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SYSTEMATICS OF THE FALSE MAP TURTLES (*GRAPTEMYS PSEUDOGEOGRAPHICA* COMPLEX: REPTILIA, TESTUDINES, EMYDIDAE)

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ABSTRACT

Taxonomic relationships in the *Graptemys pseudogeographica* complex are reviewed and redefined. Variation of head pattern within clutches, within local populations and throughout the geographic ranges of the species were compared through canonical analysis. Environmental control of head pattern characters was confirmed by laboratory manipulation of incubation temperatures. Skeletons from specimens with known head patterns, and skulls from extremes in the geographic range, were used to show species separation and subspecies affinities. Canonical analysis of 37 morphological characters (including head pattern, shell and skull morphometrics) established differentiation of *G. pseudogeographica* and *G. ouachitensis.* Electrophoresis of plasma, hemoglobin, and muscle homogenate proteins showed little variation in 16 of 19 protein systems within populations, between populations of the same species, or between species. Malate dehydrogenase was the only polymorphic protein system. Analysis of courtship behavior showed that stereotypic displays of *G. ouachitensis* and *G. pseudogeographica* from sympatric populations are distinctly different. *Graptemys pseudogeographica* and *G. ouachitensis* are shown to be widely sympatric distinct species, each with two subspecies: *G. pseudogeographica pseudogeographica* and *G. pseudogeographica kohni*; *G. ouachitensis ouachitensis* and *G. ouachitensis sabinensis.* The allopatric *G. caglei* and *G. versa* are regarded as distinct, monotypic species.

INTRODUCTION

The false map turtle complex, including the nominal forms *Graptemys pseudogeographica, G. pseudogeographica ouachitensis, G. pseudogeographica sabinensis, G. kohni, G. versa,* and *G. caglei,* has long perplexed taxonomists. *Graptemys pseudogeographica* was described by Gray (1831) from specimens collected at New Harmony, Indiana, on the Wabash River. Baur (1890) described *G. kohni* from Louisiana specimens received from Gustave Kohn. Baur characterized *G. kohni* as having "a thin yellow line, which is connected with another one running behind from the upper part of the orbit." This trait was said to distinguish *G. kohni* from *G. pseudogeographica* with its large yellow spot behind the eye. Carr (1949) considered *G. kohni* a subspecies of *G. pseudogeographica.*

Graptemys pseudogeographica versa was described by Stejneger (1925) from the Colorado River near Austin, Texas. Smith (1946) elevated *versa* to species status. This species, which is geographically isolated from other *Graptemys,* is distinguished by a J-shaped mark extending posteriorly from the orbit and the absence of distinct vertebral knobs.

Cagle (1953) described *G. pseudogeographica sabinensis* and *G. pseudogeographica ouachitensis* from the southern United States. He stated that *G. pseudogeographica sabinensis* was restricted to the Sabine River in Louisiana and Texas, and that *G. pseudogeographica ouachitensis* occurred in the Ouachita River of

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Louisiana, but its range extended north and west into Texas, Oklahoma, Arkansas, and Kansas. Cagle proposed that *sabinensis* and *versa* were related on the basis of skull characters. He claimed that intergrades between the subspecies *ouachitensis* and *pseudogeographica* occurred in Indiana (UMMZ 89742, USNM 14669), Iowa (UMMZ 92691, 92692, 92696) and Tennessee (UMMZ 99230).

Cagle (1953) suggested three hypothetical relationships for species of this complex: (1) The narrow-headed forms (*G. pseudogeographica pseudogeographica, G. p. ouachitensis, G. p. sabinensis,* and *G. p. versa*) occupy mutually exclusive ranges and *G. kohni,* a wide-headed turtle, is a separate sympatric species related to *G. pulchra* and *G. barbouri* (the occurrence of apparent intermediates between *kohni* and *pseudogeographica* complicates this interpretation); (2) *Graptemys p. pseudogeographica* may be conspecific with *G. kohni,* whereas *versa, sabinensis,* and *ouachitensis* may be associated in a separate species group (in the South *sabinensis* occurs in sympatry with *kohni,* and farther north *ouachitensis* and *kohni* are sympatric, however Cagle noted this explanation did not account for the supposed intergradation between *ouachitensis* and *pseudogeographica*); (3) *Graptemys pseudogeographica* is a separate species and intermediates between it and the other named forms might be interspecific hybrids.

Later Cagle (1954), without explanation, treated *G. versa, G. kohni,* and *G. pseudogeographica* as distinct species, with the latter having three subspecies (*sabinensis, ouachitensis,* and *pseudogeographica*). This is the arrangement generally accepted in current literature.

Graptemys caglei was described by Haynes and McKown (1974). It was hypothesized that *G. caglei* was intermediate between *G. versa* and *G. kohni,* but judged by head pattern more closely allied to the latter species. Skull characteristics also suggested affinity of *G. caglei* with *G. kohni,* although females of *G. caglei* do not exhibit the wide-headed trait characteristic of some populations of *G. kohni. Graptemys caglei* was not compared with *G. p. pseudogeographica, G. p. ouachitensis,* or *G. p. sabinensis.* The most recent review of the systematics and relationships of the members of the false map turtle complex is that of McKown (1972). He found that starch gel electrophoresis of sera demonstrated no discrete differences between *G. pseudogeographica ouachitensis, G. p. sabinensis, G. versa, G. kohni,* and *G. caglei.* He placed *G. kohni* with the *G. pulchra-G. barbouri* group on the basis of head width. *Graptemys versa* and *G. caglei* were grouped together, and *G. p. sabinensis, G. p. ouachitensis,* and *G. p. pseudogeographica* were placed together. Even though no specimens of *G. p. pseudogeographica* were examined, he stated that "intergrades" between *G. pseudogeographica ouachitensis* and *G. p. pseudogeographica* from Missouri were analyzed.

Dundee (1974) presented data supporting the separation of *G. kohni* and *G. pseudogeographica ouachitensis.* He stated that the crescentric yellow post-orbital line is diagnostic for *G. kohni* and that, even if the crescent is disrupted by neck stripes, these stripes do not reach the orbit as in *G. p. ouachitensis.* He noted that in *G. p. ouachitensis* the postorbital yellow mark is reduced to a spot. Dundee also suggested that the "large-headedness" of *G. kohni* is diagnostic in separating that taxon from *G. p. ouachitensis,* as females over 100 mm carapace length and males over 80 mm carapace length were separated by the ratio of head width to carapace length. The much greater anterior projection of the frontal bones distinguishes skulls of *G. p. ouachitensis* and *G. p. sabinensis* from those of *G. kohni,* according to Dundee. Ernst and Barbour (1972) considered *G. caglei, G. kohni,* and *G. versa* monotypic species, and *G. pseudogeographica* polytypic with three subspecies: *G. p. pseudogeographica, G. p. ouachitensis,* and *G. p. sabinensis.* In a more recent compilation (Ernst and Barbour, 1989) the same authors recognized *G. ouachitensis, G. pseudogeographica,* and *G. kohni,* along with *G. caglei* and *G. versa,* as distinct species.

I first became interested in the problem while attempting to identify Wisconsin turtles using the supposedly diagnostic head markings. The head markings of specimens collected from the Mississippi River near Stoddard, Vernon County, Wisconsin, suggested that several members of the complex occurred there sympatrically. Three possible explanations could account for the great range of head patterns in that area: (1) the variants are part of a single polymorphic species; (2) two or more species are present and their head pattern characteristics overlap; (3) two or more forms of a superspecies are present and intergradation, whether limited or extensive, has caused a confusing admixture of characteristics.

In 1971, I collected and incubated 26 clutches of eggs laid by false map turtles at Stoddard. Hatchlings with head markings reputedly characteristic of four different "taxa" emerged from these 26 clutches, in some cases multiple "taxa" coming from a single clutch. The characters of the hatchlings reinforced my first hypothesis, based on examination of adults in this population, that the four putative taxa, *G. p. pseudogeographica, G. p. kohni, G. p. ouachitensis,* and *G. p. sabinensis,* comprised a single highly polymorphic species. Smith (1961:150–151) suggested a similar explanation for variation observed in Illinois populations of false map turtles.

A study was begun in 1972 to determine the taxonomic relationships of the false map turtles at Stoddard. The principal study area, which has an unusually large population of *Graptemys,* extends northward 37.5 river km from a dam at Genoa, Vernon County, Wisconsin, to north of LaCrosse, Wisconsin (Vogt, 1980*b*).

I examined aspects of the ecology (Vogt, 1980*b*), courtship behavior, head and shell patterns, osteology, and protein characteristics in the Stoddard population. Preserved specimens from throughout the range of the complex were also examined. These were supplemented by additional collections from areas where samples were inadequate. Collections were made at 50–100 km intervals on the Mississippi, St. Croix, Chippewa, Black, and Wisconsin rivers in Wisconsin. In addition, a five-year laboratory study was conducted to determine growth rates, the effect of incubation temperature on sex determination (Bull and Vogt, 1979, 1981; Bull et al., 1982; Vogt and Bull, 1984) and head pattern inheritance, and ontogenetic change in head pattern.

METHODS

A collection of 1117 adult turtles was taken from the Stoddard study area. Turtles were captured in unbaited fyke nets using the techniques described by Vogt (1980*a*). Specimens were also obtained from the gill nets of commercial fishermen working in the area. For each specimen the following data were recorded: length, width, and height of carapace (to 0.5 mm); length and width of the plastron (to 0.5 mm); shell markings; weight; and sex. Dorsal, ventral, and both lateral surfaces of the head were photographed. The same data, exclusive of weight, were taken from over 2000 museum specimens (*see* Appendix 1).

Head photographs were taken at a standard distance and calibrated by photographing a metric ruler at the same distance. For analysis, a negative was projected onto a horizontal Tales Cybergraph tablet six times actual size. As each head spot or blotch was outlined with a stylus the outline appeared on a Tektronix

Graphics Display Keyboard, and was redrawn 15 times actual size. The outline was entered into a Harris 6024/5 computer which computed area, degree of circularity, and greatest diameter of each marking.

Thirteen characters of the head pattern of each specimen (Fig. 1) were quantified and compared at intra- and interspecific levels. Both discrete and continuous characters were examined. The discrete characters were the number of temporal lines entering the orbit and connection of the postorbital spots to the supratemporal lines. If a postorbital spot was connected to a supratemporal line a value of +1 was recorded; if not, a value of −1 was recorded. The two sides of the head were scored independently, and the sum of these two values for each specimen was treated as a single character. Thus values for this character were either −2, 0, or +2. The specimen in Fig. 1 has a value of $-1 + 1 = 0$. The number of temporal lines entering the orbit was recorded for each side of the head. If the postorbital and subocular spots were fused to form a complete crescent preventing temporal lines from entering the orbit, a value of −1 was given. If there was a space between the postorbital and subocular spots, but no lines entered the orbit, a value of 0 was given. The specimen in Fig. 1 has a value of 0 for this character for the illustrated right side of the head. Four of the continuous characters, the postorbital and mandibular spots, were measured twice from different aspects. This was done because these spots usually extended onto two head photographs. Part of each postorbital spot can be viewed from the dorsal aspect and part from lateral aspect. The mandibular spots were viewed from both the lateral and ventral aspects. Only rarely could the entirety of any of these spots be measured from one aspect. These characters were thus slightly weighted, since each occurs twice in a data set, but the area of each spot was never doubled by this process. The total area of the dorsal surface of the head was used as a covariate with pattern characters to negate the effect of overall size of the specimen. A total of 18 measurements was taken on the head pattern and shell of each specimen. The head markings of 558 turtles from 19 populations from throughout the range of the *G. pseudogeographica* complex were analyzed quantitatively (Table 1). When large series were available from a site, a sample of at least 20 was chosen at random for analysis. When possible, sites with large available samples of two or more forms in sympatry were chosen.

Separate canonical analyses (Seal, 1964) were performed on all continuous head pattern characters, on all head pattern characters, and on the head pattern characters and five shell measurements. A graph in which each individual is positioned according to the values of its first and second canonical variate shows variability within a population, and relationships between populations (Kowal et al., 1976; Kalunki, 1976). In addition, Mahalanobis' distance (1936) was calculated between all pairs of populations. This distance is measured in pooled, intra-population standard deviations and gives an index of separation between populations. For example, two populations separated by a Mahalanobis' distance of two overlap at one standard deviation from the mean, and 32% of the scores of one population

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Fig. 1.—Dorsal, lateral, and ventral aspects of head pattern characters in the *Graptemys pseudogeographica* complex: 1—supratemporal lines; 2—right postorbital spot, dorsal aspect; 3—left postorbital spot, dorsal aspect; 4—sagittal stripe; 5—right postorbital spot, lateral aspect; 6—right subocular spot; 7—right mandibular spot, lateral aspect; 8—left postorbital spot, lateral aspect; 9—left subocular spot; 10—left mandibular spot, ventral aspect; 11—right mandibular spot, ventral aspect; 12—left mandibular spot, ventral aspect; 13—chin spot; 14—throat spot.

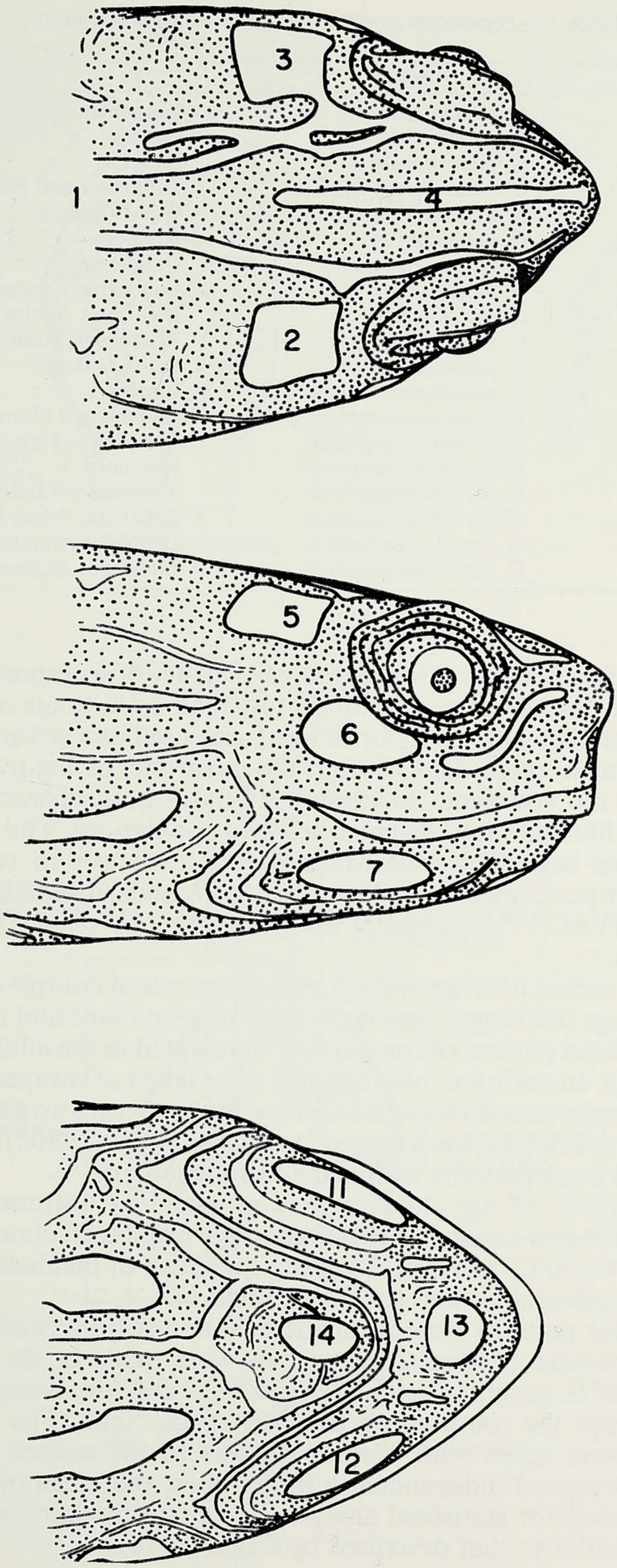
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Table 1.—*Population samples used in head pattern analysis.*

Pop.	N	Species	Locality
1	135	*G. ouachitensis*	Wisconsin, Stoddard
2	26	*G. ouachitensis*	Illinois
3	11	*G. ouachitensis*	Indiana
4	9	*G. ouachitensis*	Tennessee and Kentucky
5	6	*G. ouachitensis*	West Virginia
6	19	*G. ouachitensis*	Arkansas
7	20	*G. ouachitensis*	Oklahoma
8	19	*G. ouachitensis*	Louisiana, Catahoula Parish
9	19	*G. ouachitensis*	Louisiana, Sabine River
10	119	*G. pseudogeographica*	Wisconsin, Stoddard
11	20	*G. pseudogeographica*	South Dakota
12	24	*G. pseudogeographica*	Illinois
13	8	*G. pseudogeographica*	Indiana and Ohio
14	21	*G. pseudogeographica*	Tennessee, Tiptonville
15	4	*G. pseudogeographica*	Kentucky
16	28	*G. pseudogeographica*	Tennessee, Reelfoot Lake
17	30	*G. pseudogeographica*	Arkansas, White River
18	20	*G. pseudogeographica*	Louisiana, Catahoula Parish
19	20	*G. pseudogeographica*	Louisiana, Sabine River

fall in the range of the second. A Mahalanobis' distance of six represents an overlap at three standard deviations and connotes less than a 1% range overlap.

Untransformed data with total dorsal head area used as a covariate gave better results than untransformed data without the covariate, or log-transformed data with or without the covariate. In canonical analysis, all characters potentially contribute to the Mahalanobis' distance between populations. The first and second canonical variates best depict the Mahalanobis' distances in two dimensions. Calculations were performed at the University of Wisconsin–Madison Computing Center on a UNIVAC 1110 computer using program CANCOV (Kowal, personal communication).

In 1972, 50 clutches of *Graptemys pseudogeographica* complex eggs of known maternal parentage (640 eggs) were collected from Stoddard and incubated in the laboratory. The head pattern characteristics were noted in the adults and recorded for the hatchlings. In addition, photographs were taken of carapace and plastron. The hatchlings were raised in the laboratory for five years as part of a study of differential growth rates between species and sexes (Vogt, 1980*b*), and changes in morphology and head patterns with aging were recorded.

In 1976 and 1977, 45 egg clutches were obtained by hormonal induction of oviposition (Ewert and Legler, 1978). Some eggs from each clutch in 1977 were incubated at 25°C, 30°C, and 35°C to study the effect of incubation temperature on head pattern inheritance and sex determination.

After their color patterns were recorded, 100 adults from Stoddard were skeletonized by dermestid beetles. Comparisons were made of the skull and shell morphometrics of *G. geographica* and *G. pseudogeographica* complex turtles from Stoddard and from the southern parts of the range. Skull (Fig. 2) and plastron measurements were taken with vernier calipers to the nearest 0.01 cm. Each character was measured independently three times; the mean of the three measurements was used for statistical analysis. Carapace measurements were taken with a device similar to that described by Cagle (1946).

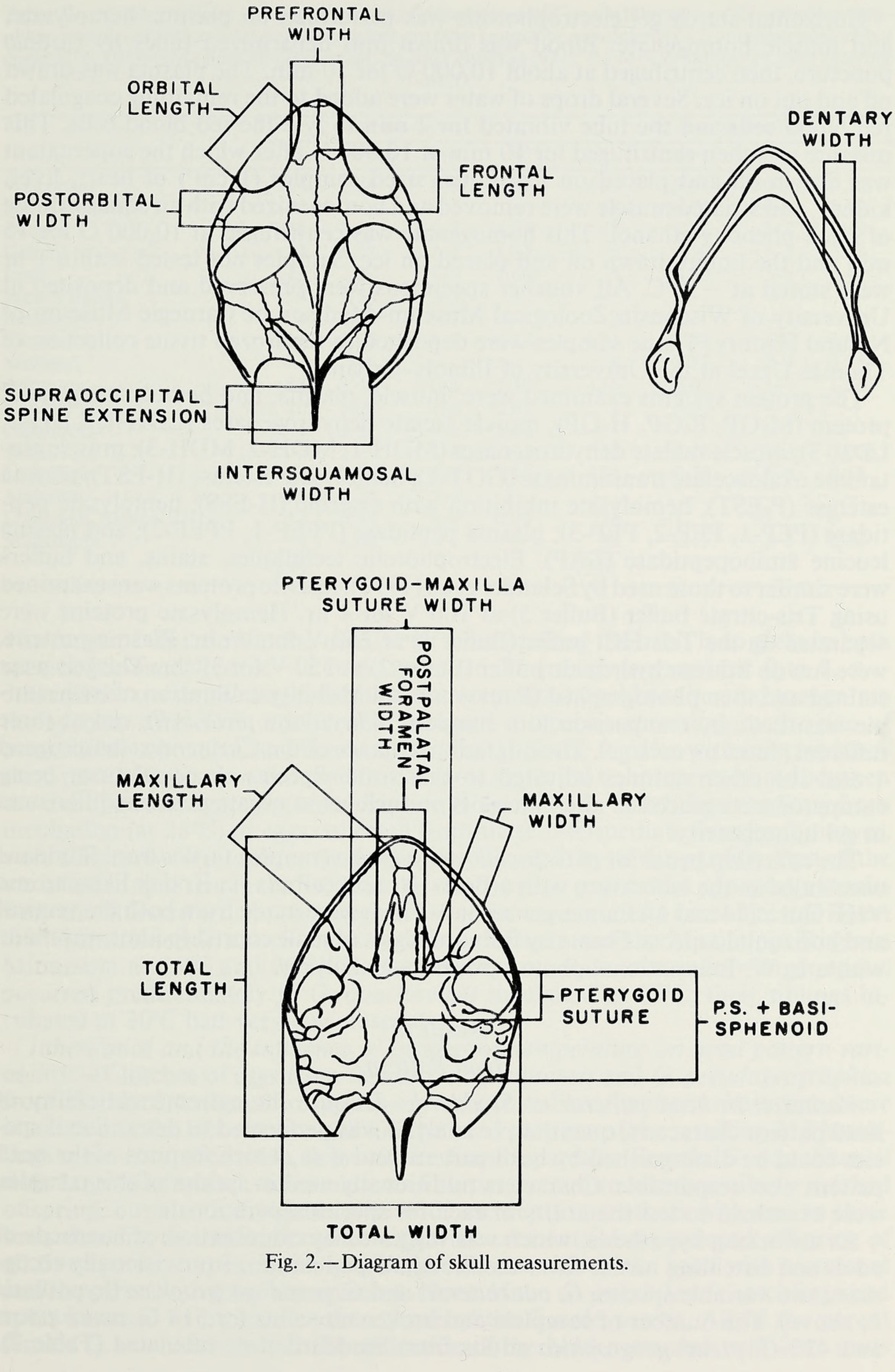

Fig. 2.—Diagram of skull measurements.

Horizontal starch gel electrophoresis was performed on plasma, hemolysate, and muscle homogenate. Blood was drawn into heparinized tubes by cardiac puncture, then centrifuged at about 10,000 G for 10 min. The plasma was drawn off and put on ice. Several drops of water were added to the remaining coagulated red blood cells and the tube vibrated for 2 min to lyse the red blood cells. This mixture was then centrifuged for 10 min at 10,000 G after which the supernatant was drawn off and placed on ice. Equal sized samples (1 cm^3) of heart, liver, kidney, and striated muscle were removed and homogenized with an equal volume of 2% 2-phenoxy-ethanol. This homogenate was centrifuged at 10,000 G for 15 min and the liquid drawn off and placed on ice. Samples not tested within 1 hr were stored at −50°C. All voucher specimens were preserved and deposited at University of Wisconsin Zoological Museum–Madison or Carnegie Museum of Natural History. Tissue samples were deposited in the frozen tissue collection of Thomas Uzzel at the University of Illinois–Urbana.

The protein systems examined were: muscle, plasma, and hemolysate general protein (M-GP, P-GP, H-GP); muscle lactate dehydrogenases (LDH-1, LDH-2, LDH-3); muscle malate dehydrogenases (MDH-1, MDH-2, MDH-3); muscle glutamate oxaloacetate transaminase (GOT-2); hemolysate esterase (H-EST); plasma esterase (P-EST); hemolysate inhibition with esserine (H-ESS); hemolysate peptidase (PEP-1, PEP-2, PEP-3); plasma peptidase (PPEP-1, PPEP-2); and plasma leucine aminopeptidase (LAP). Electrophoretic techniques, stains, and buffers were similar to those used by Selander et al. (1971). Muscle proteins were examined using Tris-citrate buffer (Buffer 5) at 100 V for 4 hr. Hemolysate proteins were separated on the Tris-HCl buffer (Buffer 1) at 250 V for 1½ hr. Plasma proteins were run on lithium hydroxide buffer (Buffer 2) at 350 V for 3½ hr. The gels were stained and then photographed (Panatomic X). Mobility calibration of each sample was made by comparison to a standard, *Chrysemys picta belli,* run at three different places on each gel. The migration distance of the *Chrysemys* was assigned 1 and the other samples adjusted to this scale. Species or populations being compared were placed in alternate slots on each gel to negate possible differences in gel homogeneity.

The courtship behavior of *G. pseudogeographica* complex turtles from Stoddard was filmed in the laboratory with a Bolex 16 mm camera on Kodak Ektachrome VHF film at 24 and 64 frames per second. Films were made from both the vertical and horizontal aspects. Frame by frame analysis of male courtship films was made with a L. W. International photo-optical data analyzer.

RESULTS

Head Pattern

Variation in head patterns at Stoddard.—Despite the extreme variability of head pattern characters, quantitative analysis was performed to determine if species could be distinguished by head pattern, and if so, which features of the head pattern were responsible. Characters traditionally used in species of this complex were examined to test the utility of each for species separation.

As a working hypothesis, which was suggested by examination of hundreds of adult and hatchling turtles from the Stoddard population, I provisionally recognized two variable species, *G. ouachitensis* and *G. pseudogeographica* (hypothesis 2, above). The number of complete and broken crescents for 514 *G. ouachitensis* and 423 *G. pseudogeographica* adults from Stoddard were tabulated (Table 2).

Table 2.—*Number of lines entering the orbit in populations of* G. ouachitensis *and* G. pseudogeographica; *samples of both species on the same line are from sympatric populations (−1, complete postorbital crescent; 0, incomplete postorbital crescent, no lines entering orbit; +1 to +9, number of lines entering orbit).*

State	*G. ouachitensis*				*G. pseudogeographica*			
	N	Mean	Range	SD	N	Mean	Range	SD
Wisconsin	514	0.76	−1–5	0.87	423	3.20	0–8	1.20
South Dakota	—	—	—	—	41	4.95	0–8	1.17
Illinois	36	2.47	−1–7	4.03	42	5.96	−1–7	3.43
Indiana	13	4.38	2–7	1.81	8	4.19	−1–7	2.53
Iowa	13	2.00	1–3	1.66	5	3.50	3–6	—
West Virginia	4	3.50	3–5	—	—	—	—	—
Kentucky	4	4.38	0–7	—	2	−1	—	—
Tennessee	25	3.62	−1–8	0.83	171	3.58	−1–8	2.54
Missouri	—	—	—	—	8	3.88	2–7	0.75
Arkansas	83	3.46	−1–6	1.30	136	0.02	−1–7	1.34
Kansas	10	3.05	1–4	0.87	1	6.00	—	—
Oklahoma	75	3.97	1–6	3.10	—	—	—	—
Texas	3	3.67	3–4	—	39	−0.54	−1–3	0.003
Louisiana	54	2.51	−1–6	1.68	314	−0.28	−1–6	0.58
Alabama	5	3.20	3–4	—	—	—	—	—
Louisiana, Sabine River	57	6.51	4–9	0.98	38	−1	−1	0
Mississippi	1	4.00	—	—	39	−0.19	−1–3	0.62
	899				1277			

The range of variation in the number of lines entering the orbit is so great in both species (*G. ouachitensis*: −1 to 5, $\bar{x}$ = 0.76; *G. pseudogeographica*: 0 to 8, $\bar{x}$ = 3.2) and the overlap so large, that this character alone could not be used to separate the species. Therefore, adults were assigned to species according to the size of postorbital, subocular, and throat spots (Fig. 1). Some females with intermediate-sized postorbital, subocular, and throat spots appeared to be intermediate between the two species, suggesting hybridization (Cagle, 1953). Hatchlings resulting from incubation (at 28°C) of eggs collected from these intermediate females, however, were all clearly *G. ouachitensis,* confirming the identity of the parents. Part of the variation in spot size in the Stoddard *G. ouachitensis* population apparently results from the different temperature regimes to which natural nests are subjected. Ewert (1979) incubated *G. ouachitensis* eggs from Indiana and the Mississippi River in Minnesota at 25°C and 30°C. He found that complete crescents (=larger spots) occurred predominately in *G. ouachitensis* incubated at 25°C; their siblings incubated at 30°C had very few crescents.

Inheritance and the influence of incubation temperature on head pattern variability.—Clutches of eggs from female *G. ouachitensis* and *G. pseudogeographica* from Stoddard, assigned to species on the basis of head pattern characters, were incubated in the laboratory at 28°C. The head patterns of the resulting 317 hatchlings were compared with those of the female parents. Female *G. ouachitensis* with large postorbital, subocular, and throat spots produced similarly marked offspring, but also individuals with wide crescents and others with one to three lines entering the orbit. Females with wide crescents also produced offspring of all three pattern types. Some hatchlings had one side of the head with a crescent and the other with a broken crescent. None of the *G. ouachitensis* hatchlings had spots as small as or smaller than those of the female parent. All of the parent female *G. ouachitensis* had the underside of the head patterned with four spots

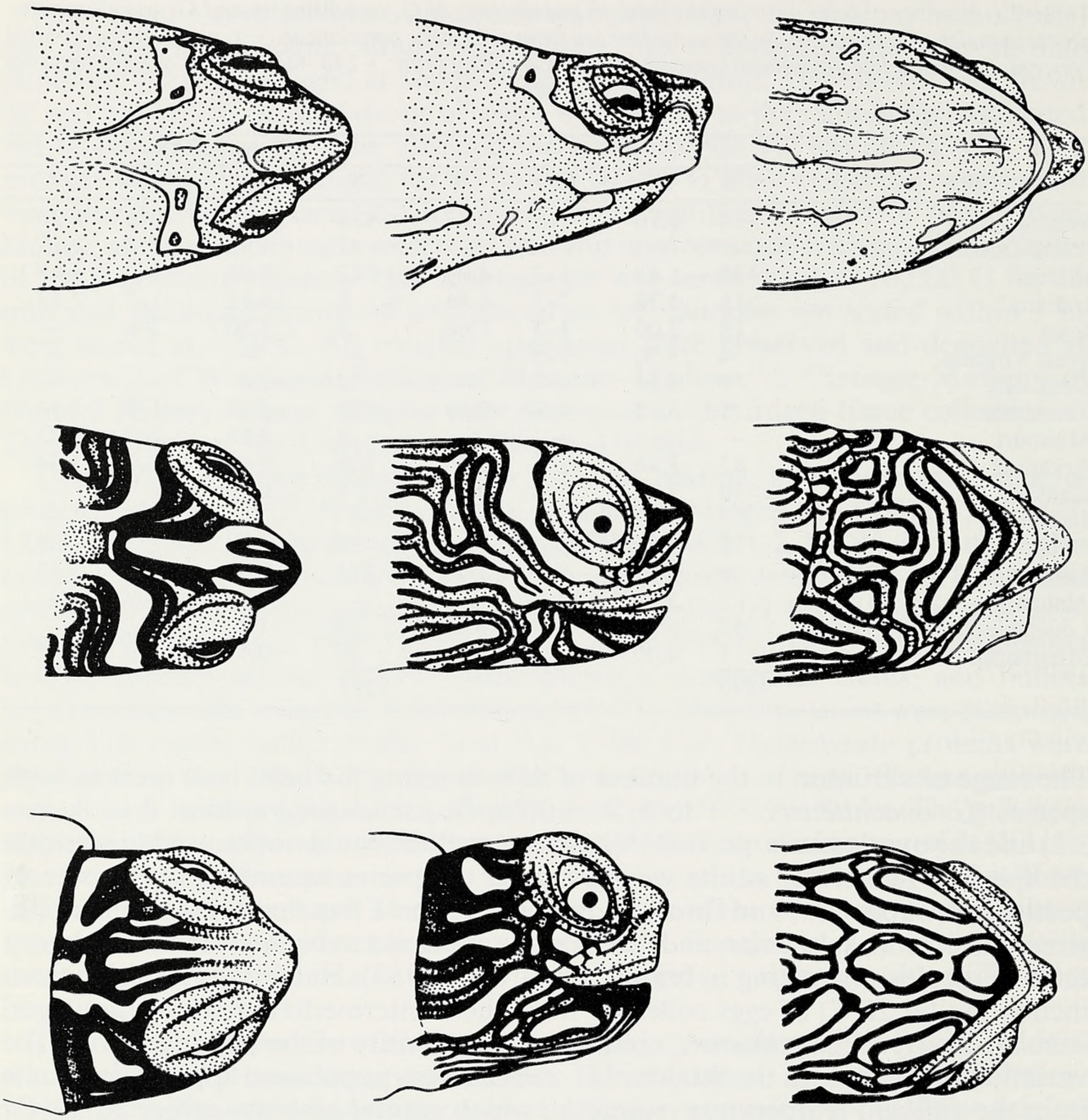

Fig. 3.—Head patterns of female *G. ouachitensis* from Stoddard, Vernon Co., Wisconsin (RCV 776, upper row) and offspring from eggs incubated at 25°C (UWZM 21658, middle row) and 35°C (UWZM 21655, lower row).

rather than crossbars. Four young, from three different clutches, had crossbars (Fig. 3).

All hatchlings of *G. pseudogeographica* had narrow postorbital spots, small subocular spots and small throat spots. No *G. pseudogeographica* females from Stoddard produced hatchlings with complete crescents. Only one hatchling had a postorbital marking that could be considered a partial crescent, which was similar to those found in Louisiana *G. pseudogeographica.*

To test the effect of various incubation temperatures on head markings, each of 11 clutches of *G. pseudogeographica* and 15 clutches of *G. ouachitensis* eggs was divided into three groups for incubation at 25°, 30°, and 35°C. The 30°C sample was lost due to equipment failure.

Only slight differences were noted between the patterns of hatchling *G. pseudogeographica* from 25°C and those of the 35°C group. No crescents were found in either group and more postorbital lines occurred in the 35°C group (3–6, $\bar{x}$ = 4.8, N = 23) than in the 25°C group (3–5, $\bar{x}$ = 3.9, N = 39). Complete wide crescents were found in six (15%) and broken crescents on three (7%) of *G. ouachitensis* hatchlings in the 25°C group, whereas none of the hatchlings in the 35°C group had crescents. Those incubated at 35°C averaged more postorbital lines on each side of the head (1–4, $\bar{x}$ = 2.5, N = 25) than those at 25°C (−1–4, $\bar{x}$ = 1.3, N = 46). In addition to the decrease in number of postorbital lines at 25°C, there was an increase in the size of the postorbital, subocular, mandibular, and chin spots, and widening of the sagittal stripe (Fig. 3). Ewert (1979) also noticed a temperature effect on sagittal stripe width.

Head marking areas of 46 *G. ouachitensis* and 39 *G. pseudogeographica* incubated at 25°C, and 12 *G. ouachitensis* and 8 *G. pseudogeographica* incubated at 35°C were compared through canonical analysis of raw data with dorsal head area used as a covariate. The first canonical variate separated *G. ouachitensis* from *G. pseudogeographica* and the second separated the effects of the two incubation temperatures (Fig. 4). Pairwise, Mahalanobis' distances between the four samples reach a maximum of 3.8 between *G. ouachitensis* incubated at 35°C and *G. pseudogeographica* at 25°C (Table 3). Separation of the two species was achieved primarily by contrast of the subocular spot area with the dorsal postorbital spot area, and chin spot area with the ventral mandibular spot area. Separation of the effects of incubation temperature was made on the basis of contrast of the ventral mandibular spot area with the subocular spot area, and ventral mandibular spot area with the dorsal postorbital spot area.

Thus much of the intrapopulation variation in head pattern in both *G. ouachitensis* and *G. pseudogeographica* can be attributed to the effect of incubation temperature. The basic pattern can be modified to the extent that *G. ouachitensis* incubated at high temperatures resemble *G. pseudogeographica.*

Geographic variation in head pattern.—A set of 100 head photographs was analyzed to test the feasibility of differentiating the forms of *Graptemys* by area and degree of roundness of specific head markings. The data were grouped into six populations: (1) 26 *G. ouachitensis* from Stoddard; (2) 24 *G. pseudogeographica* from Stoddard; (3) 20 *Graptemys* of intermediate pattern from Stoddard; (4) 10 *G. pseudogeographica* from DeVall's Bluff, Arkansas; (5) 10 *G. ouachitensis* from Illinois, Tennessee, and Oklahoma; and (6) 10 *G. pseudogeographica* from Reelfoot Lake, Tennessee. Individuals in groups 1 and 2 were chosen to represent the full range of variation in each species. Group 3 includes individuals difficult to place in either species on the basis of head pattern alone. Individuals in groups 4, 5, and 6 were chosen at random from specimens available. Canonical analysis of head pattern area is shown in Fig. 5. The first two canonical variates account for 89.4% of the variation in the six samples.

Separation of Wisconsin *G. pseudogeographica* and *G. ouachitensis* was primarily the result of contrasts between areas of the left subocular spot and dorsal left postorbital spot, chin spot and left mandibular spot, and right subocular spot and chin spot. The index of the degree of roundness of the head markings did not give a definitive separation between species or populations. Fig. 5 is a two-dimensional representation of the relationships of these populations.

Multiple discriminant analysis of head patterns separates Wisconsin *G. ouachitensis* and *G. pseudogeographica* (Table 4, Pop. 1 vs. Pop. 2), suggesting that at

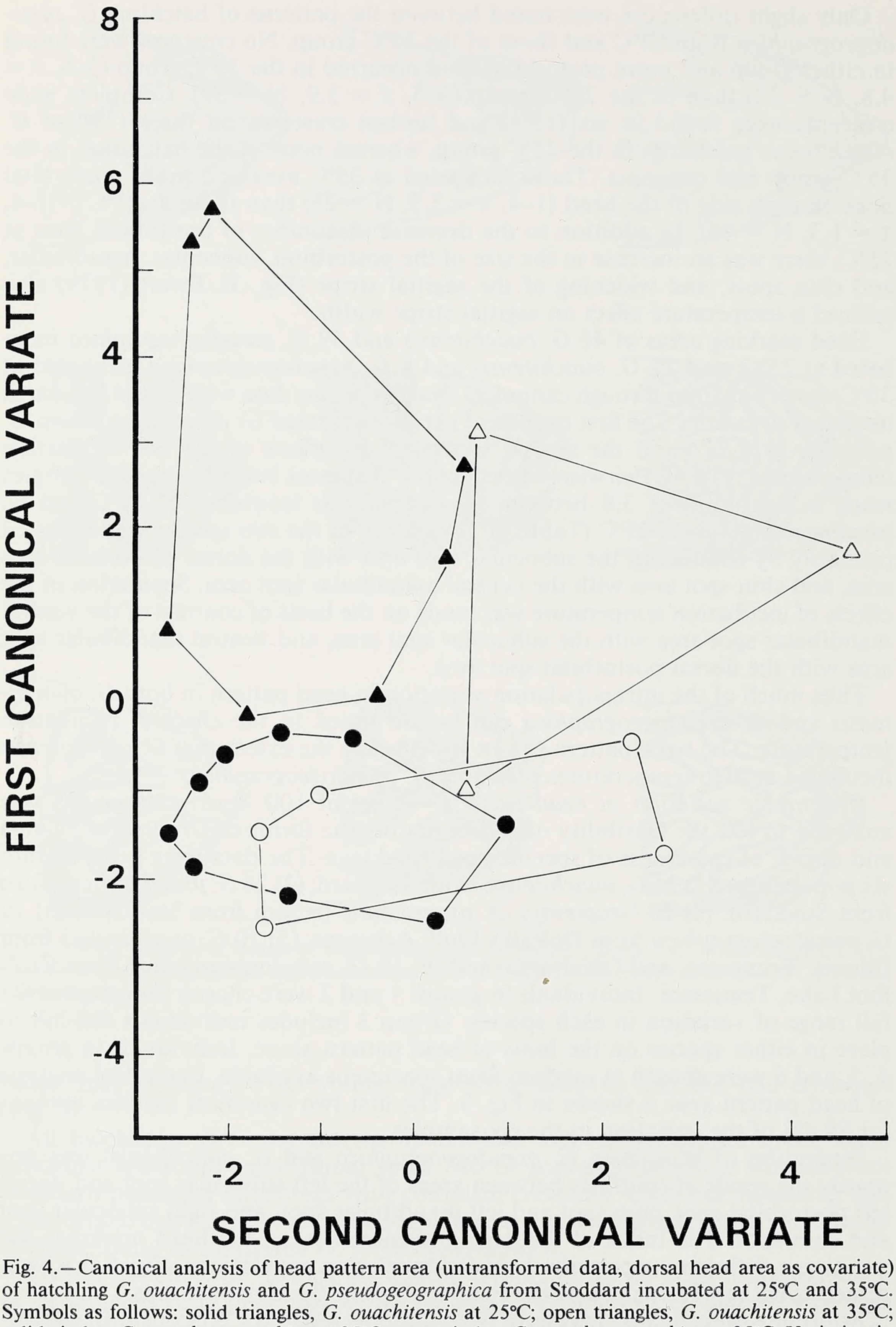

Fig. 4.—Canonical analysis of head pattern area (untransformed data, dorsal head area as covariate) of hatchling *G. ouachitensis* and *G. pseudogeographica* from Stoddard incubated at 25°C and 35°C. Symbols as follows: solid triangles, *G. ouachitensis* at 25°C; open triangles, *G. ouachitensis* at 35°C; solid circles, *G. pseudogeographica* at 25°C; open circles, *G. pseudogeographica* at 35°C. Variation in the first two canonical variates was 96.7% of variation in the four samples.

Table 3.—*Pairwise Mahalanobis' distances (untransformed head pattern area, dorsal head area as covariate) between samples of hatchling* G. ouachitensis *and* G. pseudogeographica *from eggs incubated at 25°C and 35°C: Pop. 1,* G. ouachitensis *at 25°C; Pop. 2,* G. ouachitensis *at 35°C; Pop. 3,* G. pseudogeographica *at 25°C; Pop. 4,* G. pseudogeographica *at 35°C.*

	Pop. 1	Pop. 2	Pop. 3	Pop. 4
Pop. 1	0.0			
Pop. 2	3.3	0.0		
Pop. 3	3.3	3.8	0.0	
Pop. 4	3.7	3.0	1.9	0.0

Stoddard *G. ouachitensis* and *G. pseudogeographica* are distinct species. However, the intermediacy of group 3 (Fig. 5) shows that head markings alone will not separate all individuals in the Stoddard population.

Skull Morphometrics

Skulls from Stoddard specimens of *G. ouachitensis* and *G. pseudogeographica* were qualitatively separable on the basis of flatness across the frontal, extension of the supraoccipital spine, and intersquamosal width. About 90% of skulls were consistently placed by me and an unbiased observer (E. Pilleart) into two groups. Measurements (Fig. 2) were chosen to quantify these qualitative differences in skull shape. Skull characters from 76 females were compared by canonical analysis using carapace length and width as covariates (Fig. 6). The first canonical variate primarily separated *G. ouachitensis* from *G. pseudogeographica,* whereas the second separated local populations of both species. The ratio of dentary width to carapace height and plastron width to pterygoid width were responsible for the separation of *G. ouachitensis* from *G. pseudogeographica* (Fig. 6). Intraspecific separations were made by the ratio of plastron width to dentary width. The Mahalanobis' distances (Table 5) show that the Wisconsin *G. pseudogeographica* population is closer to the southern *G. pseudogeographica* population than the Wisconsin *G. ouachitensis* population is to southern *G. ouachitensis.* The ratio of dentary width to pterygoid width separated Wisconsin *G. ouachitensis* from Wisconsin *G. pseudogeographica* by a distance of 4.36 standard deviations, when either carapace length or carapace width were used as covariates.

Canonical analysis of head pattern data combined with skeletal data for the Stoddard populations of the two species (Pop. 1 and Pop. 2) gave a separation of 11.03 standard deviations (Fig. 7). The ratios of carapace width to right mandible

Table 4.—*Pairwise Mahalanobis' distances (untransformed head pattern area, dorsal head area as covariate) between six populations of* G. ouachitensis *and* G. pseudogeographica*: Pop. 1, Wisconsin* G. ouachitensis*; Pop. 2, Wisconsin* G. pseudogeographica*; Pop. 3, Wisconsin intermediates; Pop. 4, Arkansas* G. pseudogeographica*; Pop. 5, southern* G. ouachitensis*; Pop. 6, southern* G. pseudogeographica.

	Pop. 1	Pop. 2	Pop. 3	Pop. 4	Pop. 5	Pop. 6
Pop. 1	0.0					
Pop. 2	4.7	0.0				
Pop. 3	3.2	2.8	0.0			
Pop. 4	5.1	4.2	3.1	0.0		
Pop. 5	3.1	4.0	1.5	3.4	0.0	
Pop. 6	3.9	3.0	1.0	2.6	2.0	0.0

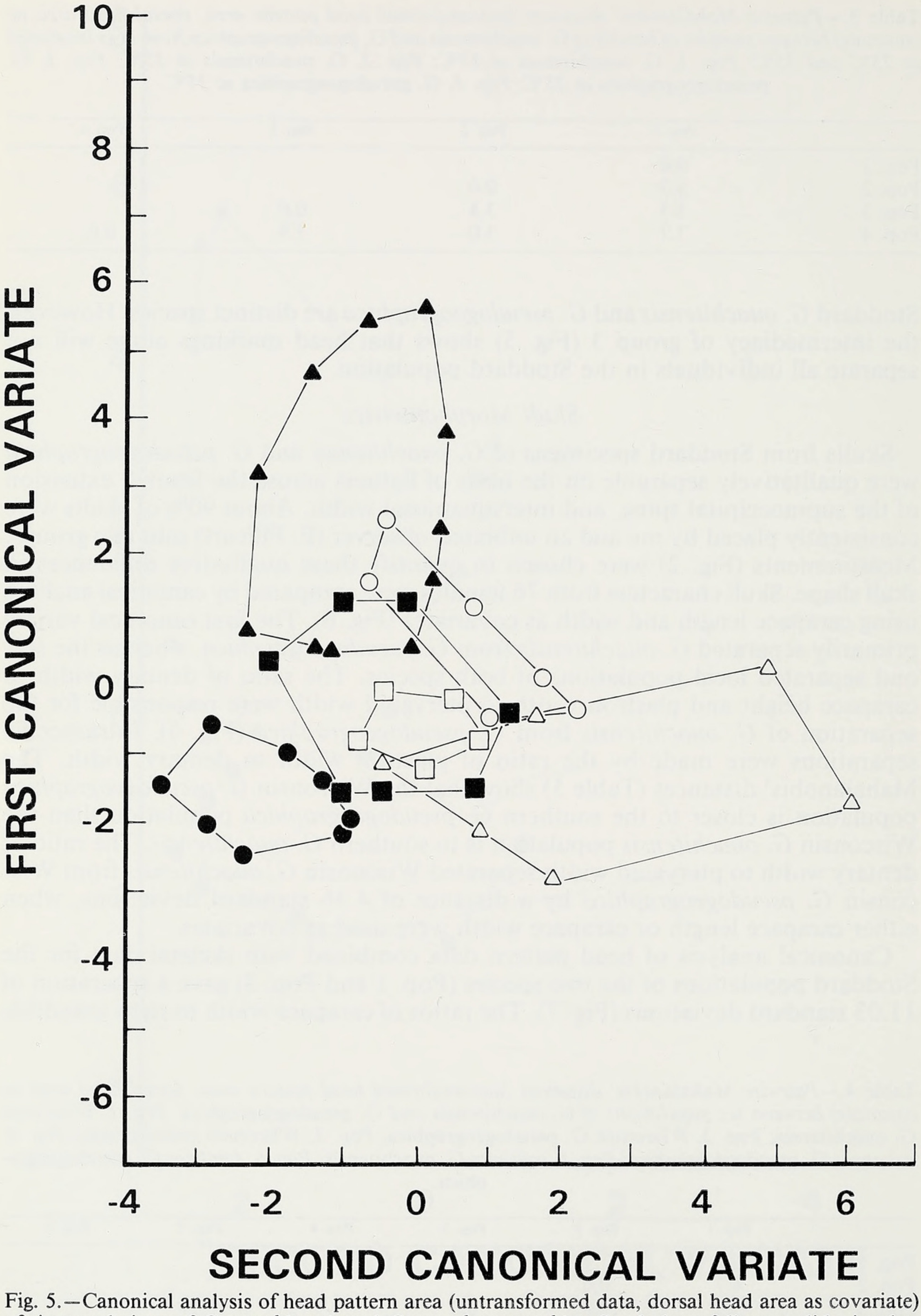

Fig. 5.—Canonical analysis of head pattern area (untransformed data, dorsal head area as covariate) of six populations of *G. ouachitensis* and *G. pseudogeographica*. Symbols as follows: solid triangles, Wisconsin *G. ouachitensis*; solid circles, Wisconsin *G. pseudogeographica*; solid squares, Wisconsin intermediates; open circles, southern *G. ouachitensis*; open triangles, Arkansas *G. pseudogeographica*; open squares, southern *G. pseudogeographica*.

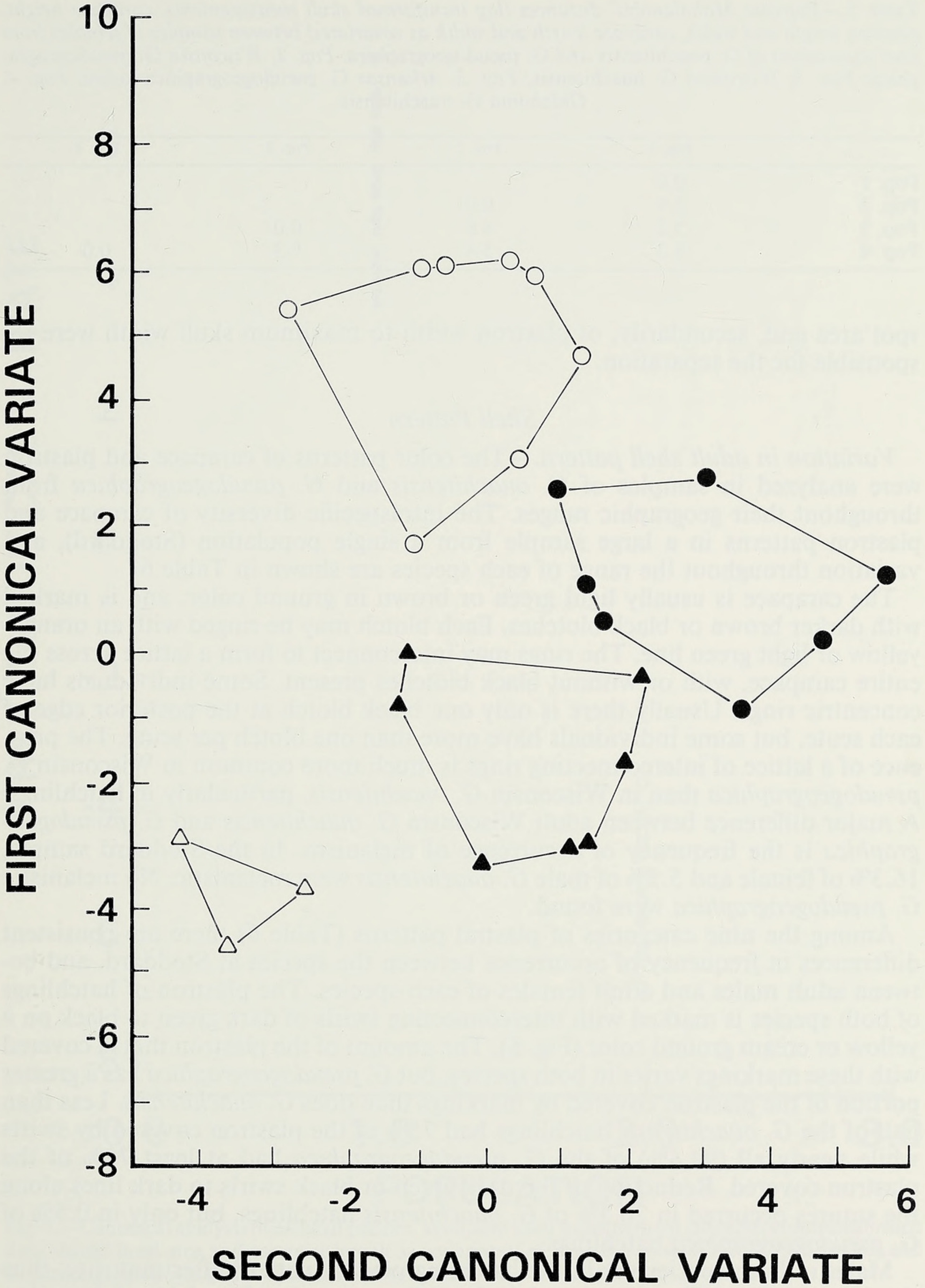

Fig. 6.—Canonical analysis of 15 skull characters, carapace height, plastron length and width (log transformed data, carapace length and width as covariates) of females from four populations of *G. ouachitensis* and *G. pseudogeographica*. Symbols as follows: solid circles, Wisconsin *G. pseudogeographica*; solid triangles, Wisconsin *G. ouachitensis*; open circles, Arkansas *G. pseudogeographica*; open triangles, Oklahoma *G. ouachitensis*.

Table 5.—*Pairwise Mahalanobis' distances (log transformed skull measurements, carapace height, plastron length and width, carapace length and width as covariates) between samples of females from four populations of* G. ouachitensis *and* G. pseudogeographica: *Pop. 1, Wisconsin* G. pseudogeographica; *Pop. 2, Wisconsin* G. ouachitensis; *Pop. 3, Arkansas* G. pseudogeographica kohni; *Pop. 4, Oklahoma* G. ouachitensis.

	Pop. 1	Pop. 2	Pop. 3	Pop. 4
Pop. 1	0.0			
Pop. 2	3.9	0.0		
Pop. 3	5.2	6.6	0.0	
Pop. 4	8.3	5.4	9.3	0.0

spot area and, secondarily, of plastron width to maximum skull width were responsible for the separation.

Shell Pattern

Variation in adult shell pattern.—The color patterns of carapace and plastron were analyzed in samples of *G. ouachitensis* and *G. pseudogeographica* from throughout their geographic ranges. The intraspecific diversity of carapace and plastron patterns in a large sample from a single population (Stoddard), and variation throughout the range of each species are shown in Table 6.

The carapace is usually light green or brown in ground color, and is marked with darker brown or black blotches. Each blotch may be ringed with an orange-yellow or light green line. The rings may interconnect to form a lattice across the entire carapace, with or without black blotches present. Some individuals have concentric rings. Usually there is only one black blotch at the posterior edge of each scute, but some individuals have more than one blotch per scute. The presence of a lattice of interconnecting rings is much more common in Wisconsin *G. pseudogeographica* than in Wisconsin *G. ouachitensis,* particularly in hatchlings. A major difference between adult Wisconsin *G. ouachitensis* and *G. pseudogeographica* is the frequency of occurrence of melanism. In the Stoddard sample, 16.3% of female and 5.5% of male *G. ouachitensis* were melanistic. No melanistic *G. pseudogeographica* were found.

Among the nine categories of plastral patterns (Table 6) there are consistent differences in frequency of occurrence between the species at Stoddard, and between adult males and adult females of each species. The plastron of hatchlings of both species is marked with interconnecting swirls of dark green to black on a yellow or cream ground color (Fig. 8). The amount of the plastron that is covered with these markings varies in both species, but *G. pseudogeographica* has a greater portion of the plastron covered by markings than does *G. ouachitensis.* Less than half of the *G. ouachitensis* hatchlings had 75% of the plastron covered by swirls while nearly all (94.4%) of the *G. pseudogeographica* had at least 75% of the plastron covered. Reduction of the dark green or black swirls to dark lines along the sutures occurred in 20.5% of *G. ouachitensis* hatchlings, but only in 0.5% of *G. pseudogeographica* hatchlings.

Males of both species retain the hatchling plastral pattern after maturity, thus the interspecific differences noted in hatchlings are also found in adult males. Adult females of *G. pseudogeographica* and *G. ouachitensis* differ very little in plastral pattern. Most have a mottled yellow-brown plastron without pattern,

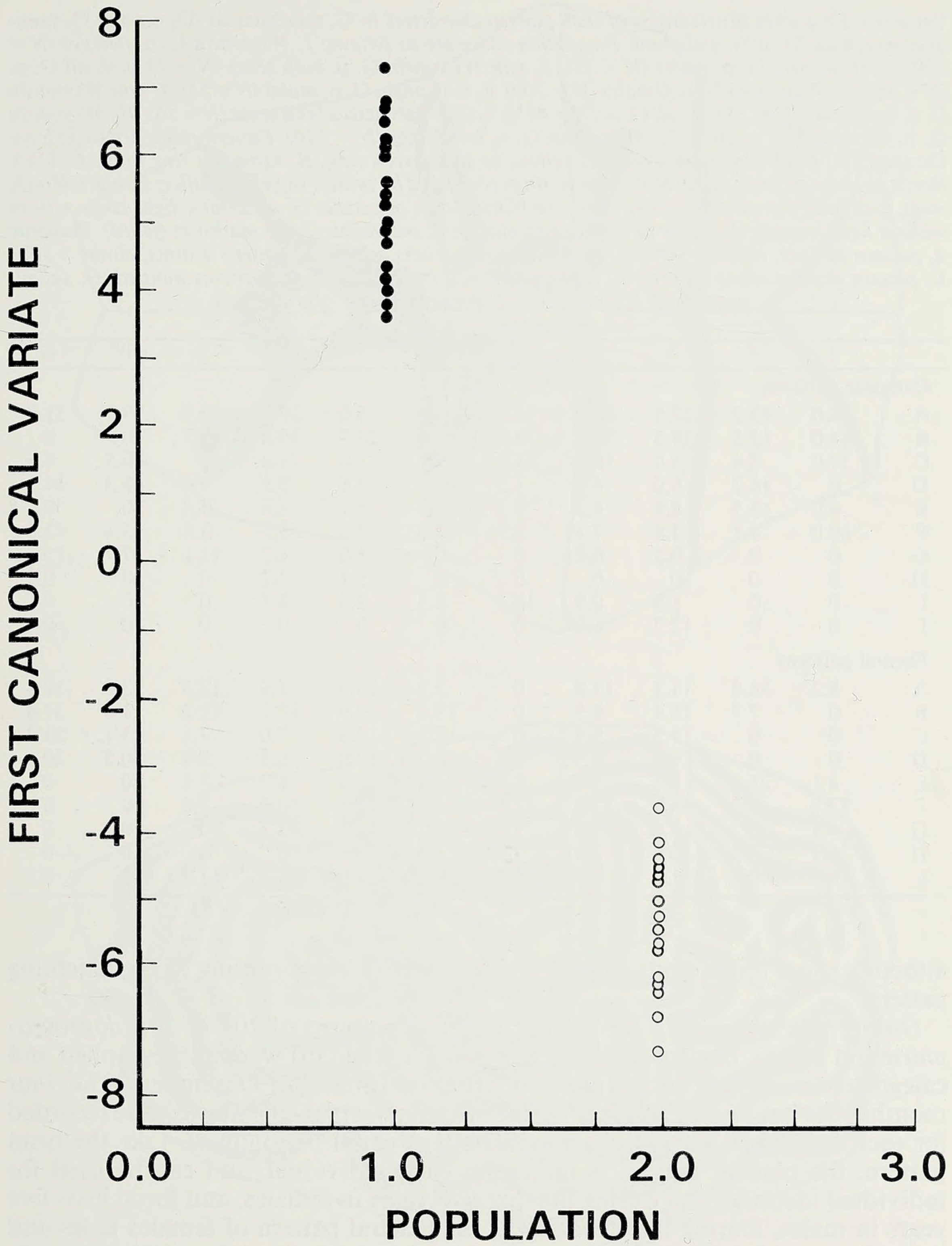

Fig. 7.—Canonical analysis of all head pattern, skull, and shell measurement characters (untransformed data, dorsal head area and carapace length as covariates) of female *G. ouachitensis* (open circles) and *G. pseudogeographica* (solid circles) from Wisconsin.

Table 6.—*Frequency distributions of shell pattern characters in* G. ouachitensis *(*G. o.*) and* G. pseudogeographica *(*G. p.*) populations. Population codes are as follows: 1, Wisconsin* G. p. *females (N = 200); 2, Wisconsin* G. p. *males (N = 37); 3, non-Wisconsin* G. p. *both sexes (N = 211); 4, all* G. p. *(N = 448); 5, Wisconsin* G. o. *females (N = 200); 6, Wisconsin* G. o. *males (N = 55); 7, non-Wisconsin* G. o. *both sexes (N = 200); 8, all* G. o. *(N = 455); 9,* G. o. sabinensis *both sexes (N = 56); 10, Wisconsin* G. p. *hatchlings (N = 207); 11, Wisconsin* G. o. *hatchlings (N = 110). Pattern codes are as follows:* Carapace: *A, black blotch with orange, yellow, or light-green ring; B, same but ring faint; C, black blotch, no orange lines; D, no black blotch, rings connected by orange or yellow lattice; E, black blotch, rings, and lattice present; F, more than one black blotch per scute; G, concentric light rings with or without light centers; H, yellow or orange reticulation; I, melanistic; J, no markings (faded).* Plastron: *A, pattern distinct, covers >90%; B, pattern distinct, covers >75%; C, pattern distinct, covers >50%; D, pattern distinct along sutures; E, pattern outlined in black; F, yellow-brown mottled; G, yellow, unmarked; H, melanistic; I, concentric dark central figure.*

	1	2	3	4	5	6	7	8	9	10	11
Carapace patterns											
A	18.0	43.2	22.5	21.9	13.9	34.6	46.0	30.3	39.3	39.1	51.0
B	34.0	13.5	38.5	34.6	34.7	41.8	23.7	30.8	10.7	0	0
C	34.0	5.4	5.6	18.3	24.8	9.1	3.0	13.4	0	0.5	4.5
D	0	16.2	6.6	4.5	1.5	1.8	9.6	5.1	1.8	48.3	14.5
E	4.0	13.5	8.9	6.5	0	3.6	5.1	2.6	3.6	0	0
F	10.0	8.1	2.8	7.1	8.9	3.6	2.5	5.5	3.6	3.4	13.6
G	0	0	0.5	0.2	0	0	3.0	1.3	41.1	7.7	15.5
H	0	0	0	0	0	0	5.1	2.2	0	0	0.9
I	0	0	1.9	0.9	16.3	5.5	2.0	8.8	0	0	0
J	0	0	12.7	6.0	0	0	0	0	0	0	0
Plastral patterns											
A	8.2	56.4	11.3	13.8	0	3.5	16.9	7.9	12.5	73.0	10.8
B	0	7.7	16.4	8.5	0	15.5	23.9	12.5	48.2	21.4	37.4
C	0	0	11.3	5.4	0	12.1	13.4	7.0	7.1	5.1	31.3
D	0	0	9.5	4.3	0	8.7	12.0	6.3	3.6	0.5	20.5
E	4.1	25.6	3.3	5.6	9.6	31.0	2.5	8.7	7.1	0	0
F	77.6	7.7	38.0	52.7	81.4	24.1	17.4	50.9	3.6	0	0
G	4.1	0	8.5	5.8	1.7	0	6.0	3.3	0	0	0
H	6.1	2.6	0	2.9	7.3	5.2	0	0	0	0	0
I	0	0	1.9	0.9	0	0	8.0	3.5	17.8	0	0

although some individuals of both species retain a black outline of the hatchling pattern.

Ontogenetic changes in shell pattern.—Shell patterns of 207 *G. pseudogeographica* and 110 *G. ouachitensis* hatchlings from Stoddard were photographed and categorized according to the patterns listed in Table 6 in December 1972, four months after hatching. Each year for the next five years shell patterns were recorded for each individual so that changes in pattern could be followed. Like the head pattern, the plastral pattern is unique in each individual, and can be used for individual identification during the first two years in females, and for at least five years in males. During the second year the plastral pattern of females fades and dark pigment begins to fill the light spaces; the entire plastral pattern is usually obliterated by the end of the third year. During the second year dark pigment begins to concentrate at the posterior edges of the plastral scutes forming dark lines along the seams. This differs from the hatchling pattern in which dark pigment is distributed on both sides of the seams. Although the hatchling plastral pattern remains distinct in most males throughout life, many of the finer lines, useful for individual identification, fade.

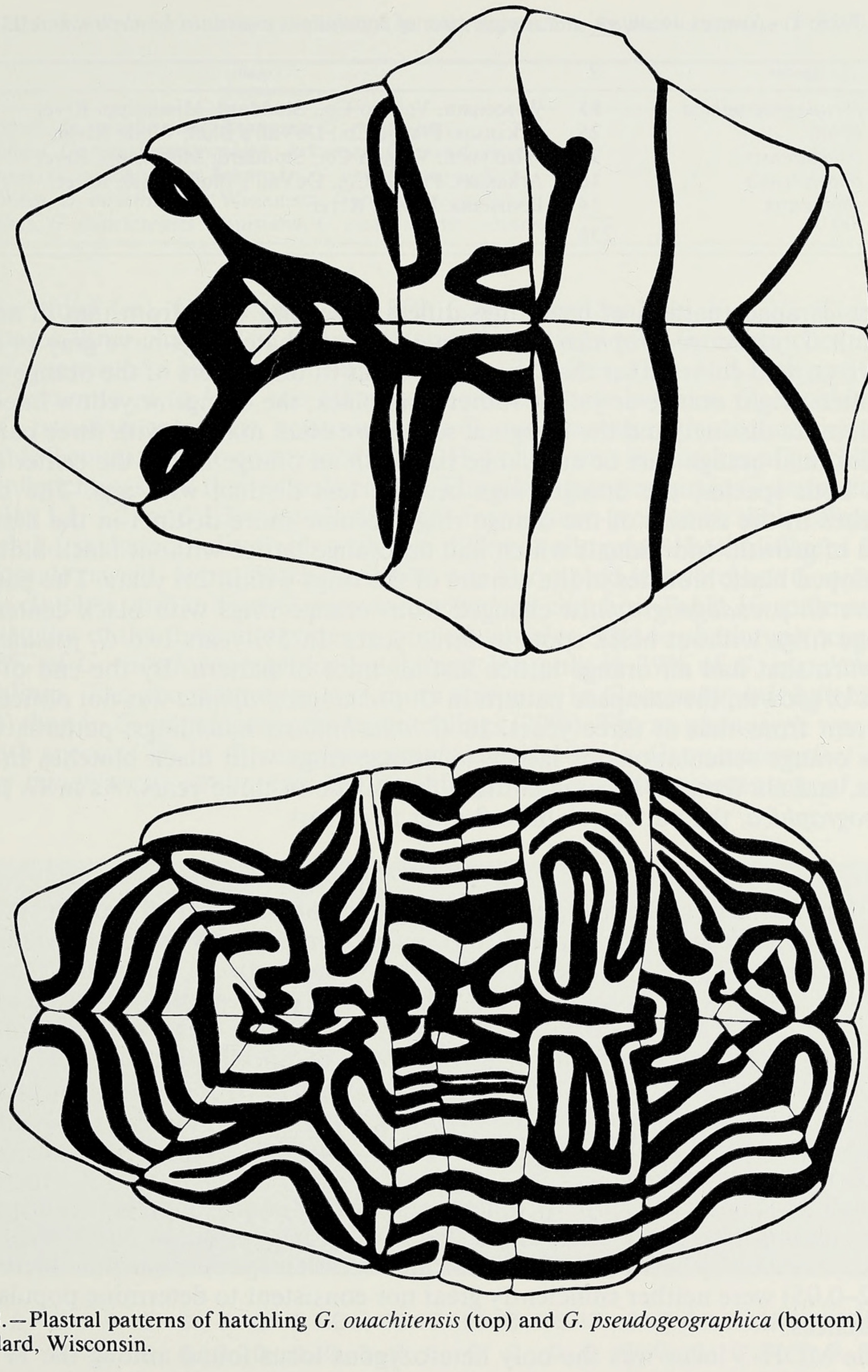

Fig. 8.—Plastral patterns of hatchling *G. ouachitensis* (top) and *G. pseudogeographica* (bottom) from Stoddard, Wisconsin.

Table 7.—*Species, localities, and sample sizes of populations examined by electrophoresis.*

Species	N	Locality
G. p. pseudogeographica	85	Wisconsin, Vernon Co., Stoddard, Mississippi River
G. p. kohni	25	Arkansas, Prairie Co., DeVall's Bluff, White River
G. o. ouachitensis	96	Wisconsin, Vernon Co., Stoddard, Mississippi River
G. o. ouachitensis	18	Arkansas, Prairie Co., DeVall's Bluff, White River
G. o. sabinensis	14	Louisiana, Sabine River
	238	

The carapace pattern of hatchlings differs in several ways from that of adults in both *G. pseudogeographica* and *G. ouachitensis*: hatchlings have gray or light brown ground color rather than green; the areas in the centers of the orange rings are often bright orange or yellow rather than black; the orange or yellow lines are much more distinct; and the marginal scutes are often marked with three parallel longitudinal orange bars or an orange ring with an orange bar in the center of it.

In both species, the orange rings become less distinct with age. The black blotches in the centers of the orange rings become more distinct in the first 3½ years of growth. Individuals which had an orange lattice without black blotches developed black blotches in the centers of the rings within 2½ years. The pattern in five *G. pseudogeographica* changed from orange rings with black centers to orange rings without black spots in three years. In 3½ years two *G. pseudogeographica* that had an orange lattice lost all trace of pattern. By the end of five years of growth, the carapace pattern in *G. pseudogeographica* was not noticeably different from that at three years. In *G. ouachitensis* hatchlings, patterns went from orange reticulations or lattice to orange rings with black blotches in two years, and six females became entirely melanistic in three years. As in *G. pseudogeographica,* the pattern stabilized after five years.

Electrophoresis

Comparisons were made of the electrophoretic mobilities of 19 protein systems in 110 *G. pseudogeographica* and 128 *G. ouachitensis* from Wisconsin, Arkansas, and Louisiana (Table 7). No differences were found between males and females, or between fresh and frozen material. Identical mobilities were displayed at the LDH-1, LDH-2, LDH-3, MDH-1, MDH-2, and GOT-2 loci for all individuals examined. Many protein systems did not show distinct bands, probably due to polymerization (McKown, 1972); they were compared by measuring the greatest distance migrated. Insignificant relative migration differences (0.01–0.03) were found at the H-EST, H-ESS, H-GEN, H-PEP-1, H-PEP-2, H-PEP-3, LAP, P-GP, PPEP-1, and M-GP loci.

Small, but consistent mobility differences (Table 8) were found between species at the plasma esterase (P-EST) locus (Fig. 9). Plasma peptidase-2 (PPEP-2) also varied in mobility between populations and between species, but the differences (0.02–0.05) were neither sufficiently great nor consistent to determine population differences.

The MDH-3 locus was the only heterozygous locus found among the 19 loci studied. Variation was present between species and between subspecies, within populations, within clutches, and between offspring and parent. The MDH-1 and MDH-2 bands were consistently light, but identical for all individuals examined. Both species were found to possess three different alleles for MDH-3, represented

Table 8.—*Relative mobility comparisons between populations for plasma esterase (P-EST).*

Populations	Mobility difference
Wisconsin, *G. ouachitensis* : Arkansas, *G. ouachitensis*	0.08
Wisconsin, *G. pseudogeographica* : Arkansas, *G. pseudogeographica*	0.03
Arkansas, *G. ouachitensis* : Arkansas, *G. pseudogeographica*	0.06
Wisconsin, *G. ouachitensis* : Wisconsin, *G. pseudogeographica*	0.08
Arkansas, *G. ouachitensis* : Louisiana, *G. ouachitensis sabinensis*	0.00

by the third (cc), fourth (aa), and fifth (abc) individuals in Fig. 10. This gel compares three clutches of *G. ouachitensis* hatchlings with three clutches of *G. pseudogeographica* hatchlings from Wisconsin. The first, 12th, and 26th positions are *Chrysemys picta belli*; the other positions alternate between *G. ouachitensis* and *G. pseudogeographica,* beginning with *G. ouachitensis* in the second position.

Table 9 compares the occurrence of MDH-3 allozymes in clutches of hatchlings, and in hatchlings and their female parent. The allozymes present in *G. ouachitensis* females L1, L2, and L3 were all different from those present in their offspring. Clutch L1 included individuals with two different allozymes, both different from the female parent. Intra-clutch variation was also noted in two other *G. ouachitensis* clutches, and in four *G. pseudogeographica* clutches. Table 10 summarizes frequencies of the three allozymes in pooled samples. The cc phenotype occurred in 78% of *G. pseudogeographica* hatchlings, but only in 29% of *G. ouachitensis* hatchlings. The abc phenotype was more common in *G. ouachitensis* hatchlings (59%) than in *G. pseudogeographica* hatchlings (20%). The aa phenotype was rare in both species: 2% in *G. pseudogeographica* and 10% in *G. ouachitensis. Graptemys ouachitensis* adults, like the hatchlings, had a greater percentage of indi-

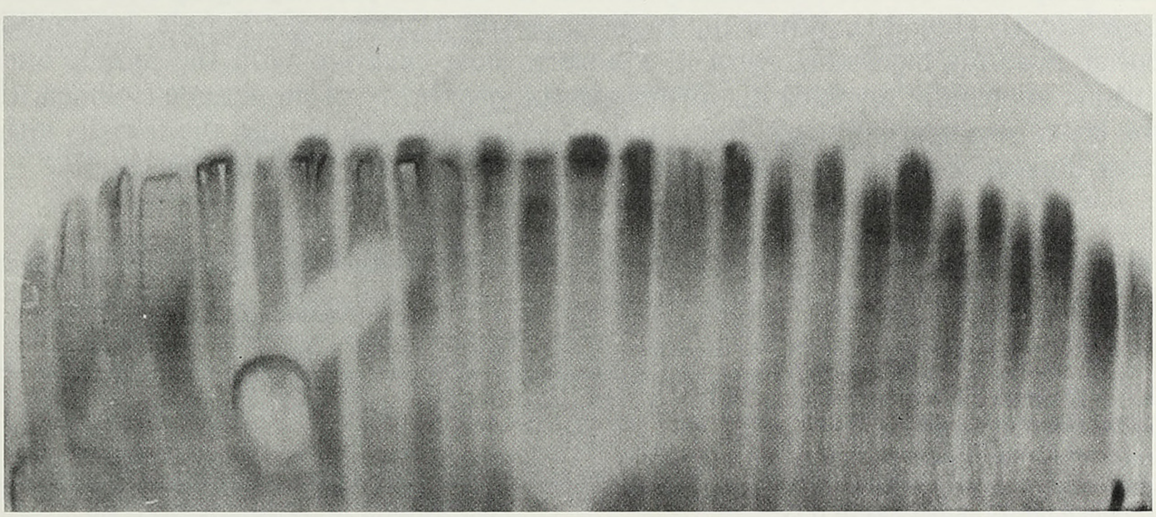

Fig. 9.—Electropherogram of plasma esterase (P-EST) in whole clutches of *G. pseudogeographica* (G. p.) and *G. ouachitensis* (G. o.) from Stoddard, Wisconsin. C. p. b., *Chrysemys picta belli.*

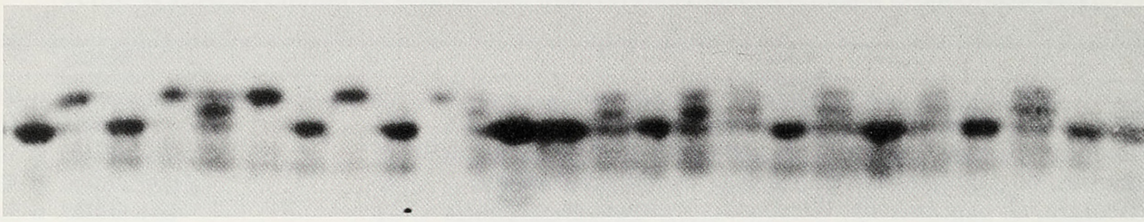

Fig. 10.—Electropherogram of malate dehydrogenase (MDH-3) in whole clutches of *G. pseudogeographica* (G. p.) and *G. ouachitensis* (G. o.) from Stoddard, Wisconsin. C. p. b., *Chrysemys picta belli.*

viduals carrying the abc phenotype than did the *G. pseudogeographica* adults in all of the populations sampled. Most (82%) of the *G. pseudogeographica* were of the cc phenotype compared to only 48% of the *G. ouachitensis.*

Courtship Behavior

Courtship behavior of *G. ouachitensis* and *G. pseudogeographica* from Stoddard was observed in the laboratory. Courtship behavior in both species is similar to that observed by Jackson and Davis (1972) for *Pseudemys.* Titillation has been reported for *G. pseudogeographica* (Cagle, 1955; Ernst, 1974), but no attempt has been made to quantify the behavioral patterns associated with courtship.

Presentation experiments were conducted with a male of one species in a 20-gallon aquarium behind one-way glass. After the male had been habituated 2 hr, one female of each species was placed in the tank with the male. The phases of courtship behavior are remarkably similar in both *G. pseudogeographica* and *G. ouachitensis* (Fig. 11). When the male observed a conspecific female, he would either raise his head and swim to a nose to nose position with the female and initiate courtship, or place his nostrils in the proximity of the female's cloaca. If the latter occurred he would then attempt to mount, trail behind the female with neck outstretched, or assume a nose to nose posture and initiate courtship.

Table 9.—*Occurrence of MDH-3 allelomorphs in* G. ouachitensis *and* G. pseudogeographica *clutches.*

	Allelomorph		
Population	cc	aa	abc
G. ouachitensis Clutch L_1 + ♀	2	♀	3
G. ouachitensis Clutch L_2 + ♀	♀	2	0
G. ouachitensis Clutch L_3 + ♀	0	3	♀
G. ouachitensis wild hatched clutch	7	0	2
G. ouachitensis hatchlings of 653	0	0	1.3
G. ouachitensis hatchlings of 76-5	3	0	6
G. pseudogeographica hatchlings of 76-1	6	0	3
G. pseudogeographica hatchlings of 76-3	11	0	4
G. pseudogeographica hatchlings of 76-4	5	0	0
G. pseudogeographica hatchlings of 418	3	0	3
G. pseudogeographica hatchlings of 651	4	0	0
G. pseudogeographica hatchlings of 659	7	0	0
G. pseudogeographica hatchlings of 663	4	1	0

Table 10.—*Summary of frequency of occurrence of MDH-3 allelomorphs (percentages) in sampled populations of* G. ouachitensis *and* G. pseudogeographica.

Population	Allelomorph			
	cc	aa	abc	N
G. pseudogeographica all hatchlings	78	2	20	51
G. ouachitensis all hatchlings	29	12	59	41
G. pseudogeographica Wisconsin adults	78	3	19	34
G. ouachitensis Wisconsin adults	44	8	48	55
G. ouachitensis Arkansas adults	72	0	28	18
G. pseudogeographica Arkansas adults	88	0	12	25
G. o. sabinensis Louisiana	64	14	22	14
Total *G. pseudogeographica*	82	2	16	110
Total *G. ouachitensis*	48	10	42	128

In the nose to nose posture the male rotated the forearms toward the medial plane and drummed the backs of the foreclaws against the ocular region of the female ("titillation"). The duration of titillation bouts in milliseconds (msec) was similar in the two species (*G. ouachitensis* $\bar{x}$ = 454 ± 126 (281–750), N = 23; *G. pseudogeographica* $\bar{x}$ = 468 ± 142 (344–843), N = 24). But the number of strokes per bout in *G. pseudogeographica* is about twice that of *G. ouachitensis* (*G. p.*, $\bar{x}$ = 10.3 ± 2.3 (7–14), N = 24; *G. o.*, $\bar{x}$ = 5.2 ± 1.28 (4–8), N = 23).

High speed motion pictures of turtles taken from the lateral aspect revealed additional species-specific differences. During the initiation of foreclaw drumming, the head of male *G. pseudogeographica* is bobbed in the vertical plane, and that of *G. ouachitensis* is held stationary. On four occasions the mouth was opened and closed in rapid succession while a male *G. pseudogeographica* was performing

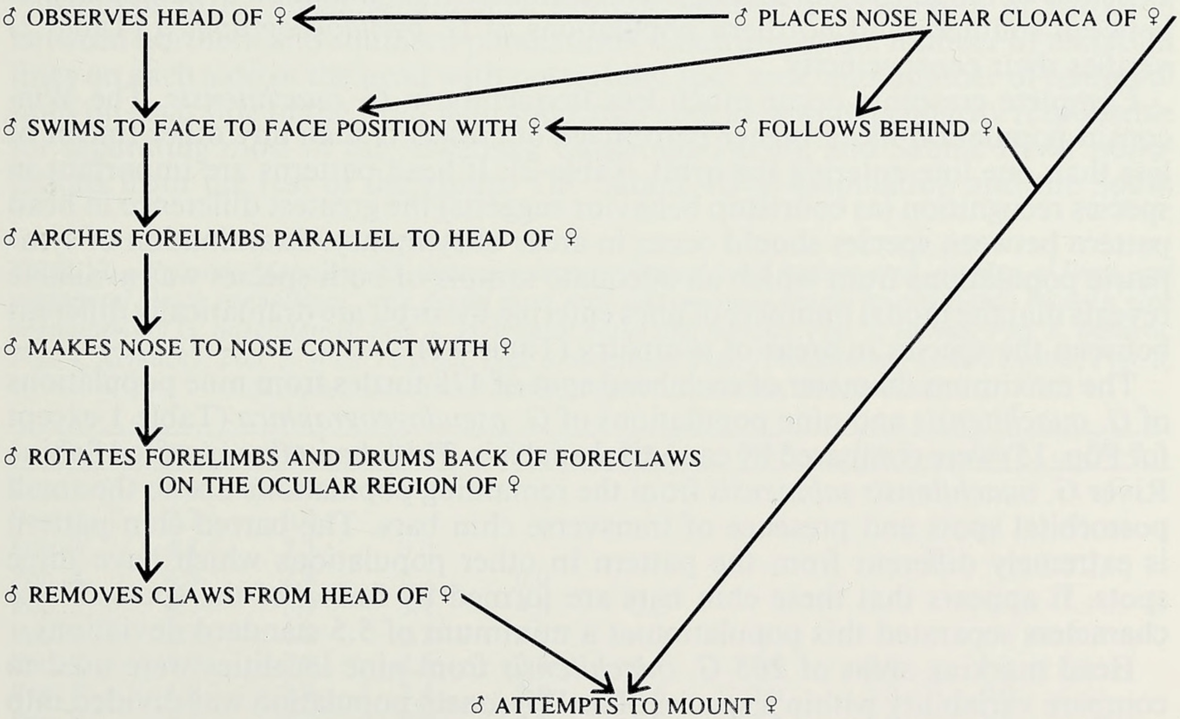

Fig. 11.—Generalized courtship sequence of male *G. ouachitensis* and *G. pseudogeographica*.

a titillation bout. Analysis of 15 bobbing sequences of *G. pseudogeographica* males showed two different patterns, either up-down-up-down-up or up-down-up. The sequence was always terminated by an upward bob. The duration of a single bob (up or down) averaged 78.1 msec. Each bobbing sequence lasted from 219–406 msec (N = 15); with a mean of 392 msec (N = 11) when five bobs were made and 230 msec (N = 4) when three bobs were made.

GEOGRAPHIC VARIATION IN THE *GRAPTEMYS PSEUDOGEOGRAPHICA* COMPLEX

Head pattern.—Specimens from throughout the geographic ranges of *G. pseudogeographica* and *G. ouachitensis* were assigned to species on the basis of the head pattern characters noted above. Each specimen was given a value related to the presence of a crescent or broken crescent, or the number of lines entering the orbit (*see* Methods). Individuals of each species were then combined into groups by state or river system (Table 1). The mean head pattern value for each group was then calculated (Table 2). The range of values throughout the geographic range of each species is nearly the same, −1 to 8 for *G. pseudogeographica* and −1 to 9 for *G. ouachitensis.*

Clinal variation in the number of lines entering the orbit occurs along a north–south gradient in both species. *Graptemys ouachitensis* has the lowest value in Wisconsin and the highest in the Sabine River, whereas *G. pseudogeographica* has a high number of lines in the northern states (South Dakota and Illinois) compared to Louisiana and Texas (Table 2).

In *G. pseudogeographica* the postorbital crescent character shows a large area of heterogeneity in Louisiana, Arkansas, Tennessee, and southern Illinois. However, the homogeneity of populations with broken crescents in Wisconsin, Iowa, South Dakota, and Nebraska, and complete crescents in Oklahoma, Texas, and Louisiana supports maintenance of subspecies designations for populations at the extremes of the geographical range. The complete intergradation of head patterns between southern and northern populations of *G. pseudogeographica* (Table 2) verifies their conspecificity.

Complete crescents occur much less frequently in *G. ouachitensis.* The Wisconsin population has a higher percentage of crescents than any other (mean of less than one line entering the orbit, Table 2). If head patterns are important in species recognition (as courtship behavior suggests) the greatest difference in head pattern between species should occur in areas of sympatry. Examination of sympatric populations from which an adequate sample of both species was available reveals that the modal numbers of lines entering the orbit are dramatically different between the species in areas of sympatry (Table 11).

The maximum diameter of each head spot of 478 turtles from nine populations of *G. ouachitensis* and nine populations of *G. pseudogeographica* (Table 1 except for Pop. 15) were compared by canonical analysis. This character separated Sabine River *G. ouachitensis sabinensis* from the remaining populations due to the small postorbital spots and presence of transverse chin bars. The barred chin pattern is extremely different from the pattern in other populations which have three spots. It appears that these chin bars are formed by fusion of the spots. These characters separated this population at a minimum of 5.5 standard deviations.

Head marking areas of 265 *G. ouachitensis* from nine localities were used to compare variability within a species. The Wisconsin population was divided into three groups (male, female, and young) to examine the effects of age and sex.

Table 11.—*Modal number of temporal lines entering the orbit in sympatric populations of* G. ouachitensis *and* G. pseudogeographica.

	G. ouachitensis	*G. pseudogeographica*
Wisconsin	1	3
Illinois	2	5
Arkansas	3	−1
Tennessee	3	1
Louisiana	3	−1
Louisiana, Sabine River	5	−1

Distances between the three divisions of the Wisconsin population are not so great as to confound the analysis. On the contrary, the multiple discriminant analysis emphasized the diversity present in a large population. The lack of discrete separation of populations from Wisconsin, Illinois, Arkansas, Oklahoma, and Catahoula Parish, Louisiana, and other Louisiana populations indicated relatedness. Combining male, female, and young from the Wisconsin populations produced little change in the results. The Wisconsin population still grouped with Arkansas, Catahoula Parish, Oklahoma, and Illinois populations, with Tennessee, Indiana, West Virginia, and Sabine River populations on the periphery. The size of the head spots is the most important character separating populations. It separated *G. ouachitensis* from Indiana, West Virginia, and Tennessee from the others. The contrast between chin spot and postorbital spot areas placed the Sabine River population and the West Virginia population at opposite extremes, and separated them partially from the rest of the group. Over 75% of the Sabine River population clustered away from the rest of the specimens examined because of its small postorbital spots and narrow transverse chin bars. The Indiana and West Virginia specimens have much larger postorbital spots and chin spots in proportion to the head area than do other populations (Table 12).

Analysis of *G. pseudogeographica* samples showed a continuum of variation between northern and southern populations. Contrasts of the number of temporal lines on each side of the head with postorbital spot area, and number of temporal lines on each side of the head with subocular spot area were primarily responsible for separating most of the Arkansas, Catahoula Parish, and Sabine River populations from the rest of the group. The Sabine River population and the South

Table 12.—*Pairwise Mahalanobis' distances (untransformed head pattern area, number of lines, and postorbital blotch connections, with dorsal head area and carapace length as covariates) between nine populations of* G. ouachitensis*: Pop. 1, Wisconsin males and females; Pop. 2, Illinois; Pop. 3, Indiana; Pop. 4, Kentucky; Pop. 5, West Virginia; Pop. 6, Arkansas; Pop. 7, Oklahoma, Lake Texoma; Pop. 8, Louisiana, Catahoula Parish; Pop. 9, Louisiana, Sabine River.*

	Pop. 1	Pop. 2	Pop. 3	Pop. 4	Pop. 5	Pop. 6	Pop. 7	Pop. 8	Pop. 9
Pop. 1	0.0								
Pop. 2	2.3	0.0							
Pop. 3	4.1	2.5	0.0						
Pop. 4	4.3	2.8	2.7	0.0					
Pop. 5	4.7	3.9	3.2	4.8	0.0				
Pop. 6	2.7	1.8	2.2	2.6	4.2	0.0			
Pop. 7	3.9	2.9	2.5	2.5	4.7	1.9	0.0		
Pop. 8	1.8	2.1	3.4	3.8	4.6	2.0	3.3	0.0	
Pop. 9	5.1	4.2	4.0	3.5	6.0	3.4	1.9	4.6	0.0

Table 13.—*Pairwise Mahalanobis' distances (untransformed all head pattern characters, dorsal head area and carapace length as covariates) between nine populations of* G. pseudogeographica*: Pop. 1, Wisconsin; Pop. 2, South Dakota; Pop. 3, Illinois; Pop. 4, Indiana; Pop. 5, Tennessee, Tiptonville; Pop. 6, Tennessee, Reelfoot Lake; Pop. 7, Arkansas; Pop. 8, Louisiana, Catahoula Parish; Pop. 9, Louisiana, Sabine River.*

	Pop. 1	Pop. 2	Pop. 3	Pop. 4	Pop. 5	Pop. 6	Pop. 7	Pop. 8	Pop. 9
Pop. 1	0.0								
Pop. 2	2.5	0.0							
Pop. 3	1.9	1.4	0.0						
Pop. 4	2.2	1.7	1.9	0.0					
Pop. 5	1.6	1.7	1.0	1.9	0.0				
Pop. 6	2.5	2.5	2.4	2.7	2.3	0.0			
Pop. 7	3.0	3.8	3.3	3.3	3.4	2.7	0.0		
Pop. 8	2.5	3.7	3.4	3.4	3.4	2.7	2.2	0.0	
Pop. 9	3.3	4.7	4.3	4.3	4.3	3.4	2.5	1.4	0.0

Dakota population are at opposite extremes for these characters. These populations also represent the extremes in geographic range of the species. Individuals from the Sabine River all have narrow crescents, small subocular spots and no temporal lines breaking the crescent. The South Dakota population has no crescents, larger subocular spots, and an average of five temporal lines entering the orbit. The Catahoula Parish and Arkansas populations are also separated from the other populations by the predominance of narrow complete crescents, but broken crescents and lines entering the orbit also occur in both of these populations. The Reelfoot Lake population is intermediate in this character between the populations to the south and populations to the north (Table 1). It is closest to the Tiptonville population both in Mahalanobis' distance (Table 13) and geographic distance. The Reelfoot Lake population has a wide variety of head patterns, including crescents and up to eight lines entering the orbit. The Wisconsin population has the narrowest postorbital spots and the smallest mandibular spots, whereas the Reelfoot Lake population has the largest, so large that individuals from that population are difficult to distinguish from *G. ouachitensis* on head markings alone.

Shell pattern.—Although some of the ten carapace pattern categories (Table 6) are more common in certain populations of one or the other species, no differences were found that consistently separate species. Carapace patterns of Sabine River *G. ouachitensis* were similar to those found in other populations of *G. ouachitensis*; however, the frequency of turtles having concentric light colored rings on each scute was nearly 50%. This character state was uncommon in other populations of *G. ouachitensis.* The carapace patterns of *G. caglei* and *G. versa* are similar to the concentric ring pattern found in Sabine River *G. ouachitensis.*

The nine categories of plastral patterns (Table 6) show no consistent differences between the species throughout their distributions. The amount of the plastron covered by dark markings is not a diagnostic character throughout the range of either species. Southern populations of *G. pseudogeographica* often have a high percentage of individuals with plastral patterns that follow the sutures. The plastron of Sabine River *G. ouachitensis* often (17.8% of specimens examined) is marked with a concentric central figure similar to that of *Chrysemys picta belli.* All of the *G. caglei* examined had the plastral pattern, when visible, primarily following the sutures. Larger individuals developed scattered black flecking. This flecking also occurred in many Sabine River *G. ouachitensis.* The plastrons of 77

G. versa were primarily unmarked yellow (91.8%); the remaining (8.2%) were mottled yellow brown.

Discussion and Conclusions

After examination of a large number of *Graptemys* from the Mississippi River at Stoddard, Wisconsin, a review of the taxonomic literature on the *G. pseudogeographica* complex, and examination of museum specimens from other localities, I concluded that the characters previously used for diagnosing taxa in the complex were not reliable.

Canonical analysis of head patterns alone did not completely separate *G. pseudogeographica* and *G. ouachitensis.* As in Darwin's Finches, there is considerable overlap between the species when the patterns of all populations are compared simultaneously. Presence or absence of a postorbital crescent, or the number of lines entering the orbit were not useful in sorting individuals to species. However, these characters did separate the two species in sympatric populations and subspecies within each species.

The size of the postorbital, subocular, and mandibular spots was most important in separating *G. ouachitensis* from *G. pseudogeographica,* regardless of the number of temporal lines entering the orbit. The combination of temporal lines and size of spots makes certain separation possible at most localities.

Reduced postorbital spots, transverse chin bars, and a large number of lines entering the orbit ($\bar{x} = 6.5$) separate over 75% of the Sabine River *G. ouachitensis* from other populations of *G. ouachitensis* studied. Since the Sabine River population is also geographically isolated, its status as a subspecies, *G. ouachitensis sabinensis,* is justified. Some individuals in this population that are indistinguishable from *G. o. ouachitensis* in head pattern are considered intergrades.

Populations of *G. pseudogeographica* from Arkansas, Catahoula Parish, Louisiana, and the Sabine River are separated from other populations of *G. pseudogeographica* primarily on the basis of fewer lines entering the orbit and smaller postorbital spots. Populations of *G. pseudogeographica* from the Sabine River and South Dakota, at the extremes of the species' geographic range, exhibit opposite extremes in head pattern. The Sabine River turtles have narrow postorbital crescents and small subocular spots, and never have any lines breaking the crescents. The Mahalanobis' distance of 4.66 between these two populations suggests that there is less than a 10% overlap between them.

The data in Table 13 show that *G. pseudogeographica* populations from Wisconsin, South Dakota, Illinois, Indiana, and Tiptonville, Tennessee, are similar. I refer these populations to the subspecies *G. pseudogeographica pseudogeographica.* All of these populations are close to at least two other populations in the group (distance of less than two standard deviations). The Arkansas, Catahoula Parish, Louisiana, and Sabine River populations have Mahalanobis' distances closer to each other than to any other group. I regard these populations as constituting the subspecies *G. pseudogeographica kohni.* The Reelfoot Lake population is intermediate between northern and southern populations. The Mahalanobis' distances between Reelfoot Lake and Arkansas, and Reelfoot Lake and Indiana are equal: 2.66. It is a geographically intermediate population wherein the subspecies *G. pseudogeographica pseudogeographica* and *G. pseudogeographica kohni* intergrade, as in other populations in Missouri and Illinois. I recognize the northern and southern populations of *G. pseudogeographica* as subspecies, even though they represent the ends of a cline in variation.

Incubation of clutches of eggs from known females at several different temperatures clarified the limits of head pattern variability. No clutches were found with hatchlings so different from the female parent that they might be considered interspecific hybrids. In addition, all female *G. ouachitensis* which had particularly small postorbital and subocular spots, suggesting possible hybridization with *G. pseudogeographica,* produced offspring that were clearly *G. ouachitensis.* The influence of incubation temperature on the size of the postorbital, subocular, and mandibular spots and on the number of temporal lines entering the orbit helps to explain intraspecific variation at a locality and emphasizes the need to examine large samples before arriving at taxonomic conclusions in this group.

Osteological comparisons showed *G. ouachitensis* and *G. pseudogeographica* males and females from both northern and southern localities to be closer to each other than to either *G. geographica* or *G. versa.*

Both shell and skull shape are important in separating *G. geographica* from the *G. pseudogeographica* complex. *Graptemys pseudogeographica kohni* females are closer to the *G. geographica* group than to any other population of *Graptemys* examined, due to their wide, massive skulls and great dentary widths. When only females from each population were used for analysis, *G. geographica* females were clearly removed from the *G. pseudogeographica* complex by the ratios of postpalatal foramen width to pterygoid width and plastron width to intersquamosal width. Differences in the skeletal characters of Wisconsin specimens substantiated separation of *G. pseudogeographica* and *G. ouachitensis.* Skeletal differences between southern and northern populations of *G. ouachitensis* were greater than between *G. pseudogeographica* populations. The ratios of dentary width to carapace height and plastron width to pterygoid width separated *G. ouachitensis* from *G. pseudogeographica.* These measurements emphasized the wider jaws and plastron of *G. pseudogeographica* and the higher carapace of *G. ouachitensis.* At Stoddard the two species were separated by 4.4 standard deviations primarily by the different ratio of dentary width to pterygoid width. When skeletal features were combined with head pattern characters, the Wisconsin population of *G. ouachitensis* was separated from sympatric *G. pseudogeographica* by a distance of 11 standard deviations. The contrasts between carapace width and size of the mandibular spot, and plastron width and maximum skull width were mainly responsible for the separation.

Several factors may help to explain the divergence of skull size in southern and northern populations of *Graptemys. Graptemys geographica* occurs with *G. ouachitensis* and *G. pseudogeographica* at the Wisconsin site, but not at the southern localities studied. A study of food partitioning (Vogt, 1981*b*) showed that *G. geographica* is a mollusk specialist in Wisconsin and has a 0.21 niche overlap with *G. ouachitensis,* whereas *Graptemys pseudogeographica* and *G. ouachitensis* in the same community have a 0.76 overlap. Competition with *G. geographica* is absent in southern turtle communities, where the species does not occur. However, the generalist *Trachemys scripta* and the herbivore *Pseudemys concinna* are abundant. In the South, *G. pseudogeographica kohni* is a mollusk specialist, developing wide crushing surfaces on the jaws as a consequence of this dietary preference. Southern *G. ouachitensis* are more insectivorous and restricted to fast-moving portions of rivers, thus avoiding competition with *T. scripta* which occurs in oxbow ponds and slower reaches (McCoy and Vogt, in preparation).

Berry (1975) observed character convergence where large-headed *Sternotherus minor* was sympatric with the narrow-headed *S. odoratus.* He suggested this was the result of competition for a limited food resource. He found the larger species, *S. minor,* becoming smaller in the presence of the small congener. In Wisconsin, *G. pseudogeographica* has been displaced as a mollusk specialist by *G. geographica* and is under selection for a head size most efficient at being a generalist (Vogt, 1980*b*). Since *G. pseudogeographica* and *G. ouachitensis* in that population overlap considerably in the types of food eaten, (primarily insect larvae and vegetation [Vogt, 1981*b*]) they have converged in head size. Absence of competition from *Trachemys* (which is an opportunist, feeding on insects, mollusks, plants, fungi, and carrion) probably permitted the evolution, in Wisconsin, of larger *G. ouachitensis* that are more capable of utilizing a generalized food resource.

Shell patterns were compared and found not to be useful taxonomic characters throughout the geographic ranges of the two species, although at specific localities plastral patterns of hatchlings were useful in separating *G. pseudogeographica* from *G. ouachitensis.*

Electrophoretic comparison of proteins is not as useful for distinguishing lower taxonomic categories of emydid turtles as it is in some other vertebrates (Selander and Johnson, 1973). I found no discrete differences between subspecies, and few at the species level. As a taxonomic tool below the generic level, electrophoresis should be used with extreme caution. Merkle (1975) found striking similarities in 17 protein systems in the genus *Clemmys,* where at least 10 systems were shared between all four species and only three separated *C. muhlenbergi* from *C. guttata* and two separated the subspecies *C. m. marmorata* from *C. marmorata pallida.* McKown (1972) found electrophoresis of blood proteins in both *Graptemys* and *Malaclemys* to be inadequate for elucidating phylogenetic relationships below the generic level. Only two of the 19 protein systems that I examined electrophoretically showed intra- or interspecific variation between populations of *G. ouachitensis* and *G. pseudogeographica.* Relative mobility differences in plasma esterase (P-EST, Table 8) were small though consistent, and showed phenotypic similarities between *G. ouachitensis sabinensis* and *G. o. ouachitensis* as well as among populations of *G. pseudogeographica.* However, differences between populations of *G. o. ouachitensis* were as great as or greater than differences between sympatric populations of *G. ouachitensis* and *G. pseudogeographica.* The only heterozygous locus, MDH-3, showed inconsistent frequencies of allozyme distributions in the three populations of *G. ouachitensis* and the two populations of *G. pseudogeographica* studied (Table 9, Table 10). However, the predominance of the cc phenotype in both populations of *G. pseudogeographica* compared to sympatric *G. ouachitensis* provided evidence that *G. pseudogeographica* from Wisconsin is conspecific with the Arkansas population. Furthermore, *G. ouachitensis* from the Sabine River possessed allozyme frequencies similar to those of the other populations of *G. ouachitensis,* supporting their status as conspecific. Although electrophoresis did not give discrete separation between the species examined, it was useful in indicating relationships.

Differences in courtship behavior further support separating *G. ouachitensis* and *G. pseudogeographica* as species. There are species-specific differences in the number of times the foreclaws are drummed against the ocular regions of the female per titillation bout (5.2 vs. 10.3). Head bobbing during titillation by both subspecies of *G. pseudogeographica,* but not by *G. ouachitensis,* also differentiates the species.

Males apparently recognize conspecific females by both visual and olfactory cues, as males did not court freeze-dried conspecific females. Auffenberg (1965) found cloacal secretions to be important in recognition of conspecifics in *Geochelone.* However, field experiments with *Chrysemys picta* (Vogt, 1980*c*) failed to demonstrate that females release species-specific pheromones to attract males in that emydine species. Preliminary laboratory observations of precopulatory or precourting *Graptemys* suggests that species-specific odors are present, but further experiments are needed.

The combination of data confirms that *G. pseudogeographica* and *G. ouachitensis* are separate species, each with two subspecies: *G. pseudogeographica pseudogeographica* and *G. pseudogeographica kohni*; *G. ouachitensis ouachitensis* and *G. ouachitensis sabinensis. Graptemys versa* is more distant from the *G. pseudogeographica* complex than is *G. geographica* as shown by skeletal anatomy. *Graptemys caglei* is thought to be related to *G. ouachitensis* on the basis of head and shell patterns. My interpretation is that the allopatric *G. caglei* and *G. versa* are distinct species, which are provisionally retained in the *G. pseudogeographica* complex pending further study.

SYSTEMATIC ACCOUNTS

Graptemys ouachitensis Cagle

Fig. 12 a–l; Fig. 13a–l; Fig. 15a–f; Fig. 16; Fig. 19

Graptemys pseudogeographica ouachitensis Cagle, 1953:10. Type locality: Ouachita River, four miles northeast of Harrisonburg, Catahoula Parish, Louisiana. Holotype, UMMZ 104345.
Malaclemys pseudogeographica ouachitensis: Cochran and Goin, 1970:149.
Graptemys ouachitensis: Vogt, 1980*b*:18. First use of present combination.

Definition.—*Graptemys ouachitensis* is a medium-sized emydid turtle: females reach 26 cm in carapace length, males 16 cm. The carapace is elevated with low black knobs on the second, third, and fourth vertebrals. The plastron is flat. The carapace is green with one to six, usually one, black blotch on the posterior border of each scute. The blotches are encircled with yellow or orange, or a lattice of interconnected circles may be present without the black blotches. The pattern is often faded in adults and melanism is frequent in northern populations. The cream to yellow plastron is marked with dark concentric swirls of alternating yellow and dark green; the green may be reduced to lines following the sutures. The pattern covers less than 50% of the plastron. This pattern fades to brown-yellow mottling in adults and is replaced by dark lines along the sutures. The head is dark green with yellow markings. A large postorbital spot extends from under the orbit around the posterior border to meet a pair of longitudinal narrow lines running the length of the head (Fig. 12a, b; Fig. 13a, b, d, e). This crescent may be broken behind the eye, and there may be 1–9 wide stripes entering the orbit (Fig. 12k; Fig. 13h, i; Fig. 15b, d, e, f). The spot below the orbit is large, and directly below this spot is a large yellow spot on the lower jaw (Fig. 12e, h, k; Fig. 13h, i). Four large yellow spots (one at the symphysis, one on each mandible, and one in the center), or alternating yellow and dark green transverse bars (Fig. 13c; Fig. 15c) mark the underside of the head.

Distribution.—*Graptemys ouachitensis ouachitensis* occurs from the Mississippi and St. Croix rivers in Minnesota and Wisconsin south in the Mississippi River Basin through Louisiana. It is found as far west as Lake Texoma, Oklahoma (Red River), and east into Indiana and West Virginia. *Graptemys ouachitensis sabinensis* is restricted to the Sabine River Drainage of Louisiana and Texas (Fig. 16).

Graptemys ouachitensis ouachitensis Cagle

Graptemys pseudogeographica ouachitensis Cagle, 1953:10.
Graptemys ouachitensis ouachitensis: Vogt, 1980*b*:107. First use of present combination.

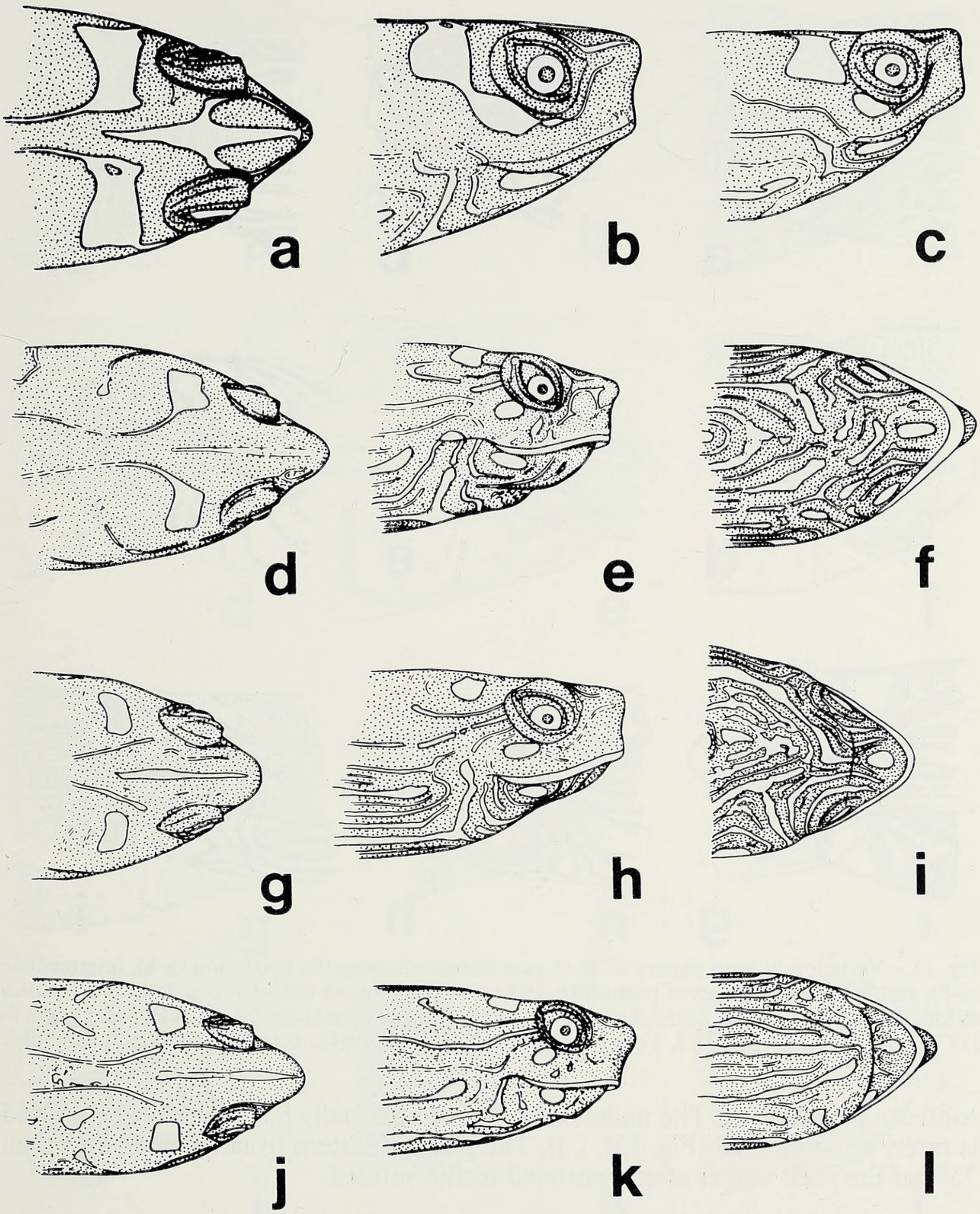

Fig. 12.—Variation in head pattern of *G. o. ouachitensis* from Stoddard, Vernon Co., Wisconsin (RCV field numbers 354, 394, 488, 537, 561) showing the maximum (a–b) and minimum (j–k) sizes of postorbital and subocular spots in northern populations.

Definition.—*Graptemys ouachitensis ouachitensis* reaches largest size in the northern United States. The postorbital spot is usually large, rarely reduced, and never has narrow yellow rings around it (Fig. 12d, e, g, h, j, k). The postorbital spot may be enlarged and connected with the subocular spot to form a wide crescent (Fig. 12a, b). This is more common in northern populations than in

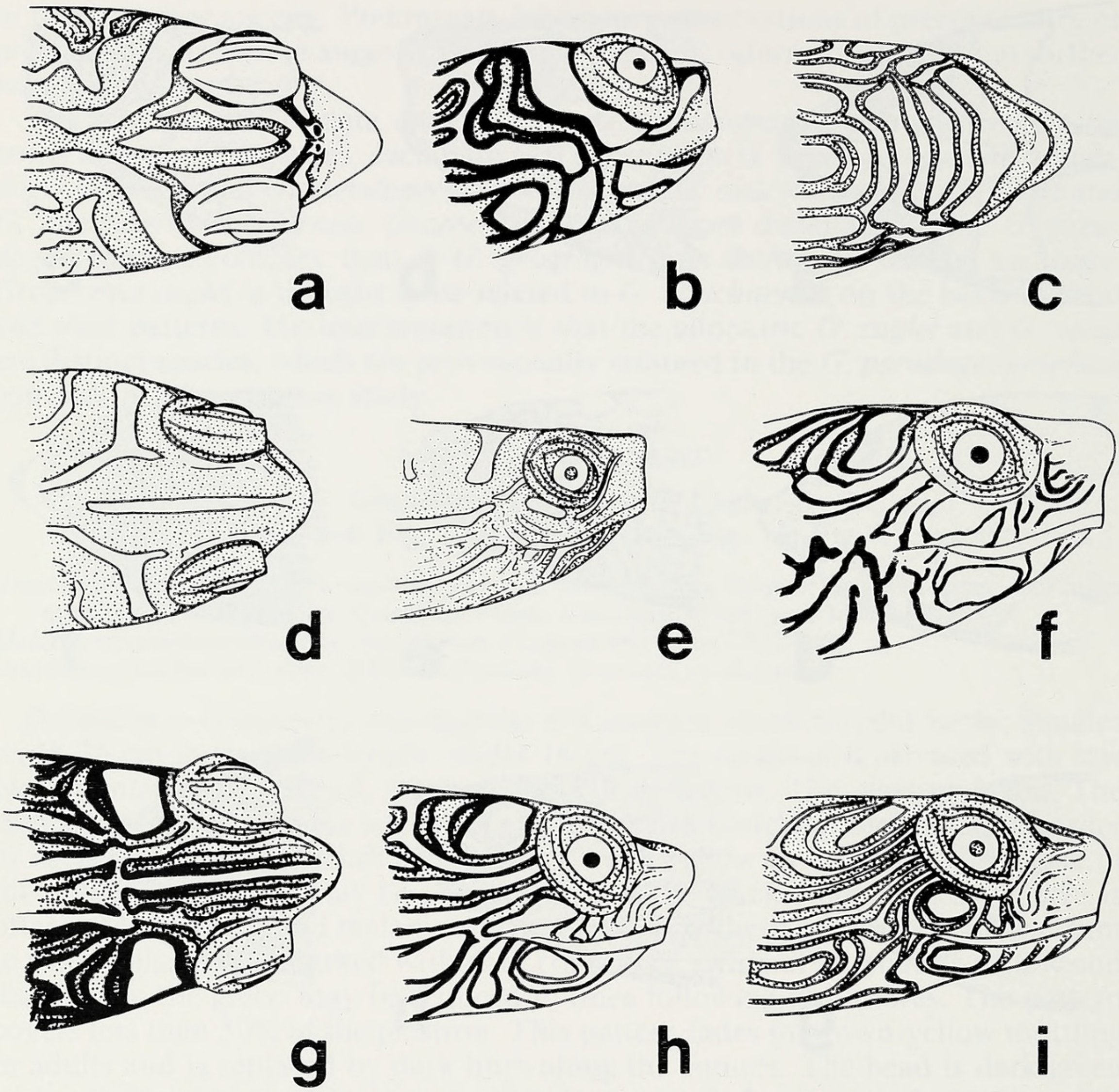

Fig. 13.—Variation in head pattern of *G. o. ouachitensis* showing the maximum (a–b), intermediate (d–h), and minimum (i) sizes of postorbital and subocular spots in southern populations. Localities as follows: a–e (TU 12535, 12658, Louisiana, Catahoula Par.; Ouachita R., 4 mi N Harrisonburg); f–i (TU 16937, 16937.1–16937.2, Tennessee, Perry Co., Tennessee R., between Saltillo and Dunville).

southern populations. The underside of the head usually has four large spots, and is rarely cross-banded (Fig. 12f, i, l). The plastral pattern usually covers less than 75% of the shell and is often restricted to the sutures.

Graptemys ouachitensis sabinensis Cagle, new combination

Graptemys pseudogeographica sabinensis Cagle, 1953:2. Type locality: Sabine River, eight miles southwest of Negreet, Sabine Parish, Louisiana. Holotype, UMMZ 104351.
Malaclemys pseudogeographica sabinensis: Cochran and Goin, 1970:149.

Definition.—Smaller in carapace length, *G. ouachitensis sabinensis* males reach 8 cm in length and females 12 cm. The postorbital yellow marking is reduced to a spot in most individuals (Fig. 15a, b, d). Six to nine yellow lines enter the orbit on each side of the head (Fig. 15b, d, e, f). At least four of these lines are wide. The throat is marked with transverse alternating yellow and dark green bars (Fig.

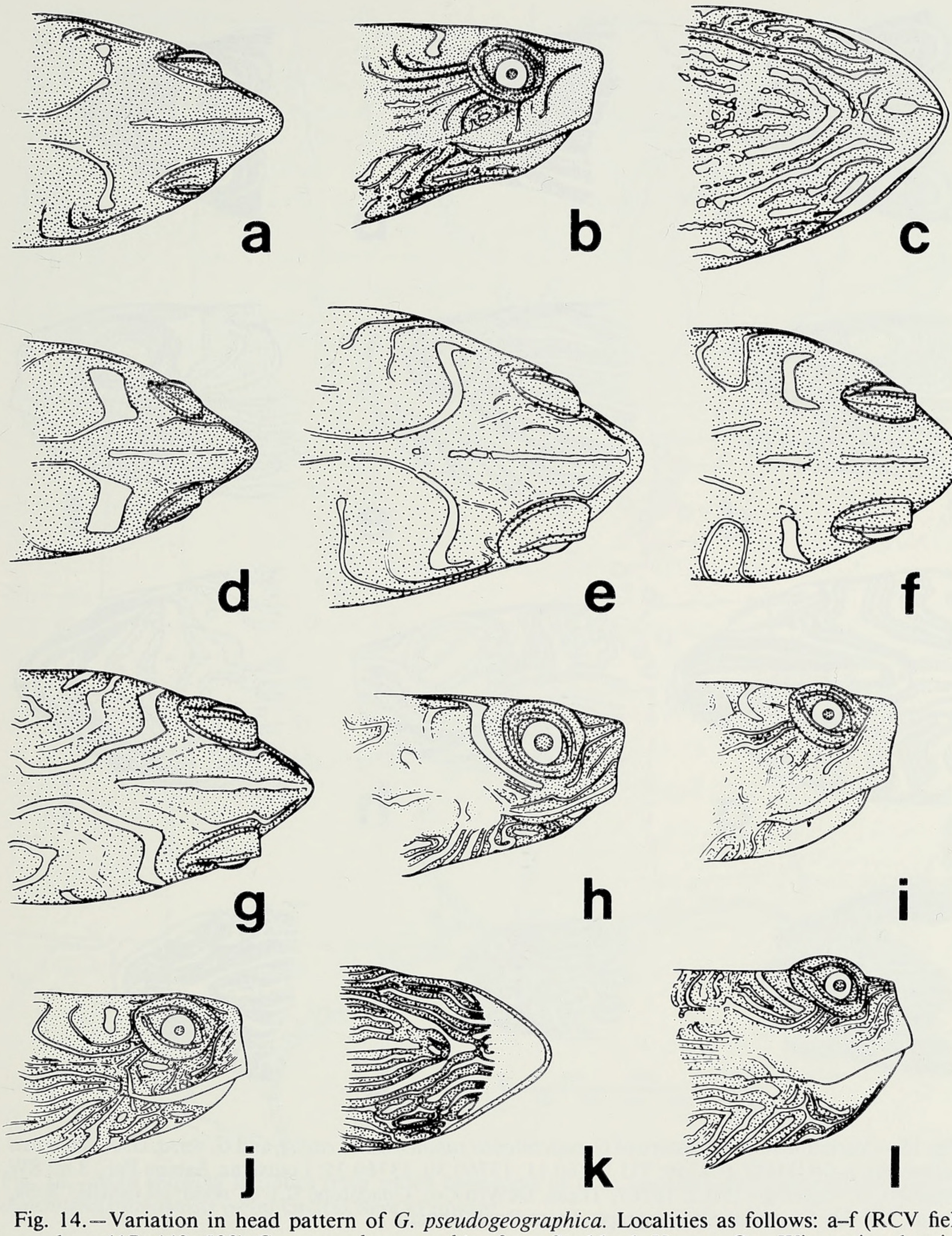

Fig. 14.—Variation in head pattern of *G. pseudogeographica.* Localities as follows: a–f (RCV field numbers 417, 443, 508) *G. p. pseudogeographica* from Stoddard, Vernon Co., Wisconsin, showing minimum (a–b) and maximum (d) sizes of postorbital and subocular spots, and postorbital crescent (f); *G. pseudogeographica kohni* g–h (CM 4258, 4259, Louisiana, Caddo Par., Red R., 1 mi W Gayle); i (MAZG 1465, Louisiana, Ouachita Par., Ouachita R., 15 mi SE Monroe); j–k (USNM 100243, Louisiana, Iberville Par., Plaquemine); l (CM 4257) same as g–h.

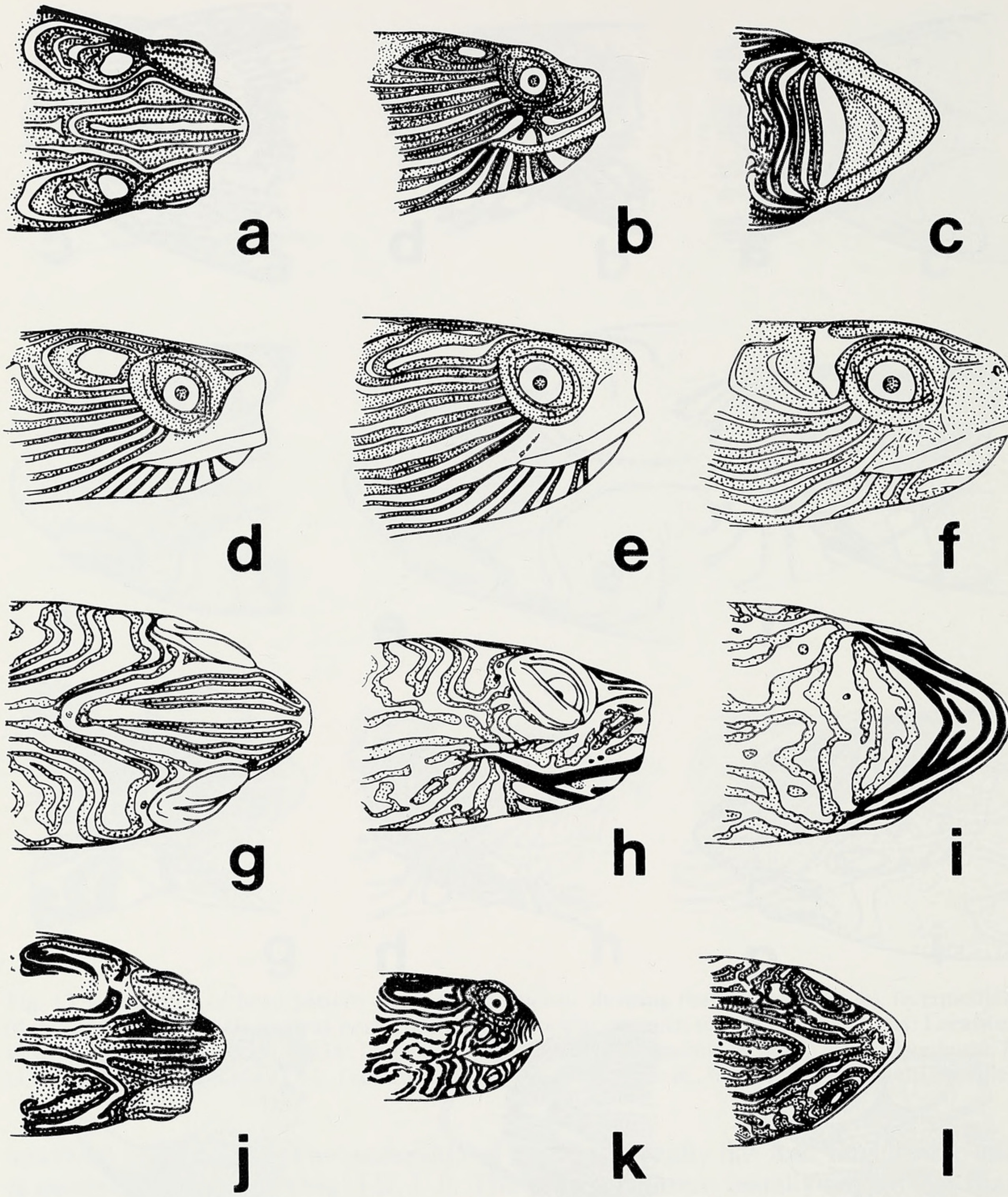

Fig. 15.—Variation in head pattern of *G. ouachitensis sabinensis, G. caglei,* and *G. versa. G. ouachitensis sabinensis*: a–f (UMMZ 104356; TU 13760.11, 13760.30, 13760.35; Louisiana, Sabine Par., 8 mi SW Negreet). *G. caglei*: g–i (MCZ 16767, Texas, DeWitt Co., Guadalupe R.). *G. versa*: j–l (SMBU 5084, Texas, Kimble Co., 3 mi SE Telegraph, Paint Rock Ranch).

15c). The central two thirds of the plastron is marked with yellow and dark green reticulations. The plastron of males is often flecked with black.

Graptemys pseudogeographica (Gray)
Fig. 14a–l; Fig. 17; Fig. 18

Emys pseudogeographica Gray, 1831:341. Type locality: Wabash River, New Harmony, Posey County, Indiana. Lectotype, MNHN 9147 (Bour and Dubois, 1983).

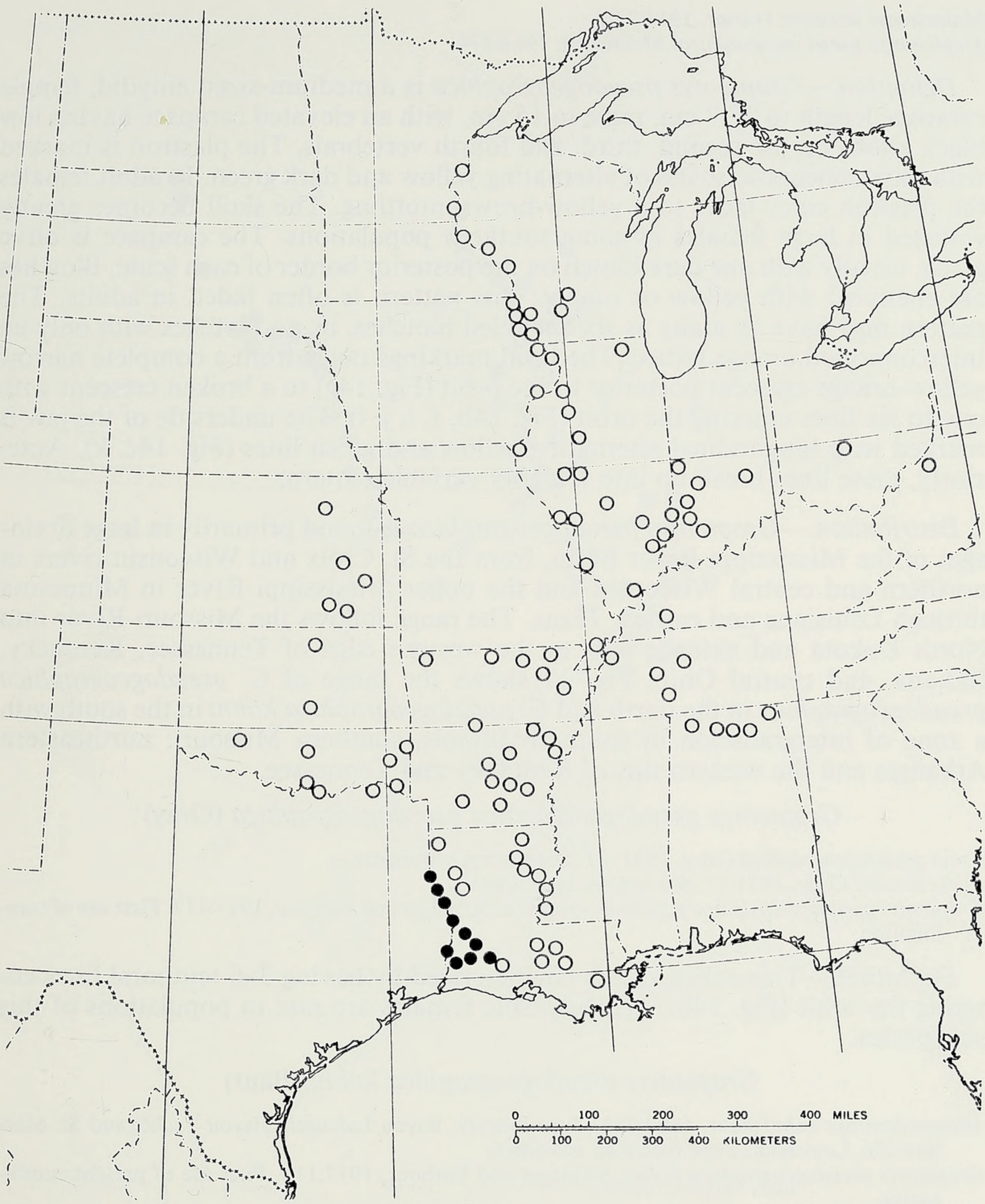

Fig. 16.—Map showing localities from which specimens of *G. o. ouachitensis* (open circles) and *G. ouachitensis sabinensis* (solid circles) were examined.

Emys lesueurii Gray, 1831:31. Type locality: Wabash River, New Harmony, Posey County, Indiana.
Emys geographica (part): Duméril and Bibron, 1835:256.
Graptemys lesueurii: Agassiz, 1857:436.
Graptemys pseudogeographica: Gray, 1863:180. First use of present combination.
Clemmys pseudogeographica: Strauch, 1862:33.
Malacoclemmys pseudogeographica: Cope, 1875:53.
Malacoclemmys lesueuri: Yarrow, 1882:34.
Malacoclemmys pseudo-geographicus: Davis and Rice, 1883:32.
Graptemys pseudogeographicus: Paulmier, 1902:393.

Malaclemys lesueuri: Hurter, 1911:243.
Malaclemys pseudogeographica: McDowell, 1964:274.

Definition.—*Graptemys pseudogeographica* is a medium-sized emydid, female carapace length to 27.7 cm, male to 15 cm, with an elevated carapace having low black knobs on the second, third, and fourth vertebrals. The plastron is marked with dark concentric swirls of alternating yellow and dark green. In adult females the plastron color fades to a yellow-brown mottling. The skull becomes greatly widened in large females in some southern populations. The carapace is olive green, usually with one dark blotch on the posterior border of each scute. Blotches are encircled with yellow or orange; this pattern is often faded in adults. The pattern may have as many as six encircled blotches, or no blotches with only an interconnected orange lattice. The head markings range from a complete narrow yellow-orange crescent posterior to the orbit (Fig. 14g) to a broken crescent with one to six lines entering the orbit (Fig. 14b, f, i, j, l). The underside of the jaw is marked with longitudinal alternating yellow and green lines (Fig. 14c, k). Anteriorly, these lines break up into a highly variable pattern.

Distribution.—*Graptemys pseudogeographica* is found primarily in large drainages of the Mississippi River Basin, from the St. Croix and Wisconsin rivers in northern and central Wisconsin and the upper Mississippi River in Minnesota through Louisiana and eastern Texas. The range follows the Missouri River into North Dakota and extends east to the western edge of Tennessee, Kentucky, Indiana, and central Ohio. Fig. 17 shows the range of *G. pseudogeographica pseudogeographica* in the north and *G. pseudogeographica kohni* in the south with a zone of intergradation in southern Illinois, southern Missouri, northeastern Arkansas and the western tips of Kentucky and Tennessee.

Graptemys pseudogeographica pseudogeographica (Gray)

Emys pseudogeographica Gray, 1831: 31. See species synonymy.
Emys lesuerii Gray, 1831:31. See species synonymy.
Graptemys pseudogeographica pseudogeographica: Stejneger and Barbour, 1917:117. First use of combination.

Definition.—This subspecies is characterized by having 3–6 temporal lines entering the orbit (Fig. 14b). Megacephalic females are rare in populations of this subspecies.

Graptemys pseudogeographica kohni (Baur)

Malacoclemmys kohni Baur, 1890:263. Type locality: Bayou Lafourch, Bayou Teche, and St. Martinsville, Louisiana. Type specimen unknown.
Graptemys pseudogeographica kohni: Stejneger and Barbour, 1917:117. First use of present combination.
Graptemys kohni: Cagle, 1954:181.
Malaclemys kohni: McDowell, 1964:274.

Definition.—This subspecies is characterized by having complete postorbital crescents (postorbital spot joined with the subocular spot, Fig. 14g), or one (Fig. 14f) to three (Fig. 14i, j) temporal lines entering the orbit. Megacephalic females are common in many populations.

G. caglei Haynes and McKown
Fig. 15g–i

Graptemys caglei Haynes and McKown, 1974:173. Type locality: Guadalupe R., 8 km NW Cuero, DeWitt Co., Texas. Holotype, TNHC 36061.

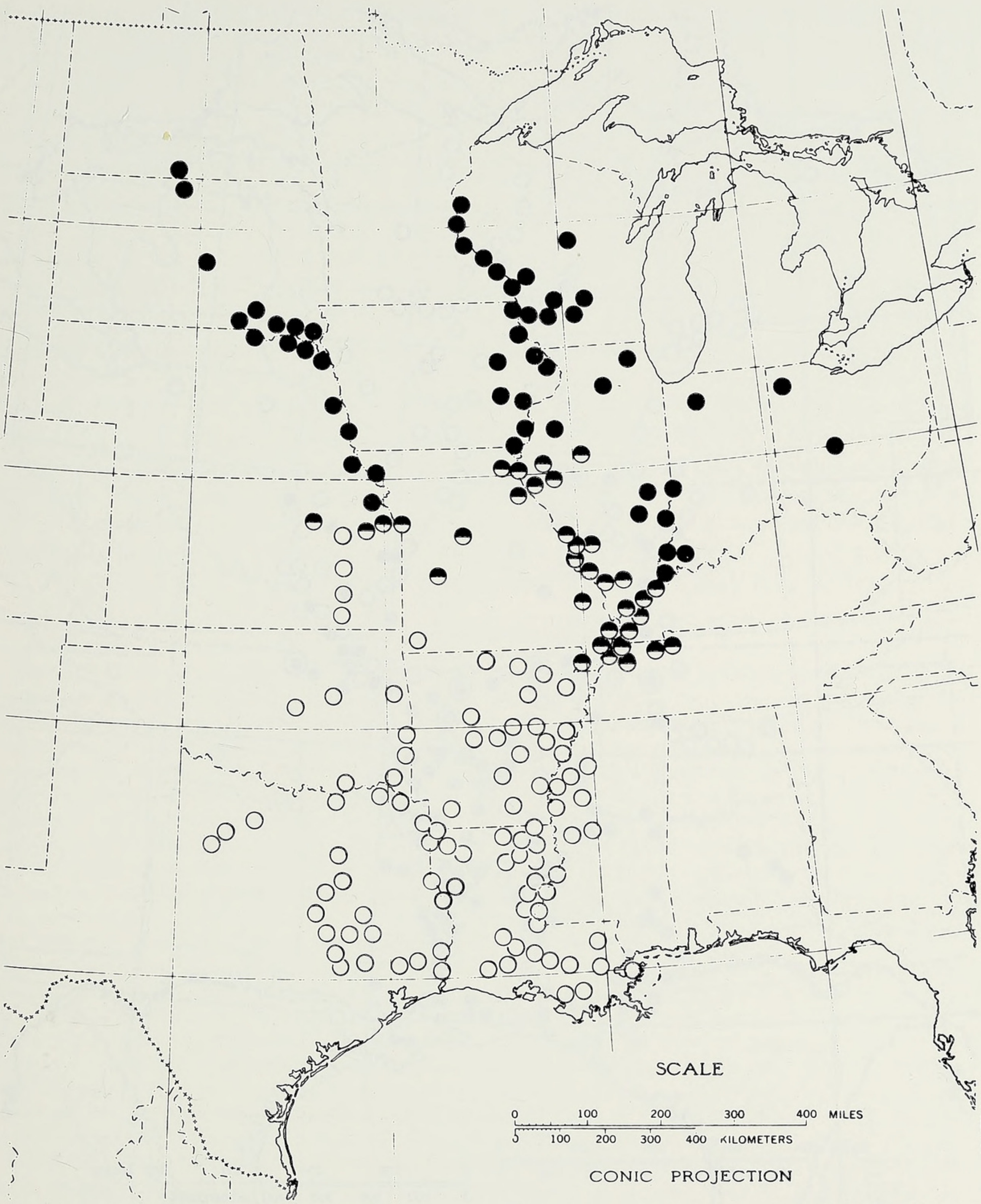

Fig. 17.—Map showing localities from which specimens of *G. p. pseudogeographica* (solid circles), *G. pseudogeographica kohni* (open circles), and intergrades (half open circles) were examined.

Definition.—*Graptemys caglei* is a medium-sized emydid: males reach 11 cm carapace length and females 16 cm carapace length. The carapace has a middorsal keel with sharp vertebral spines. The carapace is light green with cream-colored circular lines on the pleurals and marginals. The cream-colored plastron is heavily flecked with black and black lines extend along the seams. The head is black with cream stripes. Single postorbital crescents on each side extend to meet on the dorsal midline behind the orbits. The ventral side of the jaw has a transverse line.

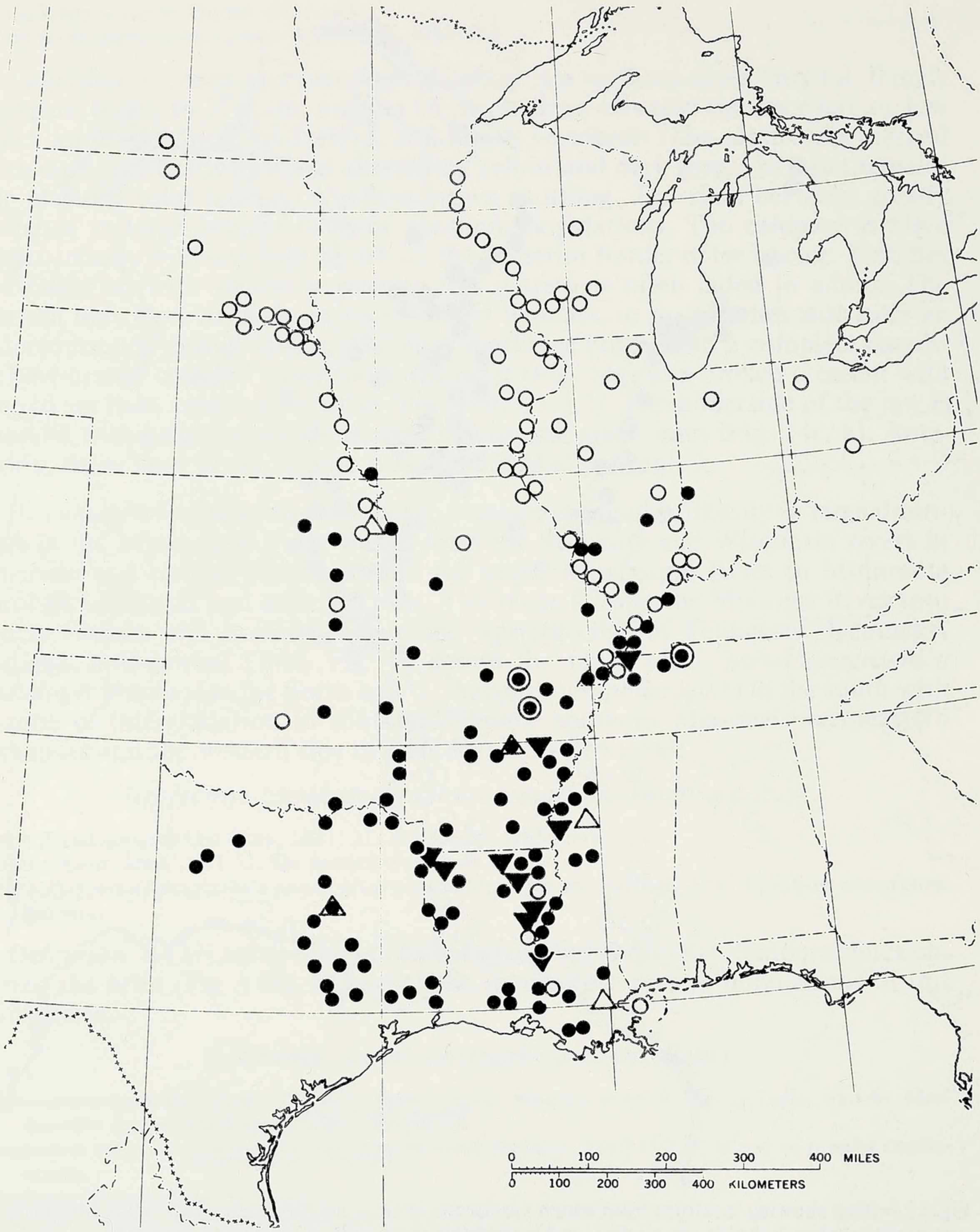

Fig. 18.—Map showing locations of populations of *G. pseudogeographica* in which individuals had the following head pattern characters: complete crescents (solid circles); incomplete crescents (triangles); incomplete crescents with lines entering orbit (open circles); all three of the preceeding (inverted triangles); complete crescents and lines entering orbit (concentric circles).

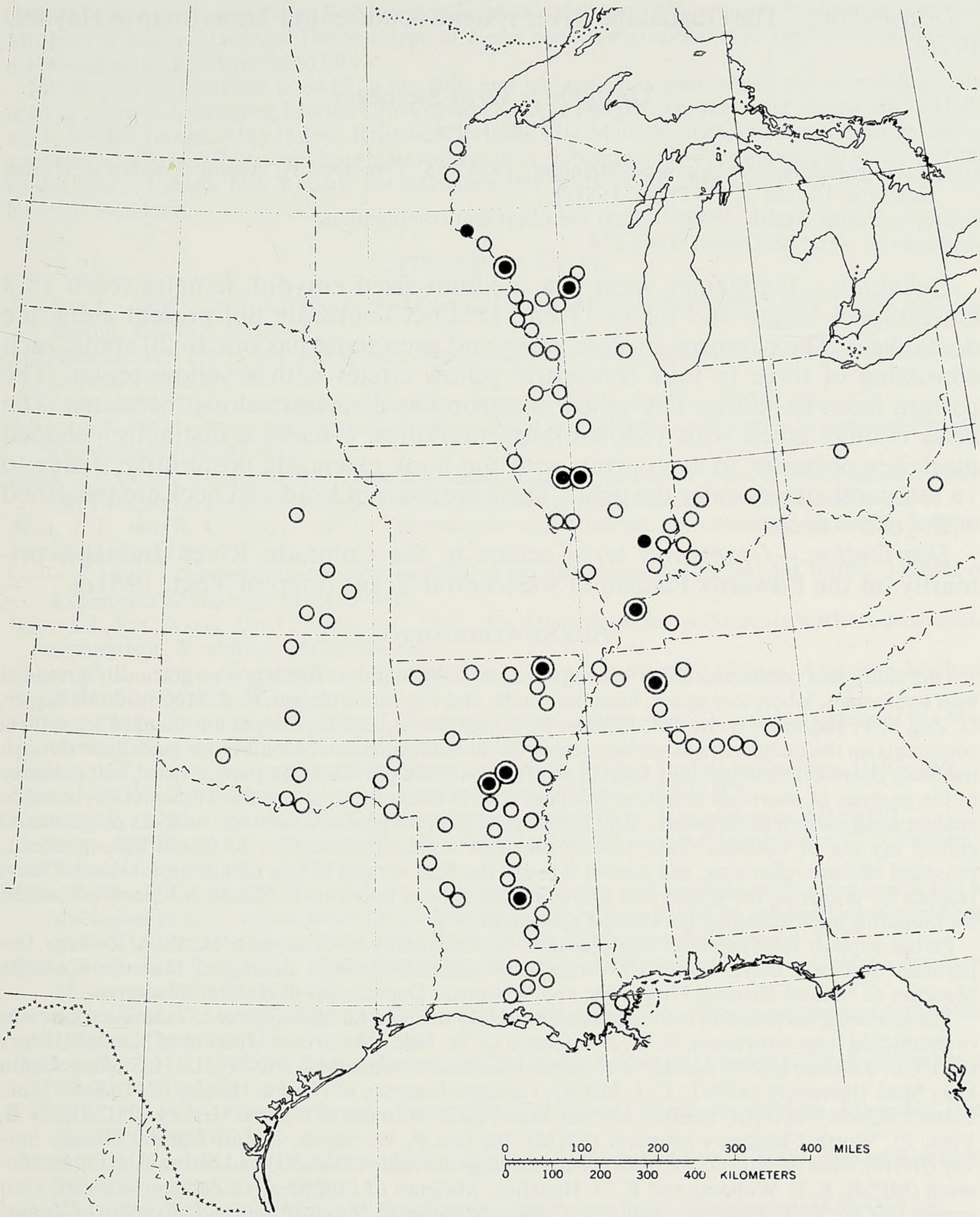

Fig. 19.—Map showing locations of populations of *G. ouachitensis* in which individuals had either complete postorbital crescents (solid circles), or incomplete postorbital crescents (open circles), or both (concentric circles).

Distribution.—The Guadalupe River system, southcentral Texas (map in Haynes, 1976).

Graptemys versa Stejneger
Fig. 15j–l

Graptemys pseudogeographica versa Stejneger, 1925:463. Type locality: Austin, Travis Co., Texas. Holotype, USNM 27473 (Vogt, 1981*c*).
Graptemys versa: Smith, 1946:60. First use of present combination.
Malaclemys versa: McDowell, 1964:274.

Definition.—*Graptemys versa* is a medium-sized emydid: females reach 18.3 cm carapace length and males 11 cm. Distinct knobs are not present along the dorsal keel. The carapace is olive green and each scute has one to 20 spots, each consisting of three to four concentric yellow circles with a yellow center. The pattern fades in adults. The yellow plastron has dark lines along the seams. The head is olive green with yellow-orange markings. Usually a distinctly j-shaped mark lies posterior to each orbit, with the hook extending posteriorly. Three to 16 temporal stripes enter the orbit. The lower part of head and neck are patterned with yellow flecks.

Distribution.—*Graptemys versa* occurs in the Colorado River drainage, primarily on the Edwards Plateau of westcentral Texas (map in Vogt, 1981*c*).

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APPENDIX

Specimens examined. Asterisk denotes skeletal specimens, others are fluid preserved. See Acknowledgments for identifications of museum acronyms.

Graptemys caglei.—TEXAS: *DeWitt Co.,* Guadalupe River, TNHC 34067, 36055–36056, 36058, 36061–36065, 36068–36070, 36075–36083, 36085–36087, 36089–36091, 36094–36096, 36098–36102, 36622–36626, 36629; MCZ 16767; CM 61699–61701. *Gonzales Co.,* no specific locality, TNHC 36054. *Kerr Co.,* no specific locality, TNHC 34022–34023.

Graptemys geographica.—MISSOURI: no specific locality, MPM 6120–6130, 6132. WISCONSIN: *Vernon Co.,* Stoddard, Mississippi River, UWZM 21807–21816, 21953, 21955, 21958, 23315*–23321*, 23329*.

Graptemys ouachitensis ouachitensis.—ALABAMA: Wheeler Reservoir, Tennessee River, USNM 118143–118144. ARKANSAS: *Benton Co.*, White River, NLU 607, 609, 615, 627, 629. *Desha Co.*, White River, near mouth, FMNH 15677; White River, near Mississippi River, FMNH 15718, 15721–15722. *Drew Co.*, Sale River, near Monticello, NLU 21458. *Garland Co.*, Pearcy, 15 mi from Hot Springs, UIMNH 28858. *Jefferson Co.*, Arkansas River at Pine Bluff Arsenal, CM 23995; USNM 55532. *Lawrence Co.*, Black River, TU 14610(19), 15154*–15159*; Powhatan, FMNH 15243–15244, 15247, 92127, 92129; MCZ 1725, 29087; Black River, 1.5 mi SW Black Rock, FMNH 73295–73297. *Marion Co.*, White River near Cotter, TU 14597. *Monroe Co.*, White River at Clarendon, TU 16854(30), 17109, 17111–17113; Indiana Bay Ferry, CM 24600. *Prairie Co.*, DeVall's Bluff, KU 3806; CM 61728–61740, 61963–61975; UWZM 22022, 22029. *Saline Co.*, Benton, Saline River, USNM 17818–17819, 20958. *Union Co.*, Ouachita River, 12 mi E Strong, TU 16849, 17110. *Yell Co.*, Petit Jean Creek, 10 m W Casa, TU 14566(7), 14568. ILLINOIS: *Calhoun Co.*, Golden Eagle, INHS 7375. *Cass Co.*, Lake Meredosia, CM 107660. *Cumberland Co.*, Greenup, INHS 1964. *DeKalb Co.*, 2 mi W Sandwich, INHS 9326. *Jersey Co.*, Mississippi River, 2 mi N Grafton, UIMNH 1123; 7 mi W Grafton, INHS 1762, 2161–2162. *Madison Co.*, Alton, N side of Mississippi River, FMNH 3464–3465. *Mason Co.*, Havana, SMBU 3104; UIMNH 55; FMNH 95, 475; Illinois River at Havana, FMNH 331. *Massac Co.*, NE edge Leon Lake, UIMNH 56449. *Morgan Co.*, Meredosia, UIMNH 2310; INHS 2131, 2134–2137, 5147–5148. *Pope Co.*, Ohio River, 2 mi S Golconda, CM 107604. *Randolph Co.*, 1 mi W Reilly Lake, INHS 9351. *Shelby Co.*, Shelbyville, INHS 2358. *Wabash Co.*, Mt. Carmel, USNM 10325, 12070, 12795(2), 12795(3). *White Co.*, 9 m SE Crossville, INHS 7170. *Whiteside Co.*, Thompson, CM 107662–107664. INDIANA: *Bartholomew Co.*, E Fork White River at Azalia, CM 65583*, 87546*, 87567*. *Gibson Co.*, Tool Pond, UMMZ 89742. *Knox Co.*, Wheatland, USNM 14669; Vincennes, USNM 22718–22719. *Owen Co.*, 4 mi SW Spencer, UMMZ 111876. *Posey Co.*, 2 mi S New Harmony, INHS 7435–7440. *Vigo Co.*, no specific locality, MCZ 16471. IOWA: *Allamakee Co.*, 1¼–3 mi NNE Lansing, UMMZ 92693, 92695–92696; Mississippi River, 1.2 mi W DeSoto, Wis., UMMZ 92589, 92689–92692. *Clayton Co.*, Clayton, Mississippi River, UMMZ 119504. *Jackson Co.*, no specific locality, UMMZ 86650; Bellevue, UMMZ 72553, 72555. *Lee Co.*, Keokuk, USNM 55259. *Muscatine Co.*, Fairport, USNM 60052–60053. KANSAS: *Cowley Co.*, Winfield, USNM 88800. *Geary Co.*, Republican River, USNM 261. *Montgomery Co.*, Verdigris River, KU 3297–3299. *Woodson Co.*, 2 mi E of Neosho Falls, KU 48251–48257. KENTUCKY: *Trigg Co.*, Sector 6J, Lake Dove, APSU 217(a), 217(b); Sector 8H, APSU 832; 1.6 mi SW 6J4 Lake Shore, APSU 911; S Redd Hollow, APSU 220, 223. LOUISIANA: south central Louisiana, TU 7693. *Bossier Par.*, Curtis, TU 6352. *Bossier/Caddo Par.*, Red River, NLU 9183, 9187, 9368–9373, 20579–20580. *Caddo Par.*, Caddo Lake, TU 7658; Gayle, 1 mi W Red River, CM 4269. *Catahoula Par.*, Ouachita River, 4 mi N Harrisonburg, TU 12535–12536, 12537*, 12545, 12615, 12631, 12651, 12655, 12658, 12664, 12666, 12670, 12695, 12701, 12705, 12707, 12710, 12783, 12968.9, 12975 (paratypes); UMMZ 104320, 104345–104351; 4 mi E Harrisonburg, USNM 139733. *Iberville Par.*, Bayou Pigeon, TU 12131. *Natchitoches Par.*, Vic. of Natchitoches, FWM 3662; Red River at Grande Ecore, CM 62160; 4 mi N Natchitoches, CM 62161. *Orleans Par.*, New Orleans, USNM 69595. *Ouachita Par.*, Monroe, TU 5870, 5872; N Monroe, Monroe Fish Hatchery, CM 39938; NLU 820, 847, 1010–1011, 1122–1125; Ouachita River, Monroe, MAZG 1470; 15 mi SW Monroe, NLU 810–812; Ouachita Bayou, NLU 1517; Ouachita River at Fondale, NLU 31464. *Red River Par.*, Red River at Coushatta, MAZG 1460. *St. Charles Par.*, pond near Mississippi River, USL 1197. *St. Landry Par.*, Bayou Teche in Arnaudville, USL 16373. *St. Martin Par.*, 1 mi S I-10 bridge, Atchafalaya River, USL 22335. MINNESOTA: *Wabasha Co.*, Wabasha, USNM 81992. MISSISSIPPI: *Adams Co.*, Mississippi R., 3 mi S International Paper Co., Natchez, NLU 35939. OHIO: *Franklin Co.*, Columbus, USNM 131884. OKLAHOMA: *Bryan Co.*, Washita Arm of Lake Texoma, UIMNH 20060. *Choctaw Co.*, Red River, opposite Arthur City, Texas, KU 128995. *Comanche Co.*, Ft. Sill, Medicine Creek, AMNH 65522. *Johnston Co.*, FMNH 15469. *Kay Co.*, E Ponca City, UMMZ 89625a–89625b. *Le Flore Co.*, 6.5 mi W Heavener, UOMZ 15708; Poteau Reservoir Stilling Basin, UOMZ 27419. *Marshall Co.*, Lake Texoma, 2 mi E Willis, KU 40168*–40169*, 40170–40171, 40172*, 40173–40174; FWM 3549–3552, 4777–4779, 5457–5459; TU 14503(14), 16661.1, 17300(2); UOMZ 26911–26912, 27129–27130, 27153, 27157, 27175, 27326–27329, 27388, 27551–27554, 27565, 27567–27568, 27573–27576, 27584–27592, 33328–33331. *McCurtain Co.*, no specific locality, UOMZ 2137; 2 mi SW Smithville, UOMZ 17137–17138; Mt. Fork River, Beaver's Bend State Park, FWM 3705; Glover River, 9 mi N Wright City, "Big Rock," CM 61741–61746; Beaver's Bend, TNHC 34020, 34034–34039. TENNESSEE: *Decatur Co.*, near Parsons, TU 14497(4). *Lake Co.*, Mississippi River, 4 mi NW Tiptonville, KU 1769, CM 107736; 3 mi W, 3 mi N Tiptonville, CM 107624, 107641. *Obion Co.*, Reelfoot Lake, UMMZ 99230; KU 88750, 88752–88757. *Perry Co.*, Buffalo River, 3.5 mi N Lobelville, TU 16048; Tennessee River between Saltillo and Dunville, TU 16937(3). TEXAS: *Grayson Co.*, Rocky Pt., Lake Texoma, USNM 20038, UIMNH 20058–20059; "Red River," USNM 69544. WEST VIRGINIA: *Wirt Co.*, Little

Kanawha River, mouth of Reedy Cr., near Palestine, CM 31245–31246, 32063, 35142. WISCONSIN: *Buffalo Co.*, approximately 12 mi above Winona, Minn., Mississippi River, CM 28807. *Columbia Co.*, Wisconsin River, T13NR8W, Sec 32, RCV 73-111-73-112. *Grant Co.*, Millville, Wisconsin River, UWZM 21930; T8NR2W, Sec 1, NE ¼ mi, RCV 73-101; T8NR1W, Sec 6, NE ¼ mi, RCV 73-102; T6NR6W, Sec 1, RCV 73-119; Mississippi River, 7 mi S Potosi, UMMZ 72508. *Iowa Co.*, Wisconsin River, T8WR2E, Sec 5, RCV 73-103; T8WR3E, Sec 19, RCV 73-104–73-105; T8NR1E, Sec 6, RCV 73-106, 73-108; T8NR3E, Sec 17, RCV 73-107; T8NR3E, Sec 19, RCV 73-109–73-110, 73-120–73-121. *Trempealeau Co.*, Mississippi River, Perrot State Park, T18NR9W, Sec 28, RCV 73-114; Fountain City, CM 107668. *Vernon Co.*, Stoddard, Mississippi River, UWZM 21212, 21296–21316, 21331–21347, 21361–21366, 21378, 21388–21390, 21403–21428, 21431, 21437–21438, 21466–21479, 21510–21515, 21532–21550, 21558–21573, 21583–21587, 21590–21593, 21601–21660, 21666–21678, 21682–21684, 21706–21721, 21732–21735, 21754–21761, 21770–21806, 21817–21856, 21867–21885, 21901–21929, 21931–21939, 21953–21954, 21957, 21959–21960, 21962, 22041–22053, 22055–22062, 22126–22127, 22129–22130, 22133–22139, 22141–22142, 22153–22160, 22179–22180, 22182–22184, 22189, 22192–22194, 22219–22220, 22224–22229, 22241–22252, 22978*, 23000*–23001*, 23009*, 23017*, 23019*–23021*, 23024*, 23029*–23030*, 23038*–23040*, 23044*, 23049*, 23193*–23197*, 23199*–23200*, 23222*–23225*, 23322*–23323*, 23325*–23328*.

Graptemys ouachitensis sabinensis.—LOUISIANA: *Allen Par.*, Calcasieu River, 3 mi W Kinder, TU 15953(.1–.14); Calcasieu River, 4 mi W Oberlin, TU 3473; Whiskey Chitto Creek between 6 Mile Creek & Hwy 26, USL 23706, 23708. *Beauregard Par.*, Merryville, Sabine River, TU 16840(14); UWZM 22022. *Sabine Par.*, 8 mi SW Negreet, TU 13109–13111, 13116, 13118–13122, 13127–13129, 13131–13150, 13152–13160, 13164, 13166–13175, 13177–13179, 13181–13190, 13192, 13194–13209, 13225–13226, 13510(2), 13760(14); UMMZ 104351–104369; FMNH 73307; USNM 134312; Sabine River at Many, TU 13564(3); TNHC 31359; Sabine River, NLU 1513–1516, 17828; Sabine River Drainage, NLU 28462–28463, 28465–28466. *Vernon Par.*, Sabine River, 1 mi N Toledo Bend Dam, NLU 8139. TEXAS: *Newton Co.*, Bonweir, CM 107771–107773. *Shelby Co.*, Sabine River, Sabine National Forest, E Hamilton Scenic Area, FWM 3565.

Graptemys pseudogeographica pseudogeographica.—ILLINOIS: *Cass Co.*, Meredosia Lake, Honey Pt., CM 107667. *McHenry Co.*, no specific locality, FMNH 2670, 2670a–2670b. *Morgan Co.*, Meredosia, INHS 2130, 2132, 5149–5150. INDIANA: "Grand Chain," MCZ 16486. *Gibson Co.*, Tool Pond, UMMZ 89741, 89743, 92588. *Posey Co.*, 2 mi S New Harmony, INHS 7441–7442. *St. Joseph Co.*, South Bend, Bowman Creek, USNM 194611. *Vigo Co.*, no specific locality, MCZ 16470; Terre Haute, USNM 79. IOWA: *Allamakee Co.*, 6 mi N Lansing, UMMZ 92694. *Des Moines Co.*, Burlington, MCZ 1726. *Jackson Co.*, Bellevue, UMMZ 72552, 72554. *Johnson Co.*, Iowa City, USNM 25394. *Mills Co.*, Mary's Bend, UMMZ 92697–92698. *Muscatine Co.*, no specific locality, TU 1714; 5½ mi SE Muscatine, INHS 7676–7680. KANSAS: *Leavenworth Co.*, Ft. Leavenworth, KU 21532. MINNESOTA: *Brown Co.*, 7 mi W New Ulm, JFBM 1320, 1322, 1354–1355. MISSOURI: *Holt Co.*, no specific locality, KU 88736, 88750. *Lewis Co.*, no specific locality, KU 88735. *Marion Co.*, no specific locality, USNM 19; KU 88747–88748. NEBRASKA: *Boyd Co.*, 5 mi N, 5 mi E Lynch, Missouri River, UN 7117. *Cedar Co.*, 2 mi E St. Helena, SD 2828; Missouri River at Yankton Bridge, UN 6633–6637. *Dakota Co.*, Sioux City, Missouri River, UN 6638. *Dixon Co.*, 1–3 mi W Vermillion (South Dakota), UN 6617–6632. *Richardson Co.*, Missouri River, Falls City, USNM 138872, 153779. *Washington Co.*, 1½ mi E Blair, Missouri River, UN 6639. NORTH DAKOTA: *Sioux Co.*, 4 mi N Ft. Yates, SD 2883. OHIO: "Maumee River," MCZ 1727. *Franklin Co.*, Columbus, USNM 7751. SOUTH DAKOTA: *Bonhomme Co.*, Sand Islands of Charles Creek, SD 1659. *Corson Co.*, ND–SD line, SD 2880, 2882. *Charles Mix Co.*, Platte Creek, SD 2345. *Clay Co.*, 2 mi S Vermillion, SD 41, 2855, 3057–3059. *Gregory Co.*, base of Ft. Randall Dam, SD 2862. *McLean Co.*, ½ mi S Big Bend Dam, SD 2860. *Union Co.*, McCook Lake, SD (Bohan #1); 3 mi SW Elk Pt., SD 12; Missouri River, SD 1534. *Yankton Co.*, below Gavins Pt. Dam, SD 1520. WISCONSIN: *Grant Co.*, Wisconsin River, T6NR5W, Sec 7, SW¼, RCV 73-100; T6NR6W, Sec 1, RCV 73-118. *Polk Co.*, Interstate Park, Lake of the Delles, T34NR19W, Sec 36, RCV 73-117. *Portage Co.*, Wisconsin River, 5 mi W Plover, T25NR7E, Sec 16, RCV 73-113. *St. Croix Co.*, Hudson, UMMZ 72505; St. Croix River, 1 mi N Hudson, JFBM 1089; St. Croix River, 1.2 mi N Somerset, T31NR19W, Sec 7, RCV 73-115–73-116. *Trempealeau Co.*, Fountain City, Mississippi River, CM 107661. *Vernon Co.*, Stoddard, Mississippi River, UWZM 21198–21203, 21317–21330, 21336–21343, 21348–21360, 21367–21377, 21379–21387, 21391–21402, 21415–21417, 21425–21426, 21429–21436, 21439–21465, 21480–21509, 21516–21531, 21551–21557, 21574–21585, 21588–21589, 21594–21600, 21661–21665, 21679–21681, 21685–21686, 21722–21731, 21736–21753, 21761–21770, 21857–21866, 21871–21881, 21886–21900, 21940–21951, 21956, 21961, 22030–22040, 22124–22125, 22128, 22131–22132, 22140, 22143–22146, 22161–22163, 22181, 22185–22188, 22190, 22195–22198, 22221–22223, 22230–22240, 22980*, 22983*–22984*, 22998*, 23002*, 23006*, 23010*–23011*, 23013*–23014*, 23018*, 23021*, 23023*, 23025*–23027*, 23031*–23032*, 23034*–23035*, 23037*, 23041*–23043*, 23047*, 23324*.

Graptemys p. pseudogeographica × *p. kohni.*—ILLINOIS: "Ohio River," UIMNH 2311. *Adams Co.*, Quincy, MCZ 6395; UIMNH 16773; AMNH 4748–4749, 46480. *Cumberland Co.*, no specific locality, FMNH 37931. *Jackson Co.*, Carbondale, SD 3563; Mississippi River, Sand Island, UMMZ 81571–81575. *Obion Co.*, Dyer Co. line, UMMZ 1938. *Madison Co.*, Alton, N side of Mississippi River, FMNH 3463. *Mason Co.*, Havana, UIMNH 53–54, 56–65, 2307; Metropolis, UIMNH 2308. *Monroe Co.*, Mississippi River, INHS 7916–7918. *Pope Co.*, Ohio River, 2 mi S Golconda, CM 107598–107606. *Randolph Co.*, 3 mi NW Chester, INHS 5009. *St. Clair Co.*, USNM 55534. *Wabash Co.*, Mt. Carmel, USNM 12795(1), 12795(4). *White Co.*, 9 mi SE Crossville, INHS 6790. KANSAS: *Douglas Co.*, 5 mi NW LeCompton, Kansas River, KU 40115; 1 mi N, 1½ mi W Lake View, KU 52290. *Geary Co.*, Republican River, USNM 7610; ANSP 260. KENTUCKY: *Ballard Co.*, 3.5 mi N Bandana, Big Turner's Lake, UIMNH 18004. *Fulton Co.*, 4½ mi S Hickman, USNM 104504. *McCracken Co.*, Paducah, USNM 102903. MISSOURI: *Boone Co.*, no specific locality, KU 88738. *Madison Co.*, no specific locality, KU 88746. *Mississippi Co.*, no specific locality, KU 88749. *St. Clair Co.*, no specific locality, USNM 55533–55534. *St. Louis Co.*, no specific locality, USNM 16494, 55529–55531; St. Louis, UIMNH 1660. TENNESSEE: *Henry Co.*, Paris Landing State Park, APSU 853. *Lake Co.*, Reelfoot Lake, UIMNH 2312; CM 107613, 107616–107617; Reelfoot Lake, 2 mi E Markham, UIMNH 1364; 2½ mi SE Tiptonville, UIMNH 1271–1275, 15791; Mississippi River, 3 mi N Tiptonville, CM 107614–107615, 107618–107623, 107625–107659; 4 mi NW Tiptonville, Mississippi River, CM 107669–107754; Edgewater, TU 16239, 17986. *Obion Co.*, Reelfoot Lake, UMMZ 74212–74220, 74612–74615, 84183, 96607; USNM 100471, 100474, 100478, 102924–102925, 102927–102937, 102939–102944, 102946, 103471; TU 19320. *Stewart Co.*, 1.8 mi S 7 PH, APSU 803; 1.2 mi S 7 RS, APSU 811, 812a–812b.

Graptemys pseudogeographica kohni.—ARKANSAS: "Horseshoe Lake," FMNH 194231. *Chicot Co.*, Lake Chicot, CM 107607–107608. *Dallas Co.*, Faringdale, USNM 95369. *Greene Co.*, Paragould, USNM 95382. *Jackson Co.*, Amagon, CM 23997. *Lawrence Co.*, Black River, Powhatan, UMMZ 91386; FMNH 15241–15242, 15248–15249, 92130–92135; Black River, TU 14611*, 15678*. *Monroe Co.*, White River at Clarendon, TU 16886(7). *Prairie Co.*, DeVall's Bluff, White River, KU 1181*, 1871*, 2463*–2464*, 2466*, 2667*–2669*, 2671*, 2679*, 2750*, 2804*, 2808*–2810*, 3107A–3107B, 3108, 3110–3112, 3232–3240, 3254, 3340–3341, 3343, 3344A–3344B, 3345, 3356, 3360, 3371, 3373–3413, 3416–3425, 3780, 3791, 3795–3798, 3800–3805, 3807–3826; CM 60401, 61708–61713, 61715–61725; UWZM 22008. *Pulaski Co.*, Lake 5 mi E North Little Rock, CM 24616–24620, 25148. *St. Francis Co.*, 5.5 mi W Forrest City, U.S. 70, CM 25067, 25072. *Union Co.*, Ouachita River, 12 mi E Strong, TU 16843(6). *Yell Co.*, Petit Jean Creek, 10 mi W Carson, TU 14567(17). KANSAS: *Coffey Co.*, Neosho River, KU 3287–3288. *Osage Co.*, Lang Creek, KU 3164. *Wilson Co.*, 1 mi S Altoona, Verdigris River, KU 3257, 46746. LOUISIANA: "South Central Mississippi Valley," TU 1348(60), 6318. *Acadia Par.*, Rayne, USL 324-3. *Bossier/Caddo Par.*, Red River, 11 mi N Bossier City, NEI 9185. *Caddo Par.*, Caddo Lake, TU 405, 416, 491–494, 496–498, 500, 635–636, 643–645(2), 684–687, 698–699, 1240, 5014, 7603–7604, 7607, 7610, 7616, 7629, 7656, 7667, 7675, 7691; Gayle, 1 mi W Red River, CM 4252–4268, 4270–4271; FMNH 8010. *Catahoula Par.*, Jonesville, TU 7533(7); Wells Lake, N Jonesville, NLU 1634; Ouachita River, 4 mi W Harrisonburg, TU 12538, 12541, 12543, 12627, 12630, 12632, 12635–12636, 12641, 12647, 12653, 12659–12660, 12662–12663, 12668, 12673–12674, 12685, 12689–12690, 12692–12694, 12698–12700, 12748, 12782, 12784, 12786, 12975, 13001, 13527(3), 16894. *Claiborne Par.*, Corney Lake, Summerfield, TU 1366. *Concordia Par.*, Deer Park, CM 107611–107612; Shaw, TU 7080, 7118, 7121, 7125, 7148, 7151, 7156–7158, 7163–7164, 7187, 7201, 7204–7205, 7218, 7222, 7235, 7246–7247, 7259, 7266, 7268–7269, 16063(22); 1–4 mi N Natchez (MS), Mississippi River, NEI 8905–8907, 8912; Riflepoint, near Natchez (MS), UMMZ 76488; Red River, Shaw, USNM 99887–99890. *DeSoto Par.*, Wallace Bayou, SMBU 2367–2368, 2372, 2376–2378, 2380–2383, 2387–2389, 2438–2441, 7753, 7760, 7767. *Franklin Par.*, Bayou Pigeon, TU 11874; Wisner, TU 7541(5), 7564(2); Turkey Cr., Winnsboro, NLU 1625–1626. *Iberville Par.*, no specific locality, TU 12121*, 16324*; Mississippi River, 2 mi N Plaquemine, CM 62151; Plaquemine, USNM 100242–100250, 100254, 100258–100263, 100265–100274, 100276–100283, 100475, 100477–100479. *Lafayette Par.*, Bayou Pkwy., USL 10640. *LaFourche Par.*, Thibodaux, CM 7518. *Morehouse Par.*, Horseshoe Lake at Oak Ridge, NLU 29172–29191. *Natchitoches Par.*, Bayou SW Natchitoches off Cane River, UIMNH 91076; Natchitoches, CM 62153; Red River at Grand Ecore, CM 62160; 4 mi W of Natchitoches, CM 62161; Cane River, CM 62152. *Orleans Par.*, New Orleans, TU 17252. *Ouachita Par.*, Monroe, TU 5869, 5871; Bayou DeSiard at Hwy 165, CM 44427–44429; 15 mi S Monroe, CM 39949; Bayou DeSiard at Webster St., CM 39950, 39951a–39951h; Bayou DeSiard at Monroe, MAZG 1456–1457, 1462, 1469; Ouachita River, 15 mi SE Monroe, MAZG 1465; Wall Lake, 9 mi E Monroe, MAZG 1455, 1458, 1463, 1466; Bayou DeSiard, NEI 8424; NLU 4971–4979; Moon Lake, Ouachita River oxbow, 3 mi W Monroe, NLU 8255; 4.8 mi N Monroe on Hwy 165, NLU 21352–21355; Monroe Fish Hatchery, NLU 4964–4965, 4986; LWFC office, W Monroe on US 65, NLU 21668; Hwy 553, 5.5 mi W of Hwy 165, NLU 22503; Hwy 553 between

Hwy 153 & Hwy 134, NLU 23263. *Pointe Coupee Par.*, False River, New Roads, USNM 100217–100219. *Richland Par.*, Kayville, USNM 100472, 100476; Brown Minnow Farm, NLU 1663; Bayou Fisheries at Archibald, NLU 4131, 4169. *Sabine Par.*, 8 mi NW Negreet, TU 13112–13114, 13117, 13123–13126, 13136, 13138, 13151, 13165, 13176, 13180, 13191, 13193, 13742(14), 13760(8). *St. Charles Par.*, no specific locality, TU 10237*. *St. James Par.*, Vacherie, TU 10235, 12074–12075. *St. Landry Par.*, Bayou Courtableau, USL 24027, 24030–24032; Courtableau Bayou, 11 mi N Butte LaRose, Exit I-10, USL 23557; Bayou Teche in Arnaudville, USL 16320–16321, 16332, 19222–19226; 2 mi W Krotz Springs, USL (uncatalogued); 3.5 mi N Three Mile Lake, USL 23296. *St. Martin Par.*, 8 mi E Henderson along Butte LaRose Canal, NLU 29541; Henderson Swamp, USL 7113; Henderson Lake, Butte LaRose Canal, USL 14171, 14382–14383, 22518; 7.1 mi S Henderson, USL 21156; 1 mi W Butte LaRose, USL 22273; Little Alabama Bayou, USL 24109–24110. *St. Mary Par.*, Morgan City, UMMZ 76447. *Tangipahoa Par.*, Ponchatoula, FMNH 22897. *Tensas Par.*, Tensas River, TU 11877, 11901(8). *Union Par.*, Ouachita River, USNM 138945; D'Arbonne Bayou, below Dam, NLU 7726–7728, 7736, 7747, 7749–7755, 17287; NEI 7728; Camp Creek at Hwy 15, NLU 20858; Bayou Bartholomew, TU 12844, 12847–12851, 12868(6), 12968(16), 13039. *Webster Par.*, Minden, AMNH 42330–42332. MISSISSIPPI: *Adams Co.*, Washington, MCZ 1728–1729; Natchez, MCZ 1730–1732, 46560. *Bolivar Co.*, Deeson, TU 19312–19315. *Humphrey Co.*, Wasp Lake, Belzoni, USNM 102704. *LeFlore Co.*, Greenwood, USNM 73670–73672. *Sunflower Co.*, Indianola, Lake Macon, USNM 102702; Shakelford, USNM 102703. *Washington Co.*, Lake Washington, UMMZ 77705, 77706a–77706f; Leroy Percy State Park, CM 107609–107610. *Yazoo Co.*, Panther Creek, W Yazoo City, UMMZ 86666–86667, 86671–86673; Yazoo River, USNM 95136–95137. *Yazoo/Madison Co.*, Big Black River on Hwy 29, TU 14581(10). MISSOURI: *McDonald Co.*, no specific locality, KU 88745. OKLAHOMA: *Cherokee Co.*, no specific locality, TU 13866*; Illinois River, between Hanging Rock and Echota Access Area, CM 61726–61727. *Le Flore Co.*, Wister, CM R3062; 6 mi S Wister, UOMZ 1638, 2138, 2540k; 1.5 mi E Zoe, UOMZ 15853, 16800. *McCurtain Co.*, Glover River, 9 mi N Wright City, "Big Rock," CM 61714, 61962; UOMZ 2139, 2142; Beaver's Bend State Park, UOMZ 29290; TNHC 34021. *Okmulgee Co.*, no specific locality, UOMZ 12415. TEXAS: "Red River," USNM 69545. *Anderson Co.*, Trinity River, USNM 17692–17695. *Brazos Co.*, Wickson Lake, TCWC 688, 690. *Cass Co.*, 5.6 mi E Linden, SMBU 16297. *Grayson Co.*, Lake Texoma, TCWC 7270. *Grimes Co.*, Navasota River, 2 mi SE Junction, FMNH 1179, 2038; TCWC 21412; Navasota River at Sulphur Springs, TCWC 23538; Navasota, 16 mi SE College Station, UIMNH 20199. *Hardin Co.*, 2 mi NE Saratoga, UIMNH 1276. *Harrison Co.*, Lake Caddo, AMNH 16967, 16984. *Henderson Co.*, Chandler, USNM 95401. *Lamar Co.*, Arthur, FMNH 460a–460c. *Leon Co.*, Clear Lake, 16 mi S Oakwood, SMBU 6694–6696. *Liberty Co.*, Big Creek near junction with Trinity River, TU 14370, 14393, 14400. *Madison Co.*, Twin Lakes, TCWC 519–520. *Newton Co.*, Bonweir, EOM 1853. *Orange Co.*, 10 mi N Orange, SMBU 13248. *Robertson Co.*, Oak Creek, Hwy 66, 3.4 mi N Ridge, TCWC 689, 30784–30785. *Shackelford Co.*, Clear Fork Brazos River, Ft. Griffin State Park, TU 14544*. *Shelby Co.*, Sabine River, 31.7 mi NW Joaquin, TU 14357. *Walker Co.*, 14.1 mi W Huntsville, TU 14354.

Graptemys versa.—TEXAS: "Colorado River," TU 14484.3*, 16190*. *Burnet Co.*, Morgan Creek, SMBU 7814. *Coleman Co.*, 20 mi S Valera, SMBU 10609–10619. *Edwards Co.*, 3 mi SW 700 Springs, FMNH 92145. *Kimble Co.*, S Llano River, SW Junction, SMBU 2112; 3 mi SE Telegraph at Paint Rock Ranch, SMBU 5074–5099, 5101–5102. *McCulloch Co.*, 3 mi SW Leaday, SMBU 3344, 5103–5104, 5106–5115, 5700. *Menard Co.*, San Saba River, 3 mi E Menard, SMBU 89410. *San Saba Co.*, 6 mi W Beaver, Royal Creek, FMNH 55556–55557, 55561; Rough Creek, 7.5 mi SE San Saba, FWM 2642; 4 mi NW Bend, FWM 3564; 11 mi NW Bend, FWM 5477; 5 mi SW Algerita, FWM 6909. *Travis Co.*, Austin, MCZ 42346; USNM 27473–27479.