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A Taxonomic Reappraisal of the Yellow Mud Turtle, *Kinosternon flavescens* (Testudines: Kinosternidae)

JOHN B. IVERSON

The taxonomy and distribution of *Kinosternon flavescens* are discussed. The three previously recognized subspecies are retained and a fourth (*K. f. durangoense*) described. Descriptions of each taxon are included as is a key. Specific distributional problems are also addressed.

KNOWLEDGE of the systematic relationships of the mud turtles of the genus *Kinosternon* has lagged far behind that for most other North American reptile genera. This has been due in part to an abundance of misidentifications and other errors in the literature, a problem so great that it has been necessary to verify each literature record by personal ex-

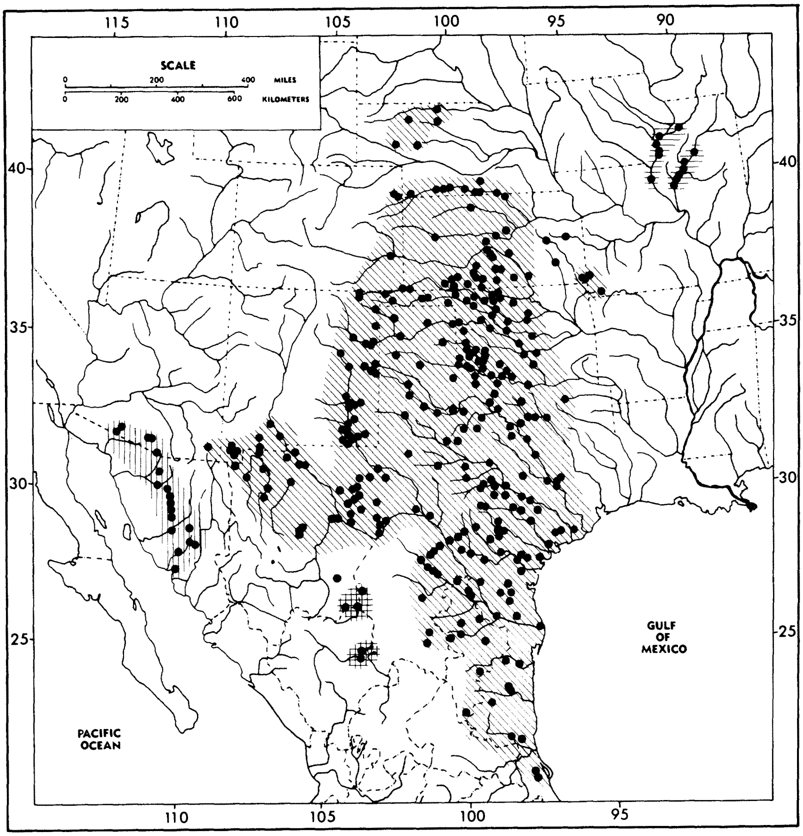

Fig. 1. Distribution of *Kinosternon flavescens flavescens* (diagonal hatching), *K. f. spooneri* (horizontal hatching), *K. f. arizonense* (vertical hatching) and *K. f. durangoense* n. ssp. (cross hatching). Plotted localities are included in Specimen List.

amination of the specimens concerned. Recent papers by Conant and Berry (1978) and Iverson (1978) have specifically addressed such problems in the American southwest. The present study deals with geographical variation in *Kinosternon flavescens.*

Materials and Methods

Nineteen shell measurements were made with dial calipers on museum specimens of *K. flavescens* from drainage basins shown in Fig. 1. Only data from specimens over 75 mm carapace length with the full complement of measurements were used in the analyses and various ratios of characters were employed to minimize ontogenetic variation.

Characters recorded and their abbreviations follow (methods of measurement were given by Iverson [1977]; plastral scute measurements were always made on each animal's left side): Carapace length (CL), carapace width (CW), maximum plastral length (PL), plastral widths measured at the lateral edges of the seams between the humeral, pectoral, abdominal, femoral and anal plastral laminae: (WA), (WB), (WC) and (WD) respectively, bridge length (BL), gular length (GL), gular width (GW), interhumeral seam length (IH), interpectoral seam (IP), interabdominal (IAB), interfemoral (IF), interanal (IAN), first vertebral width (VW) and length (VL), maximum length of plastral forelobe (FL) and maximum length of plastral hindlobe (HL). The ratios of each character to CL as well as the ratios of IH, IP, IAB, IF and IAN to PL (total 23 ratios) were employed in the analysis. Sexes were analyzed separately in all cases.

Simple statistics and canonical correlation analysis were performed using the Statistical

TABLE 1. CHARACTER PROPORTIONS USEFUL IN DISTINGUISHING SUBSPECIES OF *KINOSTERNON FLAVESCENS*. MEAN RATIOS AS PERCENTAGES ARE FOLLOWED BY ± ONE STANDARD DEVIATION. CHARACTER RANGE APPEARS BELOW MEAN. MAPIMI BOLSÓN AND RÍO NAZAS SPECIMENS REPRESENT A NEW SUBSPECIES HEREIN DESCRIBED.

	Sex	N	CL	GL/IH	IF/IAN	GL/IAN	IF/IH	CW/PL	VW/FL
K. f. spooneri	♀	8	97.4	108.0 ± 17.1	15.8 ± 2.8	61.2 ± 3.9	26.9 ± 5.6	79.5 ± 1.3	73.4 ± 2.5
			(82.9–115.9)	(80.8–134.5)	(12.4–21.3)	(55.1–66.7)	(21.8–34.3)	(77.1–80.9)	(70.6–77.1)
K. f. flavescens	♀	137	104.7	77.1 ± 19.5	16.2 ± 5.8	51.8 ± 8.7	21.0 ± 11.6	80.9 ± 2.7	75.0 ± 7.0
			(76.6–135.1)	(32.4–126.4)	(6.0–37.2)	(26.6–70.3)	(10.2–51.5)	(74.3–87.1)	(59.4–96.6)
Mapimi Bolsón specimens	♀	2	119.5	215.5	60.1	100.0	125.5	85.6	87.0
			(94.4–144.6)	(148.3–282.7)	(57.1–63.1)	(89.9–110.1)	(104.2–146.7)	(82.3–88.8)	(85.8–88.2)
Río Nazas specimens	♀	2	113.0	217.8	58.35	99.0	128.5	89.3	95.3
			(108.1–117.9)	(209.2–226.4)	(53.7–63.0)	(94.9–103.0)	(118.4–138.5)	(88.8–89.7)	(94.6–95.9)
K. f. arizonense	♀	15	123.9	194.1 ± 36.4	50.9 ± 8.0	105.8 ± 8.3	88.8 ± 26.8	76.4 ± 2.5	67.4 ± 4.9
			(95.5–141.9)	(123.8–283.3)	(33.1–63.1)	(90.3–116.7)	(58.2–121.1)	(70.9–81.1)	(60.8–76.5)
K. f. spooneri	♂	16	122.6	111.8 ± 18.2	27.0 ± 4.8	75.6 ± 6.6	38.3 ± 8.9	82.0 ± 1.8	79.4 ± 5.0
			(85.2–140.8)	(80.8–145.4)	(18.7–34.7)	(65.5–88.9)	(27.6–54.1)	(78.9–85.0)	(72.3–85.9)
K. f. flavescens	♂	158	115.5	79.4 ± 25.4	23.0 ± 7.1	63.9 ± 11.1	25.2 ± 13.0	82.4 ± 3.0	74.9 ± 7.6
			(78.0–141.9)	(32.9–142.6)	(3.1–48.4)	(31.8–96.8)	(9.0–61.2)	(75.5–91.1)	(49.9–96.3)
Río Nazas specimens	♂	2	137.8	284.5	74.4	121.9	172.4	84.1	91.0
			(134.0–141.5)	(256.6–312.5)	(68.7–80.1)	(121.1–122.7)	(169.7–175.0)	(83.1–85.1)	(85.5–96.5)
K. f. arizonense	♂	8	138.8	168.6 ± 21.0	57.9 ± 7.0	115.6 ± 11.2	83.5 ± 8.0	75.5 ± 4.7	66.5 ± 8.2
			(119.0–152.7)	(142.3–211.3)	(48.7–70.3)	(101.5–127.3)	(75.0–94.0)	(69.0–84.9)	(61.6–87.7)

Analysis System (Service, 1972). Step-wise discriminant analyses utilized the Biomedical Program BMD 07M (Dixon, 1973).

Despite recent criticism on theoretical grounds (Atchley et al., 1975, 1976) of the use of character ratios as input variables in statistical analyses, I follow Corruccini (1977) in his belief that their use can ". . . enhance (the) understanding of . . . data, despite theoretical objections." The use of character ratios has proven effective in studies of morphometric variation in *Kinosternon* turtles (Iverson, 1979). In the present paper multivariate statistical analysis of character ratio data is used only as a tool to aid my discrimination of samples and my selection of taxonomic characters. I have therefore attached no statistical significance to output based on character ratio input. As my goal is simply to discriminate samples (i.e., populations), I believe this use of character ratios is justified.

Standard deviations accompanying means in Table 1 are intended only as a relative measure of character variability, without any implication of statistical significance, because character ratio values may not generally be normally distributed (Atchley et al., 1975, 1976).

All known specimens from Mexico, Arizona, New Mexico, Colorado, Nebraska, Missouri, Iowa and Illinois are included in the appended Specimen List; only selected specimens from other states are included. Localities are plotted in Fig. 1. Specimens are listed with their catalog numbers and abbreviations for the museum or private collection according to Duellman, Fritts and Leviton (1978) except for the following: DMNH—Dallas Museum of Natural History; EAL—Ernest A. Liner, Houma, Louisiana; ENMU—Eastern New Mexico University; FWMNH—Fort Worth Museum of Natural History; JBI—John B. Iverson, Gainesville, Florida; LTU—Louisiana Tech University; MES—Michael E. Seidel, Huntington, West Virginia; MSU—Michigan State University; NMSU—New Mexico State University; SRSU—Sul Ross State University; TAI—Texas A & I University; TTU—Texas Tech University; UG—University of Georgia; UMKC—University of Missouri, Kansas City; USA—University of South Alabama; USL—University of Southwestern Louisiana.

Turtles were analyzed according to the drainage basin from which they originated. Specimens from the drainage basins listed separately in the Specimen List served as populations in the analysis. 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.

Synonymies include the reference to the original description of that taxon and all others that are considered to be junior synonyms. All types which were locatable were examined.

Due to the strong sexual dimorphism in *K. flavescens,* the included key distinguishes the sexes as well as the subspecies.

Statistical Results

For male turtles canonical correlation analysis (using all 23 character ratios) for 23 basin samples with 2 or more turtles (185 total) produced population means of the canonical variates which, when plotted on the first three canonical axes (58% of the total dispersion) revealed three distinct clusters. These phenetic groups corresponded to the three recognized subspecies of *K. flavescens* (*Kinosternon flavescens arizonense, Kinosternon flavescens spooneri* and *Kinosternon flavescens flavescens*). The first (and most distinct) included the samples from the basins in Sonora, Mexico and Arizona (*arizonense*); the second included the Illinois and Mississippi River samples (*spooneri*); and the last included the basins in Nebraska, Kansas, Colorado, southwest Missouri, Oklahoma, Texas and New Mexico in the United States, and Tamaulipas, Veracruz, Coahuila, Nuevo León and Chihuahua in Mexico (*flavescens*).

Similar analysis of 21 basin samples of females (159 total turtles) produced similar results; 69% of the total dispersion was accounted for by the first three canonical variates, and three phenetic clusters, corresponding to the three presently recognized subspecies, were revealed.

Step-wise discriminant analysis was performed with all 23 character ratios for each sex separately, using the turtles from the basins in the three respective canonical clusters as three samples. A fourth sample of four male and four female turtles from basins with small samples (including two males and four females from isolated populations in Durango) was also included for a posteriori classification by the computer. The first canonical variate produced by this analysis accounted for 80.70 and 88.50% of the total dispersion in the male and female samples, respectively. The first two variates together accounted for 99.9% of the dispersion

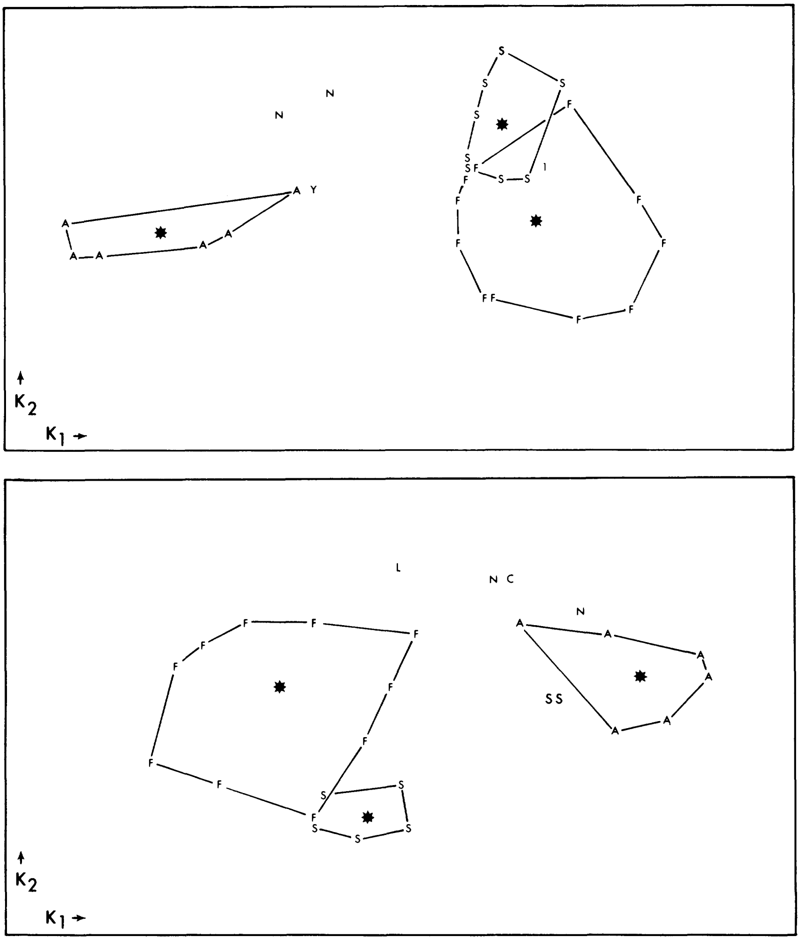

Fig. 2. Dispersion plots on the first (K_1) and second (K_2) canonical axes of *Kinosternon flavescens flavescens* (F), *K. flavescens spooneri* (S) and *K. flavescens arizonense* (A) for males (above) and females (below). Lines connect the most dispersed values about the population mean (asterisks) of the canonical variates. Values for the male "Yuma, Arizona" lectoparatype of *Platythyra flavescens* (Y), two male and two female *K. flavescens* from the Río Nazas (N), a male from the upper Río Yaqui in Arizona (I), a female from the Bolsón de Mapimi (C) and a female from southern Chihuahua (L) are individually marked. Sample sizes are in Table 1.

for each sex (Fig. 2). The discriminant analysis also determined the character ratios most important in distinguishing the three samples (or subspecies). In order of decreasing discriminatory importance, the seven best of these for male turtles were IF/CL, IF/PL, GL/CL, IH/PL, IH/CL, IAN/CL and WC/CL. The best seven for the females were IF/CL, IF/PL, IAN/PL, IAN/CL, GL/CL, IH/PL and IH/CL. Intuitive recombinations of these characters eliminated the standardizing effects of CL and PL, and produced several new character ratios which in combination discriminated the subspecific samples with nearly 100% reliability (Table 1 and Key).

Specimens of *K. flavescens* from near the Río Nazas in Durango have previously been considered representative of the Sonoran subspecies (*arizonense*). In fact, nine specimens of *K. flavescens* (including three juveniles not used in the statistical analyses) available to me from the Bolsón de Mapimi and the lower reaches of the Río Nazas in Durango are all most similar phenetically to *K. f. arizonense* (Fig. 2). However, they are morphologically distinct from that subspecies as well. In addition, geological and biogeographical evidence suggests it is unlikely that the range of *K. f. arizonense* was ever continuous from Sonora to Durango (Morafka, 1977). I therefore believe that the Durango populations represent an independent evolutionary divergence, worthy of subspecific designation, and propose the name *Kinosternon flavescens durangoense* for these populations.

A single specimen from Las Arenosas in southern Chihuahua (KU 33914; Chrapliwy and Fugler, 1955) is geographically (Fig. 1) and phenetically (Fig. 2) intermediate between *K. f. flavescens* and *K. f. durangoense.* Until additional material is available from this area, this specimen is tentatively considered a *K. f. flavescens* × *durangoense* intergrade.

Distributional Problems

Many of the distributional problems involving *K. flavescens* have been previously clarified (Iverson, 1978), but several remain. Classification by discriminant analysis of turtles from basins with very small sample sizes solved some of these problems and revealed several more. Discussions of each of these follow.

Nebraska.—*K. flavescens* is common in the Republican River drainage in Nebraska (pers. observ.), but until 1975 was known outside of that basin only on the basis of a specimen from the Blue River drainage (4.8 km NE Minden, Kearney Co.; UMMZ 101295), a specimen from the Niobrara River Valley (Valentine, Cherry Co.; UN 1982; Hudson, 1942), and two literature records from the headwaters of Blue Creek (Gimlet Lake, Crescent Lake National Wildlife Refuge, Garden Co.; Imler, 1945; Platt, 1969), a tributary of the Platte River. Recently three additional localities have been established in the Sandhills region of western Nebraska between the Platte and Niobrara rivers (John Lynch, pers. comm.; Fig. 1).

The occurrence of *K. flavescens* in Nebraska north of the Republican River is not surprising in light of Pliocene records for the species from Brown County (Fichter, 1969). The numerous fossil and recent records of *K. flavescens* in the Nebraska Sandhills do not support Hudson's (1942) speculation that the species was introduced north of the Republican River.

The populations in northwest Nebraska may be disjunct from those in southern Nebraska because the species has not been collected in between despite my extensive collecting efforts, and even though suitable habitat (especially *Typha* marshes) occurs along the intervening Platte River.

Kansas.—Collins (1974) has mapped specimens from three counties that seem to bridge the range of *K. flavescens* in central Kansas with that in southwestern Missouri and southeastern Kansas (Fig. 1). His Franklin Co. record is based on KU 3029–30 which bear no further locality data, but were (reportedly) collected by a KU Biological Survey field party in December, 1912 (J. T. Collins, pers. comm.). Collins' Greenwood Co. record stems from CAS-SU 33399 and MCZ 8432, each bearing no additional locality data. The first was recorded as having been collected by Julius Hurter sometime during the months of July and August, 1912, and received at the California Academy in December, 1912 (A. E. Leviton, pers. comm.). The second specimen was also collected by Hurter and deposited in the MCZ in 1913 (E. E. Williams, pers. comm.). The coincidence of the locations and dates (the Franklin Co. specimens were most likely deposited at KU in December, rather than collected at that time) of the Franklin and Greenwood County specimens suggests that they were all collected during the summer of 1912 by the same field party and deposited in the respective collections in December of that year or shortly thereafter. The specimen forming the basis of Collins' Lyons Co. record has not been located (J. T. Collins, pers. comm.).

The fact that no specimens have been collected since 1912 and the lack of precise locality data for all of the early turtles leads me to question the occurrence of *K. flavescens* in eastern Kansas. However, the possibility of the existence of relict populations in the area should not be ignored in light of the relict distribution of the species in many parts of its range.

Arizona and Sonora.—A single specimen known from the Río Yaqui headwaters in Arizona is *K. f. flavescens* (Fig. 1), whereas specimens from the river's lower reaches are *K. f. arizonense.* Lack of specimens from intermediate localities in the basin suggests that the ranges of the two subspecies may be completely disjunct.

Arizona, Gila River.—The Pliocene type locality of *K. arizonense* Gilmore (3.2 km S Benson, Cochise Co., Arizona) lies in the San Pedro River Valley, presently a tributary of the Gila River. *K. flavescens* is not otherwise known from the Gila Basin (Iverson, 1978, 1979); however, the species occurs today in the southward flowing Río Sonora, suggesting perhaps that the Río San Pedro was once a tributary of the Río Sonora and that *K. flavescens* was somehow extirpated from the San Pedro before it was captured by the Gila.

Systematic Accounts

Kinosternon flavescens (Agassiz)
Yellow Mud Turtle

Platythyra flavescens Agassiz, 1857:430 (lectotype, USNM 50, a male, from Río Blanco, near San Marcos, Texas; C. B. R. Kennerly, collector; type locality unjustifiably restricted to Waco, Texas, by Smith and Taylor [1950:24]).

Kinosternon arizonense Gilmore, 1922:2 (holotype, a Blancan fossil, USNM 10463, a male, from the Benson Locality Quarry, 3.2 km S Benson, Cochise Co., Arizona; J. W. Gidley, collector).

Diagnosis.—*K. flavescens* is unique among the members of the genus in the shape of the ninth marginal scutes, which are distinctly elevated above the preceding marginals in adults. It is further distinguished from other *Kinosternon* occurring sympatrically (or nearly so) by its: 1) depressed carapace, with at most one weak median keel (all but the oldest *K. hirtipes, K. integrum, K. scorpioides* and *K. sonoriense* are tricarinate); 2) bridge with distinct longitudinal groove (no such groove in *K. herrerai, K. hirtipes, K. integrum, K. scorpioides* or *K. sonoriense*); 3) reduced plastron, with a well-developed anal notch (plastron large in *K. integrum* and *K. scorpioides,* and anal notch lacking in *K. scorpioides*); 4) axillary and inguinal scutes in contact (usually not in *K. integrum* and *K. scorpioides*); 5) first vertebral scute usually contacting the second marginal scute (almost never the case in *K. herrerai* or *K. subrubrum*); 6) clasping organs on the hind limbs of males (lacking on male *K. integrum* and *K. scorpioides*); and 7) femoral scute sulcus on the hypoplastron nearly parallel to the bone's posterior margin (sulcus not parallel to the posterior margin in *K. hirtipes* and *K. sonoriense*).

Description.—*K. flavescens* is a moderate-sized turtle; males reach approximately 165 mm CL whereas females reach only 145 mm. The juvenile carapace has a single weak median keel which is lost with age. The depressed carapace is oval in adults (CW 65 to 85% of CL) and almost round in hatchlings and juveniles. The carapacial scutes are imbricated; the first or second vertebral scute (V_1 or V_2) is the longest; V_3 is nearly always the widest; V_5 is the shortest and narrowest; at least three vertebral scutes are wider than long; the vertebrals are not significantly longer than broad. The nuchal scute is small, usually broader than long. V_1 may or may not contact the second marginal (M_2). The dorsal margins of M_1 through M_8 are all aligned; none is elevated. M_9 is distinctly elevated above the preceding marginals, with its highest point at or just anterior to the seam between the third and fourth pleurals, and its dorsal margin sloping downward from that seam to its contact with M_{10}; M_{10} is also distinctly higher than M_1 through M_8, but usually not as high as M_9; M_{11} may or may not be elevated to the height of the posterior margin of M_{10} at their junction. The posterior carapace margin is shallowly notched between the eleventh marginals.

The plastron is reduced (more so in males than females), and does not completely close the ventral opening of the shell; WC averages 57.6% of CW in males and 59.5% in females. The bridge is of medium length (16 to 27% of CL) and has a longitudinal groove evident near the posterolateral margin of the abdominal scute. The anterior and posterior plastral lobes are both freely moveable; the posterior lobe is constricted at the hinge (where WC is measured) and has a distinct anal notch which is more emarginate in males than females. The plastral midlobe averages 27.7% (range, 23.7 to 38.6) of maximum PL. The sutures between the respective hyoplastra and hypoplastra along the plastral midline are ligamentous and flexible even in adults. Varying amounts of soft tissue are found between the plastral scutes of older individuals, especially above the hinges and between the abdominals. The axillary scute almost always contacts the inguinal, and the inguinal does not contact M_8.

The head is broad and the dorsal head scale is deeply furcate posteriorly even in the oldest adults. The maxillary sheath is hooked only slightly, if at all, in adult females, but often strongly hooked in older males. The eyes are located dorsolaterally on the head. One large pair of mental barbels is present near the mandibular symphysis and one smaller pair is found on the throat at the level of the tympanum. All four feet are large, fully webbed, and armed with long, sharp claws.

A well developed patch of tuberculate scales (clasping organs) is found on the posterior surface of the crus and thigh of each hind leg. The tail of adult males is elongate, approaching the plastral hindlobe in length; whereas that of the female is stubby and barely extends to the posterior margin of the carapace. The tail in both sexes bears a terminal horny spine.

The adult carapace is brown to olive in color; with darkly marked seams. The plastron is yellow to brown with darker brown seams, and the bridge area is dark brown. The hatchling carapace is colored the same, but with a yellow margin and a dark speck at the posterior border of each scute. The bridge in hatchlings is dark brown or black, and the plastron is creamy yellow with a brown to black foliate central figure applied to the seams. At all ages, the skin of the head, limbs, and tail is dark gray and the chin is yellow. A variably distinct yellow stripe extends posteriorly onto the neck from the angle of the jaws in some specimens, especially juveniles.

The third (usually), second, or fourth (rarely) cervical vertebra is biconvex; the posterior five (or four) are procoelous, with the sixth and seventh doubled posteriorly, and the seventh and eighth doubled anteriorly. The anteriormost neural bone nearly always contacts the nuchal bone. The femoral scute sulcus on the hypoplastron is nearly parallel to that bone's posterior margin. Phalangeal formula is 2-3-3-3-3.

Distribution.—The distribution of *K. flavescens* in the United States and Mexico appears in Fig. 1. Although it is primarily a Great Plains and Chihuahuan Desert form, this species also ranges into the Sonoran Desert. Its range overlaps that of *K. subrubrum* in eastern Texas and south-central Oklahoma; that of *K. scorpioides* (=*cruentatum*) in at least the area between and including the drainages of the Ríos Soto la Marina and Pánuco in southern Tamaulipas and northern Veracruz (and perhaps Nuevo León); that of *K. herrerai* in the area between and including the drainages of the Ríos San Rafael and Pánuco in southern Tamaulipas and northern Veracruz; that of *K. integrum* in the lower Río Yaqui drainage of Sonora; that of *K. hirtipes* in Presidio Co., Texas, northeastern Durango, and Chihuahua in the Ríos Conchos, Santa Clara and Santa Maria; and that of *K. sonoriense* in the Ríos Sonoyta, Magdalena, Sonora, Matape and Yaqui in Arizona and Sonora, and the Río Casas Grandes in Chihuahua. *Kinosternon flavescens* has been collected at the same locality with *K. subrubrum* in east Texas (Strecker, 1931; Olson, 1959); *K. hirtipes* in Presidio Co., Texas, and the Río Santa Maria (near Progreso), in Chihuahua (both based on museum records); and *K. sonoriense* in the Rio Sonoita basin (Quitobaquito Pond; Hulse, 1974).

Kinosternon flavescens flavescens (Agassiz)
Yellow Mud Turtle

Diagnosis.—The adults of this race differ from the other three subspecies in the shorter gular scute (21 to 59% of FL), and the longer interhumeral seam (8 to 25% of CL). The plastral hindlobe is wider (WC is 36 to 49% of CL in males; 38 to 53% in females), the plastral bridge shorter (16 to 25% of CL), the interfemoral seam shorter (1 to 9% of CL), the interanal seam longer (16 to 28% of CL in males; 23 to 35% in females), and the first vertebral scute longer (19 to 29% of CL) than in *K. f. arizonense* and *K. f. durangoense* adults. The carapace is wider (66 to 85% of CL), and the first vertebral scute wider (27 to 31% of CL) than in *K. f. arizonense.* The forelobe is longer (28 to 39% of CL) than in *K. f. durangoense.* The underside of the head and throat are distinctly yellow; the dorsum of the head is gray to grayish olive.

Distribution.—*K. f. flavescens* ranges from the Republican River Basin in southern Nebraska southward to the coastal area immediately south of the Río Pánuco Basin in Veracruz, Mexico, and west to the upper Río Yaqui in southeastern Arizona. Disjunct populations also occur in southwestern Missouri and adjacent Kansas, and the sandhill region of Nebraska. This subspecies is known from sea level to at least 1,500 m.

Kinosternon flavescens **durangoense**
new subspecies
Durango Mud Turtle

Kinosternon flavescens stejnegeri Hartweg, 1938:1 (in part).

Holotype.—FSM 16180, adult female, alcoholic; collected 8 km from Ceballos, in Lago de los Palomas, Durango, Mexico on 3 November 1963 by Walter Auffenberg (Fig. 3).

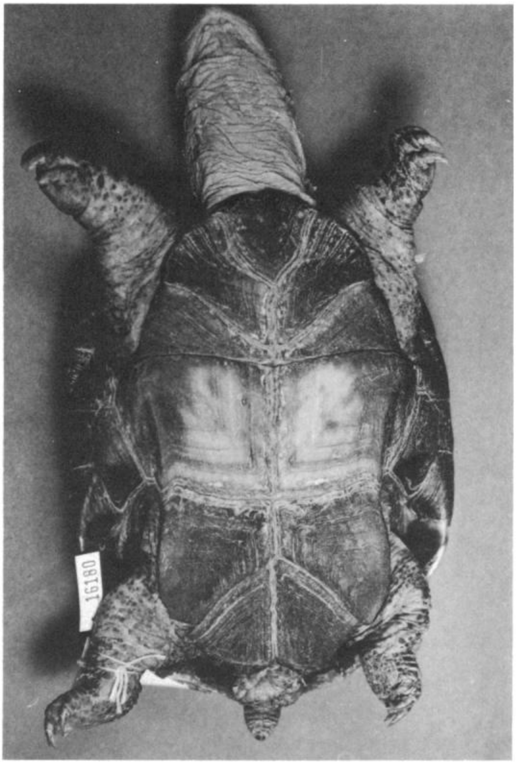

Fig. 3. Plastral view of holotype of *Kinosternon flavescens durangoense* n. ssp. (FSM 16180).

Paratypes.—(8) UTA 30524 and 30525 (both juveniles), 1.6 km NE León Gúzman on Torreón-Durango Hwy, Durango; UIMNH 19338 (adult female), and FMNH 112996 (juvenile), FMNH 112997 (adult female), FMNH 112998 (adult male), FMNH 123666 (adult male), FMNH 179224 (juvenile); all from 22.5 km NE Pedriceña, Durango (see *Remarks*).

Diagnosis.—Adults of this race differ from adults of the other three subspecies in the shorter plastral forelobe (31 to 33% of CL). This race differs from *spooneri* and the nominate subspecies in the narrower plastral hindlobe (WC is 39 to 40% of CL in males; 42 to 47% in females), the longer plastral bridge (20 to 24% of CL), the longer gular scute (54 to 69% of FL), the shorter interhumeral seam (6 to 12% of CL), the longer interfemoral seam (11 to 13% of CL), the shorter interanal seam (16 to 17% of CL in males; 19 to 22% in females), and the shorter first vertebral scute (22 to 24% of CL). The carapace is wider (73 to 82% of CL) and the first vertebral scute is wider (27 to 31% of CL) than in *K. f. arizonense* adults. The head coloration is as in *K. f. flavescens*. *Kinosternon f. durangoense* is most similar morphologically to *K. f. arizonense* (see Hartweg, 1938), but this relationship may be due to convergent adaptation to similar southerly, xeric environments; geographic proximity suggests that *durangoense* should be most closely related to the nominate subspecies. Selected character proportions appear in Table 1.

Remarks.—The paratypes of *K. f. durangoense* from near Pedriceña represent 6 of 7 specimens from that locality which were designated as paratypes of *K. f. stejnegeri* (=*arizonense*) by Hartweg (1938); I could not locate the last paratype.

Ecological notes.—Specimens of *K. f. durangoense* have been collected in or near ephemeral playa lake situations only during the period of peak rainfall in the area: 18 July, 26 August, 30 August and 3 November. This contrasts with the activity schedule of the more northern subspecies which, due to different precipitation schedules, are more active in the spring and early summer months and are generally inactive or aestivating during most of the summer and early fall (Mahmoud, 1969; Christiansen and Dunham, 1972). No standing water was present at the paratypic localities when visited on 5 and 6 May 1977; the turtles undoubtedly aestivate for much of the year, emerging when playas are filled by rain. Efforts to obtain additional material should be concentrated during that time of the year.

Additional material.—CM 59376 (adult female), 9.7 km N Escalón on Mex 49, Chihuahua; and MES uncatalogued (juvenile), Esmeralda in Sierra Mojada, Coahuila.

Distribution.—Known from the states of Chihuahua, Coahuila and Durango, Mexico, between 1,000 and 1,600 m elevation, near the lower reaches of the Río Nazas and in the Bolsón of Mapimi.

Kinosternon flavescens spooneri Smith
Illinois Mud Turtle

Kinosternon flavescens spooneri Smith, 1951:195 (holotype, INHS 4244, a female, from Henderson County State Forest, 11.3 km N Oquawka, Illinois).

Diagnosis.—The gular scute of adults is longer (40 to 55% of FL) than in *K. f. flavescens* but shorter than in *arizonense* and *durangoense.* The interhumeral seam of adults is shorter (11 to 19% of CL) than in *K. f. flavescens* and longer than in *K. f. arizonense* and *K. f. durangoense.* The plastral hindlobe is wider (WC is 36.5 to 45% of CL in males; 45 to 49% in females), the bridge shorter (17 to 22% of CL), the interfemoral seam shorter (3.5 to 7% of CL), the interanal seam longer (19.5 to 26% of CL in males; 27 to 32% in females), and the first vertebral scute longer (22 to 27% of CL) than in *K. f. arizonense* and *K. f. durangoense* adults. The carapace (68 to 81% of CL) and first vertebral scute (24 to 30% of CL) are wider than in *K. f. arizonense.* The plastral forelobe is longer (29 to 38% of CL) than in *K. f. durangoense.* Only the anterior portion of the underside of the head and neck are marked with yellow; the dorsum of the head is dark brown to black.

Distribution.—*K. flavescens spooneri* is known only from the drainages of the Illinois and Mississippi rivers in northwestern Illinois and adjacent Iowa and Missouri.

Kinosternon flavescens arizonense Gilmore
Arizona Mud Turtle

Kinosternon arizonense Gilmore, 1922:2 (see species synonymy).

Kinosternon flavescens stejnegeri Hartweg, 1938: 1 (holotype, UMMZ 72235, a female (not a male as stated in the original description), from Llano, Sonora, Mexico).

Diagnosis.—Adults of this race differ from adults of the other three subspecies in the narrower carapace (64 to 81% of CL) and the narrower first vertebral scute (21 to 27% of CL). The plastral hindlobe is narrower (WC 35 to 42% of CL in males; 39 to 45% in females), the plastral bridge longer (21 to 28% of CL), the gular scute longer (54 to 70% of FL), the interhumeral seam shorter (8 to 15% of CL), the interfemoral seam longer (7.5 to 13% of CL), the interanal seam shorter (15 to 20% of CL in males; 18 to 24% in females), and the first vertebral scute shorter (20 to 26% of CL) than in the adults of *K. f. spooneri* and the nominate subspecies. The plastral forelobe is longer (32 to 38% of CL) than in *K. f. durangoense.* The head coloration is as in *K. f. flavescens.*

Distribution.—*K. f. arizonense* is known in Arizona and Sonora, Mexico, from the San Simon Valley (near Sells) and the drainages of the Ríos Sonoyta, Magdalena, Sonora, Matape and Yaqui. All localities are between 100–1,050 m elevation. The presence of this subspecies in the Gila River Basin has not been confirmed (Iverson, 1978).

Key to the Sexes and Subspecies of *Kinosternon flavescens* >75 mm CL

1. A patch of tuberculate scales present on the posterior surface of the crus and thigh of each hind leg; tail large, extending well beyond posterior carapace margin; and maximum plastron length 80 to 98% of carapace length .... 2(Male)
   No patch of tuberculate scales on the posterior surface of the crus or thigh; tail short, barely extending to posterior carapace margin; and maximum plastron length 88 to 100% of carapace length .... 5(Female)
2. Gular length more than 140% of interhumeral seam length and more than 100% of interanal length; interfemoral seam length more than 48.5% of interanal length and more than 60% of interhumeral length 3
   Gular length less than 145% of interhumeral seam length and less than 100% of interanal length; interfemoral seam length less than 48.5% of interanal length and less than 60% of interhumeral length 4
3. First vertebral scute width less than 88% of plastral forelobe length, interfemoral seam length less than 100% of interhumeral length, and carapace width less than 86% of maximum plastron length .... *K. f. arizonense* (Sonora, Mexico and extreme southern Arizona)
   First vertebral scute width more than 85% of plastral forelobe length, interfemoral seam length more than 100% of interhumeral length, and carapace width more than 83% of maximum plastron length .... *K. f. durangoense* (Southern Chihuahua, southwestern Coahuila and northeastern Durango, Mexico)
4. Gular length 80 to 145% ($\bar{x}$ = 112%) of interhumeral length and 65 to 100% ($\bar{x}$ = 76%) of interanal seam length; interfemoral seam length 18 to 40% ($\bar{x}$ = 27%) of interanal length and 25 to 60% ($\bar{x}$ = 38%) of interhumeral length; top of head dark brown to black, yellow on chin and neck restricted to anterior half of lower jaw, and carapace dark brown or dark olive .... *K. f. spooneri* (Mississippi and Illinois River basins in Illinois, Iowa and Missouri)
   Gular length 30 to 120% ($\bar{x}$ = 79%) of interhumeral seam length and 30 to 85% ($\bar{x}$ = 64%) of the interanal seam length; interfemoral seam length 3 to 40% ($\bar{x}$ = 23%) of inter-

anal length and 9 to 45% ($\bar{x}$ = 25%) of interhumeral length; top of head gray to yellow-gray, chin and underside of neck distinctly yellow, and carapace yellow to brownish olive -- *K. f. flavescens*
(Nebraska south to extreme southeastern Arizona and northern Veracruz, Mexico)

5. Gular length more than 120% of interhumeral seam length and more than 80% of interanal length; interfemoral seam length more than 32% of interanal length and more than 58% of interhumeral length ---------------------- 6
Gular length less than 135% of interhumeral seam length and less than 80% of interanal length; interfemoral seam length less than 37% of interanal length and less than 52% of interhumeral length ------------------------------- 7
6. First vertebral scute width less than 80% of plastral forelobe length, interfemoral seam length less than 125% of interhumeral length, and carapace width less than 82% of maximum plastron length -------------- *K. f. arizonense*
First vertebral scute width more than 80% of plastral forelobe length, interfemoral seam length more than 100% of interhumeral length, and carapace width more than 82% of maximum plastron length ------ *K. f. durangoense*
7. Gular length 80 to 135% ($\bar{x}$ = 108%) of interhumeral seam length and 55 to 80% ($\bar{x}$ = 61%) of interanal seam length; interfemoral seam length 20 to 40% ($\bar{x}$ = 27%) of interhumeral length; top of head dark brown to black, yellow on chin and neck restricted to anterior half of lower jaw, and carapace dark brown or dark olive ------------------ *K. f. spooneri*
Gular length 30 to 120% ($\bar{x}$ = 77%) of interhumeral seam length and 25 to 65% ($\bar{x}$ = 52%) of interanal seam length; interfemoral seam length 10 to 35% ($\bar{x}$ = 21%) of interhumeral seam length; top of head gray to yellow-gray, chin and underside of neck distinctly yellow, and carapace yellow to brownish olive ----------------------------------- *K. f. flavescens*

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Specimen List

All specimens examined as well as all localities plotted in Fig. 1 are listed below by drainage basin sample used in the analysis. Basins are listed under the appropriate taxon (or taxa) in approximate geographical order from north to south (*flavescens*) or east to west (*spooneri* and *arizonense*). Selected literature records are also included. Specimens marked with an asterisk were not examined. A complete locality list is available from the author.

K. f. spooneri

Illinois River: Illinois. CHAS 15687 (Paratype). FMNH 39992-3* (Paratypes). INHS 4991*, 5587–89, 5987–89 (Paratypes), 6010–11 (Paratypes), 7164–66, 7920. MCZ 53932 (Paratype). TU 17864* (Paratype; formerly UIMNH 2254). UIMNH 2252–53 and 2255–56 (Paratypes). UMMZ 74654 (Paratype), 103089 (Paratype). USNM 83190 (Paratype). (Cahn, 1931, 1937).

Mississippi River: Illinois. INHS 3220–22 (Paratypes), 4244 (Holotype), 4245 (Paratype), 7937*. Iowa. JBI 591, 748–51. (Dodge and Miller, 1955; Dodge, 1956; Christiansen et al., 1975; Cooper, 1977). Missouri. UMKC 88682–83 (Anderson, 1957).

K. f. flavescens

Nebraska Sandhills: Nebraska. UN 1982, uncatalogued. (Imler, 1945).

Blue River: Nebraska. UMMZ 101295.

Republican River: Colorado. JBI 761, 763–64. UC 3402–16*, 6039–40*, 10777*, 11257*, 11697–707*, 43791*. Kansas. (Smith, 1956). Nebraska. JBI 419–38, 480–85, 758–60. UN 1558–60, 1612, 1652–57, 1981, 1983–85. USNM 90440. (Burt and Hoyle, 1934; Hudson, 1942).

Saline and Smoky Hill rivers: Kansas. KU 3753–54*, 3761*, 19480*. MCZ 32556*. UMMZ 130149.

Neosho River: Kansas. KU 20940*, 21048*, 23356*. MCZ 8432*. Missouri. UMKC 726. (Anderson, 1965; Smith and Balch, 1974).

Arkansas River: Colorado. UC 11739*. UMMZ 62502. Kansas. JBI 488. KU 3032*, 14108–12*, 18379*, 18383*, 18386*, 18388*, 18391*, 19594–95*, 20520–21*, 41712–38*, 46862*, 46898*, 50304*, 50306–09*, 51450, 69986–70010*. LSUMZ 856. MCZ 25961*, 32555*. SDNHM 22368*. Oklahoma. UO 9136–43*, 9171*, 9187*–9203*, 9246*, 9299–9300*, 9301, 19067–78*, 19080–85*, 19096*, 25268–72*. UMMZ 90001.

Cimarron River: Colorado. UC 19647*. Kansas. AMNH 62851. CM 50802 (7)*, 50803*. FSM 11023(2), 11024–25, 11072. INHS 5952–53*. KU 2791–97*, 3037–51*, 18392–3*, 46899*, 49632*. MSU 2922. UMMZ 96076, 106672–73, 127242–51, 127253–62, 127264–66, S-1211–12, S-2942–47. UNM 13277–81*. Oklahoma. JBI 770–774. UMMZ 89633. UO 5136*, 5289–5300*, 5389*, 8537*, 8596*, 8611–12*, 9454–56*, 9510–13*, 9540–41*, 9554*, 9584–86*, 9590–92*, 9681*, 24205*.

Canadian River: New Mexico. AMNH 69763*. JBI 415–18. UNM 13283–299*, 14188–90*, 20511–12*, 20516–19*, 20525*, 20529–30*, 20536–37*, 20554–56*, 20575–90*, 20685*, 20687–701*, 21167*, 22388*, 22392*, 23180–82*, 23189*, 23750–51*, 24017*, 31949–69. UMMZ 134280. Oklahoma. ENMU unnumbered (9)*. FSM 11022(2). KU 18128*, 46869*. UC 49518*. UO 467–70*, 1472*, 1513*, 1516*, 1534*, 3642–43*, 3755–56*, 4995*, 5010*, 5023*, 5028*, 5053*, 5056*, 5075*, 5101–02*, 5110–11*, 5135*, 5412–15*, 5419*, 5424–26*, 5430*, 5432*, 5433–34*, 5436–38*, 5451*, 5483*, 5876*, 6422*, 6450*, 6455–56*, 8472–74*, 8477*, 8570–73*, 8575*, 8579*, 8583–84*, 8586–88*, 8591–92*, 8833–34*, 9958*, 13752*, 19022*, 19048–49*, 19094*, 19097*, 19912–14*, 20219*, 20223*, 20225*, 22860–61*, 24215–17*, 24222–275*, 24281–82*, 25265*, 25291*, 27141*, 27504*, 27509*. Texas. TCWC 13044–46*. TU 14517*, 14525*, 14535*. UTA 10453*, 10507–12*, 10596–97*, 10699–700*, 10719–20*, 10748*, 10871*, 11527*, 11530*.

Red River: Arkansas (probably erroneous). MCZ 1919 (lectoparatype). Oklahoma. CM 42855–56*, 44722*. FWNHM 4786–89*. JBI 503. LTU unnumbered*. SDNHM 21955*. UC 14077–80*. UMMZ 77579. UO 4418–19*, 4428*, 4471*, 4530*, 4586–90*, 4592–4612*, 4614*, 4616–17*, 4619*, 4654*, 4656*, 4666*, 4684*, 8354*, 8423–24*, 10935*, 12999*, 13039*, 13041–46*, 13048–52*, 13054–63*, 13065–68*, 13070–76*, 19915–16*, 19989–91*, 19995*, 19999*, 23315*, 23765*, 23768*, 23777–81*, 23786–87*, 23791–95*, 23801*, 23804–10*, 23814*, 23817*, 23819–23*, 23828–34*, 23844–47*, 23849*, 23869–72*, 23874–78*, 23880*, 23887–88*, 23891*, 25284–85*, 25354*, 25372*, 25875*, 28624–25*, 29839*. Texas. AMNH 7488*. CM 42857*. DMNH 1087*. FWMNH 1654*, 3533*. INHS 8035*. KU 88681*. MVZ 65762*. TCWC 18754–56*, 36634*. TU 16676. UMMZ 69127–32. USL 1008. UTA T820–914*, T1039*.

Sulphur River: Texas. DMNH 691*.

Trinity River: Texas. DMNH 588*, 690*. FWMNH 623–24*, 2555*, 3490*, 3508*. JBI 514, 566. TCWC 562*. UC 16895*. UTA T3535*.

Brazos River: New Mexico. ENMU unnumbered (11)*. NMSU 2848–51*. Texas. AMNH 69761–62*. ENMU unnumbered*. FWMNH 996*, 3455–56*, 5585*, 6384*, 7038*, 46295. INHS 6015*. KU 3130–31*, 16536*. TCWC 7257*, 13963–64*, 14901*, 18430*, 20062*, 25120–25*, 30696–7*, 44478–79*. TU 16675*. UG 324*. UMMZ 70825–26, 92726. UNM 13390. USL 13492. USL 13494–95. UTA T967–68*, 9739*. UU 17417, 17427.

Colorado River: Texas. AMNH 66106*. CHAS 15049. CM 3020*, 3171*. FSM 3453. FWMNH 5375*, 6990*. INHS 6392*. LACM 7976*, 66709, 66710*, 66712–13*, 74392*. LSUMZ 16351*. MCZ 96900*. MVZ 39731*, 77913*, 99225*. TCWC 18422–27*, 21406*, 27546–47*, 31269*, 31273*, 32170*, 37947*, 40103*, 42342*. UMMZ 50153. USL 13494. UTA T41–47*, T311–12*, T362*, T677–78*, T933–34*, T6196–97*, T6345–46*, T6751–53*, T7062*, 10266*, 17491–92*, 28649*, 34018*, 46041*, 46161*.

Between Colorado and Guadalupe-San Antonio rivers: Texas. LACM 61110*. TCWC 14577*, 30698*. USA unnumbered*.

Guadalupe-San Antonio Rivers: Texas. AMNH 9339*, 32389–96*, 69758*, 69760, 72226*. CM 21120–21*. FSM 30362. KU 44945*. LSUMZ 10312*. MVZ 68390*. TCWC 14950–52*, 21101*, 36611*. TU 10834–35*. USL 20553*. USNM 50 (lectotype), 131823 (lectoparatype), (see Iverson, 1978). UTA T613*, 13991–92*, 22292*, 26681*, 26832*, 44778*, 44782*.

Between Guadalupe-San Antonio and Nueces rivers: Texas. INHS 9451*. TCWC 31271–72*. UTA 19785–86*.

Nueces River: Texas. CM 8336–43. KU 39980*. MCZ 16512*. SRSU 2036*. TCWC 4688*, 5115*, 21405*, 35591*. USL 6868. UTA 14545–46*, 21598*, 24564*, 29053*, 29057*, 42165–77*, 42179–80*, 46133*.

Between Nueces and lower Rio Grande: Texas. CM 13483*. FWMNH 6022*. TCWC 18431*, 20905–07*. UTA 28043*.

Lower Rio Grande (below Pecos River): Texas. FSM 15926–38. JBI 409. MCZ 1918 (lectoparatype). SRSU 2566*. TAI 492*. TCWC 14903*, 18428–29*. UMMZ 96631–33. UTA 29055*, 32382–84*.

Rio Pesqueria: Coahuila. FMNH 1535–36 (Hartweg, 1938), 46135*. KU 29336. Nuevo Leon. AMNH 69952. BAYUM 7494*. EAL 4163 (3 specs). UC 47379–80.

Rio Alamo: Nuevo Leon. EAL 4294.

Rio Salado: Coahuila. EAL 2394, 3144. FMNH 28840, 47355–65. KU 39950. TTU 1123*. UIMNH 48534–43 (Williams, 1961), 62779–81 (Schmidt and Owens, 1944). Nuevo Leon. BAYUM 9724*, 13142* (Casas Andreu, 1967).

Northeast Coahuila (Basins Draining to Rio Grande): Coahuila. BAYUM 9449–453*. SRSU 3671* (Schmidt and Owens, 1944).

Rio Conchos to Rio Panuco (NE Mexico): Nuevo Leon. EAL 4073* (Liner et al., 1976). UMMZ 125565. Tamaulipas. BAYUM 7479–83*, 7487*, 7493*. EAL 530*. TU 15971 (11 specs). UMMZ 103184. UNM 30809 (Seidel, 1976). USNM 108588. UU 9837*. Veracruz. BAYUM 7488–89.

Pecos River: New Mexico. AMNH 80159*. ENMU unnumbered*. JBI 504–13, 516–18, 542–562. KU 51153*. LACM 7971–75*, 105358–59. MCZ 62335*. MVZ 52255*. NMSU 3179–80*. TU 17176. UMMZ 121895–96, 123516, 123550, 123689, 134177–78, 134275–79. UNM 7519–20*, 11257*, 12506–09*, UNM 13014*, 14377*, 14489*, 14612–13*, 14741–43*, 14746*, 14865*, 14870*, 15030*, 15563–69*, 16138*, 17208–09*, 17685*, 19449–51*, 19453*, 19542*, 20485*, 20535*, 20604–08*, 20686*, 23165–66*, 23173*, 23175*, 23177*, 23363*, 23665–66*, 23745–46*, 24016*. USL 15635*. USNM 71070*. UU 8355–8440*, 11426–27*, 12418*, 12420*, 12516–18*, 13033*, 13085*. Texas. DMNH 967*. JBI 679. KU 88680*. LSUMZ 9821*, 16319*. SRSU 2039*, 2430*, 3015*. UA 27948. UC 49580*. UMMZ 65378. UNM 20524*. UTA 29056*.

Upper Rio Grande (Above Pecos River): Chihuahua. KU 45018, 51082. USNM 105019. New Mexico. KU 73479–80*. NMSU 351*, 3387*. Texas. DMNH 984*, 987*. EAL 3488. FSM 30366–68. JBI 565. LSUMZ 23049. SRSU 1501*, 1508*, 3633*. TCWC 26100*. UMKC 724–5*. UMMZ 85079*, 101291–93*, 114356*, 114358*, 116579–80. UNM 8170*, 16695*, 17191–92*. UU 11143–46*.

Rio Conchos: Chihuahua. KU 52144–46, 52158. UA 35026–30. UNM 31943–48.

Salt Basin (between Pecos River and Rio Grande): Texas. FSM 30369.

Rio Santa Clara: Chihuahua. USNM 105014–18.

Rio Santa Maria: Chihuahua. KU 44496–98. UMMZ 118272–83. UNM 30392. USNM 104976–105013, 105035.

Rio Casas Grandes: Chihuahua. UA 36375–76. UU 8441–58.

Rio Mimbres: Chihuahua. FSM 39103. USNM 19058-59. UU 8459-60. New Mexico. AMNH 68394*. BYU 14650*. TCWC 21590*.

NW Chihuahua independent basin: USNM 20974.

Playa Lakes: New Mexico. AMNH 95966. UNM 4041*, 20513-15, 20520-23, 20526, 20531-34, 20553, 20599-20603, 23752, 23753-54.

Rio Yaqui: Arizona. UA 27953.

K. f. arizonense

San Pedro River: Arizona. USNM 10463 (Holotype: Pliocene; Blancan), 10462 (Paratype).

Yaqui River: Sonora. UA 27957, 40529.

Rio Matape: Sonora. UA 27958. UNM 17663.

Rio Sonora: Sonora. CAS-SU 13184-85. UIMNH 23919-20 (Langebartel and Smith, 1954), 73495-97. UMMZ 87722. UU 7956*.

Rio Magdalena: Arizona. UA 33581. Sonora. AMNH 67502. CAS-SU 13478. LACM 105407. UA 31739-40. UMMZ 72234 (*stejnegeri* Paratype), 72235 (*stejnegeri* Holotype). (Allen, 1933).

San Simon Valley (near Sells): Arizona. UA 27949-50, 27954-55, 27964, 35394-95.

Rio Sonoyta: Arizona. INHS 8650*. MSU 11053 (Smith and Hensley, 1957). UIMNH 41218 (Williams and Chrapliwy, 1958).

Gila River: Arizona. USNM 7892 (*flavescens* Lectoparatype).

K. f. durangoense

Rio Nazas: Durango. FMNH 112996-98, 123666, 179224 (Paratypes). UIMNH 19338 (Paratype). UTA 30524-25 (Paratypes). (Hartweg, 1938).

Bolson de Mapimi: Chihuahua. CM 59376. Coahuila. MES unnumbered. Durango. FSM 16180 (Holotype).

K. f. durangoense × flavescens

Laguna de Clavos independent basin (near Rio Florido): Chihuahua. KU 33914 (Chrapliwy and Fugler, 1955).

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Genetic Studies of Melanic Color Patterns and Atypical Sex Determination in the Guppy, *Poecilia reticulata*

P. L. NAYUDU

Three guppy color patterns, with the unifying characteristic of being composed primarily of melanophores and occurring only in domestic stocks, have been subjected to genetic analysis. Each of the patterns studied in commercial populations is shown to have single gene inheritance, to be determined by a different locus, to be sex-linked on both the X and Y chromosomes, and to be dominant in expression in both sexes. The Flavus gene (a tail pattern) is found to inhibit the action of tail-fin enlarging genes; Y-linkage of the Nigrocaudatus II gene (a body pattern) is found to be associated with subnormal vigor and viability; and the likely gene order is shown to be NiII-Fla-Cp. Also reported is the occurrence of XX males constituting a quarter of the progeny of an XY male and XX female.

THE guppy is a fresh and brackish water ovoviviparous poeciliid fish which is known for intense, multiple and variable patterns of coloration (Sterba, 1962). The color patterns in wild populations are limited in their expression to the mature males. Because of the large numbers of color patterns found in the wild (Haskins et al., 1961) and the ease with