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 tur-

tles 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 Ge-

ography 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
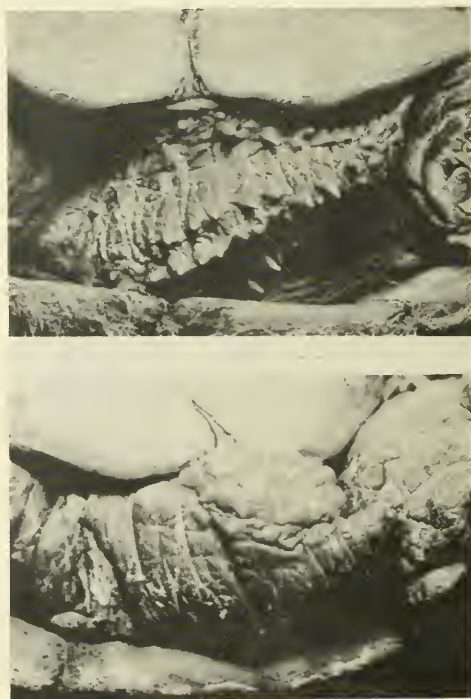

Figure 2. Comparison of papillae on the tail of female *Kinosternon hirtipes* (above; FMNH 71029; 137 mm CL; Guanajuato, Taboado) and *K. integrum* (FMNH 71031; 126 mm CL; same locality).

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.
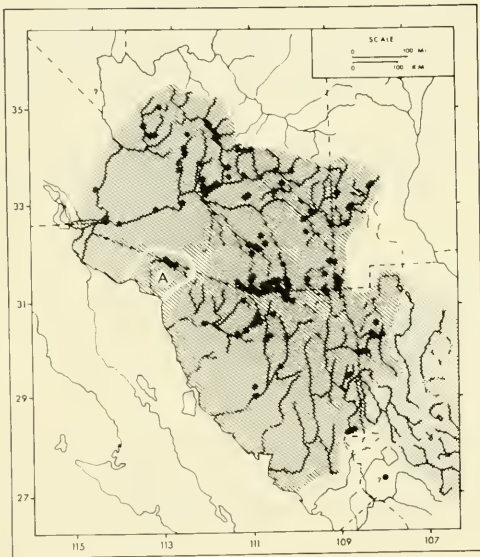

Figure 3. Distribution of the subspecies of *Kinosternon sonoriense*. Dots indicate actual records; hatching, suggested total ranges. The range of *K. sonoriense longifemorale* is marked (A); the remaining hatched area marks the range of the nominate subspecies. Question mark in Nevada is discussed in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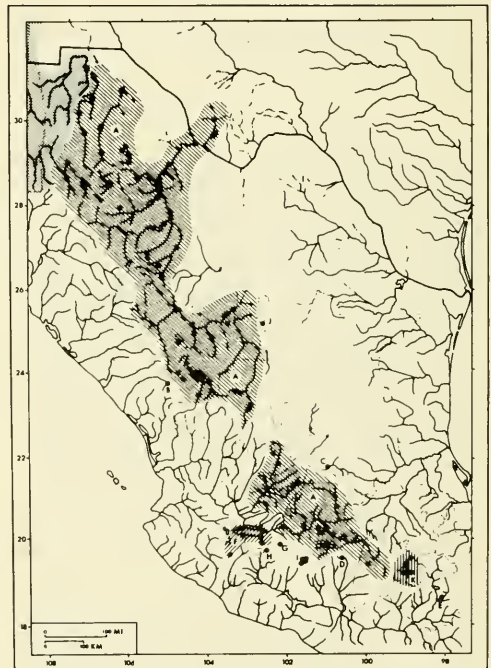

Figure 4. Distribution of the subspecies of *Kinosternon hirtipes*. Dots indicate actual records; hatchings, suggested total ranges. Subspecies ranges are marked: *K. hirtipes murrayi* (A-E); *K. h. chapalaense* (F); *K. h. chapalaense* x *K. h. murrayi* (G); *K. h. magdalense* (H); *K. h. tarascense* (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 Maria 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 evi-dene, 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 vegeta-tion and the continually changing shore-line (evident from water marks on the rocks) presented habitats which were un-doubtedly generally unsuitable for *Kino-sternon* 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 intermit-tently to the desert floor in the vicinity of the town of Sauz. It then flows intermit-tently 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-Bal-deras (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; how-ever, we trapped none at either of two sites of apparently permanent water (con-taining 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 supposed-ly recorded from this basin is *Sterno-therus odoratus,* but the single record re-mains 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. hir-tipes* 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 north-

ern 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 in-

side 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 ma-

jor 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 sub-adults) 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* co-occur 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, Aguas-calientes (AGUAS). - Because the distance between the two clusters of localities for *K. hirtipes* in the Río Aguas-calientes-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 Aguas-calientes 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; Iver-son, unpublished), but within the Rıo 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 ⁵), muddy pond immediately behind the dam. The heads of literally hundreds of *Kinosternon* werę yisible at the pool's surface on that day. The isolat-ed pools in the stream channel, however, contained few turtles, usually only one per pool. Turtles were also abúmdant 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 im-pounds a huge, muddy, unvegetated res-ervoir. 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 pro-ductive, 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 indi-cated 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 un-questionably *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, Guana-juato, 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.

Maravatío 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 Maravatío (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 km² (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 un-fortunately 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, Michoacán 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 photographs 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).

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.

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.).

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 speci-

mens 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.

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

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

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 cara-
pace length (except three females) with the
full complement of measurements were
used in the morphometric analyses; vari-
ous ratios of characters were also em-
ployed to minimize ontogenetic variation
(see STATISTICAL TECHNIQUES).
Character means and ranges by popula-
tion (Appendices 1 and 2) and taxon (Ap-
pendices 3 and 4) for each sex are avail-
able from NAPS[1].

Mensural characters recorded and their
abbreviations follow [Methods of
measurement were given by Iverson
(1977a); midline plastral scute measure-
ments were always made on the animal's
right side.]: carapace length (CL), cara-
pace 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), inter-
pectoral seam (IP), interabdominal
(IAB), interfemoral (IF), interanal (IAN),
first vertebral width (VW) and length
(VL), maximum length of plastral fore-
lobe (FL), and maximum length of plas-
tral 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 sep-
arately.

Relative shell height has been used to
distinguish *Kinosternon hirtipes* from *K.
sonoriense* (e.g., Ernst and Barbour,
1972; Wermuth and Mertens, 1961); how-
ever, 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 in-
cluded relative head size, plastral color,
and shell carination as well as the follow-
ing.

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 poster-
iorly 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 at-
tempt was made to qualify head patterns.
The procedure involved photographing
the heads of as many specimens as possi-
ble (over 500 total head photographs
available) for later simultaneous exam-
ination 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

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 disciminant 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 ref-

erence 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 record-

ed *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 morpho-geographic 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 ≥ 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.*
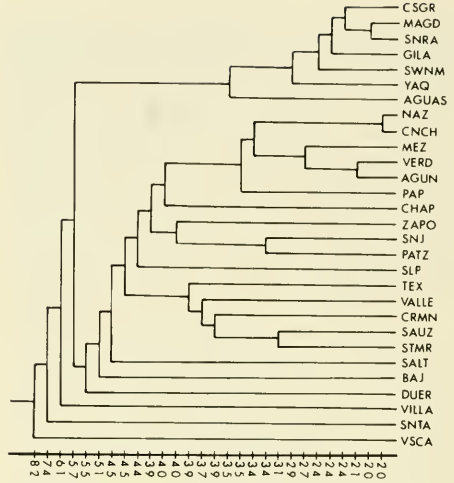

Figure 9. BMDP2M cluster of population means of all 23 character ratios (Appendices 1 and 2) for males of the *K. hirtipes* species group (including *K. sonoriense*). Abbreviations as in text. N ≥ 4 for all samples but VSCA (N = 2) and TEX (N = 3). Numbers are amalgamation distances (i.e., distance between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

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'.

Stepwise discriminant analysis of populations with N ≥ 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

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 ≥ 3 for all samples but SLP and PATZ (N = 2 each).

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
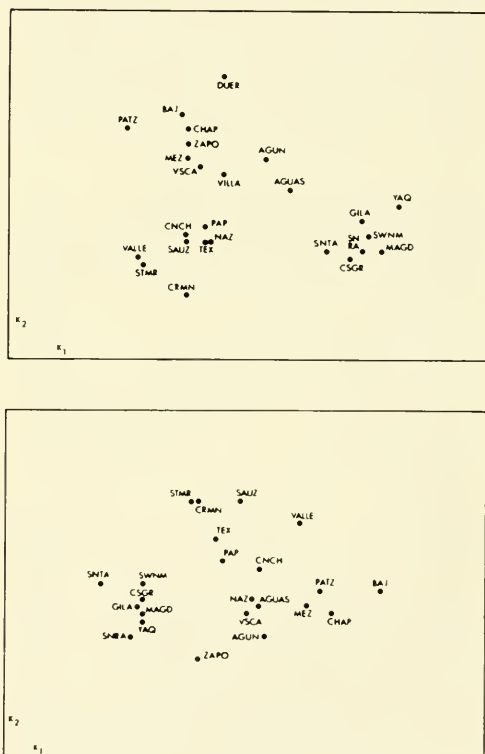

Figure 10. Plots on the first (k_1) and second (k_2) canonical axes of the population means of males (above) and females (below) of the *Kinosternon hirtipes* species group (including *K. sonoriense*). Abbreviations as in text. Analysis based on all 23 character ratios for populations with N ≥ 2. First 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
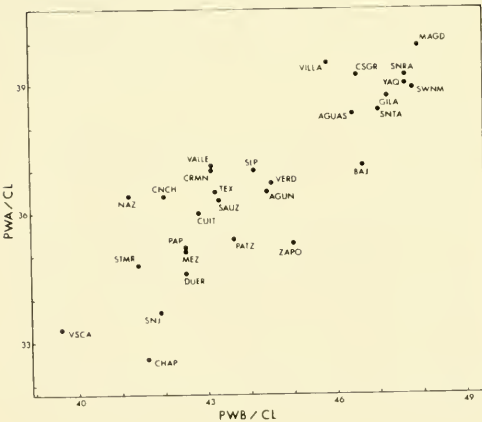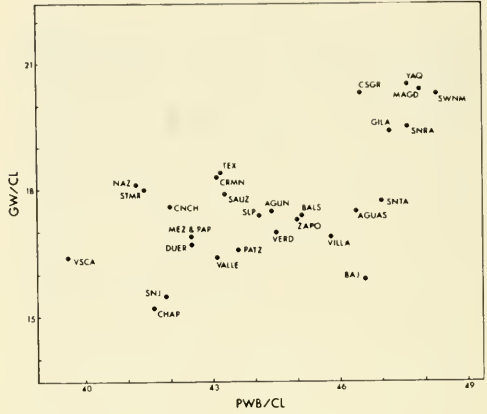

Figure 12. Graph of percent posterior width of plastral forelobe/carapace length (PWB/CL) versus percent gular width/carapace length (GW/CL) for males of all populations of the *Kinosternon hirtipes* species group (including *Kinosternon sonoriense*). Only population means are plotted. Abbreviations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

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.

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
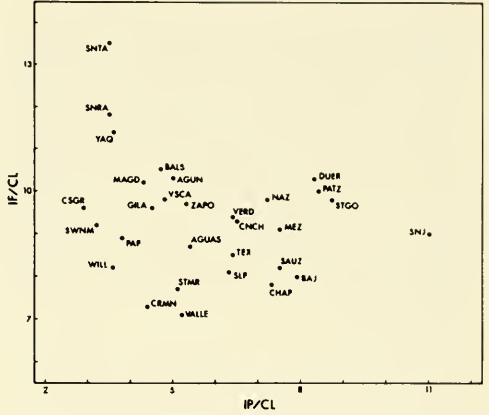

Figure 11. Graph of percent posterior width of plastral forelobe/carapace length (PWB/CL) versus percent plastral width at humero-pectoral seam/carapace length (PWA/CL) for males of all populations of the *Kinosternon hirtipes* species group (including *Kinosternon sonoriense*). Only population means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

Figure 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.
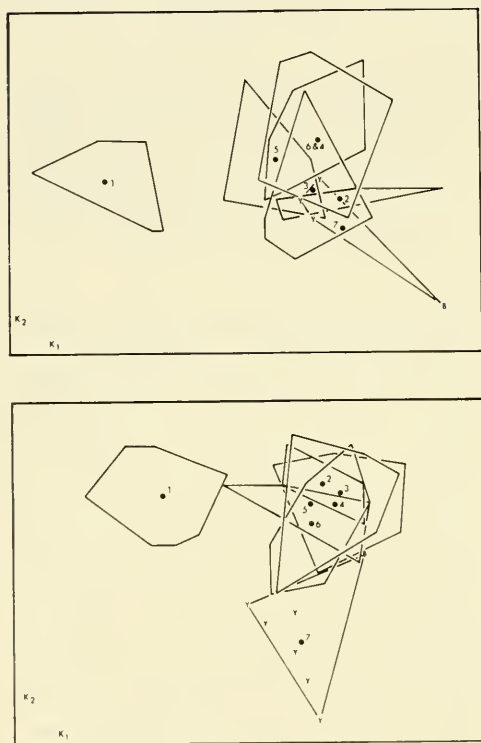

Figure 15. Plots on the first (k_1) and second (k_2) canonical axes of population means (solid dots) of males (above) and females (below) of *K. sonoriense.* Lines connect the most dispersed values about the population mean. Population mean symbols are 1, SNTA; 2, SWNM; 3, GILA and WILL; 4, MAGD; 5, 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 inter-

femoral 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
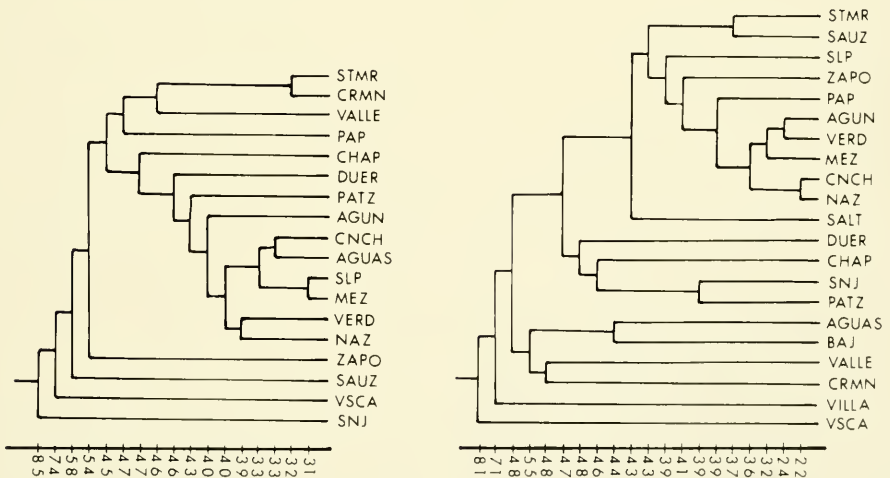

Figure 16. BMDP2M cluster of population means of all 23 character ratios (Appendices 1 and 2) for male (top) and female *K. hirtipes*. Abbreviations as in text. For males, N > 4 for all samples except VSCA (N = 2); for females, N > 5, except SNJ (N = 2) and ZAPO (N = 2). Numbers are amalgamation distances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

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

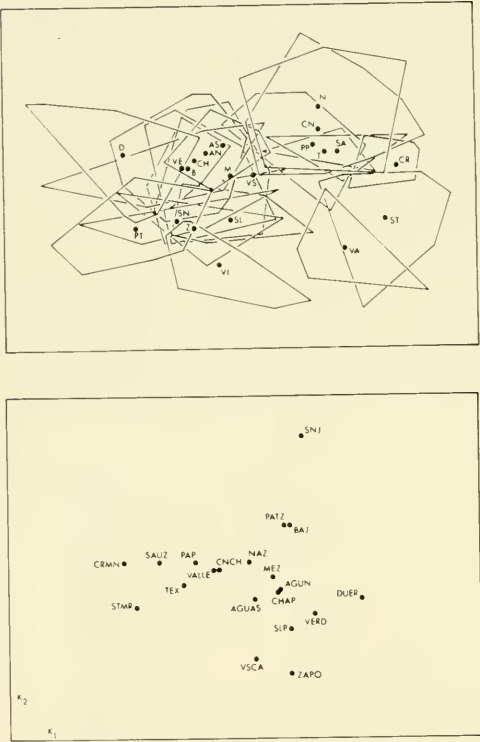Nasal scale. — The cornified epidermal shield (here called the nasal scale) found

Figure 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.
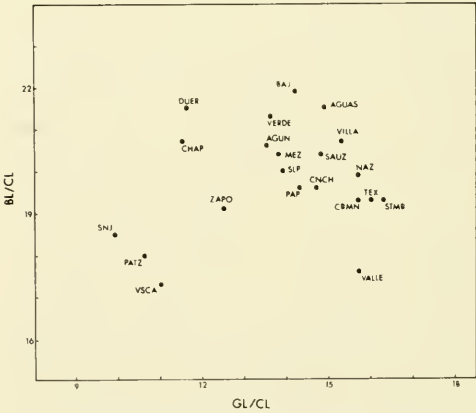

Figure 18. Graph of percent gular length/carapace length (GL/CL) versus percent bridge length/carapace length (BL/CL) for males of populations of *Kinosternon hirtipes*. Only population means are plotted. Abbreviations as in text.
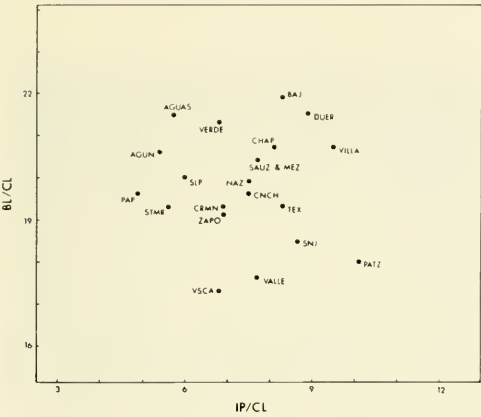
Figure 19. Graph of percent interpectoral seam length/carapace length (IP/CL) versus percent bridge length/carapace length (BL/CL) for males of populations of *Kinosternon hirtipes*. Only population means are plotted. Abbreviations as in text.

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

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
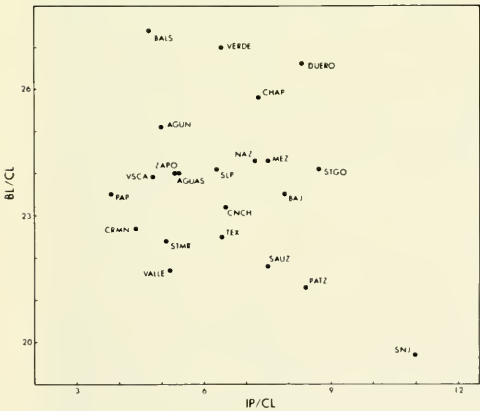

Figure 20. Graph of percent interpectoral seam length/carapace length (IP/CL) versus percent bridge length/carapace length (BL/CL) for females of populations of *Kinosternon hirtip s*. Only populations means are plotted. Abbreviations as in text.

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.
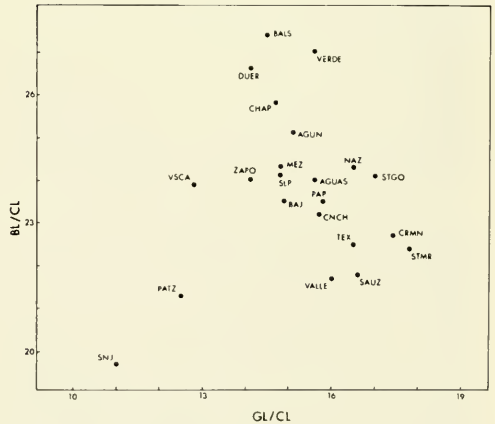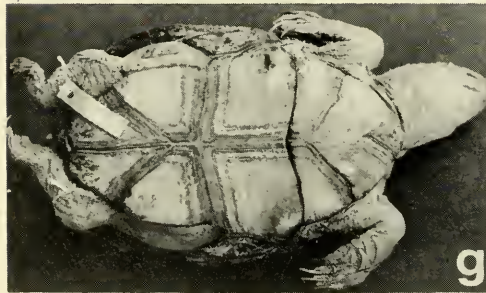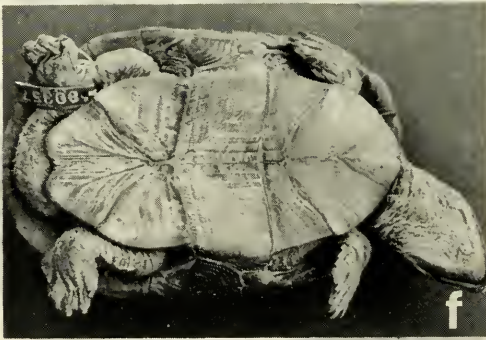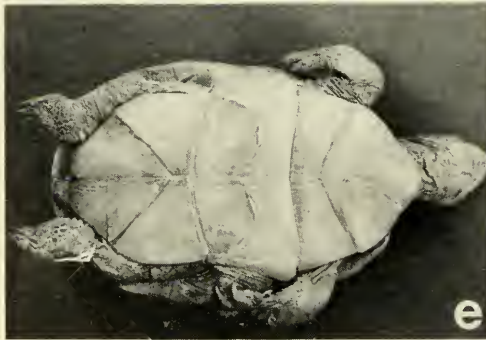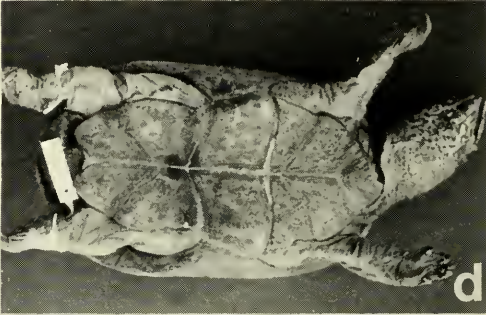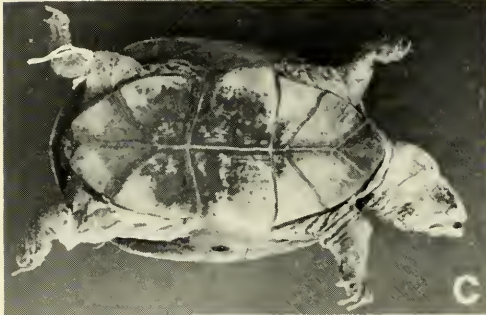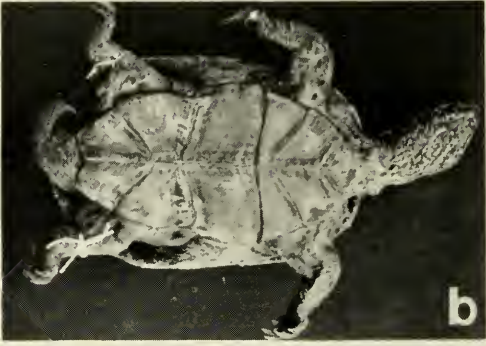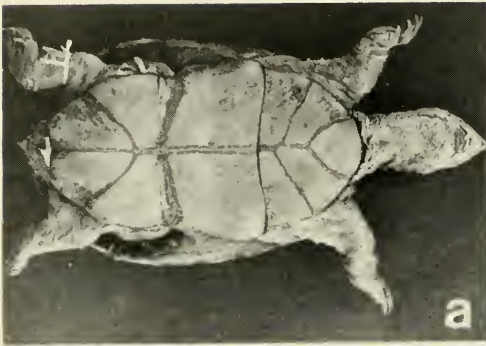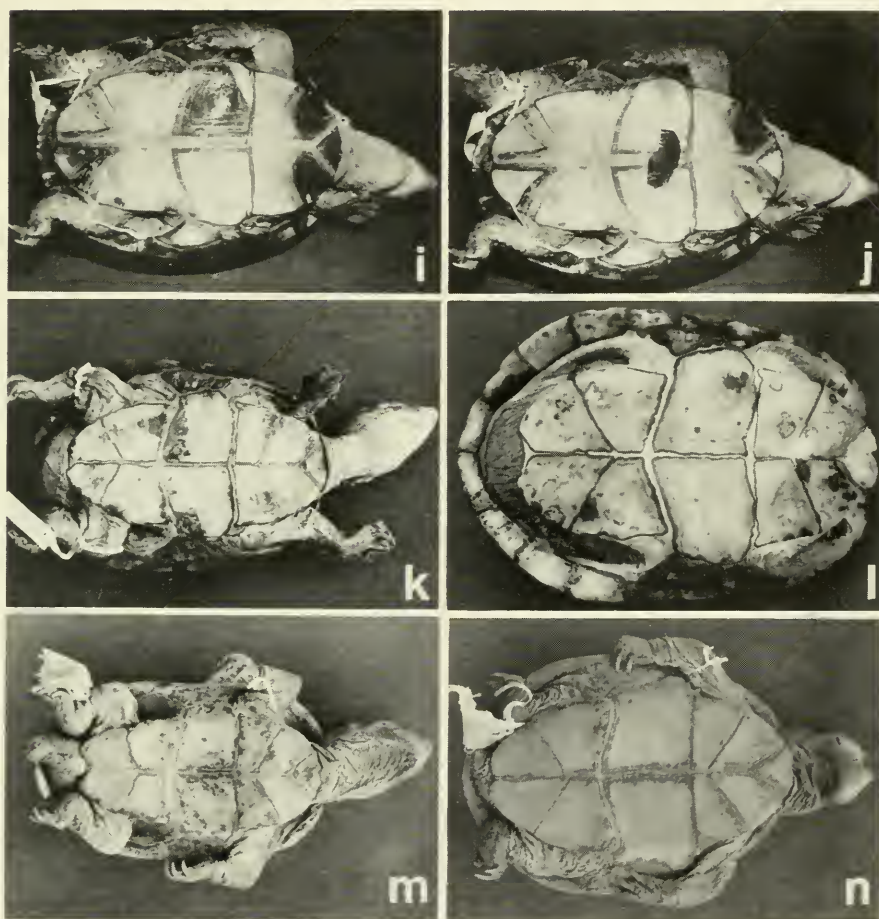
Figure 22. Plastral variation in members of the *Kinosternon hirtipes* species group: Gila River basin *Kinosternon sonoriense*, JBl 563 female (a) and JBl 386 male (b); Rio Papigochic basin *K. hirtipes murrayi*, UF 40391 female (c) and UF 40396 male (d); Valley of Mexico *K. h. hirtipes*, UMMZ 99458 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 (l); 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*).

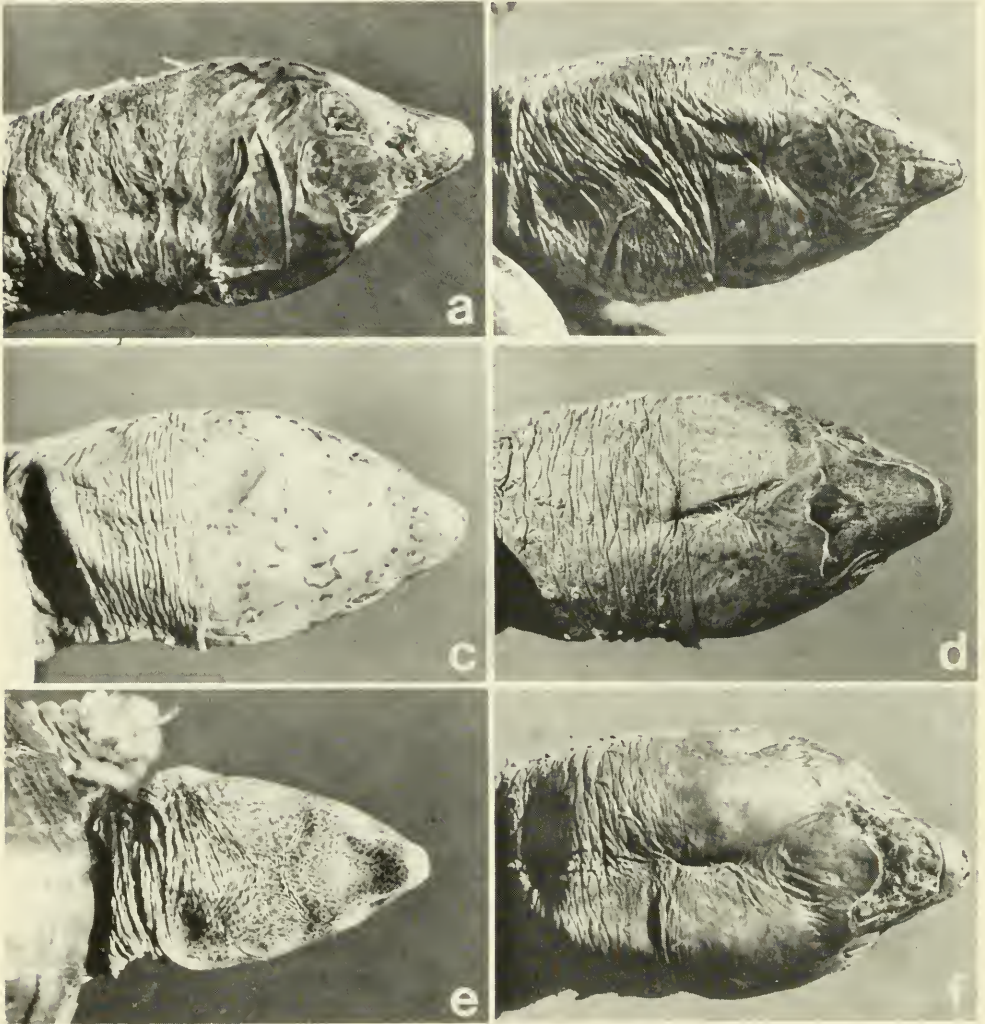Because most of the members of the

Figure 23. Nasal scale variation in members of the *Kinosternon hirtipes* species group: *K. sonoriense,* JBl 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
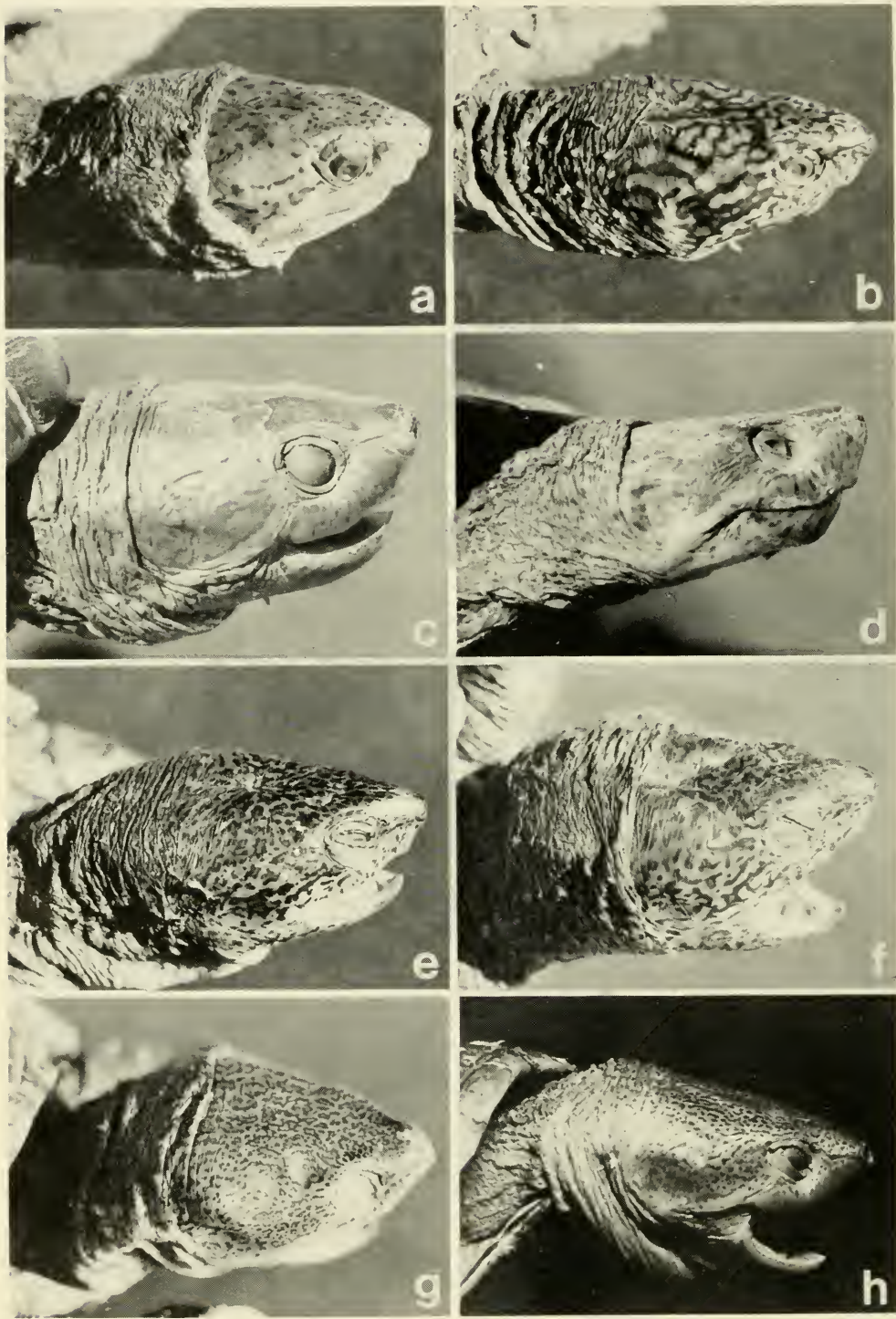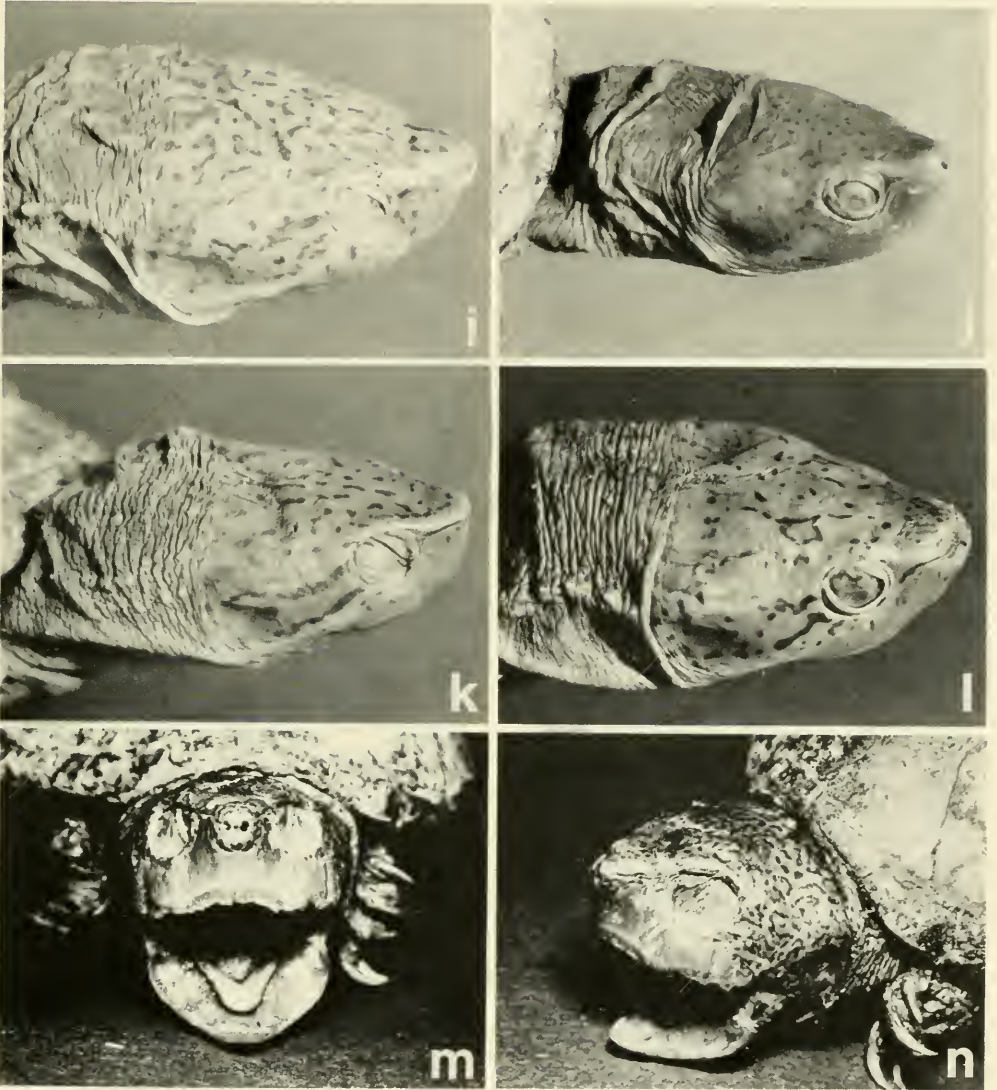
Figure 24. Head pattern variation in members of the *Kinosternon hirtipes* species group: Gila River Basin *Kinosternon sonoriense,* JBl 563 female (a) and JBl 387 male (b); Valley of Mexico, *K. hirtipes hirtipes,* UMMZ 99458 female (c) and UMMZ 80357 male (d); Rio Papigochic *K. h. murrayi,* UF 40391 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 (1); 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 kino-

sternid). 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.

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).
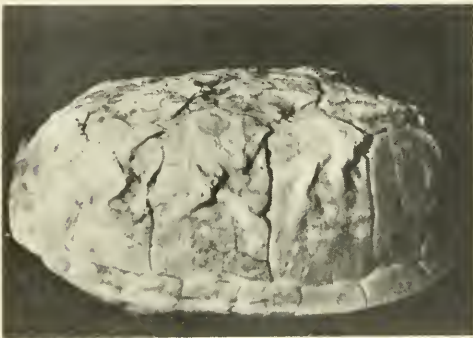

Figure 26. Articulated shell (without scutes) of adult *K. sonoriense* (JBI 800) from Sonora, near Cucurpe (Río Sonora basin). Note rugosity.

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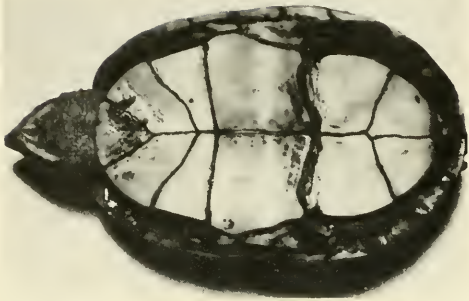
Figure 27. Plastron of female *Kinosternon sonoriense longifemorale* (UF 47720) from Quitobaquito Pond, Pima County, Arizona. Note short interanal and long interfemoral seams.

$\bar{x}$, 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 Kar-

winski, 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 Guana-

juato).

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 México (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	PL¹	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	-	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	-	-	-	2 +	-	May- ?
MEZQ	24.0² / 24.7	21.3² / 20.2	-	4 (1)	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

¹estimates from annuli   ²with 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 (maxi-

mum 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) rel-

atively short gular length (male $\bar{\bar{x}}$ GL/CL, 10.6%; female $\bar{\bar{x}}$, 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.
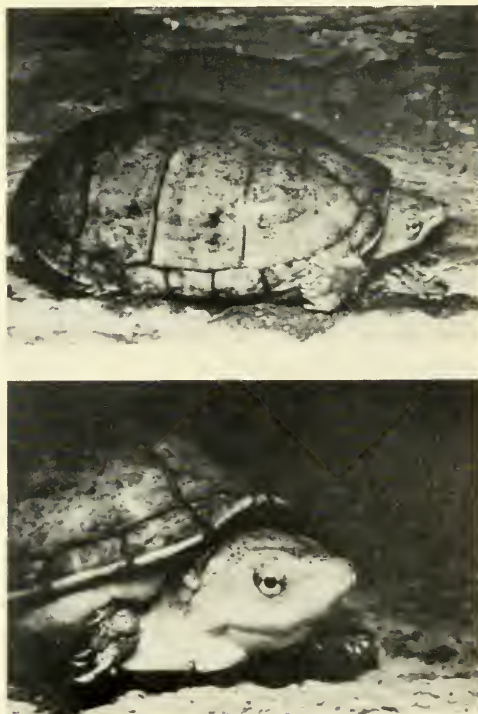

Figure 28. Holotype (UF 45035) of *Kinosternon hirtipes magdalense.*

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
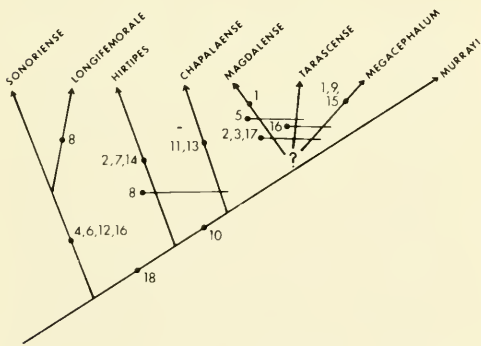

Figure 29. A theory of relationships among the subspecific taxa of the *Kinosternon hirtipes* species group. Numbers refer to derived character states listed in Table 3. Solid lines cutting lineages mark identical shifts (convergence) in character states.

(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.

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*

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 tamaño 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** (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, JB1 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 María, 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, JBl 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, JBl 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, JBl 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, JBl 896-900, UF 44064-65, 44078; 3.2 km NE Valle de Guadalupe, trib to R Verde, Hwy 80, JBl 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, JBl 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, JBl 928; 8.9 km S La Presa, JBl 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, JBl 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, BM-NH 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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