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PAINTED TURTLES (*CHRYSEMYS PICTA*) OF VERMONT: AN EXAMINATION OF PHENOTYPIC VARIATION AND INTERGRADATION

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ABSTRACT - The painted turtle, *Chrysemys picta* Schneider (family Emydidae), has been divided into four subspecies (with differing morphological characteristics), two of which intergrade in the northeastern United States. The intergradation of *C. p. marginata* (midland painted turtle) and *C. p. picta* (eastern painted turtle) has been well studied in some areas, but has been poorly studied in Vermont, an area that could contribute important information on this species and the process of intergradation. Turtles were trapped and released from three different watersheds in Vermont, and others were examined from collections at the Carnegie Museum of Natural History from within the center of the ranges of the two parent subspecies to investigate the hypotheses that Vermont's turtles are intergrades, and that the amount of influence from each subspecies differs with drainage in Vermont. For the external characteristics of scute disalignment, scute border width, and plastral figure, many of Vermont's turtles were determined to be significantly different from typical *marginata* and *picta*, and were intermediate to them, strongly suggesting that they are intergrades. Samples from the southeast corner of the state were determined to be *picta*.

INTRODUCTION

The painted turtle, *Chrysemys picta*, is found from east to west coast in the northern United States and southern Canada, and ranges south to the Gulf of Mexico from Louisiana to Alabama, though not continuously (Conant and Collins 1991). It has historically been divided into four subspecies (Ernst et al. 1994). These subspecies are: *C. p. bellii* (Gray) in the western United States and western Canada, *C. p. dorsalis* Agassiz in the south-central United States, *C. p. marginata* Agassiz in the central United States and south-central Canada, and *C. p. picta* (Schneider) along the Atlantic coast (Ernst et al. 1994). It is generally accepted that where these four subspecies overlap, they form intergrades. Intergrades are intermediate between parental forms (as are hybrids) and both sexes are completely fertile, whereas hybrids usually are partially or completely sterile in at least one sex (Gilbert 1961).

The four subspecies of *Chrysemys picta* share the smooth unkeeled carapace and red marginal scute coloration that defines the species, but differ in specific aspects of the appearance of the cara-

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pace and plastron. Two of the subspecies (*bellii*, the western painted turtle, and *dorsalis*, the southern painted turtle) will not be addressed in this paper. *C. p. marginata*, the midland painted turtle, has a plastral figure that is variable within the subspecies, but ordinarily is an oval shape and is half, or less than half, the width of the plastron (Fig. 1). It typically involves all of the plastral scutes, and does not extend along the seams. The vertebral and costal scute seams alternate (i.e., are not aligned) (Conant and Collins 1991). *C. p. picta*, the eastern painted turtle, typically has a plain yellow plastron with no plastral figure. The vertebral and costal scute seams do not alternate, but instead are aligned, unlike the other three subspecies (Fig. 2). In addition, the edges of the scutes have wide yellow or light-colored margins that form bands across the back of the turtle (Conant and Collins 1991).

Theoretically, these four subspecies are readily distinguishable in core areas far from the influence of other subspecies, but where their ranges

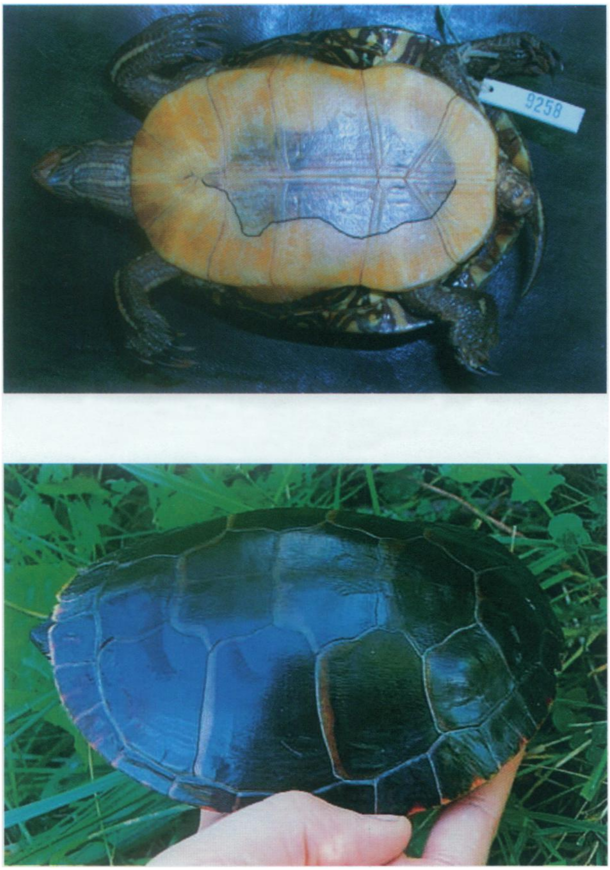

Figure 1. Typical plastron and carapace of the midland painted turtle (*C. p. marginata*). The lower half of the plastral figure has been outlined. A large plastral figure is visible, the posterior seams of the second costal and second vertebral scutes are disaligned, and there is typically a narrow border on the anterior edge of the second costal scute, although this intergrade turtle from Vermont shows larger borders than is typical of *C. p. marginata*.

overlap, their classification becomes more difficult, as the intergrades have a mixture of physical characteristics of each subspecies (Gilbert 1961). Recently, however, Ultsch et al. (2001) found that a "pure" *picta* does not exist, but shows influence from the *marginata* genome throughout its range, particularly at the extremes. Our study chose "typical" *picta* from core areas that were far from the edges of subspecific ranges given in Conant and Collins (1991), and consequently should show the least influence from *marginata*. Therefore, although no *picta* population can be considered completely pure, this study will address the *picta* specimens we chose as "typical" (the closest to "pure" that we are aware of), and will use this baseline to classify Vermont's turtles.

Intergrades have been studied extensively in several geographic areas (Allen 1899; Babcock 1933, 1938; Bishop and Schmidt 1931; Bleakney 1958a; Ernst 1967, 1970; Ernst and Ernst 1971; Ernst and Fowler 1977; Gordon 1990; Groves 1983; Hartman 1958; Johnson 1954; Klemens 1978; Pough and Pough 1968; Rhodin and Mittelhauser 1994; Waters 1964, 1969). However, there has been no systematic study in Vermont, where painted turtle accounts have been based on anecdotal observations or on data from only a few specimens. Due to this lack of

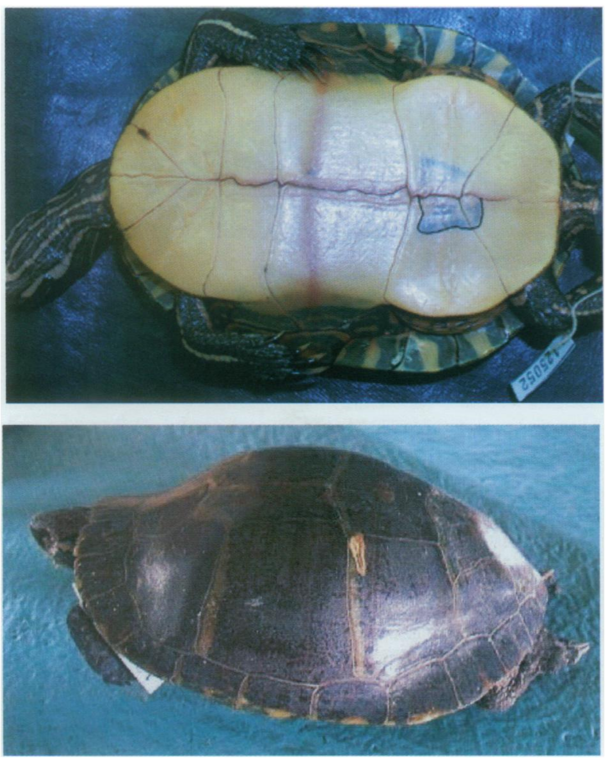

Figure 2. Typical plastron and carapace of the eastern painted turtle (*C. p. picta*). The lower half of the plastral figure has been outlined. The plastral figure is small, the posterior seams of the second costal and vertebral scutes are aligned, and there is a wide border on the anterior margin of the second costal scute.

data, there has been much speculation as to the subspecies of *Chrysemys picta* found in Vermont (Table 1).

As these reports from the past 69 years reveal, there is clearly much confusion about the painted turtles of Vermont. Because very little data exist on Vermont turtles (including *Chrysemys picta*), most conclusions about subspecies or intergrades are tenuous at best. Therefore, the current study was designed to systematically study the Painted Turtles found in Vermont, and to quantify the degree of influence from the midland and eastern subspecies.

Based on previously published hypotheses of painted turtle post-glacial movement and colonization (Bishop and Schmidt 1931; Bleakney 1958a, 1958b; Pough and Pough 1968; Rhodin and Butler 1997; Waters 1964), we might predict that: (1) Vermont's turtles are intergrades between the eastern and midland subspecies, and (2) the sites we have chosen to study will differ in the amount of influence from the two subspecies (with those in the Lake Champlain drainage showing more influence from the *marginata* gene pool and those in the Connecticut and Hudson River drainages showing more influence from the *picta* gene pool).

METHODS

Data to support our first hypothesis will come from examining museum specimens collected from areas that are far from the edge of intergradation with any other subspecies. These typical populations will allow comparison to Vermont's turtles on the basis of scute disalignment, width of the light-colored scute border, and size of the plastral figure.

Study sites

Adult painted turtles (carapace length greater than 90 mm; Pough and Pough 1968) were collected from three Vermont watersheds between 25 May 2000 and 28 June 2001 (Fig. 3). In the upper Connecti-

Table 1. Summary of studies mentioning or mapping painted turtles in Vermont. Question marks indicate unknown locations of specimens, or lack of specimens altogether. This table shows the large amount of uncertainty surrounding Vermont's painted turtles. There has been much speculation as to Vermont's subspecies of *Chrysemys picta*, but many of these ideas are based on few specimens from a limited geographic area.

Author(s) (date)	Specimens cited from:	Subspecies in Vermont
Babcock (1933, 1938)	Lake Dunmore, Lake Champlain, S. Burlington	intergrades
Bishop and Schmidt (1931)	Lake Champlain	intergrades
Bleakney (1958a)	?	none
Carr (1952)	?	intergrades
Conant and Collins (1991)	?	*marginata* and intergrades
Cook (1984)	?	*marginata* and intergrades
DeGraaf and Rudis (1983)	Bennington County	*marginata*
Hartman (1958)	Bridport	intergrades
Pope (1939)	?	intergrades
Whillans and Crossman (1977)	?	intergrades

cut River drainage (Essex County, northeastern Vermont), turtles were collected from Nulhegan Pond (Brighton), Nulhegan River (Ferdinand), Dennis Pond (Brunswick), Wheeler Pond (Brunswick), and ponds at the Great Spirit Farm (Maidstone). This field site is hereafter referred to as Essex. In the lower Connecticut River drainage (mideastern and southeastern Vermont), turtles were collected from Tunbridge Trout Pond (Tunbridge), Beaver Pond (Weathersfield), Sweet Pond and Weathershead Hollow Pond (Guilford). In the Lake Champlain drainage, turtles were collected from a farm pond (Weybridge). In the Hudson River drainage, turtles were collected from Lake Potter and South Stream Wildlife Management Area (Pownal).

Turtles from the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania were also examined. These specimens were collected from areas that are far from the edge of intergradation with any other subspecies. A total of 33 *marginata* were examined from Indiana (Brown and Whitely Counties), Michigan (Washtenaw County), Ohio (Fairfield, Knox, Mahoning, Sandusky, and Vinton Counties), and West Virginia (Cabell and Wirt Counties). Thirty-five *picta* were examined from North Carolina (Camden, Dare, and Hyde Counties), South Carolina (Pickens County), and Virginia (Accomack, Suffolk, and Virginia Beach Counties). In addition, thirteen painted turtles

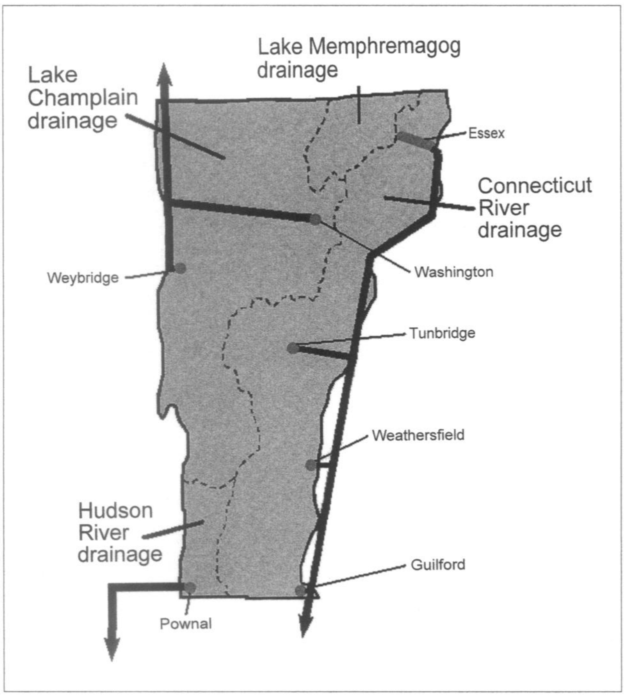

Figure 3. Map of study sites in Vermont. Dotted lines delineate watersheds, and study sites are referred to by name of town or county.

from Vermont (Washington County) were examined; this site is hereafter referred to as Washington.

Therefore, samples included six field sites in Vermont (Essex, Tunbridge, Weathersfield, Guilford, Weybridge, and Pownal) and three samples from the Carnegie Museum (*marginata*, *picta*, and Washington).

Collection methods

Trapping with 30-inch hoop net traps with one-inch mesh was the primary method for capturing turtles. Traps were baited with sardines packed in soybean oil and salt (Ernst 1965). In addition to hoop traps, seven turtles were captured on land. Four females were caught laying eggs. Two individuals were captured outside the trap while basking. One individual was found dead on the road.

Data Collection and Analysis

Field Procedures. In a procedure similar to the method described by Cagle (1939), each turtle captured in the field was marked with a saw to create triangular notches in the marginal scutes for individual numbering. The sex of each turtle was determined by measurements of the relative length of the front and rear claws as well as the location of the cloaca relative to the posterior edge of the carapace. Five measurements of each turtle were taken: straight-line length of the plastron and straight-line length of the carapace (Fig. 4) (lengths of the carapace and the plastron were measured at the extremes of the carapace and plastron using a measuring tape to the nearest millimeter), scute width of the second costal scute, width of the anterior border of this scute at the midpoint, and disalignment of the posterior edge of the second costal scute and the posterior edge of the second vertebral scute. The latter three measurements were taken on both the left and the right sides of each turtle using a 130-mm dial caliper accurate to the nearest 0.1

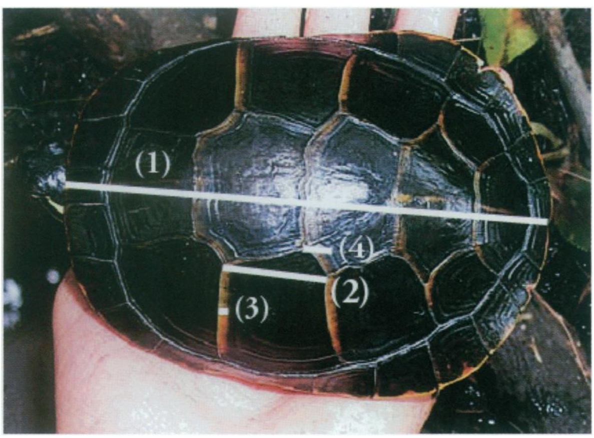

Figure 4. Measurements taken on the carapace of each turtle: (1) straight-line length of the carapace, (2) scute width of the second costal scute, (3) width of the anterior border of the second costal scute at the midpoint, (4) disalignment of the posterior edge of the second costal scute and the posterior edge of the second vertebral scute.

millimeter. In addition, the carapace and plastron of each turtle were photographed. In the case of plastral staining by tannin and other deposits, the plastron was scrubbed with a stainless steel scourer to allow visibility of the plastral figure (Klemens 1978). Any remarkable characteristics of the turtle were also recorded. Turtles were released at the site of capture after all measurements were taken.

Museum Procedures. Painted turtles from the CMNH were examined. Both skeletons and specimens preserved in alcohol were studied. Claw length was used to determine the sex of each turtle, except where skeletons were examined, in which case notes from the database were used to determine the sex of each turtle if possible. The measurements taken were the same as those taken in the field, and the plastron of each turtle was photographed.

Calculation of Distinguishing Characteristics. Using these measurements, three values were calculated that could be used to distinguish between the two subspecies-disalignment of the second vertebral and second costal scute seams, width of the anterior border of the second costal scute, and size of the plastral figure. Following the method of Hartman (1958) and subsequent studies, the percentage of disalignment of the central and lateral seams was determined for each turtle. A value of 100% indicates that the posterior edge of the second vertebral scute is exactly halfway between the seams of the second costal scute (designating *marginata*), while a value of 0% indicates that the seams are exactly aligned (characterizing *picta*). However, there is some variation in these values even in the "typical" populations.

Mean border width was determined by measuring the width of the lighter colored border on the anterior edge of the second costal scute, and dividing this measurement by the scute width. The values from the left and right side of each turtle were averaged to obtain a mean border width. Adjusting border width (by dividing by scute width) was necessary because, as shown by previous studies (Hartman 1958, Whillans and Crossman 1977), border width increases with increasing carapace length.

The size of the plastral figure was calculated in two different ways as a percentage of the area of the plastron, using a novel method of overlaying a grid over each photograph. The first method only used the part of the figure that was dark-colored (hereafter referred to as plastral figure area). Because Gordon (1990) showed that the intensity of the plastral figure decreases with increasing plastral area (i.e., age), and Whillans and Crossman (1977) suggested that the plastral figure can fade with age, plastral figure size was also calculated using a second method. The second method assumed that the area interior to the dark-colored figure was at one time a part of the figure, and so included this area in the plastral figure area measurement (hereafter referred to as solid plastral figure area).

Because of some confusion about juvenile disalignment and plastral markings (Gordon 1990, Klemens 1978, Pough and Pough 1968), juveniles <90 mm carapace length were excluded from this study, as in Klemens (1978) and Pough and Pough (1968).

Data Analysis. For both measures of plastral figure, two *marginata* specimens were excluded from analysis because their plastral figures were faded.

Scute disalignment, percent plastral figure, and percent solid plastral figure did not conform to the normal distribution (Kolmogorov-Smirnov Z test, $p < 0.05$), and so Kruskal-Wallis non-parametric tests were performed to determine if there were differences between Vermont turtles and the "typical" subspecies (museum specimens from core areas), or between the sites in Vermont. For border width, which was normally distributed (Kolmogorov-Smirnov Z, $p > 0.05$), ANOVAs were performed to determine differences among groups. Least significant difference (LSD) post hoc tests were performed for each comparison to determine which groups differed.

The ANOVAs and Kruskal-Wallis tests were used to compare means among groups. In addition, Pearson's correlations between the characteristics were calculated for each Vermont site and for the "typical" subspecies.

RESULTS

Eighty-nine adult painted turtles were collected from Vermont. Trapping success ranged from 0.16 painted turtles per trap-night in Essex to 5.40 in Guilford. In addition, 33 *marginata*, 35 *picta*, and 13 Vermont Painted Turtles from the CMNH were examined.

The nine sampling sites (seven Vermont sites, and *marginata* and *picta*) were significantly different from each other (ANOVA, $p < 0.001$) for both carapace and plastron lengths. These length differences between sites justify the adjustment of border width by dividing by scute width, and similarly the dividing of plastral figure area by the area of the plastron.

The data from measures of external appearance strongly suggest that, of the seven Vermont sites, four of them (Weybridge, Washington, Essex, and Pownal) are intergrades, two of them (Weathersfield and Guilford) are *picta*, and one (Tunbridge) could be classified as either *picta* or intergrade (Tables 2 and 3).

The mean percent disalignment of the posterior edges of the second costal and second vertebral scutes in *Chrysemys picta* was significantly different between the nine samples (Kruskal-Wallis, $p < 0.001$; Fig. 5).

C. p. marginata (midwestern USA) had the largest disalignment of vertebral and costal scutes, and was significantly larger than all other groups (LSD post hoc, $p < 0.001$). *C. p. picta* (eastern USA) showed the

Table 2. Descriptive statistics for all Painted Turtles examined in this study. For external characteristics, Vermont's turtles fall between the averages for the specimens from non-intergrading areas. In addition, their ranges are generally larger than those for the other subspecies. These data suggest that Vermont's turtles are intergrades between *C. p. marginata* and *C. p. picta*.

	C. p. m.	WE	WA	ES	PO	TU	WF	GU	*C. p. p.*
Scute Disalignment (%)									
N	33	20	13	13	14	8	7	27	35
Mean	91.7	66.6	71.1	65.0	64.3	66.4	32.6	34.8	25.4
S.E.	1.2	4.2	6.1	5.8	4.3	8.1	7.3	3.4	2.2
Minimum	68.7	22.6	27.0	24.9	31.5	21.1	13.3	13.8	6.7
Maximum	103.0	101.8	92.9	86.9	84.4	86.1	70.6	66.3	58.9
Border Width (% of Scute Width)									
N	33	20	13	13	14	8	7	27	35
Mean	6.5	12.4	12.0	9.8	12.2	12.6	13.3	13.4	13.7
S.E.	0.5	0.5	0.6	0.7	0.7	1.1	0.7	0.4	0.5
Minimum	0.0	6.3	8.7	5.7	8.6	7.3	10.2	9.3	7.6
Maximum	15.4	16.4	16.9	15.6	20.0	17.3	15.5	17.3	20.0
Plastral Figure Area (% of Plastral Area)									
N	31	20	13	13	14	8	7	27	35
Mean	20.0	12.7	7.5	7.5	7.7	3.3	0.5	3.7	4.2
S.E.	1.6	2.0	1.4	1.6	2.4	1.3	0.3	1.2	0.9
Minimum	5.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum	39.1	32.1	15.6	17.3	24.1	10.4	1.9	21.9	24.0
Solid Plastral Figure Area (% of Plastral Area)									
N	31	20	13	13	14	8	7	27	35
Mean	25.4	15.1	14.5	14.4	12.9	8.5	1.3	8.1	5.4
S.E.	1.6	2.4	3.0	3.2	3.8	3.1	0.8	2.3	1.1
Minimum	7.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum	44.3	38.0	32.1	34.1	33.9	19.3	4.7	42.1	27.7

Key: *C. p. m.* = *Chrysemys picta marginata*, WE = Weybridge, WA = Washington, ES = Essex County, PO = Pownal, TU = Tunbridge, WF = Weathersfield, GU = Guilford, *C. p. p.* = *Chrysemys picta picta*.

Table 3. Significant differences between the nine samples of this study. If a letter is present, the two samples are significantly different from each other for that characteristic. If — is present, the two samples are not significantly different for any characteristic.

	C. p. m.	WE	WA	ES	PO	TU	WF	GU	*C. p. p.*
C. p. m.	D,B,F,S	D,B,F,S	D,B,F,S	D,B,F,S	D,B,F,S	D,B,F,S	D,B,F,S	D,B,F,S	
WE	D,B,F,S		F	B,F	F	F	D,F,S	D,F,S	D,F,S
WA	D,B,F,S	F		B	—	—	D,F,S	D	D,B,S
ES	D,B,F,S	B,F	B		B	B	D,B,F,S	D,B	D,B,S
PO	D,B,F,S	F	—	B		—	D,F,S	D	D,S
TU	D,B,F,S	F	—	B	—		D	D	D
WF	D,B,F,S	D,F,S	D,F,S	D,B,F,S	D,F,S	D		—	—
GU	D,B,F,S	D,F,S	D	D,B	D	D	—		D
C. p. p.	D,B,F,S	D,F,S	D,B,S	D,B,S	D,S	D	—	D	

Key: *C. p. m.* = *Chrysemys picta marginata*, WE = Weybridge, WA = Washington, ES = Essex County, PO = Pownal, TU = Tunbridge, WF = Weathersfield, GU = Guilford, *C. p. p.* = *Chrysemys picta picta*. D = Scute Disalignment, B = Border Width, F = Plastral Figure, S = Solid Plastral Figure.

smallest scute disalignment, and was significantly smaller than all other samples (LSD post hoc, $p < 0.05$) except Weathersfield (LSD post hoc, $p > 0.05$). The seven Vermont samples were intermediate to *marginata* and *picta*. The Guilford and Weathersfield mean disalignments were much closer to *picta* than to *marginata*, not significantly different from each other, and significantly less than all others except *picta* (LSD post hoc, $p < 0.05$).

There was a significant difference in mean border width of the anterior edge of the second costal scute, as a percentage of the width of that scute, in *Chrysemys picta* from the nine sites (ANOVA, $p < 0.001$; Fig. 6). *C. p. marginata* had the smallest average border width, which was significantly smaller than that of all other samples (LSD post hoc, $p < 0.001$). *C. p. picta* had the largest border width, which was significantly larger than *marginata*, Washington, and Essex (LSD post hoc, $p < 0.001$). Again, all Vermont samples were intermediate to *marginata* and *picta*. Essex was significantly different from all other samples (LSD post hoc, $p < 0.05$), and was the closest of the Vermont samples to *marginata*. The other Vermont samples were more similar to *picta* than to *marginata*.

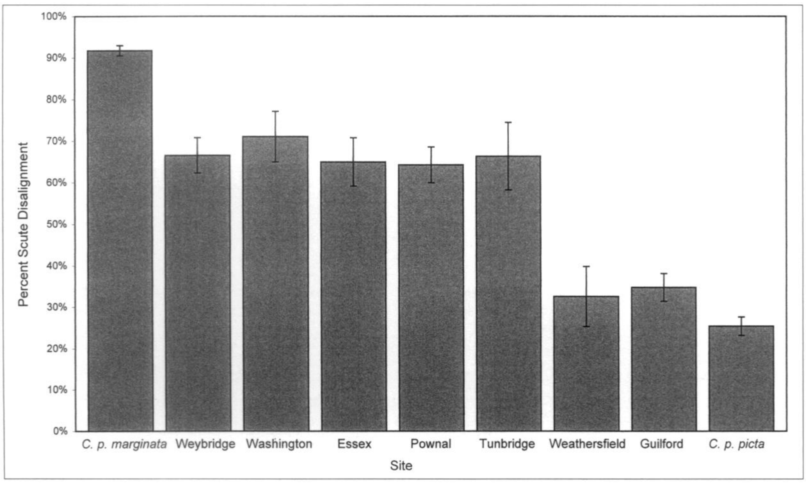

Figure 5. Plot of mean (± SE) percent disalignment of the posterior edges of the second costal and second vertebral scutes in *Chrysemys picta* for all nine areas sampled. Disalignments for the nine samples were significantly different from one another (Kruskal-Wallis, $p < 0.001$). The *C. p. marginata* sample was significantly larger than all other groups (LSD post hoc, $p < 0.001$). *C. p. picta* was significantly smaller than all other samples (LSD post hoc, $p < 0.05$) except Weathersfield (LSD post hoc, $p > 0.05$). The Guilford and Weathersfield samples are significantly less than *marginata*, Weybridge, Washington, Essex, Pownal, and Tunbridge (LSD post hoc, $p < 0.05$), but are not significantly different from each other. This suggests that Weathersfield and Guilford are *picta* populations and other Vermont sites are intergrade populations.

The mean standardized plastral figure area was significantly different between the nine samples (Kruskal-Wallis, $p < 0.001$; Fig. 7). *C. p. marginata* had the largest average plastral figure, and was significantly greater than all other groups (LSD post hoc, $p < 0.05$). The Weybridge site had the next largest plastral figure, and was significantly different from all other groups (LSD post hoc, $p < 0.05$). Interestingly, *picta* did not have the smallest plastral figure. Guilford, Tunbridge, and Weathersfield had smaller mean plastral figures than did *picta*, although these differences were not significant. The intermediate samples of Pownal, Washington, and Essex were significantly different from Weathersfield (LSD post hoc, $p < 0.05$).

There was also a significant difference in the mean standardized solid plastral figure area for *Chrysemys picta* from the nine sites (Kruskal-Wallis, $p < 0.001$; Fig. 8). Similar to the data on the plastral figure area, *marginata* had the largest solid plastral figure, which was significantly larger than all other groups (LSD post hoc, $p < 0.05$). *C. p. picta* had the second smallest solid plastral figure, surpassed only by Weathersfield. Both *picta* and Weathersfield had significantly smaller solid plastral figure areas than *marginata*, Weybridge, Washington, Essex, and Pownal (LSD post hoc, $p < 0.05$). Tunbridge,

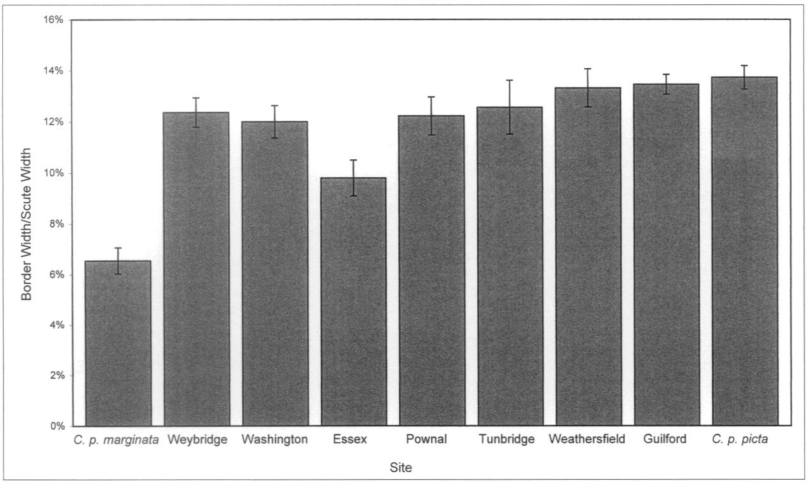

Figure 6. Plot of mean (± SE) percent border width of the anterior edge of the second costal scute, in *Chrysemys picta* from all 9 areas sampled. These percentages were obtained by dividing the width of the anterior border of the second costal scute by the width of that scute. Border widths were significantly different between groups (ANOVA, $p < 0.001$). *C. p. marginata* had a significantly smaller border width than all other samples (LSD post hoc, $p < 0.001$). Similarly, Essex was significantly different from all other samples (LSD post hoc, $p < 0.05$). Additionally, Washington had a significantly narrower border width than *C. p. picta* (LSD post hoc, $p < 0.05$).

Guilford, and Weathersfield were closer in mean value to *picta* than to *marginata*, while the other Vermont samples (Weybridge, Washington, Essex, and Pownal) were closer to *marginata*.

For all individual Vermont samples, the only significant correlation was between plastral figure and solid plastral figure (Pearson's r, $p < 0.05$), which would be expected as they are derived measures of the same characteristic. In the typical *marginata* population, the two measures of plastral figure were correlated, as were percent scute disalignment and plastral figure (Pearson's r, $p < 0.05$). In the typical *picta* population, the two measures of plastral figure were correlated, as were border width and plastral figure, and border width and solid plastral figure (Pearson's r, $p < 0.05$).

DISCUSSION

The primary results of this study suggest that many of Vermont's Painted Turtles are intergrades between *marginata* and *picta*, although a few populations in the southeast corner of the state are *picta*. The amount of influence from the two subspecies differs depending on location in the state, but not necessarily by drainage. The

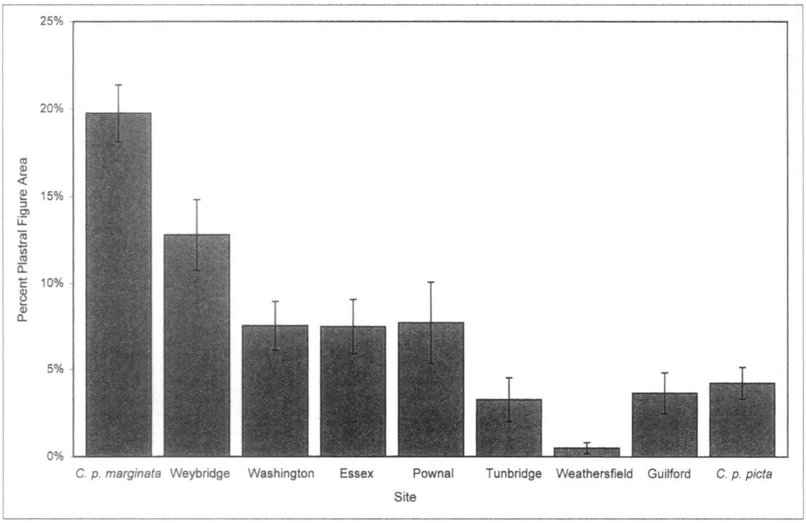

Figure 7. Plot of mean (± SE) plastral figure area, in *Chrysemys picta* from nine areas. Plastral figure areas were significantly different between groups (Kruskal-Wallis, $p < 0.001$). The *C. p. marginata* sample had a significantly larger mean plastral figure area than all other groups (LSD post hoc, $p < 0.05$). The Weybridge sample was significantly different from all other groups (LSD post hoc, $p < 0.05$). Additionally, Washington, Essex, and Pownal were significantly different from Weathersfield (LSD post hoc, $p < 0.05$).

collections also provide new records that extend *C. picta*'s documented range in Vermont.

At four of the seven Vermont sites, turtles were intermediate to the two typical subspecies for all characteristics, and did not show the correlations between characteristics shown in the typical parent populations. Lower Connecticut River drainage turtles (from Tunbridge, Weathersfield, and Guilford) were significantly more like *picta* than other Vermont populations, which partially supported our second hypothesis.

These data suggest that Vermont's turtles are unlike "typical" *marginata*. All of the Vermont samples were significantly different from *marginata* for all characteristics.

The Weathersfield and Guilford populations can be considered to be *picta*, as Weathersfield is not significantly different from *picta* for any characteristic, and Guilford is significantly different from *picta* only for percent disalignment, but is much closer in mean disalignment value to *picta* than to *marginata*. These two Vermont samples, like *picta*, are significantly different from other Vermont samples for some, if not all, characteristics. However, the Weathersfield and Guilford

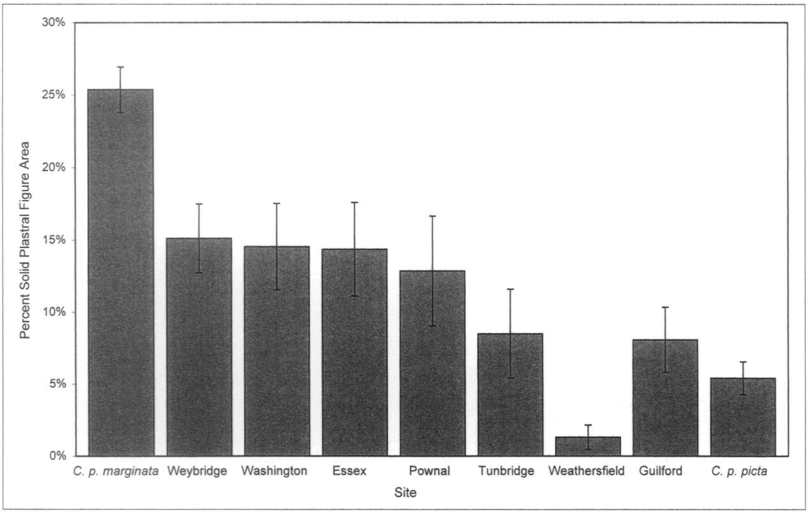

Figure 8. Plot of mean (± S.E.) percent solid plastral figure area in *Chrysemys picta* from nine areas. Percent solid plastral figure areas were significantly different between groups (Kruskal-Wallis, $p < 0.001$). The percent solid plastral figure area of the *C. p. marginata* sample was significantly larger than that of all other groups (LSD post hoc, $p < 0.01$). The Weybridge sample had a significantly larger mean solid plastral figure area than Weathersfield, Guilford, and *picta* (LSD post hoc, $p < 0.05$). *C. p. picta* and Weathersfield had significantly smaller solid plastral figure areas than *marginata*, Weybridge, Washington, Essex, and Pownal (LSD post hoc, $p < 0.05$).

samples do not show the correlations between characteristics that the *picta* sample shows. Weathersfield and Guilford only show correlations between plastral figure and solid plastral figure, while the *picta* sample additionally shows border width-plastral figure and border width-solid plastral figure correlations. This suggests that, while the Weathersfield or Guilford population as a whole can be classified as *picta*, any individual turtle would not look like a typical *picta*, but would show more influence from the *marginata* gene pool than does the typical *picta* sample.

Weybridge, Washington, Essex, and Pownal are very similar to each other. They are intermediate to *marginata* and *picta* for every characteristic, but are significantly different from both parent populations for many, if not all characteristics. These samples can be classified as intergrade populations. They do not show the correlations that the parent populations show, which suggests that any one of these turtles does not look like a typical *marginata* or *picta*, but instead shows a mixture of characteristics that do not allow the population to be classified as either *marginata* or *picta*.

The Tunbridge sample cannot be classified as clearly as the other samples. It shows a relatively large scute disalignment (a *marginata* characteristic), a relatively large border width (a *picta* characteristic), a small plastral figure (a *picta* characteristic), and a small solid plastral figure (a *picta* characteristic). It is significantly different from *picta* only for percent disalignment, which suggests it could be classified as *picta*. However, it is not significantly different from Pownal or Washington for any characteristic, and is only different from Weybridge and Essex for one characteristic, which suggests it could be classified as an intergrade population. It appears to be intermediate between an intergrade population and *picta*, potentially because it is further northwest than Weathersfield and Guilford (Fig. 3).

It was not feasible to compare border width or plastral figure across most studies, as there has been no consistent method for recording and reporting these characteristics. However, Ultsch et al. (2001) recently provided large sample sizes of "typical" *marginata* and *picta* populations with suggested values for each characteristic that would allow objective classification of painted turtles. They suggest that *picta* should show a percent scute disalignment of ±43%, a border width of 1.9–2.9% of carapace length, and a plastral figure (equivalent to my solid plastral figure) of ±9% of plastral area. *C. p. marginata* should show a percent scute disalignment of 85–93%, a border width of 1.1–1.7% of carapace length, and a plastral figure of 17–28% of plastral area. Anything between these values for *picta* and *marginata* is an intergrade. To compare to their data, we divided the border width data by carapace length instead of scute width (Table 4), and then classified each sample. Because any one turtle can show substantial individual variation and is not necessarily representative of the population (for example, the Vermont turtle with the largest solid plastral figure came from Guilford, which had the second smallest mean solid plastral figure of all Vermont samples), it is necessary to classify samples as opposed to individual turtles.

For all characteristics, our "typical" populations of *marginata* and *picta* were classified as *marginata* and *picta*, respectively, using values suggested by Ultsch et al. (2001). If each sample is classified based on 2 out of 3 according characteristics (Hartman 1958), then Weybridge, Washington, Essex, and Pownal are intergrade populations, and Tunbridge, Weathersfield, and Guilford are *picta*. This classification agrees for the most part with our conclusions, aside from the classification of Tunbridge, which was intermediate between an intergrade and *picta* population.

Apart from the recent study by Ultsch et al. (2001), it was possible to compare only the characteristic of percent scute disalignment from studies in different areas (Ernst 1967, Ernst and Ernst 1971, Ernst and Fowler 1977, Gordon 1990, Groves 1983, Hartman 1958, Pough and Pough 1968, Rhodin and Butler 1997, Waters 1964). Interestingly, when these disalignments were examined, there appeared to be a large gap in values between Pinchot State Park, York County, PA (52.4%; Ernst and Ernst 1971) and Coteau Landing, Quebec (79.2%; Gordon 1990), into which only Vermont's intergrade populations (Weybridge, Washington, Essex, and Pownal, with a mean of 66.7%) fell. This may suggest that Vermont is part of an area of high-degree intergrades, as hypothesized by Rhodin and Butler (1997). High-degree intergrades are intergrades that show a large amount of influence from the *marginata* gene pool, while low-degree intergrades show little influence from the *marginata* gene pool. However, Rhodin and Butler (1997) suggested that all of Vermont should be high-degree intergrades, which was not supported

Table 4. Descriptive statistics for all painted turtles examined in this study for the characteristic of border width as a percentage of carapace length. According to Ultsch et al.'s (2001) classification values, *C.p.m.* is *marginata*, Essex is an intergrade population, and all others are *picta*.

	C. p. m.	WE	WA	ES	PO	TU	WF	GU	*C. p. p.*
Border Width (% of Carapace Length)									
N	33	20	13	13	14	8	7	27	35
Mean	1.31	2.42	2.27	1.88	2.22	2.44	2.56	2.64	2.76
S.E.	0.10	0.11	0.11	0.11	0.10	0.20	0.13	0.08	0.09
Minimum	0	1.36	1.63	1.21	1.65	1.4	1.93	1.74	1.62
Maximum	3.27	3.28	3.31	2.42	3.16	3.33	2.93	3.43	4.07

Key: *C. p. m.* = *Chrysemys picta marginata*, WE = Weybridge, WA = Washington, ES = Essex County, PO = Pownal, TU = Tunbridge, WF = Weathersfield, GU = Guilford, *C. p. p.* = *Chrysemys picta picta*.

by our data from the southeast corner of Vermont. More samples must be analyzed from this hypothesized area of high-degree intergrades to come to any conclusions. The gap in disalignment values could simply be caused by the lack of data and reports in the regions immediately surrounding Vermont.

The results of this study do not shed much light on dispersal theories (Bleakney 1958a, 1958b; Pough and Pough 1968; Waters 1964). If our hypothesis was fully supported, Pownal and Essex should have shown more influence from *picta* than they did. Perhaps Pownal was too close to the Lake Champlain drainage, and Essex to the Lake Memphremagog drainage, to show significant influence from the *picta* gene pool. However, it is clear that turtles from the southeast corner of the state (lower Connecticut River drainage) are much more influenced by the *picta* gene pool than are the rest of Vermont's painted turtles.

In the larger picture, studies must be performed over the entire geographic range of *Chrysemys picta* to shed light onto dispersal theories, including that of Rhodin and Butler (1997) with their suggestion of high-degree and low-degree intergrades. In particular, areas directly surrounding Vermont and the watersheds of the Northeast could aid in this clarification. Future studies should ideally employ a combination of morphological characteristics and molecular techniques (Waters 1969), which together will help elucidate these theories.

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