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REVIEW OF THE *GRAPTEMYS PULCHRA* GROUP (REPTILIA: TESTUDINES: EMYDIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES

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Abstract

The *Graptemys pulchra* species group, which includes *G. pulchra* sensu lato and *G. barbouri,* is defined by the combination of large female size, extreme sexual dimorphism, head pattern with large interorbital and postorbital blotches, enlarged heads and hypertrophied jaws in females, presence of salient vertebral spines, and possibly, a diploid chromosome number of 52. *Graptemys ernsti,* n. sp. is described from the Pensacola Bay drainage, Florida and Alabama, and *Graptemys gibbonsi,* n. sp. from the Pascagoula River and Pearl River drainages, Mississippi and Louisiana. A speciation hypothesis for the group, based on successive isolation and contact of drainages due to sea level changes, agrees with data for freshwater fishes of the region.

Introduction

The North American turtle genus *Graptemys* is the most speciose in the family Emydidae. The genus is confined to the United States and Canada, and as currently recognized comprises 11 species (Ernst and Barbour, 1989). This group of turtles is characterized not only by great diversity, but also by a controversial taxonomic relationship with the genus *Malaclemys* (McDowell, 1964; Wood, 1977; Dobie, 1981). Moreover, there have been numerous recent changes in alpha taxonomy of the genus, with six species previously described in the 20th century. The diversity within the genus results in part from drainage-specific endemism, with six currently recognized species restricted to single drainage systems. The remaining species, except for *G. pulchra* and *G. geographica,* occur only in the Mississippi watershed. *Graptemys geographica* occurs in the Mississippi system, and in the Saint Lawrence, Hudson, Susquehanna, and Delaware rivers (McCoy and Vogt, 1990; Iverson, 1992). The center of diversity for the genus is along the coast of the Gulf of Mexico, from the Apalachicola River, western Florida, to the Guadalupe River, Texas.

Two species groups can be recognized among the *Graptemys* that occur in Gulf coastal rivers east of the Mississippi River. The "sawbacks" (*G. oculifera, G. flavimaculata,* and *G. nigrinoda*) are medium-sized *Graptemys* with narrow heads and hypertrophied vertebral spines. The second group of Gulf Coast species, which includes *Graptemys pulchra* (sensu lato) and *G. barbouri,* we here designate the *Graptemys pulchra* species group. This group was informally recognized by Cagle (1952), McKown (1972), Mount (1975), and Dobie (1981). The *Graptemys pulchra* group is defined by the following combination of characters, which distinguishes

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them from other species of *Graptemys*: (1) female size large (295–330 mm maximum carapace length); (2) sexual dimorphism extreme, adult SDI (sexual dimorphism index, size of larger sex divided by size of smaller sex, Gibbons and Lovich, 1990) 2.42–2.58; (3) head (especially in adult females) broad, with alveolar surfaces of jaws greatly expanded; (4) head pattern consisting of an interorbital and large postorbital blotches; (5) vertebral scutes with salient spines; and possibly, (6) diploid chromosome number 52 (McKown, 1972).

In size only *Graptemys geographica,* which reaches a maximum carapace length of 273 mm (McCoy and Vogt, 1990), approaches members of the *G. pulchra* group. All other species of *Graptemys* are smaller. Sexual dimorphism is less extreme in other species of *Graptemys.* In *Graptemys geographica,* SDI reaches a maximum of 1.97; in other species, it is between 1.50 and 2.10 (Gibbons and Lovich, 1990). Enlarged heads and expanded alveolar surfaces are also found in *Graptemys geographica* and *G. kohni,* but in those species the trait is not as extreme as in species of the *G. pulchra* group. Old females of both *G. pulchra* and *G. barbouri* have grotesquely enlarged heads and massive jaws (Cagle, 1952). The head pattern of *G. pulchra* and *G. barbouri,* in particular the presence of an interorbital blotch, is unique in the genus. All other species have head patterns that include a combination of lines and smaller spots. The salient vertebral spines of *G. pulchra* and *G. barbouri* distinguish those species from *G. geographica* and *G. versa* which lack them. Finally, all other species of the genus *Graptemys* have a diploid chromosome number of 50 (McKown, 1972). However, the chromosome number of 52 reported by McKown (1972) for *G. pulchra* and *G. barbouri* was not confirmed (in *G. barbouri* only) by Killebrew (1977), suggesting the need for further study.

The Alabama map turtle, *Graptemys pulchra* (sensu lato), is found in four major drainage systems that include the Pearl River, the Pascagoula River, rivers draining into Mobile Bay, and rivers entering Pensacola Bay (Lovich, 1985). Barbour's map turtle (*Graptemys barbouri*) occurs in the Chipola, Chattahoochee, Apalachicola and Flint rivers in Alabama, Florida, and Georgia. During the Pleistocene, the range of *G. barbouri* may have extended east to the Santa Fe River, Florida (Jackson, 1975; Sanderson and Lovich, 1988).

Graptemys pulchra was described by Baur (1893) from specimens collected near Montgomery, Alabama (Lovich, 1985). For many years the species was ignored, and the name *pulchra* was omitted from checklists and other compilations. Cagle (1952) rediscovered *G. pulchra,* redescribed the species, and defined its geographic range. Although no subspecies have been recognized, several researchers have pointed out that the species is composed of well-defined variants, each confined to a separate river system. Shealy (1976) summarized geographic variation as follows: specimens from the Mobile Bay system are characterized as much "flatter" than the other variants, the Pascagoula River form has more light pigmentation on the head and marginals than specimens from the Escambia River, and specimens from the Pearl River are intermediate in coloration between Pascagoula and Escambia forms, resembling the Escambia form most closely. Cagle (1952) noted that lower jaw markings differ between Pearl and Escambia River females, and Mount (1975) reported consistent variation in head and shell patterns among drainages. Others have reported differences in the relationships of various scutes among drainages (Tinkle, 1962; Little, 1973).

Although the existence of geographic variation has been documented, there has been no quantitative study of variation in *G. pulchra.* Our objective was to quantify patterns of morphological variation within and between populations of *G. pulchra* (sensu lato). Results were contrasted with and compared to the closely related *G. barbouri* (Cagle, 1952; Sanderson and Lovich, 1988).

MATERIALS AND METHODS

More than 596 live and preserved specimens of the *Graptemys pulchra* group were examined (Appendix 1). Straight-line, greatest length measurements were taken with dial calipers accurate to 0.1 mm for the following characters: carapace length (CL), carapace width between the second and third vertebrals (CW), carapace height from the ventral surface to the point between the second and third vertebrals (CH), plastron length (PL), central seam lengths of the six paired plastral scutes (gular = G, humeral = H, pectoral = P, abdominal = AB, femoral = F, anal = AN), jaw width from angle to angle (JW), length of the postorbital blotch (LPOB) from behind the orbit to its most posteriad extent, length of the right fifth marginal scute along the long axis of the body (MWID), width of yellow pigment on the dorsal surface of the fifth marginal scute (MPIG), and width of dark pigment on the ventral surface of the fifth marginal scute (WLMP). The following pattern variables were also recorded. The presence or absence of supraoccipital spots (SUPOC), or bulbous anterior expansions of the dorsal paramedian neck stripes was noted, as was the presence or absence of subocular spots (SUBOC). Whether postorbital blotches (POB) were connected to the interorbital blotch (IOB) or not was also recorded. A three-pronged, light colored "nasal trident" was present above the nostrils of some specimens and its presence or absence was noted. These variables were selected because preliminary analyses or previously published information suggested their discriminatory power in this group.

Operational taxonomic units (OTU) were established based on major drainage systems, as follows: OTU 1—Pensacola Bay system, including Escambia, Shoal, Conecuh, and Yellow rivers, Alabama and Florida; OTU 2—Mobile Bay system, including Alabama, Tombigbee, Coosa, Tallapoosa, Warrior, Cahaba, and Conasauga rivers, Alabama and Georgia; OTU 3—Pascagoula River system, including Pascagoula, Leaf, and Chickasawhay rivers in Mississippi; and OTU 4—Pearl River system, including the Pearl and Bogue Chitto rivers, Louisiana and Mississippi. Each of these systems enters the Gulf of Mexico separately (Fig. 1).

The relative frequency of categorical variable character states among OTUs was tested for significant departure from expected values using G statistics generated from contingency table analyses. Expected values were calculated under the null hypothesis that character states were independent of OTU. Juveniles of undetermined sex were included in the analyses with identifiable males and females since preliminary studies showed that pattern traits did not vary ontogenetically or between the sexes.

Continuous morphological variables were analyzed separately for males and females because of extreme sexual dimorphism (Lovich, 1985; Sanderson and Lovich, 1988; Gibbons and Lovich, 1990). The sex of specimens was determined on the basis of secondary characteristics including greater preanal tail length in males and greater jaw width in females. These features are apparent even in specimens that are sexually immature, thus, subadults were included with adults in the analyses. Both univariate and multivariate ANOVAs were used to compare variable means among OTUs as suggested by Willig et al. (1986). Following identification of significant differences among OTUs, a four-group discriminant analyis was conducted to classify specimens according to predicted OTU.

The significance of differences identified using discrete and continuous variables was validated using another set of variables based on the relative seam lengths of the six paired plastral scutes (G, H, P, AB, F, AN). Size relationships in these scutes have been demonstrated to vary among taxa (Lovich and Ernst, 1989; Lovich et al., 1991). Following Lovich et al. (1991), we used discriminant function analysis to classify specimens according to OTU, using scute proportions transformed as follows: scute length was divided by PL, and transformed to normality by taking the arcsine square root of the resulting proportion.

Numerous controversial analytical techniques, including the use of ratios, residuals, and analysis of covariance, have been proposed to nullify the effect of size in morphometric analyses (see reviews in Atchley et al., 1976; Packard and Boardman, 1988). Despite impassioned pleas and elegant rationale behind these suggestions, the results of morphometric studies of turtles are often identical, whether based on untransformed, log transformed, ratio, or residual-based data (Lamb, 1983; Lamb and Lovich, 1990; McCord and Iverson, 1991). Univariate and multivariate analyses of our data produced similar results using raw, log transformed, ratio, or residual-based data. Because of this, we used ratios when data presentation was enhanced by the use of proportions, and appropriate transformations when dictated by parametric assumptions. Prior to parametric statistical analysis, non-ratio data were log-transformed to reduce variance (Lewontin, 1966; Moriarty, 1977), and ratio data were arcsine square root-transformed to normality. Statistical analyses were performed using SYSTAT (Wilkinson, 1988) and STATGRAPHICS statistical software.

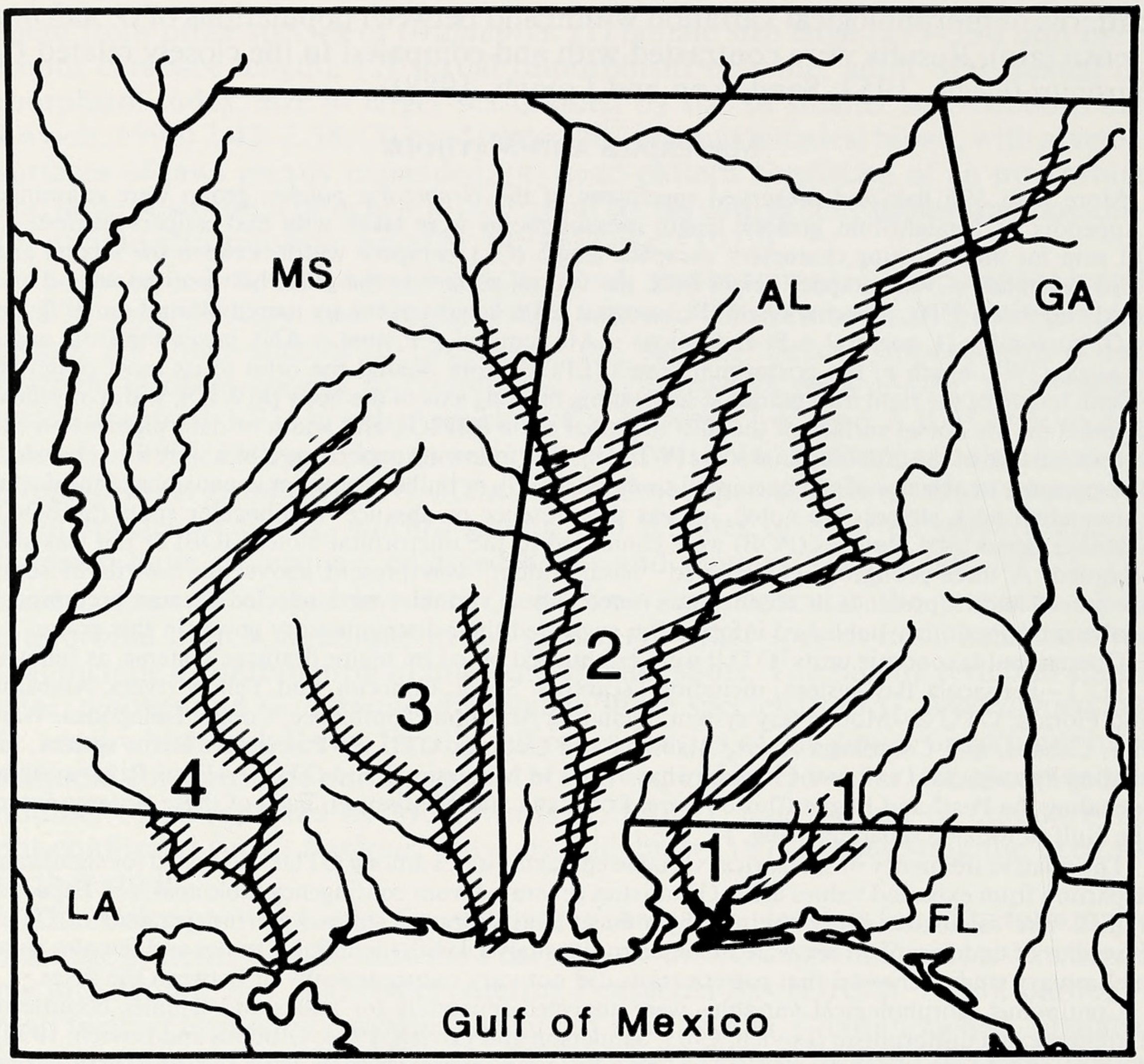

Fig. 1.—Geographic distribution of *Graptemys pulchra* (sensu lato). Operational taxonomic units (OTUs) are as follows: OTU 1 = Escambia–Conecuh River system; 2 = Mobile Bay system; 3 = Pascagoula River system; 4 = Pearl River system.

Results

Pattern characters were relatively constant within OTUs (Table 1). In the majority of specimens (95–97%) from OTUs 2–4 IOB was connected to POB. In contrast, 89 percent of specimens from OTU 1 exhibited no contact between IOB and the POB, and contacts were poorly developed in the remainder of that sample. Contingency table analysis showed that presence of a POB/IOB connection was not independent of OTU ($G = 371.7$, $df = 3$, $P < 0.001$). Approximately 95 percent of specimens from OTU 1 possessed a pair of supraoccipital spots or bulbous anterior expansions of the dorsal paramedian neck stripes. Significantly fewer specimens (2–8%) from OTUs 2–4 possessed this characteristic (Table 1). The results of contingency table analysis rejected the null hypothesis that presence of SUPOC is independent of OTU ($G = 399.7$, $df = 3$, $P < 0.001$). The presence of a nasal trident was also dependent on what OTU a specimen belonged to ($G = 249.7$, $df = 3$, $P < 0.001$). All specimens from OTU 1 exhibited a conspicuous nasal trident, while significantly fewer (11%) in OTU 2 exhibited a nasal trident,

Table 1.—*Frequency of occurrence (percentage) of pattern characters by OTU (sample sizes in parentheses). Refer to text for OTU designations.*

	OTU			
	1	2	3	4
IOB/POB connection	11% (151)	97% (109)	98% (88)	95% (94)
Supraoccipital spot	95% (151)	6% (109)	8% (90)	2% (93)
Nasal trident	100% (129)	11% (105)	66% (82)	79% (81)
Sub-ocular spot	37% (156)	3% (108)	2% (93)	0% (92)

which was often poorly, almost rudimentarily, developed. Most specimens from OTUs 3 (66%) and 4 (79%) possessed a nasal trident, but it was not as sharply defined as that seen in specimens from OTU 1. Few specimens from OTUs 2 and 3, and none from OTU 4, but significantly more (37%) from OTU 1 had a subocular spot beneath each eye. The relative frequency of occurrence varied significantly among OTUs when tested with contingency table analysis ($G = 105.8$, $df = 3$, $P < 0.001$).

Multivariate analysis of variance (MANOVA) demonstrated significant differences between OTUs when no missing value, log transformed data for CW, CH, LPOB, MWID, and WMLP were compared simultaneously for males (Wilk's lambda = 0.055; $F = 24.02$; $df = 15,93$; $P < 0.001$). Univariate ANOVAs were significant at $P < 0.05$ for all variables except CW ($P = 0.186$). MANOVA results for females were also significant (Wilk's lambda = 0.071; $F = 20.38$; $df = 15,190$; $P < 0.001$). Results based on ANOVAs were significant at $P < 0.05$ for all variables. Descriptive statistics for size-scaled derivatives of these variables are summarized in Table 2. The ratio of CH/CL was very similar between OTUs 3 and 4. Compared to OTUs 3 and 4, specimens from OTU 2 were relatively flat, while those from OTU 1 were higher domed. Relative carapace width was similar between OTUs 1 and 2, and between OTUs 3 and 4. The length of the postorbital

Table 2.—*Means and sample sizes (in parentheses) for size-scaled variables by sex and OTU, and for* Graptemys barbouri *(GB). Refer to text for OTU and character designations.*

	OTU				
Variable/sex	1	2	3	4	GB
CH/CL					
Males	0.43 (27)	0.39 (30)	0.41 (28)	0.40 (24)	0.40 (36)
Females	0.44 (49)	0.40 (40)	0.42 (25)	0.42 (21)	0.42 (39)
CW/CL					
Males	0.78 (31)	0.78 (32)	0.76 (44)	0.75 (46)	0.78 (39)
Females	0.77 (55)	0.78 (50)	0.74 (40)	0.74 (46)	0.78 (56)
LPOB/CL					
Males	0.09 (17)	0.08 (28)	0.08 (30)	0.08 (29)	—
Females	0.11 (27)	0.09 (34)	0.09 (29)	0.10 (20)	—
MPIG/MWID					
Males	0.14 (31)	0.10 (31)	0.21 (45)	0.16 (46)	0.09 (34)
Females	0.15 (53)	0.10 (46)	0.21 (40)	0.18 (47)	0.08 (54)
WLMP/MWID					
Males	0.57 (30)	0.74 (33)	0.35 (45)	0.43 (46)	0.66 (38)
Females	0.60 (53)	0.71 (50)	0.37 (40)	0.40 (47)	0.59 (53)

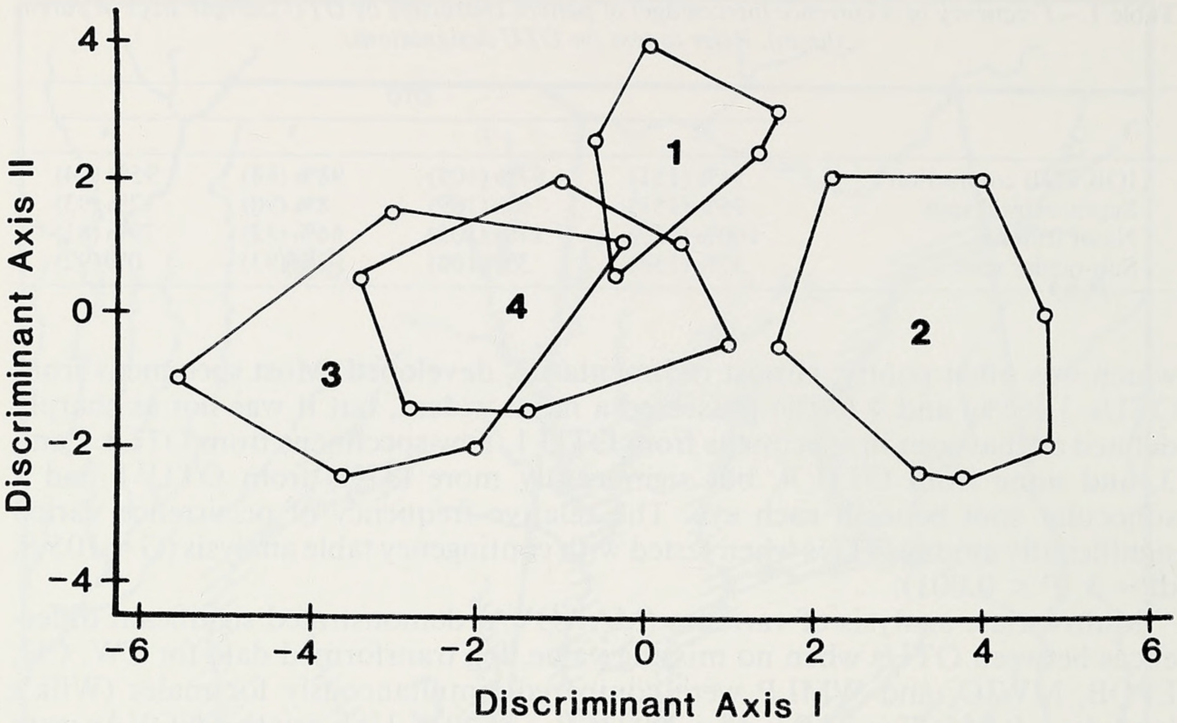

Fig. 2.—Plot of male discriminant scores on the first two canonical axes. Operational taxonomic units (1–4) are the same as in Fig. 1. Refer to text for details.

blotch (LPOB) relative to carapace length was similar in OTUs 2–4, but comparatively greater in OTU 1. The most dramatic differences between OTUs are in comparisons of MPIG and WLMP with MWID. MPIG was very narrow in OTU 2 and wide in all others, particulary OTU 3. In contrast, WLMP was wide

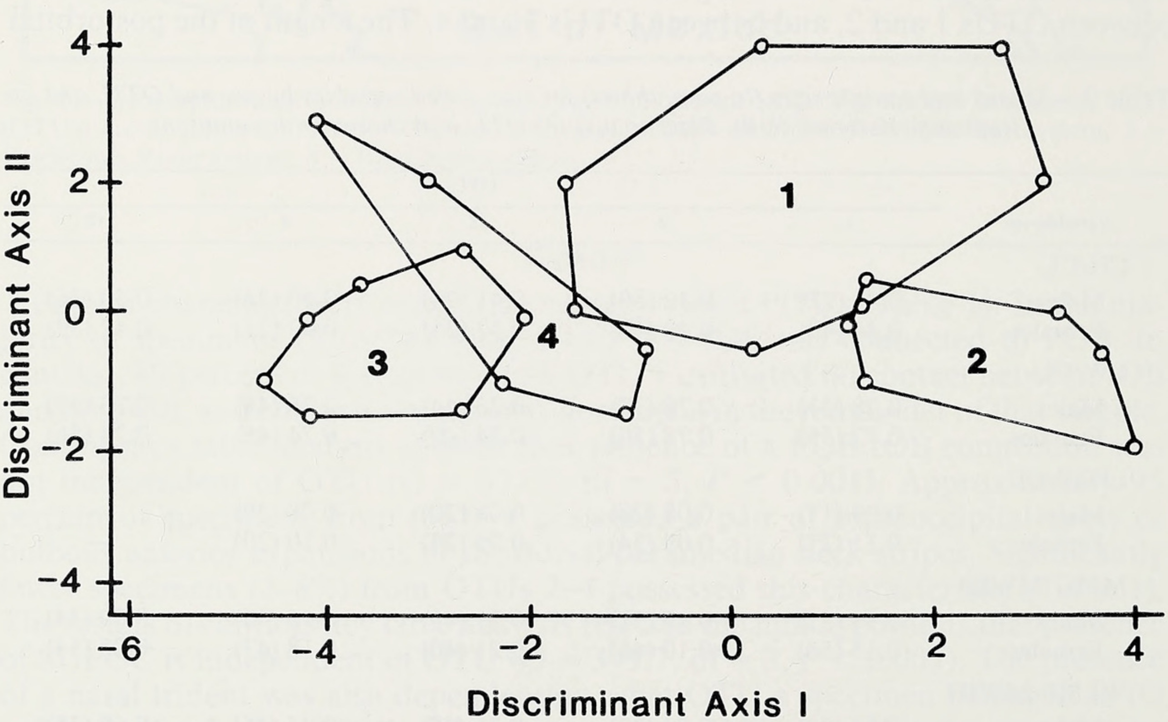

Fig. 3.—Plot of female discriminant scores on the first two canonical axes. Operational taxonomic units (1–4) are the same as in Fig. 1. Refer to text for details.

Table 3.—*Classification accuracy of discriminant function for males, based on transformations of the relative proportions of the six paired plastron scutes (refer to text for details). Rows are actual OTUs and columns are predicted OTUs. Numbers are the number of specimens assigned to each OTU.*

Actual OTU	Predicted OTU 1	2	3/4	GB
1	16	1	3	0
2	2	24	3	0
3/4	8	8	50	5
GB	2	0	2	34

in OTU 2 and narrow in all others, particularly OTU 3. Ratios of MPIG/MWID and WLMP/MWID for *G. barbouri* were most like those of OTUs 1 and 2.

Since the results of MANOVA and ANOVA revealed significant differences between OTUs, sex-specific discriminant function analyses were used to test the classification ability of CH, CW, LPOB, WLMP, and MPIG. Results for males (Fig. 2) and females (Fig. 3) suggest that OTUs 1 and 2 are phenetically distinct, when discriminant scores are projected on the first two canonical axes, while OTUs 3 and 4 overlap. Seventy-eight percent of males in the sample were correctly classified by the discriminant function. Most misclassifications occurred between OTUs 3 and 4 (29%). Ninety-two percent of females in the sample were correctly classified and most misclassifications (50%) occurred between OTUs 3 and 4.

To confirm the significance of results based on analysis of pattern characters and multivariate analysis of mensural variables, a different set of variables was tested. Sex-specific discriminant function analysis was used to classify specimens to OTU based on transformed plastron scute proportions. Because high character overlap was observed in OTUs 3 and 4 in previous analyses, they were combined (OTU 3/4). In addition, data for the closely related species *Graptemys barbouri* were included as a separate OTU (GB) for comparison. MANOVAs comparing all six transformed proportions between the four groups were significant for both sexes ($P < 0.001$). The discriminant function for males correctly classified 78% of specimens examined (Table 3) while that for females (Table 4) correctly classified 70%. Misclassifications were more frequent among OTUs 1–3/4 than between OTUs 1–3/4 and *G. barbouri.* However, the analysis still exhibits significant discriminatory power. Specimens in OTU 3/4 were correctly classified almost as often as *G. barbouri* (86% vs. 87%, respectively, in males). Females in OTU 2 were often misclassified into OTU 3/4, unlike in previous analyses.

The results demonstrate that *Graptemys pulchra* (auctorum) is composed of three distinct taxa, herein designated species (Appendix 2). The type specimens of *Graptemys pulchra* Baur were collected near Montgomery, Alabama, in the

Table 4.—*Classification accuracy of discriminant function for females, based on transformations of the relative proportions of the six paired plastron scutes (refer to text for details and* see *Table 3).*

Actual OTU	Predicted OTU 1	2	3/4	GB
1	23	4	4	3
2	2	19	6	2
3/4	1	13	30	5
GB	8	0	2	46

Table 5.—*Summary of characters that differentiate species of the* Graptemys pulchra *group: GP* = G. pulchra, *GE* = G. ernsti, *GG* = G. gibbonsi, *GB* = G. barbouri. *Presence or absence of a character is coded with a plus or minus sign.*

Character	Species			
	GP	GE	GG	GB
Relative shell height	low	high	high	high
Upper marginal pigmentation				
Width	narrow	wide	wide	narrow
Number of bars	several	several	one	one
Lower marginal pigmentation	extensive	extensive/ intermediate	limited	extensive
Nasal trident	−	+	+/−	−
Interorbital–postorbital spot connection	+	−	+	−
Subocular spots	−	+/−	−	−
Supraoccipital spots	−	+	−	−

Mobile Bay Drainage. Hence we restrict the name *G. pulchra* to populations represented by OTU 2. The allopatric populations in OTUs 1 and 3/4 are described as new species below. The characters that differentiate these taxa are summarized in Table 5.

SYSTEMATICS

Graptemys ernsti, new species
(Fig. 4, 5)

Holotype.—CM 122408; Conecuh River, 1 mile upstream from County Road 4 Bridge, 14 km east of East Brewton, Escambia County, Alabama, USA; Jeffrey E. Lovich, Anthony M. Mills, and Joshua Schachter; 30 September 1988.

Paratypes.—CM 122403–122407, 122409–122411, USNM 300604–300605; all from the type locality.

Diagnosis.—A relatively high-domed *Graptemys* with a single, vertical, yellow bar on the upper surface of each marginal scute. The seams separating the lower marginals possess dark, diffuse, wide borders sometimes forming one or two semicircles. The head pattern consists of a distinct, three-pronged yellow pattern on the snout (the nasal trident), followed first by a large interorbital blotch that is not in contact with the large postorbital blotches, and second by a pair of supraoccipital spots or bulbous anterior expansions of the first paramedian neck stripes.

Description of holotype.—Subadult female preserved in alcohol, with the following measurements: CL 132 mm, CW 102.8 mm, CH 58.3 mm, PL 125 mm, G 20.3 mm, H 8.7 mm, P 19.4 mm, AB 28.7 mm, F 20.5 mm, AN 27.7 mm, LPOB 12.5 mm, MWID 16.3 mm, MPIG 1.7 mm, WLMP 7.8 mm. Interorbital and postorbital blotches not connected, dorsal paramedian neck stripes expanded and connected at anterior ends, nasal trident distinct. Carapace olive with light, indistinct circles on anterolateral corners of pleurals 1–3. Diffuse middorsal black stripe, interrupted on vertebrals 3, 4, and 5. Marginals with a narrow, vertical light bar on dorsal side, and relatively broad black markings along seams ventrally. Plastron yellow with black lines only along transverse seams.

Variation.—Carapace length to 284 mm in females and 131 mm in males. Carapace high domed with mean individual CH/CL 0.43 (males), 0.44 (females), and 0.49 (immatures). Mean individual CW/CL 0.78 (males), 0.77 (females), and 0.92 (immatures). Large females frequently appear "hump backed" due to dramatic anterior–posterior incline of first vertebral scute. Median keel of carapace pronounced, with broken black stripe most distinct anteriorly. Posterior tips of vertebral spines black. Carapace color olive, with relatively wide yellow rings and vermiculations on distal portions of pleural

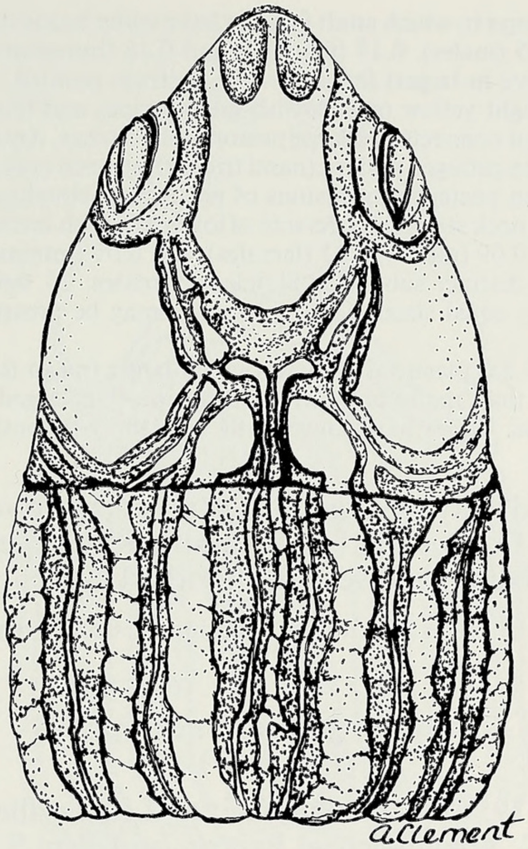

Fig. 4.—Head pattern of *Graptemys ernsti* (CM 122403) from the Conecuh River, Escambia County, Alabama.

scutes. Dark smudges present between marginals at periphery of carapace, particularly in smaller specimens. Upper marginals with relatively wide yellow bars (Fig. 5) roughly perpendicular to carapace periphery. Mean individual MPIG/MWID 0.17 for all specimens and 0.14 (males), 0.15 (females), and 0.19 (immatures). Mean individual WLMP/MWID 0.59 for all specimens and 0.57 (males), 0.60 (females), and 0.59 (immatures).

Plastron length to 251 mm in females and 123 mm in males. Plastral seam contacts usually longest between abdominals, femorals, and anals. Modal plastral formula (34%) AB > AN > F > P > G > H (n = 36). Two other formulae accounted for 21% of sample: AN > AB > F > P > G > H (n = 12) and AB > AN > P > F > G > H (n = 10). Twenty-six other plastral formulae were observed. Bridge well developed and plastron notched posteriorly. Plastron pale yellow, with seam-following dark pigment, particularly on seams perpendicular to long axis.

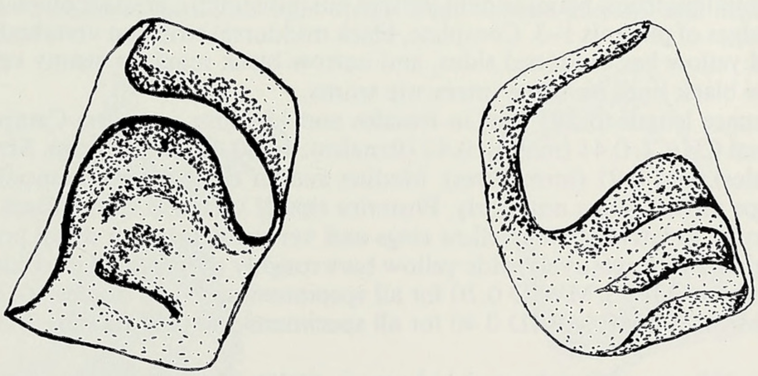

Fig. 5.—Upper (left) and lower (right) fifth left marginal patterns of *Graptemys ernsti* (CM 122403). The top of the illustration is anterior and left and right sides are distal.

A "broad headed" *Graptemys* in which adult females have wider heads than males. Mean individual JW/CL for a subsample 0.15 (males), 0.17 (females), and 0.18 (immatures). Angle between sides of upper jaw viewed from above in largest females <90°, rostrum pointed. Ground color of head and limbs brown to olive with light yellow or yellowish-green stripes and blotches. Dorsal head pattern of large interorbital blotch not connected to large postorbital blotches. Anterior portion of interorbital blotch forming a distinct three-pronged pattern (nasal trident) between eyes and nostrils. Supraoccipital spots usually present between posterior extensions of postorbital blotches. Supraoccipital spots may fuse with dorsal paramedian neck stripes. Underside of lower jaw with median longitudinal light stripe. Mean individual LPOB/CL 0.09 (males), 0.11 (females), and 0.09 (immatures). Thirty-seven percent of 75 specimens possessed distinct subocular blotches (3 males, 25 females). Dorsal neck stripes relatively broad and roughly equal sized. Thin, faint lines may be present between them. Tail and limbs striped.

Both sexes have relatively flat plastrons. Females much larger (mean female CL/mean male CL = 1.66, including immatures) than males and have conspicuously enlarged heads with hypertrophied alveolar surfaces on the jaws. Males have longer tails with the vent posterior to the margin of the carapace when extended.

Distribution.—Found only in large to medium-sized rivers emptying into Escambia Bay including: Conecuh River, Escambia River, Yellow River, and Shoal River in southern Alabama and western Florida, USA.

Etymology.—The specific epithet is a patronym honoring Dr. Carl Henry Ernst for his contributions to the study of turtles.

***Graptemys gibbonsi*, new species**
(Fig. 6, 7)

Holotype.—CM 94979; Chickasawhay River, Leakesville, Greene Co., Mississippi, USA; Richard C. Vogt, Michael Pappas, and Paul S. Freed; 21 July 1978.

Paratypes.—CM 94966–94967, 94970–94973, 94976–94978, 94980–94981, 94983, 95361–95362, 95559, 95561, 95577, all from the type locality.

Diagnosis.—A relatively high-domed *Graptemys* with a single vertical yellow bar on the upper surface of each marginal scute. The seams separating the lower marginals have dark, relatively narrow borders sometimes forming a single semicircle. The head pattern consists of a large, light interorbital blotch connected to the large postorbital blotches. A nasal trident is usually present. The dorsal paramedian neck stripes do not have bulbous anterior expansions, but may contact the postorbital blotches. Supraoccipital spots are absent.

Description of holotype.—Adult male preserved in alcohol, with the following measurements: CL 114.9 mm, CW 85.0 mm, CH 46.8 mm, PL 103.1 mm, G 11.0 mm, H 7.6 mm, P 12.3 mm, AB 25.8 mm, F 17.2 mm, AN 21.8 mm, LPOB 8.8 mm, MWID 11.7 mm, MPIG 2.0 mm, WLMP 3.5 mm. Interorbital blotch connected to large postorbital blotches, and dorsal paramedian neck stripes not in contact with postorbital blotches. Nasal trident present but indistinct. Carapace olive with light circular markings at lower edges of pleurals 1–3. Complete, black middorsal stripe on vertebrals 1–5. Marginals with broad, vertical yellow bar on dorsal sides, and narrow black mark on seams ventrally. Plastron yellow, with narrow black lines on some interscute seams.

Variation.—Carapace length to 295 mm in females and 124 mm in males. Carapace high-domed with mean individual CH/CL 0.41 (males), 0.42 (females), and 0.48 (immatures). Mean CW/CL 0.75 (males), 0.74 (females), and 0.91 (immatures). Median keel of carapace pronounced with broken or complete black stripe most distinct anteriorly. Posterior tips of vertebral spines black. Carapace color olive with grayish cast. Relatively wide yellow rings and vermiculations on distal portions of pleural scutes. Upper marginals with relatively wide yellow bars roughly perpendicular to carapace periphery (Fig. 7). Mean individual MPIG/MWID 0.20 for all specimens and 0.18 (males), 0.20 (females), and 0.24 (immatures). Mean WLMP/MWID 0.40 for all specimens and 0.39 (males), 0.39 (females), and 0.43 (immatures).

Plastron length to 250 mm in females and 113 mm in males. Plastral seam contacts usually longest between abdominals, femorals, anals, and pectorals. Modal plastral formula (51%) AB > AN > F > P > G > H (n = 73). Two other formulae accounted for 26% of sample: AB > AN > P > F > G >

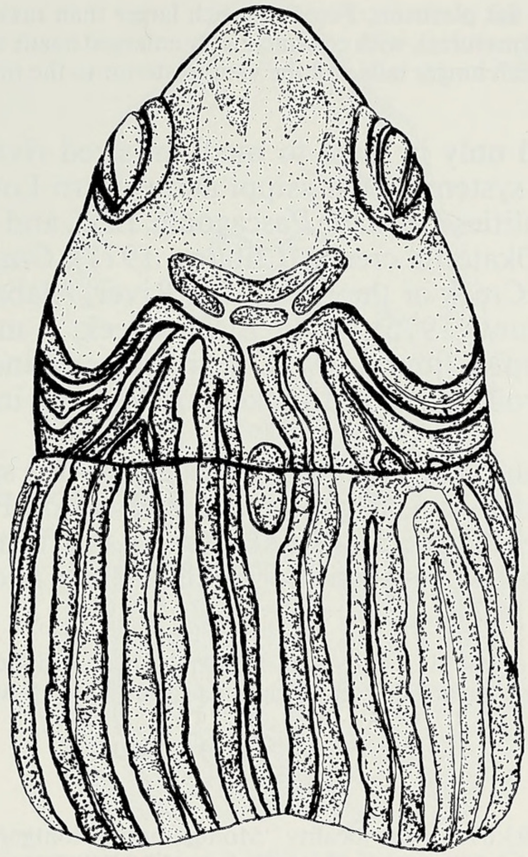

Fig. 6.—Head pattern of *Graptemys gibbonsi* (SREL 3067) from the Chickasawhay River, Greene County, Mississippi.

H (n = 28) and AB > AN > F > G > P > H (n = 9). Fourteen other plastral formulae were observed. Bridge well developed and plastron notched posteriorly. Plastron pale yellow, hingeless, with seam-following dark pigment particularly on transverse seams.

A "broad-headed" *Graptemys* with adult females possessing wider heads than males. Mean individual JW/CL for a subsample 0.15 (males), 0.19 (females), and 0.19 (immatures). Angle between sides of upper jaw viewed from above <90°, rostrum pointed. Ground color of head and limbs brown to olive with light yellow or yellowish-green stripes and blotches. Head pattern dorsally consisting of large interorbital blotch connected to large postorbital blotches; sometimes by only a thin line. Anterior portion of interorbital blotch forming a distinct three-pronged pattern (nasal trident) in 72% of a subsample (n = 118). Nasal trident more prevalent in Pearl River (79%, n = 64) specimens than in Pascagoula River specimens (65%, n = 54). Mean individual LPOB/CL 0.08 (males), 0.09 (females), and 0.08 (immatures). Dorsal neck stripes relatively broad with narrow stripes between. Underside of lower jaw with median longitudinal light stripe. Feet webbed and tail and limbs striped.

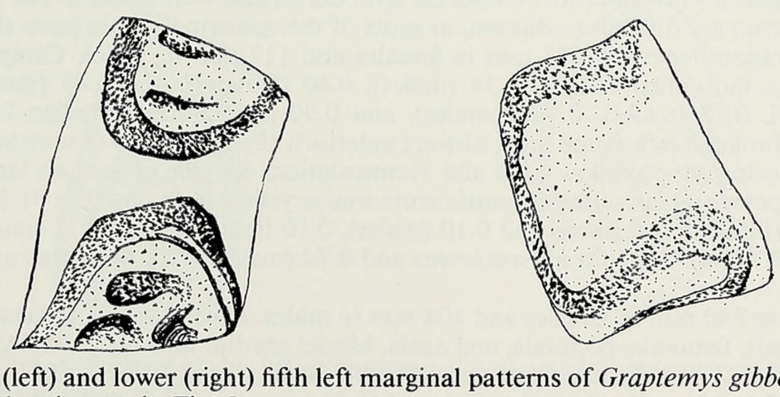

Fig. 7.—Upper (left) and lower (right) fifth left marginal patterns of *Graptemys gibbonsi* (SREL 3067). Orientation of drawings as in Fig. 5.

Both sexes have relatively flat plastrons. Females much larger than males (mean female CL/mean male CL = 1.89, including immatures), with conspicuously enlarged heads and hypertrophied alveolar surfaces on the jaws. Males with longer tails and the vent posterior to the margin of the carapace when extended.

Distribution.—Found only in large to medium-sized rivers in the Pascagoula River and Pearl River systems, Mississippi and eastern Louisiana, USA. Pascagoula River system localities are in the Pascagoula, Leaf, and Chickasawhay rivers, and Red, Bowie, and Okatoma creeks (Cliburn, 1971). *Graptemys gibbonsi* does not occur in either Big Creek or the Escatawpa River, Alabama tributaries of the Pascagoula River (Mount, 1975), or in Black Creek, a major tributary of the Pascagoula in Mississippi (Cliburn, 1971). Pearl River drainage populations occur in Ross Barnett Reservoir (Boyd and Vickers, 1963), and in the Pearl and Bogue Chitto rivers.

Dundee and Rossman (1989) published a record of this species (as *G. pulchra*) from the Tickfaw River at U.S. Highway 190, Livingston Parish, Louisiana. We question this record, as the species is unknown in the Tangipahoa, Tchefuncte, and Amite rivers, which lie between the Tickfaw River and Bogue Chitto River (Cagle, 1952; Cliburn, 1971).

Etymology.—The specific epithet is a patronym honoring Dr. J. Whitfield Gibbons for his contributions to the study of turtles, particularly in the southeastern United States.

Graptemys pulchra Baur
(Fig. 8, 9)

Graptemys pulchra Baur, 1893:675. Type locality "Montgomery [Montgomery Co.], Alabama." Lectotype: USNM 8808 (here designated), T. H. Bean and L. Kumlien, July 1876 (*see* comments). Paralectotype: USNM 318254 (*see* comments).

Diagnosis.—A relatively low-domed *Graptemys* with concentric yellow semicircles on the upper surface of each marginal scute. The seams separating the lower marginals have wide dark borders often composed of two or three concentric semicircles. The head pattern consists of a large light interorbital blotch connected to large postorbital blotches. The nasal trident is absent. The dorsal paramedian neck stripes do not have bulbous anterior expansions, but may contact the postorbital blotches. Supraoccipital spots are absent.

Description of lectotype.—Subadult female preserved in alcohol, with the following measurements: CL 176.0 mm, CW 139.0 mm, CH 72.0 mm, PL 164.0 mm, G 24.6 mm, H 10.8 mm, P 23.0 mm, AB 39.5 mm, F 22.4 mm, AN 34.3 mm, LPOB 9.0 mm, MWID 19.0 mm, MPIG 2.7 mm, WLMP 12.6 mm. Interorbital blotch narrowly connected to the postorbital blotches, dorsal paramedian neck stripes slightly expanded at anterior ends, nasal trident absent. Carapace with light reticulate markings on pleurals 1–3. Marginals with concentric circles on both dorsal and ventral sides. The patterns of both carapace and plastron are difficult to discern, as most of the epidermal scutes have sloughed.

Variation.—Carapace length to 273 mm in females and 117 mm in males. Carapace moderately domed with mean individual CH/CL 0.39 (males), 0.40 (females), and 0.45 (immatures). Mean individual CW/CL 0.78 (males), 0.78 (females), and 0.90 (immatures). Median keel of carapace pronounced with broken black stripe most distinct anteriorly. Posterior tips of vertebral spines black. Carapace ground color olive. Yellow rings and vermiculations may be present on lateral portions of pleural scutes. Upper marginals with concentric semicircular yellow markings (Fig. 9). Mean individual MPIG/MWID 0.10 for all specimens and 0.10 (males), 0.10 (females), and 0.11 (immatures). Mean individual WLMP/MWID 0.72 for all specimens and 0.74 (males), 0.71 (females), and 0.74 (immatures).

Plastron length to 240 mm in females and 108 mm in males. Plastral seam contacts usually longest between abdominals, femorals, pectorals, and anals. Modal plastral formula (33%) AB > AN > F > P > G > H (n = 24). Two other formulae accounted for 43% of sample: AB > AN > P > F > G > H (n = 17) and AB > AN > F > G > P > H (n = 14). Eleven other plastral formulae were observed.

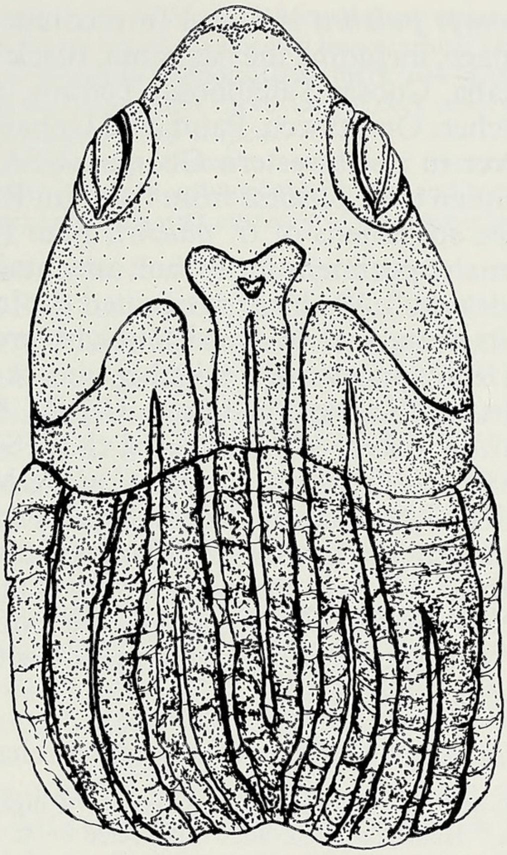

Fig. 8.—Head pattern of *Graptemys pulchra* (SREL 3343) from the Cahaba River, Dallas County, Alabama.

Bridge well developed and plastron notched posteriorly. Plastron pale yellow, hingeless, with seam-following dark pigment or dark blotches and figures.

A "broad-headed" *Graptemys* with adult females possessing wider heads than males. Mean individual JW/CL for a subsample 0.15 (males), 0.16 (females), and 0.18 (immatures). Angle between sides of upper jaw viewed from above in largest females <90°, rostrum pointed. Ground color of head and limbs brown to olive with light yellow or yellowish green stripes and blotches. Dorsal head pattern with large interorbital blotch well connected to large postorbital blotches. Anterior portion of interorbital blotch extending unbroken to nares. Mean LPOB/CL 0.08 (males), 0.09 (females), and 0.08 (immatures). Dorsal neck stripes relatively wide, of consistent width. Feet webbed and tail and limbs striped.

Both sexes have relatively flat plastrons. Females much larger than males (mean female CL/mean male CL = 1.40, including immatures) with conspicuously enlarged heads and hypertrophied alveolar surfaces. Males have longer tails with vent posterior to the margin of the carapace when extended.

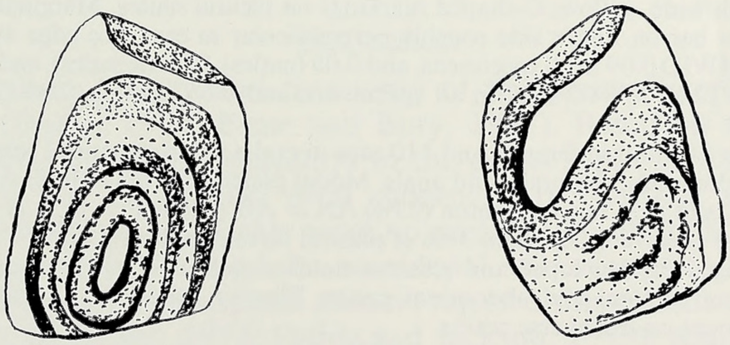

Fig. 9.—Upper (left) and lower (right) fifth left marginal pattern of *Graptemys pulchra* (SREL 3343). Orientation of drawings as in Fig. 5.

Distribution.—*Graptemys pulchra* is found in medium-sized to large streams of the Mobile Bay Drainage, including the Alabama, Black Warrior (and Mulberry and Sipsey forks), Cahaba, Coosa, Tallapoosa, Tensaw, and Tombigbee rivers, and Chewacla, Cubahatchee, Opintlocco, Paint, and Uphaupee creeks in Alabama, and the Conasauga River in northwestern Georgia, USA. Brimley (1910) erroneously reported a specimen of *G. pulchra* from the Flint River system in Georgia.

Comments.—The type specimens of *G. pulchra* Baur (USNM 8808, 318254) include two subadult female specimens in alcohol: one intact and the other without a skull, plus a separate dry skull. We have designated the intact specimen (USNM 8808) the lectotype, as its characters are consistent with provenance in the Mobile Bay Drainage. Cagle (1952) questioned whether the skull (numbered USNM 029526) belonged to the headless syntype (now USNM 318254), and suggested it might be a skull of *G. oculifera.* We compared the USNM skull with a series of skulls of adult female *G. oculifera* from Copiah County, Mississippi (CM 96224–96225, 96264–96267). The USNM skull is considerably larger than the largest *G. oculifera* skull, much heavier, and has the alveolar surfaces noticeably broadened. The ratio of skull length to width in the *G. oculifera* skulls (L/W) averages 1.68 (1.65–1.70). In the USNM skull L/W is 1.50. We conclude that the skull does not represent *G. oculifera,* and therefore is probably correctly associated with the headless paralectotype of *G. pulchra.*

Graptemys barbouri Carr and Marchand

Graptemys barbouri Carr and Marchand, 1942:98. Type locality, "Chipola River, north of Marianna, Jackson County, Florida." Holotype, MCZ 46251, collected by A. F. Carr, Jr., and T. Barbour, 1941.

Diagnosis.—A relatively high-domed *Graptemys* with a single, conspicuous, curved yellow bar on the upper surface of each marginal scute. The seams separating the lower marginals have wide, diffuse dark borders that sometimes form one or two semicircles. The head pattern consists of a distinct yellow interorbital blotch that tapers to a point near the external nares after passing between the orbits. In the center of this blotch, behind the orbits, is a heart-shaped or Y-shaped dark mark with a lighter central marking of the same shape. The interorbital blotch is broadly fused with the prominent yellow postorbital blotches. The underside of the lower jaw has a transverse light bar.

Variation.—Carapace length to 330 mm in females and 130 mm in males. Carapace high domed with mean individual CH/CL 0.40 (males), 0.42 (females), and 0.47 (immatures). Mean individual CW/CL 0.78 (males), 0.78 (females), and 0.90 (immatures). Median keel of carapace pronounced, tips of vertebral spines black. Small specimens with raised areas on anterior pleural scutes. Carapace olive to olive-brown, with wide, yellow, C-shaped markings on pleural scutes. Marginals with a relatively wide, curved yellow bar on upper side roughly perpendicular to carapace edge at outer end. Mean individual MPIG/MWID 0.09 in all specimens, and 0.09 (males), 0.08 (females), and 0.11 (immatures). Mean individual WLMP/MWID 0.62 in all specimens, and 0.66 (males), 0.59 (females), and 0.63 (immatures).

Plastron length to 252 mm in females and 110 mm in males. Plastral central seam contacts usually longest between abdominals, femorals, and anals. Modal plastral formula (36%) AB > AN > F > P > G > H (n = 38), and next most common (25%) AN > AB > F > P > G > H (n = 26). Twenty-three other formulae occurred. Less than 30% of plastral formulae shared with *G. ernsti, G. gibbonsi,* or *G. pulchra.* Bridge well developed and plastron notched posteriorly. Immatures with prominent ridges and spines on pectoral and abdominal scutes. Plastron pale yellow, hingeless, with seam-following dark pigment on transverse seams.

A "broad-headed" *Graptemys* with adult females having much wider heads than males. Mean individual JW/CL 0.12 (males) and 0.17 (females). Jaw outline broadly curved, rostrum blunt; angle between sides of upper jaw viewed from above in largest females >90°. Ground color of head and limbs dark brown to black with light yellow or yellowish-green stripes and blotches. Dorsal head pattern with large interorbital blotch broadly connected to postorbital blotches, tapering to a point in front of orbits. Heart-shaped or Y-shaped middorsal dark mark with lighter mark inside behind orbits. Chin with transverse light bar that follows jaw curve. Dorsal neck stripes relatively thick and roughly equal sized. Feet webbed and tail and limbs striped.

Both sexes with relatively flat plastrons. Females much larger (mean female CL/mean male CL = 1.71, including immatures) with conspicuously enlarged heads and hypertrophied alveolar surfaces on the jaws. Males have longer tails with vent posterior to carapace edge when extended.

Distribution.—*Graptemys barbouri* occurs in large to medium-sized rivers emptying into Apalachicola Bay, including the Chipola, Apalachicola, Chattahoochee, and Flint rivers in eastern Alabama, western Georgia, and western Florida, USA. During the Pleistocene, the range of the species may have extended eastward into the Suwannee River Drainage, northern Florida (Jackson, 1975). Cagle (1952) reported both *G. barbouri* and *G.* "*pulchra*" (=*G. ernsti*) from the Escambia River. Dobie (1972) re-examined the specimens and original field notes and concluded that data had been inadvertently transposed and the Escambia record of *G. barbouri* is erroneous (*see* Sanderson and Lovich, 1988).

KEY TO SPECIES OF THE *GRAPTEMYS PULCHRA* GROUP

1a. Interorbital and postorbital blotches separate or connected, no central dark heart-shaped figure; chin with longitudinal light stripe; rostrum (in largest females) pointed, angle formed by sides of jaw viewed from above <90° 2

1b. Interorbital and postorbital blotches fused, with a central dark heart-shaped figure; chin with transverse light bar; rostrum (in largest females) short and blunt, angle formed by sides of jaw viewed from above >90° *Graptemys barbouri*

2a. Interorbital blotch connected to postorbital blotches; supraoccipital spots or bulbous expansions of dorsal paramedian neck stripes rarely present; nasal trident present or absent.......... 3

2b. Interorbital blotch not connected, or rarely, narrowly connected to postorbital blotches; supraoccipital spots or bulbous expansions of dorsal paramedian neck stripes present; nasal trident well developed .... *Graptemys ernsti*

3a. Nasal trident usually present; single wide, yellow bar (16–21% scute width) on dorsal surface of each marginal scute .... *Graptemys gibbonsi*

3b. Nasal trident usually absent; narrow concentric yellow ocelli (no more than 10% scute width) on dorsal surface of each marginal scute .... *Graptemys pulchra*

DISCUSSION

The evolutionary history and taxonomy of the genus *Graptemys* have been controversial (Dobie, 1981; Ernst and Bury, 1982). Based on skull characters, McDowell (1964) included *Graptemys* in the genus *Malaclemys.* He concluded that *Graptemys* did not deserve even subgeneric recognition, since differences between *M. terrapin* and *G. kohni* were no greater than those between *G. kohni* and *G. geographica.* In addition, he considered *Malaclemys* to have more than two natural subgroups. Subsequent authors rejected this classification (Ernst and Barbour, 1972; McKown, 1972; Dobie and Jackson, 1979), restoring *Graptemys* to generic status. Wood (1977) recognized that the two genera were osteologically very similar, but separated them on the basis of physiological and pattern differences. He concluded that *Malaclemys* was ancestral to *Graptemys.* Dobie (1981) showed that *Graptemys* and *Malaclemys* are well differentiated in both external and osteological characters. He concluded that the Recent species of *Graptemys* were derived from other species of *Graptemys,* which were derived from a *Pseudemys* or *Pseudemys*-like ancestor.

The alpha taxonomy of *Graptemys* has been especially fluid, due in large part to relatively recent recognition of the diversity of the genus. Eight species (*barbouri, caglei, ernsti, flavimaculata, gibbonsi, nigrinoda, ouachitensis,* and *versa*) and two subspecies (*ouachitensis sabinensis* and *nigrinoda delticola*) have now been described in this century. The validity of these taxa has been confirmed in some cases (Killebrew, 1979; Bertl and Killebrew, 1983), and questioned in others (Folkerts and Mount, 1970; Freeman, 1970; Vogt, 1980).

Recognition of *Graptemys ernsti* and *G. gibbonsi* is consistent with the high level of drainage-specific endemism and speciose nature of the genus *Graptemys. Graptemys pulchra* (sensu lato) was the only Gulf Coast species of the genus that was not restricted to a single drainage. In the present arrangement, *G. gibbonsi* becomes the only Gulf Coast *Graptemys* that occurs in more than one drainage system (being found in the Pearl and Pascagoula rivers). However, this distribution is consistent with the zoogeographic evidence (*see* below).

The historical factor that we consider most important in diversification in the *G. pulchra* group is a sequence of vicariant events related to sea level fluctuations along a relatively static continental morphology during the Pliocene and Pleistocene. This hypothesis is supported by data for freshwater fish and other organisms in the southeastern United States (Avise, 1992). We consider the data for fish to be applicable to *Graptemys* since, like freshwater fish, turtles of this genus are effectively confined to rivers and neither disperse overland nor enter salt water (McCoy and Vogt, 1980). Wood (1977) emphasized the effectiveness of barriers to genetic exchange between *Graptemys* populations in independent Gulf Coast drainages which are isolated at their mouths by salt marshes.

Information summarized by Swift et al. (1985) and Bermingham and Avise (1986) indicates that sea levels were elevated 50–80 m above present levels in the Pliocene. The duration of inundation was relatively short, lasting only about one million years. The late Pliocene drop was followed by at least three Pleistocene fluctuations that rose no more than 10–20 m above present levels and fell 80–160 m below (Swift et al., 1985; Jackson, 1975; Poag, 1973). The fluctuations that occurred during the Pliocene were probably responsible for most of the speciation events due to vicariance in fish of the southeastern United States. Subsequent fluctuations during the Pleistocene probably resulted in range adjustments due to dispersal, but little speciation or extinction (Swift et al., 1985). During periods of high sea levels many Coastal Plain drainages were almost completely covered by salt water. Major drainages with headwaters above the Fall Line were isolated during these times and formed refugia for freshwater species. The results of high sea levels would be: (1) extinction of locally differentiated forms in small Coastal Plain rivers, with attendant reduction in overall levels of genetic diversity; and (2) opportunities for initiation of significant divergence between isolated lineages (Bermingham and Avise, 1986). As sea levels fell, dispersal was facilitated by coalescence of adjacent drainages into canyons beyond the present shoreline. Thus, taxa in upland drainages could colonize adjacent lowland drainages during periods of low sea level, only to be isolated once sea levels rose again.

Swift et al. (1985) considered sea level fluctuations to be largely responsible for modern patterns of distribution in freshwater fish of the southeastern United States. These patterns include: (1) a major break in faunas at the Mobile Bay drainage and the Apalachicola River, based on phenetic clustering of species occurrence data; (2) mostly allopatric distributions from Lake Ponchartrain, Louisiana, to the Choctowhatchee River in Florida; (3) lowland streams and adjacent larger upland streams generally sharing similar ichthyofaunas; and (4) the existence of two or three sister species, one each in the Mobile Bay drainage system, the Escambia to Choctawhatchee drainages, and streams west of Mobile Bay.

The results of Swift et al. (1985) are largely congruent with those of Bermingham and Avise (1986) who studied mitochondrial DNA (mtDNA) polymorphisms in four species of freshwater fish in the same region. Major genetic breaks were observed at Mobile Bay and the Apalachicola River. The latter authors also noted that the Escambia River is characterized by an unusually high number of endemic mtDNA clones. Using a molecular clock based on data for mammals they concluded that major genetic breaks occurred in the fish genus *Lepomis* 3–4.5 million years before present: an interglacial period when sea levels were 50–80 m above present levels and headwaters populations would have been isolated.

The scenario outlined above provides a possible explanation for divergence in the *G. pulchra* group. We propose that the ancestral stock which gave rise to this group was isolated in streams draining into the Mobile Bay and the Apalachicola River during periods of high sea level. Drops in sea level allowed these upland forms to invade adjacent drainages, following divergence, through drainage coalescence near river mouths. If Pliocene vicariant events are responsible for initiation of major differences among modern taxa, then it seems plausible that ancestral forms exhibited little character divergence and had widespread distributions. The existence of fossils similar to *G. barbouri* far to the east of the present distribution provides support for this hypothesis, as does the fact that representatives of the *Graptemys pulchra* group are presently distributed, almost continuously, along the northern shore of the Gulf of Mexico as far west as the Mississippi Embayment (Jackson, 1975).

In our hypothesis forms ancestral to *G. ernsti* and *G. gibbonsi* left the Mobile Bay drainage during periods of lowered sea levels and invaded drainages emptying into Pensacola Bay to the east, and the Pearl and Pascagoula rivers to the west. The endemic crawfish (Neill, 1957) and fish (Swift et al., 1985) of the Pensacola Bay system may be of similar origin. These forms were subsequently isolated when sea levels rose again, eventually leading to divergence from the ancestral stock. Similar dispersal occurred in forms ancestral to *G. barbouri* as evidenced by the presence of fossils in the Suwannee River system (Jackson, 1975). The reason for extinction of the Pleistocene *Graptemys* of the Santa Fe River, Florida, is unknown.

Independent support for our hypothesis was provided by Trip Lamb (personal communication) who is studying molecular variation in *Graptemys* and *Malaclemys* using analysis of mitochondrial DNA (mtDNA). Three of 17 restriction endonucleases revealed mtDNA polymorphisms in a small sample of *G. pulchra* (sensu lato). Four restriction site changes were observed identifying three mtDNA clones: (1) Yellow–Conecuh rivers, (2) Alabama River, and (3) Pearl River (specimens were not sampled from the Pascagoula River). There was one site gain between the Yellow–Conecuh and Alabama River genotypes, and three site losses between the Alabama River and the Pearl River genotypes. Although there was opportunity for divergence of these genotypes as early as the Pliocene, the mtDNA data suggest that differentiation was initiated more recently, perhaps during the Pleistocene. The same battery of 17 restriction endonucleases did not differentiate other groups of Gulf Coast *Graptemys.* Preliminary cladistic analysis of mtDNA data included *G. barbouri* and *G. pulchra* (sensu lato) in the same clade.

The parallel divergence exhibited by the *G. pulchra* group and many freshwater fishes is remarkable. Both show patterns of allopatric sister taxa, with one each in the Mobile Bay system, in the Escambia and Choctawhatchee Bay drainages, and in rivers to the west of Mobile Bay. In addition, adjacent lowland drainages between larger upland drainages tend to share similar faunas. In the case of *Graptemys,* the Pearl and Pascagoula rivers both have *G. gibbonsi.* This appears to contradict the usual pattern of drainage-specific endemism in Gulf Coast *Graptemys.* However, these rivers also have almost identical ichthyofaunas (Swift et al., 1985). Two other species of *Graptemys* are found in the Pearl and Pascagoula rivers: *G. oculifera* in the Pearl and *G. flavimaculata* in the Pascagoula. These two species were probably derived from a common ancestor very recently as evidenced by their morphological similarity (Cagle, 1954). They have been treated as subspecies (Wermuth and Mertens, 1961). The mouths of the Pearl and Pascagoula rivers were 20–30 km east of their present locations before the Pleistocene (Swift et al., 1985). During Pleistocene realignment of these drainages there may have been intermittent freshwater connections, or even a transitory common estuary, which could have facilitated exchange of gene pools and faunal elements. Isolation of *Graptemys gibbonsi* from *G. pulchra* in the Mobile Bay Drainage was assured by the presence of the Wiggins Uplift, a structural feature dating from the Oligocene that separates inland portions of those drainages in eastern Mississippi and western Alabama (Swift et al., 1985).

The similarity between *G. ernsti* and *G. gibbonsi* noted by Tinkle (1962) and Shealy (1976) and in this study may be due to convergence in similar selective regimes. These taxa both have relatively high shells with wide yellow bars on the upper marginals. It may be significant that yellow marginal pigmentation is most extensive in *G. gibbonsi,* which occurs in sympatry with *G. oculifera* and *G. flavimaculata,* the two species of the genus with the greatest amount of yellow pigmentation. Shealy (1976) suggested that the relatively flat shell of *G. pulchra* may be related to turbulence in Fall Line streams. The existence of the flattened musk turtle (*Sternotherus depressus*), a species endemic to the upper Mobile Bay drainage, lends support to this theory (Ernst et al., 1989). Moreover, there are local populations of "flattened" individuals of other species, such as *Pseudemys concinna,* in headwaters streams of the Mobile Bay drainage (R. C. Vogt, personal communication).

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APPENDIX 1. SPECIMENS EXAMINED
(*See* Acknowledgments for explanation of museum abbreviations)

Graptemys barbouri (total 101)—ALABAMA: *Houston Co.,* Chattahoochee R., Chattahoochee River State Park (AUM 14278). FLORIDA: no specific locality (UGAMNH 3883); *Calhoun Co.,* Chipola R. (TU 16899), Chipola R., 1 mi S Scotts Ferry (UGAMNH 3894–3895, 3898–3900), Chipola R., nr. Scotts Ferry (UGAMNH 3926); *Gadsden Co.,* Apalachicola R., Chattahoochee (CM 67334, 95997–95998); *Jackson/Calhoun cos.,* Chipola R. (TU 15399–15400, 15424–15429, 15440, 15755, 15757, 15760, 15762, 15781–15783); *Jackson Co.,* Chipola R., 2 mi S Marianna (AUM 8962, 8964, 8966–8967, 8989–8990, 9030, 11231), Chipola R., 4 mi S Marianna (TU 13410 [14], 13879 [39], 14939), Chipola R., US Hwy 90 (AUM 10101, 10104–10106), Chipola R., 3 mi S US Hwy 90 (AUM 12695–12696). GEORGIA: *Crisp Co.,* Flint R., Lake Blackshear, US Hwy 280 (AUM 19358); *Dooly Co.,* Flint R., 5 mi up from Drayton Bridge (UGAMNH 3933); *Dougherty Co.,* Flint R., Radium Springs (AUM 5955); *Upson Co.,* Flint R., US Hwy 19, S Thomaston (CM 67406, 95190).

Graptemys ernsti (total 157)—ALABAMA: *Covington Co.,* Yellow R., 5 mi E Wing, Co Rd 4 (AUM 10095, 10097–10099, 21982, 21987), Patsaliga Cr., 1 mi N Point "A" (AUM 3878); *Escambia Co.,* Conecuh R., East Brewton (AUM 22019, 22026–22028, 32754, 32756, 32770), Conecuh R., 1 mi S East Brewton, St Hwy 41 (AUM 13649–13652, 31900, 31902, 31904), Conecuh R., 8.2 mi E East Brewton, Co Rd 20 (AUM 5002–5003, 5007–5008, 5596, 5907, 6282, 6312, 13686), Conecuh R., E of Brewton, Co Rd 63 (AUM 8845, 18233, 19501, 21970, 22020–22025, 31890, 32757, 32764, 32766, AUMP 990, 1000), Conecuh R., US Hwy 29 (AUM 21972, 22017–22018, 31878–31880, 31883–31885, 32759, 32761, 32768, AUMP 942, 945, 2630, 2637, 2650), Conecuh R, 1.6 km upstream from Co Rd 4, 14 km E East Brewton (CM 122403–122407 paratypes, 122408 holotype, 122409–122411 paratypes, USNM 300604–300605 paratypes). FLORIDA: *Escambia Co.,* Escambia R., 1.2 mi E Century, St Hwy 4 (TU 13446–13448, 13456, 13458, 13461, 13463, 15827 [40], 16576 [12], 16580 [8], 16665 [6]); *Okaloosa Co.,* Yellow R., US Hwy 90, nr. Milligan (AUM 21981, 21983–21986, 21989, 32456, CM 114816–114818); *Santa Rosa Co.,* Yellow R., Harold (AUM 21980).

Graptemys gibbonsi (total 223)—LOUISIANA: *St. Tammany Par.,* Pearl River, nr. Pearl River (town) (TU 7657, 7680, 15070), Pearl R., Northeastern RR crossing (TU 15072), Pearl R., Hub Oil Field (TU 14958 [14], 14959 [4], 15330); *Washington Par.,* Bogue Chitto R. (TU 16926), Bogue Chitto R., Enon (TU 13798 [4]), Pearl River, nr. Angie (TU 12194, 12262–12263, 12274, 12360, 12370), Pearl R., Bogalusa (AUM 5949), Pearl R., Lock 1 (TU 14957 [5]). MISSISSIPPI: *Clarke Co.,* Chickasawhay R., US Hwy 45, Shubuta (CM 95879); *Copiah Co.,* Pearl R., St Hwy 28, E Georgetown (CM 62162–62163, 67473–67483, 94903–94906, 94909, 94916–94920, 94935–94936, 94938–94941, 94946, 95050, 95055–95059, 95553, 95632, 95634, 95645–95647, 95650), Pearl R., 25 mi S Jackson (Hinds Co.) (AUM 21974–21976); *George Co.,* Pascagoula R., St Hwy 26, 2 mi E Benndale (AUM 5966, 9547, 13657, TU 14739 [12], 14919 [4]), Pascagoula R., nr. Lucedale (AUM 22014), Pascagoula R., 10 mi SW Lucedale (TU 16664); *Greene Co.,* Chickasawhay R., Leakesville (AUM 10299, 22002–22003, 22009–22010, 22015, 32411–32418, CM 67454–67462, 94966–94967, 94970–94973, 94976–94978 paratypes, 94979 holotype, 94980–94981, 94983, 95361–95362, 95559, 95561, 95577 paratypes, GMU 823), Chickasawhay R., 2 mi N Leakesville (AUM 25977), Chickasawhay R., US Hwy 98 (AUM 22004–22008, 22016, 31876, 32419–32424, 32427–32429, TU 15916 [9]), Leaf R., US Hwy 98, McLain (CM 95563, 95570–95573); *Jackson Co.,* Pascagoula R., 9.6 km W Wade (CM 95875); *Lawrence Co.,* Pearl R., Monticello (AUM 25140–25144, 32430–32439, 32441–32449, 32451, CM 95663–95665), Pearl R., nr. Oma (TU 18043); *Marion Co.,* Pearl R., Columbia Water Park (CM 95674), Pearl R., 2.3 mi E Sandy Hook (TU 19344); *Pearl River Co.,* Pearl R., St Hwy 26 (E Bogalusa, Louisiana) (CM 95688); *Wayne Co.,* Chickasawhay R., 4.8 km W Waynesboro (CM 67438–67444, 94948–94949).

Graptemys pulchra (total 115)—ALABAMA: *Baldwin Co.,* Alabama R. W Chrysler (Monroe Co.) (AUM 32460–32461), Tensaw R. (AUM 16200); *Cherokee Co.,* Weiss Reservoir, Lawrence (AUM 16654); *Chilton Co.,* Coosa R., Mitchell Dam (AUM 6291); *Clarke Co.,* Tombigbee R., Jackson (AUM 5984); *Coosa Co.,* Paint Cr. nr. mouth, 7.5 mi SSW Talladega Springs (AUM 22896–22897); *Dallas Co.,* Cahaba R., 8 km W Selma (CM 95610, 95616–95618); *Elmore Co.,* Coosa R., Wetumpka (CM 95781–95784), Tallapoosa R., St Hwy 229 (AUM 5961, 9660); *Greene Co.,* Black Warrior R., 3 mi E Eutaw (TU 16613 [6], 16692, 16874 [2]); *Hale Co.,* Tombigbee R., Birdseye Landing, 12.8 km N Demopolis (CM 95852–95856), Black Warrior R., 0.5 mi above Lock 9 (TU 17151 [3]); *Jefferson Co.,* Black Warrior R., Co Rd 12, 6.4 km W Graysville (CM 95999), Black Warrior R., Taylor's Ferry, 3.4 mi NE Gilmore, Co Rd 46 (AUM 5594–5595), Cahaba R., US Hwy 280 (AUM 8743); *Lowndes Co.,* Alabama R., Prairie Creek Access, 3.2 km E Selma (CM 95792–95800), Alabama R., 7.2 mi NW White Hall (TU 16611, 16691 (2)), Tombigbee R., 7.5 mi S mouth of Bultahatchie Cr. (AUM 17131); *Macon Co.,* Chewacla Cr., Tuskegee Nat. For. (AUM 19144), Cubahatchee Cr., US Hwy 80 (AUM 22001), Tallapoosa R., Millstead (AUM 10947, 22000), Uphaupee Cr., pumping station off US Hwy 29 (AUM 12373); *Marengo Co.,* Tombigbee R., Demopolis (AUM 21998), Tombigbee R., 2.5 mi WSW Putnam (AUM 12568, 12690), Tombigbee R., 3.5 mi NW Putnam (AUM 15380); *Monroe Co.,* Alabama R., 5.5 mi E Gosport (TU 14731 [2]); *Montgomery Co.,* nr. Montgomery (USNM 8808 lectotype, 318254 paralectotype), Alabama R., US Hwy 31, W Montgomery (AUM 6305), Tallapoosa R., US Hwy 231 (AUM 32459); *Perry Co.,* Cahaba R., St Hwy 14/183, 2.2 km W Sprott (CM 67426, 94994, 94997–94998, 95007, 95010–95011); *Shelby Co.,* Coosa R., nr. Childersburg (TU 15588); *Sumter Co.,* Tombigbee R. US Hwy 11, E Epes (AUM 32463–32471, TU 16883 [3]); *Talladega Co.,* Coosa R., 8 km NW Lincoln (CM 95739–95743), Coosa R., 6 mi E Pell City (TU 16632 [3], 16865); *Tuscaloosa Co.,* Bankhead Lake, mouth of Big Yellow Creek (CM 95272, 95302), Bankhead Lake, 3.2 km S Franklin Ferry Bridge (CM 95273), Black Warrior R., above Lock 9, 17.5 mi SSW Tuscaloosa (TU 14671 [4]), Black Warrior R., 20 mi S Tuscaloosa (TU 15927); *Walker Co.,* Mulberry Fork of Black Warrior R., 9 mi E Jasper (TU 15903 [2], 16645, 16860 [2]), Mulberry Fork of Black Warrior R., Co Rd 22 (CM 95710), Sipsey Fork of Black Warrior R., Co Rd 22 (CM 95609), Black Warrior R. (TU 16060); *Wilcox Co.,* Alabama R. (TU 19265); *Winston Co.,* West Branch Sipsey Fork of Black Warrior R., 1 mi N St Hwy 33 (GMU 2806). GEORGIA: *Whitfield Co.,* Conasauga R., 10.9 mi ENE Dalton (UGAMNH 15018).

APPENDIX 2

Identifications of illustrations of species of Graptemys pulchra, *sensu lato, based on the classification proposed in this paper.*

Reference	Page	Comments
Alderton (1988)	123	Specimen is incorrectly identified as *G. pulchra.* It is actually *G. barbouri*
Ashton and Ashton (1985)	136	*G. gibbonsi*
Behler and King (1979)	Plate 284	*G. pulchra*
Carr (1952)	212	Probably *G. gibbonsi*
Conant (1975)	Plate 8	Shell pattern typical of *G. gibbonsi*
Conant and Collins (1991)	Plate 6	Shell pattern typical of *G. gibbonsi*
Dundee and Rossman (1989)	Plate 10	A composite. Head pattern is typical of *G. ernsti* and shell pattern is typical of *G. gibbonsi*
Ernst and Barbour (1972)	116 (Fig. 92)	*G. gibbonsi*
	116 (Fig. 93)	*G. ernsti*
	117 (Fig. 94)	*G. ernsti*
	117 (Fig. 95)	*G. gibbonsi*
	Plate 11 (top)	*G. gibbonsi*
	Plate 11 (middle)	*G. ernsti*
Ernst and Barbour (1989)	219	*G. gibbonsi*
Mount (1975)	279	*G. ernsti*
	280 (top)	*G. ernsti*
	281 (left)	*G. gibbonsi*
	281 (center)	*G. ernsti*
	281 (right)	*G. pulchra*
Marion (1986)	51	*G. ernsti*
Pritchard (1979)	249	*G. ernsti*
Smith and Brodie (1982)	53	A composite. Shell pattern typical of *G. gibbonsi.* Head pattern typical of *G. ernsti*
Wahlquist (1970)	10	*G. gibbonsi*