ .01	---	♂ NS
	♂ NS	---	---	---	---	♂ .001	♂ .01	♂ .01	♂ .01	♂ NS	---	♂ NS	♂ .01	---	♂ NS
<i>Tropidoclonion lineatum</i> ¹⁰ <i>Virginia striatula</i> ¹¹ <i>valentiae</i>	♂ .001	♂ NS	♂ .001	♂ .001	♂ .05	♂ NS	♂ .01	♂ NS	♂ NS	♂ NS	♂ NS	♂ .01	♂ .01	♂ NS	♂ NS
	♂ .01	♂ NS	♂ .001	♂ NS	---	♂ .02	♂ .01	♂ NS	♂ NS	♂ NS	---	♂ .05	♂ .05	♂ NS	♂ NS

¹Indicates which sex has organ position situated more posteriorly (or the longer organ); ²NS indicates, not significantly different at p>.05; ³ indicates significantly different at designated level; ⁴T. o. couchii; ⁵T. o. hydrophilus; ⁶T. elegans terrestris; ⁷T. elegans vagans; ⁸T. sirtalis fitchii; ⁹T. sirtalis sirtalis; ¹⁰T. lineatum from Nebraska; ¹¹T. valentiae elegans

Table III. Data on sexual dimorphism reported in the literature. X indicates that the organ is longer or located more caudally in sex indicated; ND that there is no appreciable dimorphism.

Taxon	Character		post. heart	ant. liver	post. liver	post. gall bl.	ant. r. kidney	post. r. kidney	ant. l. kidney	post. l. kidney	heart length	liver length	r. kidney length	l. kidney length
	♂	♀												
Colubridae, Natricinae	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<i>Natrix</i> (=Rhabdophis) <i>chrysarga</i> ¹													X	X
<i>N.</i> (=Rhabdophis) <i>subminiata</i> ²	X		X		X		X	X	X	X			X	X
<i>N.</i> (=Sinonatrix) <i>trianguligera</i> ¹									X			X	X	X
<i>N.</i> (=Xenochrophis) <i>vittata</i> ³												X	X	X
Colubridae														
<i>Ablabes</i> (=Gongylosoma) <i>balioleira</i> ⁴	X		X		X	X	X	X	X	X	ND		X	X
<i>Calamaria</i> <i>multipunctata</i> ⁵	X		X											
<i>Coluber melanurus</i> (=Elaphe <i>flavolineata</i>) ⁶	X		X		X		X	X	X	X			X	X
<i>Dendrophis</i> (=Dendrelaphis) <i>pictus</i> ⁷											ND	ND	X	X
Colubridae, Homalopsinae														
<i>Enhydryis plumbea</i> ⁸	X		X		ND	ND	X	X	X	X			X	X
<i>Fordonia leucobalis</i> ⁸												X	X	X
<i>Homalopsis buccata</i> ⁹											ND		ND	ND
<i>Hypsirhina</i> (=Enhydryis) <i>altermans</i> ⁸	X		X		X		ND	ND	ND	ND	ND	ND	ND	ND
Acrochordidae														
<i>Acrochordus granulatus</i> ¹⁰	X		X		X		X	X	X	X	ND		ND	ND
<i>A. javanicus</i> ¹⁰	X		X		X		X	X	X	X	ND			
Aniliidae														
<i>Cylindrophis rufus</i> ¹¹	ND		ND		ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Boidae														
<i>Xenopeltis unicolor</i> ¹²	ND						ND	ND	ND	ND	ND	ND	ND	ND
Elapidae														
<i>Hydrophis fasciatus</i> ¹³												X		
Viperidae														
<i>Agkistrodon piscivorus</i> ¹⁴	X										ND	ND	ND	ND
<i>Trimeresurus gramineus</i> ¹⁵	X		X		X		X		X		X	X	X	X

¹Bergman (1959a); ²Bergman (1956b); ³Bergman (1950); ⁴Bergman (1963); ⁵Bergman (1965); ⁶Bergman (1961a); ⁷Bergman (1955b); ⁸Bergman (1960); ⁹Bergman (1951); ¹⁰Bergman (1958a); ¹¹Bergman (1953); ¹²Bergman (1955a); ¹³Bergman (1962a); ¹⁴Collins and Carpenter (1970); ¹⁵Bergman (1961b).

Dice-Leraas diagrams (Figs. 1-19) was divided into three equal triads, using the highest and lowest individual values as outer parameters. In these figures each vertical bar represents the mean, each horizontal line the range expressed as a per cent, each black rectangle the 95% confidence interval, each number the quantity of specimens examined in that taxon, each horizontal dotted line the separation between genera, and each vertical dashed line the boundary between two triads. See Table IV for a comparison of taxa assigned to the lowest, middle, and highest triads. Table V shows the degree to which each taxon differs significantly from other taxa in this study. The results of this study are compared with those of other workers in Appendix A.

Posterior End of Heart. — Assuming, strictly for the sake of comparison, that the middle triad represents the normative condition, there is a clear tendency for the heart to be situated more posteriorly than

the norm in both sexes of *Nerodia rhombifera*, *Regina alleni*, *Seminatrix pygaea*, and *Thamnophis sauritus* (*T. melanogaster*, *T. proximus*, and *T. rufipunctatus* exhibit similar tendencies, but to a lesser degree). On the other hand, *Tropidoclonian lineatum* and almost half the taxa of *Thamnophis* (including some representatives from three of Ruthven's species groups) tend to have the heart displaced anteriorly relative to the norm.

Anterior End of Liver. — The anterior end of the liver lies markedly farther posteriorly than the norm in both sexes of *Regina alleni* and *Seminatrix pygaea*. It appears to extend slightly more anteriorly than the norm in about half the taxa of *Thamnophis* (the same ones having an anteriorly displaced heart) and in female *Clonophis kirtlandii*, *Nerodia erythrogaster*, *Storeria*, *Tropidoclonion*, and *Virginia*. The most posterior placement in *Nerodia* is again found in *N. rhombifera*, and in *Thamnophis* again found in *T.*

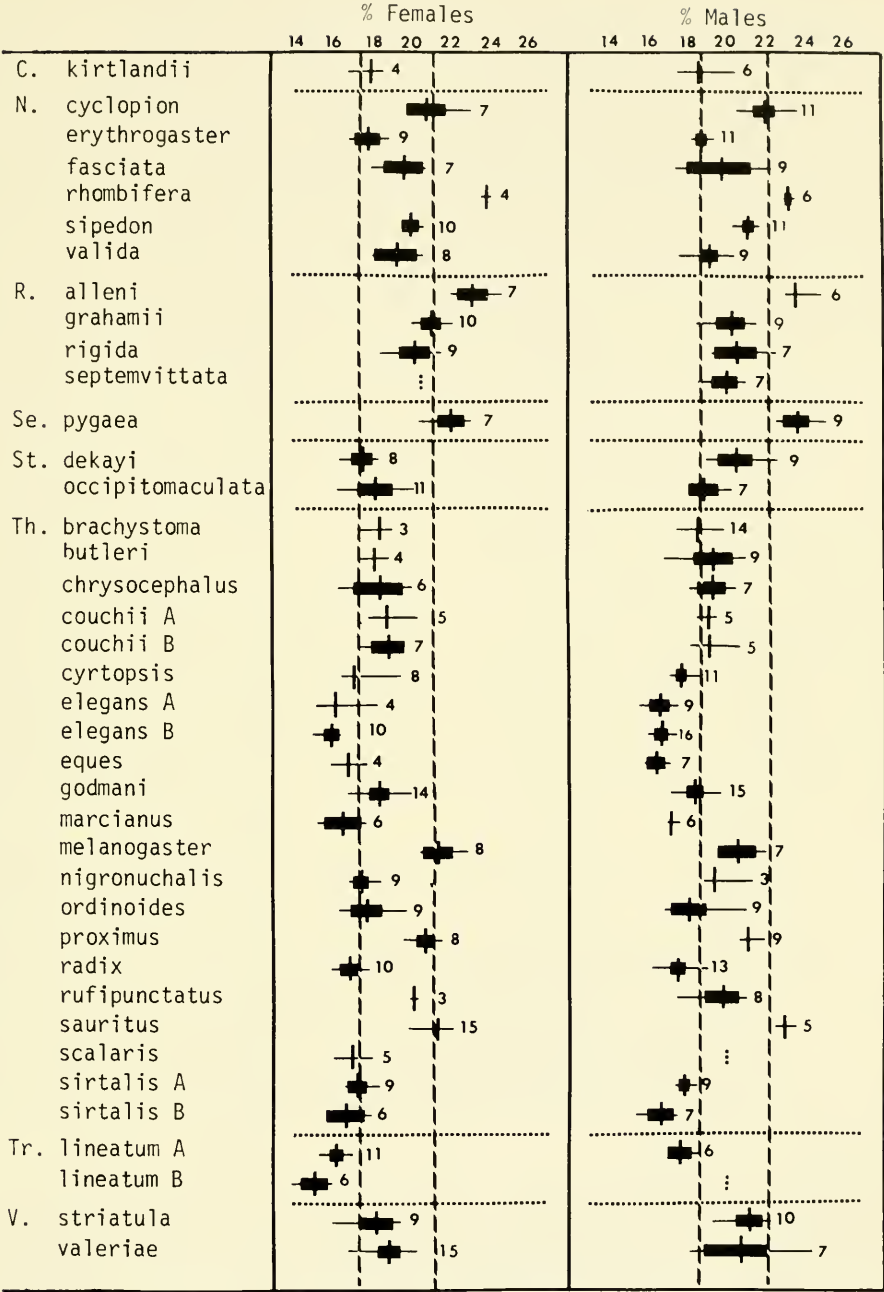


Figure 1. Location of the posterior end of the heart in thamnophiine snakes (expressed as a % of total ventrals). Construction of this and subsequent graphs is explained on pp. 127-129

Table V. Continued

Character		post. heart	ant. liver	post. liver	post. pancreas	ant. kidney	post. kidney	ant. kidney	post. kidney	liver length	r. kidney length	l. kidney length	kidney overlap	heart-liver interspace
Taxon	<i>Thamnophis couchii</i> A	63 62	54 --	79 --	65 --	81 59	76 86	73 51	59 73	42 --	43 41	43 30	51 14	15 26
	<i>couchii</i> B	53 70	68 68	84 60	35 39	78 68	73 76	73 57	59 43	21 33	38 43	24 43	43 41	19 23
	<i>elegans</i> A	89 68	82 58	79 68	53 --	89 73	78 84	89 54	73 41	21 25	43 43	57 32	54 11	37 23
	<i>elegans</i> B	92 89	82 90	79 76	76 35	86 89	78 86	92 81	78 73	21 33	62 46	76 49	49 54	15 23
	<i>melanogaster</i>	67 86	36 74	84 60	47 43	73 49	49 49	65 46	35 43	21 25	35 38	41 51	54 41	11 23
	<i>nigrougachalis</i>	54 68	-- 55	-- 76	-- 63	81 92	81 97	70 92	70 100	-- 33	19 68	32 43	41 62	-- 29
<i>Elegans</i> group	<i>ordinoides</i>	63 62	-- --	-- --	-- --	54 43	62 35	68 49	46 43	-- --	27 38	27 35	46 22	-- --
	<i>rufipunctatus</i>	60 76	61 68	-- --	-- --	78 32	81 76	76 68	81 76	-- --	46 24	32 19	35 16	44 10
	<i>scalaris</i>	-- 54	57 61	-- --	-- --	57 54	51 38	68 38	57 35	-- --	46 41	32 32	65 68	-- 26
	<i>Thamnophis chrysocephalus</i>	66 43	43 55	-- --	-- --	54 51	59 65	51 54	41 38	-- --	35 51	32 51	35 51	15 16
	<i>cyrtopsis</i>	89 54	71 71	79 88	82 65	81 78	68 62	81 78	62 73	26 79	59 84	57 43	68 51	44 26
	<i>Sirtalis godmani</i>	80 68	64 74	-- --	-- --	86 70	81 76	78 73	57 84	-- --	57 32	62 51	43 49	30 26
<i>Sirtalis</i> group	<i>sirtalis</i> A	83 65	79 65	84 80	59 35	76 59	73 35	76 51	65 35	21 25	41 49	43 49	41 43	30 19
	<i>sirtalis</i> B	89 62	61 55	-- 48	-- 22	54 59	51 49	68 54	62 38	-- 25	41 49	38 38	24 30	22 19
<i>Tropidoclonion</i>	<i>lineatum</i> A	83 86	-- --	-- --	-- --	86 84	57 27	84 84	43 43	-- --	84 92	81 92	54 73	-- 71
	<i>lineatum</i> B	-- 97	-- 42	-- 76	-- 91	-- 78	-- 38	-- 73	-- 32	-- 75	-- 81	-- 86	-- 84	-- --
<i>Virginia striatula</i>		77 57	68 52	-- 68	-- 48	92 86	51 46	78 84	30 43	-- 88	97 97	100 95	76 78	22 26
	<i>valeriae</i>	46 70	50 74	95 96	-- 48	86 84	49 35	76 84	30 54	-- 96	92 89	86 92	65 59	15 32

melanogaster (except females), *T. proximus*, *T. rufipunctatus*, and *T. sauritus*.

Posterior End of Liver. — The posterior end of the liver extends markedly farther posteriorly than the norm in both sexes of *Virginia valeriae*. In general, *Thamnophis* other than *T. proximus* and *T. sauritus* (and female *T. melanogaster*) tend to have the posterior end of the liver lying farther anteriorly than in any other thamnophiines save *Nerodia erythrogaster* and *N. valida*.

Posterior End of Pancreas. — In males the posterior end of the pancreas extends farthest posteriorly in *Thamnophis proximus* and the two species of *Storeria*; in females it extends farthest posteriorly in *Regina rigida*, *Thamnophis proximus*, *T. sauritus*, *Tropidoclonion lineatum*, and the two species of *Virginia*. About half the taxa of *Thamnophis* tend to have the pancreas located more anteriorly than in any of the other thamnophiines except female *Nerodia valida*; this condition is most pronounced in male *T. eques*. Unfortunately, the absence of data for one of the sexes in 12 of the taxa greatly reduces the value of the pancreas comparisons.

Anterior End of Right Kidney. — In all *Thamnophis* except *T. proximus* and *T. sauritus*, the right kidney in males lies anterior to the position of that organ in all other thamnophiines except *Nerodia erythrogaster*. There is a similar tendency in females, but it is neither as marked nor as consistent. On the other hand, there is marked posterior displacement from the norm in both sexes of *Seminatrix pygaea*, *Thamnophis proximus*, *T. sauritus*, and *Virginia striatula*, and a similar but slightly less pronounced tendency in both sexes of *Clonophis kirtlandii* and *V. valeriae* and in females of *Storeria occipitomaculata* and *Tropidoclonion lineatum*.

Posterior End of Right Kidney. — The pattern of variation here is generally similar to that described in the preceding account. The most notable difference, however, is that only *Thamnophis proximus*, *T. sauritus*, and female *Seminatrix pygaea* show a pronounced extension pos-

teriorly. A similar but less pronounced trend appears in males of *Clonophis kirtlandii*, all species of *Nerodia* (except *N. erythrogaster* and *N. valida*), *Regina grahamii*, and *Seminatrix pygaea*.

Anterior End of Left Kidney. — This position lies posterior to the norm in both sexes of *Clonophis kirtlandii*, *Seminatrix pygaea*, *Tropidoclonion lineatum*, both species of *Storeria*, *Thamnophis proximus*, *T. sauritus*, and both species of *Virginia*, and in females of *Regina grahamii*. *Nerodia erythrogaster* and about half the taxa of *Thamnophis* show a slight tendency toward anterior displacement from the norm (in most cases this tendency is better developed in males).

Posterior End of Left Kidney. — The end of the left kidney extends more posteriorly than the norm in both sexes of *Storeria dekayi*, *Thamnophis proximus*, and *T. sauritus*, and to a lesser degree in males of *Storeria occipitomaculata* and females of *Regina grahamii*, *Seminatrix pygaea*, and *Thamnophis radix*. Males of about half the taxa of *Thamnophis* show a tendency toward anterior displacement from the norm, as do females of *T. nigronuchalis*.

Liver Length. — The liver is relatively long in the genera *Storeria*, *Tropidoclonion*, and *Virginia*. Unfortunately we have no data for males of the latter two genera or for female *Seminatrix*. Male *Seminatrix* have an even longer liver than is found in the other three genera. Two male and two female *Clonophis*, although not shown on the Dice-Lerras diagram because of the small sample size, also have a relatively long liver (mean values of 26.3 and 26.0, respectively).

Right Kidney Length. — The right kidney is relatively short in both sexes of *Tropidoclonion lineatum* and in both species of *Virginia*, and in females of *Storeria occipitomaculata* and males of *Seminatrix pygaea*. In males there is a tendency toward a greater length than the norm in the species of *Nerodia* and about half the taxa of *Thamnophis*; the same tendency is present in females but it is developed to a

lesser degree. Notably, *Clonophis* and *Regina* separate completely from *Nerodia* on this character.

Left Kidney Length. — The left kidney is relatively short in both sexes of *Semina-trix pygaea*, *Thamnophis sauritus*, *Tropi-do-clonion lineatum*, and the two species of *Virginia*, and in females of *Clonophis kirt-*

landii, *Storeria occipitomaculata*, and *Thamnophis proximus*. The tendencies seen with regard to left and right kidney lengths are generally similar, but the distinction between *Nerodia* and *Clonophis-Regina* is less clearly defined in the left kidney length of males.

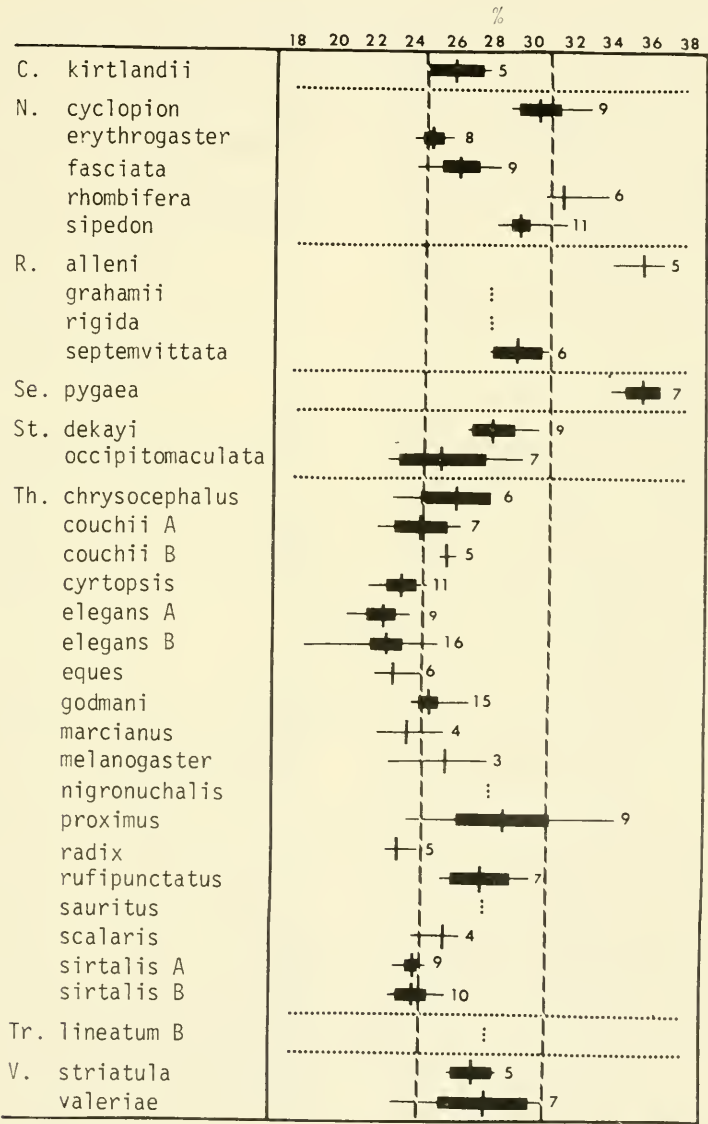


Figure 2. Location of the anterior end of the liver in male thamnophiine snakes (expressed as a % of total ventrals).

Heart-Liver Interspace. — Both sexes of *Seminatrix pygaea* and males of *Regina alleni* have a relatively long interspace, a tendency that is also seen in males of *Nerodia sipedon* and *Regina septemvittata*, and in females of *Nerodia cyclopion*, *Tropidoclonion lineatum*, and three

species of *Regina* (no data available for female *septemvittata*). The interspace is relatively short in females of *Clonophis kirtlandii*.

Kidney Overlap. — The greatest degree of kidney overlap occurs in *Nerodia* and a few *Thamnophis* (*cyrtopsis*, male

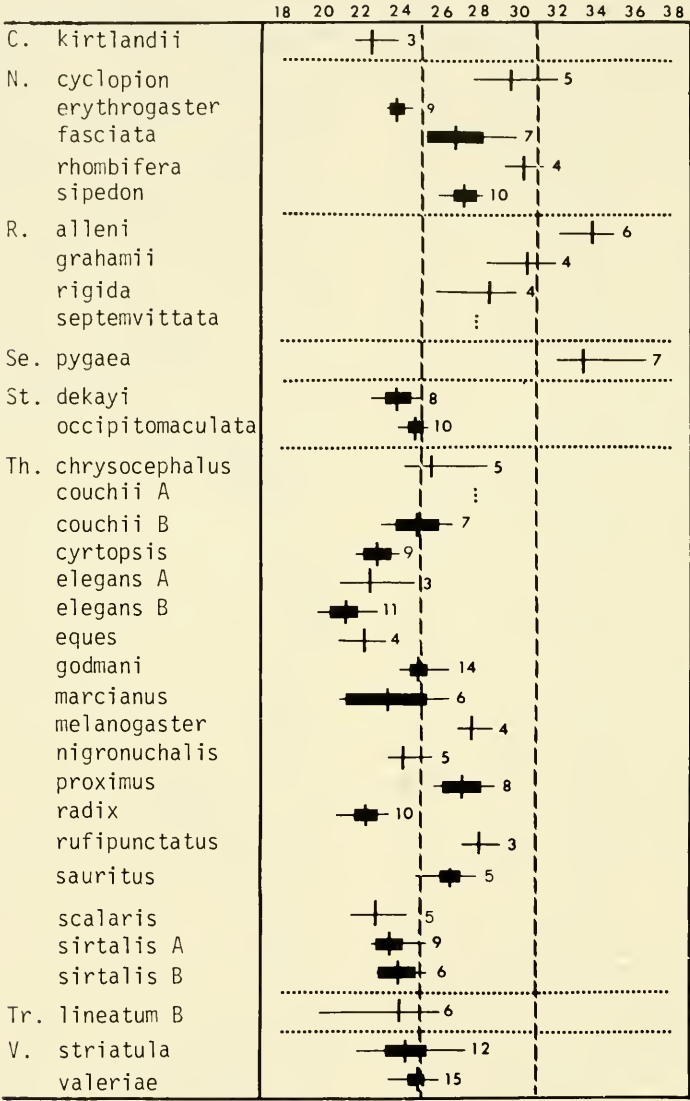


Figure 3. Location of the anterior end of the liver in female thamnophiine snakes (expressed as a % of total ventrals).

marcianus, *melanogaster*, *radix*, *scalaris*). The least amount of overlap occurs in *Storeria occipitomaculata* and *Virginia striatula*. *Clonophis*-*Regina* again separate completely from *Nerodia*.

Liver-Gall Bladder Interspace. — McDowell (1979) reported that the most striking visceral feature of all *Acrochordus* is the close proximity of the gall bladder to the liver. In *Acrochordus granulatus* the gall bladder usually lies behind the liver, but is separated from it by less than one gall bladder length; in *A. arafurae* the gall bladder lies immediately behind the liver; and in *A. javanicus* the gall bladder is usually overlapped by the posterior end of the liver. McDowell stated that *Acrochordus* seems to be the only snake genus known to have the gall bladder so near the liver, and he noted that having the gall bladder displaced far behind the liver is often cited as a distinctive feature of snakes.

A survey of Bergman's many studies (1950-1965) on the visceral topography of a wide variety of snakes reveals that the condition described by McDowell (1979) is somewhat more widespread than he had thought and that this feature exhibits sexual dimorphism in a number of species. Bergman's findings can be summarized as follows:

1. No interspace, liver overlaps gall bladder: Colubridae, Homalopsinae — female *Enhydris enhydris* (1955e), *Homalopsis buccata* (1951), male *Hypsirhina* (= *Enhydris*) *alternans* (1960); Acrochordidae — *Acrochordus javanicus* (1958a).

2. Interspace less than one gall bladder length: Colubridae, Homalopsinae — male *Enhydris enhydris* (1955e), female *Cerberus rhynchops* (1955c), *Hypsirhina* (= *Enhydris*) *plumbea* (1960); Acrochordidae — *Acrochordus granulatus* (1958a); Elapidae — *Enhydrina schistosa* (1955d).

3. Interspace one to two times gall bladder length: Colubridae, Natricinae — male *Natrix* (= *Sinonatrix*) *trianguligera* (1959b), female *Natrix* (= *Xenochrophis*) *vittata* (1950); Colubridae, Homalopsinae — female *Hypsirhina* (= *Enhydris*) *alter-*

nans (1960), male *Cerberus rhynchops* (1955c); Elapidae — female *Hydrophis fasciatus* (1962a), female *Thalassophis anomalus* (1954); Viperidae — *Ancistrodon* (= *Calloselasma*) *rhodostoma* (1961b), *Trimeresurus gramineus* (1961b).

4. Interspace more than twice gall bladder length: Colubridae, Natricinae — *Natrix* (= *Rhabdophis*) *chrysarga* (1959a), *N.* (= *Rhabdophis*) *subminiata* (1956b), female *N.* (= *Sinonatrix*) *trianguligera* (1959b), male *N.* (= *Xenochrophis*) *vittata* (1950); Colubridae, Homalopsinae — *Fordonia leucobalia* (1960); other Colubridae — *Ablabes* (= *Gongylosoma*) *baliodeira* (1963), *Calamaria multipunctata* (1965), *Coluber melanurus* (= *Elaphe flavolineata*) (1961a), *C.* (= *Elaphe*) *radiatus* (1961a), *Dendrophis* (= *Dendrelaphis*) *pictus* (1955b), *Dryophis* (= *Ahaetulla*) *prasinus* (1956a), *Elapoides fuscus* (1956-58), *Pyas korros*, *P. mucosa* (1952); Aniliidae — *Cylindrophis rufus* (1953); Boidae — *Xenopeltis unicolor* (1955a); Elapidae — *Bungarus candidus*, *B. fasciatus*, male *Hydrophis fasciatus*, *Naja tripudians* (1962b), male *Thalassophis anomalus* (1954).

We found the *Thamnophiini* to be highly variable in this character although the majority of individuals do have an interspace greater than one gall bladder length (see Table VI for details). Noteworthy exceptions are the females of *Thamnophis melanogaster* and *Virginia valeriae*, in which the mean values are 0.9 and 0.2, respectively. In general, the interspace tends to be relatively short in most *Nerodia*, *Storeria*, and *Virginia*, and relatively long in *Regina*, most *Thamnophis*, and *Tropidoclonion*. By far the greatest interspace/gall bladder values occur in *Thamnophis proximus* and *T. sauritus*, but this reflects unusually short gall bladders rather than exceptionally long interspaces in these animals.

Asymmetry of Kidney Lengths

In only 11 taxa are the differences in length between the right and left kidneys statistically significant. The left kidney is longer than the right in male *Thamnophis*

c. couchii (difference between means 1.6, significantly different at $p < .01$) and female *T. nigronuchalis* (1.4, $p < .02$). The right kidney is longer than the left in male *Thamnophis sauritus* (1.2, $p < .01$) and female *T. cyrtopsis* (1.7, $p < .02$), *T. radix* (1.9, $p < .01$), *T. sirtalis fitchi* (2.0, $p < .01$), *Nerodia cyclopion* (1.4, $p < .01$), *N. rhombifera* (1.7, $p < .05$), *N. sipedon* (1.2,

$p < .02$), *Regina alleni* (1.5, $p < .02$), and *R. grahamii* (1.2, $p < .05$).

DISCRIMINANT ANALYSIS

In an effort to ascertain which, if any, characters could be used taxonomically to separate genera and other groups, stepwise discriminant analysis was performed using the Statistical Package for the Social

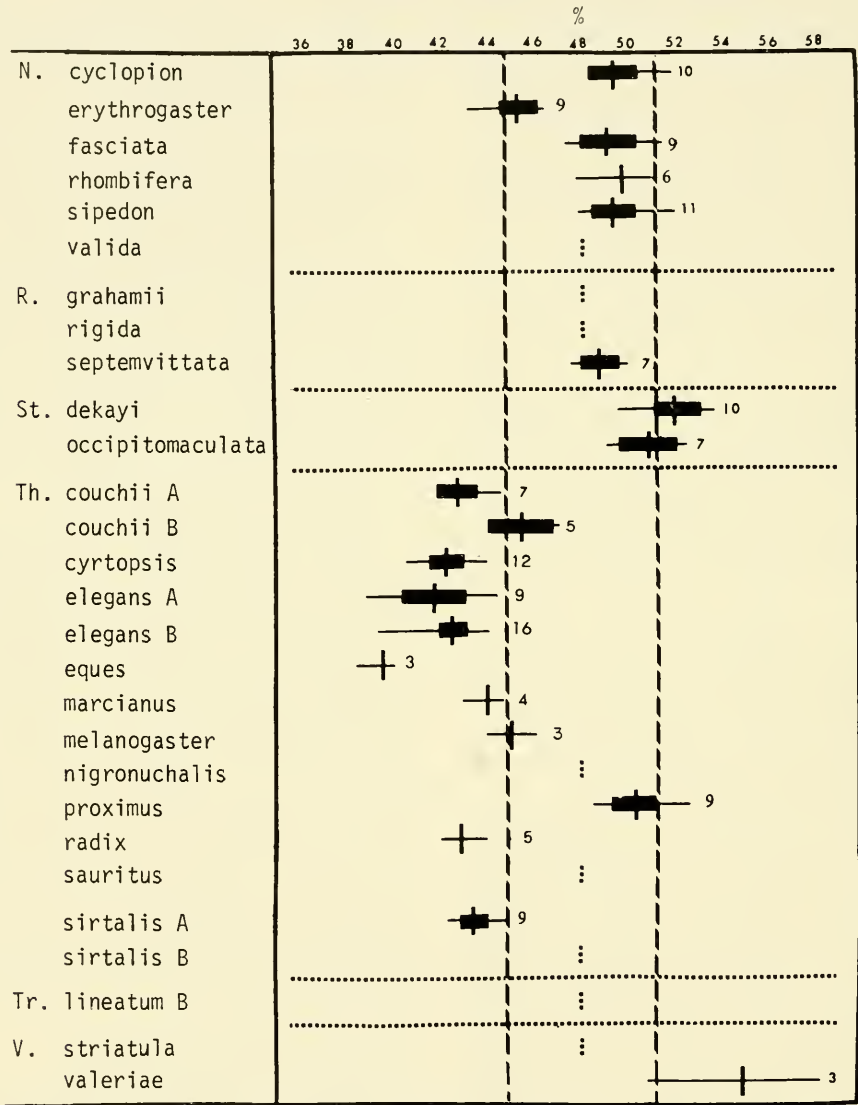


Figure 4. Location of the posterior end of the liver in male thamnophiine snakes (expressed as a % of total ventrals).

Sciences (SPSS) (Nie et al., 1975; Hull and Nie, 1979). Only adult male specimens were used in this part of the study (see Materials and Methods). Elsewhere in this paper under Materials and Methods we have discussed the details of how the specimens were treated for the discriminant analysis.

In stepwise dicriminant analysis, the variable that best discriminates among the groups enters the model first, then the next best discriminating variable enters, etc. The process terminates when there are no more variables that contribute significantly to discrimination among the groups. In this analysis four variables were found to discriminate among the groups. In the rior right kidney, (3) posterior heart, and (4) kidney overlap. In the four variable model, all groups but *Clonophis* and *Tropidoclonion* were significantly different ($p<.05$) (see Table VII).

Eleven groups were used in the discriminant analysis, and four linear discriminant functions were computed. However, only the first two were retained as

they explain 83.21% of the relative variation (function 1 accounts for 59.82% and function 2 accounts for 23.39%). Function 1 is generally a right kidney anterior dimension. Function 2 is a kidney overlap and heart posterior dimension. The all-groups scatterpoint diagram with two discriminant functions appears in Fig. 20. On dimension 1, we see that *Seminatrix*, the *Sauritus* group of *Thamnophis*, and *Virginia* are separated widely from the *Elegans*, *Sirtalis*, and *Radix* groups of *Thamnophis*. On dimension 2, we see that *Nerodia* is the most widely separated group from *Tropidoclonion* and *Storeria*. Apparently, as the right kidney anterior measure increases, the specimens are more likely to belong to *Seminatrix*, the *Sauritus* group of *Thamnophis*, and *Virginia*. Similarly, as right kidney anterior decreases, specimens are more likely to belong to the *Elegans*, *Sirtalis*, and *Radix* groups of *Thamnophis*. Also, as kidney overlap and heart posterior measurements increase, the specimens are more likely to belong to *Nerodia*. Similarly, as these mea-

Table VII. F statistics and significance between pairs of taxa in the four variable model (df=4, 280).

Taxon	1 <i>Clonophis</i>	2	3	4	5	6	7	8	9	10
2 <i>Nerodia</i>	16.557 0.0000*									
3 <i>Regina</i>	7.4392 0.0000	15.827 0.0000								
4 <i>Seminatrix</i>	11.479 0.0000	26.348 0.0000	9.4137 0.0000							
5 <i>Storeria</i>	6.7379 0.0000	52.616 0.0000	20.963 0.0000	20.288 0.0000						
6 <i>Thamnophis</i> (<i>Sauritus</i> group)	6.5426 0.0000	27.357 0.0000	11.059 0.0000	5.1882 0.0005	14.861 0.0000					
7 <i>Thamnophis</i> (<i>Radix</i> group)	8.6467 0.0000	38.890 0.0000	20.513 0.0000	37.208 0.0000	24.534 0.0000	37.326 0.0000				
8 <i>Thamnophis</i> (<i>Elegans</i> group)	24.343 0.0000	70.264 0.0000	40.509 0.0000	52.621 0.0000	58.937 0.0000	74.748 0.0000	24.394 0.0000			
9 <i>Thamnophis</i> (<i>Sirtalis</i> group)	16.569 0.0000	43.839 0.0000	27.789 0.0000	44.918 0.0000	42.816 0.0000	55.380 0.0000	7.5158 0.0000	4.7066 0.0011		
10 <i>Tropidoclonion</i>	1.2101 0.3067	23.372 0.0000	11.002 0.0000	14.360 0.0000	8.1301 0.0000	11.953 0.0000	10.465 0.0000	22.652 0.0000	16.875 0.0000	
11 <i>Virginia</i>	7.9233 0.0000	57.601 0.0000	15.848 0.0000	7.0630 0.0000	28.365 0.0000	16.768 0.0000	50.209 0.0000	76.698 0.0000	62.552 0.0000	6.9183 0.0000

* significance level

Table VI. Liver-gall bladder interspace relative to gall bladder length.

Taxon	liver-gall bladder interspace ♂♂	gall bladder length ♀♀	interspace length gall bladder length	
			♂♂	♀♀
<i>Nerodia</i>				
<i>cyclopion</i>	2.8(0.7-5.7) ⁸ 1	3.2(2.0-4.4) ⁴	2.2(1.4-2.9)	2.8(2.1-3.4)
<i>erythrogastrer</i>	6.3(4.1-8.8) ⁷	5.3(4.0-10.3) ⁹	2.2(2.0-2.1)	2.6(1.4-4.2)
<i>fasciata</i>	3.9(2.3-6.1) ⁸	5.0(3.1-6.7) ⁷	2.4(1.5-3.1)	2.7(2.2-3.1)
<i>rhombifera</i>	3.6(2.2-5.8) ⁶	3.1(2.1-4.3) ³	2.0(1.4-2.9)	2.4(2.1-2.9)
<i>sipidon</i>	3.6(0.8-6.3) ¹¹	4.2(1.4-7.4) ⁹	2.8(1.5-3.6)	2.5(2.2-3.0)
<i>valida</i>	---	5.4(3.6-7.4) ⁴	---	2.4(2.2-3.1)
<i>Regina</i>				
<i>alleni</i>	---	7.2(4.1-9.5) ³	---	2.4(1.6-3.3)
<i>grahamii</i>	---	5.7(3.5-6.7) ⁴	---	2.4(2.3-2.5)
<i>rigida</i>	---	8.4(6.0-9.6) ⁵	---	2.6(1.5-3.6)
<i>septemvittata</i>	8.0(4.9-9.4) ⁴	---	2.5(2.0-3.0)	---
<i>Storeria</i>				
<i>dekayi</i>	4.7(2.4-6.1) ⁸	4.2(2.2-5.2) ⁷	2.2(1.5-2.4)	2.4(1.5-2.9)
<i>occipitomaculata</i>	3.3(1.7-4.9) ⁶	---	2.4(1.6-3.4)	---
<i>Thamniophis</i>				
<i>couchii</i> A	6.3(3.0-9.5) ⁴	---	2.3(1.8-2.8)	---
<i>couchii</i> B	6.0(5.0-6.7) ⁵	4.4(1.9-6.9) ⁴	2.4(1.8-3.1)	2.1(1.9-2.5)
<i>cyrtopis</i>	7.5(5.3-9.0) ¹⁰	7.5(4.3-9.9) ⁹	1.8(1.2-2.3)	2.0(1.3-2.5)
<i>elegans</i> A	8.9(6.3-11.5) ⁷	9.4(7.6-12.1) ³	2.5(2.5-2.6)	2.2(1.2-2.7)
<i>elegans</i> B	7.3(4.5-10.4) ¹⁶	8.4(5.6-10.8) ¹⁰	1.7(1.2-2.5)	2.2(1.8-2.5)
<i>eques</i>	5.2(3.0-6.6) ⁶	5.9(5.1-7.6) ³	2.1(1.2-2.4)	1.7(1.3-1.9)
<i>marctianus</i>	7.8(4.5-12.2) ⁵	7.1(4.8-8.9) ⁴	2.1(1.3-2.6)	2.1(1.4-2.7)
<i>melanogaster</i>	5.2(4.9-5.4) ³	2.2(1.4-3.0) ⁴	2.0(2.0-2.1)	2.5(2.1-3.7)
<i>nigronuchalis</i>	---	3.8(0.6-5.9) ⁷	---	2.1(1.3-2.6)
<i>protrichus</i>	7.5(4.7-8.9) ⁹	7.6(6.1-9.5) ⁷	1.6(1.2-2.4)	1.7(1.2-1.8)
<i>radix</i>	7.3(4.8-10.5) ¹⁰	5.1(1.3-8.6) ¹⁰	2.0(1.3-2.5)	2.1(1.8-3.2)
<i>sauritus</i>	---	6.8(3.8-9.9) ⁵	---	1.5(1.2-2.5)
<i>sirtalis</i> A	7.6(6.6-9.2) ⁸	6.2(1.8-9.9) ⁸	2.0(1.8-2.4)	2.2(1.3-3.1)
<i>sirtalis</i> B	---	6.2(5.2-7.8) ⁶	---	2.1(1.9-2.6)
<i>Tropidocolonion</i>				
<i>luteatum</i> B	---	7.9(6.7-8.8) ⁴	---	2.2(2.2-2.3)
<i>Virginia</i>				
<i>striatula</i>	---	4.7(1.7-8.8) ⁴	---	2.4(1.7-3.1)
<i>valeriae</i>	---	1.6(-2.4-5.5) ³ 2	---	2.7(1.6-3.3)

¹ mean (range of variation) number of specimens ² negative value indicates an overlap

surements decrease, the specimens are more likely to belong to *Tropidoclonion* and *Storeria*.

The model was used to classify the 294 original specimens. The classification matrix indicates how specimens were classified by the model (see Table VIII). Over 66% of the specimens were correctly classified. The *Elegans* group of *Thamnophis*, which had the largest number of speci-

mens, had the highest prior probability of 21.4%. In the order of highest percentage to lowest, *Virginia* was classified correctly 88.2% of the time, *Nerodia* 86.3%, the *Sauritus* group of *Thamnophis* 85.7%, the *Elegans* group of *Thamnophis* 76.2%, *Seminatrix* 75.0%, *Storeria* 66.7%, the *Radix* group of *Thamnophis* 63.6%, *Tropidoclonion* 60.0%, *Regina* 58.3%, the *Sirtalis* group of *Thamnophis* 29.8%, and

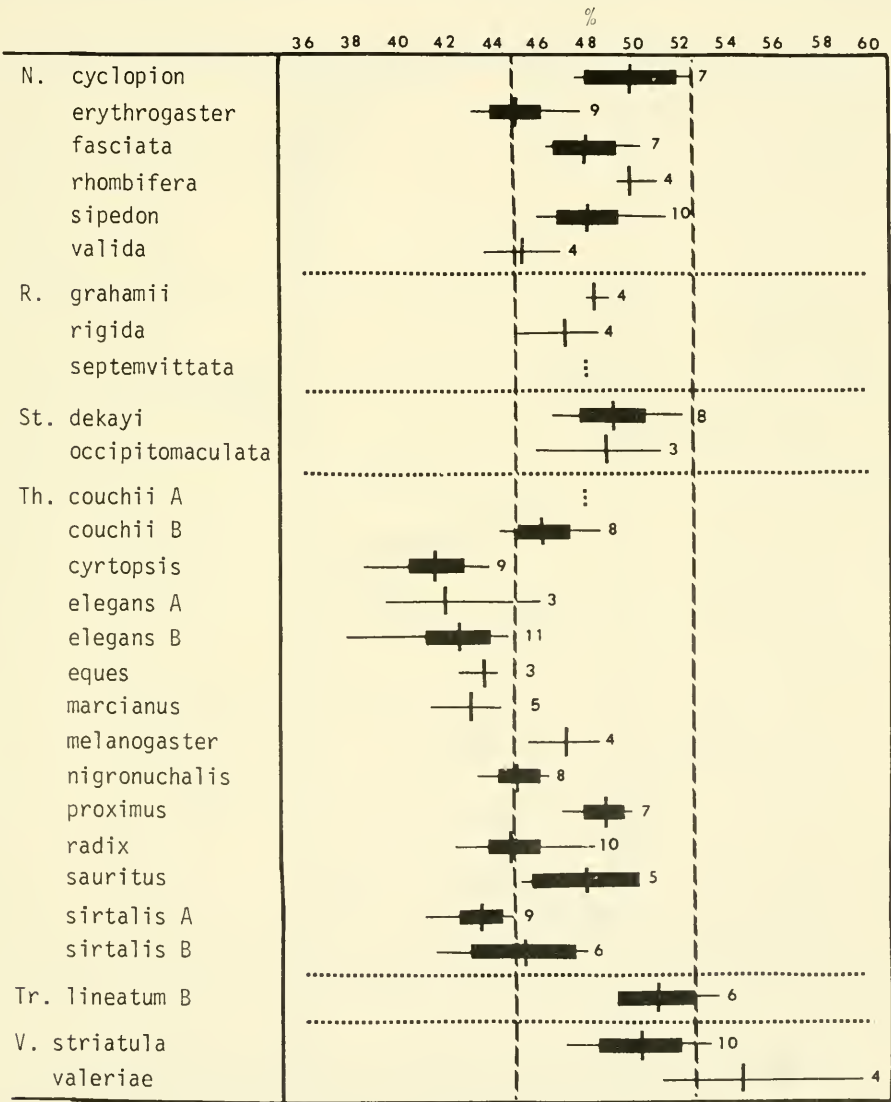


Figure 5. Location of the posterior end of the liver in female thamnophiine snakes (expressed as a % of total ventrals).

Clonophis 16.7% (less than chance). *Virginia* has the highest percentage correctly classified, the *Sauritus* group of *Thamnophis* the third highest, and *Seminatrix* the fifth highest, a notable finding inasmuch as these taxa ranked only sixth, eighth, and ninth, respectively, in terms of the number of specimens per group.

The discriminant analysis was able to distinguish among the eight genera (as well as among Ruthven's four species groups of

Thamnophis) at the 0.05 level except that *Clonophis* and *Tropidoclonion* could not be distinguished from each other. All groups except *Clonophis* could be classified by the model with greater success than the 21% prior probability obtained by placing them all in the *Elegans* group of *Thamnophis*, the numerically largest sample. Thus the visceral topographic data are remarkably concordant with the other kinds of morphological data that have

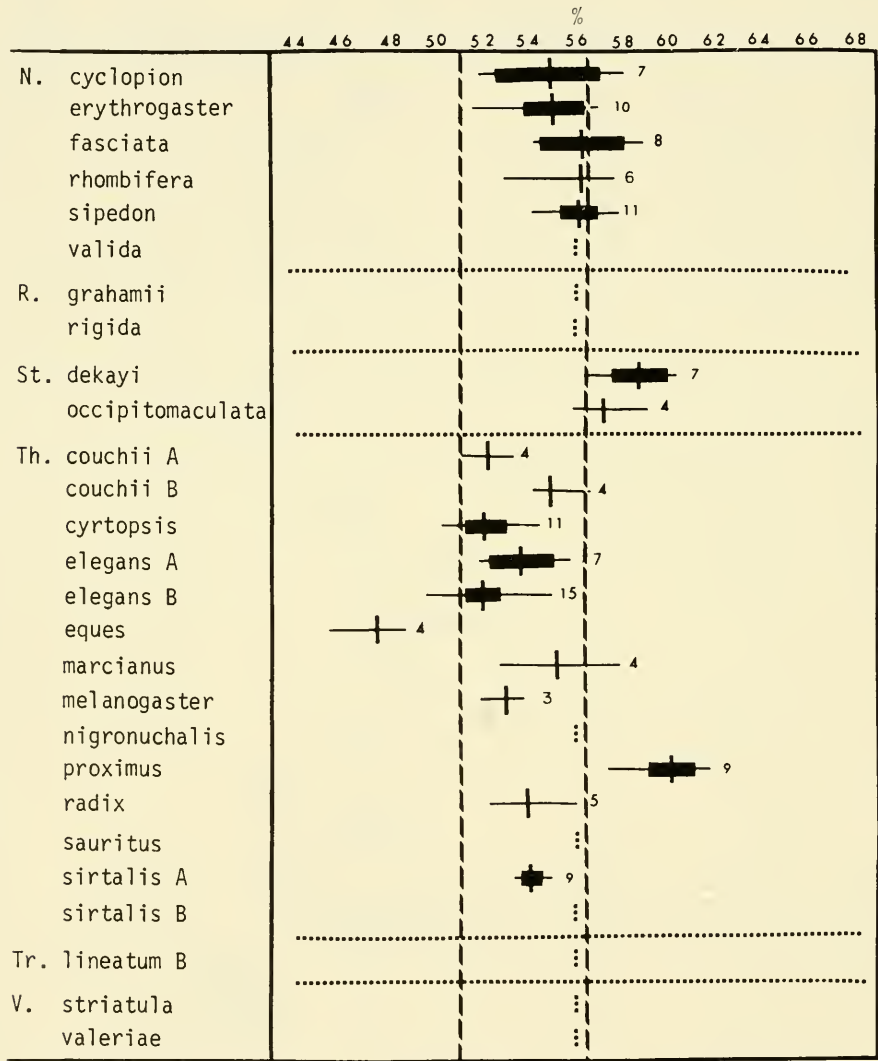


Figure 6. Location of the posterior end of the pancreas in male thamnophiine snakes (expressed as a % of total ventrals).

been used to generate the existing classification of thamnophiine snakes.

Within the genus *Thamnophis*, all of Ruthven's species groups except the *Sirtalis* group are distinguishable from each other. In the classification matrix (Table VIII), members of the *Sirtalis* group are misclassified as members of the *Elegans* group much more frequently (42.6%) than they are correctly classified (29.8%); they also are often misclassified (21.3%) as

members of the *Radix* group. One of the most interesting results of the discriminant analysis is the wide separation of the *Sauritus* group from the other three groups (see Fig. 20).

CONCLUSIONS

Visceral topographic data alone do not clearly delimit thamnophiine genera nor establish inter- or intrageneric relationships. Nevertheless, some trends are

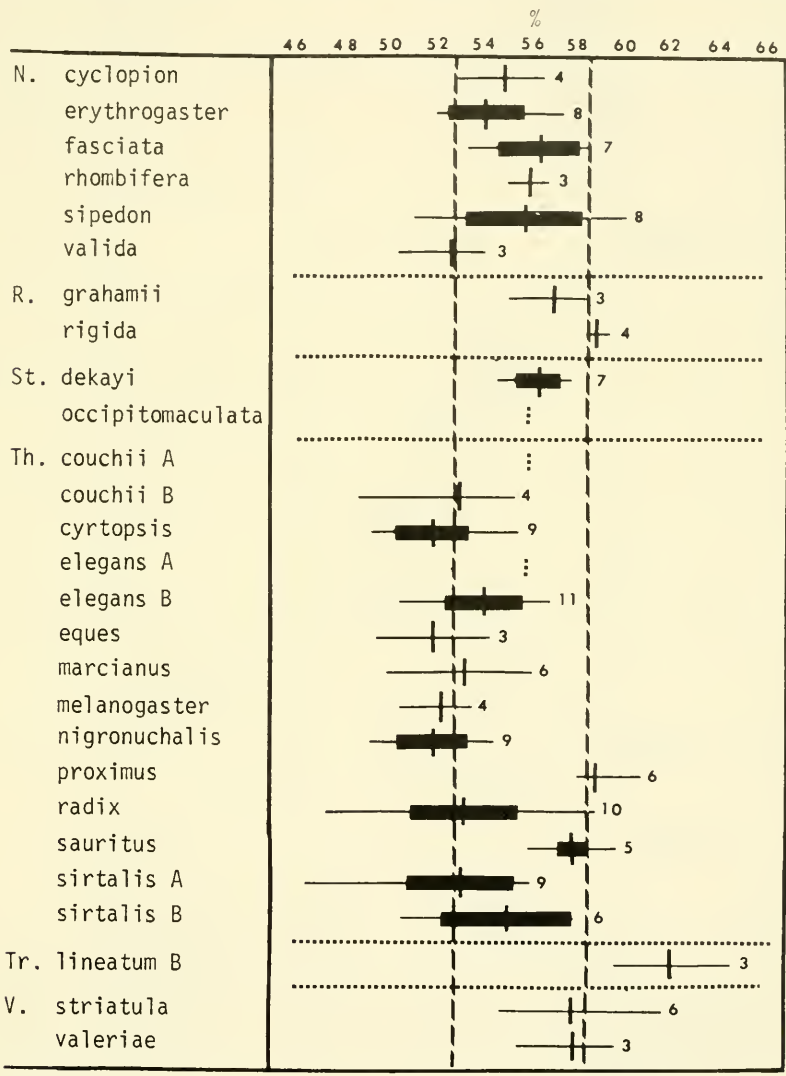


Figure 7. Location of the posterior end of the pancreas in female thamnophiine snakes (expressed as a % of total ventrals).

Table VIII. Classification matrix.

Actual Taxon	No. of Cases	Predicted Taxon Membership										
		1	2	3	4	5	6	7	8	9	10	11
1 <i>Clonophis</i>	6	1* 16.7	1 16.7	0 0.0	0 0.0	0 0.0	1 16.7	2 33.3	0 0.0	0 0.0	1 16.7	0 0.0
2 <i>Nerodia</i>	51	0 0.0	44 86.3	3 5.9	0 0.0	0 0.0	0 0.0	2 3.9	1 2.0	1 2.0	0 0.0	0 0.0
3 <i>Regina</i>	24	0 0.0	5 20.8	14 58.3	1 4.2	1 4.2	0 0.0	2 8.3	0 0.0	0 0.0	0 0.0	1 4.2
4 <i>Seminatrix</i>	8	0 0.0	0 0.0	0 0.0	6 75.0	0 0.0	1 12.5	0 0.0	0 0.0	0 0.0	0 0.0	1 12.5
5 <i>Storeria</i>	15	0 0.0	0 0.0	0 0.0	0 0.0	10 66.7	3 20.0	2 13.3	0 0.0	0 0.0	0 0.0	0 0.0
6 <i>Thamnophis</i> (<i>Sauritus</i> group)	14	0 0.0	0 0.0	1 7.1	1 7.1	0 0.0	12 85.7	0 0.0	0 0.0	0 0.0	0 0.0	0 0.0
7 <i>Thamnophis</i> (<i>Radix</i> group)	44	0 0.0	3 6.8	0 0.0	0 0.0	4 9.1	0 0.0	28 63.6	5 11.4	4 9.1	0 0.0	0 0.0
8 <i>Thamnophis</i> (<i>Elegans</i> group)	63	0 0.0	6 9.5	0 0.0	0 0.0	0 0.0	0 0.0	2 3.2	48 76.2	7 11.1	0 0.0	0 0.0
9 <i>Thamnophis</i> (<i>Sirtalis</i> group)	47	0 0.0	3 6.4	0 0.0	0 0.0	0 0.0	0 0.0	10 21.3	20 42.6	14 29.8	0 0.0	0 0.0
10 <i>Tropidoclonion</i>	5	1 20.0	0 0.0	0 0.0	0 0.0	1 20.0	0 0.0	0 0.0	0 0.0	0 0.0	3 60.0	0 0.0
11 <i>Virginia</i>	17	0 0.0	0 0.0	0 0.0	1 5.9	1 5.9	0 0.0	0 0.0	0 0.0	0 0.0	0 0.0	15 88.2

* number and percentage of specimens classified by the model into each taxon; diagonal represents correct classification.

apparent that serve to support taxonomic conclusions based on other kinds of characters.

Clonophis kirtlandii differs from all species of *Nerodia* (in which genus it was formerly placed; see Rossman, 1963b) in

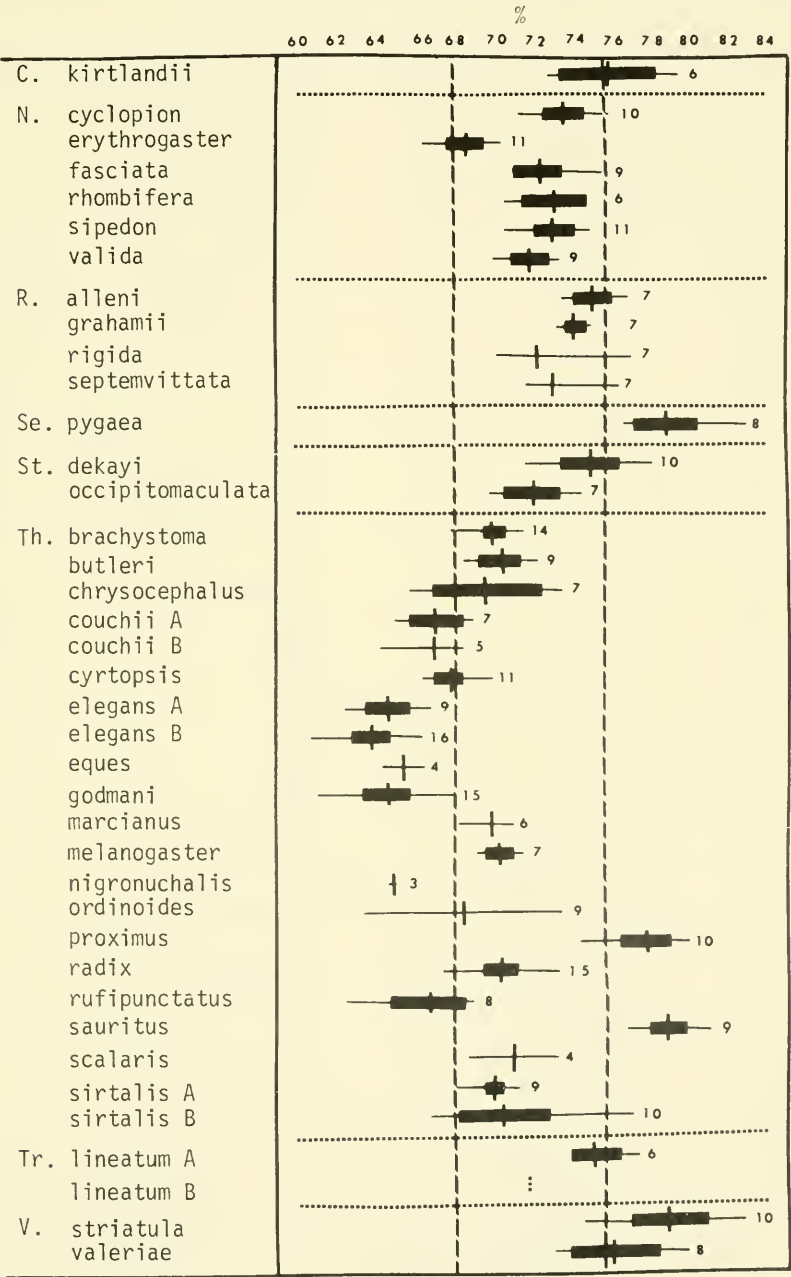


Figure 8. Location of the anterior end of the right kidney in male thamnophiine snakes (expressed as a % of total ventrals).

having a longer liver, shorter kidneys (the anterior ends have been displaced posteriorly), and less kidney overlap. Female *Clonophis* can also be distinguished from

female *Nerodia* by having a shorter heart-liver interspace, but this distinction does not apply to males.

The genus *Regina* has also been included

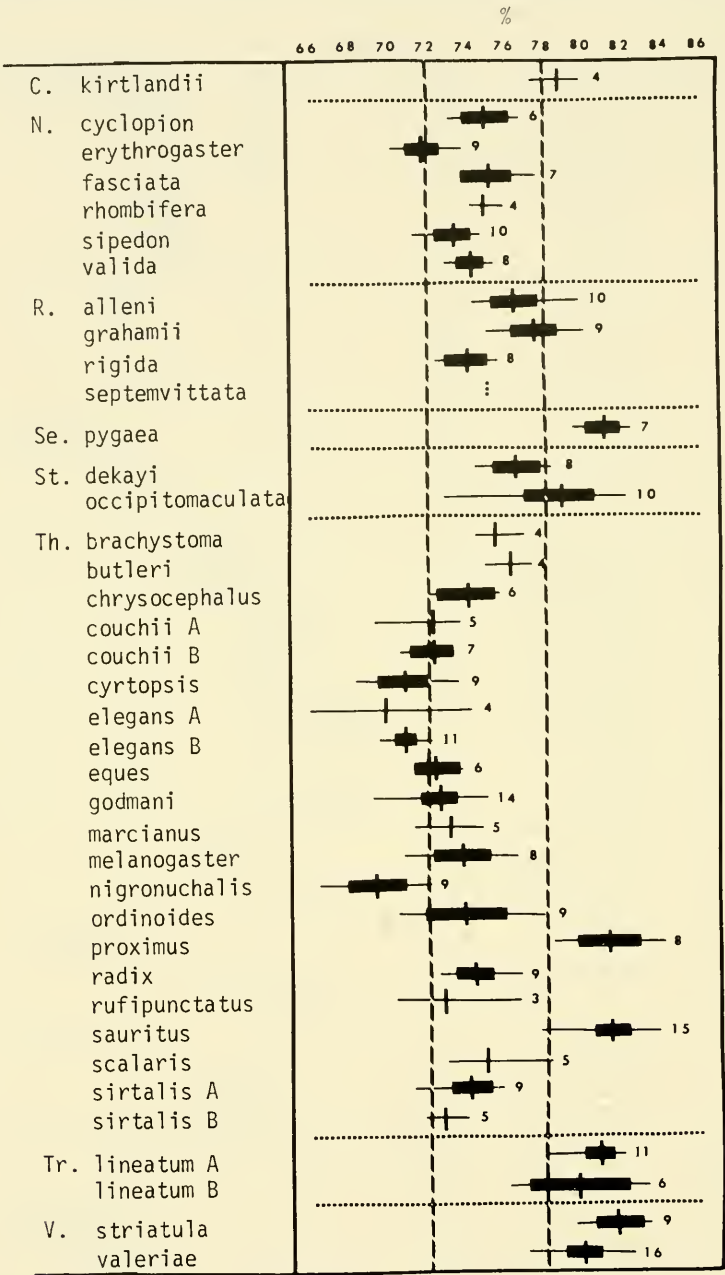


Figure 9. Location of the anterior end of the right kidney in female thamnophiine snakes (expressed as a % of total ventrals).

in *Nerodia* in the past (Smith and Huheey, 1960; Rossman, 1963b). It differs from *Nerodia* in having somewhat shorter kidneys, less kidney overlap, and a longer

liver-gall bladder interspace. *Regina alleni* has both the posterior end of the heart and the anterior end of the liver situated more posteriorly than in the other crayfish

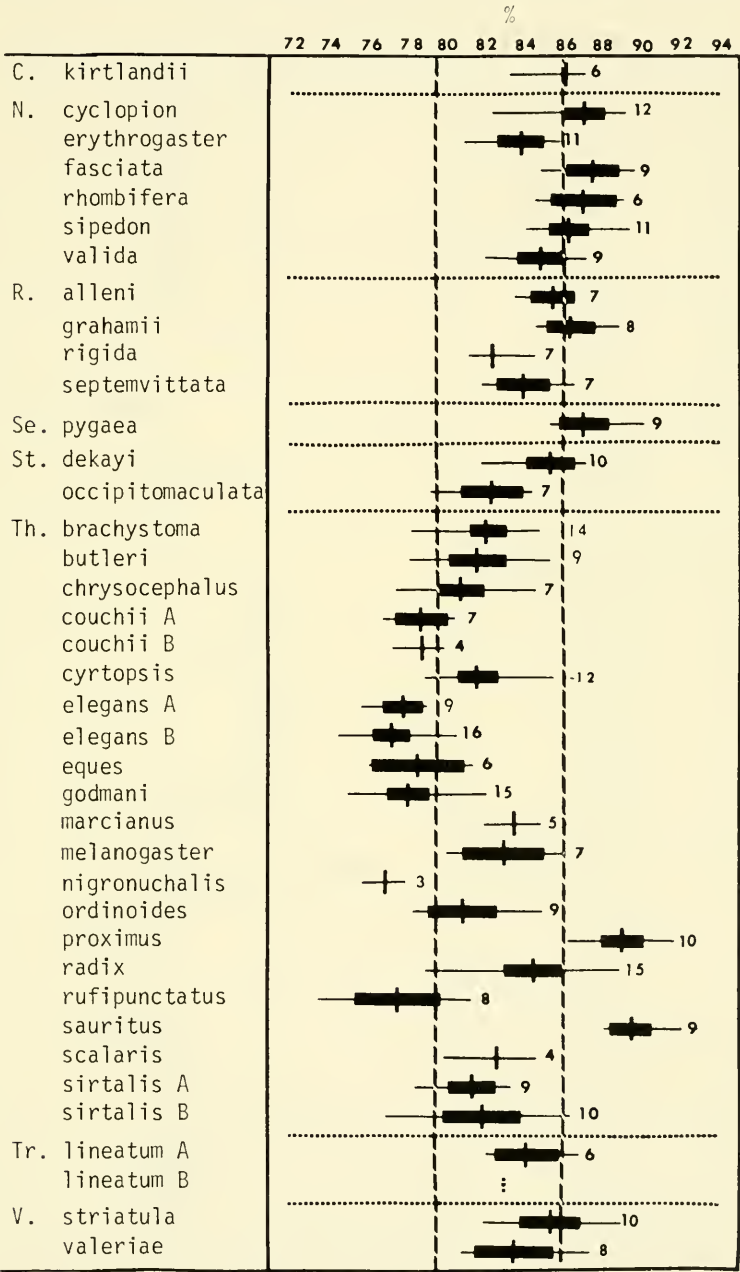


Figure 10. Location of the posterior end of the right kidney in male thamnophiine snakes (expressed as a % of total ventrals).

snakes. Male *R. alleni* have the longest heart-liver interspace of any thamnophiine in our study, but data for male *R. grahamii* and *R. rigida* are lacking. In terms of

positional characters (as opposed to organ or interspace lengths), the organs of *R. rigida* usually have the anteriormost positions within the genus.

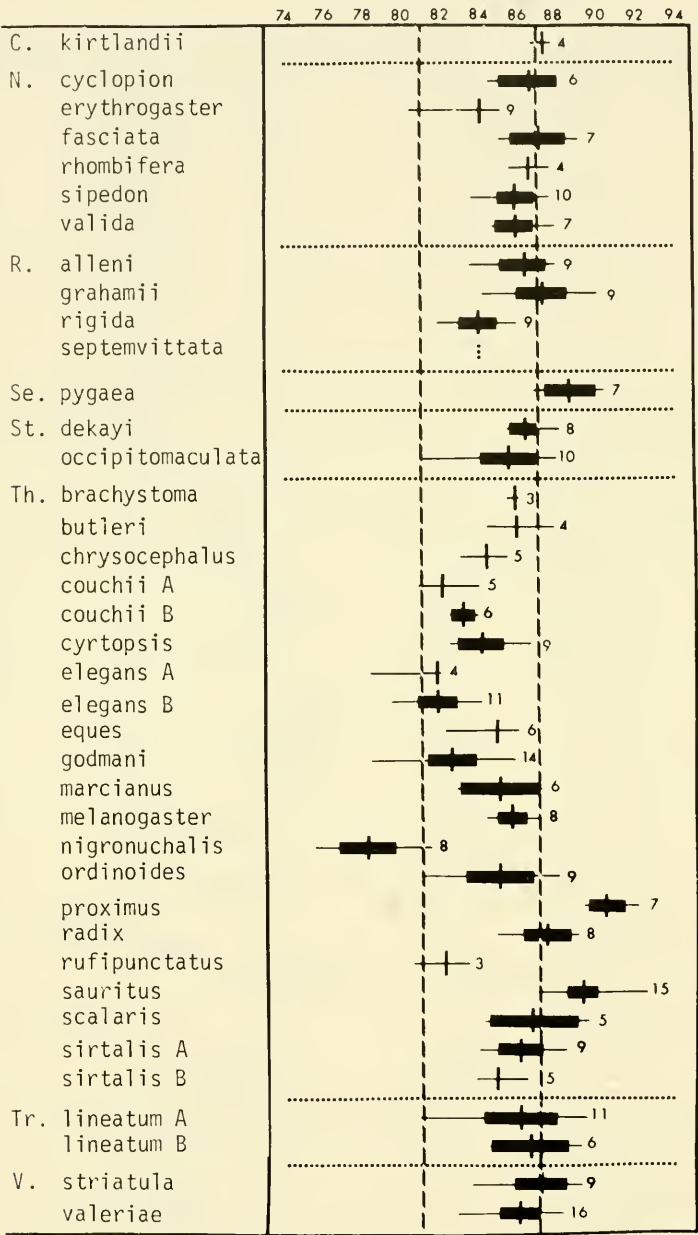


Figure 11. Location of the posterior end of the right kidney in female thamnophiine snakes (expressed as a % of total ventrals).

Within the genus *Nerodia*, where there is variation from the generic "norm," *N. erythrogaster* or, less frequently, *N. valida* invariably has the anteriormost position.

Nerodia rhombifera shows a posterior displacement of the heart and of the anterior end of the liver (but only slightly more than in *N. cyclopion*). Organ and inter-

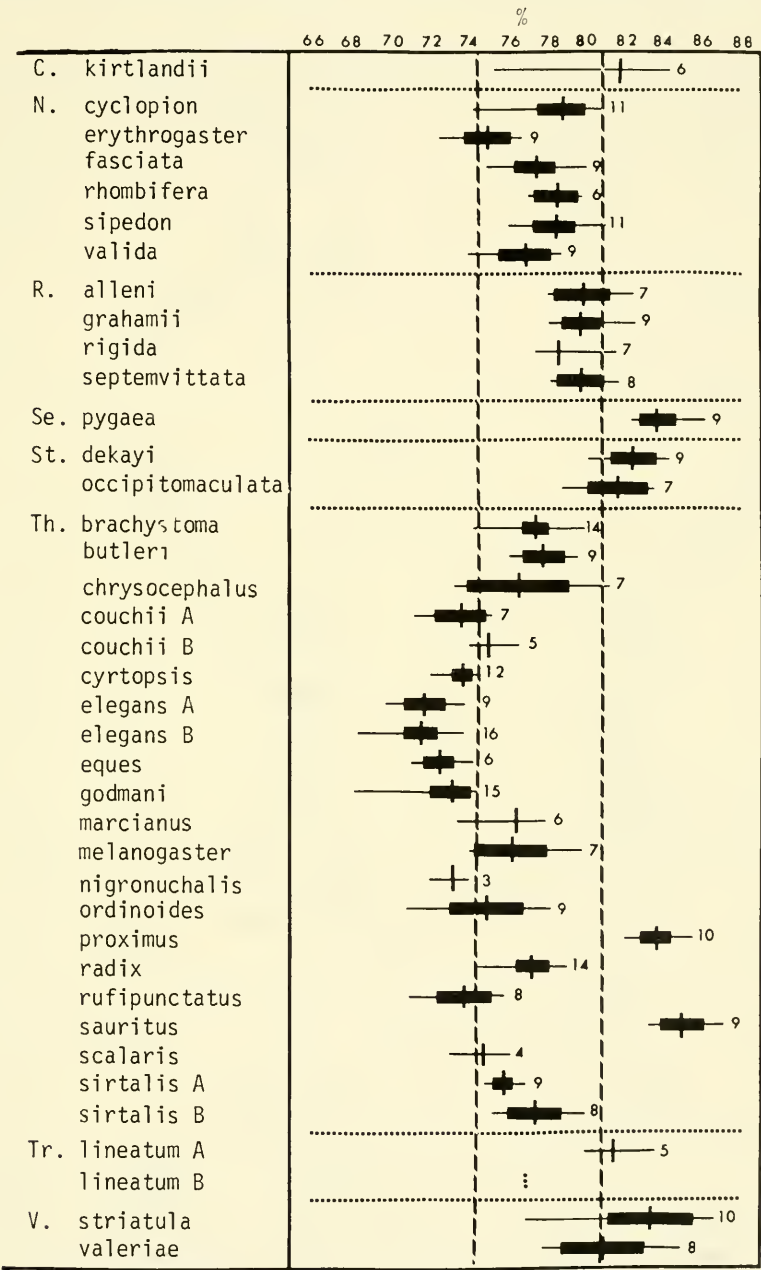


Figure 12. Location of the anterior end of the left kidney in male thamnophiine snakes (expressed as a % of total ventrals).

space lengths show no consistent intragen-
eric trends.
The only external feature that has been
used consistently to distinguish the genera

Nerodia and *Thamnophis* is the presence
of an undivided anal plate in the latter
(Conant, 1961), but Varkey (1979) has
demonstrated several consistent differ-

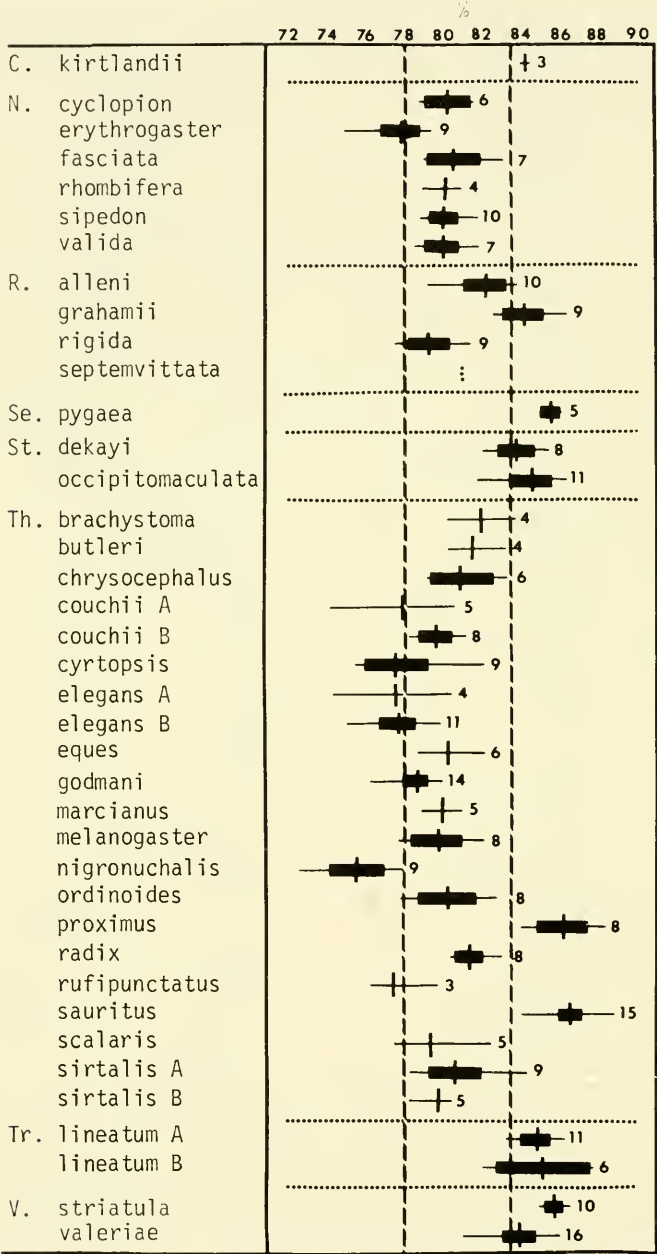


Figure 13. Location of the anterior end of the left kidney in female thamnophiine snakes (expressed as a % of total ventrals).

ences in cranial myology between the two genera. Our data on visceral topography do not provide an unequivocal picture of the *Nerodia-Thamnophis* relationship. Nevertheless, if one were to remove *N. erythrogaster* and *N. valida* from the

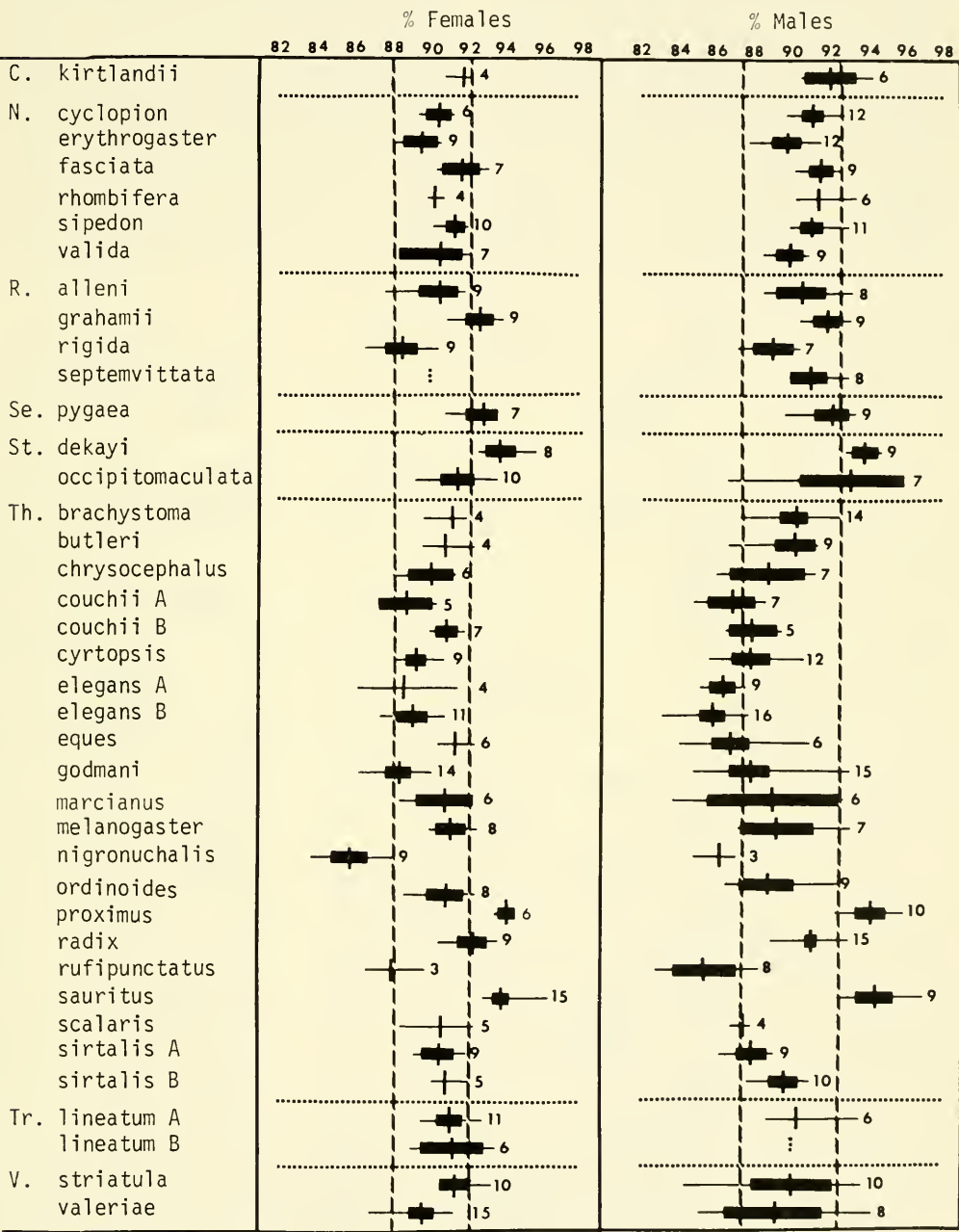


Figure 14. Location of the posterior end of the left kidney in thamnophiine snakes (expressed as a % of total ventrals).

former and *T. proximus* and *T. sauritus* from the latter, the posterior end of the liver in the remaining taxa of *Thamnophis* would lie anteriorly to its relative position in the remaining *Nerodia*; the anterior and posterior ends of the right kidney in males show a similar relationship. As a matter of fact, the anterior end of the right kidney in male *Thamnophis* (other than *T. proximus* and *T. sauritus*) lies anteriorly to that position in all other thamnophiines save *N. erythrogaster*. All taxa of *Thamnophis* (except *T. sauritus*) differ from all species of *Nerodia* (except *N. erythrogaster* and *N.*

valida) in having the posterior end of the right kidney of females lying posteriorly to that of males. All taxa of *Thamnophis* (except female *T. melanogaster* and *T. nigronuchalis*) have a liver-gall bladder interspace more than twice the length of the gall bladder; in all species of *Nerodia* (except *N. erythrogaster* and *N. valida*) the interspace is between one and two times as long as the gall bladder. Whether the frequent similarity in organ positions of *N. erythrogaster* to the garter snakes reflects phyletic affinities, convergence due to ecological similarities (*N. erythrogaster* is more ter-

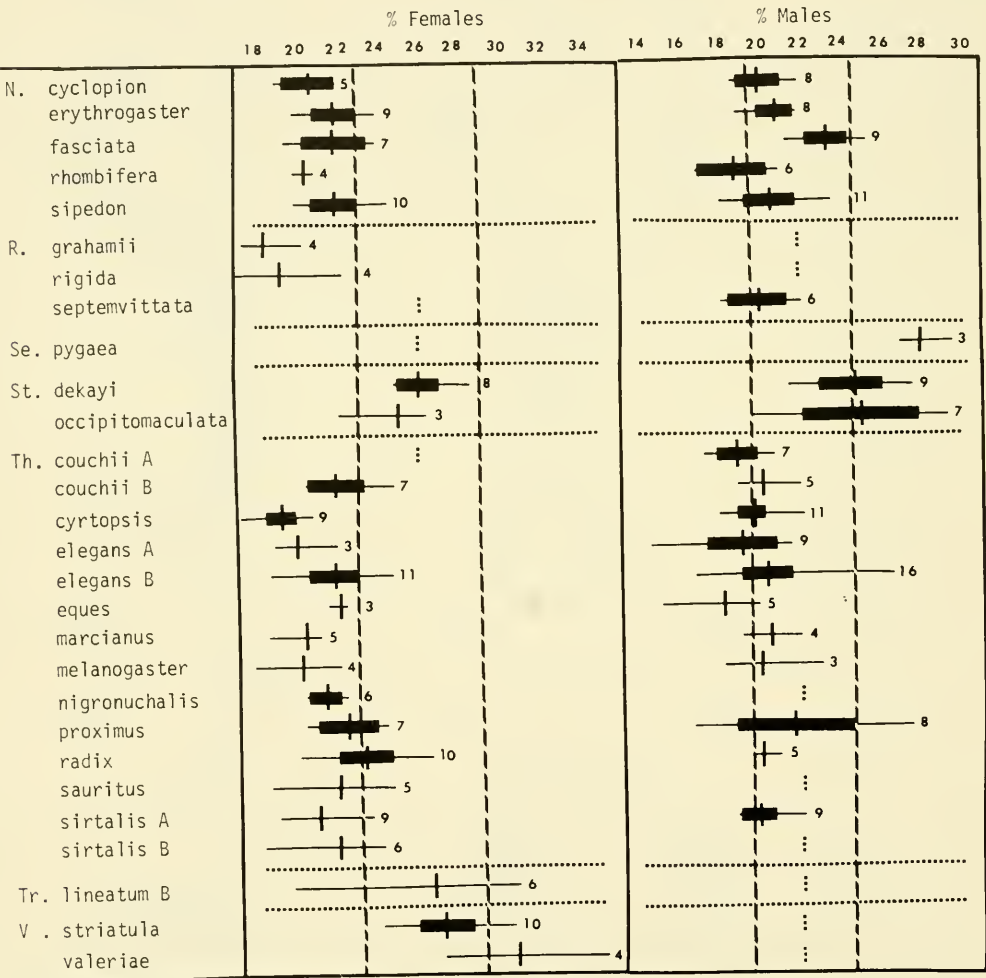


Figure 15. Liver length in thamnophiine snakes (expressed as a % of total ventrals).

restrial than its congeners and has a larger anuran component in its diet — Mushinsky and Hebrard, 1977; Kofron, 1978), or some other factors, we cannot say.

Rossman (1963a) noted that the *Sauritus* group of *Thamnophis* shows no close affinity to any of the other groups established by Ruthven (1908), and our study confirms

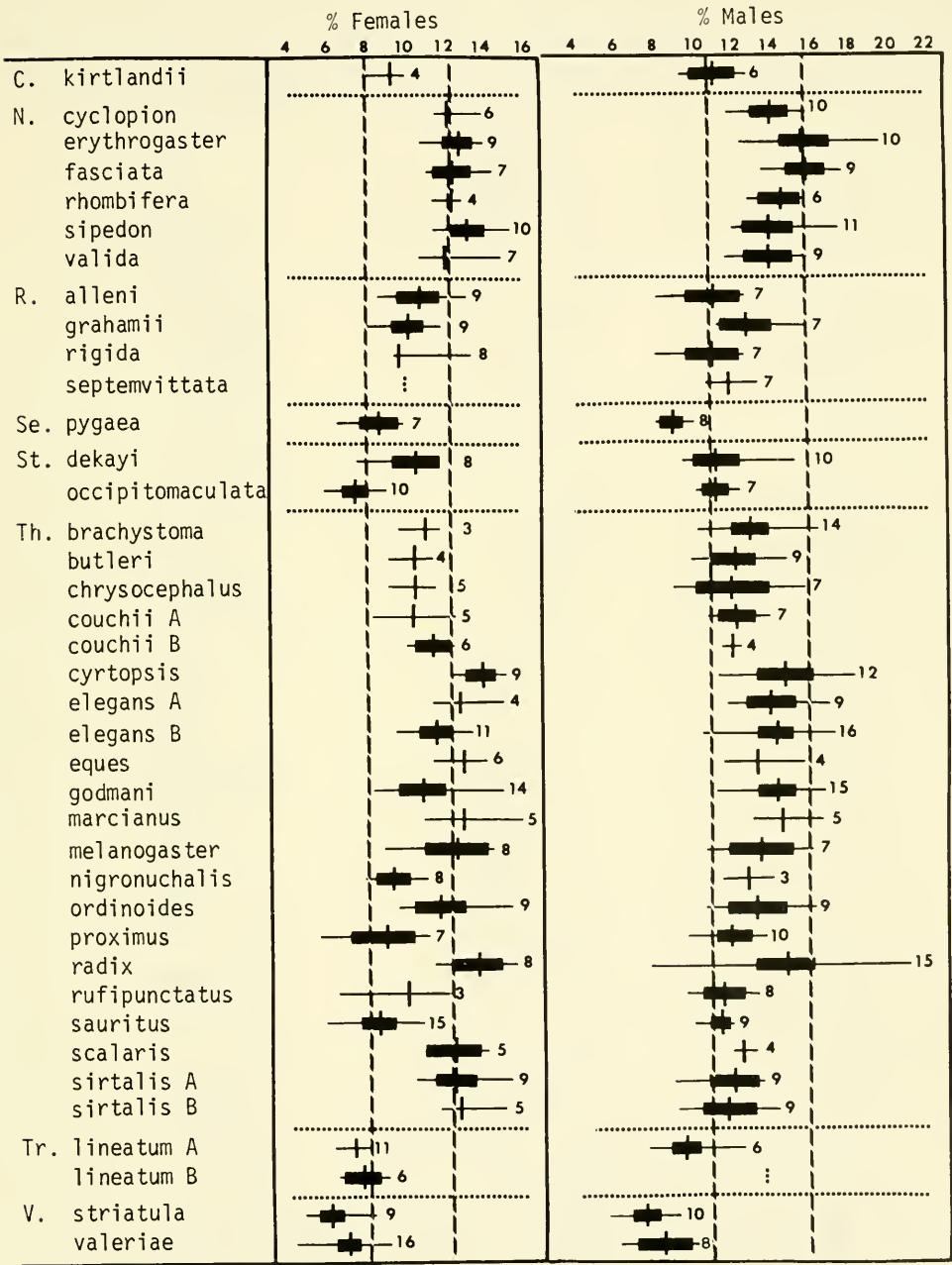


Figure 16. Right kidney length in thamnophiine snakes (expressed as a % of total ventrals).

that observation. In fact, the marked dissimilarity of the ribbon snakes (*T. proximus* and *T. sauritus*) to other *Thamnophis* in most visceral topographic features (see Table IX) proved to be the most striking,

and unexpected, discovery revealed by our study. In almost every instance the organ positions in *T. proximus* and *T. sauritus* are posterior to those in all other *Thamnophis*. In the cases of the posterior end of

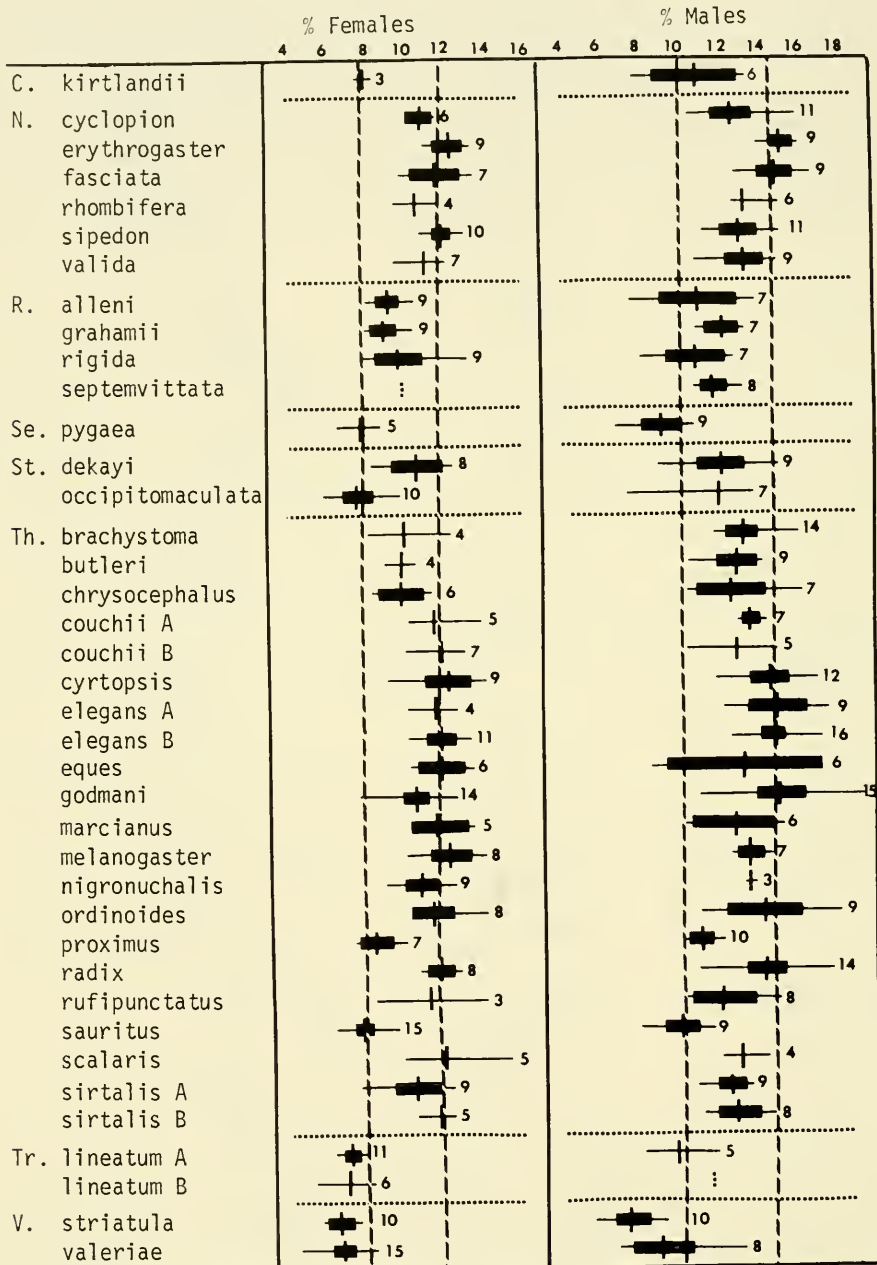


Figure 17. Left kidney length in thamnophiine snakes (expressed as a % of total ventrals).

the heart and the anterior end of the liver, the ribbon snakes share the phenomenon of posterior displacement with *T. melanogaster* and *T. rufipunctatus*, but in all other positional characters they stand alone within the genus — including possession of the highest liver-gall bladder interspace/gall bladder length values of any thamnophiine (Table VI). They also differ

from their congeners in having a relatively short left kidney. That the relatively long, slender-bodied ribbon snakes should be more similar to the stout-bodied water snakes (*Nerodia*), and especially to the short, semifossorial genera (*Clonophis*, *Seminatrix*, *Storeria*, *Tropidoclonion*, *Virginia*), than to the other *Thamnophis* poses a real enigma. Whatever the cause of the

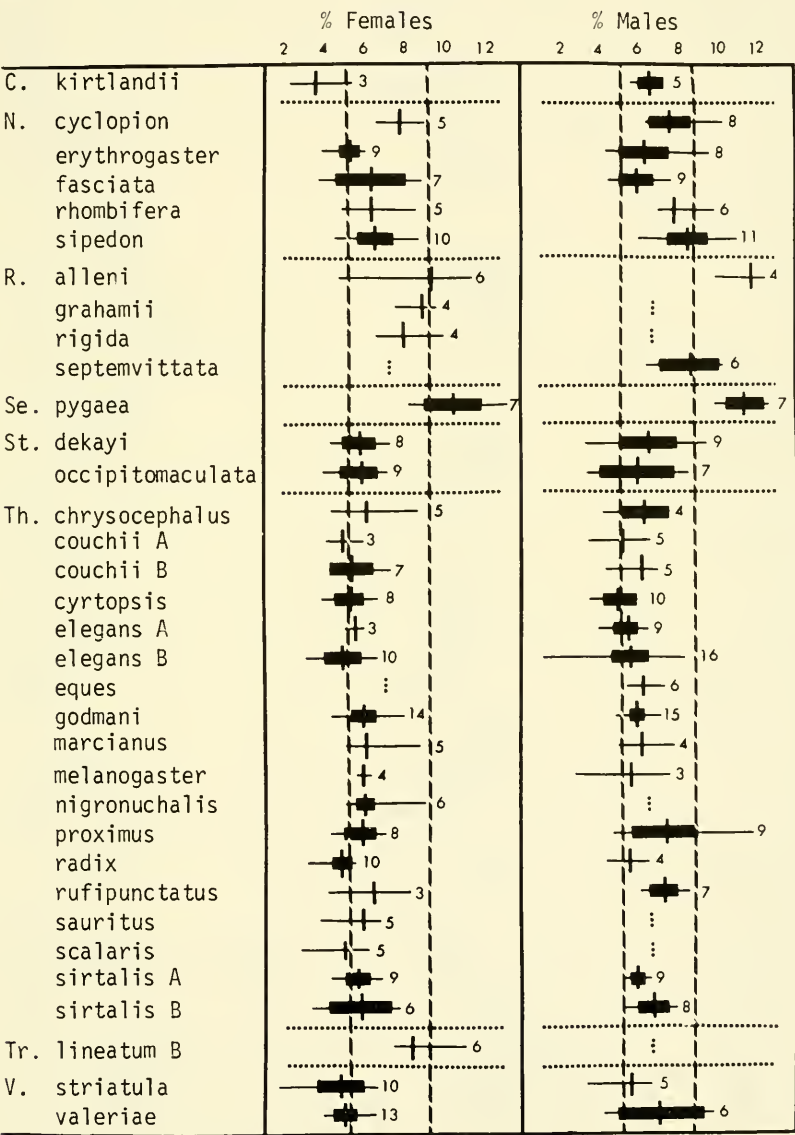


Figure 18. Heart-liver interspace in thamnophiine snakes (expressed as a % of total ventrals).

similarities, it certainly does not seem to be due to either phyletic affinity or ecological convergence. All we can reasonably conclude is that *T. proximus* and *T. sauritus*

are unique among the garter snakes. On the basis of the discriminant analysis and Student's t-test (Table IX), we would also conclude that the other three species

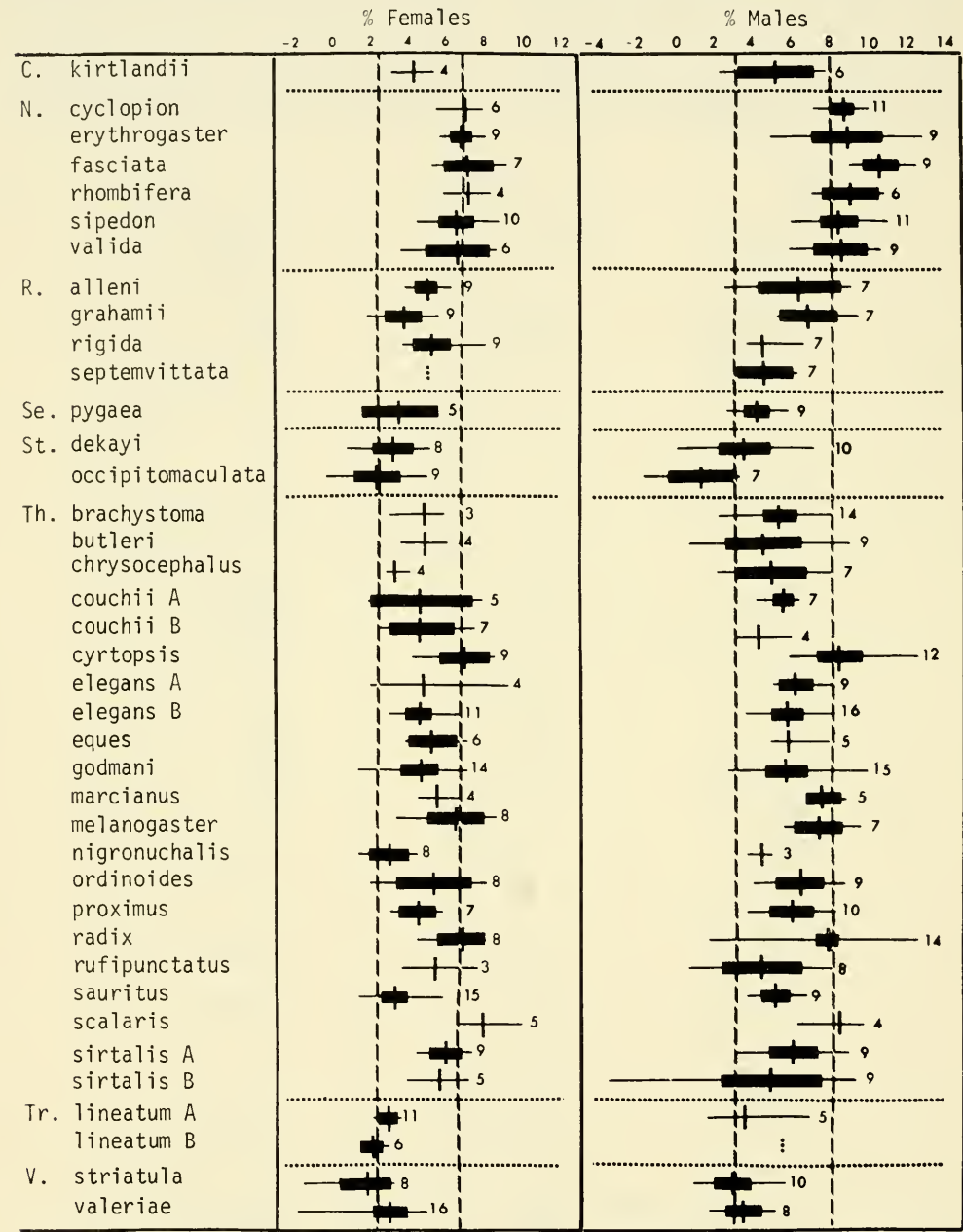


Figure 19. Kidney overlap in thamnophiine snakes (expressed as a % of total ventrals).

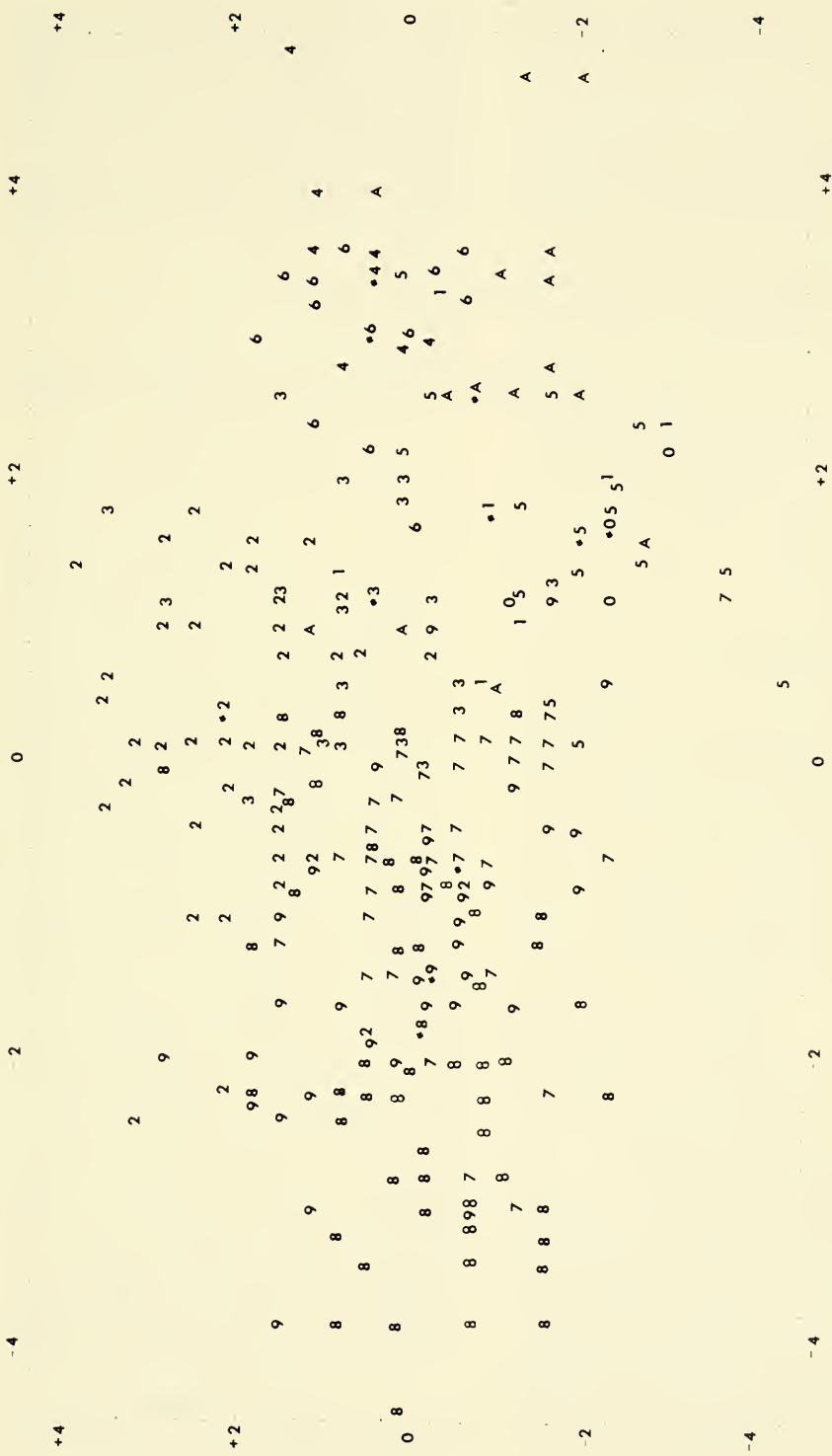


Figure 20. All-groups scatterpoint diagram of discriminant scores based on discriminant functions 1 and 2. 1 = *Clonophis*, 2 = *Nerodia*, 3 = *Regina*, 4 = *Seminatrix*, 5 = *Storeria*, 6 = *Sauritus* group of *Thamnophis*, 7 = *Radix* group of *Thamnophis*, 8 = *Elegans* group of *Thamnophis*, 9 = *Sirtalis* group of *Thamnophis*, 0 = *Tropidoclonion*, A = *Virginia*, * = group centroid.

groups designated by Ruthven (1908) do not appear to be distinguishable from one another solely on the basis of visceral topography.

As was implied above, in many cases the small, semifossorial thamnophiines tend to have a posterior displacement of organs, a condition they share frequently with the

ribbon snakes (*Thamnophis proximus*, *T. sauritus*) and occasionally with some species of *Nerodia* and *Regina*. Posterior displacement is a general trend, not an invariable phenomenon, and both inter- and intrageneric variation occur from one character to the next. The semifossorial genera also show a definite trend toward

Table IX. Significance of Ruthven's *Thamnophis* groups compared as four separate populations. NS indicates difference not significant at $p>.05$.

Character	Sex	<i>Sauritus-Radix</i>	<i>Sauritus-Elegans</i>	<i>Sauritus-Sirtalis</i>	<i>Radix-Elegans</i>	<i>Radix-Sirtalis</i>	<i>Elegans-Sirtalis</i>
post. heart	♂	.001 ¹	.001	.001	NS	NS	NS
	♀	.01	.001	.001	NS	NS	NS
ant. liver	♂	.001	.001	.001	.05	.05	NS
	♀	.001	.001	.001	.05	.001	NS
post. liver	♂	.001	.001	.001	NS	NS	NS
	♀	.001	.001	.001	NS	NS	.05
post. gall bladder	♂	.001	.001	.001	NS	NS	NS
	♀	.001	.001	.001	NS	NS	NS
post. pancreas	♂	.001	.001	.001	NS	NS	NS
	♀	.001	.001	.001	NS	NS	NS
ant. r. kidney	♂	.001	.001	.001	.001	.001	.01
	♀	.01	.001	.001	.001	.01	NS
post. l. kidney	♂	.001	.001	.001	.001	.01	NS
	♀	.001	.001	.001	.001	.001	NS
ant. l kidney	♂	.001	.001	.001	.001	.001	.01
	♀	.001	.001	.001	.001	.001	NS
post l. kidney	♂	.001	.001	.001	.001	.001	.001
	♀	.001	.001	.001	.001	.001	NS
liver length	♂	NS	.02	.01	NS	NS	NS
	♀	NS	NS	NS	NS	.02	NS
r. kidney length	♂	.01	.01	.01	NS	NS	NS
	♀	.001	.001	.001	.01	NS	NS
l. kidney length	♂	.001	.001	.001	NS	NS	NS
	♀	.001	.001	.001	NS	NS	NS
heart-liver interspace	♂	.02	.01	NS	NS	NS	NS
	♀	NS	NS	NS	NS	NS	NS
kidney overlap	♂	NS	NS	NS	NS	NS	NS
	♀	.001	.01	.001	NS	NS	NS

¹Significance levels determined using 2-tailed Student's t-test.

having relatively short kidneys, but the data for *Storeria* are equivocal and the characteristic is not unique to those genera. One unique feature that is shared by all of the semifossorial genera is the possession of a relatively long liver. We do not know why small snakes would possess a proportionally longer liver than large snakes, but perhaps there are physiological constraints that prevent the mutual reduction of body and of liver from being directly proportional — perhaps a minimum quantity of liver tissue is required for the proper functioning of that organ.

ACKNOWLEDGMENTS

For the loan of specimens and for other courtesies, we are indebted to the following curators: Charles W. Myers and Richard G. Zweifel (American Museum of Natural History); Harry A. Shankman (Arizona State University); Douglas C. Cox (Brigham Young University); C.J. McCoy, Jr. (Carnegie Museum); Hymen Marx (Field Museum of Natural History); Walter Auffenberg and Peter Meylan (Florida State Museum); Kenneth Cliffer and Philip J. Regal (James Ford Bell Museum of Natural History); Joseph T. Collins and William E. Duellman (University of Kansas Museum of Natural History); Gloria Z. Wurst and David B. Wake (Museum of Vertebrate Zoology, University of California at Berkeley); Harold A. Dundee (Tulane University); T. Paul Maslin (University of Colorado Museum of Natural History); Gary Breitenbach and Arnold G. Kluge (University of Michigan Museum of Zoology); James F. Jackson (University of Southwestern Louisiana); Jonathan A. Campbell (University of Texas at Arlington); and Robert G. Webb (University of Texas at El Paso). We are also grateful to Darrel R. Frost, Mark S. Hafner, Dominique G. Homberger, and Randy H. Vaeth for helpful suggestions at various stages in the development of this manuscript.

SPECIMENS EXAMINED¹

Clonophis kirtlandii. ILLINOIS, Christian Co.: LSUMZ 40065; Cook Co.: FMNH 23166, 25437;

/Gross Pt.: FMNH 2989; Will Co.: FMNH 55562, 65902. INDIANA, Delaware Co.: FMNH 64670; Porter Co.: FMNH 42069; /Orange Co.?/ FMNH 3060. KENTUCKY, Jefferson Co.: FMNH 25535. OHIO, Hamilton Co.: LSUMZ 7445, 13539.

Nerodia cyclopion. LOUISIANA, Ascension Par.: LSUMZ 13703; Calcasieu Par.: LSUMZ 12150; Cameron Par.: LSUMZ 18671-2; Iberville Par.: LSUMZ 18286, 20703, 24669; Jefferson Par.: LSUMZ 8670, 13704; Lafourche Par.: LSUMZ 13557, 19183; St. Bernard Par.: LSUMZ 9280; St. Charles Par.: LSUMZ 18757, 29355; St. James Par.: LSUMZ 18293, 19174; St. Tammany Par.: LSUMZ 34308; Vermilion Par.: LSUMZ 24025, 33939.

Nerodia erythrogaster. LOUISIANA, Acadia Par.: LSUMZ 20310; Cameron Par.: LSUMZ 20344; East Baton Rouge Par.: LSUMZ 17321, 17702, 19175, 20312, 20723, 22909, 24028; Iberville Par.: LSUMZ 18287, 22558-9; Jefferson Par.: LSUMZ 18716; Livingston Par.: LSUMZ 28812; St. Bernard Par.: LSUMZ 8992; St. John the Baptist Par.: LSUMZ 23864; St. Tammany Par.: LSUMZ 12983, 20279; Vermilion Par.: LSUMZ 34295; Washington Par.: LSUMZ 12540; West Baton Rouge Par.: LSUMZ 11887; West Feliciana Par.: LSUMZ 18758.

Nerodia fasciata. LOUISIANA, Ascension Par.: LSUMZ 17698; Cameron Par.: LSUMZ 12731, 17315, 20281, 28666; Jefferson Par.: LSUMZ 8947, 8953; Natchitoches Par.: LSUMZ 30410; Plaquemines Par.: LSUMZ 8653; Pointe Coupee Par.: LSUMZ 20274; St. Charles Par.: LSUMZ 7142, 7527; St. Landry Par.: LSUMZ 18113, 18122; St. Martin Par.: LSUMZ 19171, 19173.

Nerodia rhombifera. LOUISIANA, East Baton Rouge Par.: LSUMZ 17687, 17794, 17945, 20799, 23662, 28008-10; Iberville Par.: LSUMZ 13756; St. Charles Par.: LSUMZ 9216.

Nerodia sipedon. ALABAMA, Jackson Co.: LSUMZ 36375; Pickens Co.: LSUMZ 36399, 36400. ILLINOIS, Jackson Co.: LSUMZ 27610; Pope Co.: LSUMZ 27599. MISSISSIPPI, Greene Co.: LSUMZ 36379, 36381-3, 36385, 36387, 36390-3, 36396-7; Lauderdale Co.: LSUMZ 36403-4; Wilkinson Co.: LSUMZ 28712. MISSOURI, Lawrence Co.: LSUMZ 9107.

Nerodia valida. MEXICO, Colima: LSUMZ 7876; Nayarit: LSUMZ 33099, 36266, 36268; Sinaloa: AMNH 36269, 84077, 84080-2, 87575, 87577, 88889-90, 88892; Sonora: AMNH 84074-6.

Regina alleni. FLORIDA, Alachua Co.: FSM 2476, 2498, 6634, 6637, 7171, 9096, LSUMZ 13618-9; Collier Co.: LSUMZ 28992; Dade Co.: FSM 42527; Dixie Co.: LSUMZ 7473; Hillsborough Co.: FSM 42529; Indian River Co.: FSM 42524-6,

- 42530; Polk Co.: FSM 1868; Sumter Co.: FSM 11157.
- Regina grahamii*. LOUISIANA, East Baton Rouge Par.: LSUMZ 17947, 33460, USL 7623; Iberville Par.: LSUMZ 20271; Lafayette Par.: USL 20945; St. Landry Par.: LSUMZ 28665, USL 15936, 23236, 23414, 23427; St. Martin Par.: USL 22953, 24432; Terrebonne Par.: LSUMZ 36484-7; Vermilion Par.: USL 10687, 17353. TEXAS, Chambers Co.: LSUMZ 33462.
- Regina rigida*. NO DATA: USL 6067, 8820. LOUISIANA, Iberville Par.: LSUMZ 22556; Lafayette Par.: USL 24245; Natchitoches Par.: LSUMZ 12988; Orleans Par.: LSUMZ 8982-3; Sabine Par.: USL 24453; St. Charles Par.: LSUMZ 8680; St. Landry Par.: USL 15930, 17620; St. Martin Par.: USL 14365, 19471, 22425, 24433; Terrebonne Par.: LSUMZ 36483.
- Regina septemvittata*. ALABAMA, Baldwin Co.: LSUMZ 15783. NORTH CAROLINA, Orange Co.: LSUMZ 14353-4. OHIO, Montgomery Co.: LSUMZ 24476, 30184-5. TENNESSEE, Clay Co.: LSUMZ 34795; Jackson Co.: LSUMZ 34798.
- Seminatrix pygaea*. FLORIDA, Alachua Co.: FSM 9813 (-6,-12), 14146 (-4), 14147 (-1,-7), 14215 (-4), 14216 (-2,-4,-9), 14217 (-3,-5,-7), 14218 (-4,-6); Dade Co.: LSUMZ 6530, 7405, 24582.
- Storeria dekayi*. LOUISIANA, Ascension Par.: LSUMZ 18776; Cameron Par.: LSUMZ 2764, 12196, 18168-70, 24038, 28819-20, 28822, 29977, 32649; Iberia Par.: LSUMZ 2771; Iberville Par.: LSUMZ 12229, 23877; St. Landry Par.: LSUMZ 18665, 20074; Vermilion Par.: LSUMZ 24733.
- Storeria occipitomaculata*. LOUISIANA, Claiborne Par.: LSUMZ 24658; East Feliciana Par.: LSUMZ 16686; Natchitoches Par.: LSUMZ 24745, 33077-8; West Feliciana Par.: LSUMZ 12602, 17898.
- Thamnophis brachystoma*. PENNSYLVANIA, Clarion Co.: CM 28292-3, 28295, 28297-9, 28302-3, 28306-9, 28311, 28313, 28317-8, 28320-1.
- Thamnophis butleri*. CANADA, Ontario: UMMZ 90193. INDIANA, Noble Co.: UMMZ 132822. OHIO, Lucas Co.: UMMZ 68864, 99627(3). MICHIGAN, Sanilac Co.: UMMZ 98774; Washtenaw Co.: UMMZ 46523-4; Wayne Co.: UMMZ 89519. WISCONSIN, Waukesha Co.: AMNH 76178-80.
- Thamnophis chrysocephalus*. MEXICO, Guerrero: AMNH 72500-1, 72503; Oaxaca, AMNH 91094-5, 93235, 97855-6, 97865-6, 97868-9, 97871.
- Thamnophis couchii couchii*. CALIFORNIA, Amador Co.: LSUMZ 16530, 16544; Kern Co.: LSUMZ 16549; Shasta Co.: LSUMZ 22938, 34587-8, 34590, MVZ 18824-5; Tehama Co.: LSUMZ 16550; Tulare Co.: LSUMZ 16547; Tuolumne Co.: LSUMZ 34585.
- Thamnophis couchii hydrophilus*. CALIFORNIA, Humboldt Co.: LSUMZ 34578; Shasta Co.: LSUMZ 16551-4; Trinity Co.: LSUMZ 34594-5. OREGON, Jackson Co.: LSUMZ 16560-4, 16567.
- Thamnophis cyrtopsis*. ARIZONA, Coconino Co.: LSUMZ 29940, 30062, 30083, 30088; Gila Co.: LSUMZ 30061; Maricopa Co.: LSUMZ 30063, 30081; Pima Co.: LSUMZ 30066, 30090; Santa Cruz Co.: LSUMZ 10035, 30072, 30076-7; Yavapai Co.: LSUMZ 29943, 29945-6, 29948, 30064-5, 30067-8.
- Thamnophis elegans terrestris*. CALIFORNIA, Mendocino Co.: LSUMZ 34378, 34380; San Mateo Co.: LSUMZ 7922, 16502-3, 16507, 34371, 34373; Sonoma Co.: LSUMZ 34368-9, 34374-5; Sonoma-Mendocino Co.: LSUMZ 34367.
- Thamnophis elegans vagrans*. NO DATA: LSUMZ 20747-50. ARIZONA, Coconino Co.: LSUMZ 29957, 29959-62. COLORADO, Conejos Co.: LSUMZ 11571, 11609, 11611, 11615, 30051, 30055; Costilla Co.: LSUMZ 7985, 11603-5, 11607, 11614, 11618, 13929, 13931-2, 30050; Rio Grande Co.: LSUMZ 30056.
- Thamnophis eques megalops*. MEXICO, Chihuahua: AMNH 104471, 104772, BYU 22701; San Luis Potosí: LSUMZ 4374-5, 4879.
- Thamnophis eques virgatus*. MEXICO, Durango: AMNH 102521, LSUMZ 16424-6, 16429-30.
- Thamnophis godmani*. MEXICO, Oaxaca: AMNH 89604, 91101-2, 91105, 97853, 97873-4, 97884, 97888, 103090, 103092-5, 103101, 103103, 103105, 103113, 104394, 106993, 106995-8, 107002-5, 718170.
- Thamnophis marcianus*. TEXAS, Bexar Co.: LSUMZ 10315; Duval Co.: LSUMZ 23239, 23243; Hartley Co.: LSUMZ 10407; Jeff Davis Co.: LSUMZ 29608; McMullen Co.: LSUMZ 23248; Moore Co.: LSUMZ 10365; Presidio Co.: LSUMZ 23255; San Patricio Co.: LSUMZ 23249, 23252; Webb Co.: LSUMZ 30929; Zavala Co.: LSUMZ 23254.
- Thamnophis melanogaster*. MEXICO, Jalisco: LSUMZ 16434; Michoacán: LSUMZ 14489-90, 14492-3, 16435, 34346, 36277, 36279-80, 36282-6.
- Thamnophis nigronuchalis*. MEXICO, Durango: LSUMZ 11637, 16448, 16450-5, 16459-60, UTEP 3386-7.
- Thamnophis ordinoides*. CALIFORNIA, Del Norte Co.: MVZ 30276-7, 30279. OREGON, Clatsop Co.: MVZ 34265-8, 36848; Polk Co.: MVZ 24808; Tillamook Co.: MVZ 47856. WASHINGTON, Clark Co.: MVZ 34259; King Co.: MVZ 38653, 38655, 38657, 38670, 38674; Lewis Co.: MVZ 70366; Pacific Co.: MVZ 34262.
- Thamnophis proximus*. LOUISIANA, Acadia Par.: LSUMZ 17899; Cameron Par.: LSUMZ 33964;

- Claiborne Par.: LSUMZ 33966; East Baton Rouge Par.: LSUMZ 16912, 18714, 20254; Iberia Par.: LSUMZ 18077; Iberville Par.: LSUMZ 20255, 20316, 22548; Livingston Par.: LSUMZ 7960, 18974; Pointe Coupee Par.: LSUMZ 20220; St. Tammany Par.: LSUMZ 7934; Vermilion Par.: LSUMZ 24052. TEXAS, Hidalgo Co.: LSUMZ 18621-3.
- Thamnophis radix*. NO DATA: LSUMZ 20735-40, 20742-5. COLORADO, Denver Co.: LSUMZ 7465; Larimer Co.: UC 31837-40, 31842-3, 31847, 31851, 31873, 31888. ILLINOIS, Iroquois Co.: LSUMZ 8126. NEW MEXICO, San Miguel Co.: LSUMZ 7942, 7944, 7972.
- Thamnophis rufipunctatus*. ARIZONA, Coconino Co.: LSUMZ uncatalogued, LSUMZ 36815. MEXICO, Chihuahua: AMNH 4342, 68286, ASU 17042, 5304-5, 5335, UTEP 2043, 2262, 3657.
- Thamnophis sauritus*. FLORIDA, Alachua Co.: FSM 14183, 14550 (-1), 14550 (-2), 14550 (-3), 14550 (-4), 14550 (-7), 14550 (-8), 14550 (-9), 14551 (-2), 14551 (-4), 39197; Collier Co.: FSM 39198, 39200-2; Dade Co.: FSM 22874, 39204-5; Franklin Co.: LSUMZ 21805-6, 21810; Pasco Co.: LSUMZ 22003. LOUISIANA, St. Tammany Par.: LSUMZ 8302, 23770.
- Thamnophis scalaris*. MEXICO, Distrito Federal: AMNH 75934; Jalisco: UTA R-4932, R-4949, 5991, 5993; México: AMNH 71315 (2), 94714; Michoacán: AMNH 88724.
- Thamnophis sirtalis fitchi*. CALIFORNIA, Amador Co.: LSUMZ 16486-8, 16489-92; Mendocino Co.: LSUMZ 16493; Modoc Co.: LSUMZ 8215; Plumas Co.: LSUMZ 16477-8, 16481-2; Shasta Co.: LSUMZ 16496-8.
- Thamnophis sirtalis sirtalis*. INDIANA, Allen Co.: LSUMZ 7988. MINNESOTA, Carlton Co.: JFBM 1115, Cass Co.: LSUMZ 7991, 7996; Clearwater Co.: JFBM 2644-5, 2651-2, 2657, 2659; Isanti Co.: LSUMZ 23229, 23232, 23234, 24461-2; Pine Co.: LSUMZ 23230.
- Tropidoclonion lineatum*. NEBRASKA, Jefferson Co.: KU 45252-65, 45267-8; Richardson Co.: KU 52228. NEW MEXICO, San Miguel Co.: LSUMZ 29998-9, 30096-7. TEXAS, Travis Co.: LSUMZ 20078-9.
- Virginia striatula*. NO DATA: USL 5395, 15841. LOUISIANA, Acadia Par.: LSUMZ 12091; Ascension Par.: LSUMZ 12087, 18777; Caddo Par.: LSUMZ 20210; East Baton Rouge Par.: LSUMZ 1598, 1604-5, 2786, 17348, 18712, 23536, 23745; East Feliciana Par.: LSUMZ 2779; Lafayette Par.: USL 11179, 22890; Livingston Par.: LSUMZ 12126; Sabine Par.: LSUMZ 20193; St. Helena Par.: LSUMZ 18360; St. Landry Par.: USL 18277; St. Tammany Par.: LSUMZ 2773.
- Virginia valeriae*. FLORIDA, Alachua Co.: FSM 42545; Leon Co.: FSM 1942, 34858; Liberty Co.: FSM 42531-2, 42534-5; Wakulla Co.: FSM 32991. GEORGIA, Chattahoochee Co.: FSM 42546. LOUISIANA, Bossier Par.: LSUMZ 24656; Caddo Par.: LSUMZ 12094; East Baton Rouge Par.: LSUMZ 12147, 17671; East Feliciana Par.: LSUMZ 15536; Livingston Par.: LSUMZ 20256; St. Helena Par.: TU 5957; St. Tammany Par.: TU 11844, 14238, 18395; Webster Par.: LSUMZ 12142; West Feliciana Par.: LSUMZ 17901. MISSISSIPPI, Hancock Co.: TU 14304, 15056, 17681.

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- positions lie more posteriorly or which have longer organs or interspaces.
- Posterior end of heart* — non-natricine and non-homalopsine Colubridae: *Boiga*,¹ *Chamaetortus*,¹ *Coluber* (= *Gonyosoma*) *oxycephalus*,² *Dipsadoboa*,¹ and male *Zamenis rhodorhacis*,² Acrochordidae: *Acrochordus arafurae*,³ *A. granulatus*,³ *A. javanicus*,³ Boidae: male *Bolyeria*,⁴ male *Corallus*,⁴ male *Eunectes*,⁴ male *Lichanura*,⁴ male *Loxocemus*,⁴ male *Xenopeltis*,⁴ Viperidae: *Causus rhombeatus*.²
- Anterior end of right kidney* — non-natricine and non-homalopsine Colubridae: *Coluber* (= *Gonyosoma*) *oxycephalus*,² female *Philothamnus semivariegatus*,² male *Psammophis sibilans*,² male *Zamenis florulentus*,² *Z. rhodorhacis*.²
- Posterior end of right kidney* — non-natricine and non-homalopsine Colubridae: *Coluber* (= *Gonyosoma*) *oxycephalus*,² male *Leptodira* (= *Crotaphopeltis*) *hotamboeia*,² female *Philothamnus semivariegatus*,² male *Psammophis sibilans*,² Viperidae: male *Causus rhombeatus*.²
- Anterior end of left kidney* — non-natricine and non-homalopsine Colubridae: male *Coluber* (= *Gonyosoma*) *oxycephalus*,² female *Philothamnus semivariegatus*,² male *Psammophis sibilans*,² male *Zamenis florulentus*.²
- Posterior end of left kidney* — non-natricine and non-homalopsine Colubridae: male *Coluber* (= *Gonyosoma*) *oxycephalus*,² female *Philothamnus semivariegatus*,² male *Psammophis sibilans*.²
- Right kidney length* — Viperidae: *Causus rhombeatus*.²
- Heart-liver interspace* — The following taxa had an overlap — Tropidophiidae: *Trachyboa gularis*,⁶ *Tropidophis*,⁶ Viperidae: *Causus rhombeatus*.²
- Kidney overlap* — all taxa reported in the literature have an overlap, but *Causus*

APPENDIX A

Comparative data on non-thamnophiine snakes obtained from the literature fell within the outer parameters of the thamnophiine data sets generated by our study except for the following taxa whose organ

*rhombeatus*² (Viperidae) is the only one to have a greater overlap than any of the Thamnophiini.

The following taxa have an organ position lying more anteriorly or have shorter organs than any of the Thamnophiini.

Posterior end of left kidney — Tropidophiidae: female *Exiliboa placata*.⁷

Liver length — non-natricine and non-homalopsine Colubridae: female *Philothamnus semivariegatus*.²

Heart-liver interspace — Colubridae, Natricinae: male *Natrix* (= *Amphiesma*) *vibakari*³ from Japan.

Kidney asymmetry — In the present study males in 64% of the taxa have the left kidney longer than the right but the difference is significant in only 5%. However, the literature reveals that in the

males of most taxa the right kidney is longer than the left. The following are the taxa in which the left kidney is longer: Colubridae, Natricinae — *Natrix* (= *Sinonatrix*) *trianguligera*;⁸ Colubridae, Homalopsinae: *Enhydryn enhydryn*;⁹ other Colubridae: *Coluber* (= *Gonyosoma*) *oxycephalus*,² *Elapoides fuscus*.¹⁰ Females in 76% of the thamnophiines have the right kidney longer than the left (28% significantly different) as do the females of all taxa reported in the literature except: Colubridae, Natricinae — *Natrix* (= *Amphiesma*) *vibakari*;² Colubridae, Homalopsinae: *Hypsirhina* (= *Enhydryn*) *plumbea*;¹¹ other Colubridae: *Elapoides fuscus*.¹⁰

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¹Rasmussen (1979)

²Thompson (1914)

³McDowell (1979)

⁴Underwood (1976)

⁵Thompson (1913b)

⁶Brongersma (1951)

⁷Bogert (1968)

⁸Bergman (1959b)

⁹Bergman (1955e)

¹⁰Bergman (1956-58)

¹¹Bergman (1960)