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NEW ORLEANS

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CONTENTS OF VOLUME 23

TULANE STUDIES IN ZOOLOGY AND BOTANY
VOLUME 23
INDEX TO SCIENTIFIC NAMES
(NEW TAXONOMIC ENTITIES IN BOLDFACE)

TULANE STUDIES IN ZOOLOGY AND BOTANY

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Volume 23, Number 1 December 30, 1981

BIOSYSTEMATICS OF THE *KINOSTERNON HIRTIPES* SPECIES GROUP (TESTUDINES: KINOSTERNIDAE)

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ABSTRACT

Geographic variation in scute and shell measurements (via multivariate statistical analysis), body size, head scale and chin barbel morphology, size of first neural bone, shell carination, and head size and patterns in populations of the *Kinosternon hirtipes* species group were analyzed. The results support the retention of allopatric *K. sonoriense* and *K. hirtipes* as full species in the group, and the recognition of two allopatric subspecies (one new) of *K. sonoriense* and six subspecies (four new and all apparently allopatric) of *K. hirtipes.* The description of each taxon includes complete synonomies and ecological and reproductive data. Also included are a key to adults and a discussion of all taxa.

INTRODUCTION

Prior to 1970, members of the *Kinosternon hirtipes* species group were cited more than 233 times in the literature. At least half of those citations contained errors in identification, locality, and/or orthography. Iverson (1976, 1978), Conant and Berry (1978), Iverson and Berry (1979), and Berry and Legler (1980) have each addressed some of the problems dealing with members of this group in the American southwest, adjacent northwestern Mexico, and northeastern Mexico. Clearly the distribution, identification, systematics, and phylogeny of the turtles of the *Kinosternon hirtipes* species group are poorly understood. The purpose of this report, as part of a continuing analysis of relationships within the family Kinosternidae, is to rectify this situation.

My objectives here are 1) to redefine the members of this group taxonomically, 2) to analyze patterns of geographical variation in external morphological characters, 3) to develop a phylogeny of these members, and 4) to correct and bring order to the confusing and erroneous literature.

IDENTIFICATION OF THE *KINOSTERNON HIRTIPES* SPECIES GROUP

One of the primary obstacles to the study of Mexican kinosternids has been the difficulty in distinguishing members of the *K. hirtipes* species group *(K. hirtipes* and *K. sonoriense)* from those of the *K. scorpioides* group *(fide* Berry 1978; including *K. scorpioides, K. alamosae, K. oaxacae* and *K. integrum),* especially where the groups occur sympatrically. Adult males of the *hirtipes* group are readily distinguished by the presence of a patch of elevated scales on the posterior crus and thigh of each hindleg (vinculae: *fide* H. M. Smith and R. B. Smith 1980), absent in turtles of the *scorpioides* group, but adult females of the *hirtipes* group lack these structures and are thus often difficult to identify. An elaboration of the differences between *K. integrum*

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and members of the *K. hirtipes* group is therefore justified (see also Iverson and Berry 1979), especially since they coexist in several Mexican drainage basins (see MATERIALS AND METHODS). *Kinosternon scorpioides* is not sympatric with members of the *K. hirtipes* group.

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The primary criteria for distinguishing adults of *K. integrum* and the *K. hirtipes* group appear in Table 1. Juveniles are much more difficult to distinguish and remain poorly studied. In general, small specimens of the *K. hirtipes* group have smaller plastra, narrower bridges, and more axillary-inguinal scute contact than *K. integrum* (Fig. 1). More precise discrimination of small turtles must await additional data.

Members of the *K. hirtipes* group also differ from *K. integrum* ecologically. The former are virtually restricted to permanent water habitats, rarely leaving the water except to nest; migrating behavior is unreported. *Kinosternon integrum* is an excellent colonizing species (*fide* MacArthur and Wilson, 1967). It is extremely vagile, migrates considerable distances during the rainy season, and may aestivate under ground as *K. flavescens* and *K. alamosae* do. The number of specimens and locality records for *K. integrum* in museum collections (see lists in H. M. Smith and R. B. Smith, 1980) reflects the more frequent occurrence of *K. integrum* than *K. hirtipes* on roads. Thus, *K. integrum* may be found in almost any temporary pond or roadside pool, habitats where *K. hirtipes* would almost never occur.

In addition, although their thermoregulatory behavior has not been studied in detail, I suspect thermal preference and tolerance levels are higher in *K. integrum* than in the *K. hirtipes* group. This is reflected in the very different basking habits of the two forms. I have observed *K. integrum* basking at many Mexican localities in Michoacán, Jalisco, Sinaloa, and Oaxaca, but *K. hirtipes* basking only once at 2400 m elevation in Durango, and once (adult females only) at 1800 m in Jalisco. This perhaps reflects their coastal lowland *(integrum)* versus high plateau *(hirtipes)* origins. The absence of *K. integrum* in the highest (i.e. coldest) basins of the southern Mexico Plateau (Pátzcuaro, San Juanico, and Villa Victoria; see later) may be related to thermal requirements rather than to historical zoogeography. Likewise, despite its vagility, *K. integrum* ranges no farther northward in Sonora than 29 °N latitude in the Río Yaqui basin. Perhaps its range there is also limited by temperature regime. Further study may show other behavioral and ecological differences between these two groups on the Mexican Plateau.

MATERIALS AND METHODS

Specimens and field work

I have examined nearly all specimens of the species of the *Kinosternon hirtipes* group in United States museums. In addition, most of the world's museums were canvassed for locality data of other specimens. All available type specimens were examined. Each locality was pinpointed (and its elevation determined) on the

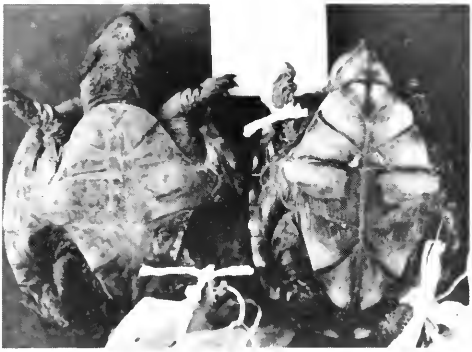

Figure 1. Plastral comparison of juvenile *Kinosternon hirtipes* (left; UMBM 2403) and *K. integrum* (UMBM 2411), both from 3.2 km SE Ocotlan, Jalisco, Mexico.

1:500,000 sheets of "La carta general de la República Mexicana" (published by the Ex-Comisión Intersecretarial de Mexico, D. F., 1958), with the help of the "Official Standard (Geographic) Names of Mexico", published by the Office of Geography of the U.S. Dept. of Interior (1956). These localities were then mapped on Miller's (1968) drainage map of Mexico (Figs. 3 and 4).

Field trips to sample critical areas for *K. hirtipes* were taken in May 1977 (12 days; 10 localities in Durango and Chihuahua), June 1978 (11 days; 12 localities in San Luis Potosí, Guanajuato, Michoacán, and Jalisco), June 1979 (part of 14 day trip; 5 localities in México State), July 1980 (12 days; 7 localities in Coahuila, Chihuahua, and Durango), and May 1981 (8 days; 10 localities in Jalisco, México State, Michoacán, and Puebla). Field work with *K. sonoriense* in Arizona was also undertaken in January 1971 (2 days), May 1974 (4 days), January 1976 (4 days), and July 1980 (1 day), and in Chihuahua in August 1980 (1 day).

All known specimens and localities for members of the *K. hirtipes* species group are in the SPECIMEN LIST and plotted in Figures 3 and 4; museum acronyms follow Duellman, Fritts, and Leviton (1978) except for the following:

CAS-SU	California Academy of Sciences - Stanford University Collections
DMNH	Dallas Museum of Natural History
EAL	Ernest A. Liner, Houma, Louisiana
ENMU	Eastern New Mexico University
FB	Thomas R. VanDevender, Tucson, Arizona
FWMNH	Fort Worth Museum of Natural History
JBI	John B. Iverson, Richmond, Indiana
JFB	James F. Berry, Elmhurst, Illinois
LTU	Louisiana Tech University
MES	Michael E. Seidel, Huntington, West Virginia
MSU	Michigan State University
MU	Midwestern University, Wichita Falls, Texas
NMSU	New Mexico State University
RSF	R. S. Funk, Normal, Illinois
SENCK	Senckenberg Museum
SM	Strecker Museum, Baylor University
SRSU	Sul Ross State University
TAI	Texas A&I University
UAZ	University of Arizona
UF	University of Florida, Florida State Museum
UG	University of Georgia
UMKC	University of Missouri, Kansas City
UNSM	University of Nebraska State Museum
UOK	University of Oklahoma
USA	University of South Alabama
USL	University of Southwestern Louisiana

This study is based on the examination of at least 1298 museum specimens of the *Kinosternon hirtipes* species group, as well as other specimens collected and released in the field. Population samples of turtles correspond to the inhabited drainage basins, which are listed and described below from approximately north to south. The reader is referred to Blasques L. (1959) and Tamayo (1962, 1964) for more general descriptions of the geography and hydrography of the drainage basins in Mexico.

Bill Williams River basin, Arizona (WILL). — The Bill Williams River and its major tributaries, the Big Sandy, Burro, and Santa Maria rivers drain a small area in west central Arizona and empty into the Colorado River at Parker Dam, about 90 km below the Nevada border. *Kinosternon sonoriense* is the only freshwater turtle known from this basin (four localities; 800-1200 m). Stebbins' (1966) *K. flavescens* records from this basin were based on *K. sonoriense* (Iverson, 1978: 477).

Gila and Lower Colorado River basins, Arizona, California, New Mexico, and Sonora (GILA). — Most of Arizona south of the Mogollon Rim and a portion of west central New Mexico are drained by this system. Miller (1961), Ohmart, et al. (1975), and McNatt (1978) described changes in the aquatic habitats along the Colorado and Gila rivers and their tributaries over the past 100 years. *Kinosternon sonoriense* occurs throughout the basin (Iverson, 1976, 1978) and reaches its maximum known elevation (2042 m) in the Gila River in western New Mexico (Niles, 1962; Degenhardt and Christiansen, 1974), and its lowest known elevation (ca. 43 m) near Yuma, Arizona.

The range of *K. sonoriense* in the Colorado River is poorly known. It apparently once occurred there at least upstream to southeastern Nevada (LaRivers, 1942, as *K. flavescens;* see Iverson 1978:476). More field work is needed along the Colorado River between Needles, California, and Yuma, Arizona, to establish the present range of *K. sonoriense*. The only other freshwater turtle which may occur naturally in this basin is *K. flavescens,* but I have elsewhere (Iverson, 1978) questioned its recent occurrence in the Gila. The introduced *Trionyx spinferus* does, however, also occur in the Gila and Colorado rivers from southwestern Utah and western New Mexico to the mouth of the Colorado River (Webb, 1973).

Southwestern New Mexico interior drainages (SWNM). — *K. sonoriense* occurs in the permanent water basins of the eastern and western slopes of the Peloncillo Mountains of Hidalgo Co. in southwestern New Mexico and adjacent Arizona from 1150 m to 1700 m (Niles, 1962, and Degenhardt and Christiansen, 1974, briefly discussed turtle habitats in

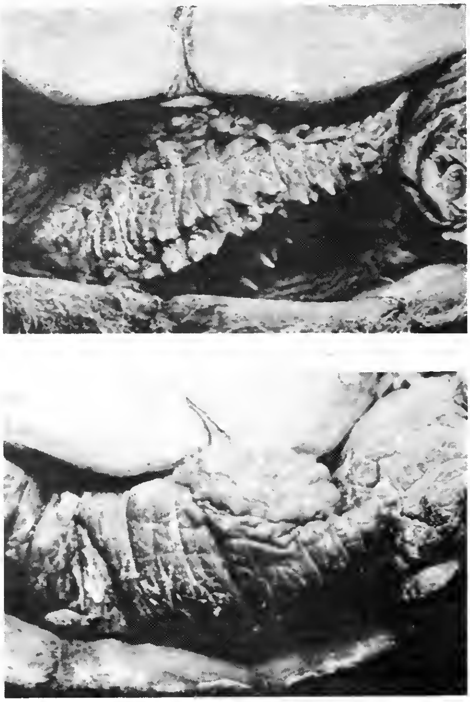

Figure 2. Comparison of papillae on the tail of female *Kinosternon hirtipes* (above; FMNH 71029; 137 mm CL; Guanajuato, Taboado) and *K. integrum* (FMNH 71031; 126 mm CL; same locality).

Table 1. Character Comparison of adults of the *Kinosternon hirtipes* species group and *Kinosternon integrum* (*K. scorpioides* species group).

Kinosternon hirtipes group	*Kinosternon integrum*
Elevated scale patches on hind legs of males	No elevated scale patches on hind legs of males
Head shield in adults geographically variable, from reduced crescent-shape to large, V-shape, or to even larger triangle or bell shape (latter characteristic only of *K. sonoriense* and Valley of Mexico *K. hirtipes*); posterior margin of shield often concave.	Adult head shield large, triangular or bell shaped, with posterior margin convex; shield not reduced or furcate behind
Axillary and inguinal scutes nearly always in broad contact.	Axillary and inguinal scutes usually not in contact; if touching, contact is narrow.
Plastron usually yellow or greenish yellow, sometimes darkly stained.	Plastron usually yellow-orange, almost never darkly stained.
If carination present on posterior carapace, then only one medial keel usually evident.	If carination present on posterior carapace, then three keels usually evident.
Skin very papillose; tail with numerous rows of large papillae (Fig. 2).	Skin hardly papillose; tail with few, very reduced papillae (Fig. 2).
Maximum carapace length, 185 mm; maximum plastron length, 160 mm.	Maximum carapace length, 210+ mm; maximum plastron length, 195+ mm.
First vertebral scute width averages 24.5 (range 20 to 32%) and 25.1% (20 to 30%) of carapace length in male *K. hirtipes* and *K. sonoriense*, respectively; 24.7 (18 to 31%) and 26.1% (20 to 32%) in females, respectively.	First vertebral scute width averages 21.3% (range 17 to 26%) of carapace length in males; 22.5% (19 to 28% in females).
Bridge length averages 20.1 (range 16 to 24%) and 21.4% (18 to 25%) of carapace length in male *K. hirtipes* and *K. sonoriense*, respectively; 23.6 (18 to 29%) and 24.8% (22 to 28%) in females, respectively.	Bridge length averages 26.1% (range 20 to 28%) of carapace length in males; 26.8% (20 to 30%) in females (excludes coastal Jalisco specimens).
Bridge length averages 82.0% (range 61 to 120%) and 85.3% (62 to 115%) of first vertebral scute width in male *K. hirtipes* and *K. sonoriense*, respectively; 95.5% (64 to 133%) and 95.0% (70 to 123%) in females, respectively.	Bridge length averages 114% (range 88 to 151%) of first vertebral scute width in males; 115% (91 to 158%) in females (excludes coastal Jalisco specimens).
Maximum posterior width of plastral forelobe averages 43% (range 36 to 51%) and 47% (range 42 to 53%) of carapace length in male *K. hirtipes* and *K. sonoriense*, respectively; 48% (42 to 54%) and 49% (44 to 54%) in females, respectively.	Maximum posterior width of plastral forelobe averages 47% (range 42 to 54%) of carapace length in males; 53% (45 to 57%) in females (excludes coastal Jalisco specimens).
Nuchal and first neural bones occasionally (41% in *K. sonoriense;* 10% in *K. hirtipes*) in contact.	Nuchal and first neural bones not in contact.

this area). Huntington (1914:70) reviewed the historical isolation of the Animas Valley, which lies to the east of Peloncillos and receives the drainages of the eastern slopes of those mountains. Hubbs and Miller (1948) examined the geography of this and other independent drainage basins in southwestern New Mexico.

Río Sonoyta (= Sonoita) basin, Arizona and Sonora (SNTA). — The Río Sonoyta lies along the northwestern boundary of the state of Sonora, Mexico. The river disappears in the desert sands near the eastern border of the Pinacate lava flows. The physical geography of the basin is reviewed by Ives (1936). *K. sonoriense* is found in the more permanent portions of the basin between about 350 and 450 m, near the U.S. border. It is abundant at Quitobaquito Pond in Organ Pipe Cactus National Monument, Pima Co., Arizona (Hulse, 1974; Iverson, field notes). The aquatic habitat at Quitobaquito was described by Cole and Whiteside (1965). Hubbs and Miller (1948:113) discussed the historical geography of the basin.

Kinosternon flavescens is the only other native aquatic or semiaquatic turtle known from the Río Sonoyta system (H. M. Smith and Hensley, 1957; Iverson, 1979), but Hulse (1974:94) reported that *Chrysemys picta dorsalis* has been introduced into Quitobaquito Spring.

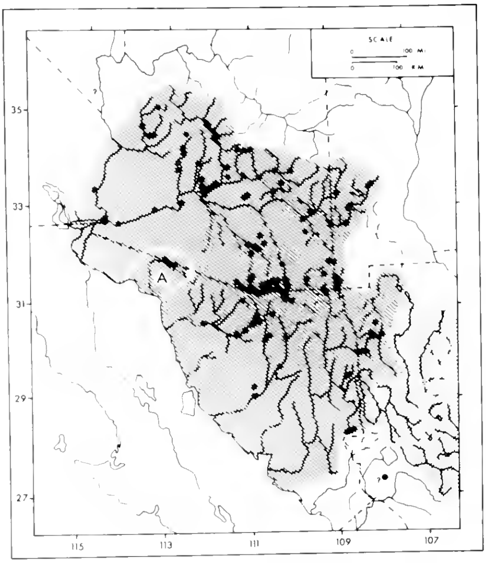

Figure 3. Distribution of the subspecies of *Kinosternon sonoriense*. Dots indicate actual records; hatching, suggested total ranges. The range of *K. sonoriense longifemorale* is marked (A); the remaining hatched area marks the range of the nominate subspecies. Question mark in Nevada is discussed in Iverson (1978); that in southeastern Chihuahua, in the present text. Stippled area illustrates portion of the allopatric range of *Kinosternon hirtipes* (see Fig. 4).

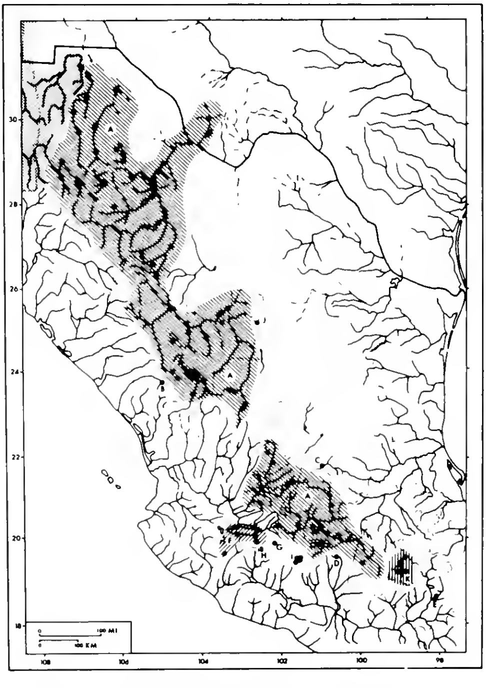

Figure 4. Distribution of the subspecies of *Kinosternon hirtipes*. Dots indicate actual records; hatchings, suggested total ranges. Subspecies ranges are marked: *K. hirtipes murrayi* (A-E); *K. h. chapalaense* (F); *K. h. chapalaense* x *K. h. murrayi* (G); *K. h. magdalense* (H); *K. h. tarascense* (I); *K. h. megacephalum* (J), and *K. h. hirtipes* (K). Problematical localities (San Luis Potosi, C; Balsas, D; and Puebla, E) are discussed in text. Stippled area indicates a portion of the allopatric range of *K. sonoriense* (see Fig. 3).

Río Magdalena, Sonora (MAGD). — The Río Concepción (the major tributary of the Rio Magdalena) arises in the hills near Nogales, Arizona, flows as a permanent stream through the Magdalena Valley, and disappears into the coastal sands of northwestern Sonora (Tamayo 1964: 102). *Kinosternon sonoriense* is known from numerous permanent water habitats between about 300 and 1200 m elevation. *Kinosternon flavescens* is also known from this basin (Iverson, 1979).

Río Sonora, Arizona and Sonora (SNRA). — Like the Río Magdalena, the Río Sonora rises near the Arizona-Sonora border and disappears (below Hermosillo) into coastal sands (Tamayo 1964:102). *Kinosternon sonoriense* is locally very abundant in this basin in permanent water habitants between at least 200 and 1200 m elevation. *Kinosternon flavescens* is the only other freshwater turtle known from this basin (Iverson, 1979).

Río Yaqui basin (excluding the Papigochic drainage), Arizona, Chihuahua, and Sonora (YAQ). — Because of the zoogeographic dissimilarity of the Yaqui basin west of the Continental Divide (Ríos Yaqui, Moctuzuma, Bavispe, and Aros) and those east of the Divide (Ríos Papigochic and Tomochic) (Meek, 1904; Miller, 1958), and because obvious differences were observed early in the study between the turtles of the *K. hirtipes* group on either side of that Divide in those rivers (*Kinosternon sonoriense* in streams to the west, *K. hirtipes* in those to the east), the Yaqui sample was divided into a Plateau portion (hereafter called the Río Papigochic sample) and a non-Plateau portion (hereafter restrictively called the Río Yaqui sample). *Kinosternon sonoriense* is known only from headwater populations in permanent water situations between 1200 and 2000 m elevation in southeastern Arizona and adjacent northeastern Sonora, and western Sonora near the Chihuahua border. A specimen from El Novillo, Sonora, catalogued as *K. sonoriense* (UAZ 36505) but unseen by me (not mapped on Fig. 3, but mapped in Iverson, 1976) is probably misidentified since it is the only record of *K. sonoriense* in the lower Río Yaqui. Additional field work in this basin is badly needed.

The freshwater turtles, *Kinosternon integrum, K. flavescens, K. alamosae,* and *Pseudemys scripta* also occur in the Yaqui basin (Legler and Webb, 1970; Iverson, 1978, 1979; Berry and Legler, 1980), but the microsympatry of any pair of species in the Yaqui basin has not been established.

Río Fuerte basin, Chihuahua and Sinaloa. — Three specimens of *Kinosternon sonoriense* (identification verified) collected by Wilmer Tanner bear the locality data "Cerocahui, Chihuahua" (question mark in Fig. 3). As mapped by Tanner and Robison (1960), and Conant (1978:466), the locality lies along a tributary of the Río Fuerte (Pacific drainage). No other members of the *K. hirtipes* group are known from this basin, whereas *K. integrum* is abundant at lower elevations (Berry, 1978; Iverson, unpublished). Contreras-Balderas (1975) suggested that the fish *Notropis (Codoma) ornatus* (primarily an inhabitant of the Mexican Plateau) may also inhabit the headwaters of the Río Fuerte. This would indicate historical faunal interchange (perhaps stream capture) between the Plateau and the upper Río Fuerte, and might have permitted *K. hirtipes,* but not *K. sonoriense,* to reach the Fuerte. The Cerocahui locality must therefore remain problematical until this rarely visited area in southwestern Chihuahua is better studied.

Río Casas Grandes Interior Basin, Chihuahua (CSGR). — The headwaters of the Río Casas Grandes are in the Sierra Madre Occidental, very close (25 km radius) to the headwaters of the Río Bavispe (Yaqui) and Río Papigochic basins. In fact, headwater streams of the Bavispe and Casas Grandes reach within 6 km of one another at about 2000 m, southwest of Pacheco, Chihuahua. The basins are there separated by a divide less than 200 meters high.

Tamayo (1962:475) provided a photograph of the Río Casas Grandes, presumably south of the town of that name, and Goldman (1951:119-122) describes several habitats in this basin. Below (north) the town of Nueva Casas Grandes, the river is diverted for agricultural purposes and can at best be called intermittent. The river terminates in Laguna Guzmán (1180 m; photographs in Henrickson, 1977) but seldom (only during floods) does that Laguna receive water via the Río Casas Grandes. *K. sonoriense* apparently occurs only above (south of) Nueva Casas Grandes (1475 m), up to an elevation of between 1500 and 1600 m in the Río Piedras Verdes near Colonia Juarez.

My trapping operations were unsuccessful on 13 May 1977 in the main channel of the Río Casas Grandes at a bridge on Highway 2 between Janos (ca. 10 km N) and Ascension; only catfish (*Ictalurus* sp.) were trapped in apparently permanent pools even though locals told me that "rock" turtles lived in the stream. Independently, Conant (1978:488) took only catfish and bullfrogs, and collected no turtles in his traps during two days of field work at the same site.

On 1 August 1980, the Río Piedras Verdes above Colonia Juarez was very shallow (average depth, 10-20 cm; maximum depth, 0.5 m) and slowly moving. In one hour, two *K. sonoriense* were collected by hand in shallow water and two more were taken in traps set in the deepest areas. Roger Conant (pers. comm.) trapped eight *K. sonoriense* near this same locality on 19 August 1974 when the river was in flood.

No other aquatic turtles are known from the Casas Grandes basin; Van Devender and Van Devender's (1975) *Chrysemys picta* record was based on specimens actually from the Río Santa María basin.

Río Santa María interior drainage, Chihuahua (STMR). — The Río Santa María rises in the Sierra Madre Occidental very close to the Río Papigochic basin, and flows northward across the desert floor in northwestern Chihuahua. The river bed terminates in Laguna de Santa María (1172 m), and like Laguna Guzmán seldom receives water from its confluent stream. The Laguna de Santa María (photographed in Henrickson, 1978) is separated from the Laguna de Guzmán by a divide of not more than 61 m elevation (Goldman, 1951:123). Geological evidence suggests the lakes were continuous during Wisconsin time when the water level reached at least 1225 m (Axtell 1978: 509).

Kinosternon hirtipes reaches its northernmost distribution in the Río Santa María, and is common in permanent water situations throughout the basin between at least 1400 and 1600 m elevation.

On 12 May 1977, in a tributary of the Río Santa María, southeast of Galeana, two assistants and I captured nearly 100 individuals of *K. hirtipes* by hand (most of which were subsequently released) in less than two hours, primarily by feeling under stream banks. Seven man hours of hand collecting on 2 August 1980 at the same locality produced 140 turtles, which were measured, marked and released as part of an ecology study. Habitats near that location were described by Van Devender and Van Devender (1975). Semmler et al. (1977) reported similar success in the Río Santa María, also near Galeana.

Both *K. flavescens* (Iverson, 1979) and *Chrysemys picta* (H. M. Smith and Taylor, 1950a; Iverson, field notes; Roger Conant, pers. comm.) also occur in the Santa María basin.

Río Carmen (= Río Santa Clara) interior drainage, Chihuahua (CRMN). — The headwaters of the Río Carmen lie in the Sierra Madre west of the Sierra del Nido. The river once flowed (at least during floods) to the Lago de Patos (1175 m) near Villa Ahumada, but since the construction of a dam (Presa de Las Lajas) just south of Ricardo Flores Magon (= El Carmen) the river no longer flows south past Ricardo Flores except in cement irrigation flumes. When visited on 11-12 May 1977, the remnants of the riparian woodland below the dam were still in evidene, but rapidly disappearing (see also Conant 1977:488). Sixty trap hours along the shores of the Presa yielded no turtles. The rocky shoreline lacks aquatic vegetation and the continually changing shoreline (evident from water marks on the rocks) presented habitats which were undoubtedly generally unsuitable for *Kinosternon* turtles. However, Conant (1978: 473) indicated that he recently obtained *K. hirtipes* in the impoundment.

Records for *K. hirtipes* are available from the Río Carmen below (north of) the dam at Ricardo Flores (1500-1600 m), up (South) to the region near Santa Clara (1800 m). *Kinosternon flavescens* is the only other aquatic turtle known from this basin (Iverson, 1979).

Río El Sauze (= Encinillas) interior drainage, Chihuahua (SAUZ). — The Río El Sauz rises in the eastern slopes of the Sierra del Nido, and flows intermittently to the desert floor in the vicinity of the town of Sauz. It then flows intermittently northward, paralleling the Sierra del Nido, until it disappears into the ground about 100 km north-northwest of Ciudad Chihuahua.

According to Hubbs (in Hubbs and Springer 1957:299; and in Miller 1961: 393) the entire Sauz Valley went dry in 1947; however, Minckley and Koehn (1965) recorded an apparently permanent, though artificial pond (with fishes) in the Sauz Valley in 1964 and Contreras-Balderas (1974:182) reported fish collections made in 1964 and 1968.

Kinosternon hirtipes has been collected from at least four localities in the Sauz Valley between 1500 and 1700 m; however, we trapped none at either of two sites of apparently permanent water (containing fishes) near Sauz on 11 May 1977. Local children at that time confirmed the occurrence of turtles in the stream, but said they were uncommon; they were also unsuccessful at securing any for us.

The only other aquatic turtle supposedly recorded from this basin is *Sternotherus odoratus,* but the single record remains problematical (Moll and Williams, 1963; Conant and Berry, 1978). Although unknown, *K. flavescens* may occur in this basin (Iverson, 1979).

Alamito Creek drainage, Presidio Co., Texas (TEX). — Alamito Creek is an ephemeral tributary of the Rio Grande, east and north of Presidio, Texas. *K. hirtipes* is known from only two permanent ponds in this drainage in Texas (about 1050 m). Conant and Berry (1978:11-15) elaborated on the specific localities and field work in the area. This species has not been found in the Rio Grande itself or its American tributaries in southwest Texas, but populations may reside in permanent Mexican tributaries between Presidio (or Ojinaga, Chihuahua) and the Big Bend of the Rio Grande.

Kinosternon hirtipes does not likely occur today above Presidio in the Rio Grande since even by 1919 that river was sometimes completely dry between the New Mexico border and the mouth of the Río Conchos (Udden, Baker, and Bose 1919:23).

Kinosternon flavescens is the only other aquatic turtle occurring in the Alamito drainage with *K. hirtipes;* based on museum records, the two species occur microsympatrically in at least one of the spring-fed ponds in this basin (Iverson, 1979).

Río Conchos drainage, Chihuahua and Durango (CNCH). — The Río Conchos is the major tributary of the Rio Grande (= Río Bravo), accounting for 18% of the latter's total flow (Tamayo 1964:89). With its headwaters in the Sierra Madre in southwestern Chihuahua and extreme northern Durango, it drains more of the state of Chihuahua than any other single river.

More specimens of *K. hirtipes* have been collected in the Río Conchos basin than in any other basin. The species is known from the mouth of the Conchos (ca. 800 m; the lowest altitudinal record for the species) near Ojinaga (Legler, 1960) to its more accessible headwaters (in the Río Florido) near Las Nieves in northern Durango (ca. 1800 m). Bushnell (1971:332) provided a photograph of Lago Boquillo on the Río Conchos, a locality from which *K. hirtipes* is known. *Kinosternon flavescens, Pseudemys scripta,* and *Trionyx spiniferus* are also known from the Conchos basin (Legler, 1960; H. M. Smith, et al., 1963; Webb, 1973; and Iverson, 1979).

Laguna Bustillos interior drainage, Chihuahua (BUST). — The small Laguna Bustillos basin (2720 square km) is in the foothills of the Sierra Madre west of Ciudad Chihuahua. The Laguna itself lies at approximately 1900 m. A single collection (UMMZ; 4 specimens) of *K. hirtipes* is available from a tributary 27.4 km north of Ciudad Cuauhtémoc. I trapped along a clear, shallow, permanent, though intermittently flowing stream with an adjacent cattle tank (pond) 24.3 km north of Cuauhtémoc on Hwy. 28 on 10 May 1977. These two localities probably are the same, since I could find no other tributaries on the road north from Cuauhtémoc. No turtles were captured, although the microhabitat seemed adequate in some of the deeper areas (maximum, 0.5 m). Populations of *K. hirtipes* may exist in the Laguna itself or in this tributary where it leaves the mountains to the west (and thus presumably has more flow). Further field work is warranted to determine if *K. hirtipes* is still extant in the Bustillos basin. No other aquatic turtle is known from the basin.

Río Papigochic, Chihuahua (PAP). — As mentioned above in regard to the Río Yaqui basin, the plateau portion of that basin, the Río Papigochic, is here considered a separate sample area. The Papigochic arises in the Sierra Madre west of Ciudad Chihuahua and flows northwestward to the vicinity of Yepómera, where it turns sharply southward for about 25 airline km to the confluence of the Río Tomóchic and another sharp turn to the northwest. It continues in that direction for almost 150 airline km before heading southwestward to its confluence with the Río Aros (tributary to the Yaqui) just inside the Sonora border. Because of this anomalous drainage pattern and because the faunal affinities of the Papigochic are with the Río Conchos and not the Río Yaqui (sensu stricto), zoogeographers believe the Río Papigochic was until recently (prehistorically) a tributary of the former stream (Meek, 1904; Miller, 1958; among others).

Kinosternon hirtipes is known from both the Tomóchic and Papigochic from elevations of 1200 to at least 2000 m. Like Van Devender and Lowe (1977), I found *K. hirtipes* very common near Yepómera. On 10 May 1977, 5 traps set in a broad, ponded stretch of a Papigochic tributary yielded 25 turtles in two hours. No other turtle species were collected (or are known from the basin), but Tom Van Devender (pers. comm.) reports that natives near Yepómera told him of a "tortuga pinta" that lives in the Papigochic basin. The validity of the report and the identity of the turtle (perhaps *Chrysemys picta*) are unconfirmed.

Río Nazas interior drainage, Durango and Coahuila (NAZ). — More of the state of Durango is drained by the Río Nazas than any other single drainage system. The Nazas rises in the Sierra Madre in western Durango as two major tributaries, the north-flowing Río Santiago and the south-flowing Río Tepehuanes. The confluence of these two streams, about 20 airline km northwest of Santiago Papasquiaro begins the Río de Ramos. The major northern tributary, the Río del Oro rises in the Sierra in northwestern Durango and joins the Río Ramos near El Palmito below which it is called the Río Nazas. The Nazas then flows eastward across the Chihuahuan desert (photographed in Spieth, 1950:34), formerly as far as the Bólson de Mayran in southwestern Coahuila. Diversion of the waters for agriculture near Torreón has, however, severed the Nazas-Mayran connection (Conant, 1963, provides an excellent description of the topography of this basin).

Trapping on the Río Nazas west of Torreón (78 trap hours, 5 - 6 May 1977, 3

Kinosternon; 156 trap hours, 23 - 24 July 1980, 6 *Kinosternon*) and near El Palmito (98 trap hours, 7-8 May, 1977, 5 *Kinosternon)* by me, and near El Palmito (30 trap hours, 20-21 July 1976, 5 *Kinosternon).* Roger Conant (pers. comm.) indicated that *K. hirtipes* is uncommon in the river itself. The absence of a large series from any one locality in the Nazas basin supports this statement. The species is known from between 1100 (Lerdo) and 1400 m (El Palmito).

Pseudemys scripta was collected at all three locations I visited and that species probably is sympatric with *K. hirtipes* in most of the Nazas drainage. *K. flavescens* is the only other aquatic turtle known from this basin (Iverson, 1979).

Viesca interior basin, Coahuila (VSCA). — Only a single collection of *K. hirtipes* (and *Pseudemys scripta*) is known from the small area south of the city of Viesca, Coahuila (symbol J in Fig. 4). Bryce Brown seined 8 *Kinosternon* and 2 *Pseudemys scripta* on 4 June 1961 from 2 drying ponds south of Viesca at about 1100 m. Natives informed Brown that the ponds were remnants of a once active hot spring (pers. comm.). At my suggestion, ichthyologist Robert Rush Miller visited the Viesca area in the spring of 1978 and verified (pers. comm.) the fact that a spring did once exist along the mountains southwest of the city, but he could find no permanent aquatic habitats suitable for turtles or native fishes.

We visited the area on 23 July 1980 and an elderly Viesca resident showed us the locations of the extinct springs (8 total; 1 hot) and confirmed the lack of permanent surface water today. He told us that the springs had gone dry "about 20 years ago" but that prior to that time there had been much water, with many turtles, snakes, and fish. The only permanent water near Viesca of which anyone there knew was a spring near the small town of La Peña, about 20 miles to the East. We visited that spring on 23 July 1980 (as Miller did in 1978), found only introduced fish and no *Kinosternon,* and failed to locate the *Pseudemys scripta*-like turtles locals told us "used to occur" in the two tiny *presas* that remain. The Viesca turtle populations must therefore be considered extinct.

The specimens of *Pseudemys scripta* from near Viesca are very similar to those in the Río Nazas immediately to the west. The *Kinosternon,* however, show little affinity with Nazas specimens and in fact have the most unique morphology of any member of the *hirtipes* group (see later).

Río Aguanaval interior drainage, Coahuila, Durango and Zacatecas (AGUN). — The Río Aguanaval rises on the Mexican Plateau in the mountains northwest of the city of Zacatecas and flows intermittently northward across the Chihuahuan Desert. It once emptied into the Laguna de Viesca in southwestern Coahuila, before its diversion for agricultural purposes (Conant 1963, 1969).

K. hirtipes is the only turtle known to occur in the Aguanaval basin and has been collected only in the headwaters immediately northwest of Fresnillo between 2000 and 2200 m. *Natrix erythrogaster alta,* endemic to the Aguanaval system, is likewise known only from the headwaters (Conant, 1969:46).

Laguna de Santiaguillo interior drainage, Durango (STGO). — The Laguna Santiaguillo is isolated at just under 2000 m in the Sierra Madre northwest of Canatlan, Durango. Only two collections (four specimens) of *K. hirtipes* have been made in the Santiaguillo basin, both apparently from the same tributary to the Laguna near the village of Guatimape. On 7 May 1977, this tributary was temporarily reduced to isolated pools (maximum depth 1 m) in the stream bed. Trapping and seining produced three *K. hirtipes.* A *presa* with permanent abundant water was subsequently located about 0.7 km upstream from the highway bridge, but was not sampled; it probably supports a good population of *K. hirtipes.* No other turtle is known from the basin.

Río Mezquital drainage, Durango (MEZ). — The Río Mezquital is the major tributary of the Río San Pedro (Pacific drainage), and drains that portion of the Mexican Plateau near Ciudad Durango, Durango (Albritton 1958: Conant 1963). Both *K. hirtipes* and *K. integrum* occur in the Plateau portion of the Río Mezquital, but only *K. integrum* is known from the Pacific coastal plain portion of the Mezquital-San Pedro system (Iverson, unpublished). Because of the inaccessibility of the area south and southeast of Ciudad Durango, the lower limit of the range of *K. hirtipes* in the Mezquital is uncertain. The locality farthest downstream is at Mezquital on the Río Mezquital, southeast of Ciudad Durango at about 1100 m. The species reaches its highest known elevation in this basin (2600 m) at Otinapa. Conant (1978:467, 473) correctly questioned the record (H. M. Smith and Taylor, 1950a:26) of *K. sonoriense* from Durango, Durango (this basin); it was apparently based on a specimen of *K. hirtipes.*

The Río Mezquital and its Plateau tributaries near Ciudad Durango contain much permanent water even at the end of the dry season. On 6 May 1977 at the Río La Sauceda (tributary to the Mezquital) bridge on Hwy 40 (Figure 5), 60 *K. hirtipes* (pre-dominately juveniles and subadults) entered 11 traps in just three hours. The most productive traps had been set along steep, undercut dirt banks; traps in areas of gently sloping shorelines were unproductive. Six traps set for 45 minutes at the same locality on 25 July 1980 produced 14 *K hirtipes.* Based on museum records, *K. hirtipes* is very common in the Mezquital system (148 specimens), whereas *K. integrum* is uncommon (I am aware of but 14 specimens); a single collection of turtles from 0.8 km N Graceros contains 12 *K. hirtipes* (KU 68733-36, 68738-45) and a single *K. integrum* (KU 68737).

El Salto area, Río Acaponeta basin, Durango (SALT). - *K. hirtipes* apparently occurs in the Río Acaponeta only in its headwaters northeast of El Salto (Symbol B in Fig. 4). On 25 July 1980, at a shallow (maximum depth 0.75 m) apparently permanent stream 9.7 road km ENE El Salto (about 2400 m) in a mountain meadow surrounded by pine-oak woodland, six *K. hirtipes* were collected in 12 trap hours and three more were taken by hand. *K. integrum* is very common in the lower Río Acaponeta basin (Berry 1978; Iverson, unpublished), but is unknown from the headwaters region.

Southwestern San Luis Potosí (interior?) basin (SLP). - In an isolated portion of the Río Santa María drainage basin (Pánuco, i.e., Atlantic drainage southwest of Villa de Reyes (symbol C in Fig. 4), *K. hirtipes* and *K. integrum* cooccur abundantly. Iverson and Berry (1979) argued that this population of *K. hirtipes* is the result of an introduction. I continue to support that view, especially since *K. integrum* has been collected at numerous localities in the Río Santa María system (see list in Iverson and Berry, 1979), yet *K. hirtipes* is known only from the Laguna de las Rusias (= Presa El Refugio; ca. 1900 m) area. As described by Iverson and Berry (1979:320) the only remaining aquatic habitat found on 11 June 1978 was a small permanent stream that was diverted entirely for agriculture within 2 km below the broken dam. The Arroyo below the dam was lined with seepage springs and quaking ground. The stream varied from one to four m wide ($\bar{x} \approx 1$) and averaged only 0.25 m deep (over a soft mud bottom at least 1 m deep). The water was quite clear along most of its length, but odor and

Figure 5. Rio La Sauceda (Rio Mezquital basin) at Highway 40 near city of Durango, 6 May 1977.

refuse in the water indicated its use as a human sewage effluent. *Kinosternon* was abundant in the stream on 11 June; 13 *K. hirtipes* and 3 *K. integrum* were dipnetted or trapped in one hour.

Río Aguascalientes drainage, Aguascalientes (AGUAS). - Because the distance between the two clusters of localities for *K. hirtipes* in the Río Aguascalientes-Verde system is so great, I have arbitrarily divided the system into two parts: the Rio Aguascalientes basin in the state of Aguascalientes and the remainder of the Río Verde, primarily in Jalisco.

Collection data for museum specimens indicate that *Kinosternon hirtipes* and *K. integrum* co-occur in the Río Aguascalientes between at least about 1900 and 2000 m elevation. Oswaldo Mooser (pers. comm.) indicated that *K. hirtipes* is much less common than *K. integrum* in Aguascalientes. The fact that 21 museum specimens of *K. integrum* are available from ten localities in Aguascalientes whereas 15 specimens of *K. hirtipes* are known from only five localities (Iverson, unpubl.) support his contention. Mooser's field observations also indicate that the former occurs only in permanent water situations, wereas the latter is common in those situations as well as temporary aquatic habitats. I have not visited the Río Aguascalientes basin.

Río Verde drainage, Jalisco (VERD). - Draining most of northeastern Jalisco, the Río Verde empties near Guadalajara into the Río Grande de Santiago, which flows through the Sierra madre Occidental to the Pacific Ocean. *K. integrum* occurs throughout the entire Verde-Santiago system (Berry 1978; Iverson, unpublished), but within the Rio Verde system (excluding Aguascalientes) *K. hirtipes* is known from only three localities. At least two are permanent water situations, their permanence enhanced by the construction of dams.

On 16 June 1978, I collected four *K. integrum* and three *K. hirtipes* in one hour at the most southerly known locality in this basin (just over 1800 m), a tributary of the Río Verde north of the city of Valle de Guadalupe. At that time the stream was reduced to a series of isolated, well-vegetated pools (one to two m across and P 1 m deep) in the channel below a large stone dam. The impounded reservoir (Presa Cañada Grande) was unvegetated and reduced to a small (50 m X 50 m), deep (2 m ^{s}), muddy pond immediately behind the dam. The heads of literally hundreds of *Kinosternon* were visible at the pool's surface on that day. The isolated pools in the stream channel, however, contained few turtles, usually only one per pool. Turtles were also abundant here on 10 May 1981, when gravid female *K. hirtipes* were seen basking.

The other locality (ca. 2000 m) below the Presa el Cuarenta on the Río del Cuarenta (= Río de Lagos = Río San Juan de los Lagos) near the village of Paso de Cuarenta, was also visited on 16 June 1978. The large cement dam impounds a huge, muddy, unvegetated reservoir. Because of the apparent lack of turtle habitat along the shoreline, the *presa* was not trapped. Below the dam, however, were numerous rocky-shored (in the main channel and well vegetated, mud-shored overflow and seepage pools. The more vegetated ponds were most productive, and eight trap settings produced 15 *K. hirtipes* and two *K. integrum* in one hour.

K. hirtipes is probably much more common in the Río Verde than is indicated by the paucity of locality records. Additional field work should verify this prediction. Of particular interest is the downstream limit of *K. hirtipes* in the Río Verde.

Río Grande de Santiago drainage. - This river links the Lago de Chapala with the Pacific Ocean and passes through the Sierra Madre Occidental. Tanner and Robison (1960) reported the collection of three unidentified *Kinosternon* from 7.5 mi. north of Magdalena, Jalisco (1000 m elevation) in this basin. One of the included specimens (BYU 14630) is unquestionably *K. sonoriense* and the locality data for that specimen must be considered in error. The other two specimens supposedly collected at the same locality (BYU 14631-32) are presently unlocatable (Tanner, pers. comm.). I doubt the natural occurrence of a *K. sonoriense*-like member of the *K. hirtipes* species group in the Río Grande de Santiago below Guadalajara. Of those major systems joining the Rio Santiago below Lake Chapala, only the Verde harbors *K. hirtipes* (see above). *K. integrum* however, ranges throughout the Lerma and Santiago basins and all their tributaries, both on the Plateau and off (Iverson, unpublished).

Conant's (1978:465; Map 10) two most southerly records for *K. hirtipes* in Durango were erroneously plotted in the Río Atengo drainage, a tributary to the Río Santiago (Roger Conant, pers. comm.); the records belong in the Río Mezquital basin near Ciudad Durango.

Río Lerma drainage, Jalisco, Guanajuato, Michaocan, and Mexico. — Most of the southern portion of the Mexican Plateau is drained by the Río Lerma and its tributaties. The Lerma originates in the springs and lakes in the southern end of the Toluca Valley at over 2400 m (Goldman 1951:185, 305, plates 59 and 60; Tamayo, 1964:104; Romero, 1965), and flows northward and then westward across the southern Plateau to Lake Chapala. The basic physiography of the river along most of its course is discussed by Barbour (1973:541) and Tamayo (1962). Like the Río Grande de Santiago, the Río Lerma's south bank tributaries are not extensive (the river flows parallel to and immediately north of the Sierra Volvanica Transversal), whereas several of those on the north bank are very large (notably the Ríos Turbio and de la Laja).

Because the Lerma basin is well over 400 airline km long, I chose to subdivide it for analysis of its resident turtle populations. I have followed Barbour (1973: 540) in his division of the Río Lerma basin into four physiographic regions: the Valley of Toluca (TOL; above the canyon below Temascalcingo in the state of Mexico), the Maravatío basin (MAR; from near Temascalcingo, Mexico through Michoacán and Guanajuato to the rapids near Salvatierra, Guanajuato), the Bajío (BAJ; from near Salvatierra, Guanajuato to the region between Piedad and Yurécuaro, Michoacán), and the Lake Chapala basin (CHAP; in Jalisco and Michoacán. [The reader is referred to Barbour (1973) for discussion of these physiographic provinces.] I have also considered the turtles in the lower Río Lerma tributary, the Río Duero (DUER) (historically a tributary of Lake Chapala; see Tamayo, 1962:404), as a separate population for purposes of analysis. Each of these subdivisions is discussed separately. *K. hirtipes* and/or *K. integrum* are the only aquatic turtles presently known to occur in these basins (But Pleistocene fossils of *Pseudemys* cf. *scripta* are known from near Lake Chapala; Tom Van Devender, pers. comm.).

Valley of Toluca basin, México (TOL). - No turtles are known from the Toluca basin, but *K. hirtipes* probably occurs in the springs and lakes near the Río Lerma headwaters in southeast México state.

Maravatió basin, México, Michoacán and Guanajuato (MAR). - Only a single broken *K. hirtipes* shell (KU 43637) is available from this basin, and this region is thus unrepresented in subsequent analysis. No *K. integrum* are known from the Maravatió (Iverson, unpublished), but both species probably occur throughout the basin.

Bajío basin, Guanajuato and Michoacán (BAJ). - This basin includes the drainages of the Lerma tributaries, the Río de la Laja and Río Turbio. Both *K. hirtipes* and *K. integrum* occur in the Bajio up to at least 1900 m (north of San Miguel de Allende; Iverson, unpublished). On 12 June 1978 I sampled two marshy areas near the Río de la Laja between San Miguel de Allende and Dolores Hidalgo, Guanajuato. An hour at each locality produced three *K. hirtipes* (two by hand; one trapped) and two *K. hirtipes* (one trapped, one seined) respectively.

Río Duero drainage, Michoacán (DUER). - *K. hirtipes* is known from only one locality in this drainage. At spring-fed, cypress-lined Lago Camécuaro (1700 m), east of Zamora (Symbol G in Fig. 4), I found *K. hirtipes* very abundant on 14 June 1978; 17 trap hours produced 20 *K. hirtipes* and one *K. integrum.* The latter species is known from several other localities in the Río Duero and likely occurs throughout the basin.

Villa Victoria basin, México (state) (VILLA). - *K. hirtipes* has been collected at only three localities within a 3 km radius in this basin (part of the Río Balsas basin; see later) at about 2500 m; *K. integrum* is therein unknown. *K. hirtipes* is apparently not common in the basin as evidenced by our collection of only two specimens in 134 trap hours at four localities below the *Presa* Villa Victoria on 21-22 June 1979.

Lago de Chapala basin, Jalisco and Michoacán (CHAP). - Lake Chapala (elevation 1525 m) is 80 km long, east to west and covers about 1685 km^2 (Debuen 1945; Deevey 1957; see photographs in Tamayo, 1962). Average depth is only 8 m (Tamayo 1964:105), and maximum depth is probably 9.8 m (Cole 1963:413). The Río Lerma flows into the extreme eastern end of the lake and the Río Grande de Santiago exits the lake about 15 km north of the Lerma's mouth. There are no other large confluent streams. All records but one (Jiquilpan; Duellman, 1961) of *K. hirtipes* from the Chapala basin are from along its shores. *K. integrum* has also been commonly collected along the lake shores (Berry 1978; Iverson, unpublished). Trapping along the south shore near Tuxcueca on 15 June 1978 produced no turtles whatsoever, although J.F. Berry (pers. comm.) obtained a series of *K. integrum* at the same locality in June 1975.

The once extensive marshes at the eastern end of Lake Chapala probably supported dense populations of *Kinosternon* turtles, but drainage operations have unfortunately nearly eliminated this habitat (Goldman, 1951:173-174).

Laguna de Zapotlán interior drainage, Jalisco (ZAPO). - The Zapotlán basin lies north of Ciudad Guzmán, Jalisco in the Sierra Volcanica Transversal. Only *K. hirtipes* is known from the basin and all specimens apparently originated at the southern end of the lake (ca. 1500 m) near Ciudad Guzman. Gadow's (1908) record of *Cinosternum integrum* from this basin must therefore be based on *K. hirtipes.*

San Juanico Valley interior drainage, Michoacán (SNJ). - The Valley of San Juanico (north of Cotija, Michoacán) was until recently an isolated, interiorly drained basin, formed prehistorically by the damming of a northward-flowing tributary of the Chapala basin by a lava flow (Alvarez 1963, 1972; Barbour 1973). The construction of the *Presa* San Juanico across the valley's southern end has enlarged Lake San Juanico, and directed its effluents southward to the Balsas system (Alvarez 1972:158; Barbour 1973; pers. observ.).

Turtles of the *Kinosternon hirtipes* group are the only turtles known from the valley behind and above the *Presa* San Juanico (ca. 1500 m; Symbol H in Fig. 4). Field work by Clyde Barbour (pers. comm.) and my own field crew (75 trap hours, 14-15 June 1978; 180 trap hours, 6-7 May 1981) in the *presa* (Figure 6) have produced only 7 specimens, three living (one seined by Barbour; two trapped by me) and four articulated shells (by my crew). Ichthyological field work in the *presa* on three dates in 1962 and 1963 by Alvarez (1963) apparently produced no turtles.

The diversion of effluents from the San Juanico Valley to the Balsas appears to be permitting *K. integrum* (known throughout the Balsas system; Berry, 1978; Iverson, unpublished) to expand its range toward the *presa.* Although no *K. integrum* are known from above the *presa,* and although we obtained no turtles 3 km below the dam in 1978 in one of the two effluent irrigation ditches (during one hour of seining and 12.5 trap hours), a single *K. integrum* observed sunning along the other ditch (ca. 100 m below the dam) was seined. An additional juvenile *K. integrum* (TUL 19504) is also known from one of the effluent ditches where it crosses the Cotija-Tocumbo road (distance below dam uncertain). *K. integrum* likely will soon invade Lake San Juanico.

In June 1978, the lake itself was very low; much of the muddy bottom was exposed due to evaporation and diversion for agriculture (Fig. 6). A small water hyacinth population represented the only obvious vegetation in the muddy lake. In 1981 the lake was even lower and new ditches were draining the lake even more. No turtles were collected and their existence seems tenuous.

Lago de Cuitzeo interior basin, Michoacan CUIT). - Lago de Cuitzeo (just over 1800 m) is the largest interiorly drained natural lake in Mexico. It is fed primarily by the Río Grande de Morelia, which heads in the mountains east of Pátzcuaro and flows southeastward to its confluence with the southeastern shore of the lake (Camacho, 1925). The lake is very shallow, and has been known to be nearly dry (Debuen, 1943). Aquatic vegetation is accordingly uncommon. When visited on 12 June 1977, the lake level was very high and therefore not trapped for turtles. Based solely on museum specimens, *K. hirtipes* (one specimen) is much less common than *K. integrum* (35 specimens, 7 localities; Iverson, unpublished). The single available specimen is a poorly preserved male.

Lago de Pátzcuaro, interior basin, Michoacán (PATZ). - Lago de Pátzcuaro (2,035 m; Symbol I in Fig. 4; see photgraphs in Tamayo, 1962:493 and Solorzano Preciado 1961:55) has been well-studied limnologically (summary in Cole, 1963), but its turtles have been only infrequently mentioned (Duellman, 1961; Altini, 1942) or completely ignored (Martin del Campo, 1940). It has a surface area of only about 111 km² and has a maximum depth of 15 m (DeBuen, 1944). Emergent vegetation (primarily *Scirpus*) is common along the shoreline, especially the southern margin (Goldman, 1951:195, plate 58; Barbour, 1973:543), where the mats often extend out 20 m or more from the shoreline (pers. observ.).

Figure 6. Presa San Juanico, Michoacán, looking northwestward from dam, on 15 June 1978. Reservoir was much reduced due to irrigation demands and the dry season. *Kinosternon hirtipes magdalense* was collected along the dredged canal in foreground.

On 12-13 June 1978, the lake was quite clear; however, we saw no turtles during the day or night in shallow water (< 1 m) in narrow strips of shoreline on the southeastern shore where emergent vegetation has been removed for docks (Fig. 7). *Kinosternon hirtipes* (the only turtle known from the lake) were, nevertheless, for sale the next day in the Pátzcuaro (city) market, an apparently frequent occurrence.

The smaller (8 km²) higher (2120 m), younger, and deeper (maximum depth 45 m) Lago de Zirahuén (DeBuen, 1943, 1944) immediately to the southwest, is believed to have been historically drained by a tributary of the Río Lerma flowing through the Lake Pátzcuaro and Lake Cuitzeo basins (DeBuen, 1943). No turtles are known from Lake Zirahuén.

Río Balsas drainages, Michoacán and Puebla (BALS). - Turtles of the *hirtipes* group have been recorded from only three localities in the Río Balsas basin, the river sytem which drains most of southern Mexico south of the Sierra Volcanica

Transversal. The Villa Victoria (VILLA) localities have already been discussed. Duellman (1961) recorded *K. hirtipes* from the Balsas on the basis of UIMNH 24707 from 8 km W Ciudad Hidalgo, Michoacan (ca. 2200 m; Río Tuxpan Valley; Symbol D in Fig. 4). I have examined the specimen and believe it to be a female *K. integrum*. However, another specimen from the same locality (AMNH 62257) is unquestionably a female *K. hirtipes*. In addition, I collected a single male *K. hirtipes* in 128 trap hours in a stream of approximately the same locality on 4-5 May 1981. *Kinosternon integrum* occurs throughout the Tuxpan (and Balsas) system (Berry, 1978; Iverson, unpublished); but *K. hirtipes* is now definitely known in the Tuxpan only near Ciudad Hidalgo.

The only other supposed Balsas specimen of *K. hirtipes* is an adult male (UU 12096) from a tributary of the Río Atoyac, 4.5 km S Molcaxac (just below 2000 m; Symbol E in Fig. 4). The identification is correct, but I question the validity of the data for three reasons. First, because of the numerous highway accesses to the Río Atoyac drainage and the fact that I know of at least 88 specimens of *K. integrum* (73 of which I have seen) from 13 localities in the Atoyac-Balsas system in the state of Puebla, additional specimens of *K. hirtipes* would likely have been collected if the species did occur in that system. Second, nine trap hours at the Molcaxac locality on 3 May 1981 produced 23 *K. integrum* and no *K. hirtipes*. Third, based on field numbers and collection dates, Clyde Barbour collected *K. hirtipes* along the Río Lerma in Jalisco (UU 12120) on 7 May 1969 and *K. integrum* in the Río Turbio in Guanajuato (UU 12083-84) on 8 May and in the Río Villeto in San Luis Potosí (UU 12085) on 12 May] immediately before he collected near Molcaxac (18 May 1969). Of the eleven turtles recorded as collected near Molcaxac, ten are definitely *K. integrum*. I submit that through a mixup, the Molcaxac locality datum was mistakenly applied to the eleventh specimen, and that the specimen possibly originated somewhere in the Lerma basin (Ríos Lerma or Turbio?) where Barbour also collected.

Figure 7. Southeastern shore (foreground) of Lago de Pátzcuaro, Michoacán, 13 June 1978.

Valley of Mexico interior basin (VALLE). - The physiography and historical geology of the Valley of Mexico in which Mexico City lies has been well-studied (Bryan 1946, 1948; De Terra et al., 1949; Arellano, 1953; Sokoloff and Lorenzo, 1953; Zeevaert, 1953; Foreman, 1955; Hibbard, 1955; Maldonado-Koerdell, 1955; Sears and Clisby, 1955; Mooser et al., 1956; Mooser, 1957, 1963; Deevey, 1957; Lorenzo, 1958; Bernal, 1959; Bribiesca Castrejon, 1960; White, 1962; Golomb, 1965; Bradbury, 1971; and an excellent summary in Barbour 1973:537). The entire basin is about 24 km wide and 113 km long (Foreman, 1955) and covers about 8000 km^2 (Maldonado-Koerdell, 1955:15). At the time of the Spanish conquest (ca. 1520), the Valley of Mexico was one of the largest interior drainage basins in the Transverse Volcanic Arc, supporting five large spring-fed lakes (Tamayo, 1964; De Terra et al., 1949; among others). So extensive were the lakes at that time, that the early city of Mexico had been built on an island and the Spaniards were forced to build ships in order to besiege the city (Huntington 1914:96). Tremendous fluctuations in water level in the Valley prompted drainage operations in the late 16th century, and by 1608 some of the Valley's water was diverted northward to the Río Tula (Atlantic drainage; Tamayo, 1964; Barbour, 1973:540). This artificial drainage system was finally completed in 1900 (Huntington, 1914:97; Bribiesca Castrejon, 1960) and they only sizeable lakes in the Valley today are Zumpango (2243 m elevation) and Texcoco (2236 m) (Barbour, 1973). Only about 10% of the Valley floor is covered with water (Foreman, 1955). For discussions of the changing conditions of the lakes since about 1500 AD, see Bribiesca Castrejon (1960). Aquatic habitats in the Valley were discussed and photographed by Gadow (1908:6) and Goldman (1951:138-39, plate 56).

Apparently the first record of a turtle from the Valley of Mexico is Wagler's (1830) description of *Cinosternon hirtipes* (see later justification). Numerous literature records (See synonymies) and museum specimens confirm the presence of *K. hirtipes* in the Valley of Mexico. *Kinosternon integrum* has possibly been collected in the Valley only three times. FMNH 116521 bears only the data "Distrito Federal". Data associated with SM 9722-23 indicate they were purchased in the Xochimilco market on 11 June 1962. Fourteen turtles purchased for me by Gustavo Casas-Andreu in the Xochimilco market in August 1977 are all *K. integrum*. The merchants told him the turtles were from the "Valle de México". Because there is no verifed record of the occurrence of *K. integrum* in the Valley before 1962, and because all three subsequent records are apparently from markets, I strongly doubt the natural occurrence of *K. integrum* in the Valley of Mexico. *K. integrum* is, however, very abundant southeast of the Valley in Puebla and Oaxaca (Berry, 1978; personal observation; see discusssion under Río Balsas), and may have been imported to the Valley for sale in the markets. Support for such an hypothesis comes from Berry's (1978:83, Fig. 17) discriminant analysis of data from the turtles sent to me by Casas Andreu (UF 41651-64), which clearly showed their affinities to be with turtles from the Upper Río Balsas (Río Mexcala) and the Upper Río Papaloapan (Río Santa Domingo basin, Puebla and Oaxaca). Whatever their true origin, *K. integrum* will likely soon establish itself in the Valley. A study of the interaction of that species with the native *K. hirtipes* would be significant.

Mittermeier (1971:16) found *Pseudemys scripta elegans,* obviously introduced, in the markets of Mexico City, where he was told that the species had been introduced into ponds near Mexico City. No other turtle is known from the Valley of Mexico.

Unrepresented or unsampled basins. - Several other isolated and/or interior drainage basins within or adjacent to the range of *K. hirtipes* should be investigated for that species. These include the Laguna de Babícora (2100 m), northwest of Gómez Farias, Chihuahua; the Laguna de Los Mexicanos (2100 m), south of Cuauhtémoc, Chihuahua; the Laguna de Zapacu and *Presa* de Copandaro, near Zacapu in northern Michoacán; the crater lakes of the Llanos of Pueblo (see Alvarez, 1949); the Río Mezquitic (= Río Balaños), tributary to the Río Grande de Santiago and accessible near Valparaíso, Zacatecas; the Laguna de Sayula (about 1300 m), north of Sayula, Jalisco; and the Laguna de San Marcos (ca. 1300 m), near Zacoalco, Jalisco. *K. integrum* occurs in the latter three basins (Iverson, unpublished), where it is the only turtle species known.

CHARACTERS

Nineteen shell measurements were made with dial calipers on museum specimens of the *hirtipes* species group from drainage basins discussed above. Only data from specimens over 80 mm carapace length (except three females) with the full complement of measurements were used in the morphometric analyses; various ratios of characters were also employed to minimize ontogenetic variation (see STATISTICAL TECHNIQUES). Character means and ranges by population (Appendices 1 and 2) and taxon (Appendices 3 and 4) for each sex are available from NAPS[1].

Mensural characters recorded and their abbreviations follow [Methods of measurement were given by Iverson (1977a); midline plastral scute measurements were always made on the animal's right side.]: carapace length (CL), carapace width (CW), maximum plastral length (PL), plastral widths measured at the lateral edges of the seams between the humeral, pectoral, abdominal, femoral, and anal laminae (WA, WB, WC, and WD respectively), bridge length (BL), gular length (GL), gular width (GW), interhumeral seam length (IH), interpectoral seam (IP), interabdominal (IAB), interfemoral (IF), interanal (IAN), first vertebral width (VW) and length (VL), maximum length of plastral forelobe (FL), and maximum length of plastral hindlobe (HL). The ratios of each character to CL as well as the ratios of IH, IP, IAB, IF, and IAN to PL (total, 23 ratios) were employed in the analysis. In some analyses, the number of variables was reduced to those thirteen (excluding the ratios CW, HL, PWD, IH, IP, IAB, IF, IAN, VW and VL to CL) with the greatest variation in the species group. Those analyses are noted in the text. Sexes (males have long tails and scale patches on the hind legs) were always analyzed separately.

Relative shell height has been used to distinguish *Kinosternon hirtipes* from *K. sonoriense* (e.g., Ernst and Barbour, 1972; Wermuth and Mertens, 1961); however, the character is difficult to measure consistently and preliminary analysis revealed it would not reliably separate the two taxa. It has therefore not been used in this analysis.

Qualitative characters also recorded included relative head size, plastral color, and shell carination as well as the following.

Nasal scale. - As described by Conant and Berry (1978:3), adult kinosternids have a patch of cornified epithelium which extends from the dorsal margin of the rostrum for a variable distance posteriorly on the dorsum of the head. A drawing of the shape and extent of the nasal scale on each individual turtle was made.

Chin barbels. - The number, relative sizes, and locations of chin and neck barbels were recorded.

Head pattern. - Although often quite variable and difficult to describe, an attempt was made to qualify head patterns. The procedure involved photographing the heads of as many specimens as possible (over 500 total head photographs available) for later simultaneous examination and comparison.

STATISTICAL TECHNIQUES

Character ratios were employed in the statistical analyses despite recent criticism of their use by Atchley et al. (1975, 1976). This decision is based on arguments in favor of their use by Corruccini (1977), Nussbaum (1976), Dodson (1978), Heyer (1978), and Iverson (1979), as well as the articulate demonstration by Berry (1978) that, for at least one other *Kinosternon* species group, the use of ratios as input variables in both multiple discriminant

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[1] See NAPS document 03915 for 20 pages of supplementary material. Order form NAPS, c/o Microfiche Publications, P.O. Box 3513, Grand Central Station, New York, NY 10017, USA. Remit in advance for each NAPS accession number. Institutions and organizations may use purchase orders when ordering; however, there is a billing charge of $5.00 for this service. Mack checks payable to Microfiche Publications. Photocopies are $5.00. Microfiche are $3.00 each. Outside the United States and Canada, postage is $3.00 for a photocopy and $1.00 for a fiche.

analysis and distance (D^2) analysis produced results almost identical to those obtained by using residual values from regression analysis as input variables (the standardization technique recommended by Atchley et al., 1976). My own unpublished data on other kinosternid species also support the effectiveness and reliability of multivariate analyses using character ratios for at least this family of turtles. Furthermore, I attach no statistical significance to multivariate output generated from ratios. The output is only used as a tool to pinpoint distinctive samples, and to suggest the characters most important to those distinctions.

Simple statistics were performed using the Statistical Analysis System (Service, 1972). Standard deviations accompany mean character ratios only as a relative measure of dispersion; no statistical significance is implied. Step-wise discriminant analyses (see Gould and Johnston, 1972, and Sneath and Sokal, 1973, for review of the procedure) utilized the Biomedical Programs BMDO7M (W.J. Dixon, 1973), and BMDP7M (W.J. Dixon, 1977). Cluster analyses employed the NT-SYS (Rohlf and Kispaugh, 1972) and BMDP2M programs. Specific applications of these analyses are outlined under MORPHOMETRIC ANALYSIS.

Because of the pronounced sexual dimorphism in members of the *K. hirtipes* species group, sexes are considered separately in all cases. Turtles from basin samples represented by only one or two individuals of either sex were included in the analysis as unknowns, and assigned to the most phenetically similar sample by discriminant analysis.

BIOSYSTEMATIC TACT

Like many evolutionary biologists before me, the problem of interpreting the genetic (and taxonomic) relationships of closely-related, allopatric vertebrate populations is a perplexing one (see Inger, 1961; Amadon, 1966, 1968; Mayr, 1970:210-211; Amadon and Short, 1976). The propensity (perhaps restriction) of members of the *K. hirtipes* group for permanent water habitats, coupled with the geographical isolation of inhabited river basins due to historical geology and desertification have produced at least thirty allopatric populations of members of this group. Many of these populations differ notably from geographically adjacent populations, but are quite similar to other populations far removed (see RESULTS). Interpreting such complex variational patterns is difficult.

In this paper I have taken a conservative approach to the species-subspecies dilemma. Within a species morphologically distinct, isolated (i.e. allopatric) populations are afforded only subspecific status even though additional data (especially breeding information) may show that some are full biological species. The genetic relationships of the populations so named are unfortunately clouded by this taxonomic designation [Amadon and Short, 1976, define "megasubspecies" and "allospecies" in an attempt to counteract this confusion]; however, complementary studies of protein variation now in progress should perhaps further clarify the specific-subspecific (i.e. genetic) relationships of these turtle populations.

LITERATURE

Because far more than half the literature records of kinosternid turtles in Mexico are in error I had to assume that *every* literature record was incorrect until personally verified by examination of the respective specimens or by analysis of distributional information (for example, in cases where only one kinosternid occurs in a particular basin). I have therefore attempted to substantiate every literature record for any kinosternid from throughout the range of the members of the *K. hirtipes* group (or stated as being from that range), and any member of the *Kinosternon hirtipes* group (i.e. *K. sonoriense* or *K. hirtipes*). Complete chronological synonymies were then compiled for *K. sonoriense* and *K. hirtipes*, and each reference was annotated to indicate the reasons for its inclusion. Copies of this annotated synonymy have been deposited in the Florida State Museum Herpetology Library (University of Florida), and are available from the author as well. Most of this information appears in this paper in the SYSTEMATICS Section, with some elaboration in the next section.

RESULTS AND DISCUSSION

Literature Corrections

Because of the past difficulty in the discrimination of the *K. scorpioides* group (including *K. integrum* and *K. alamosae)* from the *K. hirtipes* group (including *K. hirtipes* and *K. sonoriense*), the literature on Mexican *Kinosternon* has accumulated so many errors of identification that it is almost unusable. The following literature corrections (ordered by the valid taxon with which the *K. hirtipes* group member was confused) are an attempt to bring some order and accuracy to the error-plagued literature.

Sternotherus odoratus.

Apart from Meek's El Sauz, Chihuahua specimen of *Sternotherus odoratus* (see discussions in Moll and Williams, 1963 and Conant and Berry, 1978:15), that species (or its nomenclatural equivalent) has been frequently, though erroneously, recorded from Mexico. Dugès (1869:143) was apparently the first to record *"Ozotheca (odorata?)"* from "Guanajuato y Mexicó", but in a subsequent list (1888:106) he apparently changed his identification to *Cinosternon pensylvanicum.* Because *K. hirtipes* occurs in both Guanajuato and Mexico states, because it is more similar to *S. odoratus* than is *K. integrum* (the only other turtle recorded from those two states), and because Dugès was apparently not aware of Wagler's (1830) description of *K. hirtipes* from "Mexico" (the species is not on his 1869 list), Dugès' *Ozotheca* record was almost certainly based on *Kinosternon hirtipes.* The following orthographic variations of Dugès' record were apparently based on his 1869 list and are thus considered synonymous (in part) with *K. hirtipes: Ozotheca odorata,* Velasco (1890b:54, 1891:52, 1892b:40, 1893b:81, 1894:40, 1896a:30, 1898:62); *Ozothea odorata,* Velasco (1892a:76, 1892c:79, 1895:38, 1896b:37); and *Ozhoteca odorata,* Garcías-Cubas (1884:179) and Velasco (1890a:35, 1893a:64, 1897:41). In addition, Conant and Berry (1978:15) have clarified Brown's (1950:230) record of *Sternotherus odoratus* from Presidio Co., Texas; the specimen on which the record was based is TCWC 650, the holotype of *Kinosternon murrayi* Glass and Hartweg 1951(= *K. hirtipes murrayi*). The last erroneous record is that of Altini (1942:159) for *Kinosternon odoratum* in Veracruz; based on his specimen description, it is apparently referable to *K. leucostomum.*

Kinosternon subrubrum.

Testudo pensilvanica Gmelin (1788: 1042) has been recognized as a synonym of *Kinosternon subrubrum* (Lacépède, 1788:132) at least since 1917 (see Iverson, 1977b). Prior to that time, however, the former specific name had an active history in the Mexican herpetological literature, despite the fact that the species does not range in Mexico. Lichtenstein (1856:2) was the first to apply the name (as *Cinosternon pensylvanicum)* to specimens from Mexico in the Berlin Museum. Over the next 50 years, no fewer than 22 papers recorded that species name (or orthographic variations thereof) for specimens from Mexico. Based on the greater similarity of *T. pensilvanica* (i.e. *K. subrubrum*) to *K. hirtipes* than to *K. integrum,* and the fact that most of these references are based on specimens from Guanajuato (where *integrum* and *hirtipes* co-occur) and/or the Valley of Mexico (where only *hirtipes* naturally occurs; see MATERIALS AND METHODS), the following binomials and references most probably refer to *K. hirtipes: Cinosternon pennsylvanicum,* Dugès (1888:106; 1890, in Velasco 1890b:291; 1895:5; 1896a:lv; *sylvanicum,* Bocourt (1876:5), Herrera

(1890:330; 1891:46; 1893:339; 1904:5),
(1890:330; 1891:46; 1893:339; 1904:5),
Herrera and Lope (1899:281), Westphal-Castelnau (1872:278), and Strauch (1890:88); *Cinosternonus pensylvanicum,* Herrera (1899:28; for discussion see H.M. Smith and R.B. Smith, 1975:86); *Cinosternum pennsilvanicum,* Cope (1900:1229); *Cinosternum pennsylvanicum,* Gadow (1905:209); *Cynosternon pensylvanicum,* Herrera and Lope (1899:131); *Cynosternon pennsylvanicum,* Herrera (1893:342); and *Kinosternum pennsilvanicum,* Cope (1896:1021).

The failure of these person to recognize their specimens as *K. hirtipes* Wagler is probably a consequence of the lack of a nuchal scute by Wagler's only type specimen (see later). Unaware that a missing nuchal scute (actually worn away) is an uncommon, though natural anomaly, A.M.C. Duméril and G. Bibron (1834:370), A.H.A. Duméril (1870:25), Bocourt (1876:50) and Dugès (1888:106) used the absence of that scute as *the* key character in identifying *hirtipes.*

Several additional orthographic variations were not, however, based on *K. hirtipes.* Gadow's (1905:194) record of *Cinosternum pennsylvanicum* from Guerrero must be based on *K. integrum* if the datum is correct, because it is the only *Kinosternon* found there.

Lampe's (1901:185) description of *Cinosternum pensylvanicum* from north Mexico makes it clear he is referring to *Kinosternon subrubrum hippocrepis* (probably from Texas).

Siebenrock's (1905:465) erroneous record of *Testudo pensylvanica* from Veracruz is possibly based on a specimen of *K. herrerai.*

Cinosternon hippocrepis (another synonym of *K. subrubrum;* see Iverson, 1977b) was erroneously recorded from Sonora by Strauch (1865:100, 184) presumably based on a specimen of *K. sonoriense.*

Kinosternon flavescens.

Several *K. flavescens* records are in part based on members of the *K. hirtipes* species group. Most of these have been previously discussed (Iverson, 1978). In addition, Cooper (1870:66) recorded *Platythyra flavescens* from the Colorado River Valley along the California border (precise locality unknown). I have elsewhere (Iverson, 1978:477) questioned the existence of *K. flavescens* in the Colorado River basin and here suggest that Cooper's record was almost certainly based on *K. sonoriense.*

Kinosternon scorpioides group.

The true identity of the species of *Kinosternon* occuring on María Madre Island in the Tres Marías Islands off the coast of Nayarit has plagued herpetologists. Gunther (1885:15) first recorded and figured *K. hirtipes* from the island, but the same specimens were called *K. integrum* by Boulenger (1889:42). Both Strauch (1890:91) and Stejneger (1899:64) supported Boulenger's view, yet Gadow (1905:209) advocated Gunther's original designation. Siebenrock (1906:96) was the next to support Boulenger's position. H.M. Smith and Taylor (1950a:25) avoided the problem by recording both species from the islands. Zweifel (1960:94) next addressed the problem in his study of the herpetofauna of the islands. In collaboration with Norman Hartweg, he finally corrected the record; *K. integrum* is the only species of the genus occurring in the Tres Marías. Wermuth and Mertens (1961:Fig. 13, p. 20) reproduced Gunther's (1885) figures and recommitted the latter's error. Casas Andreu (1967:44) likewise repeated the error, apparently following Smith and Taylor (1950a).

Hardy and McDiarmid (1969:218) were next to discuss the problem and they supported Hartweg, Zweifel, and Boulenger's position. In what I hope is the final chapter in this prolonged story, I can only repeat and emphatically support Hartweg's opinion (in Zweifel 1960:95) that *K. integrum* is "the only species of the genus that gets to the Tres Marías."

Kinosternon hirtipes group.

Garman (1887:16) erroneously recorded *Cinosternum hirtipes* from San Luis Potosí, Mexico. Taylor (1952:793) repeated that record, listing it as "possibly doubtful". The specimen on which Garman's record was based (MCZ 4545), from the mountains of Alvarez, is unquestionably *K. integrum*. The occurrence of *K. hirtipes* in the state of San Luis Potosí has thus been verified at only one other locality (see MATERIALS AND METHODS).

J.R. Dixon et al. (1972:228) recorded *K. hirtipes* from Cadereyta, Querétero on the basis of AMNH 71570. That specimen, an articulated shell, is referrable to *K. integrum; K. hirtipes* does not occur in that part of Querétaro.

Liner (1964:221) recorded the deposition in the Tulane collections of *K. hirtipes* he collected in Guanajuato (precise locality not published). TU 17563 (adult male) from that collection, from 2 mi. N. Ojo de Agua, is not *K. hirtipes,* but *K. integrum.*

Four papers (Martin del Campo, 1937:265; Caballero y Caballero, 1938a: 103, 1938b:448; Casas Andreu, 1967:45) erroneously recorded *K. hirtipes* from Tasquillo, Hidalgo, lying in the Río Tula basin. Because only *K. integrum* occurs in that basin, those records must pertain to that species. Similarly Caballero y Caballero's (1940a:225) record of *K. hirtipes* from Uruapan, Michoacán (Río Balsas basin) is based on *K. integrum,* since only the latter species occurs in that area.

Altini (1942:154) recorded *Kinosternon hirtipes* from Lake Pátzcuaro and Lake Chapala, Mexico, and Lake Petén, Guatemala; the species occurs in both of the Mexican lakes, but clearly does not occur in Guatemala. He also recorded *K. leucostomum, K. cobanum (= K. acutum),* and *K. triliratum (= K. scorpioides)* from Lake Petén. All three of those species are known from the Petén region: *Claudius angustatus* and *Staurotypus triporcatus.* Which of the latter two species was misidentified by Altinas *K. hirtipes* cannot be determined by the data available to me. In the same paper, Altini also erroneously recorded *K. leucostomum* from Mexico's Lake Chapala; the species is not found there. Because only *K. integrum* and *K. hirtipes* occur in Lake Chapala and because Altini also recorded *K. hirtipes* from the lake (presumably correctly identified), his *K. leucostomum* record is probably based on *K. integrum.* Clearly, an examination of Altini's specimens (presumably at the University of Bologna) will be necessary to rectify these misidentifications.

Based on my discussions with the author, it is clear that Wiewandt's (1971:34; and Wiewandt et al., 1972:162) records of *K. sonoriense* from Sonora, 3.5 miles W. Alamos, were based on specimens of the recently described *K. alamosae (K. sonoriense* does not occur there). Similarly, as explained by Berry and Legler (1980), Herenghi's (1969) Sonora *K. hirtipes* are also referable to *K. alamosae.*

Morphometric Analysis

An NTSYS cluster analysis was performed early in the study (1977) employing population means for all 23 variables as OTU's (males and females separately). Two major phenetic groups were evident in both the male (Fig. 8) and female distance phenograms. The first group in each analysis included the Casas Grandes, southwest New Mexico, Magdalena, Sonora, Yaqui, and Sonoyta samples (i.e., the populations of *K. sonoriense* as previously recognized; Iverson, 1976 and 1978), and the Aguascalientes sample in the male analysis and the Nazas sample in the female analysis. Of later significance is the fact that the Sonoyta sample was the most distinct of the *sonoriense* population in both the male and female analysed. The second group in each case included all populations from the Río Santa María in Chihuahua south and eastward to soutceral Mexico (representing populations of *K. hirtipes).*

In both analyses the main *hirtipes* cluster was divided phenetically into two subgroups; however, the included samples were different in each analysis. For both sexes, one subgroup included all of the northern-most *K. hirtipes* samples (Santa María, Carmen, Sauz, and Texas); but for the males the subgroup also included several of the southern-most populations (Valley of Mexico, Villa Victoria, and Bajío) and for the females it included another northern population (Conchos), a central population (Mezquital), and two southern populations (Pátzcuaro and Chapala). No other obvious morphogeographic correlations or discontinuities were noted in these preliminary clusters, but many of the sample sizes on which the means were based were quite small. The level of differences between clusters and/or samples were generally higher in females than males, substantiating my subjective observation that there is less variation among females.

The final male (Fig. 9) cluster analysis (BMDP2M) of population means for all 23 variables for all samples with N $\geq$ 2 (Appendices 1 and 2) suggests that six groups were evident. In declining order of distinctiveness they are the 1) Viesca, 2) Sonoyta, 3) Villa Victoria, 4) *K. sonoriense,* except Sonoyta, plus Aguascalientes, 5) Duero, and 6) the remaining *K. hirtipes* samples. In the final female analysis, the nine most distinct groups are the 1) San Juanico (but N = only 2), 2) Sonoyta, 3) Viesca (no female Villa Victoria sample was included), 4) Balsas (N = only 2), 5) Zapotlan (N = 2), 6) Santiaguillo (N = 2), 7) Duero, 8) *K. sonoriense* except Sonoyta, plus Nazas and Verde, and 9) the remaining *K. hirtipes* samples. Again, the female analysis differences were not at as low levels as the males'.

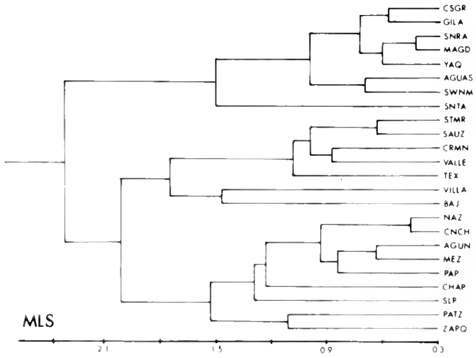


Figure 8. Preliminary NT-SYS cluster (based on the distance matrix, with complete averaging and low values considered similar) of population means of all 23 variables for males of the *K. hirtipes* species group (including *K. sonoriense*). Abbreviations as in text. N $\geq$ 3 for all samples but SLP and PATZ (N = 2 each).

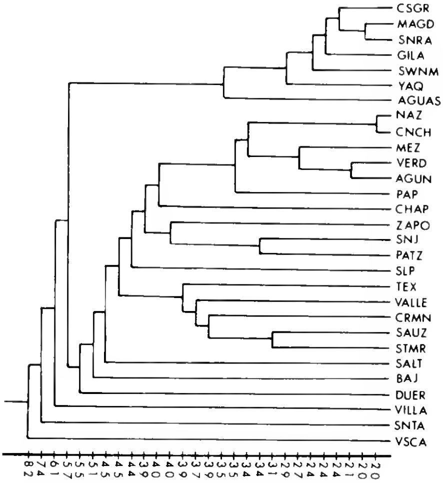


Figure 9. BMDP2M cluster of population means of all 23 character ratios (Appendices 1 and 2) for males of the *K. hirtipes* species group (including *K. sonoriense*). Abbreviations as in text. N $\geq$ 4 for all samples but VSCA (N = 2) and TEX (N = 3). Numbers are amalgamation distances (i.e., distance between the clusters joined).

Stepwise discriminant analysis of populations with N $\geq$ 2, based on all 23 character ratios, produced plots of population means on the first two (most important) canonical axes for males and females (Figure 10). Two groups separate along the first canonical axis in both analyses: 1) the seven *K. sonoriense* samples and 2) the *K. hirtipes* samples. Within the cluster of *K. hirtipes* sample means, two patterns are apparent (especially along the second canonical axis). First, the populations are arranged from northern-most (Santa María; Carmen) to central (Mexquital; Aguascalientes) to southern-most (Duero, Vajio, Pátzcuaro, and Chapala); except the Valley of Mexico sample, which falls with the northern populations. Second, there appears to be a weak phenetic break in this clinal arrangement 1) in males, between populations north of and including the Nazas (plus the Valley of Mexico) and those south and east of that basin and 2) in females, (less distinctly), between populations north of and including the Conchos (plus the Valley of Mexico) and those south and east. Other morpho-geographical discontinuities include the relative isolation of Duero, Pátzcuaro, and Aguascalientes samples (and the proximity of the latter to the *K. sonoriense* samples) in the male plot, and the relative isolation of the Zapotlan (but N = 2), Valley of Mexico, and Sonoyta samples in the female plot.

The character ratios most important for discrimination of the samples were determined in the stepwise discriminant analysis in two ways: 1) by the highest F values calculated for each variable before any were entered into the discriminant function and 2) by the order in which the variables were entered into the function. The first (most important) variable in each is always the same, but the remaining frequently are not, especially if character information is redundant in two or more variables. For males the five most important variables were PWB/CL, PWA/CL, GW/CL, BL/CL, and IP/PL by F value, and PWB/CL, IAN/PL, IP/CL, and BL/CL by order of inclusion. For females, they were IP/PL, IP/CL, IF/CL, AN/PL, and IF/PL, and IP/PL, IH/CL, IF/CL, BL/CL, and FL/CL, respectively. The analysis reveals that *K. sonoriense* in general has smaller interpectoral seam lengths, larger interfemoral seam and gular scute lengths, and a wider plastron, gular scute, and bridge (see also Appendices 3 and 4). Bivariate plots (Figures 11-14) of the most important characters (by F value) illustrate that *K. sonoriense* is both geographically and morphologically disjunct. Because they are the most morphometrically distinct groups within the species group, because they are nowhere known to hybridize, because there is no evidence of introgression (based on the morphometric calculations) in the two most geographically proximate populations (Casas Grandes and Santa María), and because several other morphological characters (see later) also show a sharp phenetic break between

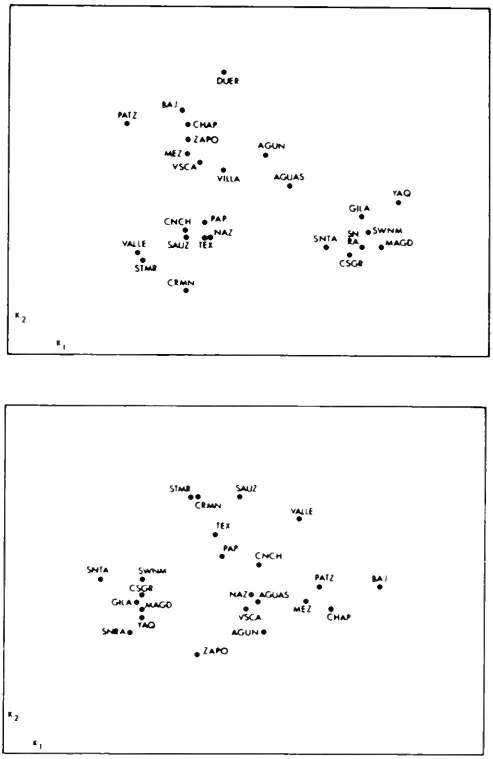


Figure 10. Plots on the first (k_1) and second (k_2) canonical axes of the population means of males (above) and females (below) of the *Kinosternon hirtipes* species group (including *K. sonoriense*). Abbreviations as in text. Analysis based on all 23 character ratios for populations with N ≥ 2. First two axes account for 30.4 and 20.6% of the total variation, respectively, in males; and 23.8 and 18.0%, respectively, in females.

the two morphometric groups, *K. sonoriense* and *K. hirtipes* are considered valid species as previously defined (Iverson, 1976, 1978; Wermuth and Mertens, 1977). Therefore, populations of each species were analyzed separately.

Variation within K. sonoriense.

The above analyses (see especially Figures 9, 10 and 12-14) suggest that the Sonoyta sample is the most distinct of the populations of *K. sonoriense*. Stepwise discriminant analyses of the seven *sonoriense* populations with N ≥ 4 (Figure 15), employing 13 variables (those indicated as the most important in the overall analyses) clearly support this suggestion.

Those plots also suggest additional variational patterns. Although most of the non-Sonoyta samples are morphologically very homogeneous (note cluster overlap in Figure 15), both the male and female Yaqui sample contain some apparently anomalous individuals. In the male plot, all but one Yaqui specimen lie within the main cluster. The outlier (BYU 14629) is the only male available from the entire Río Bavispe portion of the Yaqui basin and the only specimen available from that locality. The significance of its apparent distinctiveness must await the collection of additional material. The most important characters in the discrimination are IAN/PL, GW/CL, IF/PL, PL/CL and GL/CL by F-values, and IAN/PL, GW/CL, GL/CL, IP/PL, and PWC/CL by order of inclusion.

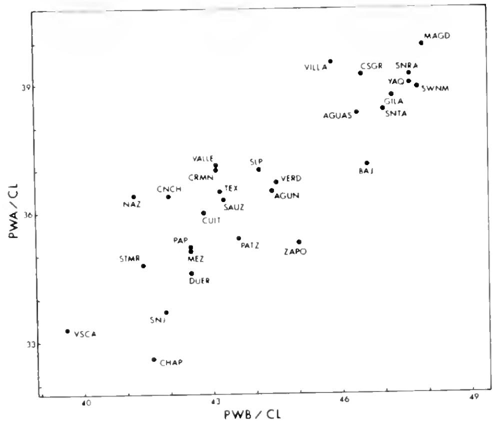


Figure 11. Graph of percent posterior width of plastral forelobe/carapace length (PWB/CL) versus percent plastral width at humero-pectoral seam/carapace length (PWA/CL) for males of all populations of the *Kinosternon hirtipes* species group (including *Kinosternon sonoriense*). Only population means are plotted. Abbreviations as in text.

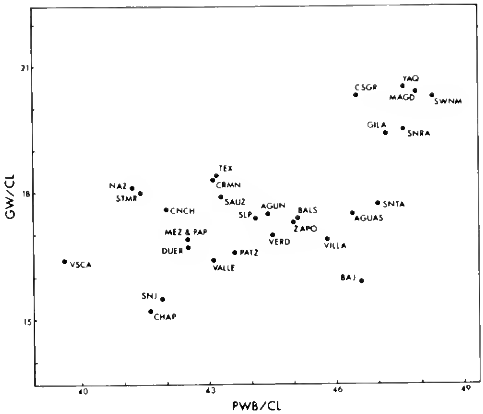


Figure 12. Graph of percent posterior width of plastral forelobe/carapace length (PWB/CL) versus percent gular width/carapace length (GW/CL) for males of all populations of the *Kinosternon hirtipes* species group (including *Kinosternon sonoriense*). Only population means are plotted. Abbreviations as in text.

In the female plot all but one of the Yaqui specimens lie *outside* the main cluster, and separate fairly well along the second canonical axis. Only a specimen from the Río Gavilan (MVZ 46646), a tributary of the Río Bavispe, falls *within* the main cluster. Although the recorded locality is clearly in the Gavilan-Bavispe drainage (see map in Marshall, 1957), the possibility exists that the specimen actually originated in the Río Casas Grandes basin; the two drainages interdigitate near the locality. The outlying cluster of female Yaqui specimens is problematical, especially since it includes specimens from the same localities that clustered in the main group in the male

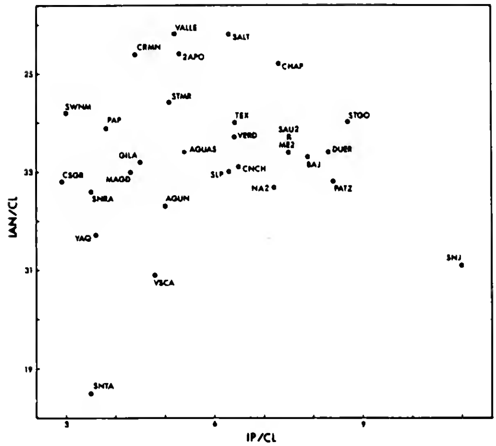


Figure 13. Graph of percent interanal seam length/carapace length (IAN/CL) versus percent interpectoral seam length/carapace length (IP/CL) for females of all populations of the *Kinosternon hirtipes* species group (including *Kinosternon sonoriense*). Only population means are plotted. Abbreviations as in text.

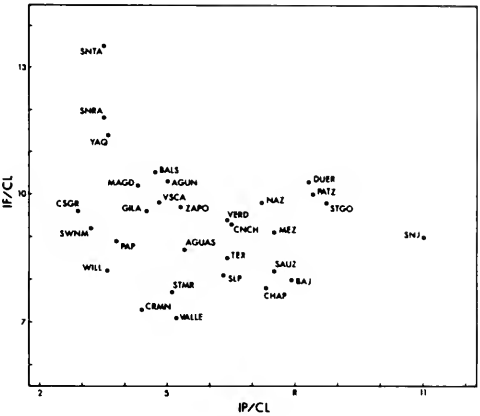


Figure 14. Graph of percent interpectoral seam length/carapace length (IP/CL) versus percent interfemoral seam length/carapace length (IF/CL) for females of all populations of the *Kinosternon hirtipes* species group (including *Kinosternon sonoriense*). Only population means are plotted. Abbreviations as in text.

analysis. Only additional field work in the Yaqui basin can clarify these variational anomalies. The most important characters in the discrimination are IF/PL, IAN/CL, PL/CL, IH/PL, and PWB/CL by F-values and IF/PL, PL/CL, IH/PL, PW/CL, and IP/PL by order of inclusion.

Two morphotypes are thus recognizable within *K. sonoriense,* represented by Sonoyta basin turtles and the other samples, respectively. The Sonoyta basin turtles have shorter plastra, longer interfemoral seams, shorter interanal seams, wider first vertebrals, and narrower gulars, than the other populations.

Variation within K. hirtipes

Cluster analysis (BMDP2M) of population means for all 23 variables, suggest that three main groups exist for males and females (Fig. 16). For males, the most distinct is the Viesca sample (but N = 2), followed by the Villa Victoria sample and all remaining *hirtipes* populations. Within the last group, the only relationship between phenetics and geography is a small subgroup including the Pátzcuaro, San Juanico, Chapala, and Duero samples. Contrary to the results of the discriminant analysis which included *K. sonoriense* (Fig. 10), no clinal relationships or phenetic breaks between northern and southern populations are evident. For females, the most distinct group is the San Juanico sample (but N = 2), followed by the Viesca sample and the remaining populations. No obvious phenetic-geographic relationships are suggested within the last group. However, Villa Victoria was not represented in the female analysis since only one female specimen is known from that basin. Raw data for that specimen (Appendix 2) suggest it might be as distinct as the male sample (see later).

Stepwise discriminant analysis of *K. hirtipes* populations with N ≥ 2, based on all 23 character ratios, produced the canonical plots in Figure 17. The male analysis reveals the same north-south clinal pattern along the first axis, the same phenetic break between the Nazas and Aguanaval basins, and the same similarity between the Valley of Mexico population and northern populations that the earlier overall discriminant analysis illustrated (Fig. 10). It further suggests the distinctiveness of the Villa Victoria population and possibly also the Pátzcuaro sample. The female analysis again reveals the general north-south clinal pattern along the first axis (although no Nazas-Aguanaval break is evident), and also suggests the distinctiveness of the Viesca, Zapotlán, San Juanico and possibly Duero populations.

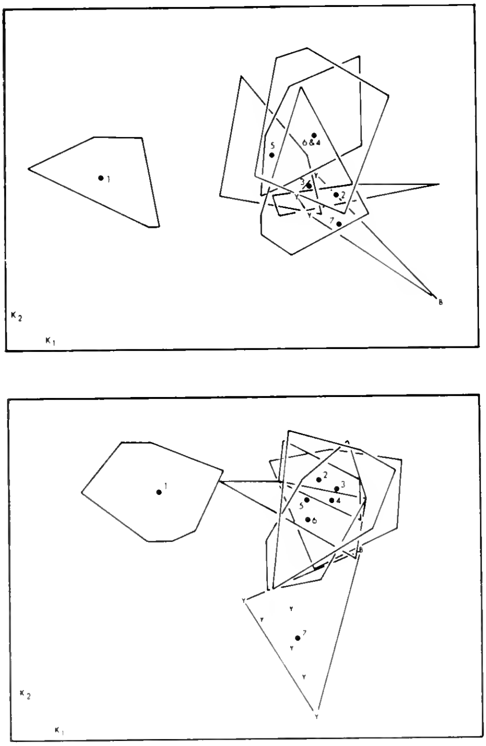


Figure 15. Plots on the first (k_1) and sec ond (k_2) canonical axes of population means (solid dots) of males (above) and females (below) of *K. sonoriense*. Lines connect the most dispersed values about the population mean. Population mean symbols are 1, SNTA; 2, SWNM; 3, GILA and WILL; 4, MAGD; 5, SNRA; 6, CSGR; and 7, YAQ. Individual Yaqui turtles are marked with Y (Yaqui River proper) or B (Bavispe River). Analysis based on 13 character ratios. First two axes account for 71.0 and 10.2% of the variation, respectively, in males; and 47.9 and 23.1%, respectively, in females.

The most important characters in the male discriminant analysis are BL/CL. GL/CL, PWC/CL, IP/CL, and IAN/PL, based on F-values and BL/CL, GL/CL, PWC/CL, IAN/PL, and PWD/CL based on order of inclusion. For the females, the important characters are IP/CL, BL/CL, IP/PL, PWB/CL, and FL/CL, and IP/CL, BL/CL, IH/CL, FL/CL, and PWB/CL, respectively. Bivariate plots of the most important characters (Figures 18-21; see also Figures 11-14) do not suggest that a significant phenetic break exists between northern and remaining populations. However, as in the previous analyses, they again indicate the distinctiveness of several samples, including the Valley of Mexico, Viesca, San Juanico, Pátzcuaro samples, and possibly also a group of three geographically adjacent samples occupying the ancestral Lake Chapala basin (Tamayo, 1964:108): Chapala, Zapotlán and Duero (see Figs. 18 and 21).

MORPHOMETRIC CONCLUSIONS

The numerous analyses have strongly suggested that 1) *K. hirtipes* and *K. sonoriense* are distinct morphometrically, 2) the Sonoyta sample within *K. sonoriense* is morphometrically distinct, 3) there is tremendous variation within *K. hirtipes,* and 4) the most morphometrically distinct populations of *hirtipes* are the San Juanico, Viesca, Pátzcuaro, Villa Victoria, and Valley of Mexico samples and possibly also the combined Chapala-Zapotlán-Duero samples.

As detailed above, the basic patterns of morphometric variation in the *K. hirtipes* species group involve several character complexes, the most important of which are 1) body size (see later), 2) relative plastron size (measured primarily as PL, PWA, PWB, PWC, and/or PWD), 3) relative bridge length, 4) the relative lengths of the gular, interhumeral seam, and interpectoral seam to the forelobe length (the forelobe length itself is not as important), and 5) (of much less importance) the relative lengths of the interfemoral and interanal seams to the hindlobe length (the hindlobe length is also not as important). Other characters clearly are important in individual population comparisons, but these complexes are apparently the most important when considering variation in the group as a whole.

Variation in relative plastron size is much greater in males than females. Females appear to be much more conservative regarding plastral reduction or modification. For relative male plastron size there is somewhat of a continuum from the relatively large plastron of *K. sonoriense* (Fig. 22b) to the small plastra of San Juanico and Viesca populations (Fig. 22, 1 and m) with the remaining populations somewhat intermediate. For females, the range is from the medium-size plastra of the San Juanico and Viesca populations (Fig. 22n) to the relatively extensive plastra of the remaining populations. Plastral reduction, typically correlated with an increase in aquatic habits among turtles (Zangerl, 1939:386; Berry, 1977; Iverson, MS1) and presumably an adaption thereto (Iverson, MS1), is considered derived.

Relative bridge length is extremely variable in the genus *Kinosternon*. Males virtually always have shorter bridges than females. For males, bridge length ranges from short in San Juanico, Pátzcuaro, Valley of Mexico, and Viesca turtles to medium length in the other populations. For females, it ranges from medium length in San Juanico, Pátzcuaro, and Valley of Mexico turtles to long (but not as long as some members of the *K. scorpioides* group) in the remaining populations. Its reduction is not necessarily correlated with plastral reduction [for example, Pátzcuaro turtles have medium (male) or large (female) plastra and relatively short bridges]. I consider relatively reduced bridge length in males or females a derived character, both because of its rarity in this species group and because many of the most specialized members of the genus have short bridges.

The components of the plastral forelobe are quite variable in this species group, but because the interhumeral seam length is essentially of medium length in all samples (except perhaps in the Villa Victoria basin), variational patterns are

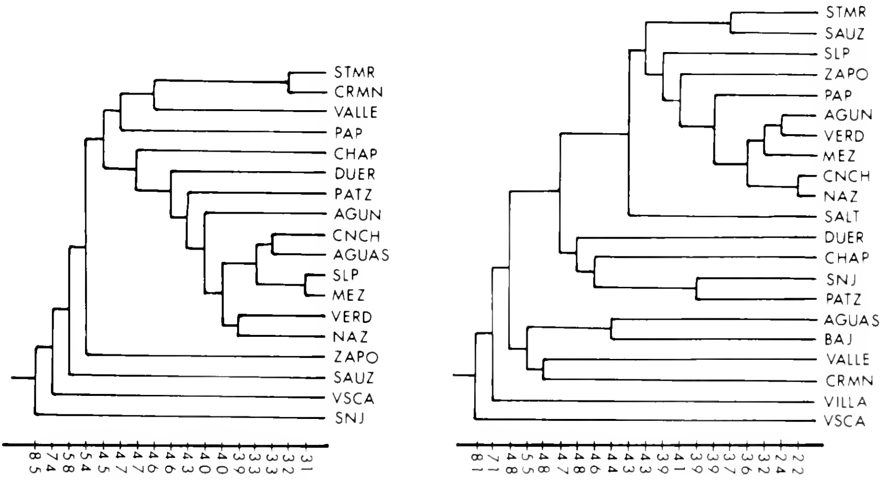


Figure 16. BMDP2M cluster of population means of all 23 character ratios (Appendices 1 and 2) for male (top) and female *K. hirtipes*. Abbreviations as in text. For males, N > 4 for all samples except VSCA (N = 2); for females, N > 5, except SNJ (N = 2) and ZAPO (N = 2). Numbers are amalgamation distances (i.e., distance between the clusters joined).

dominated by the relative lengths of the gular and the interpectoral seam. Pátzcuaro, Viesca, and San Juanico turtles have very short gulars (Fig. 22, i-n), whereas the remaining populations have medium to long gulars (*K. sonoriense* having the longest). Pátzcuaro and San Juanico turtles (and possibly Villa Victoria) have the longest interpectoral seams as well (Fig. 22, i-l); *K. sonoriense,* the shortest; and the remaining populations have intermediate lengths. Since most *Kinosternon* have interpectoral seams of medium length (frequently used to diagnose the genus; e.g., Conant, 1975), deviations from that condition are considered derived. For similar reasons, the conditions of reduced and extensive gular scutes are considered derived.

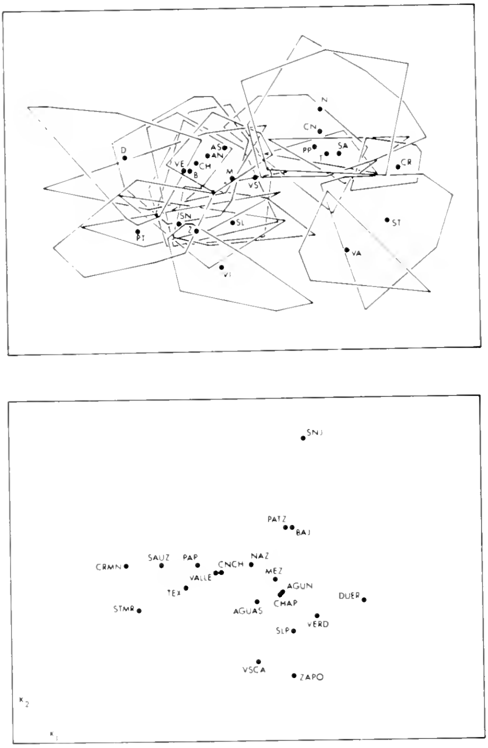


Figure 17. Plots on the first (k_1) and second (k_2) canonical axes of the population means (solid dots) of males (above) and females (below) of *Kinosternon hirtipes* (excluding *K. sonoriense*). Abbreviations as in text for females; but further shortened for males. Polygons in male plot enclose total dispersion of each population. Analysis based on all 23 character ratios for populations with N $\geq$ 2. First two axes account for 33.7 and 16.0% of the total variation, respectively, in males; and 27.4 and 14.5%, respectively, in females.

The plastral hindlobe components do not show as much variation as the other complexes, but a few patterns are evident. Hindlobe length is greater in *K. sonoriense* and Villa Victoria turtles than in remaining populations. The interfemoral seam is relatively shorter in the Valley of Mexico sample (Fig. 22, e-f) than in all other samples; and the interanal seam is relatively longer in that sample and the Chapala-Zapotlán combined sample, and shorter in the Viesca sample. Variation in these characters within *K. sonoriense* (i.e., shorter interanal and longer interfemoral seams in Sonoyta turtles) has already been discussed. Each of these deviations from the modal hindlobe condition found in the group are considered derived.

OTHER MORPHOLOGICAL CHARACTERS

Nasal scale. — The cornified epidermal shield (here called the nasal scale) found

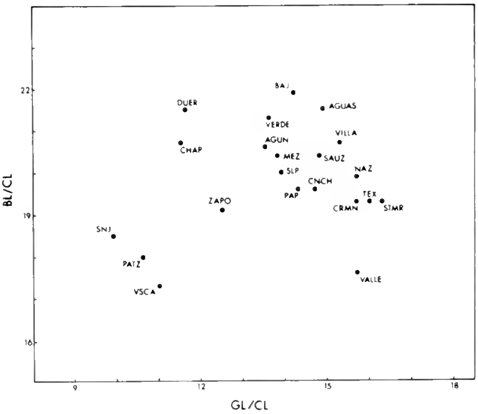


Figure 18. Graph of percent gular length/carapace length (GL/CL) versus percent bridge length/carapace length (BL/CL) for males of populations of *Kinosternon hirtipes*. Only population means are plotted. Abbreviations as in text.

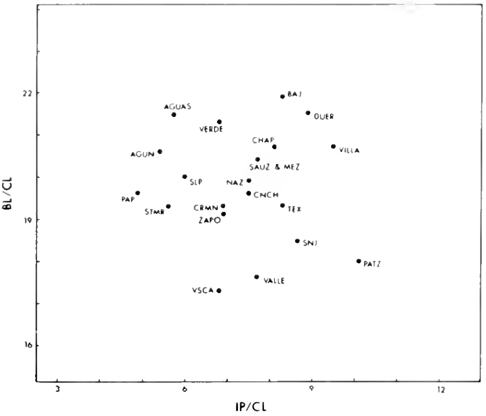


Figure 19. Graph of percent interpectoral seam length/carapace length (IP/CL) versus percent bridge length/carapace length (BL/CL) for males of populations of *Kinosternon hirtipes*. Only population means are plotted. Abbreviations as in text.

on the anterior dorsum of the head of all subadult and adult kinosternid turtles has received little attention (but see Siebenrock, 1907) until recently (Conant and Berry, 1978). Cornification of the scale begins near the rostrum in the juveniles of these turtles and spreads posteriorly with age. Development is usually more rapid laterally than medially, such that older juveniles or subadults may have V-shaped scales even though adults might have triangular to rhomboidal scales. Due to its distinctive shape in the adults of kinosternid turtle populations, it is an important taxonomic character. Intraspecific variation in nasal scale shape has already been noted in *Kinosternon subrubrum*. Ernst et al. (1974) have shown that the subspecies *Kinosternon subrubrum steindachneri* usually (81%) has a head scale that is furcate posteriorly (their "divided nasal") whereas turtles of both other subspecies *(hippocrepis and subrubrum)* usually (90 to 97%) have a non-furcate, bell-shaped scale (posterior margin convex).

Variation within the *K. hirtipes* species group is considerable but intrapopulation variation is insignificant. Three distinctive nasal scale shapes are evident in interpopulation comparisons of adults of this group. Populations from the Ríos Casas Grandes and Yaqui (excluding the Papigochic) and those westward and northward (i.e., populations of *K. sonoriense* as previously recognized; Iverson, 1976), and the population from the Valley of

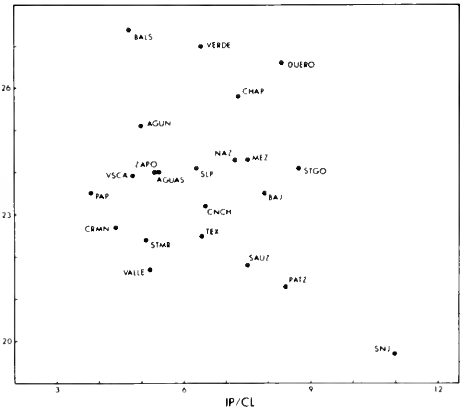


Figure 20. Graph of percent interpectoral seam length/carapace length (IP/CL) versus percent bridge length/carapace length (BL/CL) for females of populations of *Kinosternon hirtipes*. Only populations means are plotted. Abbreviations as in text.

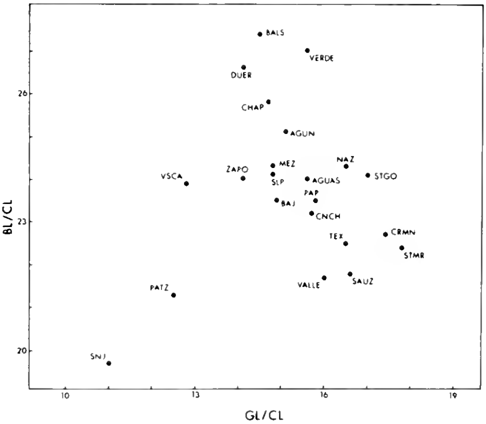
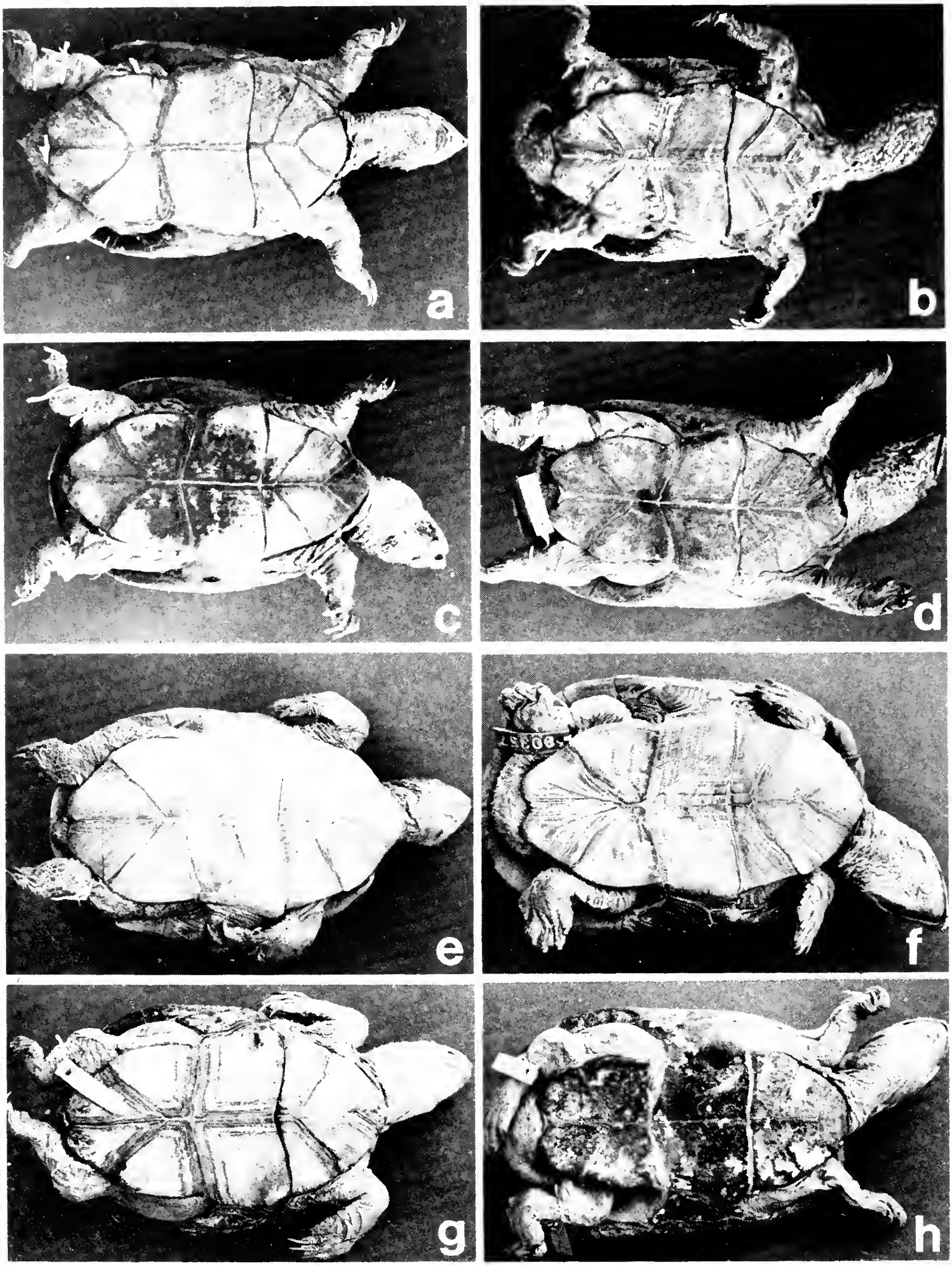


Figure 21. Graph of percent gular length/carapace length (GL/CL) versus percent bridge length/carapace length (BL/CL) for females of populations of *Kinosternon hirtipes*. Only population means are plotted. Abbreviations as in text.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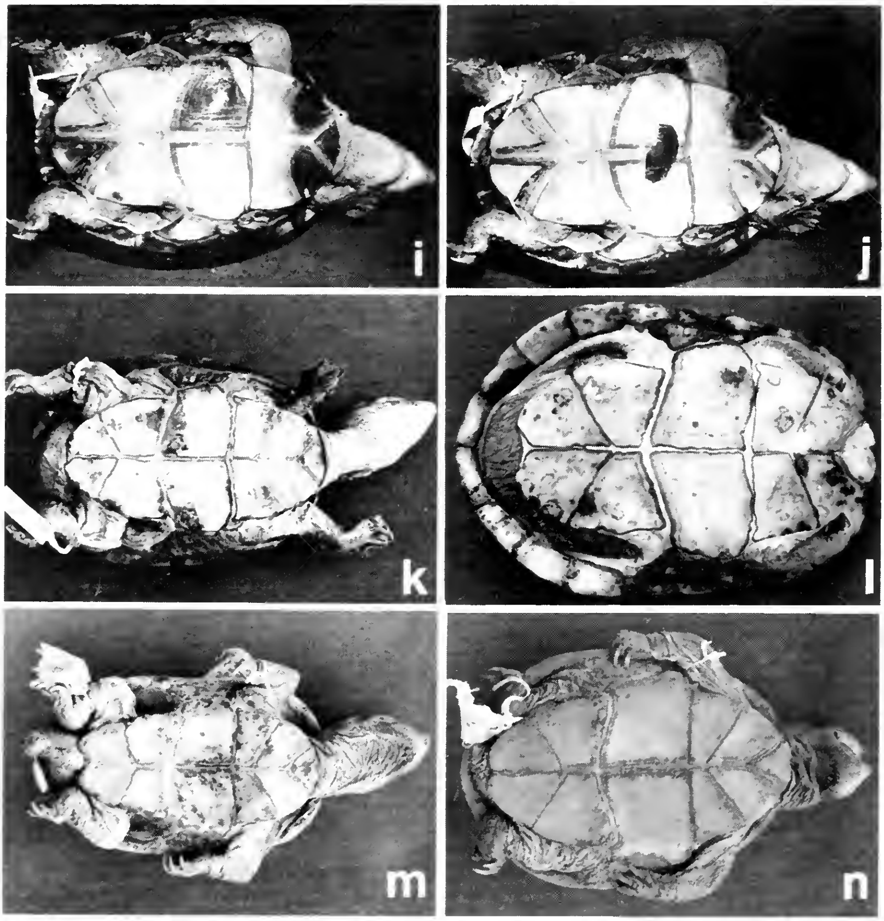


Figure 22. Plastral variation in members of the *Kinosternon hirtipes* species group: Gila River basin *Kinosternon sonoriense*, JBI 563 female (a) and JBI 386 male (b); Rio Papigochic basin *K. hirtipes murrayi*, UF 40391 female (c) and UF 40396 male (d); Valley of Mexico *K. h. hirtipes*, UMMZ 99458 female (e) and UMMZ 80357 male (f); Lake Chapala basin *K. h. chapalaense*, UMMZ 97123 female (g) and UMMZ 97128 male holotype (h); Lake Patzcuaro *K. h. tarascense*, UF 43505 female (i and j; illustrating plastral scute staining and loss of stain with scute shedding) and UF 43506 male (k); Presa San Juanico *K. h. magdalense*, UF 45035 male holotype (1); Viesca *K. h. megacephalum* SM 11464 female (m) and SM 9823 male (n).

Mexico exhibit a triangular, rhomboidal or bell-shaped nasal scale as adults (Fig. 23: a and d). Turtles from the Zapotlán, Lake Chapala, and Río Duero basins possess a nasal scale that typically is crescent-shaped and extremely reduced in size. It nearly always lies completely anterior to the orbits in turtles from the former two basins (Fig. 23: c), but may reach to mid-orbit in Río Duero turtles (Fig. 23: f). All remaining populations of this group have a nasal scale deeply furcate behind (Fig. 23: b and e; but see *Synthesis*).

Because most of the members of the

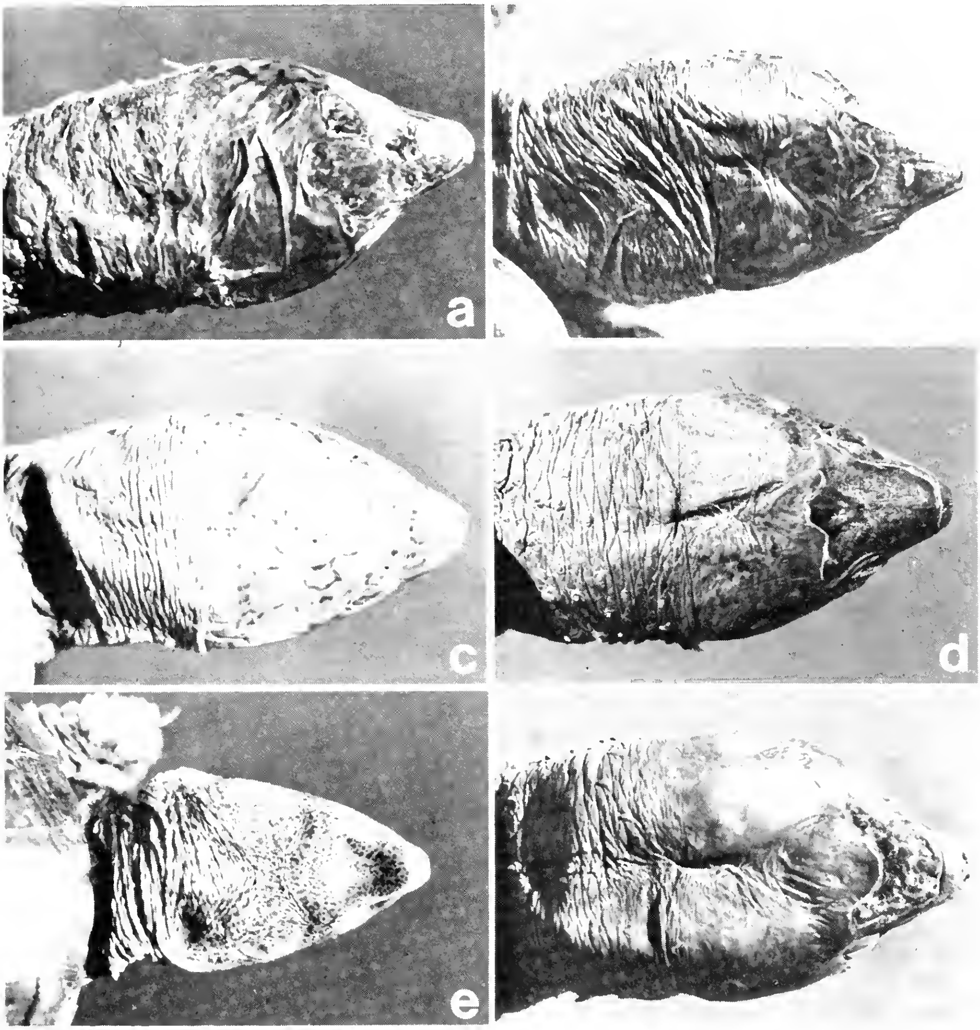


Figure 23. Nasal scale variation in members of the *Kinosternon hirtipes* species group: *K. sonoriense*, JBI 697 (a); *K. hirtipes murrayi*, UF 40396 (b); *K. h. chapalaense*, UMMZ 97130 paratype (c); *K. h. hirtipes*, UMMZ 99449 (d); *K. h. tarascense*, UF 43505 paratype (e); *K. h. chapalaense* x *K. h. murrayi*, UMMZ 97135 (f).

genus *Kinosternon* have triangular or bell-shaped nasal scales as adults (*K. dunni, K. angustipons, K. acutum, K. baurii,* most *K. subrubrum,* and all members of the *K. scorpioides* and *K. leucostomum* species groups), and because I believe that the furcate condition in *K. subrubrum steindachneri* is derived from the bell-shaped condition found in a *K. subrubrum subrubrum*-like ancestor (see also Ernst et al, 1974), I consider the large nonfurcate shape to be the primitive adult condition in the genus *Kinosternon.* Therefore, the condition in *K. sonoriense* and Valley of Mexico *K. hirtipes* is considered primitive, whereas the nasal scale reduction in remaining populations of *K. hirtipes* is considered derived.

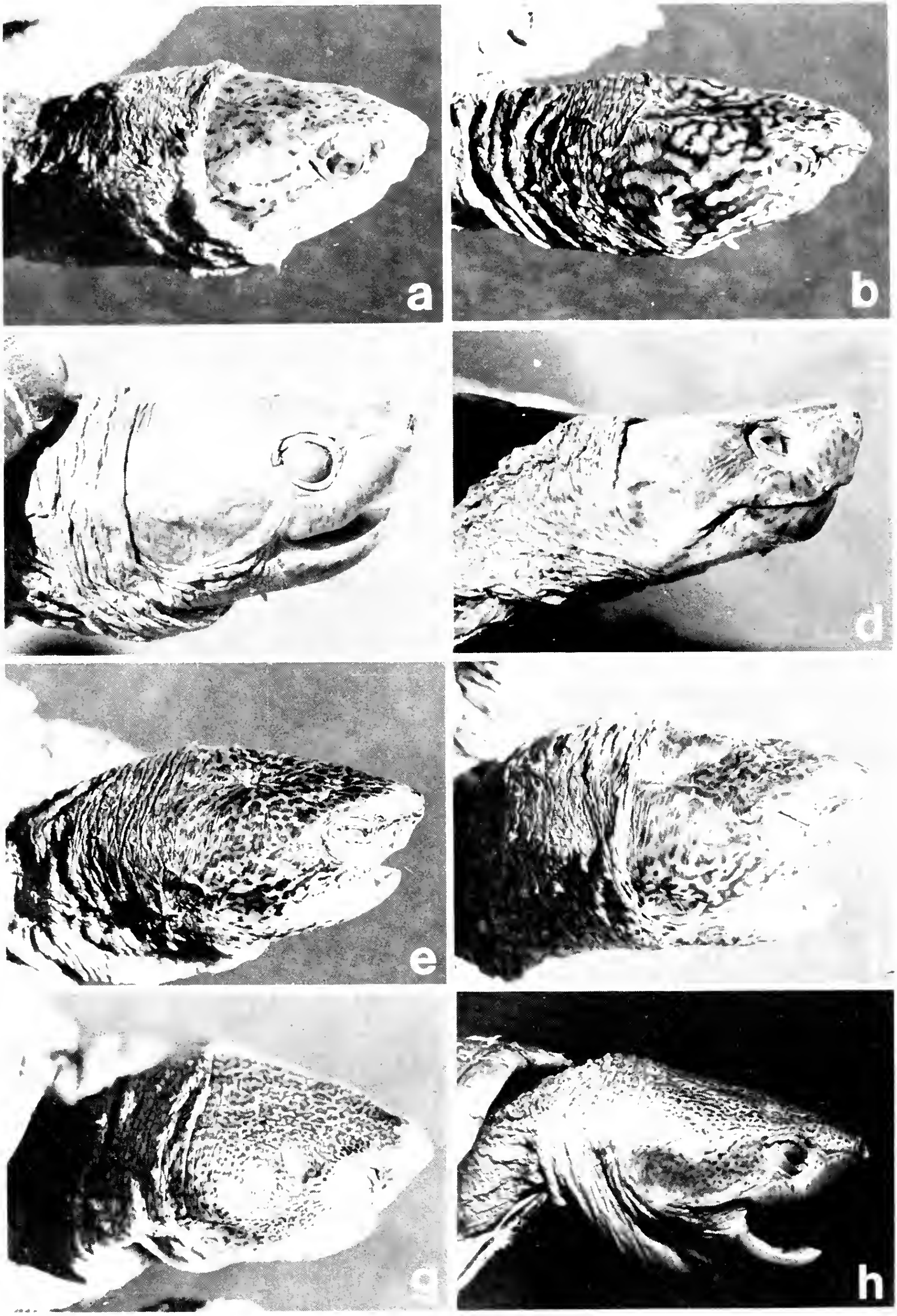
Chin Barbels. — Variable numbers of barbels are present on the chin and/or gular region of all kinosternid turtles; however, two basic patterns exist in the *K. hirtipes* species group. In the first, characteristic of all populations of *K. sonoriense* as previously defined (Iverson, 1976, 1978), 3 or 4 pairs of barbels are present and the largest 2 pairs are subequal and relatively long ($\leq$ one half orbit diameter) with one pair mentally located and the other at the level of mid-tympanum.

Populations of *K. hirtipes* are characterized by the presence of at least two pairs of chin barbels, the largest two pairs both located on the chin with the anterior pair decidedly the largest (yet ***P*** half orbit diameter). Because the typical *Kinosternon* condition is one with two mental pairs of barbels, the condition in *K. sonoriense* is considered derived and that of *K. hirtipes* ancestral.

Head color. — Head patterns in this group are extremely variable, even within populations. Patterns vary nearly continuously from broadly mottled (common in *K. sonoriense;* Fig. 24b; Conant and Berry, 1978, Fig. 7) to medium or finely reticulated (as in most populations of *K. hirtipes* from Chihuahua to Mexico City; Fig. 24: e, f, g, and n; Conant and Berry, 1978, Fig. 7) to finely spotted (common in female Pátzcuaro *K. hirtipes*; Fig. 24: h). Whatever the general pattern, however, the lateral markings are more or less longitudinally oriented, such that two yellow, cream, or white lateral stripes (one extending across the temporal region, posteriorly from the posterodorsal margin of the orbit; and the other extending posteriorly from the posteroventral margin of the orbit, along the posterodorsal margin of the maxillary sheath to the angle of the jaw) are vaguely to very well developed. The more ventral of those stripes is almost always apparent, no matter how finely reticulated or spotted the pattern, or melanistic the head coloration. Most of this general range of pattern variation may occur in a single population; however, females usually have less dark pigment on the head, have finer mottling or reticulations, and are more likely to be spotted (compare Fig. 24: a versus b or e versus f; see also Conant and Berry, 1978, Fig. 7). The jaw sheaths are also variably pigmented, but in general the more dark pigment on the head, the more darkly pigmented (streaked) are the jaw sheaths.

The only two significant deviations (considered derived conditions) from this general (considered primitive) color scheme are in *K. hirtipes* from the Lake Chapala and Zapotlán basins and the Valley of Mexico basin. Turtles from the latter basin have typical amounts of dark pigment but most specimens have both light lateral head stripes very well-defined (Fig. 24: c and d). In the former two basins, the dark markings are generally broad, but the overall amount of dark pigment is significantly reduced (compare Figure 24b versus i-l); in other populations broadness of marking is correlated with abundance of dark pigment. In addition, in Chapala and Zapotlán turtles, the lateral temporal head stripe is typically bordered ventrally by a broad dark stripe and the ventral stripe is bordered dorsally by a similar dark stripe. The general appearance is one of two dark stripes rather than two light ones (Fig. 24: i-l).

Although their nasal scales are similar


a
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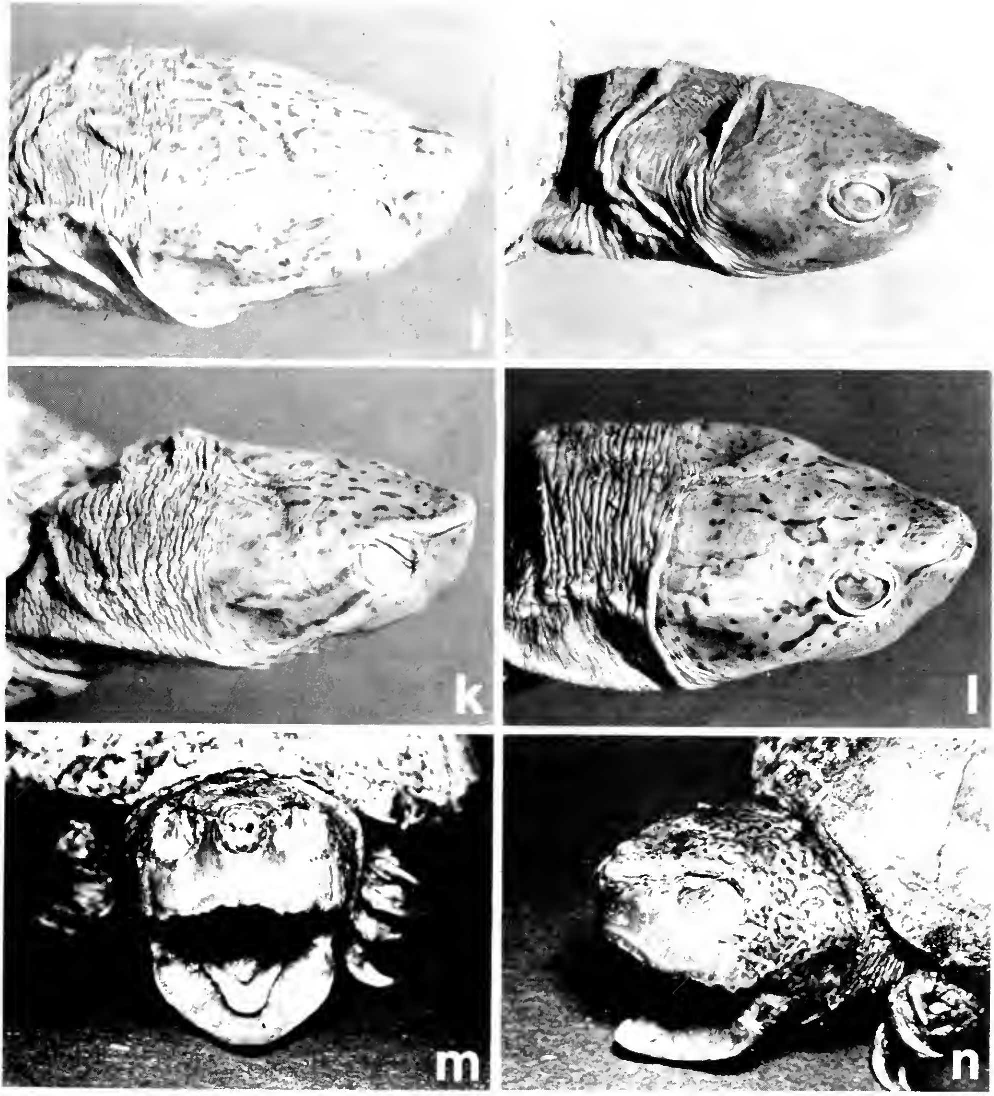

Figure 24. Head pattern variation in members of the *Kinosternon hirtipes* species group: Gila River Basin *Kinosternon sonoriense*, JBI 563 female (a) and JBI 387 male (b); Valley of Mexico, *K. hirtipes hirtipes*, UMMZ 99458 female (c) and UMMZ 80357 male (d); Rio Papigochic *K. h. murrayi*, UF 40391 female (e) and UF 40395 male (f); Patzcuaro basin *K. h. tarascense*, UF 43596 female paratype (g) and AMNH 82628 female (h); Lake Chapala basin, *K. h. chapalaense*, UMMZ 97128 male holotype (i), UMMZ 97127 male paratype (j), UMMZ 97123 female paratype (k), and UMMZ 97130 male paratype (l); Viesca, Coahuila *K. h. megacephalum*, SM 11462 female paratype (m,n).

to Chapala-Zapotlán turtles, specimens from the Río Duero have much darker head pigment as in more northerly and easterly populations.

Head size. — Only one population deviates from the typical (clearly primitive) condition. Turtles from the Viesca basin have distinctly enlarged heads (especially females) with greatly expanded alveolar surfaces (Fig. 24: m-n).

Plastral staining. — Although the plastron of members of the *K. hirtipes* group is typically cream, yellow, or yellow orange, it may be variably stained dark brown to black. The turtles from Lake Pátzcuaro have plastra consistently (and uniquely?) stained red-brown. At least in that population the color is due to environmental staining since the color is shed with the scute (Fig. 22: i-j).

Shell carination. — Due to sexual differences and considerable ontogenetic change, quantification of variation in the development of keels in members of this group is difficult. In general, adult *K. sonoriense* are much more obviously tricarinate than *K. hirtipes.* The latter species often appears almost unicarinate, the former, very rarely. The dorsum of the shell thus has a flatter appearance in *K. sonoriense* than in *K. hirtipes.*

Body size. — Average carapace lengths of males and females in Appendix 1 and 2 reveal that females average larger than males in populations of *K. sonoriense,* whereas males average larger in most populations of *K. hirtipes.* There is also considerable variation in body size among populations of *K. hirtipes.* The most obvious deviations from the mode are in turtles from the Viesca and San Juanico basins. Although these basins both have a small sample size, I believe the data truly reflect the small size of the inhabitant turtles. Pátzcuaro turtles also tend to be smaller than the mode, although not so distinctly. A more complete analysis of population and sexual variation in body size in *K. hirtipes* is in preparation.

Nuchal-neural bone contact. — Berry and Legler (1980:11) report that the nuchal bone contacts the first neural bone in 73% of the *K. sonoriense* and only 4% of the *K. hirtipes* they examined (sample sizes not reported). However, only 38.1% of the *K. sonoriense* (N = 42) and 10.2% of the *K. hirtipes* (N = 98) I examined have nuchal-neural contact. The discrepancy between our results for *K. sonoriense* is possibly due to their smaller sample size, but the character is obviously of only limited value in distinguishing the two species.

SYNTHESIS OF CHARACTER VARIATION

Analysis of geographic variation in morphological characters in the *Kinosternon hirtipes* species complex supports the recognition of two allopatric species, both previously recognized (Wermuth and Mertens, 1977; among many others): *K. sonoriense* and *K. hirtipes.* Analysis of populations of *K. sonoriense* suggests the existence of two distinct morphotypes, represented by 1) the population inhabiting the Río Sonoyta basin and 2) the remaining populations previously recognized as *K. sonoriense* (Fig. 3). Stepwise discriminant analysis of those two samples using only 13 morphometric characters is capable of distinguishing 100% of the males and 98.6% of the females. Because the holotype of *K. sonoriense* was collected in the Gila River basin (Iverson, 1976) the Río Sonoyta population is here described as a new subspecies.

Patterns of geographic variation in morphology within *Kinosternon hirtipes* suggest the existence of several undescribed taxa (Fig. 4). The most distinct morphological samples in this highly variable species are the 1) Viesca, 2) San Juanico, 3) Pátzcuaro, 4) Valley of Mexico, 5) Chapala-Zapotlán, 6) possibly the Duero sample, 7) possibly the Villa Victoria population (see below) and 8) the remaining populations of *K. hirtipes.* Stepwise discriminant analysis of the seven samples, excluding the Villa Victoria population (see below), using all 23 morphometric variables, was able to classify turtles into the correct morphotype at least 75% of the time for any given morphotype of either sex. San Juanico and Viesca turtles were always classified correctly, and only one Valley of Mexico turtle was misclassified (a female, into sample 8, above). A single male and one female from Pátzcuaro were misclassified (into San Juanico, in both cases). Two males and one female Duero turtle were misclassified into the Chapala-Zapotlán sample; and two other male Duero turtles were misclassified in the Pátzcuaro sample. Chapala-Zapotlán turtle misclassification included three males and one female into the Pátzcuaro, and one female into the Viesca sample. The large and highly variable sample of the remaining *K. hirtipes* populations included the following misclassifications: 12 males and 13 females into the Chapala-Zapotlán sample; 7 males and 6 females into the Valley of Mexico sample; 9 males and two females into the Duero sample; seven females into the Pátzcuaro sample and three females into the Viesca sample.

Based on the various morphological analyses, I conclude that at least the following samples should be recognized taxonomically: 1) Viesca, 2) San Juanico, 3) Pátzcuaro, 4) Chapala-Zapotlán, 5) Valley of Mexico, and 6) the remaining populations of *K. hirtipes* (perhaps excluding the Villa Victoria sample). I tentatively consider the Duero population as intergrading between samples 4 and 6. The first four samples have not been named and are described here. The holotype of *Kinosternon hirtipes murrayi* clearly belongs in the last group and hence that group should bear that trinomen. The status of the Valley of Mexico and Villa Victoria samples are not as clear.

Several of the early analyses (see Figures 9, 11, 16, and 17) suggested that the male Villa Victoria sample was morphometrically distinct. Unfortunately, only one female is known from that basin, and although not as distinct (see Appendix 2), it does exhibit some of the characters which seem to distinguish the males (longer hindlobe, shorter interhumeral seam, longer interpectoral seam, and longer first vertebral scute). However, the complete lack of geographically proximate comparative material from the entire upper Lerma system and the near lack of material from the Balsas drainage system (one female from 45 miles to the west) make a decision regarding the distinctiveness of this population difficult. I have therefore tentatively included the population with those of *K. h. murrayi* until field work in the upper Balsas and Lerma basins can clarify distribution and morphological variation in those regions.

Even less clear is the correct allocation of the holotype of *Kinosternon hirtipes,* a very old, worn male specimen, with no associated data except "Mexico" (see SYSTEMATIC ACCOUNTS). Plastral erosion makes clear morphometric allocation impossible (Fig. 25). In addition, the shape of the nasal scale (Fig. 25) is somewhat intermediate between a V-shaped condition of *K. h. murrayi* and the rhomboidal condition of Valley of Mexico turtles. Schmidt (1953) restricted the type-locality to "lakes near Mexico City" (in the Valley of Mexico) but without variational analyses. Because the correct allocation can only be solved by field work in the Valley of Mexico and adjacent basins, I tentatively follow Schmidt (1953) in the application of the name *K. h. hirtipes* to the populations in that Valley.

SYSTEMATIC ACCOUNTS

A chronological list of all synonyms and orthographic variations thereof is given for each valid taxon. Each orthographic combination appears with reference to its first use, including author, date and pagination (referenced in Literature Cited). Selected subsequent usages, especially those incorrect or of taxonomic significance, and including all pre-1930 references, are included in species and subspecies synonymies. Most citations are also parenthetically annotated. Localities and location of all available specimens are also included.

Figure 25. Nasal scale shape (top) and plastron shape (bottom) in holotype of *Kinosternon hirtipes* (ZSM 1374/0).

Kinosternon sonoriense LeConte
Sonora Mud Turtle

Kinosternum sonoriense LeConte, 1854: 184 [type-locality, "Tucson, in Sonora", Arizona. Type, a male, collected by Dr. J. L. LeConte (author's son) and placed in Philadelphia Academy of Sciences; presently unlocatable]; Troschel, 1855:415.

Kinosternon sonoriense Gray, 1855:79 (first use of this combination; Tucson); Stejneger, 1902:149 (Fort Huachuca and Babacomari creek, Arizona); Ruthven, 1907:594 (Sabino Canyon, Santa Catalina Mountains, Arizona); Mearns, 1907:117; Van Denburgh and Slevin, 1913:396 (Gila River and its tributaries; 8 specific localities); Grinnell and Camp, 1917:200 (in part; result of incorrect synonymy of *K. flavescens* with *K. sonoriense;* lower Colorado River, California); Stejneger and Barbour, 1917:112 (in part; southern New Mexico and Arizona into southeastern California; northern Mexico); Schmidt, 1922:618; Van Denburgh, 1922:967 (Arizona, 18 localities; California, 2 localities; and Sonora, 5 localities); Pratt, 1923:238 (in part; western Texas [= *K. hirtipes*] into southern California); Van Denburgh, 1924:229 (New Mexico; "Fort Union" locality in error, see Iverson, 1978); Strecker and Williams, 1927:15 (in part; Bexar Co., Texas locality based on *K. flavescens*); Storer, 1930:430; Ditmars, 1936:397 (in part; southwestern Texas records based on *K. flavescens*); Dunn, 1936:472 (in part; Chihuahua locality based on *K. hirtipes*); Pickwell, 1947:60 (in part; southwestern Texas record based on *K. flavescens*); Brown, 1950:228 (in part; Texas localities based on *K. flavescens*); H. M. Smith and Taylor, 1950a:26 (in part; western Texas localities based on *K. flavescens;* Chihuahua and Durango localities based on *K. hirtipes*); Carr, 1952:90 (in part; Texas records based on *K. flavescens*); Schmidt, 1953:91 (in part; Texas records based on *K. flavescens;* erroneously restricted type-locality of the synonym *Kinosternum henrici* to Las Cruces, New Mexico); Mertens and Wermuth, 1955:336 (in part; Texas records based on *K. flavescens;* Chihuahua and Durango records, on *K. hirtipes*); Cagle, in Blair et al., 1957:281 (in part; Texas records based on *K. flavescens*); Gijzen and Wermuth, 1958:44 (in part; photograph apparently *K. integrum*); Wermuth and Mertens, 1961:27 (in part; Texas records based on *K. flavescens* ; Chihuahua and Durango records based on *K. hirtipes*); Casas Andreu, 1965:382 (in part; Chihuahua and Durango records based on *K. hirtipes*); Stebbins, 1966:82 (in part; Texas records based on *K. flavescens;* Durango records based on *K. hirtipes*); Casas Andreu 1967:51 (in part; Chihuahua and Durango records based on *K. hirtipes*); Pritchard, 1967: 37 (in part; Coahuila records incorrect; Texas records based on *K. flavescens*); Cochran and Goin, 1970:136 (in part; Texas records based on *K. flavescens*); Legler and Webb, 1970:163 (in part; Chihuahua records based on *K. hirtipes*); Wiewandt, 1971:34 (in part; southern Sonora records based on *K. alamosae*); Wiewandt, Lowe and Larson, 1972:162 (in part; southern Sonora records based on *K. alamosae*); Ernst and Barbour, 1972:64 (in part; Chihuahua and Durango records based on *K. hirtipes*); Hambrick, 1976:291 (in part; Texas records invalid); Iverson, 1976:1 (in part; upper Río Yaqui records in Chihuahua based on *K. hirtipes*); Wermuth and Mertens, 1977: 10; Conant and Berry, 1978:1; Iverson, 1978:476; H. M. Smith and R. B. Smith, 1980:156; Berry and Legler, 1980:1.

Thyrosternum sonoriense Agassiz, 1857: 428; Blair, 1859:3, Troschel, 1860:270; Garman, 1885:8.

Cinosternum sonoriense Agassiz, 1857: Plate V, fig. 8-11; Cope, 1875:52, Coues, 1875:589; Yarrow, 1883:31; Gunther, 1885:13; Boulenger, 1889:40; Siebenrock, 1907:551; Siebenrock, 1909:444.

Kinosternum henrici LeConte, 1859:4 (type-locality, "New Mexico"). Type, a male, collected by Dr. T.C. Henry and placed in Philadelphia Academy of Sciences (ANSP 83). Locality data with type is "Gila River, New Mexico." Type-locality erroneously restricted by Schmidt (1953:91) to vicinity of Las Cruces; Cope, 1880:13 (in part; Texas record based on *K. flavescens).*

Thyrosternum henrici Troschel, 1860: 270; Garman, 1884:8.

Cinosternon henrici Strauch, 1862:41; Strauch, 1865:101; Strauch, 1890:89 (in part; Dallas, Texas record based on *K. subrubrum*).

Cinosternon sonoriense Strauch, 1862:41; Strauch, 1865:100.

Thylosternum sonoriense Müller,1865: 598.

Kinosternon punctatum Gray, 1870:67 (in part; Sonora; eastern United States records based on *K. subrubrum*).

Swanka henricii Gray, 1870:69.

Platythyra flavescens Cooper, 1870:66 (possibly in part; see Iverson, 1978; Colorado River Valley).

Cinosternum henrici Cope, 1875:52; Yarrow, 1875:583; Coues, 1875:590; Yarrow, 1883:31; Boulenger, 1889:40; Ditmars 1907:26; Strecker, 1915:10 (in part; Texas records based on *K. flavescens*); Malnate, 1971:353.

Aromochelys carinatus Yarrow, 1875:582 (in part; Arizona); Coues, 1875:589 (in part; Arizona).

Cinosternum flavescens Yarrow, 1883:31 (in part; "Utah" and "Fort Mora", specimens actually *K. sonoriense,* see Iverson, 1978).

Cinosternum hirtipes Gunther, 1885:15 (in part; result of his synonymy of *K. henrici* LeConte with *K. hirtipes* Wagler); Cope, 1887:23 (in part; result of his synonymy of *C. henrici* with *C. hirtipes*); Gadow, 1905:209 (in part; Arizona and New Mexico).

Cinosternon integrum Strauch, 1890:91 (in part; result of his synonymy of *C. hirtipes* Gunther with *C. integrum* LeConte).

Kinosternon flavescens Van Denburgh, 1922:972 (in part; Ft. Verde and Graham Co. records actually *K. sonoriense;* see Iverson, 1978); LaRivers, 1942:66 (in part; Nevada; see Iverson, 1978); Stebbins, 1966:82 (in part; northwest Arizona; see Iverson, 1978).

Kinosternon sp. Little, 1940:264 (Roosevelt Reservoir and Sallymae Creek, Gila Co., Arizona); Tanner and Robison, 1960:59 (in part; specimens are *K. sonoriense* but locality doubtful).

Kinosternon sonoriensis Bogert and Oliver, 1945:396; Smith and Buechner, 1947:10; H. M. Smith, Williams and Moll, 1963:207.

Kinosternon hirtipes H. M. Smith and E. H. Taylor, 1950a:25 (in part; Arizona).

Kinosternon sonorensis Weise, 1962: 165.
Kinosternon seonoriense Berry and Shine, 1980:189.

Type. Lost; see synonymy.

Content. Two subspecies, one new, are described: *K. s. sonoriense and K. s. longifemorale.*

Diagnosis. A *Kinosternon* of the *hirtipes* species group with: 1.) the adult nasal scale large and triangular, rhomboidal or bell shaped (not furcate behind); 2.) usually three or four pairs of relatively long chin or neck barbels (at least one pair more than half orbit diameter); 3.) male plastron relatively wide (PWB 42-53% of CL; $\bar{x}$ = 47.2%); 4.) first neural often (38.1%) in contact with nuchal bone; 5.) the female generally larger than the male; and, 6.) populations confined to Arizona, California, New Mexico, Sonora, western Chihuahua, and possibly Baja California.

Description. The adult carapace generally is tricarinate with the medial keel most apparent; some turtles possess well-defined keels, others have only the median keel present with mere hints of the two lateral keels, and still others have a virtually smooth shell. The algae covered shells of some individuals are extremely rugose and densely pock-marked (Fig. 26; found in 15 of 164 turtles by Hulse, 1976:347), a condition perhaps induced by the algae (the condition is known for no other kinosternid). The average female is larger than the average male. Maximum female size is 175 mm carapace length; males 155 mm. The nasal scale is not furcate behind in adults. The first vertebral scute usually touches the second marginal. The axillary is nearly always in broad contact with the inguinal, and the inguinal contacts the eighth marginal. The ninth marginal scute is not elevated above the preceding marginals. The tenth marginal is higher than the ninth marginal and the eleventh marginal may or may not be elevated to the height of the posterior portion of the tenth marginal. Interpectoral seam length is less than one-half of gular length. The nuchal bone often contacts the first neural bone. The carapace is brown to olive in color, the seams darker. Well-developed transverse plastral hinges border the abdominal scutes. The male plastron is relatively extensive (PWB = 42 to 53% CL). The plastron is yellow to brownish with darker brown seams. The bridge area is dark brown. The skin is dark gray and the head and neck bear cream colored mottlings that tend to form at least one pair of stripes extending back from the orbit, one above and the other below the typanum after intersecting the angle of the jaw. A yellow or cream stripe also extends from the palmar surface of each foot to the base of the limb along its posterior surface in some adults. Three to four pairs of relatively long chin or neck barbels usually are present. Mature females possess short, stubby tails, with a small terminal spine, whereas males possess long, thickened tails with a large terminal spine and a patch of elevated (tubercular), acute, nonimbricated scales on the posterior surface of the crus and thigh of each hind leg.

Figure 26. Articulated shell (without scutes) of adult *K. sonoriense* (JBI 800) from Sonora, near Cucurpe (Río Sonora basin). Note rugosity.

Remarks. Iverson (1976) has synthesized most of the literature. Additional important references include Hulse (1976); Morafka (1977); Bowler (1977); Conant and Berry (1978); Iverson (1978); H.M. Smith and R.B Smith (1980); Berry and Legler (1980); and Iverson and Weyman (MS).

Kinosternon sonoriense is the largest *Kinosternon* in which the females are generally larger than the males. Perhaps concomitantly it produces the largest number of eggs per clutch of any kinosternine — up to at least eight (Hulse, 1974; Iverson, unpublished data). I have observed copulation in the field near Fort Huachuca, Arizona (Gila River basin) on 4 May 1974, much later than the March-April records of Hulse (1974). The smallest turtles I measured were 22.3 mm CL (20.0 mm PL), 23.9 mm CL (18.3 mm PL), and 25.7 mm CL. In the southern part of its range, this turtle is apparently active year round; I have observed activity at Quitobaquito Pond, Arizona on several occasions in January.

Range. Kinosternon sonoriense occurs in the United States from the Lower Colorado and Gila rivers in Arizona and New Mexico, southward to and including the Río Yaqui basin west of the continental divide, and eastward through the Río Casas Grandes basin of northwestern Chihuahua. It is known from between at least 43 and 2042 m elevation. The species may also occur in the Río Fuerte (see MATERIALS AND METHODS).

Specimens examined and Additional Records. See Locality list.

Etymology. The specific name *sonoriense* refers to the Sonoran Biotic Province, wherein the turtle is found.

Kinosternon sonoriense sonoriense (LeConte)

Sonora Mud Turtle

Synonymy. See species synonymy, except those references in synonymy of *K. sonoriense longifemorale.*

Holotype. Lost; see species account.

Diagnosis. A subspecies of *K. sonoriiense* with 1) a relatively long interanal seam (male $\bar{x}$ IAN/CL, 19.5%; female $\bar{x}$, 23.0%); 2) a relatively short interfemoral seam (male X, IF/CL, 10.1%; female $\bar{x}$, 10.1%); 3) a first vertebral scute of medium width (male $\bar{x}$, VW/CL, 24.4%; female $\bar{x}$, 25.5%); and 4) a relatively wide gular scute (male $\bar{x}$, GW/CL, 20.0%; female $\bar{x}$, 19.4%).

Range. Kinosternon s. sonoriense is definitely known from the Bill Williams, lower Colorado, Gila, Sonora, Magdalena, Yaqui, southwest New Mexico, and Casas Grandes basins of Arizona and New Mexico, and Sonora and western Chihuahua, Mexico.

Specimens examined and Additional Records. See locality list.

Etymology. See species account.

Kinosternon sonoriense longifemorale ssp. nov.

Sonoyta Mud Turtle

Kinosternon sonoriense Mearns, 1907:117 (Sonoyta); Van Denburgh, 1922:969. (Sonoyta River three miles from Sonoyta); Stebbins, 1966:83 (Quitobaquito Spring); Hulse, 1974:15, 94 (Quitobaquito Spring); H.M. Smith and R.B. Smith, 1980:160 (3 localities in Sonoyta basin).

Holotype. USNM 21710, young male, preserved whole, from "artificial pond fed by springs", Sonoyta, Sonora, Mexico (31°51'N, 112°50'W); collected 15 January 1894, apparently by E.A. Mearns.

Paratypes. USNM 21709 and 21711, topotypic male and female, preserved whole, and USNM 21708, adult female, preserved whole, from Sonoyta River, 3 mi. from Sonoyta, collected on 22 January 1894 by B.A. Wood; UAZ 27987 and 27996, adult male and female, respectively, preserved whole, Quitobaquito Springs, Organ Pipe Cactus National Monument, Pima County, Arizona, collected on 14 May 1967 and 10 April 1965, respectively, by R.D. Krizman and T.J. Cox, respectively; and UF 47719 and 47720 (Fig. 27), skeletal adult male and female, respectively from Quitobaquito Pond, Pima County, Arizona, collected on 19 January 1976 by John B. Iverson.

Diagnosis. A subspecies of *K. sonoriense* with 1) a relatively short interanal seam (male $\bar{x}$, IAN/CL, 14.4%; female

Figure 27. Plastron of female *Kinosternon sonoriense longifemorale* (UF 47720) from Quitobaquito Pond, Pima County, Arizona. Note short interanal and long interfemoral seams.

$\bar{x}$, 18.5%); 2) a relatively long interfemoral seam (male $\bar{x}$, IF/CL, 12.8%; female $\bar{x}$, 13.5%); 3) a wide first vertebral scute (male $\bar{x}$, VW/CL, 28.9%; female $\bar{x}$, 28.8%); and 4) a relatively narrow gular scute (male $\bar{x}$, GW/CL, 17.7%; female $\bar{x}$, 17.8%).

Range. Kinosternon sonoriense longifemorale is known only from the Río Sonoyta basin in Arizona and Sonora, Mexico.

Specimens examined and Additional Records. See locality list.

Etymology. The subspecific name *longifemorale* is from the Latin *longus* (long) and *femoralis* (of the femur; here the femoral scute) and refers to the long interfemoral seam which, along with the short interanal seam, diagnoses the taxon.

Kinosternon hirtipes (Wagler)

Rough-footed Mud Turtle

Cinosternon hirtipes Wagler, 1830:137, plate 5, fig. 29-30 (Type-locality, "Mexico", restricted to "lakes near Mexico City" by Schmidt 1953:89, but see REMARKS under *K. h. hirtipes).* Holotype, München Museum (Germany) 1374/0, a male, collected by Baron Karwinski, collecting date unknown. Type-locality incorrectly restricted to "Mazatlan, Sinaloa" by H.M. Smith and E.H. Taylor 1950b:25; see discussion in Hardy and McDiarmid, 1969:70, 218); Wagler, 1833:plate 30; Fitzinger, 1835:125; A.M.C. Duméril and Bibron, 1834:370; A.M.C. Duméril and Duméril, 1851:17; Gray, 1855:46 (in part; "Brazils" record in error); Strauch, 1862:41; Strauch, 1865:101; A.H.A. Dumeril, 1870:25; Westphal-Castelnau, 1872:278; Gray, 1873:113; Bocourt, 1876:8; Dugès, 1888:106.

Kinosternon oblongum Gray, 1844:33 (in part).

Cinostermon hirtipes Gray, 1844:33 (in synonymy).

Kinosternum hirtipes LeConte, 1854:186; LeConte, 1859:5; Müller, 1885:716.

Kinosternon hirtipes Gray, 1855:47, 1869: 183, 1870:67; Stejneger, 1899:64; Rust, 1934:59; Taylor, 1936:529 (in part; Sinaloa records based on *K. integrum)*; Martin del Campo, 1937:265 (in part; Hidalgo record based on *K. integrum)*; Rust, 1938:22; Caballero y Caballero, 1938a:103 (in part; Hidalgo record based on *K. integrum)*; Caballero y Caballero, 1940a:225 (in part; Uruapan, Michoacán locality based on *K. integrum)*; H.M. Smith and E.H. Taylor, 1950a:25 (in part; Chihuahua, Michoacán, Guanajuato, México, and Distrito Federal; other locality based on *K. sonoriense, K. flavescens,* or *K. integrum)*; H.M. Smith and E.H. Taylor, 1950b:342 (in part; type-locality restriction to Mazatlan, Sinaloa invalid); Glass and Hartweg, 1951:50; Taylor, 1952:793; Schmidt, 1953:89; Mertens and Wermuth, 1955:336; Cable in Blair et al. 1957:281 (in part; Arizona records based on *K. sonoriense)*; Malkin, 1958:75 (in part; Nayarit records based on *K. integrum)*; Zweifel, 1960:94 rejects Tres Marías records; Wermuth and Mertens, 1961:19; Croulet, 1963:4 (in part; Nayarit record based on *K. integrum)*; Liner, 1964:221 (in part; Guanajuato records on *K. integrum)*;

Casas Andreu, 1965:285 (in part; Sinaloa, Colima, and Hidalgo records based on *K. integrum)*; Pritchard, 1967:37; Casas Andreu, 1967:44 (in part; Sinaloa, Colima, Hidalgo and Nayarit records based on *K. integrum)*; Hardy and McDiarmid, 1969:104 (rejects Sinaloa records, including H.M. Smith and Taylor's 1950b:343 type-locality restriction); Cochran and Goin, 1970:135 (in part; Arizona records based on *K. sonoriense)*; Ernst and Barbour, 1972: 66 (in part; Arizona records based on *K. sonoriense)*; Dixon, Ketchersid, and Leib, 1972:228 (in part; Querétaro record based on *K. integrum)*; Greene, 1972: 2 (in part; Puebla record based on *K. integrum)*; Bravo-Hollis and Caballero Deloya, 1973:109; Conant and Berry, 1978:1; Iverson, 1978:1, Iverson and Berry, 1979:318; Pritchard, 1979:537; H.M. Smith and R.B. Smith, 1980:137; Berry and Legler, 1980:1.

Cinosternon pensylvanicum Lichtenstein, 1856:2 (in part; Mexico); Westphal-Castelnau, 1872:278 (in part; Guanajuato); Bocourt, 1876:5 (in part; Mexico); Herrera, 1890:330, 1891:46 (in part; Valley of Mexico); Strauch, 1890:88 (in part; Mexico); Herrera, 1893:339 (in part; Mexico); Dugès, 1898:40 (in part; Mexico); Herrera and Lope, 1899:281 (in part; Mexico); Herrera, 1904:5 (in part; Mexico).

Thryrosternum hirtipes Agassiz, 1857:429.

Ozotheca hirtipes LeConte, 1859:6; Troschel, 1860:270.

Ozotheca odorata Dugès, 1869:143 (in part; states of Guanajuato and Mexico); Velasco, 1890b:54 (in part, Guanajuato); Velasco, 1891:52 (in part; Querétaro record unsubstantiated); Velasco, 1892b:40 (in part; Tlaxcala record incorrect); Velasco, 1893b:81 (in part; Sonora record incorrect); Velasco, 1894:40 (in part; Zacatecas record unsubstantiated); Velasco, 1896a:30 (in part; Aguascalientes record unsubstantiated); Velasco, 1898:62 (in part; Chiapas record incorrect).

Ozhoteca odorata García Cubas, 1884: 179 (in part; Mexico); Velasco, 1890a: 35 (in part; Nuevo Leon record incorrect); Velasco, 1893a:64 (in part; Durango record unsubstantiated); Velasco 1897:41 (in part; Coahuila record incorrect).

Cinosternum hirtipes Gunther, 1885:13 (in part; Sinaloa records based on *K. integrum;* Arizona and New Mexico records based on *K. sonoriense)*; Cope, 1885:390; Cope, 1887:23 (in part; Colima and Sinaloa records based on *K. integrum)*; Garman, 1887:16 (in part; San Luis Potosí record based on *K. integrum)*; Boulenger, 1889:38; Gadow, 1905:209 (in part; Arizona and New Mexico records based on *K. sonoriense);* Siebenrock, 1906:94, 1907: 551; Gadow, 1908:5; Siebenrock, 1909: 444; Gadow, 1930:50.

Cinosternon pennsylvanicum Dugès, 1888:10 (in part; Valley of Mexico and Guanajuato state); Velasco, 1890b:291 (in part; Guanajuato); Dugès, 1895:5 (in part; Guanajuato); Dugès, 1896a:1v (in part; Mexico); Dugès, 1896b:329 (in part; Mexico); Dugès, 1896c:479 (in part, Guanajuato).

Ozothea odorata Velasco, 1892a:76 (in part; Guerrero record incorrect); Velasco, 1892c:79 (in part; Tamaulipas record incorrect); Velasco, 1895:38 (in part; Campeche record incorrect); Velasco, 1896b:37 (in part; Colima record incorrect).

Cynosternon pennsylvanicum Herrera, 1893:342 (in part; Valley of Mexico).

Cinosternum pennsylvanicum Gadow, 1905:209 (in part; Valley of Mexico).

Kinosternum pennsilvanicum Cope, 1896: 1021 (in part; Austrocentral district of Mexico).

Cinosternonus pensylvanicum Herrera, 1899:28 (in part; Mexico).

Cynosternon pensylvanicum Herrera and Lope, 1899:131 (in part; Valley of Mexico).

Cinosternum pennsilvanicum Cope, 1900: 1229 (in part; Valleys of Mexico and Toluca northward through Guanajuato).

Cinosternum pensylvanicum Lampe, 1901:184-85 (North Mexico).

Cinosternon sp. Herrera, 1904:6 (Valley of Mexico).

Cinosternum integrum Gadow, 1908:518 (in part; Laguna de Zapotlán, Jalisco).

Kinosternon sonoriense Dunn, 1936:472 (in part; Chihuahua); H.M. Smith and E.H. Taylor, 1950a:26 (in part; Chihuahua and Durango); Mertens and Wermuth, 1955:338 (in part; Chihuahua to Durango); Casas Andreu, 1965: 386, 1967:52 (in part; Chihuahua and Durango); Legler and Webb, 1970:163 (in part; western Chihuahua); Iverson, 1976:1 (in part; upper Río Yaqui, Chihuahua; see Iverson, 1978).

Chinosternum hirtipes Caballero y Caballero, 1938b:449 (in part; Hidalgo locality based on *K. integrum).*

Sternotherus odoratus Brown, 1950:230 (in part; Presidio Co., Texas; see Conant and Berry, 1978).

Kinosternon murrayi Glass and Hartweg, 1951:50 (type-locality, "Harper Ranch, 37 miles south of Marfa, Presidio County, Texas." Holotype, Texas Cooperative Wildlife Collection 650, a young male, collected by S.H. Wheeler on 12 August 1941); Peters, 1952:54; Legler, 1960:139 (Lajitas, Texas record in error); Cochran, 1961:232.

Kinosternon flavescens Stebbins, 1966:82 (in part; Durango; see Iverson, 1978); Morafka, 1977:70, Map 25 (in part; some northern Mexico records based on *K. hirtipes.*).

Kynosternon hirtipes Lopez 1975:2 (Valley of Mexico).

Kinosternon hertipes Semmler et al., 1977: 18 (Chihuahua).

Types. Only the holotype (Fig. 25), an adult male, preserved whole, is available, contrary to Bocourt's (1876:8) suggestion that Wagler's (1830, 1833) figures (Plate 5:fig. 29-30 and Plate 30:figs. 1-3, respectively) of *Cinosternon (= Kinosternon) hirtipes* were based on two different specimens.

Content. Six subspecies, four new, are described: *K. h. hirtipes, K. h. chapalaense, K. h. murrayi, K. h. magdalense, K. h. tarascense,* and *K. h. megacephalum.*

Diagnosis. A *Kinosternon* of the *hirtipes* species group with 1) the adult nasal scale reduced and crescent-shaped, or larger and furcate behind, or still larger and triangular or bell shaped (the latter combination characteristic only of Valley of Mexico turtles); 2) usually three pairs of relatively short chin barbels (< half orbit diameter); 3) male plastron relatively narrow (PWB 36 to 50% of CL; $\bar{x}$ = 43%); 4) first neural rarely (10.2%) contacting nuchal bone; 5) the male generally larger than the female; and 6) populations confined to Central Mexico from Chihuahua (and adjacent Texas) to Jalisco, Michoacán, and Mexico (state). Despite its anomalous absence on the holotype (Fig. 25), a nuchal scute is typically present.

Description. As for *K. sonoriense* except as stated above, and 1) the carapacial keels are almost never absent (i.e., the median keel is virtually always evident at least posteriorly); 2) maximum female size is 157 mm carapace length, male 182 mm; 3) carapace light to dark brown to nearly black in color; 4) plastron usually yellow to brown with darker brown seams but sometimes (stained ?) nearly black; 5) head markings extremely variable (coarsely mottled, reticulated or spotted to almost unmarked; see subspecific accounts).

Remarks. Most of the literature is synthesized in Iverson (in press). A discussion of the evolutionary significance of the geographically variant sexual size dimorphism of this species appears in Iverson (MS 2). Reproductive parameters are summarized here (Table 2) and in Iverson (MS 2). Clutch size data (4-5 and 4-7 eggs) in Moll and Legler (1971) are all referable to the subspecies *murrayi.* Scaling of skeletal components is discussed in Iverson (MS 1) and Iverson and Weyman (MS).

Table 2. Reproductive data by population for *Kinosternon hirtipes*. Estimated number of annual clutches based on multiple sets of corpora lutea plus sets of enlarged follicles. Clutch size range appears below mean.

Basin	Smallest turtle < 1 year			Clutch size based on:			Estimated number of annual clutches	$\bar{X}$ Egg size	Estimated Reproductive Season
	CL	PL	PL[1]	Oviducal Eggs	Corpora lutea	Enlarged Follicles			
STMR	-	-	17.0 18.9	2.8 (9) 2-3	2.7 (10) 2-4	2.9 (21) 2-5	3 - 4	29.5 x 16.8 (22)	May-August
CRMN	23.9	18.5	-	-	-	-	-	-	-
CNCH	-	-	-	4.5 (2) 4-5	-	-	-	-	-
PAP	-	-	-	4.0 (2) 3-5	4.0 (2) 3-5	4.0 (8) 1-6	2 - 3	-	May-July
NAZ	22.8	19.5	17.9	4 (1)	4 (1)	5.5 (2) 5-6	3 - 4	31.3 x 16.9 (4)	May- ?
AGUAN	26.5	21.1	-	-	-		-	-	-
STGO	-	-	16.8	-	-	4 (1)	2+	-	May- ?
MEZQ	24.0[2] 24.7	21.3[2] 20.2	- -	4 (1)	4 (1)	-	2+	29.2 x 16.2 (4)	May ?-July
SALT	-	-	-	5 (1)	5 (1)	6 (1)	2+	30.9 x 17.4 (5)	June ?-August
SLP	-	-	-	-	-	2.75 (4) 2-4	2+	-	June- ?
VERDE	-	-	-	3.5 (2) 3-4	3.5 (4) 3-4	3.5 (4) 3-5	2 - 4	30.8 x 17.6 (7)	May-July (?)
DUER	-	-	-	6 (1)	6 (1)	9 (1)	2	29.0 x 18.3 (6)	May-July (?)
PATZ	-	-	-	4.5 (2) 3-6	4.5 (4) 3-6	4.5 (2) 4-5	2	31.8 x 17.4 (9)	May-June
LERMA	-	-	-	-	-	3 (1)	2	-	June

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[1] estimates from annuli

[2] with egg tooth

Range. Primarily distributed on the Mexican Plateau, *Kinosternon hirtipes* ranges from Alamito Creek in Texas in the United States and the Ríos Santa María, Carmen, and Conchos in northern Mexico south and eastward to the Chapala, Zapotlán, San Juanico, Pátzcuaro, and Valle de México basins of the Sierra Volcanica Transversal of southern Mexico. It is known from between at least 800 and 2600 m in elevation.

Specimens examined and Additional Records. See locality list.

Etymology. The specific name *hirtipes* is from the Latin, *hirtus,* meaning rough, and *pes* meaning foot, and refers to the rough scales on the feet of the species.

Kinosternon hirtipes hirtipes Wagler

Valley of Mexico Mud Turtle

Cinosternon hirtipes Wagler, 1830:187 (see species synonymy).

Ozotheca odorata Dugès, 1869:143 (in part; State of México).

Cinosternon pennsylvanicum Dugès, 1888:107 (in part; Valley of Mexico).

Cinosternum hirtipes Boulenger, 1889:38; Siebenrock, 1906:94, 1907:551 (State of México); Gadow, 1908:5 (Chalco lakes, Valley of Mexico).

Cinosternon pensylvanicum Herrera, 1890:330, 1891:46 (in part; Valley of Mexico).

Cynostenum pennsylvanicum Herrera, 1893:342 (in part; Valley of Mexico).

Cynosternon pensylvanicum Herrera and Lope, 1899:131 (in part; Valley of Mexico).

Cinosternom pennsilvanicum Cope, 1900: 1229 (in part; Valley of Mexico).

Cinosternon sp. Herrera, 1904:6 (Mexicalzingo, Valley of Mexico).

Cinosternum pennsylvanicum Gadow, 1905:209 (in part; Valley of Mexico).

Kinosternon hirtipes Martin del Campo, 1938:391 (Valley of Mexico); Caballero y C., 1939:279 (Xochimilco, Mexico, Distrito Federal); H.M. Smith and Taylor, 1950a:25 (Distrito Federal); Glass and Hartweg, 1951:50 (Valley of Mexico); Schmidt, 1953:89; Beltz, 1954:124 (Mexico City, Mexico); Martin del Campo, 1955:66 (Valley of Mexico); Deevey, 1957:240 (Valley of Mexico); Casas Andreu, 1965:385 (Distrito Federal); Kranz, Smith, and Smith, 1971:23 (near City of Mexico); Greene, 1972:2 (in part; Mexico City, Puebla locality based on *K. integrum)*; Perez Villegas and Reyna Trujillo, 1978:215 (southern region of Valley of Mexico).

Kinosternon hirtipes hirtipes Mertens and Wermuth, 1955:336 (first use of this combination; in part; State of México); Wermuth and Mertens, 1961:20 (in part; State of México); Duellman, 1961:57, 1965:653 (in part; Michoacán localities not this subspecies); H.M. Smith, Williams and Moll, 1963:209; Liner, 1964:221 (in part; Guanajuato records not this subspecies); Pritchard, 1967:37 (in part; State of Mexico); Casas Andreu, 1967:44 (in part; State of México); Parsons, 1968:1238; Legler and Webb, 1970:163 (in part; Chihuahua records based on *K. h. murrayi)*; Mittermeier, 1971:16 (Mexico City); Moll and Legler, 1971:92 (in part; Chihuahua records based on *K. h. murrayi)*; Wermuth and Mertens, 1977: 7; Pritchard, 1979:537 (in part; Mexico City).

Kynosternon hirtipes Lopez 1975:2 (Valley of Mexico.

Kinosternon sp. Niederberger, 1979:134 (Valley of Mexico archeological remains: 5500 BC).

Types. Only the holotype (Fig. 25) is available (see *Remarks* below).

Diagnosis. A subspecies of *Kinosternon hirtipes* with 1) the adult nasal scale triangular, rhomboidal, or bell-shaped (furcate behind in subadults, but not in large adults); 2) a mottled head pattern, typically organized into a light streak extending posteriorly from the angle of the jaw, with a similar light postorbital streak variably evident; 3) one or (typically) two pairs of mental chin barbels, the anterior pair largest; 4) medium body size (maximum male size 140 mm CL; female, 140 mm); 5) relatively short bridge length (male BL/CL, 17.6%; female , 21.7%); 6) relatively short interfemoral seam length (male IF/CL, 6.9%; female , 7.1%); 7) relatively long interanal seam length (male IAN/CL, 20.6%; female , 25.8%) and 8) populations confined to the Valley of Mexico.

Remarks. As mentioned under SYNTHESIS (above), the allocation of the holotype of *Kinosternon hirtipes* to the Valley of Mexico must remain uncertain until additional material is available from the southern and southwestern margins of the Mexican Plateau.

Specific natural history data are unavailable for *Kinosternon hirtipes hirtipes.* A photograph of the plastron of UMMZ 99449, an adult female, appears in H.M. Smith and R. B. Smith (1980; plate 19, bottom).

Range. Kinosternon hirtipes hirtipes is known only from the drainages of the Valley of Mexico.

Specimens Examined and Additional Records. See locality lists.

Etymology. See species account.

Moll and Legler, 1971:92 (in part; Chihuahua records based on *k. h. murrayi)*; Wermuth and Mertens, 1977: 7; Pritchard, 1979:537 (in part; Mexico City).

Kynosternon hirtipes Lopez 1975:2 (Valley of Mexico.

Kinosternon sp. Niederberger, 1979:134 (Valley of Mexico archeological remains: 5500 BC).

Types. Only the holotypes (Fig. 27) is available (see *Remarks* below).

Diagnosis. A subspecies of *Kinosternon hirtipes* with 1) the adult nasal scale triangular, rhomboidal, or bell-shaped (furcate behind in subadults, but not in large adults); 2) a mottled head pattern, typically organized into a light streak extending posteriorly from the angle of the jaw, with a similar light postorbital streak variably evident; 3) one or (typically) two pairs of mental chin barbels, the anterior pair largest; 4) medium body size (maxi-

mum male size 140 mm CL; female, 140 mm); 5) relatively short bridge length (male $\bar{x}$ BL/CL, 17.6%; female $\bar{x}$, 21.7%); 7) relatively short interfemoral seam length (male $\bar{x}$ IF/CL, 6.9%; female $\bar{x}$, 7.1%); 8) relatively long interanal seam length (male $\bar{x}$ IAN/CL, 20.6%; female $\bar{x}$, 25.8%) and 9) populations confined to the Valley of Mexico.

Remarks. As mentioned under SYNTHESIS (above), the allocation of the holotype of *Kinosternon hirtipes* to the Valley of Mexico must remain uncertain until additional material is available from the southern and southwestern margins of the Mexican Plateau.

Specific natural history data are unavailable for *Kinosternon hirtipes hirtipes.* A photograph of the plastron of UMMZ 99449, an adult female, appears in H.M. Smith and R. B. Smith (1980; plate 19, bottom).

Range. Kinosternon hirtipes hirtipes is known only from the drainages of the Valley of Mexico.

Specimens examined and Additional Records. See locality lists.

Etymology. See species account.

Kinosternon hirtipes murrayi
Glass and Hartweg

Murray's Mud Turtle

Ozotheca odorata Dugès, 1869:143 (in part; Guanajuato); Velasco 1890b:54 (in part; Guanajuato).

Cinosternon hirtipes Westphal-Castelnau, 1872:278 (Guanajuato).

Cinosternum hirtipes Cope, 1887:23 (in part; city of Chihuahua, Guanajuato).

Cinosternum pennsylvanicum Dugès, 1896c:479 (Guanajuato).

Cinosternon pennsilvanicum Cope, 1900: 1229 (Toluca Valley northward through Guanajuato.

Kinosternon sonoriense Dunn, 1936:472 (in part; Río Conchos, Julimes, Chihuahua); H.M. Smith and Taylor 1950a:26 (in part; Chihuahua and Durango); Mertens and Wermuth, 1955: 338 (in part; Chihuahua and Durango);

Casas Andreu, 1965:386 (in part; Chihuahua and Durango); Legler and Webb, 1970:163 (in part; Ríos Papigochic and Tomuchic in western Chihuahua); Iverson, 1976:1 (in part; Upper Río Yaqui, Chihuahua; see Iverson, 1978).

Kinosternon hirtipes Caballero y C., 1940b:562 (Río Lerdo, Guanajuato); Caballero y C. y Cerecero, 1943:534 (Rio Lerdo del Valle de Santiago, Guanajuato); H.M. Smith and Taylor, 1950b:25 (in part; Chihuahua, Guanajuato); Williams, Smith, and Chrapliwy, 1960:36 (Chihuahua, 1 mi. E La Cruz); Casas Andreu, 1965:385 (in part; Chihuahua, Guanajuato); Conant, 1978: 465 (Texas, Chihuahua, Durango and Zacatecas).

Sternotherus odoratus Brown, 1950:230 (in part; Presidio Co., Texas; based on holotype of *K. murrayi*; see Conant and Berry, 1978:15).

Kinosternon murrayi Glass and Hartweg, 1951:50 (Type-locality, "Harper Ranch, 37 miles south of Marfa, Presidio County, Texas." Holotype, TCWC 650, a young male, collected 12 August 1941 by S.H. Wheeler.); Peters, 1952:54 (Texas); Legler, 1960:139 (Jct. Río San Pedro and Conchos, and Ojinaga, Chihuahua).

Kinosternon hirtipes murrayi Schmidt, 1953:89 (first use of combination; Texas); Mertens and Wermuth, 1955: 336 (Texas); H.M. Smith, Williams and Moll, 1963:207 (Chihuahua); Casas Andreu, 1967:45 (Texas, Chihuahua, and Durango); Parsons, 1968:1238; Cochran and Goin, 1970:135 (Texas); Moll and Legler, 1971:92 (Durango and Chihuahua); Ernst and Barbour, 1972: 66 (Texas); Hambrick, 1976:292 (Texas); Wermuth and Mertens, 1977:7 (Texas); Conant and Berry, 1978:1 (Texas and Chihuahua); Iverson, 1978: 476 (Chihuahua).

Kinosternon hirtipes hirtipes Mertens and Wermuth, 1955:336 (in part; Chihuahua); Duellman, 1961:57 (in part ?; Michoacán, 8 km W Ciudad Hidalgo and Lago de Cuitzeo); Casas Andreu, 1967:44 (in part; Chihuahua, Michoacán, and Guanajuato); Legler and Webb, 1970:163 (in part; Ríos Papigochic and Tomuchic, western Chihuahua); Moll and Legler, 1971:92 (in part; Chihuahua); Wermuth and Mertens, 1977:7 (middle and western Mexico); Pritchard 1979:537 (in part).

Kinosternon flavescens Stebbins, 1966:82 (in part; Durango; see Iverson, 1978).

Kinosternon hirtipes murryi Ashton et al., 1976:51 *(lapsus pro murrayi)*.

Kinosternon hertipes Semmler, et al., 1977:18 (near Galeana, Chihuahua).

Types. Holotype: see subspecies synonymy. Paratypes: USNM 15860, adult male, preserved whole, from "Marfa, Presidio County, Texas", collected by Vernon Bailey: UMMZ 101294, adult male, preserved whole, and UMMZ S-1083, shell of adult male, both topotypic and collected 12 June 1950 by Herndon G. Dowling.

Diagnosis. A subspecies of *Kinosternon hirtipes* with: 1) a large posteriorly furcate nasal scale (typically exending posterior to the orbits); 2) an extremely variable mottled to reticulated head pattern; 3) typically two pair of mental chin barbels, the anterior pair largest; 4) medium to large body size (maximum known male size, 182 mm CL; female, 157 mm); 5) relatively long bridge length (male $\bar{x}$ BL/CL, 20.0%; female $\bar{x}$, 23.7%); 6) relatively long gular length (male $\bar{x}$ GL/CL, 14.7%; female $\bar{x}$, 15.8%); and 7) populations confined to the Big Bend region of Texas and adjacent Chihuahua southward across the Mexican Plateau to northern Jalisco, northern Michoacán, and eastern México (state).

Remarks. As discussed in the results, there appears to be a slight morphometric distinction between populations of *K. h. murrayi* in the Río Nazas northward, and populations in the Río Aguanaval southward. This difference is not considered significant enough to warrant subspecific designation, but has some interesting zoogeographic implications.

Range. Kinosternon hirtipes murrayi is known from the following basins in Aguascalientes , Chihuahua, Coahuila, Durango, Guanajuato, Jalisco, México, Michoacán, San Luis Potosí, Texas, and Zacatecas: Santa Maria (Chihuahua), Carmen, El Sauz, Conchos, Bustillos, Papigochic, Nazas, Viesca, Aguanaval, Santiaguillo, Mezquital, El Salto, Santa Maria (San Luis Potosi; presumably introduced), Aguascalientes, Verde, Lerma (except Chapala), Cuitzeo, Balsas, and Villa Victoria (with reservation).

Specimens examined and Additional Records. See locality lists.

Etymology. The subspecific name *murrayi* is a patronym, honoring Dr. Leo T. Murray of Texas A & M College.

Kinosternon hirtipes chapalaense ssp. nov.

Lake Chapala Mud turtle

Cinosternum integrum Gadow, 1908:518 (in part; Laguna de Zapotlán, Jalisco).

Kinosternon hirtipes Altini, 1942:153 (in part; Lake Chapala, Jalisco).

Kinosternon hirtipes hirtipes Duellman, 1961:57, 1965:653 (in part; Jiquilpan, La Palma, Lago de Camécuaro = 14 km E Zamora, Michoacán).

Kinosternon hirtipes chapalaense Pritchard, 1979:557 (*nomen nudum;* Lake Chapala).

Holotype. UMMZ 97128, adult male, preserved whole, from Lake Chapala, 0.25 mile off Chapala, Jalisco, Mexico [20°18'N, 103°12'W]; collected 15 July 1947, by Norman Hartweg.

Paratypes. All preserved whole: UMMZ 97122-23, topotypic adult females; UMMZ 97124, topotypic subadult male; 97125-27 and 97129-30, topotypic adult males; and UU 12126-12128, adult male, subadult female, and juvenile, Lago de Chapala, 3.2 km W Chapala; and UU 12125, adult female, Lago de Chapala, 6.1 km W Ajijic, all collected on 21-22 June 1969 by Clyde Barbour.

Diagnosis. A subspecies of *Kinosternon hirtipes* with 1) a reduced crescent-shaped nasal shield, which nearly always lies anterior to the orbits (Figure 23); 2) a reduction of dark pigment on the head and neck, dark markings confined to isolated spots or reticulations dorsally (Figures 23 and 24), but laterally sometimes organized as two dark, nearly parallel postorbital stripes; 3) the neck and chin virtually unmarked and the mandibular and maxillary sheaths bearing only a few dark streaks, if any; 4) one, two, or three pairs of mental barbels present, the anteriormost pair (near the mandibular symphysis) usually the largest; 5) medium body size (maximum known size for males is 152 mm CL; females, 149 mm); 6) relatively long bridge length (male $\bar{x}$ BL/CL, 20.3%; female $\bar{x}$, 25.3%); 7) relatively long interanal seam (male $\bar{x}$ IAN/CL, 19.1%; female $\bar{x}$, 25.2%); and 8) populations confined to the Chapala and Zapotlán (and possibly Duero) basins of Jalisco and Michoacán.

Remarks. Field notes accompanying the topotypes provide no additional geographical and ecological information. However, Clyde Barbour (pers. comm.) obtained the non-topotypic paratypes (during the night 21-22 June 1969) along the shore of Lake Chapala, on trot-lines baited with liver. These lines were necessarily buoyed off the lake bottom with floats to avoid bait removal by crabs. Peter Meylan found a single rotten carcass of this species on the south shore of Lake Chapala just east of Tuxcueca during my field trip to the area on 15 June 1978; trapping at that locality produced no turtles. Trapping in isolated spring-fed pools just northeast of the town of Chapala on 9 May 1981 produced only *K. integrum.*

Range. Kinosternon hirtipes chapalense is known only from the Lago de Chapala and Laguna de Zapotlán drainage basins in Jalisco and Michoacán, Mexico. Specimens from the Río Duero basin are tentatively considered intergrades with *K. h. murrayi.*

Specimens Examined and Additional Records. See locality list.

Etymology. The subspecific name *chap-*

alaense refers to Lake Chapala wherein the type series was collected.

†*Kinosternon hirtipes* **megacephalum** ssp. nov.

Viesca Mud Turtle

Holotype. SM(BCB) 11466, adult male, preserved whole, from 3.2 km SE Viesca [25°21'N, 102°48'W], Coahuila; collected 4 June 1961 by Bryce C. Brown and John Wottring by seining a drying pond.

Paratypes. SM(BCB) 11460-65, adult females, preserved whole, all topotypic (11461 photographed in H.M. Smith and R.B. Smith, 1980); and SM(BCB) 9823, adult male, preserved whole, from 9.7 km SW Viesca, also collected on 4 June 1961 by Brown and Wottring (see Figs. 22 and 24).

Diagnosis. A subspecies of *Kinosternon hirtipes* with: 1) enlarged head, hypertrophied head musculature, and broad alveolar jaw surfaces (Fig. 24); 2) the nasal scale furcate posteriorly; 3) the head pattern mottled or reticulated as in *K. h. murrayi;* 4) three to four pairs of chin barbels are present, two to three mental pairs (anterior usually the largest) and one small pair at level of anterior edge of tympanum; 5) small body size (maximum known size for males 99 mm CL; females, 117 mm); 6) plastron extremely reduced in size (Fig. 22); 7) relatively short bridge length (male $\bar{x}$ BL/CL, 17.3%; female $\bar{x}$, 23.9%); 8) relatively short gular length (male $\bar{x}$ GL/CL, 11.0%; female $\bar{x}$, 12.8%); 9) relatively short interanal seam length (male $\bar{x}$ IAN/CL, 15.9%; female $\bar{x}$, 20.9%); and 10) populations confined to southwestern Coahuila.

Remarks. This subspecies is known only from the type series. Field work in the area of the type locality (see MATERIALS AND METHODS) suggests that *K. h. megacephalum* is now extinct; natural permanent water habitats apparently no longer exist near Viesca. Future field work should be concentrated in the mountains south of the city of Viesca in hope of discovering permanent water situations where turtles (and fishes?) might still exist.

The distinctive trophic apparatus of this subspecies is likely an adaptation to stenophagous molluscivory.

Range. Known only from the two localities in Coahuila at which the type series was collected.

Etymology. The subspecific name *megacephalum* is from the Greek *mega,* meaning large, and *kephale,* meaning head, and refers to the enlarged head, diagnostic of the subspecies.

Kinosternon hirtipes **tarascense** ssp. nov.

Pátzcuaro Mud Turtle

Kinosternon hirtipes Altini, 1942:153 (in part; Lake Pátzcuaro, Michoacán).

Kinosternon hirtipes hirtipes Duellman, 1961:57, 1965:653 (in part; Lago de Pátzcuaro, Michoacán); Casas Andreu, 1967:45 (in part; Pátzcuaro, Canal de la Tzipecua, Michoacán).

Holotype. UF 43506, adult male, preserved whole, from Lago de Patzcuaro, adjacent to city of Pátzcuaro [19°32'N, 101°36'W]; purchased in Pátzcuaro market 13 June 1978 by John B. Iverson.

Paratypes. All topotypic and preserved whole: UF 43505 and 43596, adult females; and UF 43507 and 43595, adult males.

Diagnosis. A subspecies of *K. hirtipes* with: 1) a typically finely mottled to spotted head (Fig. 24); 2) variable red-brown to brown staining on the otherwise light yellow plastral scutes [The dark plastral scutes are apparently a result of natural staining; the character is exhibited to variable degrees by individuals and the dark color is lost when plastral scutes are shed (Fig. 22)]; 3) the large nasal scale posteriorly furcate; 4) two pairs of mental chin barbels typically present; 5) small to medium body size (maximum known size for males 136 mm CL; females, 132 mm); 6) relatively short bridge length (male $\bar{x}$ BL/CL, 18.0%; female $\bar{x}$, 21.4%); 7) relatively short gular length (male $\bar{x}$ GL/CL, 10.6%; female $\bar{x}$, 12.6%); 8) relatively long interpectoral seam length (male $\bar{x}$ IP/CL, 10.1%; female $\bar{x}$, 8.5%); and, 9) populations confined to the Lago de Pátzcuaro drainage basin.

Remarks. Despite considerable study of other components of the biota of the Lago de Pátzcuaro (see review in Cole, 1963 and Barbour, 1973), the mud turtles have been ignored. Reproductive information resulting from my studies appears in Table 2.

Range. Known only from the basin of the Lago de Pátzcuaro, Michoacán.

Specimens examined and Additional Records. See locality list.

Etymology. The subspecies name *tarascense* honors the native tribe of Indians, the Tarascas, inhabiting the Pátzcuaro area.

Kinosternon hirtipes magdalense ssp. nov.

San Juanico Mud Turtle

Holotype. UF 45035, an adult male, preserved whole, from along the face of the dam at *Presa* San Juanico, Michoacán [ca. 19°50'N, 102°40'W] (Fig. 28). Holotype collected 15 June 1978 by John B. Iverson, Peter A. Meylan, and Ron Magill.

Paratypes. UF 45036, a subadult female, UF 45038, female shell; UF 45039-40, male shells, all topotypic; and TUL 18677, adult male, collected atop *Presa* San Juanico 9 August 1963 by Clyde D. Barbour and Salvador Contreras-Balderas.

Diagnosis. A subspecies of *Kinosternon hirtipes* with: 1) a finely mottled to spotted head pattern with jaw streaking minimal or absent; 2) a large nasal scale, furcate behind; 3) two pairs of mental chin barbels present; 4) small body size (maximum known male size 94 mm CL; female, 91 mm); 5) a relatively small plastron (male $\bar{x}$ PWB/CL, 41.9%; female $\bar{x}$, 43.5%); 6) relatively short bridge length (male $\bar{x}$ BL/CL, 18.5%; female $\bar{x}$, 19.7%); 7) relatively short gular length (male $\bar{x}$ GL/CL, 9.9%; female $\bar{x}$, 11.0%); 8) relatively long interpectoral seam length (male $\bar{x}$ IP/CL, 8.7%; female $\bar{x}$, 11.0%); and, 9) populations restricted to the Magdalena Valley, Michoacán.

Remarks. As mentioned earlier (MATERIALS AND METHODS), the turtles inhabiting the *Presa* San Juanico are poorly known. Future field work in the area should help delimit the subspecific range within the Magdalena Valley and also provide basic natural history information.

Range. Kinosternon hirtipes magdalense is known only from the type series, all from the reservoir above *Presa* San Juanico in the Magdalena Valley of Michoacán, Mexico.

Etymology. The subspecific name *magdalense* refers to the Magdalena Valley of Michoacán to which the subspecies is apparently endemic.

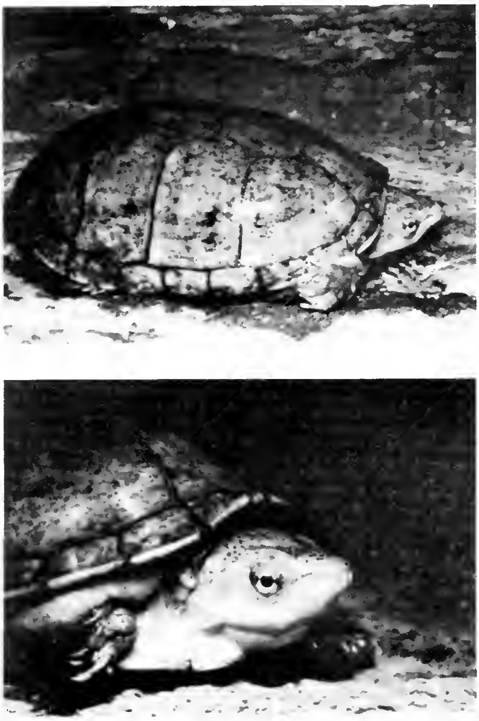

Figure 28. Holotype (UF 45035) of *Kinosternon hirtipes magdalense.*

EVOLUTION

Based on the derived characters of the turtles of the *Kinosternon hirtipes* species group (Table 3), I have constructed a phylogeny of the included taxa (Fig.29). For reasons discussed by Farris (1966) and Kluge and Farris (1969) (e.g., high intrafamilial variation and indiscrete character shifts), I have not always assumed that taxa sharing derived *morphometric* characters are closely related. In fact, the distribution of some character states among taxa clearly indicates that those characters are not a result of single origin, but rather of convergence. For example, the lengthening of the interanal seam in *K. sonoriense (longifemorale)* and *K. hirtipes (hirtipes* and *chapalaense)* certainly illustrates multiple origin of a derived character state. In addition, Viesca *(megacephalum),* Pátzcuaro *(tarascense),* and San Juanico turtles *(magdalense)* all share a relatively short bridge (with Valley of Mexico turtles), a short gular, and small body size (the latter two also share a long interpectoral seam), yet geographically and zoogeographically (Iverson, in preparation) the three populations likely do not represent a monophyletic divergence from a pre-*murrayi* stock. Rather, the evolution of these character states is more likely a response to selection in similar, very narrow adaptive zones (i.e., isolated, *very* small basins). Unfortunately, the functional significance of those characters is unknown, as is that of most of the other characters herein examined (but see Iverson, MS 2)

Table 3. Tally of subspecific taxa exhibiting derived character states in the *Kinosternon hirtipes* species group. Primitive states are discussed in the text.

	Derived Character	Taxa exhibiting derived character
1	small plastron	*magdalense, megacephalum*
2	short bridge	*magdalense, tarascense, hirtipes, megacephalum*
3	short gular	*magdalense, tarascense, megacephalum*
4	long gular	*sonoriense* and *longifemorale*
5	long interpectoral	*magdalense, tarascense*
6	short interpectoral	*sonoriense, longifemorale*
7	short interfemoral	*hirtipes*
8	long interanal	*chapalaense, hirtipes, longifemorale*
9	short interanal	*megacephalum*
10	V-shaped nasal	*murrayi, magdalense, tarascense, megacephalum, chapalaense*
11	reduced nasal	*chapalaense*
12	multiple, long chin barbels	*sonoriense, longifemorale*
13	reduced head pigment	*chapalaense*
14	well-developed head stripes	*hirtipes*
15	large head	*megacephalum*
16	female > male	*sonoriense, longifemorale* (possibly *tarascense, megacephalum*)
17	small body size	*magdalense, tarascense, megacephalum*
18	tendency toward unicarination	*murrayi, hirtipes, magdalense, tarascense, megacephalum, chapalaense*

The *Kinosternon hirtipes* species group apparently evolved on the Mexican Plateau from an ancestor as yet unknown. Despite the fact that several coastal streams have come to drain the Plateau due to headwater stream erosion (e.g., Ríos Yaqui, Mezquital, Santiago, Balsas; see Fig. 4), *K. hirtipes* has nowhere left the Plateau. This is surprising since *K. integrum* has apparently moved both up and down several of these basins (Balsas, Santiago-Lerma, and Mezquital; Iverson, unpublished). *K. sonoriense* apparently evolved from a *K. hirtipes*-like ancestor isolated in the Sonoran Desert, possibly following migration across the well-documented Sonora Desert-Chihuahua Desert filter barrier in southeastern Arizona, southwestern New Mexico and adjacent Mexico (see review in Morafka, 1977). Because so much geological information concerning the Mexican Plateau is now available (see reviews in Barbour, 1973 and Wauer and Riskind, 1978), a discussion of the historical zoogeography of the *K. hirtipes* species group will appear elsewhere (Iverson, in preparation).

The relationship between the *Kinosternon hirtipes* species group and other *Kinosternon* is unclear. Siebenrock (1907:551) included *K. hirtipes* and *K. sonoriense, K. baurii, K. subrubrum, K. flavescens,* and *K. steindachneri (= K. subrubrum)* in the *K. subrubrum* species group. However, I believe that *K. baurii* and *K. subrubrum* (including *steindachneri)* represent a species group distinct from the *K. hirtipes* group, and that *K. flavescens* is similarly distinct. Perhaps the closest relative of the *hirtipes* group is *K. herrerai* (found in the Tampico Embayment of eastern Mexico; i.e., non-Plateau), which shares with most *K. hirtipes* the elevated scale patches on the hindlegs of males, the tendency toward unicarination in adults, the furcate nasal scale, the reduced plastron, the broad inguinal-axillary contact, and several morphometric plastral characters. Unfortunately, the determination of the phylogenetic relationship of the *K. hirtipes* group to the other species groups in the genus must await further analysis.

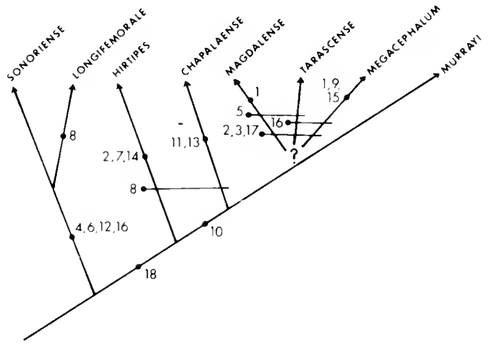

Figure 29. A theory of relationships among the subspecific taxa of the *Kinosternon hirtipes* species group. Numbers refer to derived character states listed in Table 3. Solid lines cutting lineages mark identical shifts (convergence) in character states.

KEY TO ADULT TURTLES OF THE *Kinosternon hirtipes* SPECIES GROUP

1A. Nasal shield triangular, rhomboidal, or bell shaped; largest 2 pairs of chin barbels relatively long (at least one pair > half orbit diameter, with one pairmental and other at mid-tympanum level); interpectoral length averages 5.0% of plastron length in males (less than 8% in 95% of cases) and 4.0% in females (less than 7% in 96% of cases); posterior width of plastral forelobe (PWB) averages 47.2% of carapace length in males (more than 44% in 95% of cases) and 49.0% in females (more than 45% in 96% of cases); maximum gular width averages 19.7% of carapace length in males (more than 18% in 94% of cases) and 19.1% in females (more than 17% in 94% of cases); first neural bone often (38.1%) in contact with nuchal bone; northwestern Chihuahua and Sonora, Mexico and adjacent New Mexico, Arizona and California .... *Kinosternon sonoriense*..............2

1B. Nasal shield large and deeply notched posteriorly (V-shaped), or reduced to crescent-shaped scale lying fully anterior to level of orbits, or triangular, rhomboidal, or bell shaped if from Valley of Mexico; largest 2 pairs of chin barbels relatively short (< half orbit diameter), mentally located, with anterior pair larger; interpectoral length averages 8.2% of plastron length in males (more than 4.5% in 97% of cases); and 6.6% in females (more than 3.5% in 94% of cases); posterior width of plastral forelobe (PWB) averages 42.8% of carapace length in males (less than 48% in 98% of cases) and 47.6% in females (less than 51% in 95% of cases); maximum gular width averages 17.3% of carapace length in males (less than 20% in 98% of cases) and 17.0% in females (less than 20% in 98% of cases); first neural rarely (10.2%) in contact with nuchal; Chihuahua, Mexico and adjacent Texas southward to Jalisco, Michoacán, and México, México (state)....................*Kinosternon hirtipes*.......3

2A. Interanal seam length averages 19.5% of carapace length in males (more than 16.5% in 97% of cases) and 23.0% in females (more than 21% in 90% of cases); interfemoral seam length averages 10.1% of carapace length in males (less than 13% in 93% of cases) and 10.1% in females (less than 12.5% in 95% of cases); maximum first vertebral width averages 24.4% of carapace length in males (less than 28% in 97% of cases) and 25.5% in females (less than 28% in 90% of cases); and gular width averages 20.0% in males (more than 18.5% in 93% of cases) and 19.4% in females (more than 17.5% in 90% of cases); Bill Williams, lower Colorado, Gila, Sonora, Magdalena, Yaqui, southwest New Mexico, and Casas Grandes basins......*K. s. sonoriense*

2B. Interanal seam length averages 14.4% of carapace length in males (less than 16% in 90% of cases), and 18.5% in females (less than 22% in 100% of cases); interfemoral seam length averages 12.8% of carapace length in males (more than 10% in 100% of cases) and 13.5% in females (more than 11.5% in 91% of cases); maximum first vertebral width averages 28.9% of carapace length in males (more than 28% in 90% of cases) and 28.8% in females (more than 26% in 100% of cases); and gular width averages 17.7% of carapace length in males (less than 19% in 100% of cases) and 17.8% in females (less than 20% in 100% of cases); Río Sonoyta basin, Arizona, and Sonora, Mexico...............................*K. s. longifemorale*

3A. Nasal shield reduced to crescent-shaped scale lying anterior to level of orbits; dark reticulate head markings reduced or nearly absent; plastral width at humero-pectoral seam (PWA) averages 33.3% of carapace length in males (less than 35.5% in 100% of cases) and 37.0% in females (less than 40% in 93% of cases); bridge length averages 20.3% of carapace length in males (over 18% in 100% of cases) and 25.3% in females (more than 22% in 100% of cases); gular length averages 11.8% of carapace length in males (less than 13% in 93% of cases) and 14.5% in females (less than 18.5% in 100% of cases); forelobe length averages 30.5% of carapace length in males (less than 33.5% in 100% of cases) and 31.8% in females (less than 34% in 100% of cases); interhumeral seam length averages 14.0% of maximum plastron length in males (more than 12% in 93% of cases) and 12.7% in females (more than 10% in 88% of cases); interabdominal seam length averages 28.6% of maximum plastron length in males (more than 26% in

93% of cases) and 29.3% in females (more than 25.5% in 100% of cases); Lake Chapala and Lake Zapotlán basins, Michoacán and Jalisco, Mexico..........................
....*Kinosternon hirtipes chapalaense*

3B. Nasal shield large and deeply notched posteriorly, triangular, rhomboidal or bell shaped; head with abundant dark head markings; plastral width at humero-pectoral seam (PWA) averages 36.1% of carapace length in males (more than 32.5% in 98% of cases) and 38.1% in females (more than 35% in 97% of cases); bridge length averages 19.9% of carapace length in males (less than 22% in 95% of cases) and 23.4% in females (less than 26% in 93% of cases); gular length averages 14.6% of carapace length in males (more than 12% in 95% of cases; excluding turtles from Pátzcuaro, San Juanico, Cuitzeo, and Viesca basins) and 15.6% in females (more than 12.5% in 97% of cases; excluding turtles from Pátzcuaro, San Juanico, Cuitzeo, and Viesca basins); forelobe length average 31.2% of carapace length in males (more than 28.5% in 100% of cases) and 34.4% in females (more than 30% in 98% of cases); interhumeral seam length averages 11.8% of maximum plastron length in males (less than 15% in 90% of cases) and 12.6% in females (less than 17% in 96% of cases); interabdominal seam length averages 28.1% of maximum plastron length in males (less than 31% in 96% of cases) and 28.0% in females (less than 31% in 95% of cases); Chihuahua, Mexico and adjacent Texas southward to Jalisco, Michoacán, and México, México, except Chapala and Zapotlán basins..........................4

4A. Gular length averages 10.5% of carapace length in males (less than 13% in 100% of cases) and 12.4% in females (less than 14% in 93.0% of cases); plastron width at humero-pectoral seam (PWA) averages 34.6% of carapace length in males (less than 38% in 100% of cases) and 35.9% in females (less than 38% in 93% of cases); posterior width of plastral forelobe (PWB) averages 42.5% of carapace length in males (less than 45.6% in 100% of cases) and 45.8% in females (less than 47.5% in 88% of cases); anterior width of plastral hindlobe (PWC) averages 39.3% of carapace length in males (less than 43% in 100% of cases) and 42.8% in females (less than 46% in 93% of cases); maximum carapace length 140 mm in males, 135 mm in females; Pátzcuaro, San Juanico, and Viesca basins......
populations with small plastron....5

4B. Gular length averages 14.8% of carapace length in males (more than 12% in 94% of cases) and 15.9% in females (more than 13% in 94% of cases); plastron width at humero-pectoral seam (PWA) averages 36.2% of carapace length in males (more than 33% in 97% of cases) and 38.3% in females (more than 35.5% in 96% of cases); posterior width of plastral forelobe (PWB) averages 42.9% of carapace length in males (more than 39% in 94% of cases) and 47.6% in females (more than 45% in 94% of cases); anterior width of plastral hindlobe (PWC) averages 38.0% of carapace length in males (more than 34% in 96% of cases) and 43.2% in females (more than 40% in 97% of cases); maximum carapace length 185 mm in males, 160 mm in females; Chihuahua and Texas to Jalisco, Michoacán, and Mexico, except Chapala, Zapotlán, Pátzcuaro, San Juanico, and Viesca basins.......populations with large plastron..........7

5A. Head enlarged, jaws with extremely broad alveolar surfaces; carapace width averages 61.9% of carapace length in males (less than 65% in 100% of cases) and 68.1% in females (less than 71.5% in 100% of cases);

plastral forelobe length averages 28.7% of carapace length in males (less than 30% in 100% of cases) and 29.0% in females (less than 30.5% in 100% of cases); plastral width at femoro-anal seam (PWD) averages 28.2% in males (less than 29% in 100% of cases) and 31.4% in females (less than 32.5% in 100% of cases); interpectoral seam length averages 6.8% of carapace length in males (less than 8% in 100% of cases) and 4.8% in females (less than 6.5% in 100% of cases); bridge length averages 17.3% of carapace length in males (less than 17.5% in 100% of cases) and 23.9% in females (more than 23% in 100% of cases); Viesca area, Coahuila. . . . . *K. h. megacephalum*

5B. Head not enlarged, jaws with narrow alveolar surfaces; carapace width averages 72.0% of carapace length in males (more than 65% in 100% of cases) and 72.7% in females (more than 66.5% in 100% of cases); plastral forelobe length averages 31.2% of carapace length in males (more than 29.5% in 100% of cases) and 33.3% in females (more than 30.5% in 100% of cases); plastral width at femoro-anal seam (PWD) averages 29.1% in males (more than 28% in 100% of cases) and 34.0% in females (more than 31% in 100% of cases); interpectoral seam length averages 9.6% of carapace length in males (more than 8% in 100% of cases) and 8.9% in females (more than 6% in 100% of cases); bridge length averages 18.2% of carapace length in males (more than 16% in 100% of cases) and 20.9% in females (less than 23.5% in 100% of cases); Pátzcuaro and/or San Juanico basins, Michoacán 6

6A. Plastral scutes usually immaculate, not darkly stained; maximum plastral hindlobe length averages 30.1% of carapace length in males (less than 32% in 100% of cases) and 31.5% in females (less than 33% in 100% of cases); plastral width at humero-pectoral seam (PWA) averages 33.7% of carapace length in males (less than 38% in 100% of cases) and 34.8% in females (less than 36% in 100% of cases); posterior width of plastral forelobe averages 41.9% of carapace length in males (less than 43% in 100% of cases) and 43.5% in females (less than 45.5% in 100% of cases); interpectoral seam length averages 10.3% of maximum plastron length in males (less than 12% in 100% of cases) and 12.3% in females (more than 11.5% in 100% of cases); first vertebral scute width averages 22.3% of carapace length in males (less than 23.5% in 100% of cases) and 21.4% in females (less than 22.5% in 100% of cases); San Juanico basin, Michoacán. . . . . *K. h. magdalense*

6B. Plastral scutes often stained red-brown to dark brown; maximum plastral hindlobe length averages 31.3% of carapace length in males (more than 29% in 100% of cases) and 34% in females (more than 32% in 100% of cases); plastral width at humero-pectoral seam (PWA) averages 35.4% of carapace length in males (more than 33.5% in 100% of cases) and 36.8% in females (more than 35% in 100% of cases); posterior width of plastral forelobe averages 43.6% of carapace length in males (more than 41% in 100% of cases) and 46.8% in females (more than 43.5% in 100% of cases); interpectoral seam length averages 11.7% of maximum plastron length in males (more than 9% in 100% of cases) and 9.1% in females (less than 12% in 100% of cases); first vertebral scute width averages 22.9% of carapace length in males (more than 20.5% in 100% of cases) and 24.5% in females (more than 22% in 100% of cases); Lake Pátzcuaro basin, Michoacán. . . . . *K. h. tarascense*

7A. Nasal scale triangular, rhomboidal, or bell shaped; maximum plastron length averages 86.4% of carapace length in males (less than 90.5% in 100% of cases) and 91.6% in females (less than 94% in 100% of cases); bridge length averages 17.6% of carapace length in males (less than 19.5% in 100% of cases) and 21.7% in females (less than 23% in 94% of cases); interabdominal seam length averages 22.7% of carapace length in males (less than 23.5% in 100% of cases) and 24.3% in females (less than 26% in 94% of cases); interfemoral seam length averages 6.9% of carapace length in males (less than 8.5% in 100% of cases) and 7.1% in females (less than 8.5% in 100% of cases); interanal seam length averages 20.6% of carapace length in males (more than 19% in 100% of cases) and 25.8% in females (more than 23.5% in 100% of cases); Valley of Mexico............... *K. h. hirtipes*

7B. Nasal scale deeply notched posteriorly (V-shaped); maximum plastron length averages 86.0% of carapace length in males (more than 81% in 95% of cases) and 92.6% in females (more than 88% in 96% of cases); bridge length averages 20.0% of carapace length in males (more than 18% in 97% of cases) and 23.7% in females (more than 21% in 95% of cases); interabdominal seam length averages 24.2% of carapace length in males (more than 21.5% in 98% of cases) and 26.0% in females (more than 23% in 96% of cases); interfemoral seam length averages 9.0% of carapace length in males (more than 6% in 98% of cases) and 9.0% in females (more than 6% in 99% of cases); interanal seam length averages 18.6% of carapace length in males (less than 22% in 95% of cases) and 23.4% in females (less than 26% in 93% of cases); Chihuahua and Texas south to Michoacán, Jalisco, and México.............. *K. h. murrayi*

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RESUMEN

Se analizaron las variaciones geograficas del escudo y las medidas de las conchas (mediante analisis estadístico multivariado), tamaño del cuerpo, morfologia de las escamas de la cabeza y del menton, tamaño del primer hueso neural, escamación irregular, asi como tamano de la cabeza y los patrones de poblaciónes de la especie *Kinosternon hirtipes*. Los resultados sustentan la retención de las especies alopátricas *K. sonoriense* y *K. hirtipes* como especies completas dentro del grupo, y el reconocimiento de dos subespecies alopatricas (una de ellas nueva) de *K. sonoriense* y de seis subespecies (cuatro de ellas nuevas y todas aparentemente alopátricas) de *K. hirtipes*. La descripción de cada taxon incluye datos completos de sinonimias, ecología y reproducción. También estan incluidas claves para adultos y una discusion de todos los taxa.

SPECIMEN LIST

All specimens examined as well as localities plotted in Figure 1 are listed below by drainage basin sample used in the analysis. Basins are listed under the appropriate taxon in approximate geographic order from northwest to southeast. Localities (including literature records) within each basin are listed alphabetically by state, county, and specific locality. Specimens marked with an asterisk were not examined. All distances are in km. The following abbreviations are used throughout the list: C = city or ciudad; Cn = canyon; Cr = creek; Hwy = highway; Mtn(s) = mountain(s); nr = near; R = river or río; Rd = road; Spg(s) = spring(s); trib = tributary; and vic = vicinity.

K. sonoriense sonoriense.

BILL WILLIAMS (BIG SANDY) RIVER *(WILL)*.

ARIZONA. Mojave Co.: Big Sandy Basin, NW Wickenburg, UAZ 30826*; Burro Cr Campground, ASU 13785; 14.5 km E Burro Cr Campground, ASU 13786; Trout Cr (Hulse, 1974).

GILA and LOWER COLORADO RIVERS *(GILA)*.

ARIZONA. Cochise Co.: Babacomari R, ca. 4.8 km W Huachuca C, UAZ 38861*; Bear Cn, 16.1 km W Coronado International Memorial, ASU 13783*; Bear Cn, Huachuca Mtns, Montezema Pass Rd, UAZ 27982*; Fort Huachuca, first cienega above post, USNM 17780-81*, 19680*, 21718-19*, 45305* (Stejneger, 1902); nr Hereford, San Pedro R, KU 15927*, CAS-SU 48886-87*; Huachuca Mtns, AMNH 19450, USNM 20975-77*, 20979-80* (Van Denburgh and Slevin, 1913; Van Denburgh, 1922); Lewis Spgs, AMNH 15165-69, 18103, 18656-57, UMMZ 118269; 3.2 km S Miller's Peak, Huachuca Mtns, Cochise Cn, CAS-SU 13888*; Pyeatt Ranch nr West Gate Fort Huachuca, JBI 410-14; San Pedro R, USNM 20547-55*; San Rafael Valley, UMMZ 88476*; Hwy 80 at St. David (Kauffeld, 1943); Vasquez Ranch, St. David, UAZ 32960*. Gila Co.: Cibecue Cr nr Salt R, ASU 10530* (Hulse, 1974); Coyote Cn, ASU 10903-04* (Hulse, 1974); 66 km NNE Globe, Salt R, UMMZ 105791 (Duellman, 1955); Mezquite Flat at Salt R, ASU 10527-29* (Hulse, 1974); Natural Spgs, just N Payson (J. F. Berry, pers. comm.); Payson, ASU 4142*; 4.8 km N Punkin Center on Tonto Creek, ASU 12061-68*; Rice, San Carlos Indian Reservation, USNM 59738*; Roosevelt Reservoir (Little, 1940); San Carlos River, N San Carlos, UMMZ 105821 (Duellman, 1955); Spring Cr, 16.1 km W Young, UMMZ 105756 (Duellman, 1955); Tonto Cr nr Gisela, ASU 2372* (Hulse, 1974, 1976). Graham Co.: Bonita Cr, NE of Safford, UMMZ 105792 (Duellman, 1955); Marijilda Cr (Nickerson and Mays, 1971); 8.0 km S Safford (Nickerson and Mays, 1971); 9.7 km S Safford, UMMZ 105765, 105293 (Duellman, 1955); no further data, USNM 55627-28 (Van Denburgh, 1922 as *K. flavescens;* Iverson, 1978). Greenlee Co.: Virden, 1.6 km W New Mexico State line, UNM 15561. Maricopa Co.: Agua Caliente, CAS-SU 39102*; Box Cn, 8.0 km N Wickenburg (Gates, 1957); Cave Cr, CAS-SU 17282*, KU 15926*, UAZ 35948*; Cave Cr, Fairbank, CAS-SU 20643*, 35157* (Van Denburgh and Slevin, 1913; Van Denburgh, 1922); Granite Reef Dam, ASU 4549*; Guadalupe, ASU 1972*; Hassayampa R, 8.0 km S Wickenburg, CHAS 16177 (Gates, 1957); Hassayampa R, 8 km SE Wickenburg, UIMNH 85839, 85842; Mesa, ASU 336*; Phoenix, AMNH 73821-22*, ASU 4268*, UMMZ 69417-20, 72497, USNM 55625-26* (Van Denburgh, 1922); Phoenix, Salt R, KU

2908, UMMZ 15755*, USNM 15755* (Iverson, 1978); 48.3 km SW Phoenix, Gila R, KU 15928*, Sycamore Cr at Sunflower, ASU 13801-03*, CM 57121, 57113-14 (Hulse, 1974, 1976); Sycamore Cr at Hwy 87, ASU 12105*; Sycamore Cr, 1.6 km S. Sunflower, UU 11537-39*; Tempe, ASU 1004*. Navajo Co.: Fort Apache (Hulse, 1974); Rock Cr Cn, S. Camp Apache, USNM 1103* (Yarrow 1875 as *K. henrici;* Van Denburgh, 1922). Pima Co.: Annilo Tank, R17E, T14S, Sec 3, NE ¼, UAZ 36510*; Arivaca, 0.8 km SW of Post Office, UAZ 30821, 30823; 0.8 km E Arivaca, UAZ 30824; Madrona Cn, Rincon Mtns, UAZ 27985*, 36512*, FB 1551; Molina Basin, Santa Catalina Mtns, UAZ 27998*; Posta Quemada Cn, SE side Rincon Mtns, UAZ 24753*; Rincon Mtns, end of Kennedy Rd via Speedway, UAZ 30825*; Rincon Stock Farm, nr Tucson, UMMZ 89871-73; Sabino Cn, Santa Catalina Mtns, CAS-SU 8637-38*, FMNH 74777, SDNHM 14225, UAZ 27997* (Van Denburgh and Slevin, 1913; Van Denburgh, 1922); Santa Catalina Mtns, AMNH 4520; Tanque Verde Ranch, SDNHM 16232-37; Tucson, Santa Cruz R, AMNH 2565, 20538, CAS-SU 33850-66*, MCZ 1920, USNM 67*, 17018-21*, 16835-36* (LeConte, 1854; Agassiz, 1857; Baird, 1859; Yarrow, 1883; Gunther, 1885; Van Denburgh and Slevin, 1913; Van Denburgh, 1922); Tucson Sewage Disposal Area, UAZ 28002*; nr Xavier, 16.1 km S Tucson, CM 19287. Pinal Co.: Boyce Thompson SW Arboretum, 6.4 km W Superior, AMNH 66336, CHAS 9494-97, 9644, 9648, 10324, UMMZ 85076 (14 specs); Queen Cr, Arboretum, CHAS 9879-80, 13634-44; Superior, CHAS 10325, UAZ 27994-95*. Santa Cruz Co.: Alamo Cn, 4.0 km SW Pena Blanca Camp, Pajarito Mtns, MVZ 50903-06, UAZ 15104*; Babacomari R at Babacomari Ranch, ASU 12107-113*; G. A. Jones Ranch at Parker Cn, UAZ 27986*; Lochiel, ASU 13804*; Monkey Spg, ASU 12077*; Nogales, USNM 17127-36*, ASU 13787* (Van Denburgh, 1922); 19.3 km W Nogales, CM 25209; 6.8 km S Patagonia on Hwy 82, LACM 64223; Pena Blanca Spg, TUL 15040-41, UMMZ 75814, 75855 (Campbell, 1934); Santa Rita Mtns, CAS-SU 48885* (Van Denburgh, 1922); SW of Tucson, AMNH 2559-62, UMMZ 118268; Tumacacori Mtns, SDNHM 5720, CAS-SU 81457-58*; Turkey Cr at Canelo, UAZ 27988*. Yavapai Co.: Bard, SDNHM 33866; 12.9 km S Camp Verde, SDNHM 17889; 4.8 km N Clarksdale, Verde R, UU 15078-84*; Ft. Verde, USNM 14807-09, 15708 (Van Denburgh, 1922 as *K. flavescens* and *K. sonoriense;* Iverson, 1978); Fossil Cr, 9.7 km N Verde R, ASU 12151-56* (Hulse, 1974); Hassayampa R at Wagoner, CHAS 16631; Hassayampa R, 3.2 km S Wagoner, CHAS 15834; Montezuma's Well, ASU 4573*, UU 13031*; Peck's Lake, NE Clarksdale, JBI 386-88; Rock Spgs, CM 47751, MSU 3578; Stehr Lake, ASU 13790*; Sycamore Cr, E of Dugas, UMMZ 105822 (Duellman, 1955); Sycamore Cr at Verde R, ASU 12074-76*; Tule Stream, ASU 10962-67*, CM 57115, 57122 (Hulse, 1974, 1976); Entrance to Tuzigoot National Monument, ASU 13789*; Verde R, above Camp Verde, UMMZ 105823* (Duellman, 1955); Verde R in Cottonwood, JBI 524. Yuma Co.: Gila C, Gila R, USNM 21716-17*, 21817*; Gila R, Adonde Siding, USNM 21715* (Van Denburgh, 1922); North Gila East Main Canal, 1.6 km SW Laguna Dam, RSF 468* (Funk, 1974); Warshaw, Mex. Boundary line, USNM 21712-14*; Yuma (Van Denburgh and Slevin, 1913; Van Denburgh, 1922).

CALIFORNIA. Imperial Co.: Palo Verde, MVZ 6282 (Van Denburgh, 1922); No further data, CAS-SU 33408 (Van Denburgh and Slevin, 1913; Van Denburgh, 1922).

NEVADA. Clark Co.: Pyramid Cn (LaRivers, 1942, as *K. flavescens,* but see Iverson, 1978).

NEW MEXICO. Catron Co.: Glenwood, San Francisco R, CM 18310; Taylor Cr, 2.4 km NE Wall Lake, UMMZ 134282-84, UNM 2568 (Niles, 1962); Wall Lake, 13.7 rd km SSE Beaverhead, UMMZ 134281, UNM 20552, 20609-10 (Niles, 1962). Grant Co.: Bennett Ranch, W Cliff, UNM 8157-69; 3.2 km ENE Cliff (Niles, 1962); 1.6 km E Bedrock Post Office, S side Gila R, UNM 20611. Undetermined Co.: Gila R, ANSP 83 (holotype of *Kinosternum henrici).*

SONORA. R Nutrias, above Nutrias Dam, UMMZ 105817; R San Pedro, above Elias Dam, UMMZ 105816, 105818-20; R Santa Cruz, 6.4 km S Arizona border, UMMZ 105814-15; San Pedro R, USNM 20968 (Van Denburgh, 1922); Sierra Magallones, UAZ 36497*.

SW NEW MEXICO INTERIOR DRAINAGES *(SWNM).*

ARIZONA. Cochise Co.: N of Rodeo, nr New Mexico border, UMMZ 86081-86 (Niles, 1962).

NEW MEXICO. Hidalgo Co.: Clanton Cn, 16.1 km N Cloverdale, LACM 7967-70, 7994; 8 - 9.7 km W Cloverdale Store, UNM 20558; Guadalupe Cn, 3.1 km E, 2.3 km N Arizona-New Mexico border, UNM 14061; W slope Peloncillo Mtns, T32S, R21W, Sec 16, NE ¼, UNM 15618; 24.1 km N Rodeo, San Simon Marsh, NMSU 3050*; San Simon Cienega, UMMZ 105800 (Niles, 1962); Skeleton Cn, Peloncillo Mtns, AMNH 109056, MVZ 70350.

RIO MAGDALENA *(MAGD)*.

ARIZONA. Santa Cruz Co.: California Gulch, ASU 13633-37*, CM 57116-20; Ruby, UIMNH 4129, UMMZ 107480 (Duellman, 1955); Sycamore Cn, UAZ 28000*, 30822*, 33582*.

SONORA. Imuris, UIMNH 85832; 14.5 km N Imuris, KU 44503-25; 14.5 km NNE Imuris, KU 48562-63, 50734*, 51429; 1.1 km S Magdalena, UAZ 28010; nr Magdalena, MCZ 46649*; 25.1 km NNE Magdalena, UMMZ 126442; 42 km S Nogales, Rancho de Tascara, AMNH 73004; 69.5 km S Nogales on Hwy, 2, LACM 61107; R Arizona, vic. Rancho de la Arizona, UAZ 28010-11; R Magdalena, 1.6 km SE Caborca, MVZ 51355 (Zweifel and Norris, 1955).

RIO SONORA *(SNRA)*.

SONORA. Arispe, UAZ 27976, 28003-07, 28012-14, 28016-18, 28020-21; 24.1 km W Cananea, AMNH 67503-05, 67507; 4.8 km downstream from Cucurpe, UAZ 36509; Hermosillo, AMNH 74945; 24.1 km N Hermosillo (Taylor, 1936); Cienega nr Rancho Agua Fria, E Cucurpe, JBI 799-803, 866-870; 16.1 km E Ures, R Sonora, NMSU 4101*.

RIO YAQUI. *(YAQ)*.

ARIZONA. Cochise Co.: Ashton Spg, nr San Bernardino Ranch, UAZ 28001*; Black Dam, San Bernardino Ranch, UAZ 27999*; Chiricahua Mtns, USNM 33929-30* (Van Denburgh, 1922); 8.0 km S McNeal on Hwy 666, LSU 9861; San Bernardino Ranch, 27.4 km E Douglas, CM 40407, ASU 13784*; San Bernardino Ranch, Mex. boundary, USNM 21104*; nr Turkey Cr Ranger Station, UMMZ 105675 (Duellman, 1955).

CHIHUAHUA. Bavispe R, below 3 Rivers, Chihuahua-Sonora border, BYU 14629; R Gavilan, 11.3 km SW Pacheco, MVZ 46646.

SONORA. Guadalupe Cn, nr Monument 72, Mex. boundary line, USNM 20970 (Agassiz, 1857; Baird, 1859; Yarrow, 1883; Van Denburgh and Slevin, 1913; Van Denburgh, 1922); 14.2 km W Maicova, UAZ 39968; Ranchito Pinos Altos, Sierra Nacori, UAZ 31613-14; San Bernardino Ranch, USNM 20981-88 (Van Denburgh, 1922). Yecora, UAZ 28211, 35209-11*; 18.0 km E Yécora, UAZ 40105.

RIO CASA GRANDES INTERIOR BASIN *(CSGR)*.

CHIHUAHUA. 3.2 km N Old Casas Grandes, BYU 14132-33; Colonia Juarez, R Piedras Verdes, FMNH 1873 (2), UNM 30393-99, UU 11522-36; 2.6 km NW Colonia Juarez, UF 47642-43, JBI 946-47; 10.5 km NW Colonia Juarez, ASU 5207-08*; Ramos, MVZ 46647-50.

RÍO FUERTE *(FRTE)*.

CHIHUAHUA. Cerocahui, BYU 14625, 14627, 14628 (see text).

QUESTIONABLE DATA.

JALISCO. 12.1 km N Magdalena, BYU 14630 (Tanner and Robison, 1960).

Kinosternon sonoriense longifemorale

RIO SONOYTA *(SNTA)*.

ARIZONA. Pima Co.: Quitobaquito Pond, JBI 391, 696-699, 701-706, UF 47719-20 (paratypes); Organ Pipe National Monument Collection (4 uncatalogued specimens), LACM 105399, SDNHM 47316, UAZ 27987 (paratypes,) 27993, 27996 (paratypes) (Stebbins, 1966).

SONORA. Sonoyta, USNM 21709-11 (paratype, holotype, and paratype, respectively); Sonoyta R, USNM 21725; Sonoyta R, 4.8 km from Sonoyta, USNM 21708 (Van Denburgh, 1922) (paratype); 29.0 km W Sonoyta on Hwy 2, LACM 105400.

Kinosternon hirtipes murrayi

RÍO SANTA MARÍA INTERIOR BASIN *(STMR)*.

CHIHUAHUA. Galeana, R Santa María, BYU 15266-76; nr Galeana, R Santa María, BYU 16846-47, UMMZ 117783-84 (Semmler et al, 1977); 4.8 km N and 3.2 km W Galeana, R Santa María, UU 4457-80, 12511; ca. 4.8 km SE Galeana, UAZ 36349*; 9.7 km NW Galeana, R Santa Maria, MCZ 62516-22; Ojo de Galeana, 7.2 km SE Galeana, ASU 5169-82*, 5185-95*, FB 1695*, 1844*, JBI 808-09, 815-20, 838-43, 850, 958-61, UAZ 27965-70*, 34766*, UF 40536-49, UNM 32600-12; outflow of Ojo de Galeana, 3.4 km S Galeana, ASU 5196-205*; nr Progreso, R Santa Maria, UMMZ 118284-89, USNM 105026-28, 105031-34; R Santa María, USNM 30841-43; San Buenaventura, below Presa El Tintero, R Santa María (Casas Andreu, 1967).

RÍO CARMEN (= SANTA CLARA) INTERIOR BASIN *(CRMN)*.

CHIHUAHUA. 3.2 km W Carmen, R Carmen, UU 8539-43; 1.6 km S and 0.8 km E Santa Clara, R Santa Clara, MVZ 72819-43, 89676-77; 3.2 km S Santa Clara, MVZ 70688-95; R Carmen at Ricardo Flores Magon, UMMZ 125362.

RÍO SAUZ INTERIOR BASIN *(SAUZ)*.

CHIHUAHUA. Arroyo El Sauz, El Sauz, UU 8549-53; 5 mi N Cerro Campana, MVZ 68915;

nr Encinillas, UMMZ 117781-82, 117785; Ojo Laguna, MVZ 70696-98; Sauz, FMNH 1405 (5); UMMZ 117426-29.

ALAMITO CREEK DRAINAGE. *(TEX).*

TEXAS. (See discussion in Conant and Berry, 1978). Presidio Co.: Casa Piedra, Willie Russell Ranch, DMNH 985, 1095-96; Marfa, USNM 15860 (paratype) (Glass and Hartweg, 1951) (data obviously in error; see Conant and Berry, 1978); 48.3 km S Marfa, Harper Ranch, USNM 198055; 59.5 km S Marfa, Harper Ranch, TCWC 650 (holotype) (Glass and Hartweg, 1951); 60.3 km SSE Marfa, UMMZ S1083, 101294 (paratypes) (Glass and Hartweg, 1951; Peters, 1952).

RÍO CONCHOS *(CNCH).*

CHIHUAHUA. Boquilla Culebra, UIMNH 52198 (Smith et al, 1963); 1.6 km N Camargo, UU 8548; 8 km N Camargo, UMMZ 118075; 20 km W Camargo, Arroyo del Vado o La Paloma, Presa La Boquilla (Casas Andreu, 1967); 27.4 km SW Camargo, UU 8469-89, 8490-98; 27.5 km SW Camargo, UIMNH 43528; R Catalina, 24.1 km N Villa Ocampo, Durango, UU 12758-59; 8 km N Chihuahua, MVZ 66121*; 8 km N Falomir, UIMNH 52199-201 (Smith et al, 1963); 0.8 km N Guadalupe Victoria, KU 51237-38*, 51259-60; Guardiola, UIMNH 52194-97 (H.M. Smith et al, 1963); 4.8 km S Hidalgo del Parral, UU 8468; 12.9 km SW Hidalgo del Parral, TCWC 20812; 4.8 km SW Jimenez, KU 53758-84; Julimes, ANSP 20106-08, UIMNH 52190-93, UU 8546-47 (Smith et al, 1963); 9.7 km NE La Boquilla, UNM 467; 0.8 km E La Cruz, KU 48259-62; 0.4 - 1.6 km E La Cruz, UIMNH 43511-27 (Williams et al, 1963); cited erroneously as Lago Toronto by Casas Andreu, 1967); Meoqui, R San Pedro, MVZ 52256; 8 km N and 8 km E Meoqui, KU 33903*; nr Ojinaga, AMNH 113858-59* (Conant and Berry, 1978); 1.6 km NW Ojinaga, KU 52159, 69849 (Legler, 1960); R San Pedro, 78.8 km SE Chihuahua, MVZ 57467; Mouth of R San Pedro, KU 51221-33, 51239-56, 51276, 51291-98, 51316-20, 52147-57, 56163-64, 9136572 (Legler, 1960); 1.6 km upstream from mouth of R San Pedro, KU 51234-36, 51257-58; 12.9 km SE Santa Barbara at Rafael, AMNH 6792325; Santa Rosalia, FMNH 5930 (2).

DURANGO. 4.8 km E Las Nieves, R Florido, MSU 3180-89.

LAGUNA BUSTILLOS INTERIOR BASIN *(BUST).*

CHIHUAHUA. 27.4 km N Cuauhtémoc, trib to Laguna Bustillos, UMMZ 125358-61.

RÍO PAPIGOCHIC DRAINAGE *(PAP).*

CHIHUAHUA. 8 km N, 1.6 km W Cd Guerrero, R Papigochic, KU 45020-25, 51425-26, 87854; El Riyito, 17.7 km WNW Cocomorachic, KU 51311, 51313-14; Minaca, FMNH 1102, MVZ 58967-70; 3.2 km W Minaca, KU 51261-309, 52142-43, 87853, 91364, 91373-78; 5.5 km NE Minaca, BYU 16848; Ríos Papigochic and Tomochic (Legler and Webb, 1970; erroneously recorded as *K. sonoriense* and *K. hirtipes hirtipes)*; Yepómera, FB 1545-46, 1595-97, JBI 403-404, MSU 3579, UAZ 34168*; 1.6 km N Yepómera, JBI 821-23, 835-37, UF 40389-400, UNM 32588-599; 3 km N Yepómera, UAZ 34169-70*; 3 km W Yepómera, MCZ 79029-38, 79039-46; 4 - 5 km N Yepómera, Arroyo de la Huachin, UAZ 34171-72*.

RIO NAZAS INTERIOR DRAINAGE *(NAZ).*

DURANGO. Lerdo, USNM 61687-88; 24.1 km SW Lerdo, AMNH 67496-500, UMMZ 118267; between Lerdo and La Goma, USNM 105262-64; R Nazas, at Cardenas Dam, nr El Palmito, JBI 826-31, UU 8461-66; 22.5 km NE Pedriceña UIMNH 19339; La Concha, nr Penon Blanco, AMNH 88883; Presa Francisco Zarco on R Nazas nr Graseros, ENCB 10893-94, JBI 948-50, UF 47602; Trib to R San Juan at Hwy 45, 5.6 km N turnoff to Primo Verdad, UU 12075-77; Rodeo, AMNH 87654-57, 96589; 13.5 km S San Jacinto, R Nazas, UF 40425-27; 16.1 km W Torreón, R Nazas, USNM 105270-71.

RÍO AGUANAVAL INTERIOR DRAINAGE *(AGUN).*

ZACATECAS. 24.1 km NW Fresnillo, R Florido AMNH 85285-91; 25.7 km N Fresnillo, UMMZ 118056-057, and 118060*; La Florida, R Florido, UU 12078-80; Rancho Grande, R Medina, AMNH 85296; 1.6 km N Rancho Grande, R Nieves, UU 8499-538, 8544-45; 17.7 km E Sombrerete, UIMNH 28155; 46.7 km E Sombrerete, UMMZ 126284.

LAGO SANTIAGUILLO INTERIOR DRAINAGE *(STGO).*

DURANGO. 22.5 km SE Chinacates, AMNH 88882; trib to Lago Santiaguillo, at bridge in Guatimape, UF 40428-30.

RÍO MEZQUITAL DRAINAGE *(MEZ).*

DURANGO. ca. 5 km from Colonia Hidalgo, km 937, Torreón-Durango Hwy (Casas Andreu, 1967); 4.8 km E Durango, AMNH 85294; 9.7 km E Durango, R Tunal, AMNH 85292-93; 10.5 km E Durango, R Tunal, UU 4481-520, 12512-15; 15.8 km N Durango, UIMNH 7051, 23844; 16.1 km N Durango, R Canatlan, MVZ 57333-35; 17.7 km E Durango on Hwy 45, TUL 18680; 17.7 km E Durango, R Santiago, MVZ 58222; 6.4 km E and 11.3 km S Durango, R Santiago, MSU 4245-56; 25.4 km SW Durango, R Chico on Hwy 40, LSU 34319, JBI 954-55, UF 47603-04; ENCB 10904-08; 27.4 km N Durango, CU 46115-16; 37 km N Durango, MSU 7869; kilometer 48.5, N of Durango, Hwy 45, UF 40424; nr Durango, 6.4 km E and 3.2 km NE jct. hwys to Torreón and Fresnillo, UMMZ 122245-54; 0.8 km N Graceros, KU 68733-36, 68738-45 (KU 68737 is *K. integrum*!); 6.4 km SW La Pila, KU 51083-84, MSU 2680-82, 2684, 2686-89, 10197-98; 9.7 km NW La Pila, KU 51085-86; R Mezquital, at Mezquital, 86.7 km SSE Durango, TUL 18670; 6.4 km S Morcillo, MSU 4243-44 (basis of Stebbins' 1966 southern Durango *flavescens* record; see Iverson, 1978); Ojo de Agua de San Juan, 1.6 km N Los Berros, UMMZ 129824-28; Otinapa, AMNH 68382; R La Sauceda at Hwy 40, ENCB 10894-903, JBI 825, 832-34, 951-53, UF 40401-23, UNM 32588-99; R Soledad, La Soledad, MSU 2683, 2685; 6.4 km S Villa Union jct. Hwy 45, CM 53987.

EL SALTO (ACAPONETA) BASIN *(SALT)*.

DURANGO. 9.7 km ENE El Salto, Hwy 40, ENCB 10909-14, JBI 956-57, LSU 34320, UF 47605-06.

RÍO SANTA MARÍA BASIN *(SLP)*.

SAN LUIS POTOSI. Laguna de las Rusias, LSU 7873-75 (Williams and Wilson, 1966); Arroyo la Hilada, ca. 1 km N *Presa* El Refugio (= Laguna de las Rusias), UF 42803-815.

RÍO AGUASCALIENTES DRAINAGE *(AGUAS)*.

AGUASCALIENTES. Aguascalientes, MCZ 79047; Aguascalientes, R Morcinique, MU 793; 2.1 km E Aguascalientes, UIMNH 43582; R Penuela nr Aquido, CAS-SU 19702-03; R Jocoque Dam, SE end *Presa* Jocoque, CAS-SU 19692-95; 1.2 km W Santiago, R Jocoque, CAS-SU 19696-701.

RÍO VERDE DRAINAGE *(VERD)*.

JALISCO. El Olivo, 19.3 km W Lagos de Moreno, AMNH 117953; Presa el Cuarenta nr Paso de Cuarenta, JBI 896-900, UF 44064-65, 44078; 3.2 km NE Valle de Guadalupe, trib to R Verde, Hwy 80, JBI 893-95, TUL 18671, UF 44077.

MARAVATIÓ BASIN *(MAR)*.

GUANAJUATO. 1.6 km SE Inchamacuaro, KU 43637.

BAJIO BASIN *(BAJ)*.

GUANAJUATO. No further data (Westphal-Castelnau, 1872); R Turbio, 12.9 km E Penjamo, UU 12081-82; R Lerdo, Valle de Santiago (Caballero y C. y Cerecero, 1943; Caballero y C., 1940a); 16.1 km N San Miguel de Allende, AMNH 93363; 22.5 km N San Miguel de Allende, AMNH 85295; Arroyo el Sauz, ca. 10.5 km N Yuriria-Salvatierra Hwy (Casas Andreu, 1967); Taboado, 9.7 km NW San Miguel Allende, AMNH 71033, FMNH 71029; Hwy 51, 6.0 km S jct. Hwys 51 and 110, UF 43613-15; 11.9 km S jct. Hwys 51 and 110 at Sebastian, UF 44074, JBI 908.

JALISCO. R Lerma, 0.8 km NW jct. Hwys 90 and 110, UU 12120.

LAKE CUITZEO INTERIOR BASIN *(CUIT)*.

MICHOACÁN. Lago Cuitzeo (Casas Andreu, 1967); Lake Cuitzeo, San Agustin, UMMZ 97136 (Duellman, 1961).

VILLA VICTORIA BASIN *(VILLA)*.

MEXICO. 11.3 km W Villa Victoria, USNM 108719-26, UMMZ 118295-296; 3.7 km S La Presa, JBI 928; 8.9 km S La Presa, JBI 927.

RÍO BALSAS DRAINAGES *(BALS)*.

MICHOACÁN. 8 km W C Hidalgo, AMNH 62257 (UIMNH 24707 from the same locality is *K. integrum*, not *K. hirtipes*, as listed in Duellman, 1961).

PUEBLA. Trib to R Atoyac, 4.5 km S Molcaxac, UU 2096 (Data questionable).

Kinosternon hirtipes megacephalum

VIESCA INTERIOR BASIN *(VCSA)*.

COAHUILA. 3.2 km SE Viesca, SM 11460-66 (paratypes and holotype); 9.7 km SW Viesca, SM 9823 (paratype).

Kinosternon hirtipes tarascense

LAGO PÁTZCUARO INTERIOR BASIN *(PATZ)*.

MICHOACÁN. Lago Pátzcuaro, FMNH 1397, 2036, JBI 880-84, UF 43505-07 (paratype, holotype, and paratype), 43595-96 (paratypes), UMMZ 96988-91, 97131, 99762, 117798 (Duellman, 1961); Lago Pátzcuaro, nr E end, UF 7075; Isla Janitzio, Lago Pátzcuaro, CU 16142; Canal de la Tzipecua, SW margin Lago Pátzcuaro (Casas Andreu, 1967); Tzintzuntzan, AMNH 82128.

Kinosternon hirtipes magdalense

SAN JUANICO (= MAGDALENA or TOCUMBO) VALLEY INTERIOR BASIN *(SNJ)*

MICHOACÁN. Atop Presa San Juanico (road to dam meets Hwy 15 ca. 56.3 km W of Zamora), TUL 18677 (paratype); *Presa* San Juanico, at dam, UF 45035-36 (holotype and paratype), 45038-40 (paratypes), and 45041.

Kinosternon hirtipes hirtipes

VALLEY OF MEXICO *(VALLE)*

DISTRITO FEDERAL. Mexico C, Senck 47875* (Greene, 1972); vic Mexico C (Beltz, 1954); San Juan Tezompa, 19.3 km E Xochimilco, UMMZ 99446-60; Valley of Mexico, Xochimilco, USNM 61247; Xochimilco, UMMZ 69264 (Caballero y C., 1939); Lake Xochimilco, nr Mexico C, MCZ 7866, UMMZ 80356-57.

MEXICO. Chalco, FMNH 1406 (Gadow, 1908); Teotihuacan, San Juan, AMNH 17859-62; Lake Texcoco, nr Mexico C, AMNH 68699; Valle de Mexico, CAS-SU 5849-50 (Martin del Campo, 1938; Hartweg and Glass, 1951; Deevey, 1957; Kranz et al, 1970).

STATE UNCERTAIN. "Mexico", ZSM 1374/0 (Holotype of *Cinosternon hirtipes;* Wagler, 1830).

Kinosternon hirtipes chapalaense

LAGO DE CHAPALA BASIN *(CHAP).*

JALISCO. Lago de Chapala, Beach at Chapala, UMMZ 97190; Lago de Chapala, 0.4 km off Chapala, UMMZ 97121-130 (includes holotype and paratypes); Lago de Chapala, 3.2 km W Chapala, UU 12126-28; (paratypes) Lago de Chapala, 0.8 km E Tuxcueca, JBI 890; Lago de Chapala, 6.1 km W Ajijic, UU 12125; paratype 3.2 km S Jamay, AMNH 17856; 3.2 km SE Ocotlan (El Fuerte), UMBM 2403; Ocotlan, UMMZ 76129, 117796-97 (UMMZ 117801 from this locality is *K. integrum.)*

MICHOACÁN. Jiquilpan (Duellman, 1961); La Palma, USNM 108718 (Duellman, 1961).

LAGO DE ZAPOTLÁN INTERIOR BASIN *(ZAPO).*

JALISCO. 1.6 km NW C Guzman, Lago de Zapotlán, UMMZ 117259-66; 3.2 km N C Guzman, UMMZ 102154; Laguna Zapotlán, BMNH 1906.6.1.253-5* (Gadow, 1908 as *K. integrum).*

Kinosternon hirtipes chapalaense x *murrayi*

RÍO DUERO DRAINAGE *(DUER).*

MICHOACÁN. Lake Camecuaro, 14.5 km E Zamora, JBI 885-889, UF 43603-610, 44062-63, 44075-76, UMMZ 97132-35, 102150-53 (Duellman, 1961).

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LIFE HISTORY OF *ETHEOSTOMA COOSAE* (PISCES: PERCIDAE) IN BARBAREE CREEK, ALABAMA

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ABSTRACT

Collections of *Etheostoma coosae* (Coosa darter) were made from April 1977 to April 1978 in Barbaree Creek (Coosa River system), Clay County, Alabama. The principal habitat of this species was cobble and/or gravel raceways, riffles and pools. Spawning occurred on the surface of rocks and small boulders from mid March to late May with peak activity in mid April. The spawning position was either inclined or semi-inverted horizontally. Individuals reached sexual maturity and spawned by the first year. Maximum age was three years. By the end of the second year, the average size of males and females was 41.0 mm and 36.5 mm SL, respectively. The sex ratio, 1:1.3, was significantly different from 1:1. The principal diet consisted of Copepoda, Cladocera, Ephemeroptera *(Isonychia)* and Diptera (Chironomidae, Simuliidae).

INTRODUCTION

Etheostoma (Ulocentra) coosae is endemic to the Coosa River system of Alabama, Georgia, and Tennessee. The biology of the subgenus as a whole is largely unknown. Published papers include studies by Winn (1958a, 1958b) on the reproduction of two undescribed forms, Stiles (1975) on the reproductive behavior of *Etheostoma simoterum,* and Ultsch et al. (1978) on habitat selection by *Etheostoma duryi.* This study reports on the life history of *E. coosae* in Barbaree Creek, an eastern Alabama stream.

STUDY AREA

A section along Barbaree Creek, T.18S., R.7E, Sec. 22, Clay County, Alabama (Coosa River system) was chosen as the study site. Barbaree Creek is a perennial stream flowing through northern Piedmont physiography. Its headwaters originate in the Talladega Mountains.

The substrate consisted of gravel and sand shoals interspersed with patches of cobble and boulders that were regularly broken by cobble or slab riffles. Bedrock was usually exposed below riffles whereas the pools contained unconsolidated material. The ranges of measured water quality values were: disssolved oxygen, 7.9-13.0 ppm; pH, 6.8-7.3; turbidity, 0.7-2.8 JTU; conductivity, 17-45 umhos; and stream temperature 3.7-25 °C (Boschung and O'Neil, 1980).

METHODS

Specimens of *E. coosae* were collected monthly from April 1977 through April 1978. Small mesh minnow seines, 3/16 inch delta weave, and a backpack shocker were each operated approximately 1.5 hours during each monthly collection, sampling a variety of habitats. Upon capture the fishes were preserved in a 20-percent formalin solution.

In the lab, fishes were blotted dry and then weighed to the nearest .01 g on a Mettler electronic balance. Standard length (SL) and sex were determined. The specimens are deposited in the University of Alabama Ichthyological Collection.

Aging to year class was determined by

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scale annuli. From 5 to 10 scales per fish were analyzed to reduce the chance of aging error due to the presence of false annuli and regenerated scales. Aging to month was accomplished by the technique outlined by Page (1974). The following symbols were used to indicate year classes: -1, 0 to 12 months; 1 +, 13 to 24 months; 2 +, >24 months.

Reproductive condition and length of the spawning season were determined by field observations and by determination of female gonosomatic indices (GSI). The GSI is the ratio of gonad weight to corrected body weight. Corrected body weight is total weight minus the viscera and gonad weight (Mathur and Ramsey, 1974).

Fecundity is defined as the number of ova equal to or exceeding 0.2 mm diameter. A large number of ova less than 0.2 mm diameter were present in each ovary, but past studies of darters with retracted spawning seasons (Fahy, 1954; Winn, 1958a; Scalet, 1973) have suggested that these minute oocytes never differentiate into fully yolked, enlarged ova and were, therefore, not spawned that year. The smallest differentiating ova of the larger egg group was 0.2 mm diameter, so this size was used as the lower limit.

For food and feeding studies, whole stomachs were removed, and the contents were identified to family and enumerated.

RESULTS AND DISCUSSION

Habitat

Etheostoma coosae adults and juveniles were consistently collected over rubble in raceways and around boulders, near sand bars and occasionally in the foot of riffles. This habitat preference was maintained seasonally with no indication of age or size specific habitat utilization for foraging or reproduction.

The basis of habitat selection by darters is influenced, if not determined, by physiological and/or ecological requirements of the species. Ultsch et al. (1978) conducted a series of critical O_2 experiments with six species of *Etheostoma* and observed that four ecological groups exist with respect to oxygen requirements versus habitat selection. They suggested that one such group, typified by *E. (Ulocentra) duryi* and *E. (Catonotus) flabellare,* preferred relatively fast water but maintained its ability to tolerate periods of hypoxia. This group was the most diverse physiologically in terms of oxygen use strategies. As a result of this, these darters maintained a diverse array of habitat types. The applicability of this explanation to habit selection by *E. coosae* lies in the close phylogenetic and ecological relationships between it and *E. duryi.*

Demography

Etheostoma coosae was the dominant percid species in Barbaree Creek. It comprised 5.9 percent of the total number of fish specimens collected (Table 1). The overall age class distribution of *E. coosae* for the year studied is seen in Table 2. Approximately 64 percent of the population occupied the − 1 age class, 29 percent the 1 + age class, and 7 percent the 2 + age class.

Seasonal changes in age class composition (Figure 1) indicate that maximum contribution to population size occurred during winter in the − 1 age class as it approached 12 months of age. From this point, percent contribution to population size declined throughout the older age classes.

Of the 750 specimens examined, 32.9 percent and 55.6 percent of the males and females, respectively, survived from the − 1 to the 1 + age class, whereas 10.8 percent and 10.3 percent of the males and females respectively, survived from the 1 + to the 2 + age class (Table 2).

The overall sex ratio, 1:1.3, was significantly different ($\chi^2 = 9.86$; $p < .01$) from the expected 1:1. This skewed sex ratio was most evident in the 1 + age class, 1:1.8 ($\chi^2 = 18.96$; $p < .01$), whereas the − 1 and 2 + age class sex ratios were not statistically different from 1:1.

Age and Growth

The oldest individuals collected, two females and one male (Figure 2), were 36

Table 1. Percent relative abundance and frequency of occurrence of fishes collected in Barbaree Creek from April 1977 through April 1978.

Species	Abundance	Occurrence
Family Cyprinidae		
Campostoma anomalum	1.69	91.7
Notropis asperifrons	5.87	100.0
Notropis callistius	8.81	100.0
Notropis lirus	0.19	25.0
Notropis stilbius	2.97	75.0
Notropis trichroistius	45.62	100.0
Notropis venustus	0.34	41.7
Notropis xaenocephalus	16.90	100.0
Phenacobius catostomus	0.01	8.3
Semotilus atromaculatus	0.09	25.0
Family Catostomidae		
Hypentelium etowanum	2.00	100.0
Moxostoma duquesnei	0.39	66.7
Family Ictaluridae		
Ictalurus natalis	0.04	8.3
Family Centrarchidae		
Ambloplites rupestris	0.07	41.7
Lepomis cyanellus	0.01	8.3
Lepomis gulosus	0.07	33.3
Lepomis macrochirus	0.04	8.3
Lepomis megalotis	0.76	66.7
Micropterus coosae	1.11	91.7
Micropterus punctulatus	0.06	25.0
Family Cyprinodontidae		
Fundulus stellifer	0.02	25.0
Family Percidae		
Etheostoma coosae	5.93	100.0
Etheostoma jordani	1.18	100.0
Etheostoma stigmaeum	0.97	100.0
Percina caprodes	0.31	66.7
Percina nigrofasciata	0.96	91.7
Family Cottidae		
Cottus carolinae	2.94	100.0
Total	99.35	

Table 2. Age-class distributions and survival of *Etheostoma coosae* collected in Barbaree Creek from April 1977 through April 1978. S_1 and S_2 equal survival calculated from the −1 and 1+ age classes, respectively.

Sex	Year class	Number of specimens	Survival S_1	Survival S_2
Males	−1	231	1.000	–
	1+	76	0.329	1.000
	2+	25	0.108	0.329
Females	−1	252	1.000	–
	1+	140	0.556	1.000
	2+	26	0.103	0.185
Combined Sexes	−1	483	1.000	–
	1+	216	0.447	1.000
	2+	51	0.106	0.236

months of age assuming a May hatching. Each specimen had two annuli and the third was in the process of being established. Scale studies of *E. coosae* in Barbaree Creek indicated that annuli are established in early to middle spring.

Males grew faster than females, and were on the average significantly longer ($p < .05$) by the first spawning season (Figure 3). Females attained 70.3 percent and 90.0 percent of their average maximum standard length (40.5 mm) in 12 and 24 months, respectively, whereas males attained 69.5 percent and 94.5 percent of their average maximum standard length (43.1 mm) in 12 and 24 months. The longest male and female were 47.0 mm and 44.1 mm, respectively (Figure 2). There were no significant differences ($p > .05$) between male and female length-weight equations as tested by analysis of covariance ($F_S = 0.867$, df = 1,136). The relationship for combined sexes was log wt. (grams) = 3.1657 log SL − 5.1200, N = 140, r = .978.

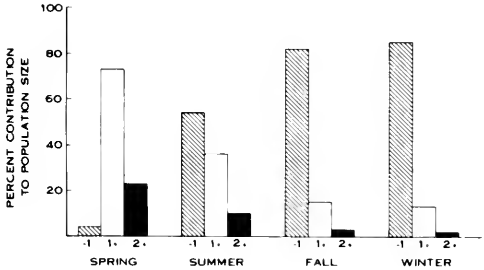


Figure 1. Seasonal changes in age-class composition of *Etheostoma coosae* collected in Barbaree Creek. Age-class designations are: −1, 1 to 12 months; 1+, 13 to 24 months; and 2+, >24 months.

Page and Schemske (1978) stated that one possible factor affecting size in darters of the subgenus *Catonotus* was interspecific competition. They concluded that maximum size in sympatric populations of *Catonotus* was determined by the presence or absence of *Etheostoma squamiceps*. In the presence of *E. squamiceps*, other *Catonotus species* were reduced in size, whereas in the absence of *E. sqamiceps* their maximum size was greater. They suggested that the major function of the size differences was for size-specific utilization of potential reproductive habitats.

The overall growth trend of *E. coosae* was for rapid growth, both sexes reach-ing approximately 70 percent of the average maximum standard length, the first year of life, with a subsequent reduction of this rate in later years (Figure 3). This pattern is quite common in darters (Page, 1974 and 1975; Page and Burr, 1976; Starnes, 1977) and in fishes generally. As Ricker (1971) has pointed out, this phenomenon is usually attributed to physiological size limitations primarily influenced by the heavier reproductive effort by older individuals.

Reproduction

Female gonosomatic indices (Figure 4) and field observations indicate that *E. coosae* spawned from mid March through early to mid May with peak spawning in April. The spawning periods for species of the subgenus *Ulocentra* are similar. Winn (1958a, 1958b) reported that males of *Etheostoma* sp. (Barren River form) in Tennessee established territories near the beginning of April, and spawning began in about one week. Stiles (1975) reported that *E. simoterum* spawned from early April to the end of May throughout its entire range. *Etheostoma duryi* females had ripe ova and males were in extreme breeding color in late April in Cypress Creek, Lauderdale County, Alabama (pers. obs.).

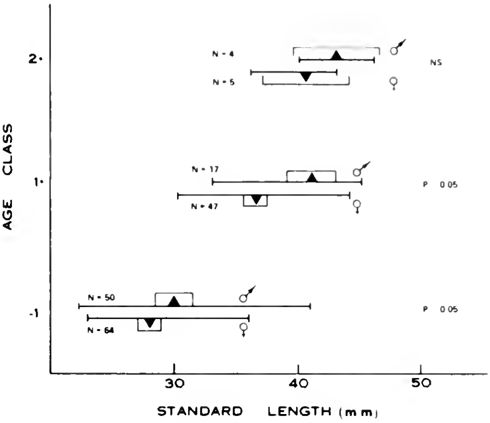


Figure 3. Annual growth of *Etheostoma coosae* males and females collected in Barbaree Creek. N equals sample size; NS equals not significant; and P equals probability level. Solid line equals range; triangle equals mean; and rectangle equals 95% confidence interval.

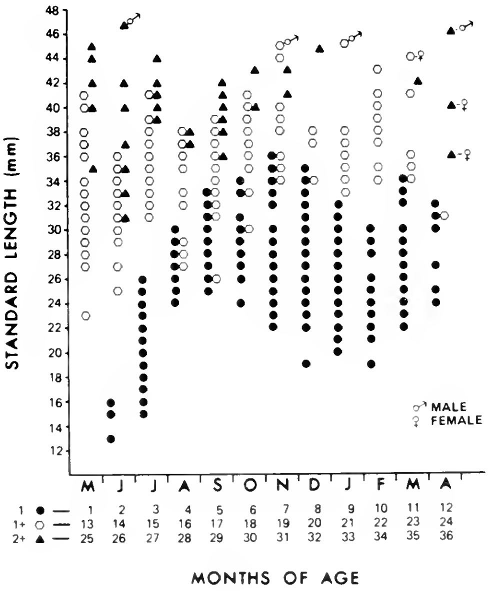


Figure 2. Length-age relationship of *Etheostoma coosae* collected in Barbaree Creek.

One month prior to spawning, male testicular tissue was swollen with a white granular appearance. During spawning, the tissue was extremely swollen with a subdued beige color. Approximately two months after spawning the testes were reduced to transparent, filamentous structures. The reproductive cycle of females was shorter in length when compared to males. Fully yolked mature ova were present for about 6 to 8 weeks. Mature testes and fully yolked ova were present in yearling darters indicating the possibility of spawning within the first year of life.

The spawning site of *E. coosae* consisted of almost any inclined, creviced surface within pools or raceways. Aquarium observations revealed that *E. coosae* spawned at angles from 0° to 90°, or in a horizontally inverted position while wedged in rock crevices or under ledges.

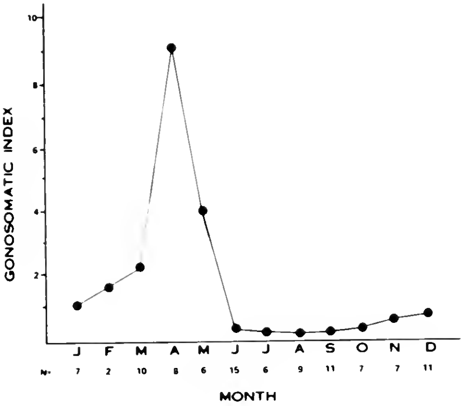


Figure 4. Monthly average gonosomatic index of *Etheostoma coosae* females collected in Barbaree Creek. N equals sample size.

In typical percid fashion, a male would display to a female as well as physically stimulate her nape with his head, attempting to elicite a spawning response. On occasion, a female would assume the dominate courtship role nudging and displaying her dorsal fins to a male, attempting to incite responses from him. Once an egg site, usually a small protective nook or crack, was selected, the female arched her body, placed the genital papilia over the site, and deposited one egg. The male quickly arched his body, placed the genital papilia over the egg and fertilized it. The eggs were deposited with no definable pattern or arrangement.

At the approach of spawning season *E. coosae* males acquired a light aqua-green tint around the gular region, along the tips of the spinous dorsal fin, on the first three membranes of the anal fin, and on

Table 3. Standard length, egg-size distribution, total egg complement (TEC), and age in years of selected *Etheostoma coosae* females collected in Barbaree Creek during March, April, and May, 1977 and 1978.

Standard length	Egg diameter in mm			TEC	Age
	0.2-0.4	0.5-1.0	>1.0		
40.1	194	156	72	422	2
38.5	300	116	80	496	2
36.0	278	56	4	330	2
35.9	320	118	54	492	2
34.5	284	92	34	410	1
33,7	220	92	42	354	1
33.5	172	78	38	288	1
31.5	280	46	22	348	1
30.5	260	39	0	299	1
Mean	256.4	88.0	38.4	382.8	
Percent	67.0	23.0	10.0	100.0	

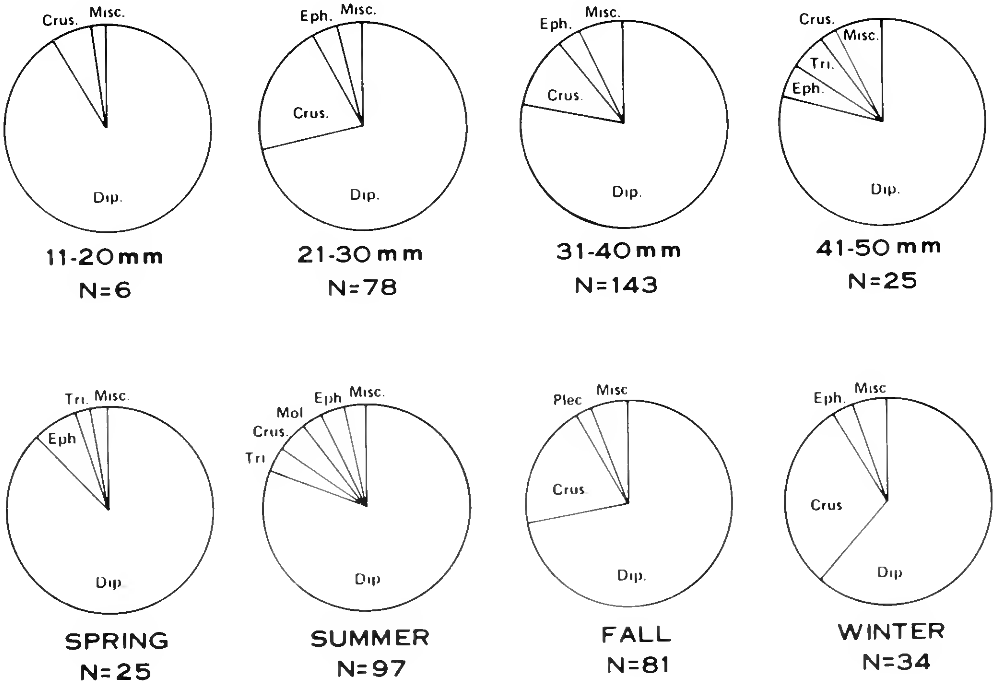
the anterior dorsal and ventral interradial membranes of the caudal fin. The interradial membranes throughout the length of the spinous and soft dorsal fins had rusty-red quadrate spots. Females maintained a ground color of light tan overlaid by brown to black lateral blotches and mottling above the lateral line.

The total egg complement increased proportionally with length, r = .682 (Table 3).Fecundity studies of other darters have substantiated positive size-fecundity relationships: *E. squamiceps,* r = .692 (Page, 1974); *E. barbouri,* r = 530 (Flynn and Hoyt, 1979); *E. kennicotti,* r = .631 (Page, 1975); and *Percina nigrofasciata,* r = .721 (Mathur, 1973). An exception to this general relationship was reported for *E. proeliare* (r <.1) by Burr and Page (1978). This vagary was attributed to the short life span (one year) of the population studied, which yielded females of a similar size.

Feeding

The overall diet of *E. coosae,* consisted of 78 percent Diptera (Chironomidae and Simuliidae), 12 percent Crustacea (Copepoda and Cladocera), 3 percent Ephemeroptera (Baetidae and Siphlonuridae) and 5 percent miscellaneous items (Acarina, Mollusca, Nematoda, Trichoptera, and sand). The diet of various size classes as well as the seasonal diet of combined age and size classes is seen in Figure 5.

Etheostoma coosae consumed midge larvae as juveniles and expanded their diet as adults to include mayflies and caddisflies. Midge larvae decreased whereas crusaceans increased in importance from spring to winter. Mayflies, caddisflies, and molluscs were important items during summer months.



11-20mm
N=6

21-30mm
N=78

31-40mm
N=143

41-50mm
N=25

SPRING
N=25

SUMMER
N=97

FALL
N=81

WINTER
N=34

Figure 5. Stomach contents of *Etheostoma coosae* collected in Barbaree Creek by size class of darter and season collected. Seasonal analyses include all size and age classes. Food items are abbreviated as follows: (Crus)tacea, (Dip)tera, (Eph)emeroptera, (Mis)ellaneous, (Mol)lusca, (Plec)optera, and (Tri)choptera. N equals sample size.

The feeding mode of darters has been reported to be largely selective in some species: *E. fonticola* (Schenck and Whiteside, 1977), *E. nigrum* (Roberts and Winn, 1962), and *E. radiosum cyanorum* (Scalet, 1972); and largely opportunistic in others: *E. acuticeps* (Bryant, 1979), *E. blennioides* (Fahy, 1954), and *E. gracile* (Braasch and Smith, 1967). These papers have illustrated that within the genus *Etheostoma* feeding behaviors are quite variable and complex. Based on the literature and my own studies, I believe that feeding behavior is not so restrictive but rather lies along a dynamic continuum between selectivity and opportunism. Species will adapt to prey abundance and type assuming the most energetically rewarding feeding response. Prey switching as a possible behavioral mechanism involved in feeding is supported by the studies of Murdoch et al. (1975) on *Poecilia reticulatua* and Roberts and Winn (1962) on the role of visual cues in the feeding of *E. nigrum*.

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December 30, 1981

THE TAXONOMIC RELATIONSHIP BETWEEN *MALACLEMYS* GRAY, 1844 AND *GRAPTEMYS* AGASSIZ, 1857 (TESTUDINES: EMYDIDAE)

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Abstract

The turtle genus *Graptemys* is a distinctive group clearly separable from *Malaclemys* on the basis of external and osteological features. The difference between the groups indicate that the degree of genetic relationship is no closer than that resulting from their both having presumably arisen from a *Pseudemys* - like stock or *Malaclemys* from a *Graptemys* stock.

INTRODUCTION

Investigators of *Malaclemys* and *Graptemys* have based their taxonomic allocations on penial, skull, shell, hind limb and pelvic girdle morphology and on head patterns. Osteological comparisons, when indicated, were usually limited to the skull, and in most cases, head patterns were used to distinguish taxa. The degree of evolutionary conservatism and parallelism exhibited by turtles argues against the use of external characters (e.g., head striping), alone in determining taxonomic and phylogenetic relationships. Thus, both osteological and surficial features have been examined in this study.

HISTORICAL REVIEW

The controversy about the relationship between *Malaclemys* and *Graptemys* began as a result of the lumping of *Graptemys* with *Malaclemys* by Boulenger (1889) and the re-establishment of the genus *Graptemys* by Baur in 1890. Since that time, W.P. Hay (1904) and O.P. Hay (1908) followed Baur in recognizing the two genera, as did Carr in 1949. Later, however, Carr (1952) questioned the validity of separating the two genera and McDowell (1964), without presenting supporting data, lumped *Graptemys* with *Malaclemys.* Zug (1966, 1971), on the basis of similiar penial, pelvic girdle, and hind limb morphology for the two genera considered them congeneric, and Parsons (1960, 1968) found the choanal structures of both genera to be so variable that the evidence did not particularly support or refute the congeneric idea. Several other authors (Ernst and Barbour, 1972; McKown, 1972; Dundee, 1974; Killebrew, 1979; Dobie and Jackson, 1979; Pritchard, 1979; Vogt, 1978, 1980) have not supported the synonymy of *Graptemys* with *Malaclemys;* they evidently must believe that sufficient evidence has not been presented to lump the two genera together.

The purpose of this study is to clarify the generic status of *Malaclemys* and *Graptemys.*

MATERIALS AND METHODS

Representatives of each of the ten extant *Graptemys* species (Vogt, 1980) and their subspecies and individuals of several subspecies of the monotypic *Malaclemys* were examined. External features, includ-

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ng scute contracts, plastral patterns, and striping on the head and leg were analyzed in juvenile and adult turtles of both sexes. Skull and shell characters were analyzed on large sub-adult and adult females. Skull terminology is that of Gaffney (1972 a); scute and bone terminology is that used by Zangerl (1969).

The method used to elucidate the relationship between *Malaclemys* and *Graptemys* and to other North American emydid turtles is the search for taxa that have shared derived characters. This method was described by Hennig (1966), and has been used by others (Gaffney, 1972 b, 1975; W.E. Clark, 1978) and is called phylogenetic systematics or cladism.

DIAGNOSTIC CHARACTERISTICS

The diagnostic characteristics of *Graptemys, Malaclemys* and an outgroup comparison of those genera with the other North American emydid genera are listed in Table 1. Each feature is also designated as either ancestral (primitive) or advanced (derived).

SIGNIFICANCE OF DIAGNOSTIC CHARACTERISTICS

The number (s) in a bracket refers to the number of the diagnostic features in Table 1.

SKULL FEATURES

(1) Quadratojugal - maxilla contact. If the absence of contact between these two bones represents the primitive state, then the possession of the derived condition in three *Graptemys* species (in one *pseudogeographica* and in all *pulchra* and *barbouri)*, in *M. terrapin,* and in some *Pseudemys* species suggests that *M. terrapin* could have been derived from one of these *Graptemys* or *Pseudemys* species. *Graptemys* could have come from any group lacking contact between the two bones.

(2) Spoon-shaped symphysis of lower jaw (Fig. 1). The flattened spoon-shaped nature of the symphyseal part of the lower jaw apparently is a derived feature in *Graptemys*. The absence of such a structure in *Malaclemys* suggests that *Graptemys* was not ancestral to *Malaclemys* and that *Malaclemys* may have arisen from some *Pseudemys* species.

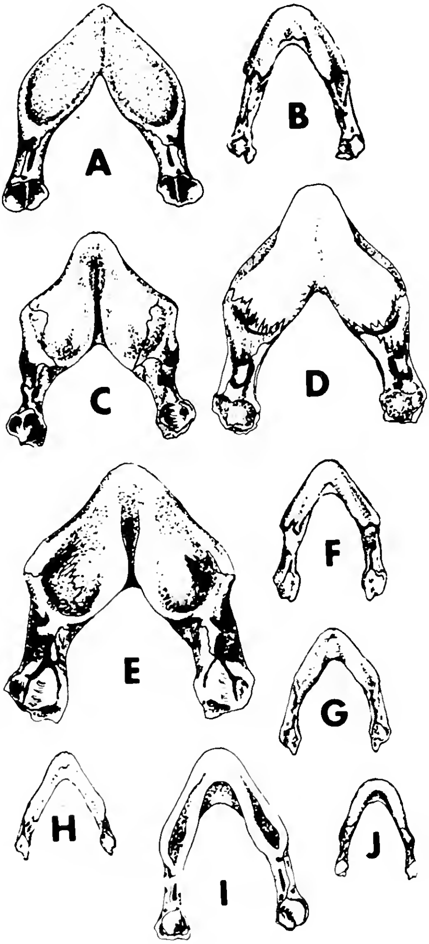

Figure 1. Shape of the symphyseal area of the lower jaw in mature females of (A) *Malaclemys terrapin,* (B) *Graptemys pseudogeographica,* (C) *G. geographica,* (D) *G. pulchra,* (E) *G. barbouri,* (F) *G. caglei,* (G) *G. versa,* (H) *G. ouachitensis sabinensis,* (I) *G. o. ouachitensis,* and (J) *G. flavimaculata* (the shape of the symphysis is the same for *flavimaculata, oculifera,* and *nigrinoda).*

(3) Bones surrounding the foramen palatinum posterius (Fig. 2). The bones surrounding that foramen in *Terrapene* and in the species of the *Pseudemys rubriventris* complex are the same as *Graptemys;* the other species of *Pseudemys* and the other N.A. emydid genera are like *Malaclemys.* Therefore, *Graptemys* and *Malaclemys* were possibly derived from different species of *Pseudemys.*

(4) The absence of contact between the ophisthotic and pterygoid due to the involvement of the exoccipital. If the condition in *Malaclemys* and *Deirochelys* represents a derived feature, this would strongly suggest that *Malaclemys* was not the ancestral stock from which *Graptemys* evolved. It could also indicate that a *Graptemys, Deirochelys,* or any other species of North American emydid turtle could have been ancestral to *Malaclemys.*

(5) The lack of a notch in the premaxillary bones. The lack of a notch in those bones in *Graptemys* and the presence of a notch in *Malaclemys* and the rest of the N.A. emydids, precludes determination of the possible ancestor for *Graptemys* and *Malaclemys* based on this feature.

SHELL FEATURES

(6) Flaring of carapace. The presence of such in *Graptemys* and to varying degrees in all other N.A. emydids except *Malaclemys* and some *Terrapene,* may indicate that flaring is an ancestral feature. If so, the upturning of the carapace in the last two genera would be a derived feature. This implies that *Graptemys* did not come from a *Malaclemys* stock.

(7) Double notching of some peripherals. The double notching of some of the peripherals is found only in *Graptemys* and in some individuals of *Pseudemys scripta* and *P. concinna.* This could indicate that *Graptemys* was not ancestral to *Malaclemys* and that a *Pseudemys* species was ancestral to *Graptemys.*

(8 and 9) The keel and its associated bosses (Fig. 3). A number of reports have dealt with the extent and development of the keel in *Malaclemys.* The last vertebral scute is variable with respect to keel development. Say (1825) reported that the last vertebral in *M. terrapin centrata* was unkeeled; Wied (1865) noted that all of the vertebrals of *M. t. pileata* have a well developed keel. The keel in *Malaclemys t. centrata* was stated by W.P. Hay (1904) "to be rather low and rounded," whereas it was "always well developed," in *M. t. macrospilota.* A keel is thus not always present on the last vertebral, and I have not observed the end of the keel (the fifth boss area) to extend more than four-fifths the length of the last vertebral scute. W.P. Hay's (1904) statement about the keel and bosses of *M. t. littoralis* was: "the first vertebral plate is raised on the middle line to form a broad, low carina; on the second plate the elevation is greater, and stands out as a smooth boss . . . ; the elevation on the third plate has the form of a hemispherical button with a well-marked constriction around the posterior half of the base . . . ; on the fourth plate the elevation is raised into a knob-like protuberance from a base which is constricted all around . . . ; the fifth vertebral plate is flat or with only a trace of an elevation." Thus Hay's statement suggests that four or five bosses are present on the keel in *Malaclemys.* This is not always the case. Auburn University Museum of Paleontology (AUMP) specimen 2179 has only three bosses, and its shell structures are normal.

Concerning the total number of bosses on the keel in *Graptemys pulchra,* Carr and Goin (1955) said, "the dorsal keel . . . comprises a boss on each of the first four centrals, . . . weak to nearly lacking on the first and completely lacking on the fifth." A boss on the fifth central (vertebral) is not lacking in *pulchra.* Although it is not prominent in *G. pulchra* or in any other species of *Graptemys,* a terminal boss can be detected in all species. Cagle (1954), p. 182, Fig. 11) illustrated a juvenile *G. flavimaculata* that had five bosses on the carapace. I have never examined any specimen of *Graptemys,* including *G. flavimaculata,* in which the

TABLE 1

Diagnostic Characteristics of *Graptemys* and *Malaclemys* and An Outgroup Comparison of Those Genera with the Other North American Emydid Genera. Each Feature is Designated As Either Ancestral (Primitive = P) or Advanced (Derived = D)[1].

Graptemys	*Malaclemys*	Other N. A. Emydines and *Rhinoclemmys*, a Batagurine
1. Sutural contact of maxilla with quadratojugal lacking. (P?)	In contact. (D?)	Lacking in *Terrapene*, *Emydoidea*, *Clemmys*, *Deirochelys*, *Pseudemys scripta*, *Chrysemys*, *Rhinoclemmys* and in some *P. floridana*. (P?) In contact in *P. concinna* and in the members of the *P. rubriventris* complex. (D?)
2. Rounded-shaped symphyseal part of lower jaw. (D)	Symphysis pointed. (P)	Like *Malaclemys*. (P)
3. Foramen palatinum posterius bounded on mediolateral and outer lateral sides by palatine. (D)	Bounded on outer later side by maxilla. (P)	The members of the *P. rubriventris* complex, *Terrapene*, and *Clemmys*-like *Graptemys*. (D). (Chrysemys, Pseudemys scripta, P. *concinna*, *P. floridana*, *Emydoidea*, and *Rhinoclemmys*-like *Malaclemys*. (P)
4. Exoccipital not responsible for the separation of the opisthotic and pterygoid when the latter two are not in contact. (P)	Exoccipital responsible for the separation of the two bones. (D)	*Chrysemys*, *Pseudemys*, *Emydoidea*, *Terrapene*, *Clemmys*, and *Rhinoclemmys*-like *Graptemys*. (P) *Deirochelys*-like *Malaclemys*. (D)
5. Premaxillae without medial notch. (D)	With medial notch. (P)	Like *Malaclemys*. (P)
6. Hind edges of carapace flared but not curved upward. (P)	Fore, lateral and hind margins of carapace normally curled upward. (D)	Like *Graptemys* except for some *Terrapene*. (P)
7. Posterior ends of some peripherals emarginate with double notching on at least some of those peripherals in juveniles and some adults. (D)	Same as in *Graptemys* except none with double notching. (P)	Like *Malaclemys* except double notching in some *Pseudemys scripta* and some *P. concinna*. (P)
8. Carapace with a medial keel. (P) It normally reaches from anterior end of first vertebral scute to posterior of end of fifth vertebral scute.	Carapace usually with medial keel. (P) It normally reaches from posterior end of first verteral scute to approximately four-fifths of the length of the fifth vertebral scute.	A medial keel present in most *Terrapene*, in *Emydoidea*, most *Pseudemys*, in *Deirochelys*, in two species of *Clemmys*, and in some *Rhinoclemmys*. (P) A very slight keel is present in some *Chrysemys*.
9. Keel with 5 bosses. (D)	Keel with from 3-5 bosses. (D)	No bosses. (P)

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[1] I am at present following the separation of *Chrysemys* into *Chrysemys* and *Pseudemys* based on the recent paper by Vogt and McCoy (1980). I am not following their division of *Pseudemys* into the genera *Pseudemys* and *Trachemys*.

10.	Ventrolateral sides of nuchal bone (costiform process normally absent) extend laterally to contact the midline side of the first peripheral bone. (P)	Ventrolateral sides of nuchal bone (costiform process present) extend laterally to beyond the medial side of first peripheral bone (contact with second peripheral not unusual). (D)	Not in contact with second peripheral in *Pseudemys, Clemmys, Rhinoclemmys, Terrapene,* and *Emydoidea.* In fact, contact is on medial side of first peripheral in the latter two genera. (P) Just makes contact with second peripheral in *Deirochelys.* (D) No costiform process in *Emydoidea.* Costiform process in some *Clemmys* and in some *Rhinoclemmys.* Costiform process in *Deirochelys, Pseudemys,* and *Terrapene.*
11.	Posterolateral borders of the nuchal bone at the area of the pleural scute sulci are notched. (P)	Not notched (except in one specimen). (D)	Notched in all Terrapene and in most *Chrysemys, Pseudemys,* and *Clemmys.* (P). Not notched in most *Deirochelys* and in all *Emydoidea.* (D) Notched in some *Rhinoclemmys.*
12.	That part of the anterior border of the first costal bone is extended outward and notched. (P)	Border is straight and unnotched except in one specimen. (D)	Same as in 11.
13.	Lateral edges of nuchal bone overlapped broadly by first pleural scute. (D)	Not overlapped or slightly overlaped by first pleural scute. (P)	Broad overlap in *Pseudemys.* (D) Slight to broad overlap in *Terrapene.* Not overlapped or only slightly overlapped in *Deirochelys, Chrysemys, Clemmys,* and *Rhinoclemmys.* (P) No overlap in Emydoidea.
14.	Anterolateral border of the first vertebral scute confined to nuchal bone. (D)	Not always confined to nuchal bone. (P)	Not confined to nuchal bone in *Emydoidea, Clemmys, Rhinoclemmys;* only rarely in *Deirochelys* and *Chrysemys.* (P) Confined to nuchal bone in *Pseudemys.* (D) May or may not be confined to nuchal bone in *Terrapene.*
15.	Amount of nuchal scute underlap is small and distal width of nuchal scute underlap broader than length of nuchal scute underlap. (D)	Same as in *Graptemys.* (D)	Large amount of nuchal scute underlap in all N.A. emydid turtles, except in some *Rhinoclemmys.* Distal width smaller than length in all except some *Pseudemys* and *Terrapene.* (P)
16.	Amount of nuchal scute overlap is small except in *G. geographica.* (D)	Small amount of overlap (D)	Large amount in *Pseudemys, Clemmys, Chrysemys, Emydoidea,* Deirochelys, and in some *Rhinoclemmys.* (P) Small amount of overlap in *Terrapene.* (D)
17.	Eighth costal contacts the eighth neural but not the seventh neural (all of the *G. pulchra* examined from the Conecuh River in Alabama have lost the eighth neural; the contact between the eighth costal and the seventh neural is therefore an abnormal condition in that population of *G. pulchra).* (P)	Contact of eighth costal with seventh and eighth neural bones. (D)	With eighth neural in all except for some *Terrapene* (some of the latter have lost the eighth neural and thus contact is with seventh neural). (P) Derived for some *Terrapene.*

Table 1 continued on next page

18. Well developed lateral ridges on the undersides of the first and fifth costal bones. (D)	Not well developed. (P)	Like *Malaclemys.* (P)
19. Distal widths of the three widest costal bones $1>5>3$ or $1>3>5$. (P? or D?)	Distal widths of three widest costal bones extremely variable but with costal 1 widest. Closest pattern to that for *Graptemys* was $1>3>5>6$ and that condition found in a single specimen. (P? or D?)	Variable within all.
20. Scutes of carapace sculptured but not concentrically so. (P)	Scutes of carapace concentrically sculptured. (D)	Same as for *Graptemys* except for some Antillean *Pseudemys, Clemmys insculpta,* and some *Terrapene.* (P). No scupturing in *Chrysemys.*
21. Carapace with pattern. (P)	Carapace with pattern dissimilar to that of any *Graptemys.* (D)	Same as in *Graptemys* except for *Clemmys guttata.* (P)
22. Bridge relatively wide. (P)	Bridge relatively narrow. (D)	Same as for *Graptemys.* (P)
23. Seventh marginal scute normally separated from abdominal scute by inguinal scute (except in some individual *G. pseudogeographica).* (P)	Seventh marginal contacts abdominal scute. (D)	Like *Graptemys.* (P)
24. Axillary and inguinal scutes not reduced in size or absent. (P)	Axillary and inguinal scutes reduced in size or absent. (D)	Like *Graptemys.* (P)
25. Typical plastral formula is gular< humeral< pectoral<abdominal> femoral<anal (89%). (P? or D?)	Typical plastral formula is gular humeral<pectoral<abdominal>femoral <anal (76%). (P? or D?)	Variable.
26. Among plastral scutes the abdominal longest in longitudinal dimensions 82% of cases; anal longest 18% of cases. (P? or D?)	Among plastral scutes the abdominal longest in longitudinal dimensions 53% of the time; anal longest 47% of the time. (P? or D?)	Variable.
27. Plastron of juveniles with generally an ornate plastral pattern (except in most *G. geographica* and in all *G. barbouri)* (P) Some individuals have dark spots as in *Malaclemys.*	Plastron of juveniles with generally an ornate plastral pattern. The pattern is not similar to that of any *Graptemys* except for one *G. nigrinoda.* (D)	Ornate plastral pattern in juveniles of *Chrysemys,* most *Pseudemys,* most *Terrapene, Clemmys, Emydoidea,* and *Rhinoclemmys.* (P) No pattern in *Deirochelys.* (D) Patterns of none are like those of *Malaclemys* except some mature *Pseudemys* males have dark spots.
28. Head, neck and limbs striped. (P)	Not striped but blotched or spotted. (D)	Like *Graptemys* except some *Rhinoclemmys* have stripes and spots on the head. (P)
29. Diploid chromosome number of 50. (D) Primitive number is 50 for emydines.	Same as in *Graptemys.* (D)	Same as in *Graptemys* except for *Rhinoclemmys* (52). Primitive number in batagurines may be 52.

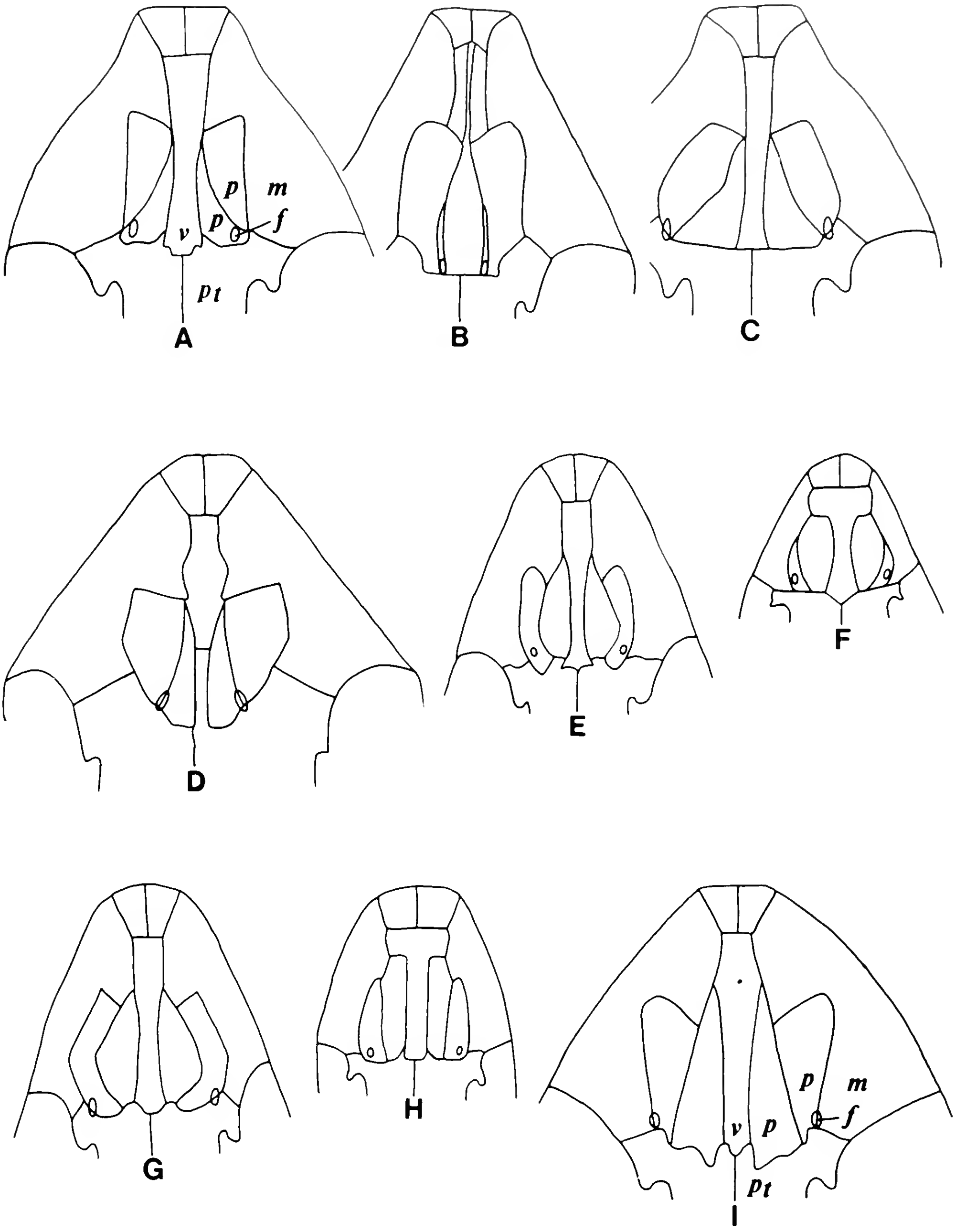

Figure 2. The location of the foramen palatinum posterius. The foramen is bounded on its mediolateral and outer lateral sides by the palatine in *Graptemys* (A) *pseudogeographica,* (B) *geographica,* (C) *pulchra,* (D) *barbouri,* (E) *caglei* and *versa,* (F) *o. sabinensis,* (G) *o. ouachitensis* and (H) *nigrinoda, oculifera,* and *flavimaculata.* It is bounded on its mediolateral and outer sides by the palatine and maxilla, respectively, in *Malaclemys terrapin* (I). Palatine (p). Maxilla (m). Foramen (f). Vomer (v). Pterygoid (pt).

fifth boss was located in the position illustrated by Cagle; the fifth boss is always at the posterior end of the last vertebral scute. The similar location of each boss in *Graptemys* and *Malaclemys* indicates their close relationship.

(10) Amount of ventrolateral extension of the nuchal bone and the costiform process of the nuchal bone. *Graptemys* normally lacks a costiform process; *Malaclemys* has one. Even though the nuchal of *Graptemys* is as wide as the same bone in *Malaclemys,* the distance the nuchal extends ventrolaterally is less in *Graptemys* than in *Malaclemys.* Therefore, the degree of such extension must not be solely a function of the width of the nuchal bone. This seems to be the case since the distal width of the first peripheral is proportionately greater in *Graptemys* than in *Malaclemys.* Therefore, the presence of a narrower first peripheral and a costiform process in *Malaclemys* results in a greater ventrolateral extension of the nuchal in that genus than in *Graptemys.*

The other North American emydids that have a costiform process are *Pseudemys, Terrapene,* some *Clemmys* and *Deirochelys,* and the latter genus is the only group that has a ventrolateral extension similar to that of *Malaclemys.* I think it unlikely that *Deirochelys* was ancestral to *Malaclemys;* therefore, perhaps some *Pseudemys* turtle was the stock from which *Malaclemys* arose. The ancestral stock for *Graptemys* can not be determined with respect to this feature.

(11 and 12) The notching of the posterolateral borders of the nuchal bone and the anterior border of the costal bone (Figs. 4 and 5). The presence of such notching in *Graptemys, Terrapene* and in most *Clemmys* (14 of 16), *Pseudemys* (29 of 31), and *Chrysemys* (15 of 20), and not in *Malaclemys* (except in one specimen), *Emydoidea,* and most *Deirochelys* suggests that *Malaclemys* was not ancestral to

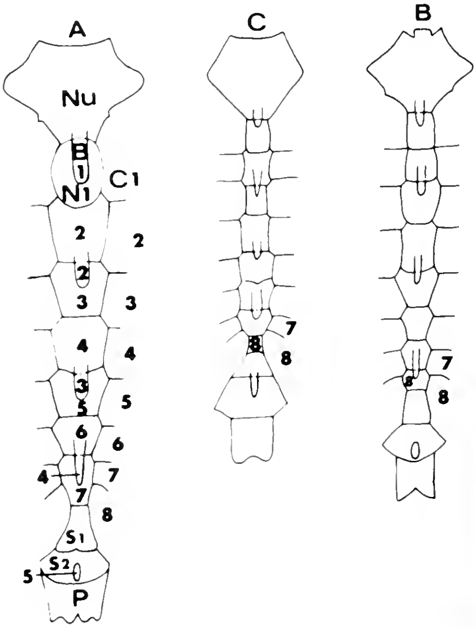

Figure 3. The location of the bosses in *Graptemys* (A) *pulchra,* (B) nigrinoda, and (C) *Malaclemys terrapin* and the contact of the eighth costal with the seventh neural in some *G. pulchra* due to the loss of the eighth neural bone. The normal contact is between eighth costal and eighth neural in *Graptemys* and eighth costal and seventh and eight neurals in *Malaclemys.* Nuchal bone (Nu). Bosses)B 1-5). Neural bones (N 1-8). Suprapygal bones (S 1-2). Pygal bone (P). Costal bones (C 1-8).

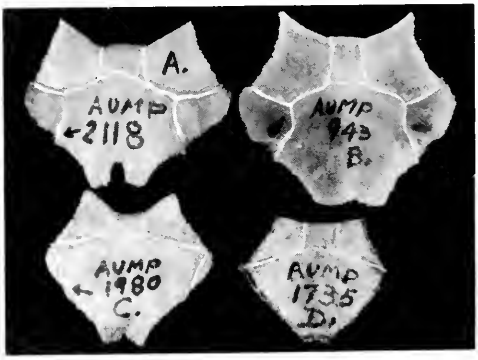

Figure 4. Dorsal view of the nuchal bone in *Graptemys* (A) *pseudogeographica,* (B) *pulchra* and (C and D) *Malaclemys terrapin.* Arrows indicate notches. The position of the anteromedial edge of the first pleural scute and the anterolateral borders of the first vertebral scute are not on the nuchal bone in some *Malaclemys* (D).

Graptemys if the absence of notching is a derived feature. However, *Graptemys* could have given rise to *Malaclemys,* as could have *Clemmys, Chrysemys, Pseudemys, Terrapene, Emydoidea,* and *Deirochelys. Emydoidea* and *Deirochelys* presumably would be the best candidates from which to derive *Malaclemys* if relationships are based on the presence of shared derived features. In spite of the presence of a shared derived feature between those genera and *Malaclemys,* I do not believe that either one is a good candidate for being the progenitor of *Malaclemys.* Therefore, *Graptemys, Pseudemys,* and *Chrysemys* are considered to be more likely candidates.

(13 and 14) The amount of pleural scute overlap on the nuchal bone and first vertebral scute - nuchal bone relationships. A great deal of pleural scute overlap exists in *Graptemys, Pseudemys,* and in some *Terrapene* and the pleural scute always contacts the margin of the first vertebral scute on the nuchal bone in the first two of the the three above (Dobie and Jackson, 1979). *Malaclemys* resembles most *Chrysemys* and some *Terrapene, Clemmys,* and *Deirochelys* in that there is little overlap of the pleural scute on the nuchal and the pleural scute does not always contact the first vertebral scute on the nuchal bone (Dobie and Jackson, 1979).

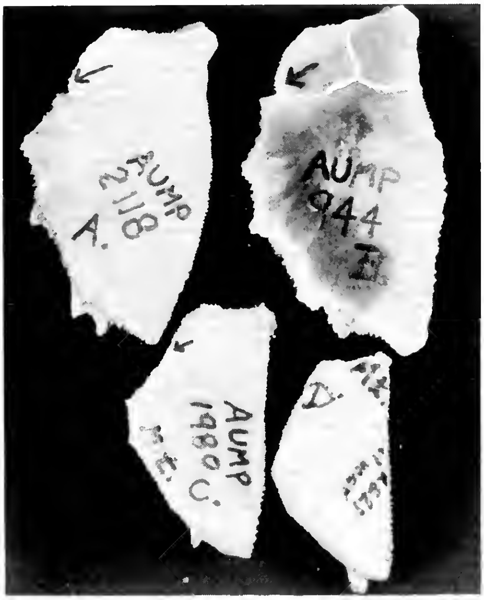

Figure 5. Dorsal view of the first left costal bone in *Graptemys* (A) *pseudogeographica,* (B) *pulchra* and (C and D) *Malaclemys terrapin.* That part of the anterior border of the costal bone that would adjoin the nuchal generally is straight and unnotched in *Malaclemys* as in (D). Arrows indicate notches.

Malaclemys terrapin could have evolved from *Chrystemys* in which the extent of pleural scute overlap was minimal and the margin of the first vertebral scute did not always meet the pleural scute on the nuchal bone. If *M. terrapin* evolved from any species of *Graptemys* or *Pseudemys* that had a large amount of pleural scute overlap and contact between the two scutes on the nuchal bone, then presumably a reduction in the amount of pleural scute overlap must have occurred. *Graptemys* could have arisen from a *Pseudemys* stock.

(15 and 16) Amount of nuchal scute overlap and underlap and the width-length relationships of the underlap part of the nuchal scute (Figs. 6 and 7). The amount of nuchal scute overlap is small in *Malaclemys,* in some *Terrapene,* and in all extant species of *Graptemys,* except *G. geographica* (Dobie and Jackson, 1979). Both *Malaclemys* and *Graptemys* have smaller amounts of nuchal scute underlap than any other North American emydid turtle, and the distal width of the underlap part of the nuchal scute is broader than its length in both of those genera and in some *Pseudemys* and *Terrapene* (Dobie and Jackson, 1979). Based on these features, *Malaclemys* would seem to be more closely related to *Graptemys* than to any other extant North American emydid genus.

(17) Contact of the eighth costal bone with the seventh and eighth neurals (Fig. 3). The presence of such contacts in *Malaclemys* and the contact of the eighth costal with only the eighth neural in *Graptemys*

(except for a single population of *G. pulchra)* and in all other North American emydid genera except *Terrapene* (the eighth neural is absent in some *Terrapene)* indicates that contact with the seventh neural is a derived character. The stock from which *Malaclemys* was derived presumably could have been any genus of North American emydid turtles; *Graptemys* could have come from *Pseudemys* or from any other North American emydid genus except *Malaclemys.*

(18) Lateral ridges on undersides of first and fifth costals (Fig. 8). The lateral ridges extending toward the midline of the carapace from the anterior and posterior ends of the bridge are well developed in *Graptemys* in constrast to those of *Malaclemys* and the rest of the North American emydid genera. The functional significance of those ridges is not known but they may serve as supportive units for the carapace. *Malaclemys* and *Graptemys* presumably could have been derived from any one of those genera.

(19) Distal widths of the three widest costal bones. An attempt to indicate the degree of relationships of *Malaclemys* to any other emydid genus on the basis of this character would be impractical because of the extremely variable nature of the widths of the costal bones. The fairly consistent widths in the species of *Graptemys* does indicate that they are closely related.

(20) Sculpturing on the carapace. The sculpturing on the carapacial bones in *Graptemys* is similar to that of some species of *Pseudemys (P. floridana* and *P. concinna)* although the degree of sculp-

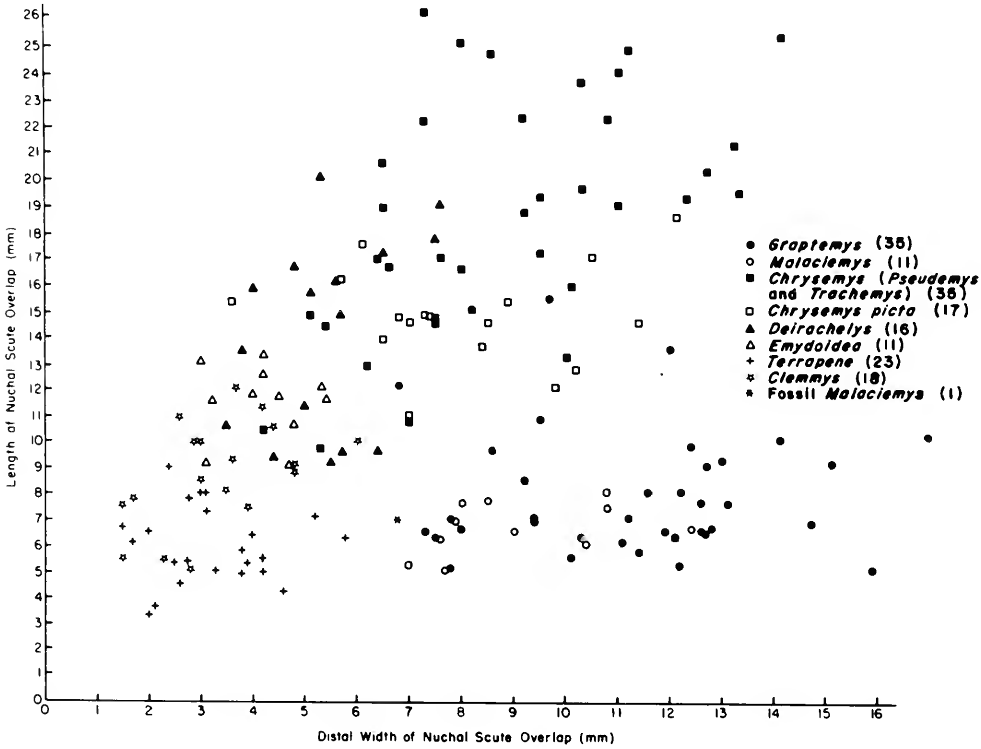

Figure 6. Length of nuchal scute overlaps versus distal width of nuchal scute overlap in various emydines including *Graptemys* (35) and *Malaclemys* (11).

turing in *Graptemys* is generally less than in any species of *Pseudemys* and more than that of *Chrysemys*. The type of concentric sculpturing in *Malaclemys* is unique and represents a derived feature (the species of *Terrapene*, some Antillean *Pseudemys*, and *Clemmys insculpta* also have concentric sculpturing (Zangerl, 1969; Dobie and Jackson, 1979) but the sculpturing patterns in the species of *Terrapene*, Antillean *Pseudemys*, and in *C. inscultpa* are not the same as that demonstrated by *Malaclemys*. *Graptemys* may have arisen from *Pseudemys*; *Malaclemys* from any one of these genera including *Graptemys*.

(21) Carapacial pattern. The patterns on the carapace of the various *Graptemys* justify the name, "map turtle". Those patterns, although more similar to those patterns found in other North American emydids, except *Clemmys guttata*, are distinctive and were probably modified from a less elaborate carapacial pattern. The lack of similarity of the carapacial patterns of *Graptemys* and *Malaclemys* could mean that the patterns of both were independently derived from different ancestors or that they came from the same ancestor that had a less elaborate pattern.

(22) Bridge width (Fig. 9). The width of the bridge in *Graptemys* resembles that of most aquatic emydids. The relatively narrow bridge in *M. terrapin* is distinctive, presumably derived, and perhaps is an adaptation for increasing the animal's ability for bottom walking in that a narrow bridge could allow the limbs to be advanced to a greater degree anteriorly than in a turtle having a wide bridge. *Malaclemys* could have come from any one of several different genera on the basis of this feature.

(23 and 24) The separation of the seventh marginal scute from the abdominal scute by the inguinal scute and the sizes of the inguinal and axillary scutes. The separation of the two scutes by the inguinal scute in *Graptemys* indicates that the size of the inguinal scute is about the same size as that found in most other North American emydids. The contact between the abdominal and seventh marginal scutes in *Malaclemys* is due to the small size of the inguinal scute or the absence of that scute. The condition in *Malaclemys* is probably derived.

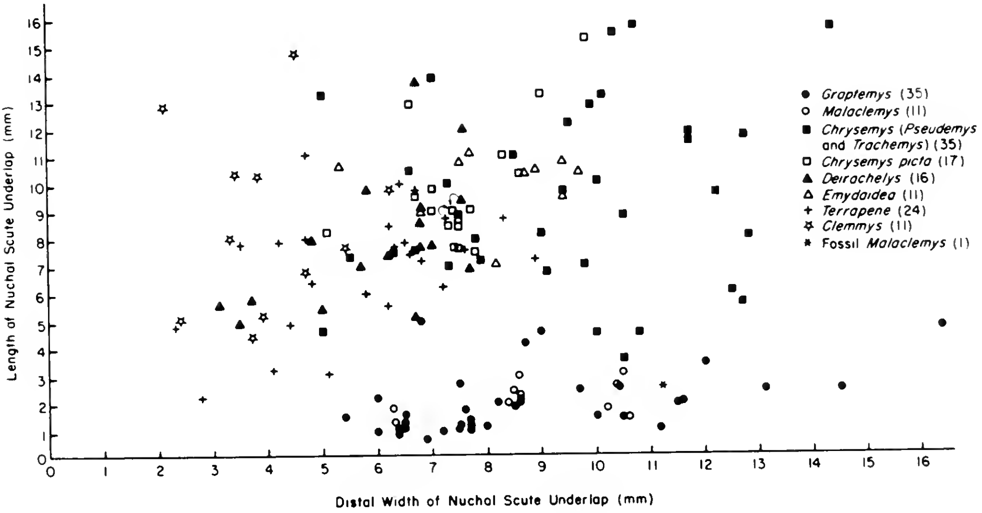

Figure 7. Length of nuchal scute underlap versus distal width of nuchal scute underlap in various emydines including *Graptemys* (35) and *Malaclemys* (11).

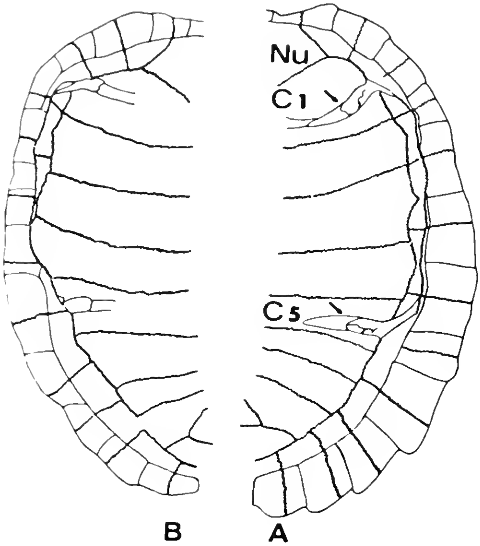

Figure 8. Lateral extensions of ridges on the ventral sides of the first and fifth costal bones in (A) *Graptemys nigrinoda* and (B) *Malaclemys terrapin*. The arrows indicate the ridges. Nuchal bone (Nu). Costal bone (C 1). Costal bone (C 5).

The size of the axillary scute in *Graptemys* is like that of most other emydids. It is either absent or very small in *Malaclemys*. The reduction in the size or loss of both the axillary and inguinal scutes is perhaps a result of the decrease in bridge width. Based on these features, *Graptemys* and *Pseudemys* are more similar than either is to *Malaclemys*.

(25 and 26) Plastral formulae and the length of the abdominal plastral scute. The two genera are more similar to each other in these two features than either is to any other North America emydid genus; they would thus appear to be closely related.

(27) Plastral patterns. The ancestral plastral pattern of *Graptemys* was probably ornate because to varying degrees ornate plastral patterns appear in all species of *Graptemys* except *G. barbouri*. The plastral patterns in *Malaclemys*, although ornate, do not resemble the pattern of any *Graptemys* species except for a single specimen of *G. nigrinoda*. The ornate plastral patterns of both were probably derived from different ancestral stocks.

HEAD, NECK AND LIMB STRIPING

(28) Head, neck and limbs striped. The striping of such units is a typical emydid condition and *Graptemys* is no exception. According to Wood (1977), *Malaclemys* is striped although I and evidently Pritchard (1979) have never seen a striped individual and Ernst and Barbour (1972) use the absence of striping in *Malaclemys* as a feature in their key to U.S. turtles. If striping does occur in *Malaclemys*, it must be a rare condition. The absence of striping in *Malaclemys* is a derived feature. *Malaclemys* could have been derived from *Graptemys* or from any other North American emydid genus.

DIPLOID CHROMOSOME NUMBER

(29) Chromosome count. Because all emydines presumably have 50 chromosomes (Killebrew, 1977), *Graptemys* and *Malaclemys* could have been derived from each other, from any one of several different groups, or perhaps from a batagurine if in fact the 50 chromosome number of emydines is a derivation of the 52 chromosome number of the batagurines.

DISCUSSION AND CONCLUSION

All indications are that *Graptemys* represents a distinct group of closely related turtles. *Malaclemys* is undoubtedly more closely related to *Graptemys* than it is to any other extant genus, as would be evidenced by (1) the pterygoid forming a suture with the exoccipital except in some species of *Graptemys (G. nigrinoda* for example) and in some individuals of *M. terrapin*, (2) similarities in penial, pelvic girdle and hind limb morphology, (3) similarity in carapacial seam contacts (Tinkle, 1962), (4) similarity in the amount of nuchal scute underlap, and (5) similarity in the width-length relationships of the underlap of the nuchal scute. In addition, the plastral scute formulae are the same for the two genera as are, generally, the locations of the bosses on the carapace.

The Oligocene species of *Graptemys*, *G. inornata* (Loomis, 1904) and *G. cordifera* (J. Clark, 1937) do not have shell characteristics that indicate a close relationship with *Malaclemys*. No other remains of *G. inornata* and *G. cordifera* are known. No fossils intermediate between *Graptemys* and *Malaclemys* are known, and only recently were fossil remains for *M. terrapin* discovered (Pleistocene age: South Carolina, [Dobie and Jackson, 1979]). Examination of an Eocene specimen (South Dakota School of Mines and Technology, SDSM&T, 59187) identified as *Graptemys* by Bjork (1967), reveals that it is not *Graptemys* or *Malaclemys* because it lacks, among other things, a keel and bosses. The absence of the uniform fine granular tubercles on the external surface of the carapace of the Eocene fossil prevents its inclusion within *Compsemys* (a baenid turtle, Gaffney, 1972b) and the absence of a keel and rugosities rules out its inclusion within any genus of North American emydids except *Chrysemys* (some *Chrysemys* do have a slight keel). On the basis of the absence of the latter two features it is like *Chrysemys picta*. However, it cannot be

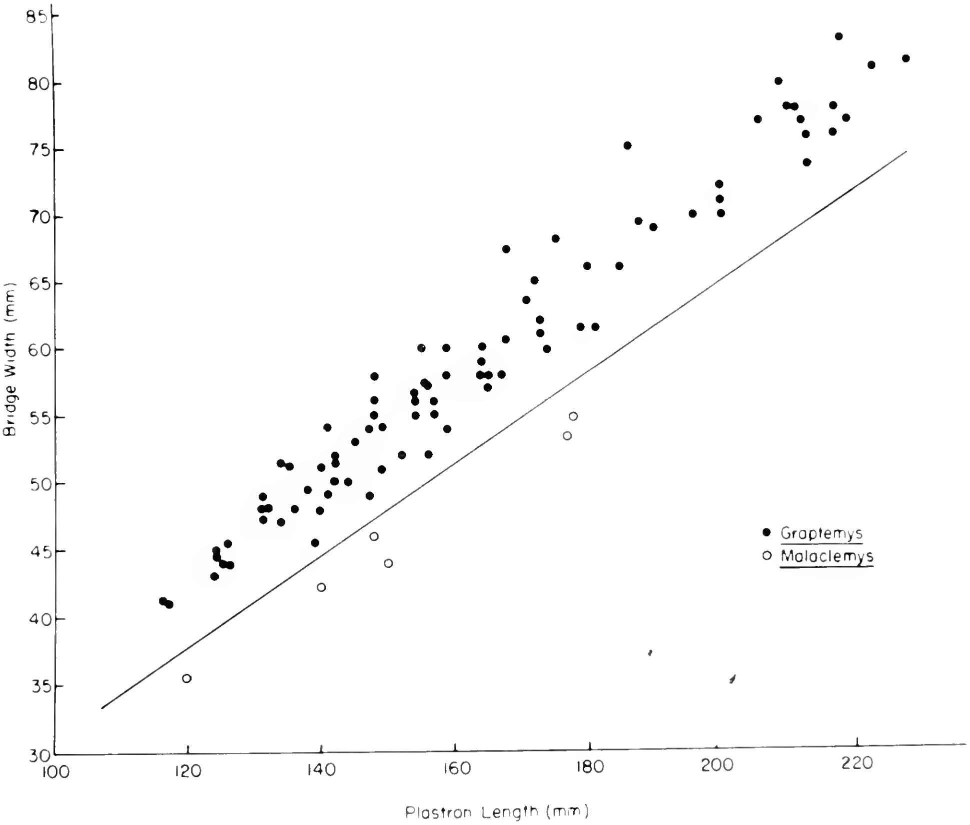

Figure 9. Relative bridge width in *Graptemys* and *Malaclemys*. The solid line depicts the separation of the two genera.

included within *Chrysemys picta* as the length of the sixth neural in *C. picta* is about twice as long as that of the fossil and the posterior width of the first suprapygal of the fossil is about twice the width of the same bone in *C. picta*. The neural bones of the fossil are narrow as compared to those of *Deirochelys carri, D. reticularia, Emydoidea blandingi, Malaclemys terrapin, Clemmys guttata,* and *C. insculpta* and this rules out the inclusion of the fossil into any of those genera.

The features possessed by the Eocene fossil do not fit those of *Graptemys, Malaclemys* or any extant North American emydid genus, thus, it may be a new taxon.

Although *Graptemys* and *Malaclemys* have several characteristics in common with some of the species of the Eocene emydid fossil turtles assigned to the genus *Echmatemys* (Table 2), I do not believe that either one of the two taxa nor any other new world emydine genus came from *Echmatemys*. O.P. Hay (1908) and Weaver and Rose (1967) proposed that *Chrysemys* came from *Echmatemys* and Hay (1908) also believed that *Echmatemys* was the ancestral stock for most other North American emydine genera. I reject the ancestral status of *Echmatemys* because to me many if not most of the species of *Echmatemys* appear to be members of *Rhinoclemmys* (e.g., McDowell, 1964, believed that *E. pusilla* belonged in the Neotropical batagurine genus *Rhinoclemmys)* and because most of the characters used to indicate relationships between *Echmatemys* and *Chrysemys* (in the sense of Weaver and Rose, 1967) were primitive characters and such can never be used to determine relationships. The *Graptemys* line may have arisen from some Eocene pre-*Pseudemys* of *Pseudemys* stock; *Malaclemys* may be an additional derivation of a *Pseudemys* stock or of a *Graptemys* stock, but its origin was probably somewhat later in the Tertiary (post-Miocene or later).

Loveridge and Williams (1957) believed that *Graptemys* may have arisen from a *Pseudemys* stock, as did McDowell (1964), Ernst (1974), and Pritchard (1979), and that the ancestral *Malaclemys* was close to a *Graptemys* stock. The former is in disagreement with O.P. Hay's (1908) conclusion that *Graptemys* was from *Malaclemys*. Wood (1977) also considered *Graptemys* a *Malaclemys* derivative, and according to him, "most or all of these species evolved independently and perhaps also at different times during the latter part of the Pleistocene from *Malaclemys* rather than giving rise to one another." Assuming that each species of *Graptemys* was independently derived from *M. terrapin* as Wood believes, then each feature common to two or more *Graptemys* but absent in *M. terrapin* must exemplify convergence. A total of 24 features, at least 10 of which appear to be derived, are shared by all *Graptemys*, only six of these feature, at least three of which appear to be derived, are possessed by *Malaclemys*. It is highly unlikely that the remaining 18 features (seven derived and 11 ancestral) would have arisen independently in all *Graptemys* species.

Because of the number of features held in common by the species of *Graptemys* and because it is obvious to me and to other individuals (Cagle, 1952, 1953a, 1953b, 1954; McKown, 1972; Dundee, 1974; Killebrew, 1977; Vogt, 1978, 1980) that there are closely related complexes of *Graptemys* turtles, e.g., *G. nigrinoda, G. flavimaculata,* and *G. oculifera; G. pulchra* and *G. barbouri; G. pseudogeographica, G. ouachitensis, G. versa,* and *G. caglei, (G. geographica* belongs in a group by itself), I conclude that the various species of the *Graptemys* turtles were derived from other species of *Graptemys*. (The species of *Graptemys* are thus more closely related to each other than any one species is to *M. terrapin.)*

Wood (1977) apparently was unaware that there are two Oligocene fossil species of *Graptemys*. If the fossils are correctly assigned, the various species of *Grapt-*

TABLE 2

Characteristics of Various Genera of Emydine Turtles and of *Echmatemys,* a Genus that Presumably Has Members of the Batagurine Genus *Rhinoclemmys* Included Within It[1].

	Graptemys	*Malaclemys*	*Chrysemys*	*Pseudemys*	*Echmatemys*
1. Extensive overlaps of pleural scute on nuchal bone	+	–	–	+	–
2. Contact between first vertebral scute and pleural scutes always on nuchal bone	+	–	–	+	–
3. Extensive nuchal scute overlap on nuchal bone	±	–	+	+	+
4. Nuchal scute underlap short and length not exceeding its distal width	+	+	–	±	+
5. Inguinal scute normally separates the seventh marginal scute from the abdominal scute	+	–	+	+	+
6. Axillary and inguinal scutes always present and always relatively large	+	–	+	+	–
7. Premaxillae with medial notch	–	+	+	+	?
8. Exoccipital not responsible for the separation of opisthotic and pterygoid when the latter two bones are not in contact	+	–	+	+	?
9. Double notching on some peripherals	+	–	–	±	–
10. Eighth costal bone normally contacts only the eighth neural	+	–	+	+	+
11. Scutes of carapace sculptured but not concentrically so	+	–	+	+	+
12. Bridge width broad	+	–	+	+	+
13. Hind edges of carapace flared	+	–	+	+	+

[1]The designations + and – indicate the presence or absence respectively of the feature.

emys obviously could not have been derived independently from *M. terrapin* during the Pleistocene.

Adult female *Malaclemys terrapin* and adult females of some species of *Graptemys (pseudogeographica, pulchra, barbouri* and *geographica)* resemble one another closely in general skull shape. The resemblance of *M. terrapin* to those *Graptemys* species is probably not due to common ancestry but rather to the development by each species of similar kinds of anatomical features (e.g., broad heads) as adaptations for feeding on similar kinds of food items (mussels.) *Graptemys pulchra, barbouri,* and *geographica* are also farther from the base of the *Graptemys* phylogenetic tree than is *G. pseudogeographica* (a species which is presumed to represent more nearly the ancestral-like stock) and both *G. geographica* and *G. barbouri* appear to be highly specialized, derived terminal end forms with respect to skull features. None of those species appears to be closely related to *Malaclemys terrapin* even though all have broad heads.

Mature females of some of the species of *Graptemys, G. nigrinoda, G. oculifera, G. flavimaculata, G. versa, G. caglei, G. ouachitensis* and some *G. pseudogeographica,* have narrow alveolar surfaces. The genus *Graptemys* cannot be differentiated, therefore, from *Malaclemys* on the basis of wide alveolar surfaces, as O.P. Hay (1908) contended.

The evidence is clearly against the lumping of *Graptemys* and *Malaclemys.* A subsequent paper will clarify the phylogenetic relationships of the *Graptemys* turtles.

ACKNOWLEDGMENTS

I am grateful to Drs. Robert Mount and George Folkerts for their advice on various aspects of this study. Several museums and one individual loaned me specimens and Robert Mount, John Pritchett and Lacy Hyche reviewed this manuscript. Theresa Rodriguez and Dr. Jeanne Stuart did most of the drawings.

SPECIMENS EXAMINED

Chrysemys picta: (74) (AUM 426, 605, 749, 829, 1170, 1553, 1915, 2062, 3827, 3872-73, 3875-76, 3884-85, 3999, 5669, 5885, 7072, 9514, 9747, 10091, 10126, 12587, 12589, 13616, 14133-34, 16231, 17366-67, 17871-72, 18033-34, 18218, 18812-14, 23478, 24109, 25088); (AUMP 132, 1713-23, 1965, 1967, 1983, 1985, 1990, 2117, 2171-76, 2318-20, 2351-54, 2405).

Clemmys guttata: (9) (AUM 21554, 22433, 26741, three classroom specimens); (AUMP 308, 2251); (UF/FSM 41018).

C. insculpta: (5) (AUM 29257); (AUMP 279); (UF/FSM 19016, 41525-26).

C. marmorata: (9) (AUMP 2260-62, 2264-66, 2310-11); (UF/FSM 41523).

C. muhlenbergi: (1) (UF/FSM 14116).

Deirochelys reticularia: (44) (AUM 1705, 1733, 3378, 3898, 8747-48, 9320, 10090, 10109, 10152, 11564, 12394, 13495, 15791, 18236, 18484, 18999, 19729, 22706, 22998, 23001); (AUMP 125-26, 897, 935, 1924, 2315, 2910); (UF/FSM T736, 6530, 7744, 14192, 14244-48, 30348, 34880, 35026, 38433, 40824, 41524, 41533).

Emydoidea blandingi: (17) (AUMP 1724-26, 1959, 1962, 1971, 2014-15, 2017, 2115, 2117, 2119, 2252-54, 2417-18).

Graptemys barbouri: (35) (AUM 3380-81, 5956, 6238, 6326-27, 6329, 6388, 6621, 8793, 8966, 9470-71, 9500, 9548, 9659, 10101, 10104-05, 10276, 11231, 12694-95, 13653-54, 14278, 21606, 22662); (AUMP 297, 325, 328-29, 931, 1733, 2357).

G. caglei: (10) (TNHC) 36066, 36071, 36084, 36088, 36093, 36097, 36103, 36621, 36627-28).

G. flavimaculata: (48) (AUM 5941, 5968-74, 6147, 6387, 8792, 8941-43, 8982-83, 9238-31, 9348, 9492-95, 9538-40, 9542-46, 10150-51, 10294, 10296-98, 13660-61, 23664); (AUMP 925, 940, 998-99, 2129, 2247).

G. geographica: (31) (AUM 5976-77, 6622, 9319, 9446-47, 10858, 11805, 11830, 12410-18, 12240-41, 13002, 21613, 22910, 23111, 23242, 29574); (AUMP 300, 909, 1940, 2355); (NLSC 622).

G. nigrinoda: (33) (AUM 5665, 5939, 5942, 5964, 5983, 5989, 8948, 8968, 8970, 9233, 9235, 9237, 9261-62, 9268, 10127, 10143-44, 10149, 10292, 10301, 12562, 12575, 12630, 12635, 21553, 22988-89); (AUMP 927, 1730, 2255-56, 2419).

G. oculifera: (23) (AUM 5951-53, 5979, 9333, 14289, 23665-69, 25136-39); (AUMP 304, 2125-28, 2215-16, 2248).

G. ouachitensis ouachitensis: (27) (AUM 9136-38, 25983-84, 25988, 26431-34, 26648); (AUMP 278, 309, 1738, 1997, 2131-32, 2136, 2200-04, 2273-75): (NLSC 9383).

G. ouachitensis sabinensis: (32) (AUM 24019, 24022-23, 24239-46, 24253-55, 25129-35); (AUMP 2121-24, 2244-46); (NLSC 10137-39, 10142).

G. pseudogeographica pseudogeographica: (24) (AUM 25985, 27090, 27101, 27113), (AUMP 2905, 2902, 2277-84); (SUSD 1520, 2855, 2860, 2862, 2880-83, two uncatalogued specimens).

G. pseudogeographica kohni: (81) (AUM 6843, 20715, 23985, 23989, 23991-97, 24020, 24191, 24224-25, 24247-52, 24259-60, 24263, 25989, 26385, 26401-02, 26406, 26422-25, 27093-98); (AUMP 305-08, 326-27, 2118, 2133-35, 2161-66, 2185-88, 2191-99, 2221, 2267-72, 2276, 2402, 2901); (KU 1183); (NLSC 2304, 5263).

G. pulchra: (37) (AUM 4997, 5000-01, 5004-06, 5597, 5742, 5961, 6302, 6311, 9467-69, 9532, 9535, 12556, 19898, 23482, 25140-44, 25977); (AUMP 301, 443, 926, 930, 936, 943-44, 989-91, 1000, 1960).

G. versa: (14) (AUM 16653, 22816, 23984, 24202, 24222, 26030-34, 29302); (AUMP 924, 2130 2137).

Malaclemys terrapin: (23) (AUM 8839, 14277, a classroom specimen); (AUMP 706, 932, 954, 963, 1732, 1734-37, 1956, 1980, 2157-58, 2179, 2403); (TU 15194, .2, 15195.1); (UF/FSM 22849a-49b).

Pseudemys alabamensis: (41) (AUM 4840, 9346, 9957, 10072, 11598-99, 11601-02, 11608, 11813-14, 12580, 12591, 16870-71, 17032-33, 19362, 26998, 27003-05, 27007, 27009-10, 27018, 27020, 27023); (AUMP 277, 298, 938, 1706, 1710, 1906, 2285, 2356, 2360-62); (USA 1501-02).

P. concinna: (142) (AUM 4560, 5901, 5994, 7432, 7567, 8918, 10140, 10147, 10396, 11294, 12650, 13553, 13639, 13743, 16906, 17139, 18483, 18975, 19140, 21802-05, 22825, 23248, 24201, 24208, 24214-16, 24223, 24227-28, 24280-81, 25126-28, 26413, 26416, 29298-01); (AUMP 17, 284, 288, 290, 311, 318-19, 693-94, 697, 881, 900-01, 911-12, 917-19, 933-34, 950, 1707-09, 1904-05, 1941, 1976, 1989, 1993, 2000, 2148, 2156, 2167-69, 2181-84, 2189-90, 2221 2286-90, 2292-94, 2316 2410-12); (FMNH 55646, 55649-52); (KU 33526); (SFA 2769, 2803, 2858, 2989, 3460); (TCWC 13735, 13965-67, 42345); (TNHC 536-37); (TU1637, 3605-06, 11940, 13464, 14414, 14421-22, .1-.3, .9-.10, 14441, .2-.3, .10, 14451, .2-.3, 14506.1, 14541, 16030); (UNM465, 30345).

P. floridana: (53) (AUM 1670, 7672, 8976, 9505, 9563, 10102, 10290-91, 10725-29, 11596, 12428, 12430, 12602, 13834, 17133-34, 19000, 19927-29, 21609, 21831, 22658, 23201, 23490, 23703, 27706, 27945); (AUMP 289, 440-42, 447-48, 700, 1703, 1712, 1727-29, 1902, 1948, 1963, 1981, 1998, 2249, 2291, 2309, 2404).

P. nelsoni: (19) (AMNH 80234); (AUM 27948); (AUMP 299, 446, 449, 913, 1702, 1946, 1964, 1982, 1992, 1994, 2200, 2413-16); (USNM 101393, 101398).

P. rubriventris: (25) (AMNH 69909-12, 77114, 77587, 77613, 99145); (AUMP 445, 2116, 2120); (CM 14022-29); (UF/FSM 1821 - six specimens).

P. scripta: (84) (AUM 3828, 6993-97, 7574-76, 7578-80, 11557-58, 11560, 13319, 21540, 24203, 24258, 24261-62, 24264-68, 25125, 27016); (AUMP 11.0-11.21, 12-15, 16.1-.5, 285-87, 317, 692, 1720, 1969-70, 1972-73, 1984, 1988, 1999, 2001, 2149, 2155, 2173, 2214, 2222-24, 2406-09).

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December 30, 1981

ADDENDUM

Tulane Studies in Zoology and Botany Volume 23, number 1

The addendum below is a continuation of the left hand paragraph of page 101 in the article by Dobie. It ends where the right hand paragraph begins LITERATURE CITED.

P. stejnegeri: (5) (AUMP 2363, four uncatalogued specimens).

Rhinoclemmys areolata: (1) (AUMP 2111).

R. pulcherrima: (2) (AUMP 910, uncatalogued specimen).

R. unidentified species: (1) (AUMP 2299).

Terrapene ornata: (AUM 10732); (AUMP 122-23, 962, 1939).

T. carolina: (52) (AUM 551, 1394, 1899, 3909-11, 4998, 5925, 8866, 9414, 11611, 14295, 17634, 20942, 23851, 25096-97); (AUMP 116-20, 124, 128, 130-31, 136-42, 702, 712, 914-16, 2250, 2257, 2312, 2317); (UF/FSM 7570, 14204, 35023, 38341, 40388, 41508-09, 41518, 41521-22).

Unidentified genus and species: (1) (SDSM & T 59187).

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CHANGES IN MELANIN MIGRATION INDUCED BY NORADRENERGIC AND HISTAMINERGIC AGENTS IN THE FIDDLER CRAB, *UCA PUGILATOR*[*]

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ABSTRACT

The effects of the H_1 receptor blocker SA-97, the H_2 receptor blocker cimetidine, the tyrosine hydroxylase inhibitor α-methyl-para-tyrosine and the H_1 receptor and norepinephrine uptake, blocker diphenhydramine on histamine- or 4-methyl histamine-induced inhibition of melanin dispersion in the fiddler crab, *Uca pugilator* undergoing a background transfer from white to black were determined. Only cimetidine significantly antagonized the 4-methyl histamine-evoked decrease in melanin dispersion. α-Methyl-para-tyrosine by itself significantly diminished whereas diphenhydramine by itself significantly potentiated the amount of this centrifugal melanin migration in the fiddler crabs. None of these drugs affected melanin migration *in vitro*. The results are consistent with the hypotheses that norepinephrine triggers release of a melanin-dispersing hormone and that H_2 receptor activation decreases impulse-mediated norepinephrine release in this crab.

INTRODUCTION

Translocation of the melanin in the melanophores of the fiddler crab, *Uca pugilator,* is regulated by antagonistic neurohormones, a melanin-dispersing hormone (MDH) and a melanin-concentrating hormone (Carlson, 1935; Sandeen, 1950; Fingerman, 1956). Norepinephrine (NE) triggers release of MDH in this crab (Fingerman et al., 1981; Hanumante and Fingerman, 1981a,b; 1982a,b,c; Hanumante et al., 1981). Recently histamine (HA) has been shown to inhibit melanin dispersion in a dose-dependent manner (Hanumante and Fingerman, 1981b). Use of a variety of histaminergic agonists and antagonists led to the hypothesis that two types of HA receptors, called H_1 and H_2, are present on NE neurons that trigger MDH release and that HA exerts its inhibitory action by stimulating the H_2 receptors. The present investigation was devised to obtain further support for this hypothesis. This objective was carried out by observing the effects of specific mammalian histaminergic and noradrenergic agents not used previously on the inhibitory action of HA and 4-methyl histamine (4-MeHA; a selective H_2 receptor agonist, Owen et al., 1979; Douglas, 1980; Polanin et al., 1981) on melanin dispersion in *Uca pugilator* transferred from a white to a black background.

MATERIALS AND METHODS

Adult male fiddler crabs, *Uca pugilator,* from the vicinity of Panacea, Florida, (Gulf Specimen Company) were used. Their melanophores were staged according to the system of Hogben and Slome (1931) whereby stage 1.0 represents maximal pigment concentration, stage 5.0 maximal pigment dispersion and stages 2.0, 3.0, and 4.0 the intermediate conditions. When intact crabs were used, the melanophores seen through the cuticle on the anteroventral surface of the second walking leg on the right side were staged at the time a sub-

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stance was injected and 15, 30, 60, 90, and 120 minutes thereafter. To facilitate comparison of the responses of the experimental and control crabs, mean differences between the 15 through 120 minute melanophore stages for the control and experimental groups were calculated for use in Table 1. The depicted data are based on the mean melanophore stages of 20 intact crabs (10 experimental and 10 control) or 20 isolated legs (10 experimental and 10 control). When assays were performed on isolated legs, the melanophores were staged only at the time the legs were removed from the crab (at which time the legs were perfused with the test or control solution) and 15, 30, 45, and 60 minutes thereafter. The second and third walking legs from both sides of the crab were removed; the legs from the right served as experimentals and the legs from the left side received control solution; the melanophores on the anteroventral surface of these isolated legs were observed for staging. The assays were performed using isolated legs having initially either maximally concentrated melanin (stage 1.0) or maximally dispersed melanin (stage 5.0). Melanophores in isolated legs of this crab remain responsive for at least 120 minutes (Herman and Dallmann, 1975). The statistical significance of the data was determined using Standard Errors of the Means (SEM) the Student's *t* test with significance set at the 95% confidence interval. None of the data for isolated legs were statistically significant.

The volume of the solution injected into each crab or isolated leg was always 0.05 ml. The experiments with intact crabs and isolated legs were performed at 24 °C under an illumination of 1190 lx. 4-MeHA dihydrochloride (Smith, Kline and French), cimetidine (N''-Cyano-N-methyl-N'-{2-(5-methylimidazol-4-yl) methylthioethyl} guanidine) (Smith, Kline and French) and SA-97 (homochlorcyclizine) (Eisai) were generous gifts. In addition, HA, α-methyl-para-tyrosine (α-MPT) and diphenhydramine HCl (all from Sigma) were used. The concentration used for each drug, whether injected alone or in combination, was 20 ug/dose of the free compound. All drugs except cimetidine were dissolved in Pantin's physiological saline (Pantin, 1934). Cimetidine was dissolved in acidified (a drop of 1.2 M HCl) saline. Consequently, a drop of HCl (1.2 M) was added to control saline for the cimetidine experiments. The rest of the controls received pure saline.

RESULTS AND DISCUSSION

4-MeHA, an H_2 receptor agonist, slowed the rate of melanin dispersion, as observed earlier by Hanumante and Fingerman (1981b), in intact crabs transferred from a white to a black background (Table 1). Cimetidine, which selectively blocks mammalian H_2 receptors (Douglas, 1980; Polanin and McNeill, 1981) significantly antagonized the 4-MeHA. On the other hand, the H_1 receptor blocker SA-97 not only did not antagonize the 4-MeHA but the combination of 4-MeHA plus SA-97 resulted in significantly further inhibition. None of these drugs affect melanin migration *in vitro* nor do SA-97 and cimetidine by themselves have an effect on the rate of melanin dispersion in crabs undergoing a background change from white to black (Hanumante and Fingerman, 1981b), a black background fostering melanin dispersion (Brown and Hines, 1952) which will be effected by MDH.

α-MPT selectively inhibits tyrosine hydroxylase. This enzyme catalyzes the synthesis of dihydroxyphenylalanine from tyrosine. At least in mammals this is the rate-limiting step in the biosynthesis of NE (Terrasawa et al., 1975; Lofström and Backström, 1978). α-MPT by itself significantly decreased melanin dispersion. HA by itself, as reported earlier (Hanumante and Fingerman, 1981b), significantly reduced centrifugal melanin migration in intact crabs transferred from a white to a black background. However, in the crabs that were co-administered either 4-MeHA and α-MPT or HA and α-MPT (Table 1), 4-MeHA and HA were not able to produce further, significant reduction of the melanin dispersion. Diphenhydramine, a blocker of H_1 receptors and NE uptake, in mammals (Isaac and Goth, 1965; Fantozzi et al., 1975; Marco et al., 1980), by itself significantly enhanced melanin dispersion. However, when HA was co-administered with diphenhydramine, the HA-induced inhibition in melanin dispersion was still evident (Fig. 1).

The present data, in light of our earlier report (Hanumante and Fingerman, 1981b) and the pharmacological actions of noradrenergic and histaminergic agents in mammals, further strengthen the hypothesis that (a) NE serves as a neurotransmitter triggering release of MDH and that (b) activation of H_2 receptors located on NE neurons which control MDH release results in a decrement of melanin dispersion in *Uca pugilator* transferred from a white to a black background. The observations that cimetidine, a selective H_2 receptor blocker, antagonized the 4-MeHA-induced inhibition in melanin dispersion, whereas the H_1 blocker SA-97 did not, reveal that this effect is mediated specifically by activation of HA H_2 receptors. The marked increase in inhibitory effect of 4-MeHA when co-administered with the H_1 antagonist SA-97 was probably due to the fact that excitation of H_1 receptors evokes enhanced melanin dispersion (Hanumante and Fingerman, 1981b), blocking them would prevent any endogenous H_1 stimulation of the crabs. This would enable 4-MeHA, an agonist of H_2 receptors, to produce an even greater inhibition of the melanin dispersion. On the contrary, in the crabs whose H_2 receptors were blocked by cimetidine, 4-MeHA was unable to significantly decrease the action potential-mediated release of NE, which in turn resulted in a near normal quantity of MDH being released into the hemolymph of these crabs transferred to the black background. The fact that metiamide, another H_2 receptor blocker, significantly antagonized the 4-MeHA-stimulated decrease in centrifugal melanin migration (Hanumante and Fingerman, 1981b) *in vivo* further strengthens this conclusion.

NE has been found (0.51 µg/g) in the supraesophageal ganglia of male fiddler crabs (Hanumante and Fingerman, 1982b). Also, we have provided evidence that H_1 and H_2 receptors occur on NE neurons because in fiddler crabs pretreated with 6-hydroxydopamine (which presumably destroys NE neuroterminals in *Uca* as it does in vertebrates) (Hanumante and Fingerman, 1982b,c) HA is unable to significantly reduce further the melanin dispersion (Hanumante and Fingerman 1981b). We have not determined (i) the levels of NE in α-MPT injected crabs or (ii) the exact mechanism of action of α-MPT in *Uca puilator.* However, data that we obtained using noradrenergic and histadrenergic agents (Hanuamante and Fingerman, 1981b) reveal that 20 MPT clearly interferes with NE neurotransmission. This probably was either by way of its well-established (at least in mammals) pharmacological NE synthesis-inhibiting effect (Terraswawa et al., 1975; Lofström and

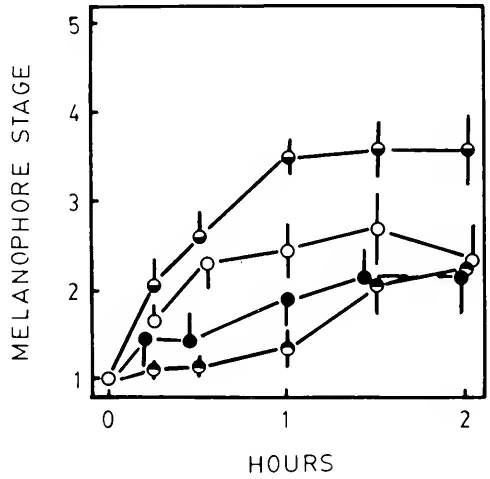

Figure 1. Relationships between melanophore stage and time. Circles with bottom-half darkened, crabs that received diphenhydramine; circles with top-half darkened, crabs that received histamine; solid circles, crabs that received histamine plus diphenhydramine; open circles, saline-injected controls. Vertical bars indicate SEM.

TABLE 1. The means (± SEM) of the differences between the melanophore stages determined at 15, 30, 60, 90, and 120 minutes of the intact crabs that received a drug versus the saline-injected controls. The minus sign indicates decreased melanin dispersion relative to the controls. *Statistically significant $p \leqq .05$ relative to respective controls.

4-Methyl histamine (4-MeHA)	−0.67* (± 0.08)
Cimetidine	−0.17 (± 0.01)
4-MeHA plus cimetidine	−0.39 (± 0.07)
4-MeHA plus SA-97	−1.43* (± 0.12)
α-Methyl-p-Tyrosine (α-MPT)	−1.15* (± 0.15)
4-MeHA plus α-MPT	−1.44* (± 0.21)
Histamine (HA)	−1.18* (± 0.18)
HA plus α-MPT	−1.01* (± 0.12)

Backström, 1978; Douglas, 1980) or by stimulating H_2 receptors, thereby leading to the observed decrement in MDH release (Table 1). Hence, the melanin of these α-MPT-treated crabs did not disperse to the extent it did in the control animals.

As stated above, in the crabs co-injected with 4-MeHA and α-MPT or HA and α-MPT, neither 4-MeHA nor HA significantly affected the melanin dispersion compared with that which occurred in response to α-MPT alone (Table 1). This presumably was due to the interference with NE neurons by α-MPT in such a way that the impulse-mediated decrement in NE secretion by the H_2 stimulators 4-MeHA and HA was not large enough to affect significantly the NE-mediated MDH release.

The diphenhydramine-evoked increment in melanin dispersion (Fig. 1) was presumably due to its blocking action on NE uptake$_1$ (Marco et al., 1980). NE uptake$_1$ inhibitors like nisoxetine (Koe, 1976) have already been shown to potentiate MDH release (Hanumante and Fingerman, 1981a). Diphenhydramine antagonizes H_1 receptors (Isaac and Goth, 1965; Fantozzi et al., 1975; Marco et al., 1980) also. However, because H_1 receptor blockers do not significantly abolish HA- or 4-MeHA- (an H_2 receptor agonist) mediated inhibition of melanin dispersion, we suggest that the NE uptake$_1$ blocking action of diphenhydramine is responsible for the potentiation of melanin dispersion. The observation that even when HA is co-administered with diphenhydramine there is still a decrease in melanin dispersion (Fig. 1) indicates that HA does not evoke its effect by stimulating NE uptake$_1$; uptake$_1$ being the major mechanism of inactivating the postsynaptic actions of monoamines including NE (Fuller and Wong, 1977). That none of these drugs affect significantly melanin migration in isolated legs (Hanumante and Fingerman, 1981b) is consistent with the hypothesis that these drugs elicit changes in melanin dispersion indirectly by interacting with the neuroendocrine system of *Uca pugilator*.

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ADDITIONAL TREMATODES OF MAMMALS IN LOUISIANA WITH A COMPILATION OF ALL TREMATODES REPORTED FROM WILD AND DOMESTIC MAMMALS IN THE STATE

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ABSTRACT

The following trematodes were collected from hunter-trapped mammals in the Atchafalaya basin of Louisiana during the winters of 1981 and 1982: *Alaria alarioides* (Dubois, 1937) Dubois, 1970 from mink, *Mustela vison* Schreber, and river otter, *Lutra canadensis* (Schreber); *Alaria marcianae* (La Rue, 1917) Walton, 1949 from raccoon, *Procyon lotor* (Linn.) and bobcat, *Lynx rufus* (Schreber); *Alaria mustelae* Bosma, 1931 from raccoon and mink; *Amphimerus speciosus* (Stiles and Hassal, 1896) Barker, 1911 from raccoon and the domestic cat, *Felis domesticus* Linn.; *Baschkirovitrema incrassatum* (Dies., 1850) Skrjabin, 1944 from mink and river otter; *Brachylaima virginiana* Dickerson, 1930 from opossum, *Didelphis virginiana* Kerr; *Carneophallus basodactylophallus* Bridgman, 1969 from raccoon; *Cryptocotyle concava* (Creplin, 1825) Luhe, 1899 from mink; *Fibricola cratera* (Barker and Noll, 1915) Dubois, 1932 from mink, opossum, and raccoon; *F. lucida* (La Rue and Bosma, 1927) Dubois and Rausch, 1950 from mink and opossum; *Gyrosoma singulare* Byrd, Bogitsh, and Maples, 1961 from raccoon and mink; *Hasstilesia texensis* Chandler, 1929 from muskrat, *Ondatra zibethica* (Linn.); *Heterobilharzia americana* Price, 1929 from mink, raccoon, and bobcat; *Isthmiophora melis* (Schrank, 1788) Luhe, 1909 from raccoon and mink; *Linstowiella szidati* (Anderson, 1944) Anderson and Cable, 1950 from opossum and raccoon; *Maritreminoides nettae* (Gower, 1938) Rankin, 1939 from raccoon and mink; *Microphallus opacus* (Ward, 1894) Ward, 1901 from raccoon and mink; *Paragonimus kellicotti* Ward, 1908 from opossum; *Pharyngostomoides procyonis* Harkema, 1942 from raccoon; *Quinqueserialis quinqueserialis* (Barker and Laughlin, 1911) Harwood, 1939 from muskrat; *Rhopalias macracanthus* Chandler, 1932 from opossum; and *Sellacotyle vitellosa* Sogandares-Bernal, 1961 from mink. *Alaria alarioides*, *A. marcianae*, *Amphimerus speciosus*, *Cryptocotyle concava*, *Isthmiophora melis*, *Microphallus opacus*, *Paragonimus kellicotti*, and *Quinqueserialis quinqueserialis* have not been previously reported from Louisiana mammals. Diagnoses are presented for the species representing state records along with pertinent notes on the biology of each. New host records include *Heterobilharzia americana*, *Cryptocotyle concava*, and *Maritreminoides nettae* from mink; *Alaria marcianae*, *Amphimerus speciosus*, and *Linstowiella szidati* from raccoon; and *Hasstilesia texensis* from muskrat. A compilation of trematodes previously reported from Louisiana mammals is presented.

INTRODUCTION

Recently, we reported some trematodes collected from mammals in south Louisiana (Shoop and Corkum, 1981a). Since that time we have continued our examination of hunter-trapped mammals from the Atchafalaya basin of Louisiana during the winters of 1981 and 1982. The following mammals were examined for trematodes: 42 minks, *Mustela vison* Schreber; 37 raccoons, *Procyon lotor* (Linn.); seven river otters, *Lutra canadensis* (Schreber); five muskrats, *Ondatra zibethica* (Linn.); three bobcats, *Lynx rufus* (Schreber); four domestic cats, *Felis domesticus* Linn.; two opossums, *Didelphis virginiana* Kerr; and three red foxes, *Vulpes fulva* (Desmarest). The red foxes were found uninfected with trematodes.

Trematodes were fixed in steaming 10%

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formalin and stained in Semichon's acetocarmine. All measurements are in micrometers unless otherwise stated; means are followed by the ranges in parentheses. Line drawings were prepared with the aid of a microprojector. Representative specimens of the species for which diagnoses are given were deposited in the Manter Laboratory, University of Nebraska State Museum, Lincoln, Nebraska.

Table I lists the trematodes recovered from the eight species of mammals. Lumsden and Zischke (1961) reported and diagnosed *Fibricola cratera, F. lucida, Hasstilesia texensis, Brachylaima virginiana,* and *Rhopalias macracanthus* from Louisiana mammals. Our specimens agree in all respects with Lumsden and Zischke's (1961) diagnoses. Our specimens of *Hasstilesia texensis* from the muskrat represent a new host record. Shoop and Corkum (1981a) reported and diagnosed *Alaria mustelae, Baschkirovitrema incrassatum, Gyrosoma singulare, Maritreminoides nettae,* and *Pharyngostomoides procyonis* from Louisiana mammals. In that report we noted *M. nettae* in raccoons; it is herein reported from the mink as well (new host record). In a more recent note, we (Shoop and Corkum, 1982) commented further on the status of *G. singulare* in this state. *Heterobilharzia americana* has been reported from Louisiana mammals by Malek et al. (1961) and Kaplan (1964). Our collections of *H. americana* from mink represent a new host record. *Carneophallus basodactylophallus* was originally described by Bridgman (1969) from raccoon in Louisiana as was *Sellacotyle vitellosa* from mink by Sogandares-Bernal (1961). Lumsden and Winkler (1962) reported *Linstowiella szidati* from opossum. We have found it in opossum as well as in raccoon. In addition to these trematodes, we identified eight other species that have not been previously reported from Louisiana mammals and that are of importance from epidemiological or zoogeographical standpoints. Table II compiles all trematodes reported heretofore from mammals in the state of Louisiana.

Family DIPLOSTOMIDAE Poirier, *1886*
Alaria alarioides (Dubois, 1937) Dubois, 1970

(Figure 1)

Synonyms: Diplostomum alarioides Dubois, 1937; *Enhydrodiplostomum alarioides* (Dubois, 1937) Dubois, 1944.

Hosts: Mustela vison Schreber and *Lutra canadensis* (Schreber).

Location: Small intestine.

Locality: Belle River, Assumption Parish, Louisiana.

Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21367.

Diagnosis (based on ten mature specimens): Body elongate, distinctly bisegmented, 1650 (1400-1800) long by 540 (450-650) at the widest point. Forebody spathulate, 777 (640-940) long by 540 (450-650) wide; pseudosuckers present as depressions on either side of the oral sucker, never observed evaginated. Hindbody claviform, 907 (760-1050) long by 430 (400-480) wide, containing reproductive organs. Forebody tegument covered with small spines; hindbody smooth. Oral sucker terminal, 92 (80-100) long by 106 (90-120) wide; acetabulum weak, spherical, 75 (60-80) long by 76 (60-90) wide, often covered by the tribocytic organ; tribocytic organ broadly elliptical when evaginated, 348 (240-400) long by 280 (240-330) wide, with a longitudinal cleft.

Prepharynx and esophagus extremely short or absent; pharynx usually in contact with oral sucker, 77 (70-90) long by 65 (50-80) wide; paired ceca extend to the posterior end of body. Testes tandem, not equal; anterior testis asymmetrical, laterally disposed on either side of midline, 215 (200-250) long by 317 (290-350) wide; posterior testis symmetrical, dumbbell-shaped, much wider than anterior testis, 218 (190-250) long by 394 (350-410) wide, with a ventro-median groove to allow passage of ceca, uterus, and vitellaria; ejaculatory duct opens into the genital atrium; genital atrium opens posterior, subterminally on the dorsal surface. Ovary spherical, located in hindbody just in front of

TABLE I. Trematodes recovered from hunter-trapped mammals in Louisiana during the winters of 1981 and 1982.

Trematode	Hosts	No. Examined	No. Infected	%	Location
Alaria alarioides (Dubois, 1937) Dubois, 1970	otter	7	2	29	Sm. Int.
	mink	42	24	57	"
A. marcianae (La Rue, 1917) Walton, 1949	raccoon	37	2	5	"
	bobcat	3	2	67	"
A. mustelae Bosma, 1931	raccoon	37	1	3	"
	mink	42	1	2	"
Amphimerus speciosus (Stiles and Hassal, 1896) Barker, 1911	raccoon	37	1	3	Liver
	domestic cat	4	1	25	"
Baschkirovitrema incrassatum (Dies., 1850) Skrjabin, 1944	otter	7	2	29	Sm. Int.
	mink	42	21	50	"
Brachylaima virginiana Dickerson, 1930	opossum	2	1	50	"
Carneophallus basodactylophallus Bridgman, 1969	raccoon	37	2	5	"
Cryptocotyle concava (Creplin, 1825) Luhe, 1899	mink	42	22	52	"
Fibricola cratera (Barker and Noll, 1915) Dubois, 1932	mink	42	4	10	"
	raccoon	37	12	32	"
	opossum	2	2	100	"
F. lucida (La Rue, and Bosma, 1927) Dubois and Rausch, 1950	mink	42	26	62	"
	opossum	2	2	100	"
Gyrosoma singulare Byrd, Bogitsh, and Maples, 1961	raccoon	37	7	19	"
	mink	42	2	5	"
Hasstilesia texensis Chandler, 1929	muskrat	5	1	20	Cecum
Heterobilharzia americana Price, 1929	raccoon	37	20	54	Mes. Ven.
	mink	42	2	5	"
	bobcat	3	1	33	"
Isthmiophora melis (Schrank, 1788) Luhe, 1909	raccoon	37	6	16	Sm. Int.
	mink	42	2	5	"
Linstowiella szidati (Anderson, 1944) Anderson and Cable, 1950	raccoon	37	1	3	"
	opossum	2	1	50	"
Maritreminoides nettae (Gower, 1938) Rankin, 1939	mink	42	3	7	"
	raccoon	37	6	16	"
Microphallus opacus (Ward, 1894) Ward, 1901	raccoon	37	5	14	"
	mink	42	4	10	"
Paragonimus kellicotti Ward, 1908	opossum	2	1	50	Lungs
Pharyngostomoides procyonis Harkema, 1942	raccoon	37	31	84	Sm. Int.
Quinqueserialis quinqueserialis (Barker and Laughlin, 1911) Harwood, 1939	muskrat	5	2	40	Cecum
Rhopalias macracanthus Chandler, 1932	opossum	2	1	50	Sm. Int.
Sellacotyle vitellosa Sogandares-Bernal, 1961	mink	42	2	5	"

the anterior testis, 103 (90-120) long by 114 (110-120) wide; uterus courses anteriad into the forebody and turns immediately posteriad where it opens in the genital atrium; vitellaria penetrate the forebody and extend in two bands through the ventro-medial grooves of the testes to the level of the genital atrium; vitelline reservoir median, intertesticular. Eggs large, operculate, 101 (90-110) long by 55 (50-60) wide. Excretory system not observed.

Discussion: Dubois (1937) originally described *Diplostomum alarioides* from a Brazilian otter. He (Dubois, 1944) subsequently purged the genus *Diplostomum* of all mammalian parasites, retaining it for avian parasites, and erected the new genus *Enhydrodiplostomum* for *D. alarioides* and a second otter parasite, *D. fosteri.* Chandler and Rausch (1946) assigned two additional species, *Alaria clathrata* and *A. pseudoclathrata,* both also parasites of the otter, to the genus *Enhydrodiplostomum.* In a later revision, Dubois (1970) agreed that these four species are closely related, but reassigned them to the genus *Alaria* where additional mustelid parasites are found.

Sawyer's (1961) collection of *A. alarioides* from river otter in Georgia was the first report from North America. Since then, Miller and Harkema (1964, 1968) reported *A. alarioides* from both mink and river otter in North Carolina, and Fleming et al. (1977) reported it from river otter in Alabama. *A. alarioides* is also a common parasite of mink and river otter in Louisiana. Measurements of *A. alarioides* from the two hosts compare favorably with the descriptions of Dubois (1937, 1970).

Alaria marcianae (La Rue, 1917) Walton, 1949

(Figure 2)

Synonyms: Cercaria marcianae La Rue, 1917; *Agamodistomum marcianae* (La Rue, 1917) Cort, 1918; *Alaria americana* Hall and Wigdor, 1918; *Alaria canis* La Rue and Fallis, 1934; *Alaria minnesotae* Chandler, 1954.

Hosts: Lynx rufus (Schreber) and *Procyon lotor* (Linn.).

Location: Small intestine.

Locality: Pierre Part, Assumption Parish, Louisiana.

Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21368.

Diagnosis (based on ten mature specimens): Body elongate, distinctly bisegmented, 1375 (1000-1600) long by 478 (350-600) at the widest point. Forebody spathulate with lateral margins folded ventrally where they meet at the midline, the entire forebody serving as an organ of attachment, 883 (650-1050) long by 478 (350-600) wide; ear-like appendages present on either side of the oral sucker, rarely observed invaginated to form pseudosuckers. Hindbody conical, 535 (400-650) long by 363 (280-500) wide, containing reproductive organs. Forebody tegument covered with small spines, hindbody tegument smooth. Oral sucker terminal 90 (60-105) long by 73 (60-81) wide; acetabulum weak, spherical, 74 (60-95) long by 75 (60-95) wide, rarely covered by the tribocytic organ; tribocytic organ elongate when evaginated, 453 (310-550) long by 200 (155-225) wide, with a longitudinal cleft. Prepharynx present, 5 (4-6) long; pharynx pyriform, 102 (75-215) long by 64 (55-85) wide; esophagus 6 (4-10) long; paired ceca extend to the posterior end of the body. Testes tandem, not equal; anterior testis asymmetrical, typically wedge-shaped, laterally disposed on either side of the midline, 160 (128-215) long by 225 (175-300) wide; posterior testis symmetrical, dumbbell-shaped much wider than anterior testis, 210 (165-276) long by 340 (275-425) wide, with a ventro-medial groove to allow passage of ceca and uterus; muscular ejaculatory pouch lies posterior to the testes and empties into the genital atrium; genital atrium located in the posterior end of the body, opening on the dorso-subterminal side. Ovary reniform, located in front of the anterior testis on either side of midline, 72 (60-99) long by 167 (100-180) wide; Mehlis' gland opposite the ovary; uterus courses briefly into the forebody and turns immediately posteriad where it empties into the genital atrium; vitellaria located only in the forebody, from just in front of the acetabulum to the forebody-hindbody juncture; vitelline reservoir prominent, located in the hindbody at the level of the anterior testis. Eggs few, large, operculate, 122 (110-128) long by 65 (60-75) wide. Excretory pore terminal, remainder of excretory system not observed.

Discussion: Apparently, adult *Alaria marcianae* have not previously been reported from Louisiana. A single specimen of *A. americana* (= *A. marcianae*) from a dog from Baton Rouge was deposited by G. Dikmans (USNM Helm. Coll. No. 25159). We examined that specimen and identify it as *A. marcianae,* being similar to our material from the bobcat.

In a previous report, the epidemiology of *A. marcianae* mesocercariae was studied in Louisiana and evidence was presented that this species was responsible for an authochtonous human infection (Shoop and Corkum, 1981b). In experimental infections only juvenile raccoons served as definitive hosts for *A. marcianae.* Adult raccoons proved to be refractory to the development of the mesocercarial stage, which remained undifferentiated in the subcutaneous fat. These findings were corroborated in the present study because no adult raccoons were found infected. Two yearlings, however, harbored several adult *A. marcianae* in their duodena. This is the first report of raccoon naturally infected with this species. Though these worms from the yearlings exhibited no morphological anomalies, they were smaller than specimens from the bobcat.

The known definitive hosts for *A. marcianae* in Louisiana now include the domestic dog, bobcat, and juvenile raccoons. In experimental laboratory infections we have found that the domestic cat is a suitable definitive host and that it, as well as feral cats, may play a significant role in the maintenance of *A. marcianae* in Louisiana.

Family OPISTHORCHIIDAE
Braun, 1901

Amphimerus speciosus
(Stiles and Hassal, 1896) Barker, 1911
(Figure 3)

Synonyms: Amphimerus caudalitestis Caballero, Grocott, and Zerecero, 1953; *A. guayaquilensis* (Rodriguez, Gomez, and Montalvan, 1948) Caballero, Grocott, and Zerecero. 1953; *A. interruptus* (Braun, 1901) Barker, 1911; *A. minimus* Thatcher, 1970; *A. neotropicalis* Caballero, Montero-Gei, and Caballero, 1963; *A. parciovatus* Franco, 1967; *A. pricei* (Foster, 1939) Yamaguti, 1958; *A. pseudofelineus* (Ward, 1901) Barker, 1911.

Hosts: Felis domesticus Linn. and *Procyon lotor* (Linn.).

Location: Liver and bile ducts.

Locality: Ramah, Iberville Parish, Louisiana.

Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21369.

Diagnosis (based on ten mature specimens): Body elongate, sharply tapered anterior to the acetabulum, 10.25 (8.0-12.25) mm long by 2010 (1150-2400) at the widest point. Tegument beset with small, stout spines. Oral sucker 268 (240-300) long by 313 (270-340) wide; acetabulum 200 (150-240) long by 218 (170-250) wide. Prepharynx absent; pharynx 183 (160-200) long by 173 (150-190) wide; esophagus 170 (120-200) long; paired ceca extend to the posterior end of body. Testes tandem, in posterior ⅓ of body, transversely elongate, slightly lobed; anterior testis 498 (410-600) long by 925 (550-1150) wide; posterior testis 573 (450-720) long by 925 (550-1150) wide; seminal vesicle elongate, coiled, opens into the genital atrium which is immediately preacetabular. Ovary oval to reniform, may be slightly lobed, 325 (240-450) long by 470 (370-610) wide; seminal receptacle large, lying immediately postovarian, 525 (200-700) long by 473 (320-600) wide; Laurer's canal present, opening on dorsal surface; Mehlis' gland preovarian, sinistral to midline; uterus forming transverse, intercecal coils between the ovary and acetabulum; vitellaria lateral, extracecal, consisting of two pairs of disjunct bundles on each side, each pair separate at level of the ovary; four vitelline ducts fuse mesially at the level of the ovary to form a vitelline reservoir. Eggs small, 28 (25-32) long by 12 (11-14) wide. Excretory pore terminal or slightly subterminal; excretory vesicle sigmoid, coursing anteriorly between the testes and bifurcating immediately posterior to the seminal receptacle.

Discussion: Reports of species of *Amphimerus* from North American mammals have almost exclusively been *A. pseudofelineus* and this name has become well entrenched in veterinary literature. However, Nasir and Diaz (1972) synonymized the following species with *A. speciosus: A. caudalitestis; A. guayaquilensis; A. interruptus; A. minimus; A. neotropicalis; A. parciovatus; A. pricei;* and *A. pseudofelineus.*

Lumsden and Zischke (1963) reported *Amphimerus interruptus* from a yellow-crowned night heron, *Nyctanassa violacea.* Their measurements fall within the ranges we recorded and the specimen figured is remarkably similar to ours, indicating that they are the same species. Lumsden and Zischke also noted similarities between their specimens and the description of *A. speciosus.* These observations corroborate, in part, Nasir and Diaz's (1972) synonymies and further indicate the ability of these organisms to live in both avian and mammalian hosts.

A. speciosus has been reported in cats and dogs from several states in the United States (Rothenbacher and Lindquist, 1963). Chronic morbidity associated with infection includes liver and biliary cirrhosis and pancreatitis. Also, Thatcher (1970) commented on the unassessed possibility of human infection with this species. *A. speciosus* was collected from the liver and bile ducts of one of four domestic cats and two of 37 raccoons in Louisiana. The raccoon apparently is a new host record for this species.

Family HETEROPHYIDAE (Leiper, *1909*) Odhner, *1914*

Cryptocotyle concava (Creplin, 1825) Luhe, 1899

(Figure 4)

Synonyms: Distoma concava Creplin, 1825; *Tocotrema concava* Looss, 1899; *Cryptocotyle echinata* Linstow, 1878.

Hosts: Mustela vison Schreber.

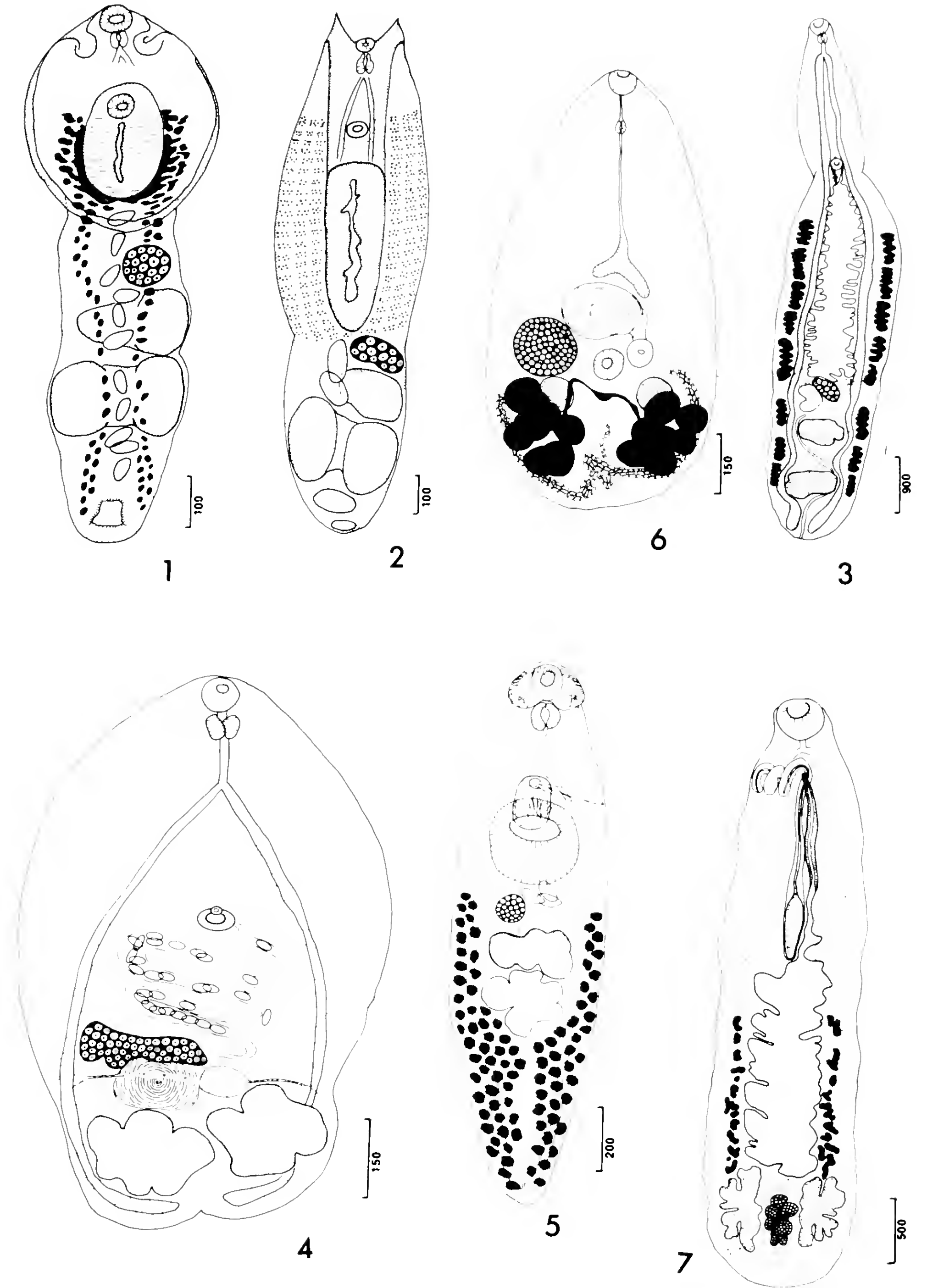
Location: Small intestine.

Locality: Belle River, Assumption Parish, Louisiana.

Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21370.

Diagnosis (based on ten mature specimens): Body foliate, 904 (780-1050) long by 612 (560-680) wide. Tegument beset with small spines. Oral sucker terminal, 47 (35-55) long by 54 (40-65) wide; acetabulum 41 (35-50) in diameter, found within the genital atrium and comprising a part of the acetabulogenital apparatus; acetabulogenital apparatus 67 (60-75) long by 91 (70-125) wide, located medially and equatorially. Prepharynx 10 (5-15) long; pharynx 49 (40-55) long by 48 (45-60) wide; esophagus 76 (65-100) long; paired ceca extend to the posterior end of body where they turn medially just posterior to the testes. Testes opposite, distinctly lobate, 152 (125-175) long by 233 (210-250) wide, located in posterior end of body; seminal vesicle courses from testes to the acetabulogenital apparatus; cirrus pouch absent. Ovary wedge-shaped, lobate, 93 (70-115) long by 138 (100-175) wide, located dextral to the midline, between the ovary and right testis; uterus makes 3-4 intercecal loops before opening into the acetabulogenital complex; vitellaria mostly lateral, commence behind the level of the cecal bifurcation and extend to the posterior end of body where they meet at the midline; vitelline reservoir is located medially, at the level of the seminal vesicle. Eggs small, operculate, 36 (33-40) long by 15 (13-20) wide.

Discussion: Wootton (1957) first reported *Cryptocotyle concava* from North America and elucidated the life cycle. It included an operculate snail, *Amnicola longiqua,* in which rediae gave rise to pleurolophocercous cercariae; these penetrated and



Figures 1-7. 1. *Alaria alarioides* from mink and river otter. 2. *Alaria marcianae* from bobcat and raccoon. 3. *Amphimerus speciosus* from raccoon and the domestic cat. 4. *Cryptocotyle concava* from mink. 5. *Isthmiophora melis* from raccoon and mink. 6. *Microphallus opacus* from raccoon and mink. 7. *Quinqueserialis quinqueserialis* from muskrat. Scales in micrometers.

encysted in three-spined sticklebacks, *Gasterosteus aculeatus.* When infected fish were fed to both chicks and ducklings adult worms were recovered. Hoffman (1957) found metacercariae of *C. concava* in suckers, *Catostomus commersoni,* and also obtained adults from experimentally infected chicks.

The only other report of *C. concava* from North America was that of Burrows and Lillis (1965) who collected specimens from a dog in New Jersey. We compared our specimens with theirs (USNM Helm. Coll. No. 60902) and find no differences between them.

Our report is the first record of *C. concava* from mink. Its occurrence in them is not surprising due to the prevalence of fish in their diet and the lack of definitive host specificity common in heterophyids. Quite possibly, Louisiana veterinarians may encounter eggs of this trematode in routine stool examination of pets. In addition, the possibility of human infection can not be overlooked because *Cryptocotyle* eggs have already been reported from humans elsewhere (Babbot et al., 1961).

Family ECHINOSTOMATIDAE (Looss, 1902) Poche, 1926

Isthmiophora melis (Schrank, 1788) Luhe, 1909

(Figure 5)

Synonyms: Fasciola putori Gmelin, 1790; *Fasciola trigonocephala* Rud., 1802; *Euparyphium melis* (Schrank, 1788) Railliet, 1919; *Echinocirrus melis* (Schrank, 1788) Mendheim, 1943. Mendheim, 1943.

Hosts: Procyon lotor (Linn.) and *Mustela vison* Schreber.

Location: Small intestine.

Locality: Belle River, Assumption Parish, Louisiana.

Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21371.

Diagnosis (based on ten mature specimens): Body lanceolate, 2450 (2000-3500) long by 650 (520-700) wide. Anterior tegument densely covered with spines until the posterior level of the acetabulum, where they diminish in number towards the posterior end of the body. Head collar reniform, bearing 27 spines; each side with 4 corner spines, 59 (57-61) long by 13 (12-14) wide; six marginals on each side, 46 (43-48) long by 11 (9-13) wide; and a double, uninterrupted row of dorsal spines composed of four oral and three aboral spines, 40 (36-44) long by 11 (8-12) wide. Acetabulum large relative to the oral sucker, 380 (350-410) long by 385 (350-430) wide. Prepharynx not discernible; pharynx 130 (110-160) long by 115 (110-140) wide; esophagus 173 (110-210) long; ceca bifurcate immediately anterior to the cirrus sac and extend to the posterior end of the body. Testes tandem, irregular in shape, from strongly indented to completely lobed, posterior testis always more indented or lobate than the anterior testis, both testes wider than long; anterior testis 242 (200-310) long by 348 (310-370) wide; posterior testis 285 (220-410) long by 341 (320-360) wide; cirrus sac ovate, extending from middle of the acetabulum to just posterior to the cecal bifurcation, 265 (220-300) long by 168 (130-200) wide; seminal vesicle distinct; cirrus long, coiled when withdrawn, beset with minute spines. Ovary spherical, dextral to midline, 111 (90-130) long by 114 (90-130) wide, located between the acetabulum and anterior testis; Mehlis' gland broadly oval to reniform, lying immediately in front of the anterior testis; seminal receptacle absent; uterus short, with 3-5 intercecal coils; vitellaria extend from the level of the ovary to the posterior end of body; vitelline reservoir well developed, at the anterior half of the anterior testis. Eggs large, operculate, 97 (95-100) long by 53 (50-60) wide. Excretory pore dorsal and subterminal.

Discussion: Dawes (1946) and Skrjabin and Bashkirova (1956) transferred all the species of *Isthmiophora* to the genus *Euparyphium,* however, Yamaguti (1971) retained the former based on: (1) body shape (lanceolate in *Isthmiophora* whereas *Euparyphium* is subcylindrical); and (2) shape of testes (irregular with lateral indentations in *Isthmiophora* whereas in

Euparyphium they are longitudinally elongated). Based upon a comparative study of several hundred specimens from Louisiana mink and raccoons, our specimens agree with the generic diagnosis of *Isthmiophora* as presented by Yamaguti.

This is the first report of *Isthmiophora melis* from the raccoon and, to our knowledge, the only report of this species from North America. We have found this species in the small intestine of six of 37 raccoons and two of 42 minks. The only other echinostomes found in raccoon are *Euparyphium beaveri* reported by Harkema and Miller (1964) and Bufundo et al. (1980) and *Echinostoma revolutum* which was regarded as an aberrant condition (Larson and Scharf, 1975). Because *Euparyphium beaveri* is also found in minks we compared the type material deposited by Beaver (1941) to our specimens. We find they are very similar in head collar spination and body anatomy, but that they differ strikingly in two respects: (1) the range in size of our specimens (2000-3500) is not concordant with the ranges provided by Beaver (3860 -10500) and the averages are markedly dissimilar (2450 for our material to 6100 for that of Beaver's); and (2) the testes in our specimens are broader than long with either deep marginal indentations or completely lobate, whereas that of *Euparyphium* is longitudinally oval with only slight evidence of indentations in the larger specimens. We conclude that our material is distinct from *Euparyphium beaveri.*

Lumsden and Zischke (1961) rediagnosed *Euparyphium beaveri* from Louisiana minks. A close inspection of their diagnosis indicates they probably were not dealing with *E. beaveri* but with the closely related *Baschkirovitrema incrassatum.* At the time of their diagnosis *B. incrassatum* had not been reported from North America. It is now known to be a common inhabitant of mustelids from the Gulf and Atlantic coasts (Sawyer, 1961; Miller and Harkema, 1964; Fleming et al., 1977; Shoop and Corkum, 1981a). At the time we diagnosed *B. incrassatum* from a river otter in Louisiana we had only specimens from a single otter. We now, however, have a large series of *B. incrassatum* from both river otter and mink and they include the ranges of both our previous material and that given by Lumsden and Zischke (1961). We, therefore, regard *Euparyphium beaveri* of Lumsden and Zischke, 1961 conspecific with *Baschkirovitrema incrassatum.*

Family MICROPHALLIDAE
Travassos, 1920
Microphallus opacus (Ward, 1894)
Ward, 1901
(Figure 6)

Synonyms: Microphallus ovatus Osborn, 1919.

Hosts: Procyon lotor (Linn.) and *Mustela vison* Schreber.

Location: Small intestine.

Locality: Belle River, Assumption Parish, Louisiana.

Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21372.

Diagnosis (based on ten mature specimens): Body oval to pyriform, 1233 (1160-1300) long by 664 (620-700) wide. Tegument spined throughout. Oral sucker subterminal, 67 (60-70) long by 80 (75-90) wide; acetabulum 86 (80-90) long by 91 (90-100) wide. Prepharynx 60 (35-85) long; pharynx weak, 36 (35-40) long by 29 (25-30) wide; esophagus 340 (275-400) long; ceca short, rarely extending beyond the seminal vesicle, occasionally with a single sac. Testes two, opposite, 190 (150-230) long by 135 (75-190) wide, very often the testes are not discernible in gravid specimens; seminal vesicle saccular, preacetabular, opening into the genital atrium; genital atrium lies sinistral to the acetabulum, 62 (55-75) long by 74 (65-80) wide. Ovary spherical to oval in shape, dextral to midline, 150 (110-175) long by 160 (130-205) wide; oviduct sinistral to ovary, courses posteriad to the Mehlis' gland; Mehlis' gland prominent, on the midline of the body between the two bundles of vitellaria; uterus makes several loops in posterior half of body and opens into the genital atrium; vitellaria in two symmetrical clusters of spherical follicles, located in the posterior ⅓ of body; vitelline ducts fuse in the middle of the body at the level of the Mehlis' gland to form a vitelline reservoir. Eggs small, numerous, 25 (25-26) long by 13 (12-14) wide. Excretory vesicle V-shaped, extending to the anterior level of the vitellaria; a single collecting duct arises from each side of the vesicle and courses anteriad to the level of the pharynx.

Discussion: Though *Microphallus opacus* is generally regarded as a fish parasite (Yamaguti, 1971) it has been experimentally established in various reptilian species as well as opossum and raccoon by Rausch (1947) and in white mice by Sogandares-Bernal (1965a). Rausch (1946) also reported it from a naturally infected raccoon from Ohio and provided a brief diagnosis. Our material from raccoon and mink agrees well with that description.

Sogandares-Bernal (1965a) surveyed the crayfish parasites in Louisiana and found *Cambarellus puer* and *Procambarus clarkii* naturally infected with the metacercariae of *Microphallus opacus.* He noted that snails of the genus *Amnicola,* "probably *integra*", released several different types of microphallid cercariae at his study site (Rosedale, Louisiana), one of which he believed to be *M. opacus.* The definitive host at that time was unknown. The life-cycle of *M. opacus* in Louisiana can be postulated using Sogandares-Bernal's report and that of the present work to include the following; an amnicolid snail as first intermediate host; several crayfish species as second intermediate hosts; and the raccoon and mink as definitive hosts. At present, the extent to which *M. opacus* uses fishes as definitive hosts in Louisiana is unassessed as it has yet to be reported from fishes in this state.

Family PARAGONIMIDAE
Dollfus, 1939
Paragonimus kellicotti Ward, 1908

Hosts: Didelphis virginiana Kerr.
Location: Lungs.
Locality: Baton Rouge, East Baton Rouge Parish, Louisiana.
Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21394.

Discussion: We have recovered three mature *Paragonimus kellicotti* from the lungs of a single opossum. We have not figured or diagnosed *P. kellicotti* owing to the paucity of specimens in our possession and to the fact that our specimens are similar to those described by Byrd et al. (1942) which came from the lungs of a Tennessee opossum.

Paragonimus kellicotti metacercariae were reported from crayfish in Louisiana by Ameel (1934) and La Rue and Ameel (1937). Sogandares-Bernal (1965b) reported natural infections of the snail, *Pomatiopsis lapidaria,* with *Paragonimus kellicotti.* Since those accounts, *P. kellicotti* is commonly acknowledged to be present in Louisiana although neither the adult nor the definitive host have been reported from this state.

That the infected opossum was trapped in residential Baton Rouge *is* epidemiologically significant. The location was an upper middle class neighborhood which borders on the flood plain of the Mississippi River. The area of the flood plain in heavily treed, with numerous bayous, and low lying grounds which are nearly always water laden. This scenario is a classical nidus capable of maintaining all of the hosts essential to the life-cycle of *P. kellicotti* and has the potential of including man into the life-cycle owing to his close proximity and crustacean cuisine.

Family NOTOCOTYLIDAE
Luhe, 1909
Quinqueserialis quinqueserialis
(Barker and Laughlin, 1911)
Harwood, 1939
(Figure 7)

Synonyms: Notocotylus quinqueserialis Barker and Laughlin, 1911; *Quinqueserialis hassali* (McIntosh and McIntosh, 1934) Harwood, 1939; *Notocotylus urbanensis* of Harrah, 1922.
Hosts: Ondatra zibethica (Linn.).
Location: Cecum.
Locality: Belle River, Assumption Parish,

TABLE II Compilation of all trematodes reported from Louisiana mammals with pertinent references

Trematode	Hosts	References
[illegible] 1937) [illegible]	mink, otter	(present study)
[illegible]	raccoon, opossum (larval) raccoon, bobcat, dog	Shoop and Corkum, 1981b (present study)
[illegible] 1931	skunk raccoon raccoon, mink	Babero, 1960 Shoop and Corkum, 1981a (present study)
Amphimerus speciosus (Stiles and Hassal, 1896) Barker, 1911	cat, raccoon	(present study)
Allassogonoporus marginalis Olivier, 1938	free tail bat	Martin, 1976
Apophallus venustus (Ransom, 1920) Cameron, 1936	raccoon	Shoop and Corkum, 1981a
Baschkirovitrema incrassatum (Dies., 1850) Skrjabin, 1944	otter otter, mink	Shoop and Corkum, 1981a (present study)
Brachylaima virginiana Dickerson, 1930	opossum skunk mink opossum opossum	Dikmans, 1931 Babero, 1960 Lumsden and Zischke, 1961 Shoop and Corkum, 1981a (present study)
Carneophallus basodactylophallus Bridgman, 1969	raccoon raccoon	Bridgman, 1969 (present study)
C. choanophallus Bridgman, 1969	raccoon, black rat	Bridgman, 1969
Conspicuum icteridorum Denton and Byrd, 1951	free-tail bat	Martin, 1976
Cryptocotyle concava (Creplin, 1825) Luhe, 1899	mink	(present study)
Dicrocoelium rileyi Macy, 1931	free-tail bat free-tail bat	Byrd and Macy, 1942 Martin, 1976
Echinochasmus schwartzi Price, 1931	muskrat muskrat	Byrd and Reiber, 1942 Penn, 1942
Echinostomum sp	opossum	Dikmans, 1931
Echinostoma revolutum (Frohlich, 1802) Looss, 1899	nutria	Babero and Lee, 1961
Euparyphium beaveri Yamaguti, 1958	mink	Lumsden and Zischke, 1961*
Eurytrema procyonis Burrows and Lillis, 1960	red wolf X coyote	Custer and Pence, 1981
Fasciola hepatica Linn 1758	cattle, sheep	Bennett, 1938
Fascioloides magna (Bassi, 1875) Ward, 1917	cattle	Dikmans, 1945
Fibricola cratera (Barker and Noll, 1915) Dubois, 1932	mink, raccoon mink, raccoon, opossum mink, raccoon, opossum	Lumsden and Zischke, 1961 Shoop and Corkum, 1981a (present study)
F. lucida (La Rue and Bosma, 1927) Dubois and Rausch, 1950	opossum opossum, mink raccoon, gray fox mink, opossum	Dikmans, 1931 Lumsden and Zischke, 1961 Shoop and Corkum, 1981a (present study)
Gyrosoma singulare Byrd, Bogitsh, and Maples, 1961	raccoon raccoon, mink raccoon, mink	Shoop and Corkum, 1981a Shoop and Corkum, 1982 (present study)
Hasstilesia texensis Chandler, 1929	swamp rabbit swamp rabbit muskrat	Lumsden and Zischke, 1961 Shoop and Corkum, 1981a (present study)
Heterobilharzia americana Price, 1929	dog, raccoon, nutria nutria opossum opossum, raccoon red wolves, coyotes bobcat, mink, raccoon	Malek et al., 1961 Babero and Lee, 1961 Kaplan, 1964 Shoop and Corkum, 1981a Custer and Pence, 1981a (present study)
Isthmiophora melis (Schrank, 1788) Luhe, 1909	raccoon, mink	(present study)
Linstowiella szidati (Anderson, 1944) Anderson and Cable, 1950	opossum opossum, raccoon	Lumsden and Winkler, 1962 (present study)
Maritrematoides nettae (Gower, 1938) Rankin, 1939	raccoon raccoon, mink	Shoop and Corkum, 1981a (present study)
Microphallus opacus (Ward, 1894) Ward, 1901	raccoon, mink	(present study)
Nudacotyle novicia Barker, 1916	muskrat	Penn, 1942
Ochoterenatrema labda Caballero, 1943	free-tail bat	Martin, 1976
Paragonimus kellicotti Ward, 1908	opossum	(present study)
Parametorchis complexus (Stiles and Hassal, 1894) Skrjabin, 1913	raccoon	Shoop and Corkum, 1981a
Paramonostomum pseudalveatum [illegible]	muskrat	Penn, 1942
Paramphistomum microbothrioides Price and McIntosh, 1944	cattle cattle, sheep	Bennett and Jenkins, 1936 Bennett, 1938
Phagicola angrensis (Travassos, 1916) Yamaguti, 1971	muskrat raccoon	Byrd and Reiber, 1942 Sogandares-Bernal and Bridgman, 1960
Pharyngostomoides procyonis Harkema, 1942	raccoon raccoon	Shoop and Corkum, 1981a (present study)
Plagiorchis vespertilionis (Muller, 1784) Braun, 1900	free tail bat	Martin, 1976
Prosthodendrium swansoni Macy, 1936	free-tail bat	Byrd and Macy, 1942
Psilostomum sp †	skunk nutria (larval)	Babero, 1960 Babero and Lee, 1961
Quinqueserialis quinqueserialis (Barker and Laughlin, 1911) Harwood, 1939	muskrat	(present study)
Rhopalias macracanthus Chandler, 1932	opossum opossum, mink opossum opossum	Dikmans, 1931 Lumsden and Zischke, 1961 Shoop and Corkum, 1981a (present study)
Ribeiroia ondatrae (Price, 1931) Price, 1942†	skunk	Babero, 1972
Sellacotyle vitellosa Sogandares Bernal, 1961	mink mink	Sogandares Bernal, 1961 (present study)
Stichorchis subtriquetrus (Rud., 1814) Looss, 1902	beaver	Bennett and Humes, 1939
Urotrema scabridum Braun, 1900	free-tail bat	Martin, 1976
Zonorchis komareki (McIntosh, 1939) Travassos, 1944	rice rat	Lumsden and Zischke, 1961

*We regard *E. melis* of Lumsden and Zischke, 1961 as a synonym of *Baschkirovitrema incrassatum*. Refer to our discussion of *Isthmiophora melis* in this paper.

†In a recent paper (Shoop and Corkum, 1982) we have stated our reasons for regarding *Psilostomum* sp. and *Ribeiroia ondatrae* as junior synonyms of *Gyrosoma singulare*.

Louisiana.
Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21373.
Diagnosis (based on ten mature specimens): Body elongate, oval, slightly attenuated anteriorly, 3850 (3420-4150) long by 1050 (960-1300) at the greatest width. Tegument aspinous. Ventral surface with five longitudinal rows of spherical glands. Oral sucker subterminal, 335 (320-350) in diameter; acetabulum absent. Pharynx absent; esophagus short, paired ceca extend to posterior end of body. Testes opposite, highly branched, in posterior end of body, 513 (405-610) long by 305 (260-390) wide; external seminal vesicle tubular, coursing anteriad to the base of the cirrus sac; cirrus sac elongate, claviform, 1277 (1050-1500) long by 145 (125-170) at the greatest width; cirrus often extruded and much coiled, densely beset with spines; genital pore median, near intestinal bifurcation. Ovary deeply lobed, intertesticular, 334 (300-390) long by 210 (150-250) wide; Mehlis' gland immediately anterior to ovary; uterus comprised of transverse loops which may extend beyond the ceca; metraterm distinct, 775 (700-900) long; vitellaria pretesticular, in two, extracecal bands. Eggs oval, 17 (16-18) long by 8 (7-9) wide, without polar filaments. Excretory system not observed.
Discussion: Penn (1942) examined 1,780 muskrats from coastal Louisiana and recovered the trematodes *Nudacotyle novicia, Echinochasmus schwartzi,* and *Paramonostomum pseudalveatum.* Byrd and Reiber (1942) examined three muskrats from the New Orleans area and reported *E. schwartzi* and *Phagicola nana* (= *P. angrense*). Because of their declining numbers, we were unable to obtain a large series of muskrats from trappers, but we were successful in obtaining five carcasses. Two of the muskrat harbored hundreds of *Quinqueserialis quinqueserialis* in their ceca. Although this species is considered a ubiquitous parasite of muskrats in North America, this is the first report of it from Louisiana. Our measurements agree well with those provided by Kinsella (1971) in his study of intraspecific variation of *Q. quinserialis.* The life-cycle has been elucidated by Herber (1942) and includes the freshwater snail, *Gyraulis parvus,* from which monostome cercariae are released and encyst on vegetation. The muskrat becomes infected while grazing on vegetation containing the cysts.

Incidentally, one muskrat was infected with thousands of *Hasstilesia texensis* in the cecum (new host record). We have found *H. texensis* in all of the swamp rabbits, *Sylvilagus aquaticus,* that we have examined in Louisiana. As all of the specimens from the muskrat were gravid and showed neither stunting nor any anomalies, we presume that the muskrat may serve occasionally as a normal, definitive host for this species.

SUMMARY

The following trematodes were collected from hunter-trapped mammals in the Atchafalya basin of Louisiana during the winters of 1981 and 1982: *Alaria alarioides* (Dubois, 1937) Dubois, 1970; *Alaria marcianae* (La Rue, 1917) Walton, 1949; *Alaria mustelae* Bosma, 1931; *Amphimerus speciosus* (Stiles and Hassal, 1896) Barker, 1911; *Baschkirovitrema incrassatum* (Dies. 1850) Skrjabin, 1944; *Brachylaima virginiana* Dickerson, 1930; *Carneophallus basodactylophallus* Bridgman, 1969; *Cryptocotyle concava* (Creplin, 1825) Luhe, 1899; *Fibricola cratera* (Barker and Noll, 1915) Dubois, 1932; *Fibricola lucida* (La Rue and Bosma, 1927) Dubois and Rausch, 1950; *Gyrosoma singulare* Byrd, Bogitsh, and Maples, 1961; *Hasstilesia texensis* Chandler, 1929; *Heterobilharzia americana* Price, 1929; *Isthmiophora melis* (Schrank, 1788) Luhe, 1909; *Linstowiella szidati* (Anderson, 1944) Anderson and Cable, 1950; *Maritreminoides nettae* (Gower, 1938) Rankin, 1939; *Microphallus opacus* (Ward, 1894) Ward, 1901; *Paragonimus kellicotti* Ward, 1908; *Pharyngostomoides procyonis* Harkema, 1942; *Quinqueserialis quinqueserialis* (Barker and Laughlin, 1911) Harwood, 1939; *Phopalias macracanthus*

(Chandler, 1932; and *Sellacotyle vitellosa* Sogandares-Bernal, 1961.

Adult trematodes reported from Louisiana for the first time are: *Alaria alarioides, A. marcianae, Amphimerus speciosus, Cryptocotyle concava, Isthmiophora melis, Mircophallus opacus, Paragonimus kellicotti,* and *Quinqueserialis quinqueserialis.*

New host records include *Heterobilharzia americana, Cryptocotyle concava,* and *Maritreminoides nettae* from mink; *Alaria marcianae, Amphimerus speciosus,* and *Linstowiella szidati* from raccoon; and *Hasstilesia texensis* from muskrat.

Natural infections of adult *Alaria marcianae* were found only in juvenile raccoons. This substantiates previous experimental work which demonstrated that adult raccoon are unsuitable for the maturation of this trematode. The larvae, however, are able to employ the adult raccoon as a paratenic host where they remain undifferentiated in the subcutaneous fat.

Amphimerus speciosus is a well known pathogen of dogs and cats in North America, being herein reported from a domestic cat and a raccoon. Synonymization of the better known *A. pseudofelineus* with *A. speciosus* is corroborated by our observations.

Whether *Isthmiophora* is distinct from *Euparyphium* has been debated by several authors. We place our specimens in the genus *Isthmiophora* on the basis of body shape and testicular morphology. We compared our specimens to those of *Euparyphium beaveri* and conclude they are distinct. This is the first report of *I. melis* from a raccoon and, to our knowledge, the only report of this species from North America. We consider *Euparyphium beaveri* of Lumsden and Zischke, 1961 to be a synonym of *Baschkirovitrema incrassatum.*

Microphallus opacus is a common parasite in the mink and raccoon in Louisiana. Sogandares-Bernal (1965a) stated that the aquatic snail, *Amnicola,* probably served as first intermediate host and that several species of crayfish served as second intermediate hosts. Therefore, a hypothetical life-cycle of *M. opacus* from Louisiana can be proposed: the first intermediate host is the aquatic snail, *Amnicola;* several crayfishes serve as second intermediate; and the raccoon and mink are definitive hosts. Fishes have yet to be reported with *M. opacus* from Louisiana.

The first and second intermediate hosts, as well as the larval stages, of *Paragonimus kellicotti* have been previously reported from Louisiana. However, this is the first report from this state of the adult fluke in a naturally infected definitive host, the opossum. The locality of the infection is noteworthy in that it was found in an upper middle class Baton Rouge residential area.

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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 amount of descriptive anatomical work has appeared in print, very little has 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. virgatenuis.*

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.*

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[1] taxon described since Ruthven (1908)

[2] taxon 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 ($p \leq .05$) from ♀♀
post. heart[1]	35	77%	17%	6%	37%
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 11. Sexual dimorphism in certain thamnophiine snakes as reflected by a comparison of male and female means for each taxon.

Character / Taxon	post. heart	ant. liver	post. liver	post. gall. bl.	ant. r. kidney	post. r. kidney	ant. l. kidney	post. l. kidney	liver length	gall bl. length	r. kidney length	l. kidney length	heart-liver interspace	kidney overlap
Clonophis kirtlandii	♂[1]NS	♂ .01[3]	---	---	♀NS	♀NS	♀NS	♂NS	---	---	♂.05	♂.05	♂.01	♂NS
Nerodia cyclopion	♂ .05	♂ NS	♀NS	♀NS	♀NS	♂NS	♀NS	♂NS	♀NS	♀NS	♂.02	♂.02	♀NS	♂.01
erythrogaster	♂ .01	♂ .001	♂NS	♂NS	♀.001	♀NS	♀.001	♂NS	♀NS	♀NS	♂.01	♂.001	♂NS	♂.05
fasciata	♂ NS	♀ NS	♂NS	♂NS	♀.01	♂NS	♀.01	♀NS	♂NS	♀NS	♂.001	♂.001	♀NS	♂.001
rhombifera	♀ NS	♂ NS	♀NS	♀NS	♀NS	♂NS	♀.001	♂NS	♀.05	♀NS	♂.01	♂.01	♂NS	♂NS
sipedon	♂ .001	♂ .02	♂NS	♂NS	♀NS	♂NS	♀.02	♀NS	♀NS	♂NS	♂NS	♂.05	♂.001	♂.01
valida	♀ NS	---	---	---	♀.001	♀NS	♀.01	♀NS	---	---	♂.05	♂.01	---	♂.05
Regina alleni	♂ NS	♂ .02	---	---	♀.05	♀NS	♀.01	= NS	---	---	♂NS	♂.05	♂NS	♂NS
grahamii	♀ NS	---	---	---	♀.001	♀NS	♀.001	♀NS	---	---	♂.01	♂.001	---	♂.001
rigida	♂ NS	---	---	---	♀NS	♀NS	♀NS	♂NS	---	---	♂NS	♂NS	---	♂NS
Seminatrix pygaea	♂ .01	♂ .01	---	---	♀.02	♀NS	♀.01	♀NS	---	---	♂NS	♂NS	♂NS	♂NS
Storeria dekayi	♂ .001	♂ .001	♂.001	♂.05	♀NS	♀NS	♀NS	♂NS	♀NS	♂NS	♂NS	♂NS	♂NS	♂NS
occipitomaculata	♂ NS	♂ NS	♂NS	---	♀.001	♀.01	♀.01	♂NS	= NS	---	♂.001	♂.001	♂NS	♀NS
Thamnophis brachystoma	♂ NS	---	---	---	♀.001	♀.01	♀.001	♀NS	---	---	♂NS	♂.001	---	♂NS
butleri	♂ NS	---	---	---	♀.001	♀.01	♀.01	♀NS	---	---	♂NS	♂.001	---	♀NS
chrysocephalus	♂ NS	♂NS	---	---	♀.01	♀.05	♀.01	♀NS	---	---	♂NS	♂.01	♂NS	♂NS
couchii A[4]	♂ NS	---	---	---	♀.001	♀.01	♀.01	♀.05	---	---	♂NS	♂.01	♂NS	♂NS
couchii B[5]	---	♂NS	♀NS	♂NS	♀.001	♀.001	♀.001	♀.001	♀NS	♂NS	♂.01	♂NS	♂NS	♀NS
cyrtopsis	♂ NS	♂NS	♂NS	♂NS	♀.001	♀.01	♀.001	♀.02	♂NS	♀NS	♂NS	♂.01	♀NS	♂NS
elegans A[6]	♂ NS	= NS	♀NS	♀NS	♀.01	♀.05	♀.001	♀.05	♀NS	♂NS	♂NS	♂.01	♀NS	♂NS
elegans B[7]	♂ .01	♂.01	♀NS	♀.02	♀.001	♀.001	♀.001	♀.001	♀NS	♀.01	♂.001	♂.001	♂NS	♂.05
eques	♀ NS	♂NS	♀.01	♀.05	♀.001	♀.001	♀.001	♀.01	♀.02	♂NS	♂NS	♂NS	---	♂NS
godmani	= NS	♀NS	---	---	♀.001	♀.001	♀.001	♀NS	---	---	♂.001	♂.001	♀NS	♂NS
marcianus	♂ NS	♂NS	♂NS	♂NS	♀.01	♀NS	♀.01	♀NS	♂NS	♀NS	♂NS	♂NS	♀NS	♂NS
melanogaster	♀ NS	♀NS	♀NS	♂NS	♀.001	♀.02	♀.01	♀.05	♀NS	♀NS	♂NS	♂.05	♀NS	♂NS
nigronuchalis	♂ .001	---	---	---	♀.01	♀NS	♀NS	♂NS	---	---	♂.01	♂.001	---	♂NS
ordinoides	♂ NS	---	---	---	♀.01	♀.01	♀.001	♀.02	---	---	♂NS	♂.02	---	♂NS
proximus	♂ NS	♂NS	♂.05	♂.01	♀.001	♀NS	♀.01	♀NS	♀NS	♀NS	♂.01	♂.001	♂NS	♂NS
radix	♂ .05	♂.05	♀.02	♂NS	♀.001	♀.02	♀.001	♀.05	♀.01	♀NS	♂NS	♂.01	♂NS	♂NS
rufipunctatus	♀ NS	♀NS	---	---	♀.01	♀.05	♀.02	♀NS	---	---	♂NS	♂NS	♂NS	♀NS
sauritus	♂ .01	---	---	---	♀.001	♂NS	♀.01	♂NS	---	---	♂.001	♂.001	---	♂.01
scalaris	---	♂.01	---	---	♀.05	♀.01	♀.01	♀.01	---	---	= NS	♂NS	---	♂NS
sirtalis A[8]	♂ .05	♂NS	= NS	♂NS	♀.001	♀.001	♀.001	♀.001	♀NS	♀NS	♀ NS	♂ .01	♂NS	= NS
sirtalis B[9]	= NS	♂NS	---	---	♀NS	♀NS	♀.02	♀.05	---	---	♀ NS	♂NS	♂NS	♀NS
Tropidoclonion lineatum[10]	♂ .001	---	---	---	♀.001	♀NS	♀.001	♀NS	---	---	♂.001	♂.001	---	♂NS
Virginia striatula	♂ .001	♂.01	---	---	♀.02	♀NS	♀.05	♀NS	---	---	♂.01	♂NS	♂NS	♂NS
valeriae[11]	♂ .01	♂.001	♂NS	---	♀.001	♀.02	♀.01	♀NS	---	---	♂.05	♂.001	♂.02	♂NS

[1] indicates which sex has organ position situated more posteriorly (or the longer organ); [2] NS indicates not significantly different at p>.05; [3] indicates significantly different at designated level; [4] *T. c. couchii*; [5] *T. c. hydrophilus*; [6] *T. elegans terrestris*; [7] *T. elegans vagrans*; [8] *T. sirtalis fitchi*; [9] *T. sirtalis sirtalis*; [10] *T. lineatum* from Nebraska; [11] *V. valeriae 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.

Character / Taxon	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																								
Natrix (=Rhabdophis) chrysarga[1]																						X		X
N. (=Rhabdophis) subminiata[2]	X		X		X					X		X		X		X					X		X	
N. (=Sinonatrix) triangulígera[1]																			X		X		X	
N. (=Xenochrophis) vittata[3]																					X		X	
Colubridae																								
Ablabes (=Gongylosoma) baliodeira[4]	X		X		X		X			X	X			X	X		ND				X		X	
Calamaria multipunctata[5]	X		X		X																			
Coluber melanurus (=Elaphe flavolineata)[6]	X		X		X					X		X		X		X								
Dendrophis (=Dendrelaphis) pictus[7]																	ND		ND		X		X	
Colubridae, Homalopsinae																								
Enhydris plumbea[8]	X		X		ND		ND			X		X		X		X					X		X	
Fordonia leucobalia[8]																			X		X		X	
Homalopsis buccata[9]																	ND				ND		ND	
Hypsirhina (=Enhydris) alternans[8]	X		X		X				ND		ND		ND		ND		ND		ND		ND		ND	
Acrochordidae																								
Acrochordus granulatus[10]	X		X		X					X		X		X		X	ND				ND		ND	
A. javanicus[10]	X		X		X					X		X		X		X	ND							
Aniliidae																								
Cylindrophis rufus[11]	ND		ND		ND		ND		ND		ND		ND				ND		ND		ND		ND	
Boidae																								
Xenopeltis unicolor[12]	ND								ND		ND		ND		ND		ND		ND		ND		ND	
Elapidae																								
Hydrophis fasciatus[13]																			X					
Viperidae																								
Agkistrodon piscivorus[14]	X																ND		ND		ND		ND	
Trimeresurus gramineus[15]	X		X		X					X				X			X		X		X		X	

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

Table IV. A comparison of various taxa in terms of the triads into which they fall. L represents the lowest triad, M the middle triad, and H the highest triad.

Character Taxon	post. heart		ant. liver		post. liver		post. pancreas		ant. r. kidney		post. r. kidney		ant. l. kidney		post. l. kidney		liver length		r. kidney length		l. kidney length		kidney overlap		heart-liver interspace	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Clonophis kirtlandii	L	M	M	L	-	-	-	-	H	H	H	H	H	H	M	M	-	-	M	M	M	M	M	M	M	L
Nerodia cyclopion	M	M	M	M	M	M	M	M	M	M	H	M	M	M	M	M	M	L	M	M	M	M	H	H	M	M
erythrogaster	L	M	M	L	M	M	M	M	M	L	M	M	M	L	M	M	M	L	M	H	H	H	H	M	M	M
fasciata	M	M	M	M	M	M	M	M	M	M	H	H	M	M	M	M	M	L	H	H	H	M	H	H	M	M
rhombifera	H	H	H	M	M	M	M	M	M	M	H	M	M	M	M	M	L	L	M	H	M	M	H	H	M	M
sipedon	M	M	M	M	M	M	M	M	M	M	H	M	M	M	M	M	M	L	M	H	M	H	H	M	M	M
valida	M	M	-	-	-	M	-	L	M	M	M	M	M	M	M	M	-	-	M	M	M	M	H	M	-	-
Regina alleni	H	H	H	H	-	-	-	-	M	M	M	M	M	M	M	M	-	-	M	M	M	M	M	M	H	H
grahamii	M	M	-	M	-	M	-	M	M	M	H	H	M	H	M	H	-	L	M	M	M	M	M	M	-	M
rigida	M	M	-	M	-	M	-	H	M	M	M	M	M	M	M	M	-	L	M	M	M	M	M	M	-	M
septemvittata	M	-	M	-	M	-	-	-	M	-	M	-	M	-	M	-	M	-	M	-	M	-	M	-	M	-
Seminatrix pygaea	H	H	H	H	-	-	-	-	H	H	H	H	H	H	M	H	-	-	L	M	L	L	M	M	H	H
Storeria dekayi	M	M	M	L	H	M	H	M	M	M	M	M	H	H	H	H	H	M	M	M	M	M	M	M	M	M
occipitomaculata	M	M	M	L	M	M	H	-	M	H	M	M	H	H	H	M	H	M	M	L	M	L	L	L	M	M
Thamnophis proximus	M	M	M	M	M	M	H	H	H	H	H	H	H	H	H	H	M	L	M	M	M	M	M	M	M	M
Sauritus sauritus	H	H	-	M	-	M	-	M	H	H	H	H	H	H	H	H	-	L	M	M	L	L	M	M	-	M
group[1]																										
Thamnophis brachystoma	L	M	-	-	-	-	-	-	M	M	M	M	M	M	M	M	-	-	M	M	M	M	M	M	-	-
butleri	M	M	-	-	-	-	-	-	M	M	M	M	M	M	M	M	-	-	M	M	M	M	M	M	-	-
Radix eques	L	L	L	L	L	L	L	L	L	M	L	M	L	M	L	M	L	L	M	H	M	H	M	M	M	-
group *marcianus*	L	L	L	L	L	L	M	M	M	M	M	M	M	M	M	M	M	L	M	H	M	M	M	M	M	M
radix	L	L	L	L	L	L	M	M	M	M	M	H	M	M	M	H	M	M	M	H	M	H	M	H	M	L
Thamnophis couchii A	M	M	L	-	L	-	M	-	L	M	L	M	L	L	L	M	L	-	M	M	M	M	M	M	M	L
couchii B	M	M	M	L	M	M	M	M	L	M	L	M	M	M	M	M	M	L	M	M	M	H	M	M	M	M
elegans A	L	L	L	L	L	L	M	-	L	L	L	M	L	L	L	M	L	L	M	H	H	M	M	M	M	M
elegans B	L	L	L	L	L	L	M	M	L	L	L	M	L	L	L	M	M	L	M	M	H	H	M	M	M	L
Elegans melanogaster	M	H	M	M	M	M	M	L	M	M	M	M	M	M	M	M	M	L	M	H	M	H	M	M	M	M
group *nigronuchalis*	M	M	-	L	-	M	-	L	L	L	L	L	L	L	L	L	-	L	M	M	M	M	M	M	-	M
ordinoides	L	M	-	-	-	-	-	-	M	M	M	M	M	M	M	M	-	-	M	M	M	M	M	M	-	-
rufipunctatus	M	M	M	M	-	-	-	-	L	M	L	M	L	L	L	L	-	-	M	M	M	M	M	M	M	M
scalaris	-	L	M	L	-	-	-	-	M	M	M	M	M	M	M	M	-	-	M	H	M	H	H	H	-	L
Thamnophis chrysocephalus	M	M	M	M	-	-	-	-	M	M	M	M	M	M	M	M	-	-	M	M	M	M	M	M	M	M
cyrtopsis	L	L	L	L	L	L	M	L	L	L	M	M	L	L	M	M	M	L	M	H	M	H	H	H	L	M
Sirtalis godmani	L	M	M	L	-	-	-	-	L	M	L	M	L	M	M	M	-	-	M	M	H	M	M	M	M	M
group *sirtalis A*	L	L	L	L	L	L	M	M	M	M	M	M	M	M	M	M	M	L	M	H	M	M	M	M	M	M
sirtalis B	L	L	L	L	-	M	-	M	M	M	M	M	M	M	M	M	-	L	M	H	M	M	M	M	M	M
Tropidoclonion lineatum A	L	L	-	-	-	-	-	-	M	H	M	M	H	H	M	M	-	-	L	L	L	L	M	M	-	-
lineatum B	-	L	-	L	-	M	-	H	-	H	-	M	-	H	-	M	-	M	-	L	-	L	-	L	-	M
Virginia striatula	M	M	M	L	-	M	-	M	H	H	M	H	H	H	M	M	-	M	L	L	L	L	L	L	M	L
valeriae	M	M	M	L	H	H	-	M	H	H	M	M	H	H	M	M	H	H	L	L	L	L	M	M	M	L

[1] Ruthven's species groups

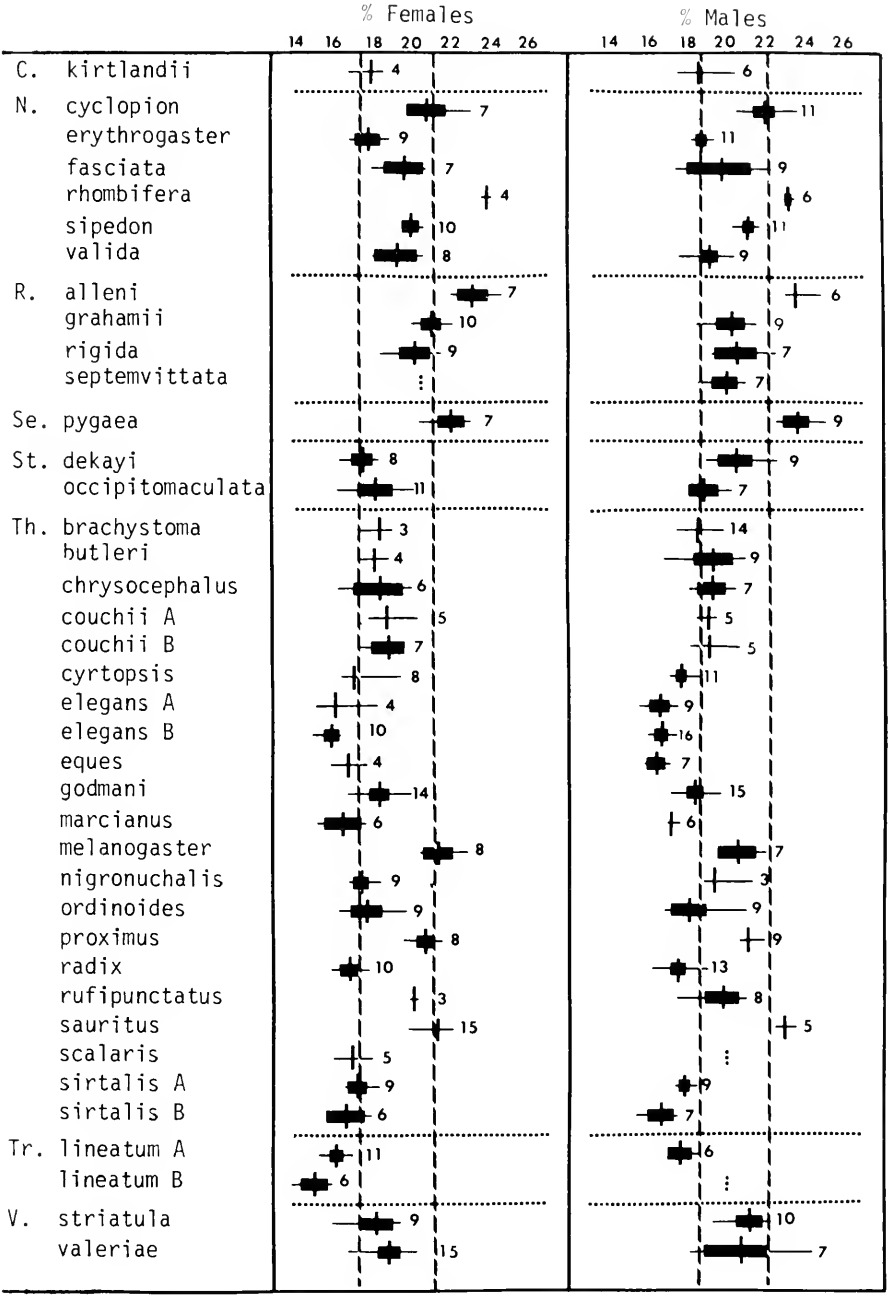

Figure 1. Location of the posterior end of the heart in thamnophiine snakes (expressed as a % of total ventrals). Construction of this and subsequent graphs is explained on pp. 127-129

Table V.--Frequency of significant differences between one taxon and all other taxa in this study expressed as a per cent.

Character / Taxon	post. heart		ant. liver		post. liver		post. pancreas		ant. r. kidney		post. r. kidney		ant. l. kidney		post. l. kidney		liver length		r. kidney length		l. kidney length		kidney overlap		heart-liver interspace	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Clonophis kirtlandii	58	46	61	55	--	--	--	--	81	89	65	51	73	84	62	41	--	--	49	59	76	76	48	38	26	61
Nerodia cyclopion	94	78	82	84	68	64	29	26	78	62	81	43	70	49	57	43	21	33	54	49	62	43	81	57	33	74
erythrogaster	69	62	68	74	89	72	35	48	78	73	62	62	70	81	57	57	42	38	76	62	78	65	68	57	11	26
fasciata	49	68	64	77	74	68	53	57	76	59	81	49	68	49	62	46	79	25	73	49	76	38	70	54	26	13
rhombifera	89	97	96	90	68	68	53	39	70	59	76	43	65	49	54	35	26	42	57	43	38	35	76	54	41	19
sipedon	81	86	86	84	74	60	59	22	78	57	70	41	65	62	54	51	32	35	43	62	43	54	73	51	77	55
valida	69	62	--	--	--	60	--	43	78	62	65	43	62	57	57	35	--	--	49	35	38	35	70	43	--	--
Regina alleni	89	97	96	94	--	--	--	--	86	78	70	38	73	84	43	35	--	--	46	54	49	81	24	57	96	81
grahamii	66	86	--	87	--	60	--	43	73	84	68	51	78	84	43	84	--	79	30	68	46	76	35	43	--	81
rigida	66	84	--	74	--	60	--	83	65	57	54	68	62	49	51	81	--	50	49	57	62	54	49	49	--	71
septemvittata	66	--	79	--	79	--	--	--	70	--	65	--	78	--	49	--	16	--	41	--	59	--	43	--	74	--
Seminatrix pygaea	89	92	96	97	--	--	--	--	92	84	81	84	86	84	78	84	95	--	89	78	89	81	62	27	96	90
Storeria dekayi	67	62	79	65	89	52	88	57	78	81	68	43	81	86	92	92	84	88	51	57	35	35	65	51	15	23
occipitomaculata	66	51	46	71	79	44	53	--	73	86	57	32	84	78	62	43	79	67	62	84	32	84	95	68	15	23
Thamnophis proximus	78	84	64	74	74	60	94	83	92	84	97	97	89	89	95	95	5	38	43	59	78	81	38	46	19	23
Sauritus sauritus	89	84	--	81	--	48	--	61	92	84	97	95	95	89	92	95	--	29	57	78	78	92	46	68	--	23
group																										
Thamnophis brachystoma	71	57	--	--	--	--	--	--	76	57	65	38	73	70	51	35	--	--	41	38	43	38	43	19	--	--
butleri	51	59	--	--	--	--	--	--	73	70	65	30	68	65	49	35	--	--	43	49	41	59	32	46	--	--
Radix *eques*	92	59	75	74	100	60	100	43	81	65	68	49	84	49	57	32	32	33	24	57	11	41	38	38	26	16
group *marcianus*	86	73	50	42	79	68	35	35	73	54	57	35	65	59	16	35	26	42	54	41	27	38	59	27	15	10
radix	83	81	61	81	68	72	41	35	76	65	58	57	70	76	54	76	26	50	54	57	49	49	57	51	**22**	35

Table V. Continued

Taxon	**Character**	post. heart	ant. liver	post. liver	post. pancreas	ant. r. kidney	post. r. kidney	ant. l. kidney	post. l. kidney	liver length	r. kidney length	l. kidney length	kidney overlap	heart-liver interspace
Thamnophis	*couchii* A	63 62	54 --	79 --	65 --	81 59	76 86	73 51	59 73	42 --	43 41	43 30	51 14	15 26
	couchii 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
	elegans 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
	elegans 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
Elegans	*melanogaster*	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
group	*nigrouchalis*	54 68	-- 55	-- 76	-- 63	81 92	81 97	70 92	70 100	-- 33	19 68	32 43	41 62	-- 29
	ordinoides	63 62	-- --	-- --	-- --	54 43	62 35	68 49	46 43	-- --	27 38	27 35	46 22	-- --
	rufipunctatus	60 76	61 68	-- --	-- --	78 32	81 76	76 68	81 76	-- --	46 24	32 19	35 16	44 10
	scalaris	-- 54	57 61	-- --	-- --	57 54	51 38	68 38	57 35	-- --	46 41	32 32	65 68	-- 26
Thamnophis	*chrysocephalus*	66 43	43 55	-- --	-- --	54 51	59 65	51 54	41 38	-- --	35 51	32 51	35 51	15 16
	cyrtopsis	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
Sirtalis	*godmani*	80 68	64 74	-- --	-- --	86 70	81 76	78 73	57 84	-- --	57 32	62 51	43 49	30 26
group	*sirtalis* 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
	sirtalis B	89 62	61 55	-- 48	-- 22	54 59	51 49	68 54	62 38	-- 25	41 49	38 38	24 30	22 19
Tropidoclonion	*lineatum* A	83 86	-- --	-- --	-- --	86 84	57 27	84 84	43 43	-- --	84 92	81 92	54 73	-- 71
	lineatum B	-- 97	-- 42	-- 76	-- 91	-- 78	-- 38	-- 73	-- 32	-- 75	-- 81	-- 86	-- 84	-- --
Virginia	*striatula*	77 57	68 52	-- 68	-- 48	92 86	51 46	78 84	30 43	-- 88	97 97	100 95	76 78	22 26
	valeriae	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 prounced 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 posteriorly. 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 *Seminatrix pygaea, Thamnophis sauritus, Tropidoclonion lineatum,* and the two species of *Virginia,* and in females of *Clonophis kirtlandii, 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.

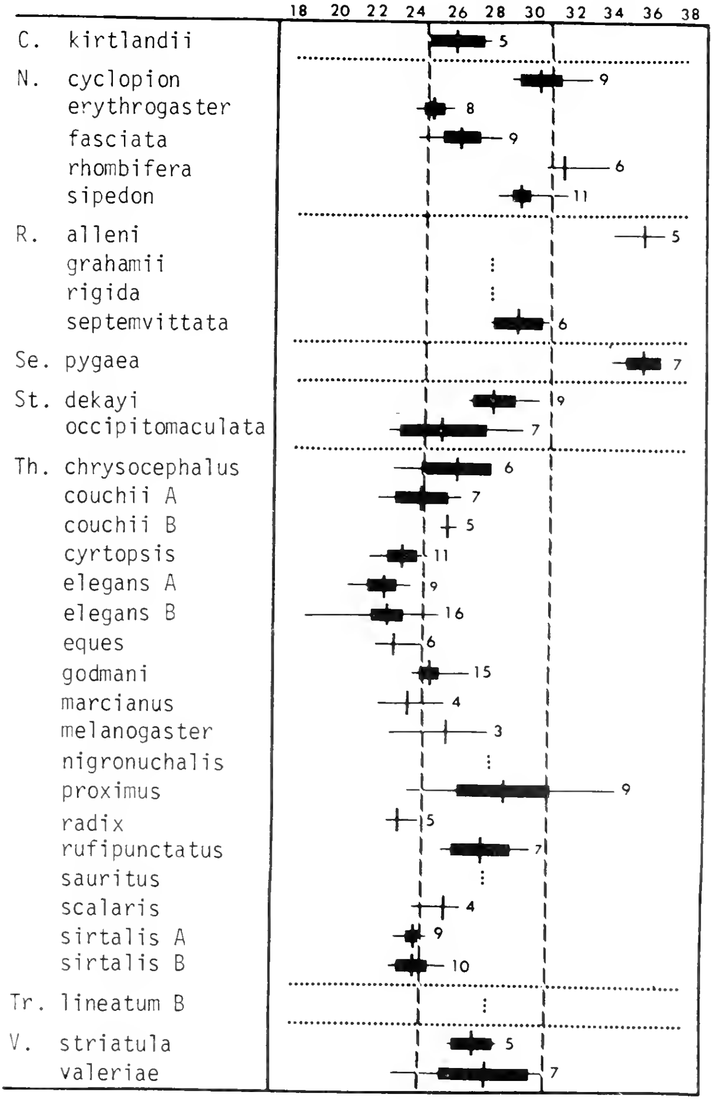

Figure 2. Location of the anterior end of the liver in male thamnophiine snakes (expressed as a % of total ventrals).

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

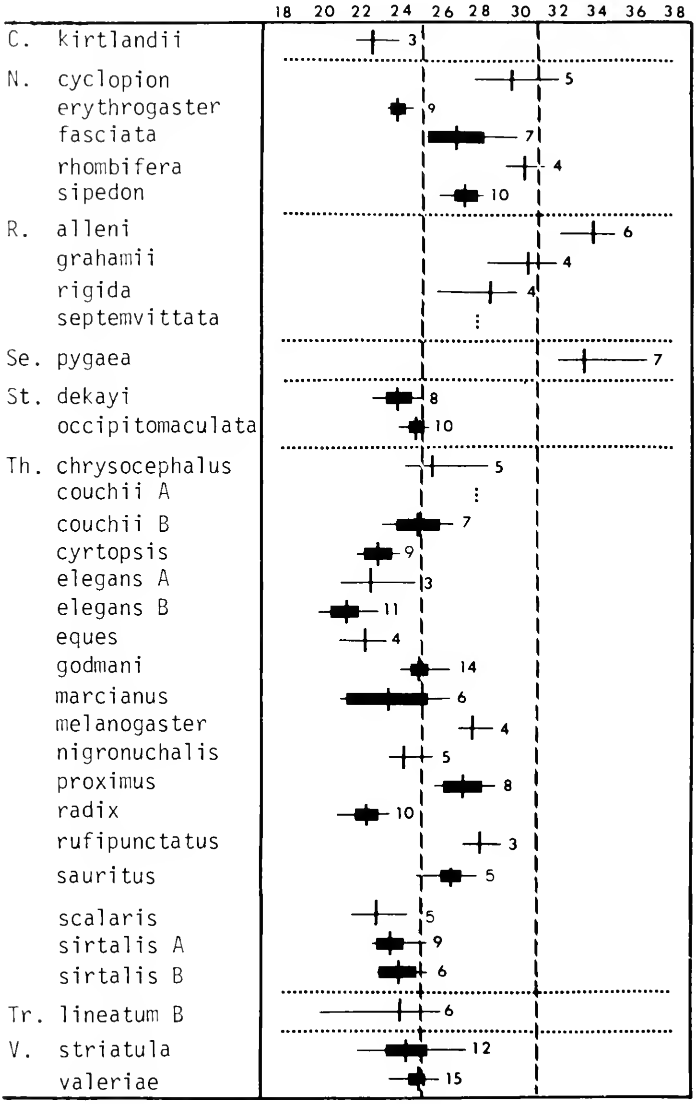

Figure 3. Location of the anterior end of the liver in female thamnophiine snakes (expressed as a % of total ventrals).

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*) *alternans* (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 Colubribae — *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), *Ptyas 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

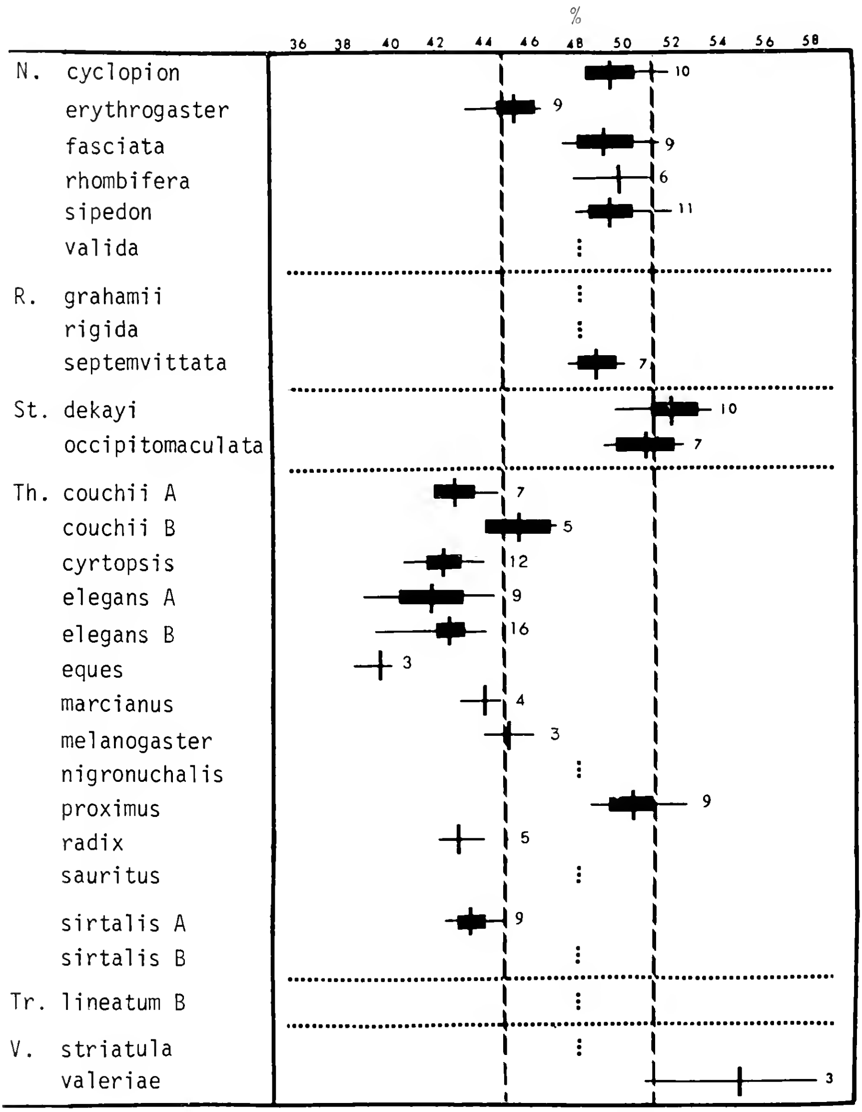

Figure 4. Location of the posterior end of the liver in male thamnophiine snakes (expressed as a % of total ventrals).

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 *Clonophis*	2	3	4	5	6	7	8	9	10
2 *Nerodia*	16.557 0.0000*									
3 *Regina*	7.4392 0.0000	15.827 0.0000								
4 *Seminatrix*	11.479 0.0000	26.348 0.0000	9.4137 0.0000							
5 *Storeria*	6.7379 0.0000	52.616 0.0000	20.963 0.0000	20.288 0.0000						
6 *Thamnophis* (*Sauritus* group)	6.5426 0.0000	27.357 0.0000	11.059 0.0000	5.1882 0.0005	14.861 0.0000					
7 *Thamnophis* (*Radix* 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 *Thamnophis* (*Elegans* 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 *Thamnophis* (*Sirtalis* 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 *Tropidoclonion*	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 *Virginia*	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	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Nerodia						
cyclopion	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)	1.3(0.5-2.7)	1.2(0.6-2.0)
erythrogaster	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)	2.9(2.0-4.0)	2.3(1.0-3.8)
fasciata	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)	1.7(1.0-2.7)	1.8(1.3-3.0)
rhombifera	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)	2.0(1.0-4.1)	1.3(1.0-1.5)
sipedon	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)	1.5(0.3-4.0)	1.8(0.6-3.4)
valida	---	5.4(3.6-7.4)4	---	2.4(2.2-3.1)	---	2.2(1.6-3.4)
Regina						
alleni	---	7.2(4.1-9.5)3	---	2.4(1.6-3.3)	---	3.5(1.2-5.9)
grahamii	---	5.7(3.5-6.7)4	---	2.4(2.3-2.5)	---	2.4(1.5-2.8)
rigida	---	8.4(6.0-9.6)5	---	2.6(1.5-3.6)	---	3.6(2.1-6.4)
septemvittata	8.0(4.9-9.4)4	---	2.5(2.0-3.0)	---	3.4(1.8-4.4)	---
Storeria						
dekayi	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)	2.3(1.0-3.9)	2.1(1.0-2.5)
occipitomaculata	3.3(1.7-4.9)6	---	2.4(1.6-3.4)	---	1.6(0.5-3.1)	---
Thamnophis						
couchii A	6.3(3.0-9.5)4	---	2.3(1.8-2.8)	---	2.9(1.3-5.3)	---
couchii 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)	2.6(2.0-3.7)	2.3(1.0-3.6)
cyrtopsis	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)	4.3(2.3-6.8)	3.9(2.4-6.4)
elegans A	8.9(6.3-11.5)7	9.4(7.6-12.1)3	2.5(2.5-2.6)	2.4(2.1-2.7)	3.5(2.5-4.6)	3.8(3.0-4.5)
elegans 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)	4.2(2.5-8.7)	3.9(2.2-5.6)
eques	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)	2.7(1.7-4.1)	3.5(2.7-4.0)
marcianus	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)	3.2(1.7-8.7)	3.9(1.8-6.4)
melanogaster	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)	2.6(2.3-2.7)	0.9(0.7-1.4)
nigronuchalis	---	3.8(0.6-5.9)7	---	2.1(1.3-2.6)	---	1.9(0.2-2.7)
proximus	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)	5.0(3.0-7.4)	5.2(3.4-6.7)
radix	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)	3.8(2.0-5.5)	2.5(0.4-4.2)
sauritus	---	6.8(3.8-9.9)5	---	1.5(1.2-2.5)	---	5.2(2.3-8.3)
sirtalis 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)	4.0(2.8-5.1)	2.7(0.7-3.7)
sirtalis B	---	6.2(5.2-7.8)6	---	2.1(1.9-2.6)	---	3.1(2.0-4.1)
Tropidoclonion						
lineatum B	---	7.9(6.7-8.8)4	---	2.2(2.2-2.3)	---	3.5(3.0-4.0)
Virginia						
striatula	---	4.7(1.7-8.8)4	---	2.4(1.7-3.1)	---	2.0(1.0-4.0)
valeriae	---	1.6(-2.4-5.5)3[2]	---	2.7(1.6-3.3)	---	0.2(-1.5-1.7)[2]

[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 specimens, 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

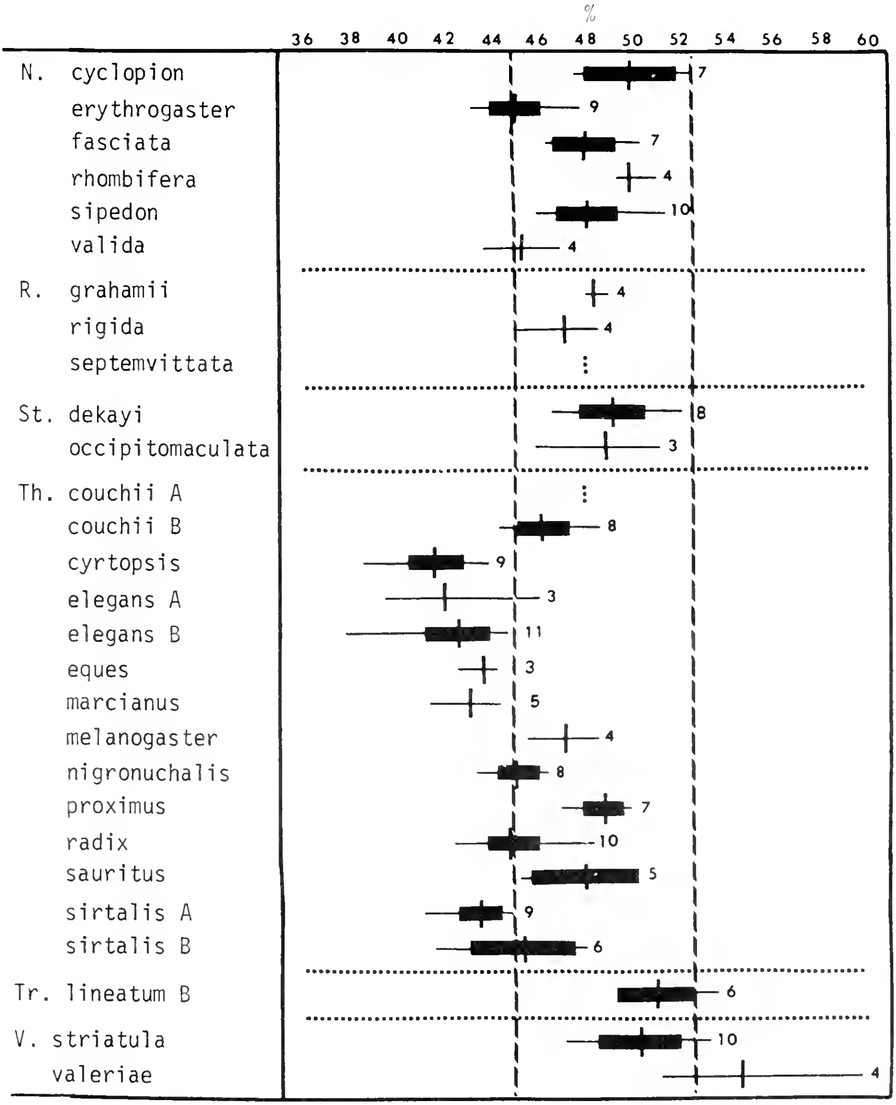

Figure 5. Location of the posterior end of the liver in female thamnophiine snakes (expressed as a % of total ventrals).

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

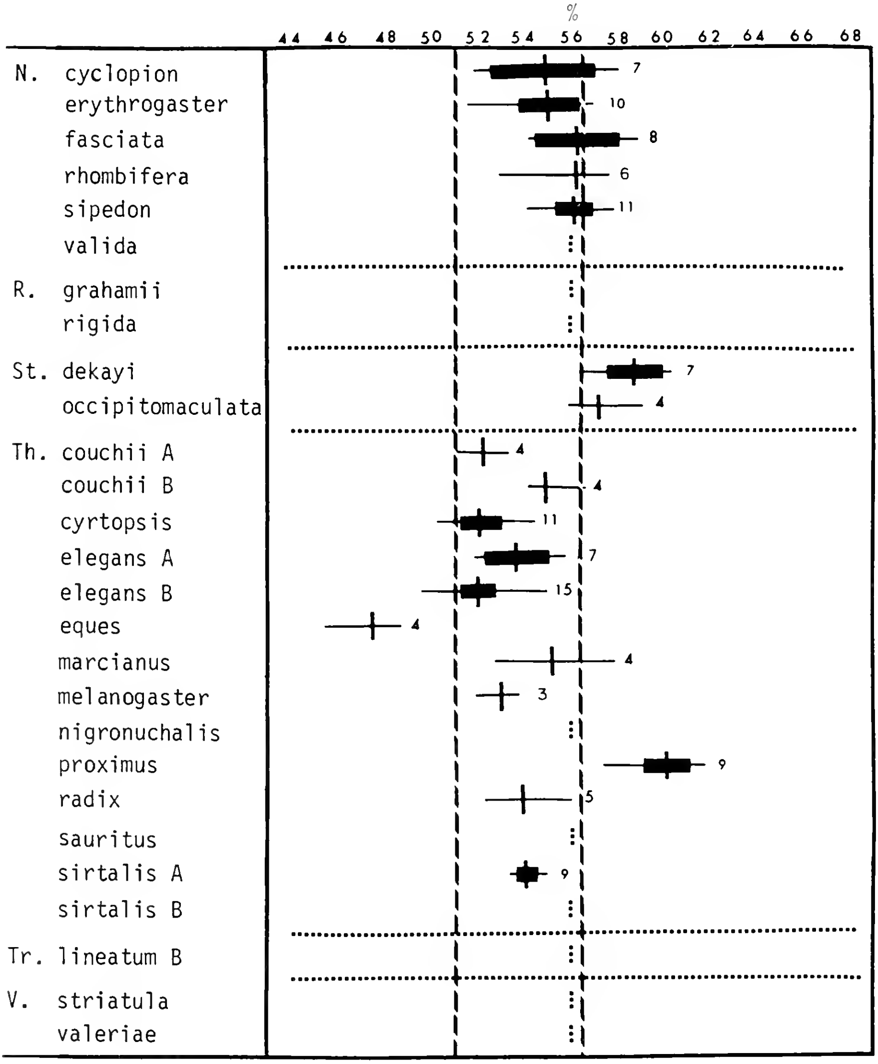

Figure 6. Location of the posterior end of the pancreas in male thamnophiine snakes (expressed as a % of total ventrals).

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

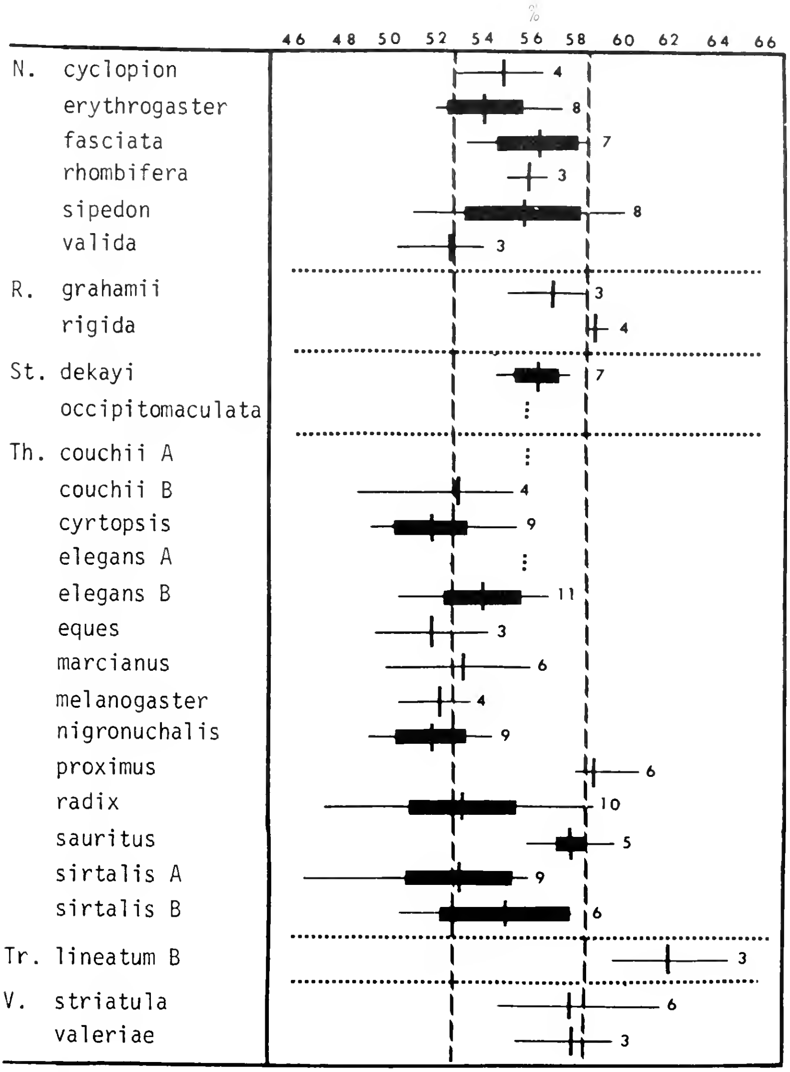

Figure 7. Location of the posterior end of the pancreas in female thamnophiine snakes (expressed as a % of total ventrals).

Table VIII. Classification matrix.

Actual Taxon	No. of Cases	Predicted Taxon Membership 1	2	3	4	5	6	7	8	9	10	11
1 *Clonophis*	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 *Nerodia*	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 *Regina*	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 *Seminatrix*	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 *Storeria*	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 *Thamnophis* *(Sauritus 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 *Thamnophis* *(Radix 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 *Thamnophis* *(Elegans 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 *Thamnophis* *(Sirtalis 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 *Tropidoclonion*	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 *Virginia*	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

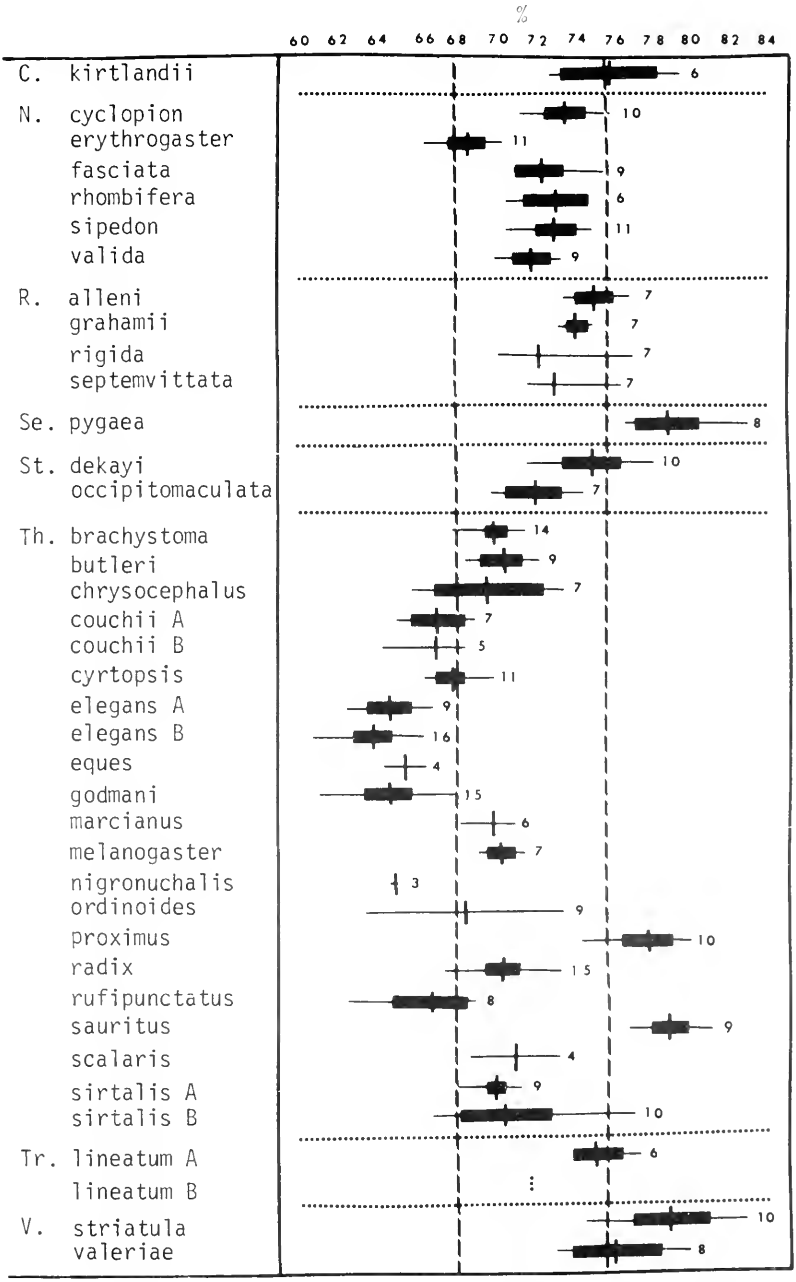

Figure 8. Location of the anterior end of the right kidney in male thamnophiine snakes (expressed as a % of total ventrals).

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

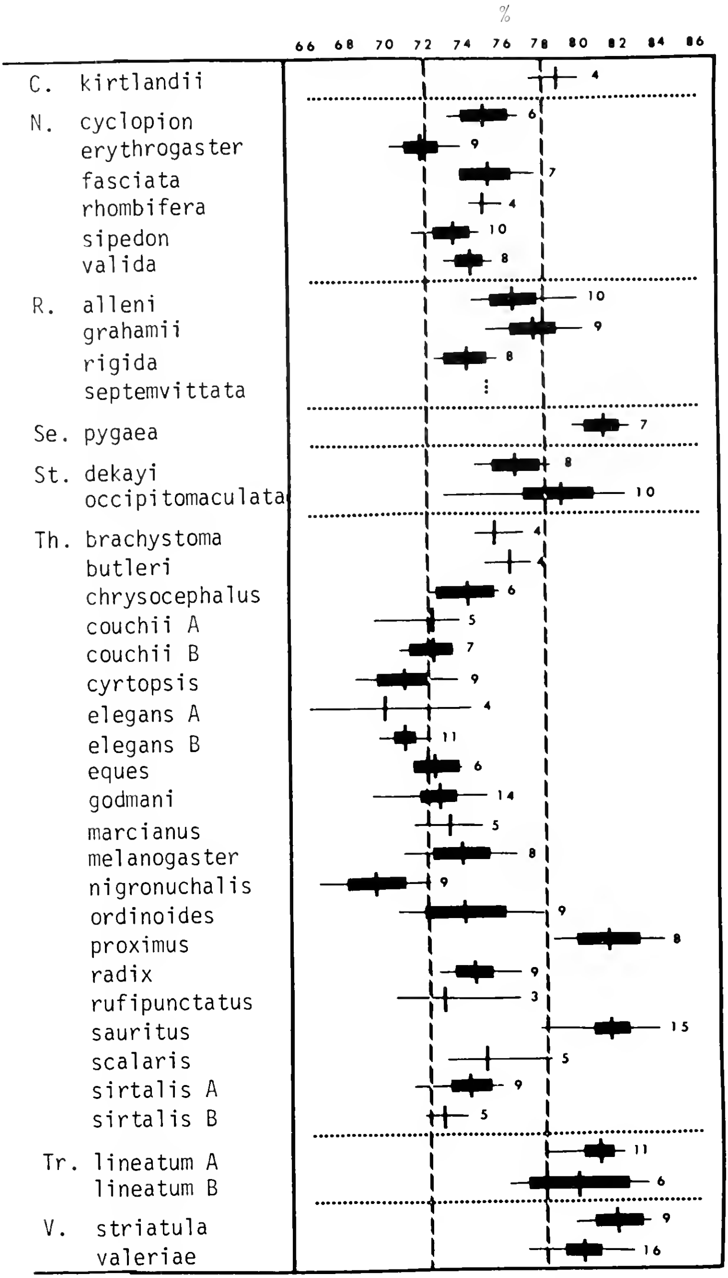

Figure 9. Location of the anterior end of the right kidney in female thamnophiine snakes (expressed as a % of total ventrals).

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

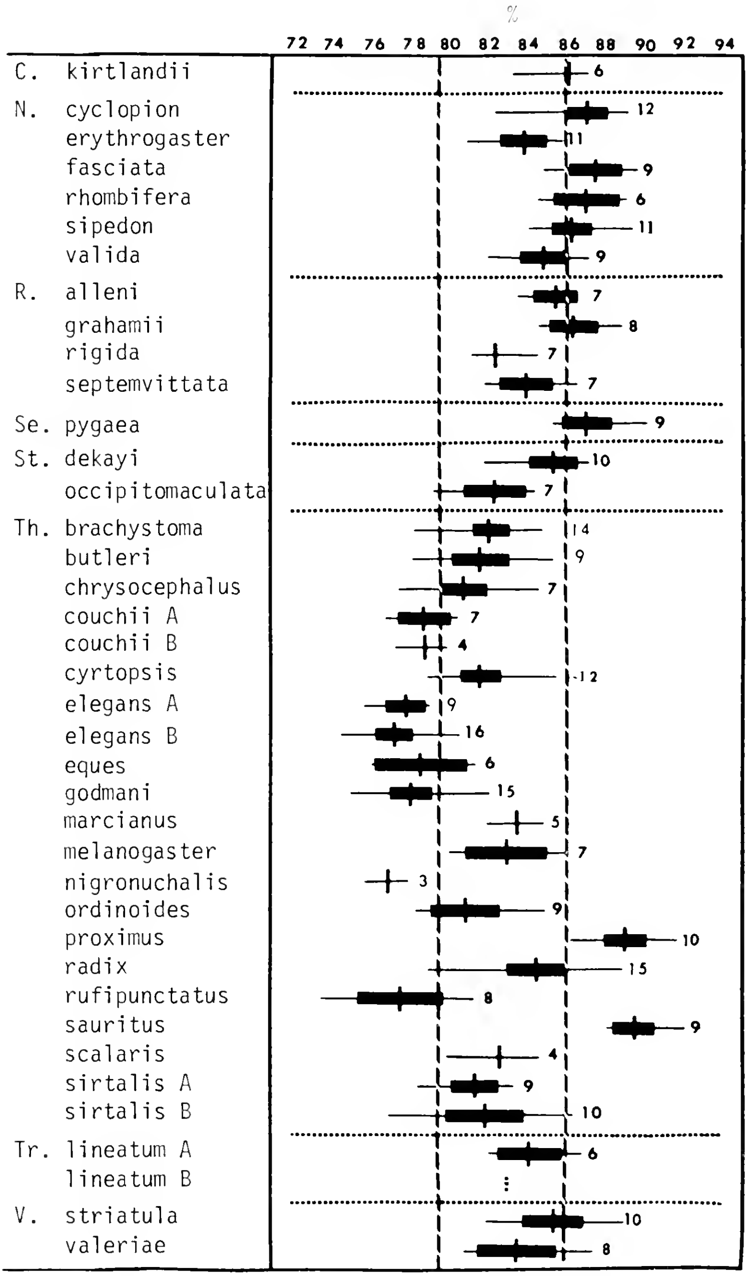

Figure 10. Location of the posterior end of the right kidney in male thamnophiine snakes (expressed as a % of total ventrals).

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.

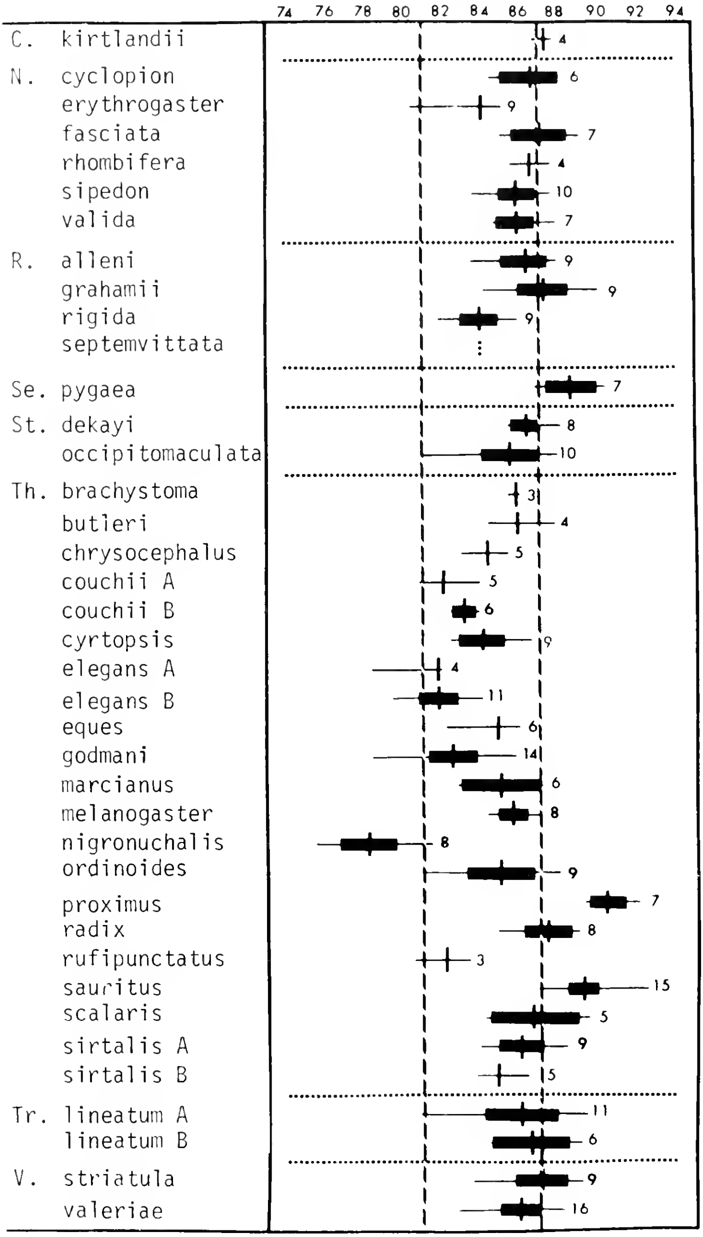

Figure 11. Location of the posterior end of the right kidney in female thamnophiine snakes (expressed as a % of total ventrals).

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-

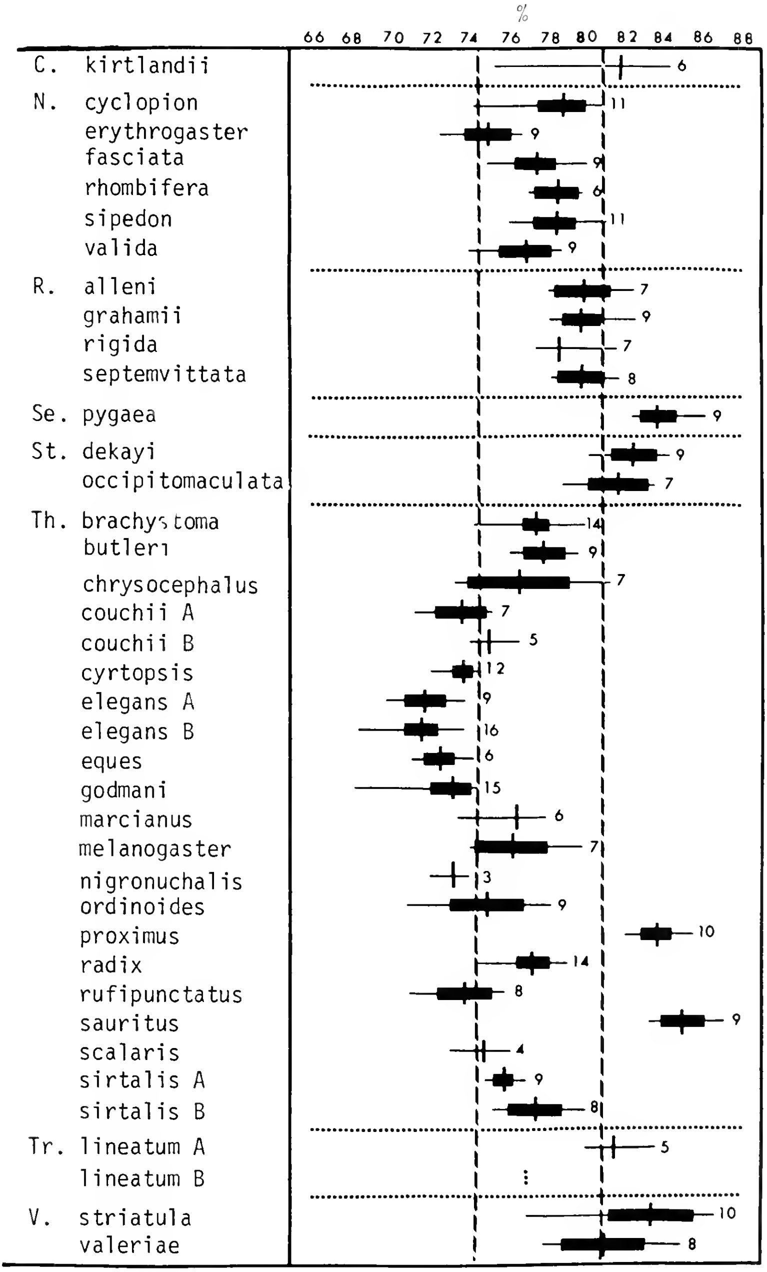

Figure 12. Location of the anterior end of the left kidney in male thamnophiine snakes (expressed as a % of total ventrals).

space lengths show no consistent intrageneric 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-

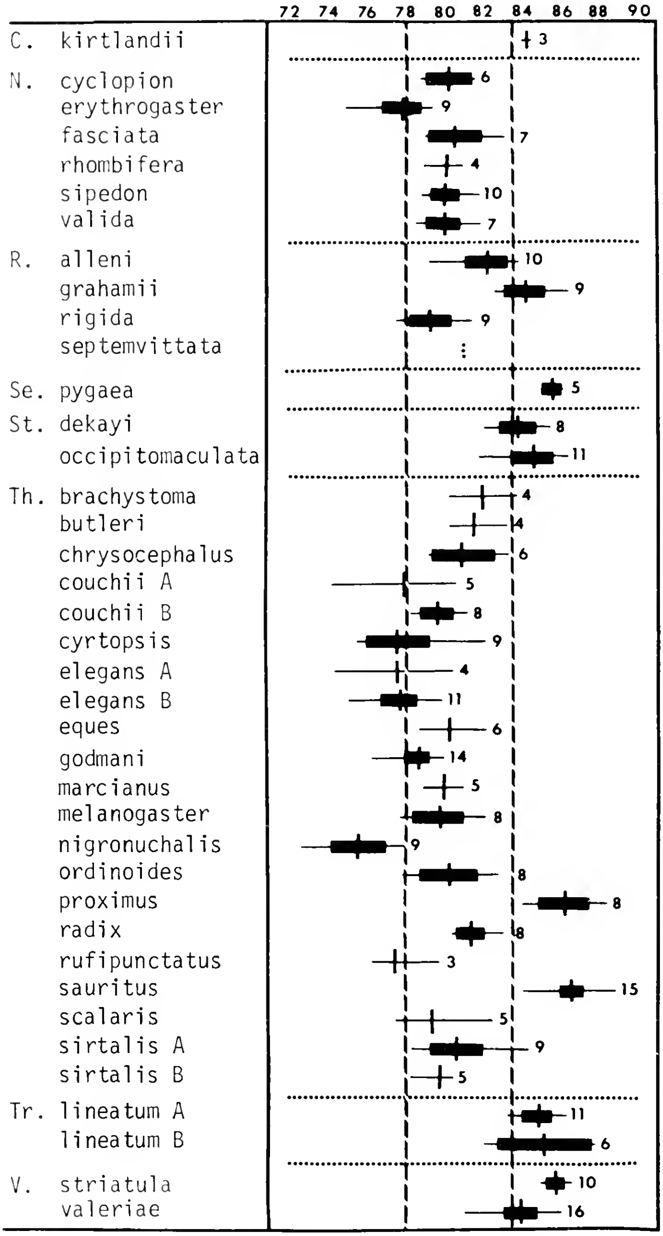

Figure 13. Location of the anterior end of the left kidney in female thamnophiine snakes (expressed as a % of total ventrals).

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

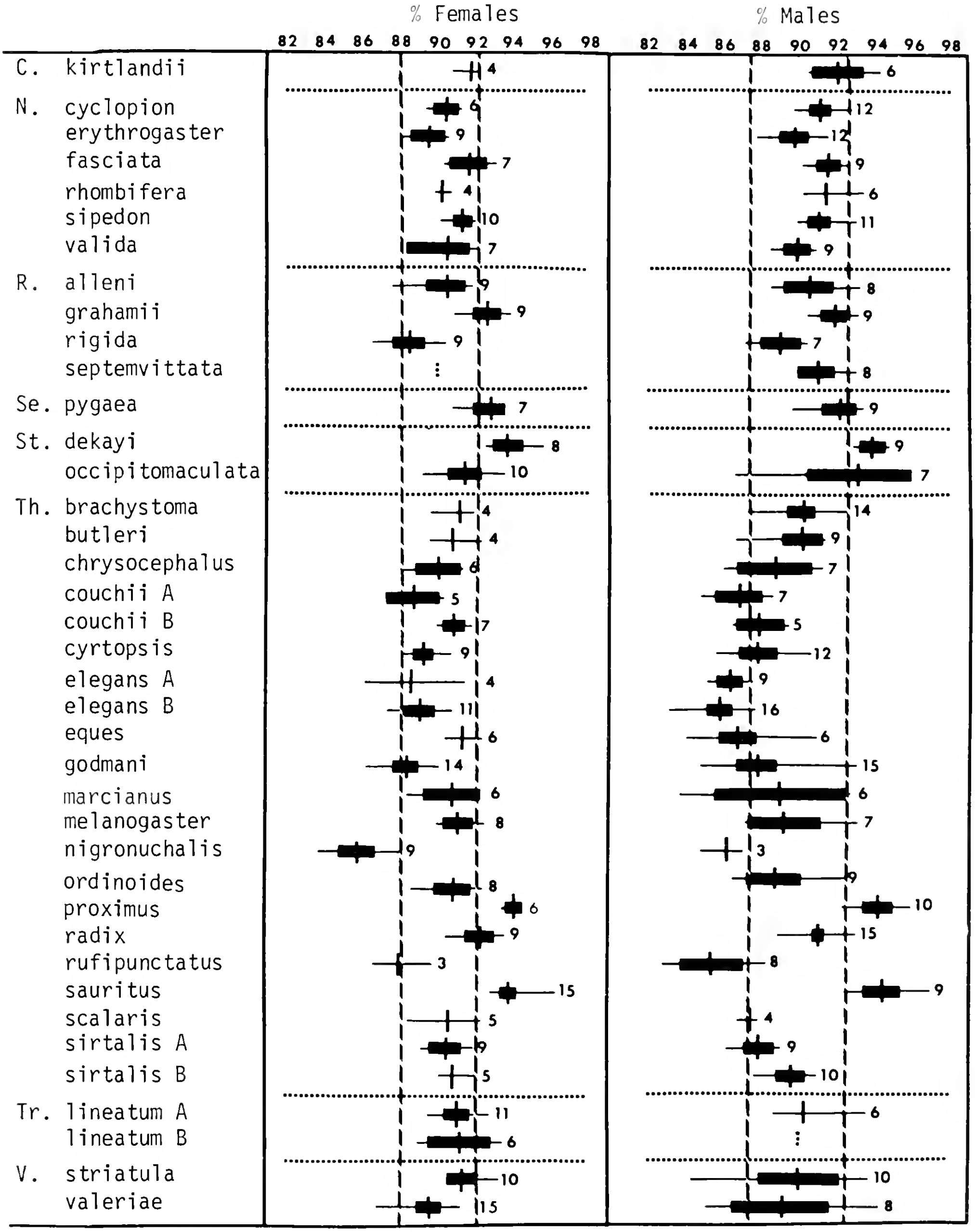

Figure 14. Location of the posterior end of the left kidney in thamnophiine snakes (expressed as a % of total ventrals).

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-

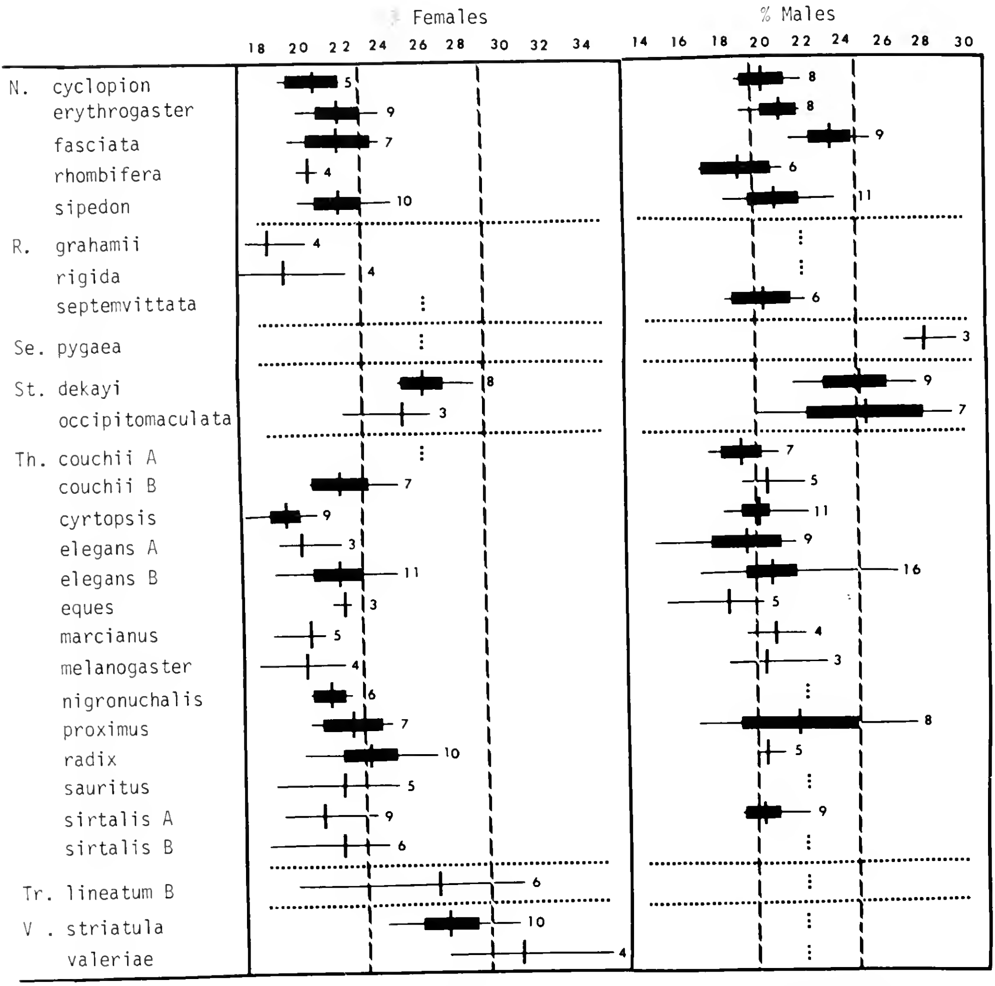

Figure 15. Liver length in thamnophiine snakes (expressed as a % of total ventrals).

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

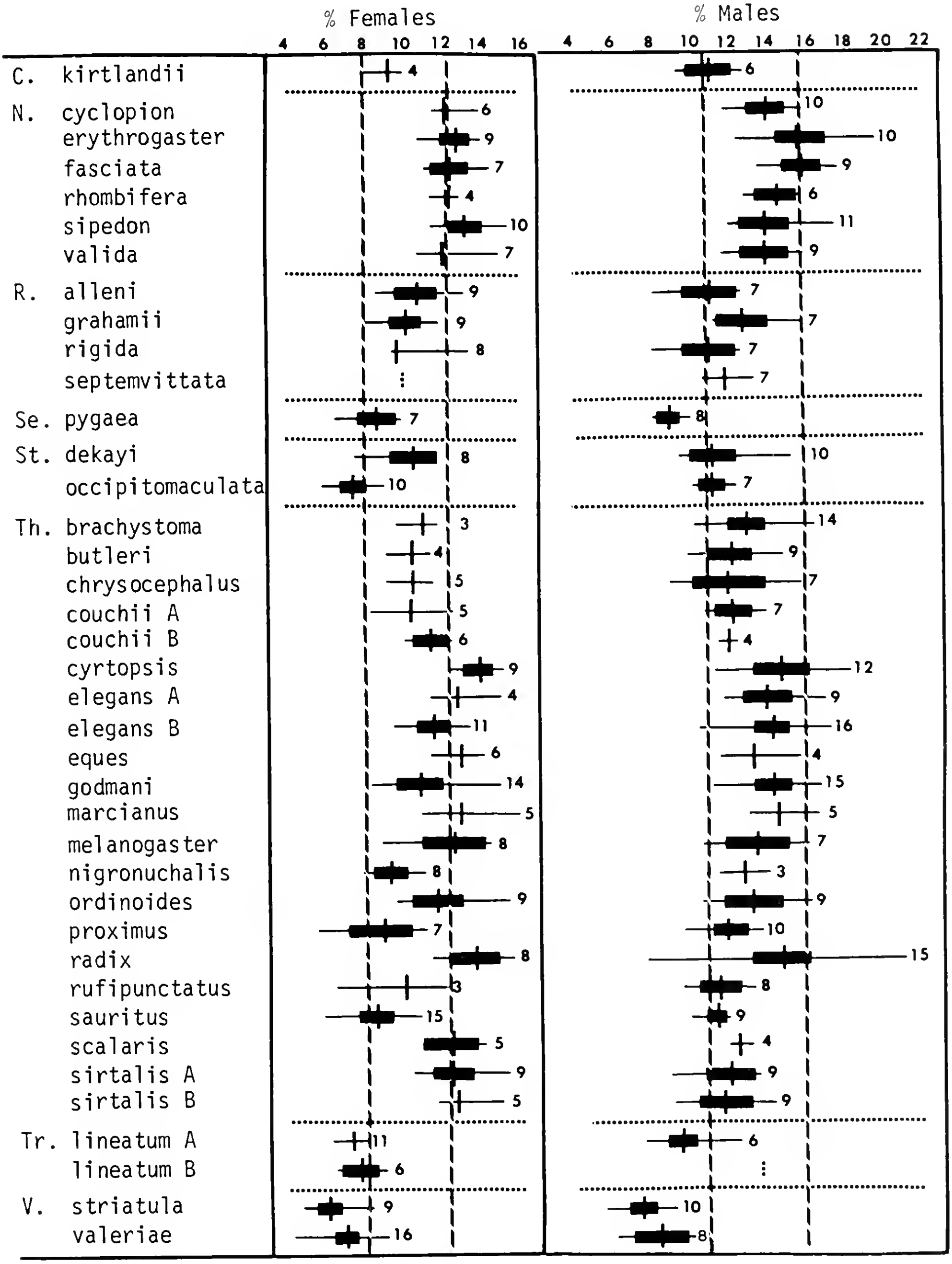

Figure 16. Right kidney length in thamnophiine snakes (expressed as a % of total ventrals).

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

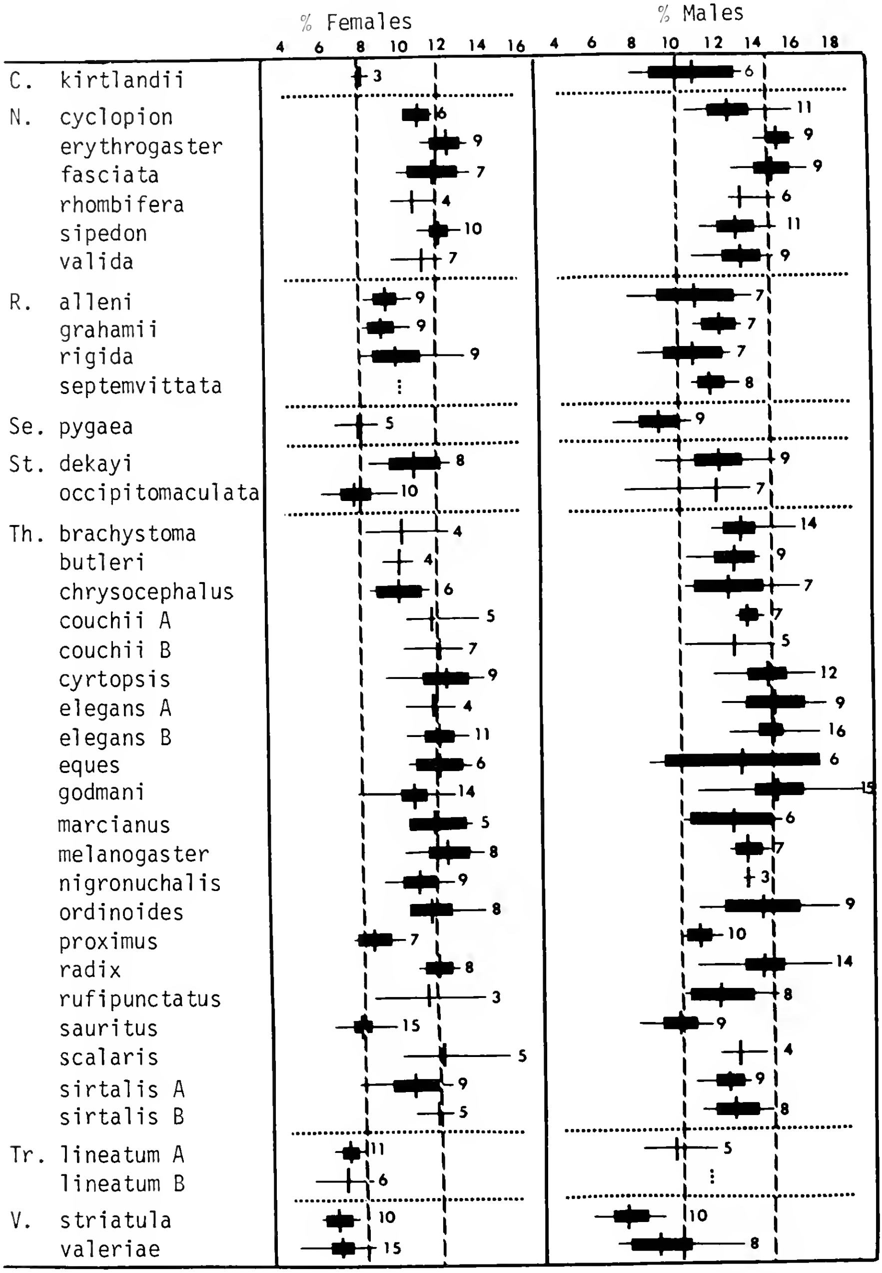

Figure 17. Left kidney length in thamnophiine snakes (expressed as a % of total ventrals).

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

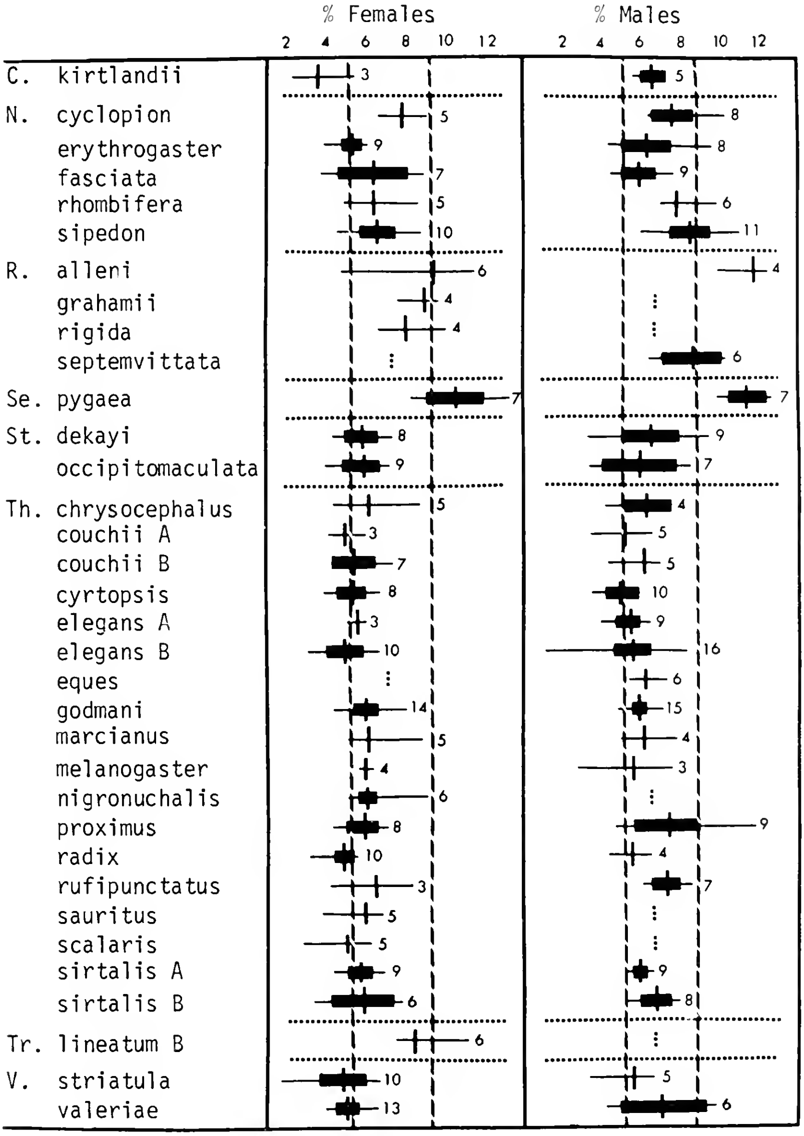

Figure 18. Heart-liver interspace in thamnophiine snakes (expressed as a % of total ventrals).

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

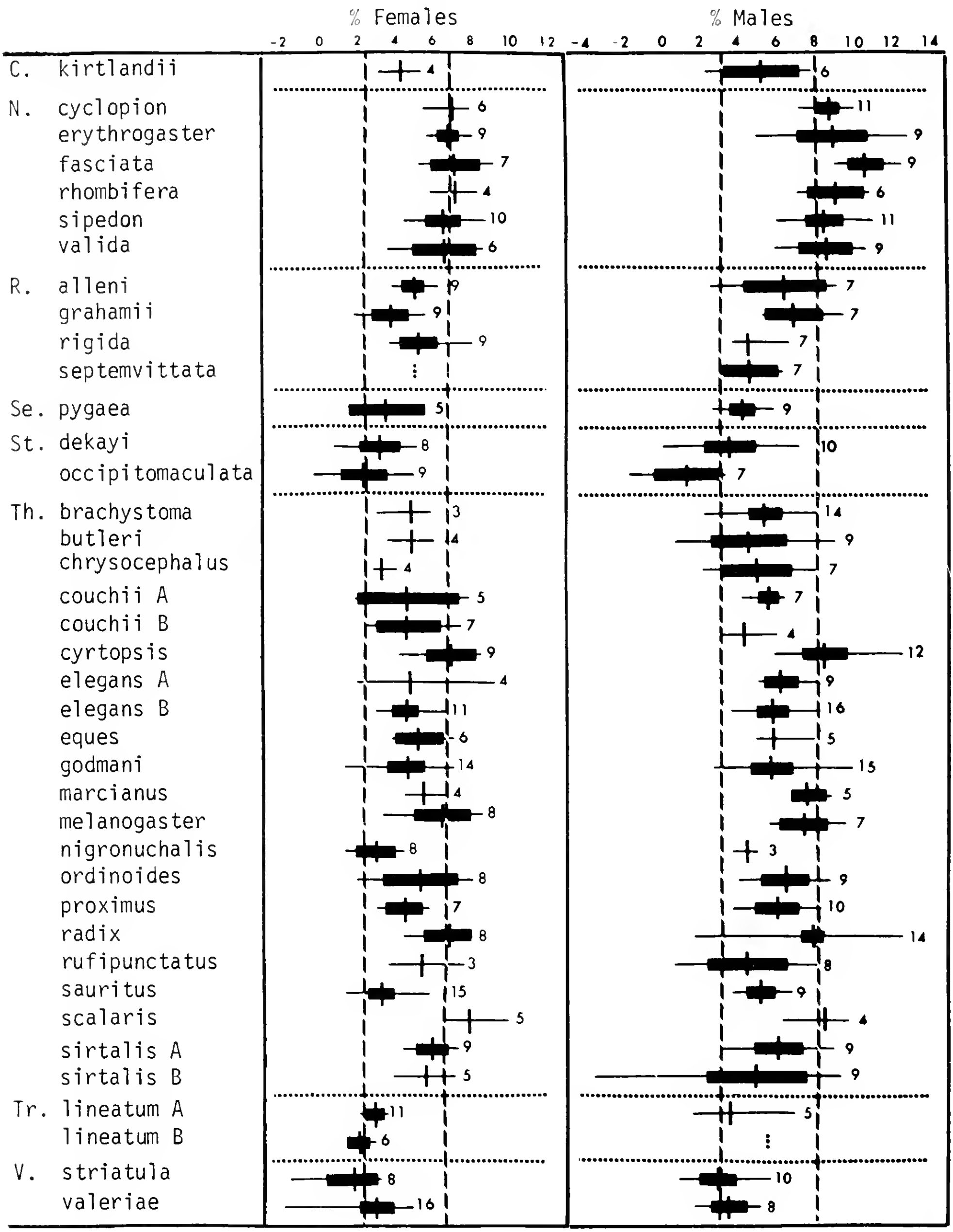

Figure 19. Kidney overlap in thamnophiine snakes (expressed as a % of total ventrals).

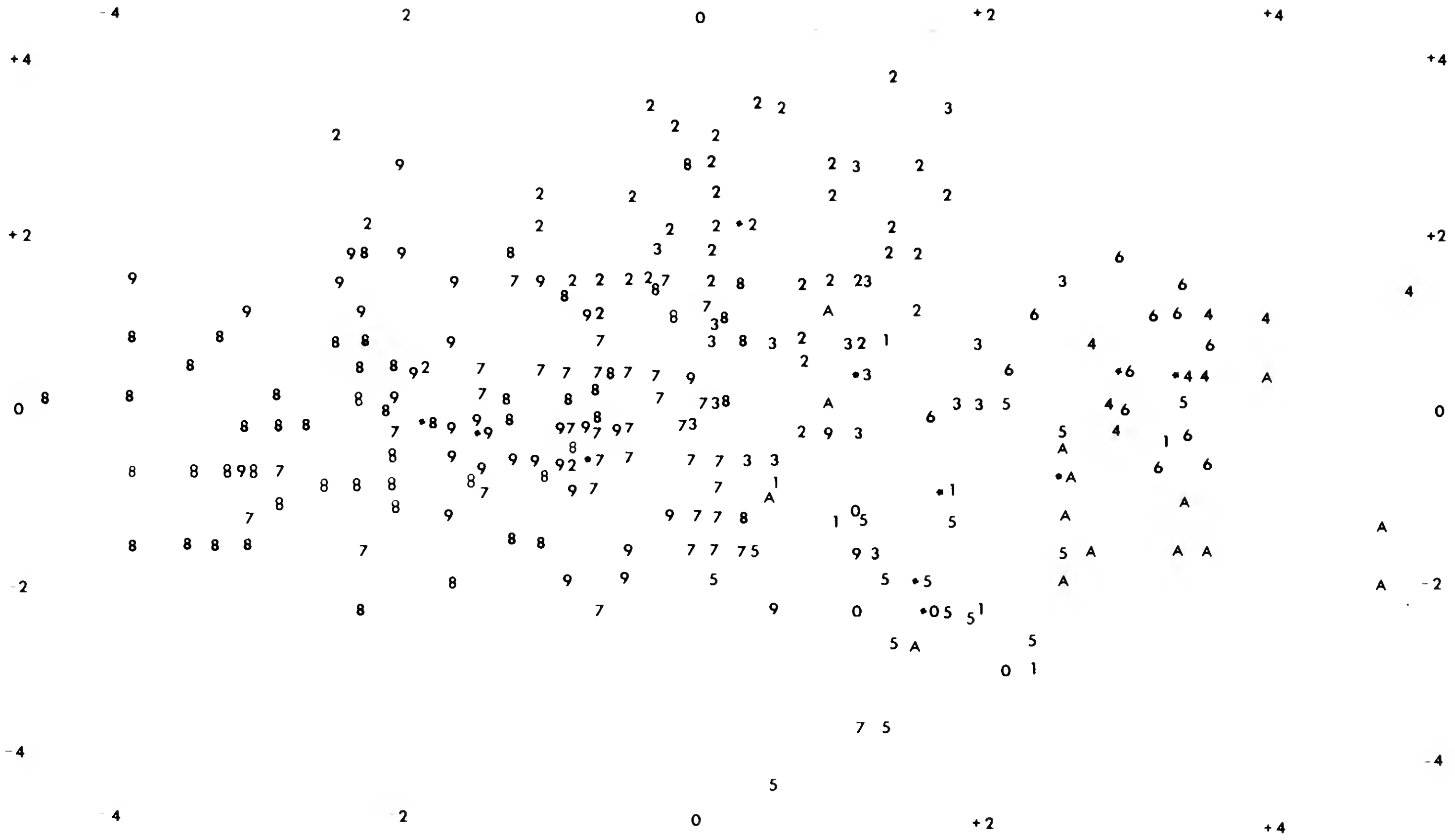

Figure 20. All-groups scatterpoint diagram of discriminant scores based on discriminant functions 1 and 2. 1 = *Clonophis*, 2 = *Nerodia*, 3 = *Regina*, 4 = *Seminatrix*, 5 = *Storeria*, 6 = *Sauritus* group of *Thamnophis*, 7 = *Radix* group of *Thamnophis*, 8 = *Elegans* group of *Thamnophis*, 9 = *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	*Sauritus-Radix*	*Sauritus-Elegans*	*Sauritus-Sirtalis*	*Radix-Elegans*	*Radix-Sirtalis*	*Elegans-Sirtalis*
post. heart	♂ ♀	.001[1] .01	.001 .001	.001 .001	NS NS	NS NS	NS NS
ant. liver	♂ ♀	.001 .001	.001 .001	.001 .001	.05 .05	.05 .001	NS NS
post. liver	♂ ♀	.001 .001	.001 .001	.001 .001	NS NS	NS NS	NS .05
post. gall bladder	♂ ♀	.001 .001	.001 .001	.001 .001	NS NS	NS NS	NS NS
post. pancreas	♂ ♀	.001 .001	.001 .001	.001 .001	NS NS	NS NS	NS NS
ant. r. kidney	♂ ♀	.001 .01	.001 .001	.001 .001	.001 .001	.001 .01	.01 NS
post. l. kidney	♂ ♀	.001 .001	.001 .001	.001 .001	.001 .001	.01 .001	NS NS
ant. l kidney	♂ ♀	.001 .001	.001 .001	.001 .001	.001 .001	.001 .001	.01 NS
post l. kidney	♂ ♀	.001 .001	.001 .001	.001 .001	.001 .001	.001 .001	.001 NS
liver length	♂ ♀	NS NS	.02 NS	.01 NS	NS NS	NS .02	NS NS
r. kidney length	♂ ♀	.01 .001	.01 .001	.01 .001	NS .01	NS NS	NS NS
l. kidney length	♂ ♀	.001 .001	.001 .001	.001 .001	NS NS	NS NS	NS NS
heart-liver interspace	♂ ♀	.02 NS	.01 NS	NS NS	NS NS	NS NS	NS NS
kidney overlap	♂ ♀	NS .001	NS .01	NS .001	NS NS	NS NS	NS NS

[1] Significance 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.

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SPECIMENS EXAMINED[1]

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 virgatenuis. 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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[1] Standard museum acronyms (Duellman, Fritts, and Leviton, 1978) are used throughout this paper.

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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 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* *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*[5] 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: *Enhydris enhydris;*[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* (=*Enhydris*) *plumbea;*[11] other Colubridae: *Elapoides fuscus.*[10]

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[1] Rasmussen (1979)
[2] Thompson (1914)
[3] McDowell (1979)
[4] Underwood (1976)
[5] Thompson (1913b)
[6] Brongersma (1951)
[7] Bogert (1968)
[8] Bergman (1959b)
[9] Bergman (1955e)
[10] Bergman (1956-58)
[11] Bergman (1960)