A review of morphological and pattern variation in the Painted turtle, *Chrysemys picta*, in Missouri, USA, with an alternate hypothesis of the origin of *Chrysemys picta marginata*

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THE Painted turtle, *Chrysemys picta*, as traditionally recognized, is composed of four distinct subspecies (Ernst, 1971; Ernst *et al*., 1994). *Chrysemys picta picta*, the Eastern painted turtle, ranges from southeastern Canada through New England south along the Atlantic coastal plain to Georgia and west into eastern Alabama. It has the vertebral and pleural scutes of its carapace aligned (the only turtle with this condition) light borders along the carapace seams, a narrow light vertebral stripe, and a mostly unpatterned plastron (some dark spotting may occur). *Chrysemys p. dorsalis*, the Southern painted turtle, occurs from extreme southwestern Kentucky and southeastern Missouri southward in the Mississippi Valley to the Gulf Coast of Louisiana and eastward through Mississippi into Alabama, and formerly in a relict population in southeastern Oklahoma and adjacent Texas. It is distinguished by having a conspicuous, broad, red or yellow, vertebral stripe, light borders along the carapace seams, the vertebral and pleural scutes disaligned, and an unpatterned plastron. *Chrysemys p. marginata*, the Midland painted turtle, is found from southern Quebec and Ontario south in the central United States to Tennessee and northern Alabama. Its range is east of the Mississippi River, extending eastward to New England, Pennsylvania, Maryland, Virginia, and the Carolinas. It has disaligned pleural and vertebral scutes, dark or no border along the carapace seam, a narrow often interrupted or absent vertebral stripe, and a variable dark pattern that is commonly less than half the width of the plastron. *Chrysemys p. bellii*, the Western painted turtle, ranges from western Ontario across southern Canada to British Columbia and south to Missouri, northern Oklahoma, eastern Colorado, Wyoming, Idaho, and northern Oregon. It also occurs in scattered localities in the southwestern United States and at one site in Chihuahua, Mexico. It is the largest subspecies (CL_{max} 25.1 cm), and has alternating vertebral and pleural scutes, a light reticulate pattern on the carapace, narrow light borders along the carapace seams, a narrow sometimes interrupted light vertebral stripe, and a plastron pattern which branches outward along the seams to occupy most of the plastron.

Where the ranges of the subspecies of *C. picta* meet, zones of intergradation occur, and these have been well studied at various areas of the geographical range. Data on intergradation are known from the Northeast and adjacent Canada (Babcock, 1933; Hartman, 1958; Waters, 1964, 1969; Pough & Pough, 1968; Klemens, 1978; Gordon, 1990; Rhodin & Butler, 1997; Wright & Andrews, 2002), Pennsylvania (Ernst & Ernst, 1971); Maryland (Groves, 1983), Kentucky and Tennessee (Johnson, 1954; Ernst, 1970), the southern Gulf states (Ernst, 1967; Muir, 1989), and the Upper Peninsula of Michigan (Ernst & Fowler, 1977). In addition, overall subspecific variation in morphology and colour patterns has been examined by Bishop & Schmidt (1931), Hartweg (1934), Bleakney (1958), and Ultsch *et al*. (2001).

Bleakney (1958) proposed a theory as to the places of origin of the four subspecies, and how they subsequently migrated into their present geographical ranges after the Wisconsinian glacial period. He thought that at the end of the last North American glacial period painted turtles (*Chrysemys*) were divided into three separate populations, which may well have represented separate incipient species that had not yet evolved reproductive isolation: *C. picta* in the southeastern Atlantic coastal region, *C. dorsalis* in the lower Mississippi River Valley, and *C. bellii* in the Rio Grande River and Pecos River watersheds of New Mexico.

According to Bleakney, these three populations extended their ranges northward with the retreat of the glaciers. *Chrysemys dorsalis* moved up the Mississippi River and met *C. bellii* in the region of St. Louis 'near the Missouri-Mississippi-Ohio [rivers] junctures.' There, Bleakney hypothesized, the two hybridized and produced the species, *C. marginata*. *C. marginata* then spread up the Mississippi River and Ohio River watersheds, eventually reaching the northeastern United States and adjacent Canada. There it met and interbred with *C. picta*, which had migrated up the Atlantic Coast. It also met and interbred with *C. bellii* in Wisconsin and Michigan. Because the four 'species' had not evolved reproductive isolating mechanism to prevent gene exchange when their populations met, broad zones of intergradation were established.

Recently, Starkey *et al*. (2003) studied the molecular systematics of the four subspecies of *C. picta* by analyzing the variation in the rapidly evolving mitochondrial DNA control region. The genetic data gathered indicated that two monophyletic evolutionary clades exist in extant *Chrysemys*; one containing only *C. p. dorsalis*, and a second, extremely wide-ranging and genetically undifferentiated, clade that includes the other three subspecies. Based on this, Starkey *et al*. concluded that *C. p. dorsalis* should be elevated to the full species *C. dorsalis*, and that the other three subspecies should remain within the current species *C. picta*.

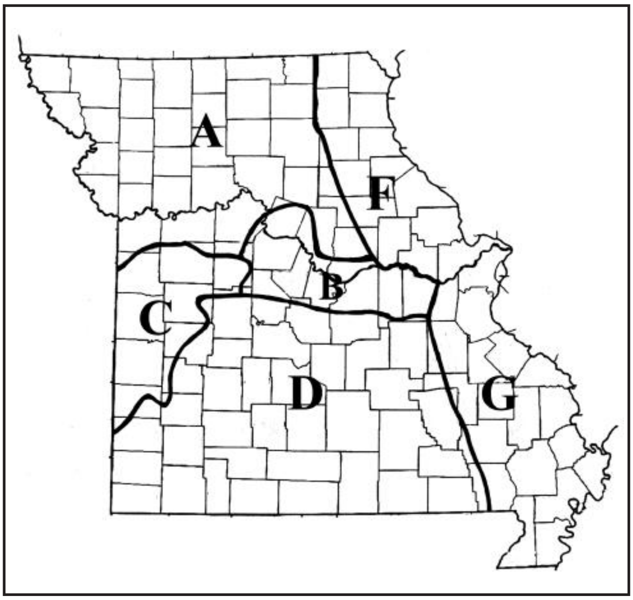

Figure 1. Map of Missouri, USA showing the Physiographic Provinces denoted by Thom & Wilson (1980), but with Province E deleted and intergrade Zones F and G inserted.

We examined specimens of *C. picta* from throughout Missouri to document their subspecific status, and especially that of painted turtles from the St. Louis area, the proposed centre of hybrid origin of *C. p. marginata*. We present our results below, and offer an alternate hypothesis concerning the region of origin of *Chrysemys p. marginata*.

METHODS

A total of 195 specimens of *Chrysemys picta* from 58 counties in Missouri was examined. All were sexed using the characters of Ernst (1971), and their greatest carapace and plastron lengths recorded. All measurements were made with metric dial calipers accurate to 0.1 mm. Scute terminology used was that of Ernst *et al*. (1994).

The methods of measurement of Hartman (1958) were used to compare the degree of disalignment of the carapace laminal seams. When

Clockwise from top left: *Chrysemys picta belli* (adult), *C. p. belli* (juvenile), *C. p. marginata* (adult), *C. p. dorsalis* (male). Photographs © C. Ernst.

the seams between the central vertebral scutes and the lateral pleural scutes lie in the same transverse line, they were considered to be 0% disaligned; if the seams alternate exactly they were 100% disaligned. The base point for measuring is the inner end of the seam between the second and third pleural scutes. The imaginary line from the base point forward and parallel to the longitudinal axis of the carapace, to the point opposite the inner end of the seam between the first and second pleurals was measured, and was denoted 1a on the left side of the carapace, and 2a on the right side. The part of this same imaginary line starting at the base point between the second and third vertebrals was measured, and was denoted as 1b on the left side, and 2b on the right side. The average percent disalignment was then calculated as 1b/1a + 2b/2a.

The light border of the anterior seam of the second pleural scute was measured at its widest point and its colour noted. Red, orange, or yellow borders were considered characters of *C. dorsalis* and *C. p. bellii*; black, olive, or no border pigmentation were considered characters of *C. p. marginata* (Ernst, 1971). The greatest width of the medial dorsal stripe on the carapace was measured on the second vertebral scute. Cagle (in Johnson, 1954) discovered the dorsal stripe to be wider than the widest foreleg stripe in *C. dorsalis*, but narrower in other subspecies of *C. picta*. The greatest width of the dorsal stripe was expressed as a percentage of the greatest width of the foreleg stripe. Percentages greater than 100 were regarded a character of *C. dorsalis*. The condition of the dorsal stripe was also noted. A complete, uninterrupted dorsal stripe was a character of *C. dorsalis* and *C. p. bellii*, but a discontinuous, interrupted stripe was characteristic of *C. p. marginata*, as was also the absence of a dorsal stripe. The widths of both the pleural seam border and the dorsal stripe were scaled against the greatest carapace length of the turtle. In addition, the presence of (*C. p. bellii*) or the absence of a

				Character			
Zone	**Plastron Mark**	**Carapace Seam Disalignment**	**Carapace Seam Width**	**Carapace Stripe Condition**	**Carapace Stripe Width**	**Carapace Stripe/ Foreleg Stripe**
A *n* = 42	b = 40 (95.2%) b x m = 1 (2.4%) m = 1 (2.4%)	94.5% (70.3-104.4)	1.77 mm (0.6-4.0)	Cont. 25 (59.5%) Disc. 14 (33.3%) None 3 (7.1%)	0.63 mm (0-1.10)	47.9 (10.0 – 77.7)
B *n* = 25	b = 23 (92%) b x m = 2 (8%)	95.7% (93.4-98.3)	2.25 mm (0-4)	Cont. 25 (68%) Disc 8 (32%)	1.13 mm (0.9-1.3)	64.4 (40.9-80.0)
C *n* = 14	b = 14 (100%)	91.1% (88.1-93.7)	1.95 mm (1.3-2.5)	Cont. 13 (93%) Disc. 1 (7%)	0.80 mm (0.50-1.10)	46.1 (27.7-64.7)
D **n = 6**	b = 6 (100%)	95.7% (93.4-98.3)	1.30 mm (1.0-1.5)	Cont. 2 (33.3%) Disc. 4 (66.7%	0.7 mm (0.6-0.9)	35.9 (26.1-50.0)
F *n* = 41	b = 13 (31.7%) b x m = 20(48.7%) m = 8(19.5%)	95.6% (91-100)	1.4 mm (0-2.3)	Cont. 23 (56.1%) Disc. 17(41.5%) None 1 (2.4%)	1.03 mm (0.5-1.6)	54.8 (35.7-76.2)
G *n* = 23	d = 18 (78.3%) m x d = 2 (8.7%) m = 3 (13.0%)	76.6% (54.7-112.9)	2.68 mm (0-4.8)	Cont. 23 (100%)	2.8 mm (0.9-5.6)	161.1 (56.2-373.0)
Ky *n* = 96	m = 96 (100%)	36.8% (61.1-102.9)	1.68 mm (0.5-3.3)	Cont. 61 (63.5%) Disc. 31 (32.3%)	1.03 mm (0-2.0)	58.2 (1.1-100)
LM *n* = 80	d = 80 (100%)	54.8% (5.5-96.2)	1.70 mm (0.7-4.0)	Cont. 79 (98.8%) Disc. 1 (1-2%)	2.10 mm (1.0-3.8)	147.2 (70-345)
MN *n* = 61	b = 65 (100%)	93.5% (79.0-108.7)	1.99 mm (0.9-5.3)	Cont. 34 (55.7%) Disc. 22 (36.1%) None 5 (8.2%)	0.98 mm (0-2)	58.1 (24-100)

Table 1. Phenotypic characters by zones for Missouri *Chrysemys picta* (b = *bellii*, d = *dorsalis*, m = *marginata*, b x m = *bellii* x *marginata*, m x d = *marginata* x *dorsalis*).

pattern of reticulating light lines on the carapace (*C. dorsalis, C. p. marginata*), were also noted.

Three patterns of dark markings occur on the plastron of the *Chrysemys* turtles (Bishop & Schmidt, 1931; Ernst, 1971). The pattern of each specimen was noted. The absence of a dark plastron pattern was considered a character of *C. dorsalis*. A large pattern of dark lines covering most of the plastron and extending outward from the centre along the seams was considered characteristics of *C. p. bellii*, and a more narrow central dark pattern lacking outward seam extensions was considered to be of *C. p. marginata*. Intermediate patterns between the latter two were considered intergrade, as was a pattern of only a few dark pigmented spots.

Data on Missouri *Chrysemys* were placed for comparison into five groups corresponding to the physiographic provinces of Missouri (Fig. 1) proposed by Thom & Wilson (1980) and described by Johnson (1987): A) The Glaciated Plains comprise the northern third of the state (28 counties sampled) and mark the southern-most limits of the Kansan Glacial Period. They feature rolling hills and wide flat valleys, with soils composed of glacial till and loess. Most of these occur within the Missouri River watershed, but waterways of the easternmost counties flow into the Mississippi River (Pflieger, 1975); B) The Ozark Border (14 counties sampled) forms a narrow system of river hills and sandstone bluffs, deciduous forests, wide river valleys, and deep soils along the lower Missouri River. Its southeasternmost watersheds flow into the Mississippi River (Pflieger, 1975); C) The Osage Plains (7 counties sampled) is an unglaciated region of rolling hills, streams, and tallgrass prairies with deep soils in west central Missouri. Waterways in most of the zone flow northeast into the Missouri River, but those of the southern portions drain southwestward out of the state

(Pflieger, 1975); D) The Ozark Plateau (4 counties sampled) is a rugged mountainous region of limestone bluffs, clear streams, and thin soils south of the Missouri River and east of the Ozark Plains. The northern counties drain into the Missouri River, waterways of the southwest flow out of the state in that direction, and the southern portions of the zone drain southward into Arkansas (Pflieger, 1975); and E) The Mississippi Lowlands (5 counties sampled) lie in the southeastern corner of the state on the floodplain of the Mississippi River, and contain swamps and bottomland harwood forests.

In addition, 81 adult specimens of *Chrysemys dorsalis* from Louisiana and Mississippi, 99 adult specimens of *Chrysemys p. marginata* from Kentucky, and 61 adult specimens of *Chrysemys p. bellii* from southwestern Minnesota were included in the data set to ensure pure characters from these taxa for comparison with painted turtles from the supposed site of hybrid origin of *Chrysemys p. marginata* in the vicinity of St. Louis. These specimens were from localities outside the zones of hybridization or intergradation between the respected taxa (Ernst, 1967, 1970; Ernst & Fowler, 1977).

Statistics were run using SAS package 8.2; levels of significance were set *a priori* at $P = 0.05$. To compare possible hybrids or intergrades, Fisher's discriminant analysis was run on combined data from both sexes using the following nonsexually dimorphic variables: scute disalignment, seam width, carapace stripe width, and the width of the foreleg stripe. Normality was checked visually using probability plots. To analyze the data, first, a training data set was created using data from the known pure taxa (Ultsch *et al.* 2001, Starkey *et al.* 2003) under investigation from Kentucky, Mississippi and Louisiana, and Minnesota. The remaining specimens (from eventually newly created zones F and G) were then compared and analyzed by comparing them with the training data set. Canonical discriminant analyses were performed on grouped data from each of the five physiographic zones. Cross validation was then used to test the taxonomic identification of each individual in each physiographic zone which had complete data (some specimens lacked soft parts or parts of the shell making statistical comparisons difficult).

Table 2. Classification by cross validation of individual turtles from zones F and G with complete data (b = *belli*, d = *dorsalis*, m = *marginata*, b x d = *bellii* x *dorsalis*, b x m = *belli* x *marginata*, and d x m = *dorsalis* x *marginata*).

Taxon Frequency

Zone	b	d	m	b x d	b x m	d x m	Total
F	10	0	5	0	22	0	37
G	0	9	0	9	2	3	23
Total	10	9	5	9	24	3	60

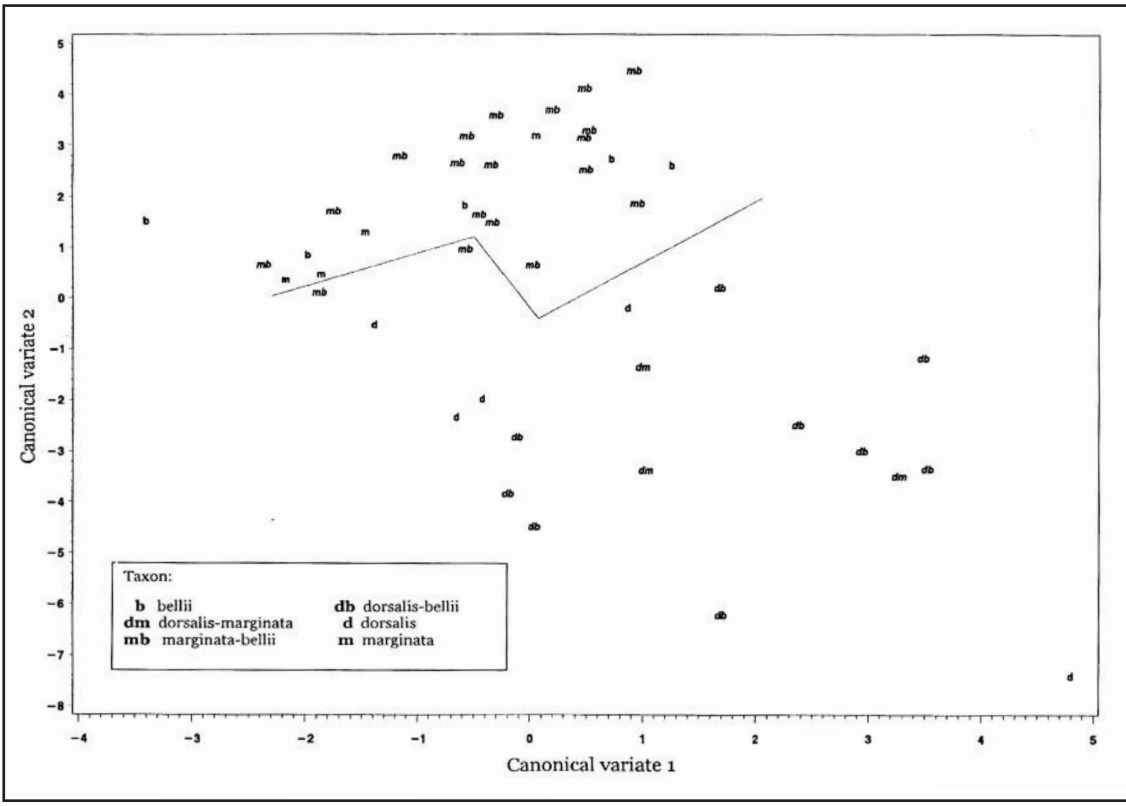

Figure 2. Discriminant analysis of individuals of *Chrysemys* in Zones F (above) and G (below).

RESULTS

Plastron pattern was different by frequency for all zones (Table 1). Examination of the phenotypic characters of colour and shell patterns, and of carapace seam alignment of each specimen, showed that 100 percent of the individuals from populations of *Chrysemys* in the Osage Plains (C) and Ozark Plateau (D) zones could be assigned to the subspecies *C. p. bellii* (Table 1). However, the Glaciated Plains (A), Ozark Border (B), and Mississippi Lowlands (E) zones contained hybrid specimens of *C. p. bellii* X *C. dorsalis* (zone B, 7/65, 10.8%; zone E, 8/34, 23.5%) and *C. p. marginata* X *C. dorsalis* X (zone B, 1/65, 1.5%; zone E, 10/34, 29.4%), and intergrade specimens of *C. p. bellii* X *C. p. marginata* (zone A, 12/73, 16.4%; zone B, 13/65, 20%). *Chrysemys p. marginata* patterns were found in only a few individuals (zone A, 1/73, 1.4%; zone B, 5/65, 7.7%). Individuals of *Chrysemys p. marginata* totaled only 6/195 turtles (3.1%) examined from Missouri, and they were from eastern counties north of the Missouri River.

All but two of the intergrade individuals (Fig. 2, Table 1) were from eastern counties where the waterways flow primarily into the Mississippi River (Pflieger, 1975). The other two intergrade specimens were from Franklin and Montgomery counties, respectively, on the plateau of the Ozark Border just west of the Mississippi floodplain. These data indicate that eastern Missouri has received genes of *C. dorsalis*, *C. p. bellii*, and *C. p. marginata* to form a *Chrysenys* population with a mixed genotype in an extensive hybrid/intergrade zone along the western floodplain of the Mississippi River. North of the confluence of the Missouri and Mississippi rivers the intergrades are *C. p. bellii* X *C. p. marginata*, as determined by variation in the dark plastron mark, absence or interruption of the vertebral stripe, and the presence or absence of reticulate light markings on the carapace. South of the

Missouri River *C. dorsalis, C. p. bellii*, and *C. p. marginata* have each contributed genes to the mixed swarm, as indicated by the presence or absence of a dark plastron mark and, if present, variation in it; the degree of prominence and width of the vertebral stripe; disruption of the vertebral stripe in some specimens; the width of the light seam border on between pleural scutes 2 and 3; and the presence or absence of light reticulations on the carapace.

In view of the apparent interbreeding based on shell morphology and colour patterns, and for more meaningful comparisons, we removed the eastern intergrade populations from the Glaciated Plains (A) and Ozark Plateau (B), but retained the nonintergrade populations in them. We designated the intergrade populations in 6 counties occurring north of the Missouri River the Northeastern Intergrade Zone (F), and combined those occurring in 3 counties south of the Missouri River with turtles from the original 5 counties of the Mississippi Lowlands zone (E) into a second Southeastern Intergrade Zone (G), abandoning the original designation of zone E for the Mississippi Lowlands (Table 1). Results of cross validation for the new zones F and G are presented in Table 2.

DISCUSSION

Ultsch *et al*. (2001) conducted a study of *Chrysemys* from throughout the genus' geographic range in an attempt to better define the morphological phenotypes of its four morphs. Their data revealed no reason to accept or reject Bleakney's (1958) theory of the distribution of the subspecies of *C. picta* at the height of the Wisconsinian glaciation, or Bleakney's conjecture that *C. marginata* was derived from hybridization between *C. bellii and C. dorsalis*. They speculated that, if *C. marginata* is a hybrid, it could have originated as one between *C. bellii* and *C. picta*; however, nowhere at present do the ranges of *bellii* and *picta* meet, and, although they may possibly have in the past, there is no supporting fossil evidence. Unfortunately, the possible flaw in their hypothesis that *C. marginata* may be a hybrid of *C. bellii* and *C. dorsalis* is that Ultsch *et. al*. (2001) examined no specimens from Missouri or adjacent Illinois. If the centre of origin of *C. marginata* is in the St. Louis area, than pure *marginata* specimens should be present there today in identifiable numbers.

Figure 2 and Tables 1 and 2 indicate that this is not the case. Only 5 (11.6%) of the 43 turtles from the Northeastern Intergrade Zone (F), which includes the St. Louis area, could be assigned to *C. p. marginata*. A sixth specimen of *C. p. marginata* was recorded from Audrain County, just west of the Northeastern Intergrade Zone. Phenotypic *marginata* characters were also found in 24 (55.8%) *C. p. bellii* x *C. p. marginata* from the Northeastern Intergrade Zone (F) and one turtle showing phenotypic *marginata* characters was recorded in each of Franklin and Montgomery counties on the Ozark Border just west of Zone F. Under cross validation of the 37 turtles in Zone F having complete data 5 (13.5%) were classified as *C. p. marginata*, 10 (27.0%) were classified as *C. p. bellii* and 22 (59.4%) as *C. p. bellii* x *C. p. marginata* (Table 2). No turtle from north of the Missouri River possessed *C. dorsalis* characters, which is to be expected if *C. p. marginata* is a hybrid creation between *C. dorsalis* and *C. p. bellii*, as proposed by Bleakney (1958).

In addition, only 3 (13%) turtles from the Southeastern Intergrade Zone (G) had a phenotype like *C. p. marginata*, 2 (8.7%) individuals were *C. dorsalis* x *C. p. marginata*, and the remaining 18 (78.3%) turtles were *C. dorsalis* (Table 1). Under cross validation of the 23 turtles from Zone G with complete data, none were classified as *C. p. marginata*, 2 (8.7%) were *C. p. bellii* x *C. p. marginata*, 9 (39.1%) were classified as *C. dorsalis*, and 9 (39.1%) were *C. dorsalis* x *C. p. bellii* (Table 2). Individuals with a phenotype like that of *C. p. marginata* comprised only 12.4% (11/89) of the *Chrysemys* turtles examined from the Mississippi watershed in eastern Missouri, 9% (8/89) from localities north of the Missouri River (F) and 3.4% (3/89) from south of that river (G) (Table 1). Cross validation only classified 8.3% (5/60) turtles as *C. p. marginata* in the Mississippi watershed in eastern Missouri, 13.5% (5/37) from localities north of the Missouri River (F) and none from localities south of the Missouri River (Table

2). If the hybrid creation of *C. p. marginata* proposed by Bleakney (1958) occurred south of the Missouri River, some pure *C. p. marginata* should probably be present, but our data do not show this.

Hartweg (1934) surmised that “west of the Mississippi River little *marginata* influence can be detected except in the region of St. Louis. Our data agree, but evidence supporting Bleakney’s (1958) theory is very weak at best. Our data indicate that those watersheds flowing into the Mississippi River in eastern Missouri (F, G) can be interpreted as containing a narrow north-south hybrid/intergrade swarm (Fig. 2) that has received genes from southern *C. dorsalis*, western *C. p. bellii*, and eastern *C. p. marginata*, and not as the region of hybrid origin of *C. p. marginata*. Where then did *Chrysemys p. marginata* originate?

Fossil evidence (Holman, 1995) supports the proposed centres of origin of Bleakney for both *C. bellii* and *C. picta*, but fossils are lacking in the area of Louisiana and Mississippi where he thought *C. dorsalis* originated.

Is there fossil evidence to support another region of origin of *C. marginata*? If *C. marginata* invaded Missouri from its present eastward range, we should look for evidence of its possible origin east or southeast of the Mississippi River. At its maximum, the Laurentide ice sheet of the late Wisconsinian did not reach the vicinity of the present channel of the Ohio River. Remains of turtles referable to the genus *Chrysemys* have been found at several Pleistocene sites in the Tennessee River watershed. The Blackbelt Complex of fossil sites in northeastern Mississippi has yielded remains of *Chrysemys* that date to the Sangamonian interglacial age and the Wisconsinian glacial stage (Holman, 1995). Fossil *Chrysemys* have also been found in Bell Cave, Colbert County, Alabama, which date to between 11,800-26,500 YBP (Holman *et al*., 1990), and Guy Wilson Cave, Sullivan County, Tennessee has yielded fossil *Chrysemys* that date from about 19,700 YBP (Fay, *in* Holman, 1995). In addition, late Wisconsinian remains of *Chrysemys* have been uncovered at Ladds Quarry, Bartow County, in northwestern Georgia (Holman, 1985a, 1985b, 1995). These fossils show that turtles of the genus *Chrysemys* occupied the Tennessee River watershed at the same time as other *Chrysemys* occurred at the sites proposed by Bleakney (1958) as the centres of origin of both *C. bellii* and *C. picta* (Holman, 1995). If *C. marginata* originated in the region of the Tennessee River Valley, it could easily have migrated north, then west and east into its present geographical range, forming the present intergrade zones where it met *C. bellii*, *C. dorsalis* and *C. picta* (Hartweg, 1934; Cagle, 1954; Carr, 1952; Ernst, 1971; Ernst & Fowler, 1977; Conant & Collins, 1998; Ernst *et al*. 1994). The geological history of the Tennessee River Basin presented in Fitzpatrick (1986) also supports this conclusion. Therefore, we believe that the Tennessee River Valley is a more plausible centre of origin of the population of *C. picta* that eventually evolved into the subspecies *C. p. marginata*.

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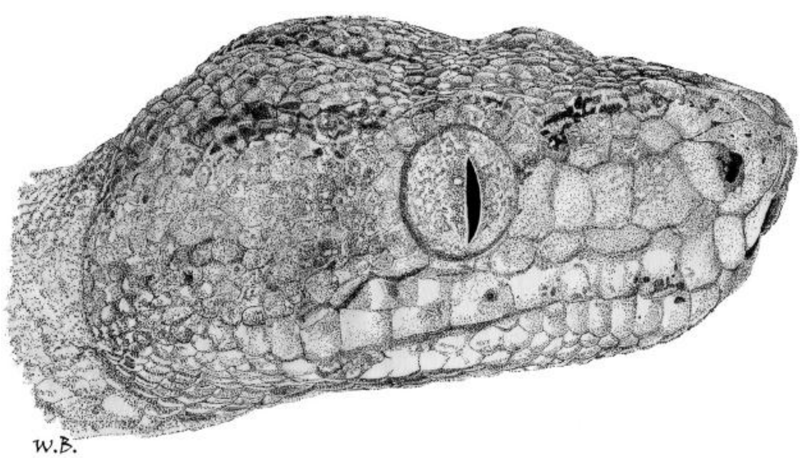

Amazon tree boa, *Corallus hortulanus*. Pen and ink illustration by Will Brown.
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