VARIATION IN SHELL MORPHOLOGY OF NORTH AMERICAN TURTLES
I. THE CARAPACIAL SEAM ARRANGEMENTS

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This study is the first of two papers devoted to variations in the arrangements and relative size of the laminae of North American turtles, and in the position of seams between some of the carapacial laminae. These studies have been supported by a grant from the American Philosophical Society to which I express my appreciation. I am also indebted to many individuals and institutions for permitting me to examine their research collections, particularly to Archie Carr and Walter Auffenberg at the University of Florida, Fred R. Cagle and Harold Dundee at Tulane University, Doris Cochran at the United States National Museum, and Norman Hartweg, at the University of Michigan. The terminology for carapace and plastral structures are those of Carr (1952) to which the reader is referred for details.

Tinkle (1958) demonstrated that the positions of the contacts of the seams between the lateral laminae of the carapace with the marginal laminae, or with the seams between the latter were variable and sometimes could be used to indicate divergence of turtles *(Sternothaerus)* at the infrasubspecific level. Because the number of laminae of the trutle shell is so constant, there are few morphological characters that can be used to show such divergence. Therefore, our knowledge of variation below the species level in turtles is not as detailed as in many reptiles in which scutellation is more variable than in turtles.

This study was undertaken to determine the extent of variation in carapace characters in several species of North American turtles to show how these data might be useful as taxonomic criteria at several taxonomic levels, as indications of genetic divergence at an infrasubspecific level, and as an aid to paleontologists who sometimes use these characters in studies of fossil turtles without sufficient information of the extent of their variation in recent species.

Only turtles without obvious abnormalities such as supernumerary laminae or obviously malformed ones were used. Several studies on abnormalities in the turtle shell have appeared (Newman, 1906; Coker, 1910; Zangerl and Johnson, 1957) with various interpretations of the increase or decrease in number or of the odd arrangements. In each turtle examined, note was made whether the seams between lateral laminae contacted the anterior half of a marginal, the posterior half, or the midline, as determined with dividers. In some instances the interlateral seam contacted an intermarginal seam. For a more thorough discussion of these conditions see Tinkle *(op. cit.)*. The sex, carapace length plastron length, number of "annuli", and the length of each plastral lamina was determined. The data on plastral morphology will appear in another paper.

Interlateral Seam Contacts

The five carapacial seams contacting the marginal laminae were designated from anterior to posterior as A, B, C, D, and E. If the A seam contacted a marginal in the anterior one-half, at the midpoint, or in the posterior one-half, these contacts would be designated 1<, 1½ and 1>, respectively. The data for the contacts of each of the five seams are shown in Tables 1 to 5; the tables are discussed below.

The position of contacts of seam A, which lies between the precentral lamina and the first lateral lamina, shows striking similarity in most species (Table 1). The kinosternids (*sensu* Williams, 1950) are the most divergent from the other species; of these, *Chelydra and Macroclemmys* may be the most primitive. At least, the fossil record of these extends further back than that of the other kinosternids. Sufficient data are lacking for *Macroclemmys,* but *Chelydra* has a seam A contact with its highest frequency at 2>, a position found in only 5 of 2177 non-kinosternid turtles. *Chelydra* also has a high frequency (40%) of contacts between seam A and 2<, a contact relatively infrequent in most turtles, but common in some kinosternids and in *Chelonia.*

TABLE 1.
Seam A contacts in turtles *

Species	1<	1½	1>	s2	2<	2½	2>	s3	3<
Chelonia mydas (31)					100				
Chelydra serpentina (110)			1		40	6	54		
Macroclemmys temmincki (10)					100				
Kinosternon subrubrum (164)	3	1	87	8	1				
Kinosternon flavescens (43)			19	16	65				
Kinosternon sonoriense (23)				4	96				
Kinosternon bauri (52)	2	4	90	4					
Sternothaerus odoratus (847)	26	10	63	1					
Sternothaerus minor (422)	62	21	18						
Sternothaerus depressus (41)	63	32	5						
Sternothaerus carinatus (87)	61	20	20						
Gopherus polyphemus (36)			94	3	3				
Terrapene carolina (144)			99	1					
Terrapene ornata (63)			100						
Emys blandingi (44)			2		96		2		
Clemmys guttata (33)			49	42	9				
Clemmys muhlenbergi (13)			92	8					
Clemmys insculpta (19)	11	11	79						
Clemmys marmorata (5)				20	80				
Malaclemmys terrapin (34)			62	21	18				
Graptemys geographica (25)			56	40	4				
Graptemys pseudogeographica (168)	1	1	95	2	1				
Graptemys kohni (158)	5	3	91	1					
Graptemys versa (64)	9	5	83	3					
Graptemys barbouri (139)	1	1	99						
Graptemys pulchra (146)	6	5	89						
Graptemys oculifera (100)	1		99						
Graptemys flavimaculata (64)			100						
Graptemys nigrinoda (87)	1	3	95						
Pseudemys scripta (347)	12	2	86						
Pseudemys floridana (190)	3	6	89	2					
Chrysemys picta (212)	1	1	62	28	8	1	1		
Deirochelys reticularia (53)	4				91	2	2		
Totals 3975	16	6	66	4	7	0	2		

* Numerals at top indicate marginal laminae; the letter s denotes a seam. Figures in the table are percentages. Number of specimens examined is shown after species name. Figures may not add to 100% because all were rounded to nearest whole per cent.

Kinosternon flavescens and *K. sonoriense* are divergent from the other *Kinosternon* and show closer relationship to each other than to *K. subrubrum* and *K. bauri,* as should be expected. The contact percentages are much the same for *Sternothaerus* species except *S. odoratus* which is considerably different from the other species in the genus in having a low percentage of contacts at 1<. Most emydid species show more than 75% of the individuals with a seam A contact at 1>. Exceptions are *Emys blandingi*[1] *with* 96% at 2< and *Dierochelys reticularia* with 91% at the same point. *Clemmys guttata* (49%), *Malaclemmys terrapin* (62%), *Graptemys geographica* (56%) and *Chrysemys picta* (62%) have less than 75% of the contacts at 1>. Most *Pseudemys* and *Graptemys* are much the same in percentage contacts.

In 66% of the 3824 turtles studied, seam A contacts 1>, and in 88% of all specimens the contact is in the first marginal. The contact most frequent in 3 species (9%) is at 1<, at 1> in 22 (67%), at 2< in 7 (21%), and at 2> in 1 (3%).

Chelydra serpentina is the most divergent species in seam B contacts; there is no overlap with any other species studied (Table 2). The contacts of seam B are between 4> and 5> in 98% of the 3962 specimens examined and in 97% of the species. In 26 (82%) species the contact is somewhere on the fifth marginal. Seam

[1] The author has retained this combination throughout the paper because of its familiarity. Loveridge and Williams (1957) have indicated that *Emys blandingi* should be restricted to the monotypic genus *Emydoidea.*

B most commonly contacted 4> in 2 species (6%), seam 5 in 3 (9%), 5< in 22 (69%), 5> in 4 (13%), and 6< in 1 (3%). The emydid turtles are not so uniform in this contact as in seam A contacts. Fifteen species have the most common contact at 5<, two at 5>, three at s5 and one at 4>. The kinosternids, except *Chelydra* and probably *Macroclemmys,* are fairly uniform with six of eight species having the most common contact at 5< and two at 5>.

Seam C contacts were studied in 3945 specimens (Table 3). In 90% of these, the contacts were on the seventh marginal, with about equal numbers of contacts on the anterior (41%) and posterior (46%) portions. Of the 32 species examined, 88% had the most common point of contact on the seventh marginal. Two species were conspicuously divergent: *Gopherus polyphemus* shows 32 (91%) of the specimens with the most frequent contact of seam C at 6< and *Chelydra serpentina,* at the other extreme, has 95% of 104 specimens with contact at 8>. The kinosternids, exclusive of *Chelydra* and probably *Macroclemmys,* are fairly consistent with 6 of 8 species having 7> as the most frequent point of contact and two of eight with 7< most frequent. The emydid turtles were less consistent with 6>, s7, 7< and 7> the most common contact points in one, one, 14 and five species, respectively. Seam C most frequently contacted 6< in 1 (3%) of the species studied, 6> in one, s7 in one, 7< in 16 (50%), 7> in 12 (38%) and 8> in one.

The contact of seam D with the marginals was examined in 3957 specimens (Table 4). Ninety-one percent had a seam D contact at the ninth marginal. In 88% of the 33 species studied, the ninth marginal was the most frequently contacted.

TABLE 2.
Seam B contacts in turtles *

Species	3>	s4	4<	4½	4>	s5	5<	5½	5>	s6	6<	6½	6>
Chelonia mydas (31)	3				3	13	77		3				
Chelydra sepentina (110)											93	4	4
Macroclemmys temmincki					no analysis possible								
Kinosternon subrubrum (164)							48	6	46	1			
Kinosternon flavescens (43)							98		2				
Kinosternon sonoriense (23)							70	13	17				
Kinosternon bauri (52)							96	2	2				
Sternothaerus odoratus (845)							71	8	22				
Sternothaerus minor (422)							61	20	19				
Sternothaerus depressus (41)							12	34	54				
Sternothaerus carinatus (87)							28	31	41				
Gopherus polyphemus (35)			11	3	86								
Terrapene carolina (143)							22	10	69				
Terrapene ornata (63)					2		5	5	89				
Emys blandingi (44)						2	91		7				
Clemmys guttata (35)							57	14	29				
Clemmys muhlenbergi (13)						15	85						
Clemmys insculpta (19)							100						
Clemmys marmorata (5)							60	40					
Malaclemmys terrapin (34)					9	3	88						
Graptemys geographica (25)							100						
Graptemys pseudogeographica (169)					2	10	88						
Graptemys kohni (158)					1	14	85						
Graptemys versa (64)					22	38	41						
Graptemys barbouri (139)		1			33	39	27						
Graptemys pulchra (146)					44	38	18						
Graptemys oculifera (99)					30	56	14						
Graptemys flavimaculata (62)					10	32	58						
Graptemys nigrinoda (88)					35	47	18						
Pseudemys scripta (347)							99		1				
Pseudemys floridana (192)						4	95	1					
Chrysemys picta (211)						1	90	4	5				
Deirochelys reticularia (53)							100						
Totals 3962					6	8	63	6	15		3		

* Numerals at top indicate marginal laminae; the letter s denotes a seam. Figures in the table are percentages. Number of specimens examined is shown after species name. Figures may not add to 100% because all were rounded to nearest whole per cent.

The most divergent species are *Gopherus polyphemus* in which 77% of 35 individuals had a contact at 8>, and *Chelydra serpentina* and *Macroclemmys temmincki* in which 84% and 91%, respectively, had the most frequent contact at 10>. The kinosternine species are quite uniform. The most frequent contact is at 9< in seven of eight species and at s9 in the other. The emydid turtles, likewise, are extremely uniform with 20 of the 21 species having the most frequent contact at 9<. Of 33 species studied, one (3%) had 8> as the most frequent seam D contact; one (3%) had s9, 28 (85%) had 9<, one (3%) had 9> and two (6%) had 10>.

Seam E contacts were analyed in 3947 specimens (Table 5). Sixty-seven percent had a contact at 11< and an additional 23% at the s11 seam preceding that lamina. *Chelydra serpentina* and *Macroclemmys temmincki,* once again, were widely divergent from the other species with 84% of 107 specimens and 100% of 11 specimens, respectively, having a 12> contact. The kinosternids show considerable variability, with the most frequent contact at 10>, s11, and 11< in two, four, and two species respectively. Of the other species, *Gopherus* is unusual in having the most frequent contact of seam E on the tenth rather than the eleventh marginal. The emydids are, again, uniform with all species having the most frequent contact on the anterior half of the eleventh marginal. Of 33 species studied the most frequent contact was at 10>, s11, 11< and 12> in three (9%), four (12%), 24 (73%) and two (6%) species, respectively.

Discussion of Modal Formulae For Seam Contacts

The modal formula for seam contacts can be determined by the most frequent

TABLE 3.
Seam C contacts in turtles *

Species	6<	6½	6>	s7	7<	7½	7>	s8	8<	8½	8>	s9
Chelonia mydas (31)			3				97					
Chelydra sepentina (110)									5	1	95	
Macroclemmys temmincki					No analysis possible							
Kinosternon subrubrum (163)					26	2	70	2				
Kinosternon flavescens (43)					9	12	77	2				
Kinosternon sonoriense (23)					48	22	30					
Kinosternon bauri (52)					62	6	33					
Sternothaerus odoratus (839)					4	2	89	4				
Sternothaerus minor (421)					2	5	92	2				
Sternothaerus depressus (41)					5	20	76					
Sternothaerus carinatus (87)					8	23	69					
Gopherus polyphemus (35)	91		10									
Terrapene carolina (142)					11	3	85	1				
Terrapene ornata (63)						2	98					
Emys blandingi (44)					5		95					
Clemmys guttata (35)					31	3	66					
Clemmys muhlenbergi (13)					92	8						
Clemmys insculpta (19)					100							
Clemmys marmorata (5)					60		40					
Malaclemmys terrapin (34)					100							
Graptemys geographica (25)					100							
Graptemys pseudogeographica (169)			2	11	88							
Graptemys kohni (158)			1	4	94							
Graptemys versa (64)				3	97							
Graptemys barbouri (139)				2	98							
Graptemys pulchra (147)				10	90							
Graptemys oculifera (99)			3	39	58							
Graptemys flavimaculata (61)			8	51	41							
Graptemys nigrinoda (83)			60	34	6							
Pseudemys scripta (346)					95	2	3					
Pseudemys floridana (192)				2	98		1					
Chrysemys picta (211)					45	6	49					
Deirochelys reticularia (52)					75	8	17					
Totals 3945	1		2	4	41	3	46	1			3	

* Numerals at top indicate marginal laminae; the letter s denotes a seam. Figures in the table are percentages. Number of specimens examined is shown after species name. Figures may not add to 100% because all were rounded to nearest whole per cent.

TABLE 4.
Seam D contacts in turtles *

Species	8<	8½	8>	s9	9<	9½	9>	s10	10<	10½	10>
Chelonia mydas (31)			3		74		23				
Chelydra serpentina (109)									10	6	84
Macroclemmys temmincki (11)									9		91
Kinosternon subrubrum (162)				2	97		1				
Kinosternon flavescens (43)					91	5	5				
Kinosternon sonoriense (23)					96	4					
Kinosternon bauri (51)					100						
Sternothaerus odoratus (842)				2	96		1				
Sternothaerus minor (422)			2	31	67						
Sternothaerus depressus (41)			24	54	22						
Sternothaerus carinatus (87)				7	91	1	1				
Gopherus polyphemus (35)	20	3	77								
Terrapene carolina (145)					65	10	25				
Terrapene ornata (63)					91	3	6				
Emys blandingi (44)					18	5	77				
Clemmys guttata (35)					74	11	14				
Clemmys muhlenbergi (12)					92	8					
Clemmys insculpta (19)					95		5				
Clemmys marmorata (5)					60	20	20				
Malaclemmys terrapin (32)					66	9	25				
Graptemys geographica (25)					100						
Graptemys pseudogeographica (169)				1	97	2					
Graptemys kohni (158)					99		1				
Graptemys versa (64)					100						
Graptemys barbouri (139)				1	94	4	1				
Graptemys pulchra (147)					97	2	1				
Graptemys oculifera (100)					96	3	1				
Graptemys flavimaculata (64)			2	3	95						
Graptemys nigrinoda (87)				6	94						
Pseudemys scripta (342)					83	6	11				
Pseudemys floridana (192)			1		82	7	10				
Chrysemys picta (209)					63	7	30				
Deirochelys reticularia (51)			2	2	57	14	26				
Totals 3957			1	5	82	3	6				3

* Numerals at top indicate marginal laminae; the letter s denotes a seam. Figures in the table are percentages. Number of specimens examined is shown after species name. Figures may not add to 100% because all were rounded to nearest whole per cent.

point of contact of each interlateral seam with a marginal or intermarginal seam. The modal for all turtles studied is shown in Table 6.

Similarly, a modal formula can be devised for each genus. These formulae obviously cut across taxonomic lines with two genera in the same family having widely differing modal formulae (Table 7). Thus, although four genera of emydids have the same modal formula, another shares a different formula with *Sternothaerus*, while others have unique formulae. Therefore, it is not possible to choose a formula except in *Gopherus, Chelydra,* and *Macroclemmys* which will show little overlap with other species; not even in these genera would such a formula have taxonomic value. However, a *particular* seam contact does have taxonomic value at the generic or species level in indicating degree of divergence in such closely related genera as *Pseudemys* and *Graptemys, Sternothaerus* and *Kinosternon* and between the species of these genera.

Taxonomic Consideration of Specific Seam Contacts

Refer to the list of species and their respective modal formulae for the percentage of each contact and for a listing of the number of individuals of each species examined (Table 8).

Seam A Contacts: *Chelydra serpentina* is unique in having most of the seam A contacts at 2>. Ninety percent of *Kinosternon bauri* and 87% of *K. subrubrum* have this contact at 1>, while only 19% of *K. flavescens* and no *K. sonoriense* show this contact. Also, 65% of *flavescens,* 96% of *sonoriense* have a contact at 2< which

TABLE 5.
Seam E contacts in turtles *

Species	10>	s11	11<	11½	11>	s12	12<	12½	12>
Chelonia mydas (31)			97	3					
Chelydra serpentina (107)							9	7	84
Macroclemmys temmincki (11)									100
Kinosternon subrubrum (150)	8	88	4						
Kinosternon flavescens (42)	76	21	2						
Kinosternon sonoriense (22)	55	45							
Kinosternon bauri (51)	25	63	12						
Sternothaerus odoratus (833)	1	29	70						
Sternothaerus minor (422)	1	58	41						
Sternothaerus depressus (41)	5	61	34						
Sternothaerus carinatus (87)		14	85	1					
Gopherus polyphemus (35)	77	6	17						
Terrapene carolina (142)	2		89	3	6				
Terrapene ornata (63)	13	6	79	2					
Emys blandingi (44)			91	5	5				
Clemmys guttata (35)		9	91						
Clemmys muhlenbergi (12)		8	92						
Clemmys insculpta (19)	5	5	79	11					
Clemmys marmorata (5)		20	80						
Malaclemmys terrapin (34)	3	3	85		9				
Graptemys geographica (25)			92	4	4				
Graptemys pseudogeographica (169)	9	21	68	1	1				
Graptemys kohni (158)	1	10	88		1				
Graptemys versa (64)	2	2	91	2	5				
Graptemys barbouri (139)		5	94		1				
Graptemys pulchra (150)	1	15	80	3	2				
Graptemys oculifera (100)		1	83	11	5				
Graptemys flavimaculata (64)		6	91	2	2				
Graptemys nigrinoda (87)		3	87	2	7				
Pseudemys scripta (344)	7	6	86	1					
Pseudemys floridana (192)	9	9	81		2				
Chrysemys picta (210)	5	12	81	1	1	1			
Deirochelys reticularia (49)	2	10	86	2					
Totals 3947	5	23	67	1	1				3

* Numerals at top indicate marginal laminae; the letter s denotes a seam. Figures in the table are percentages. Number of specimens examined is shown after species name. Figures may not add to 100% because all were rounded to nearest whole per cent.

occurs in one percent of *K. subrubrum,* not at all in *K. bauri.*

Among sternothaerine turtles, only *S. odoratus,* probably the oldest phylogenetically of this group (Tinkle, 1958), shows considerable overlap in position of seam A contacts with species of *Kinosternon. Sternothaerus minor, S. depresssus* and *S. carinatus* have, respectively, 83%, 95% and 81% of the contacts at 1< or 1½; i.e. at or anterior to the midpoint of the first marginal. Contact is in similar positions in a maxmum of 6% of any species of *Kinosternon* in which the majority of contacts are at 1> or posterior to this point. The usefulness of these contacts for distinguishing between species of *Sternothaerus* are quite limited and have been discussed previously in sufficient detail (Tinkle *op. cit.*). *Sternothaerus odoratus* has not been discussed previously, but on the basis of this contact further reason exists for considering *S. odoratus* divergent from other species of the genus. It shows at 1> a frequency of 63% compared to a high of 20% in any other species of *Sternothaerus.*

TABLE 6.
Modal formula for seam contacts in 33 species of turtles

	% of species	% of individuals
A - m 1 (>½)	67	66
B - m 5 (<½)	69	63
C - m 7 (<½)	50	41
D - m 9 (<½)	85	82
E - m 11 (<½)	73	67

Among the species of *Graptemys,* the percentage of contacts at 1> are above 83% in all species except *Graptemys geographica* (56%) which is most divergent from the other species.

TABLE 7.
Modal formula for each genus

1> 5< 7< 9< 11<	Clemmys (68), Malaclemmys (34), Graptemys (952), Pseudemys (537)
1> 5< 7> 9< 11<	Chrysemys (213), Sternothaerus (1397)
1> 5< 7> 9< s11	Kinosternon (281)
1> 5> 7> 9< 11<	Terrapene (207)
1> 4> 6< 8> 10>	Gopherus (36)
2< 5< 7< 9< 11<	Deirochelys (53)
2< 5< 7> 9> 11<	Emys (44)
2< 5< 7> 9< 11<	Chelonia (31)
2> 6< 8> 10> 12>	Chelydra (110)

* Modal formulae (as in Table 6) for each genus of turtle studied. Numbers in parentheses are numbers of specimens examined in each group.

The genera *Emys* and *Deirochelys* which are similar in many other aspects have 96% and 91% of their contacts, respectively, at 2<. Such a contact occurs at most in 18% of any other emydid turtle (excluding *Clemmys marmorata* in which the sample size is too small for conclusions), and supports the conclusions reached by Loveridge and Williams (1957) of the close relationships of *Emys* and *Deirochelys*.

Seam B Contacts: In all specimens of *Chelydra,* the seam B contact is on the sixth marginal. This contact occurs in no other species of turtle examined and is hence diagnostic at the generic level. Among the other species of chelydrid turtles there are no diagnostic differences in seam B contacts. On the basis of this contact, a closer relationship exists between *Sternothaerus odoratus* and *S. minor* than between these two and other *Sternothaerus*.

Gopherus polyphemus with 86% of the contacts on 4> is fairly distinctive and overlaps to any extent only with *Graptemys pulchra.*

Among the emydid turtles, seam B contacts typically the fifth marginal anterior to the middle or contacts the fifth intermarginal seam. The contact at 5< is about twice as common or more in *Graptemys geographica G. pseudogeographica* and *G. kohni* than in the other species of *Graptemys.* Otherwise, the seam contacts reinforce concepts of relationship of *Graptemys* species based on other characters. The major exception to this statement is the big (58%) percentage of contacts at 5< in *Graptemys flavimaculata* compared with 14% in *G. oculifera* and 18% in *G. nigrinoda,* the two other members of the distinct narrow-headed (and presumably closely related) complex of *Graptemys* species in the southeastern United States (see Cagle, 1954).

Seam C Contacts: There is no overlap in seam contacts of *Chelydra serpentina* with any other species studied, so a seam C contact on the eighth marginal can be considered a diagnostic generic character. Among the other chelydrids, the seam contacts are virtually limited to the seventh marginal, but there is great variability in the position of this contact in the seventh marginal so that no generalization can be made concerning them, except that in both *Kinosternon* and *Sternothaerus* the point of contact is in the middle or posterior part of the seventh marginal.

Gopherus polyphemus shows almost no overlap with any other turtle with regard to this seam contact. Ninety-one percent have a seam C contact on the anterior one-half of the sixth marginal. This contact occurs in no other species studied.

The emydid turtles are fairly consistent in having most seam C contacts at 7< or anterior to this point. The major exceptions are the two species of *Terrapene* (85% and 98% at 7>), *Emys blandingi* (95% at 7>), *Clemmys guttata* (66% at 7>) and *Chrysemys picta* (49% at 7>). This contact is found in only three other species for which sufficient numbers were available, and at most in 17% of the individuals *(Deirochelys reticularia)*. The high frequency (60%) of contacts between seam C and 6> in *Graptemys nigrinoda* is unusual. The greatest percentage shown by another *Graptemys* is eight percent by *G. flavimaculata,* a species closely related to *nigrinoda.* As a matter of fact, none of the other emydids shows a higher (than 8%) frequency of occurrence at this contact. This may be taken as evidence additional to that presented by Cagle (1954) to demonstrate the divergence of this species *nigrinoda* from others in the genus. The high frequency (49%) of seam C contacts at 7> that occurs in *Chrysemys picta* is interesting because this contact is found in only 3% of any species of *Pseudemys* examined.

Seam D Contacts: In *Chelydra* and *Macroclemmys,* the seam D contacts are on the tenth marginal, a contact not found in any specimen of other turtle species. Most of the remaining chelydrids are much alike in having 90% or more of the seam D contacts at 9<. A partial exception is *S. minor* with 67% and *S. depressus* with a low 22% showing additional evidence of the distinctiveness of this form, but a closer relationship to *S. minor* than to other sternothaerine turtles. Most of the emydid turtles have over 90% of the seam D contacts at 9<. Notable exceptions are *Emys blandingi* with only 18% and *Deirochelys* with 57%. All others are 60% or above. The *Graptemys* species all show at least 94% of the contacts at 9<.

Seam E Contacts: Chelydra and *Macroclemmys* have most of their contacts at 12> and all of them on the twelfth marginal. No other turtle was seen with this contact. In the other chelydrids the seam E contacts are almost always at 10>, s11, or 11<, but there is little consistency in which of these three contacts is most frequent. In *Kinosternon subrubrum* 88% of the specimens have an s11 contact, while in *K. flavescens* this contact occurs in 21% of the specimens. *Kinosternon flavescens* and *K. sonoriense* show closer relationship to one another in this contact, as do *K. subrubrum* and *K. bauri. Sternothaerus odoratus* and *S. carinatus* show close relationship in this character, as do *S. minor* and *S. depressus.* However, none of these contacts has a high enough frequency to be diagnostic.

Seventy-seven percent of *Gopherus polyphemus* have seam E contacts at 10>. This contact occurs in a maximum frequency of 13% of other turtles, exclusive of those of the genus *Kinosternon.*

The emydid turtles consistently have 80% or more seam E contacts at 11< with the exception of *Terrapene ornata* (79%), *Clemmys insculpta* (79%) and *Graptemys pseudogeographica* (68%). None of the contacts in emydid turtles is diagnostic.

Discussion of Taxonomic Value of Seam Contacts. Consistency of Relationships as Revealed by Percentage Contacts

With the exception of seam A contacts in which *Chelydra* shows considerable overlap with other chelydrid and emydid turtles, all other contacts of *Chelydra* are unique. The scant information available on *Macroclemmys* indicates that it, too, has the same contacts as *Chelydra.*

Chelonia is not unusual in its seam contacts and shows close relationship in this character to the emydid and kinosternid species.

In the genus *Kinosternon,* these contacts do not consistently indicate the same taxonomic relationships. Seam A contacts indicate a close relationship between *K. subrubrum* and *K. bauri* while in seam B contacts *bauri* and *flavescens* are most closely related. In seam C contacts, *bauri* and *sonoriense* are most alike. If the modal seam formula (Table 8) is considered, however, it is clearly evident that *K. subrubrum* and *K. bauri* show more likeness to one another than to *flavescens* and *sonoriense.*

TABLE 8.

Modal formulae for each turtle species for which 10 or more specimens were studied *

	N	A	B	C	D	E
Chelonia mydas	(31)	2< (100);	5< (77);	7> (97);	9< (74);	11< (97).
Chelydra serpentina	(110)	2> (54);	6< (93);	8> (95);	10> (84);	12> (84).
Kinosternon subrubrum	(164)	1> (87);	5< (48);	7> (70);	9< (97);	s11 (88).
Kinosternon flavescens	(43)	2< (65);	5< (98);	7> (77);	9< (91);	10> (76).
Kinosternon sonoriense	(23)	2< (96);	5< (70);	7< (48);	9< (96);	10> (55).
Kinosternon bauri	(51)	1> (90);	5< (96);	7< (62);	9< (100);	s11 (63).
Sternothaerus odoratus	(847)	1> (63);	5< (71);	7> (89);	9< (96);	11< (70).
Sternothaerus minor	(422)	1< (62);	5< (61);	7> (92);	9< (67);	s11 (58).
Sternothaerus depressus	(41)	1< (63);	5> (54);	7> (76);	s9 (54);	s11 (61).
Sternothaerus carinatus	(87)	1< (61);	5> (41);	7> (69);	9< (91);	11< (85).
Gopherus polyphemus	(36)	1> (94);	4> (86);	6< (91);	8> (77);	10> (77).
Terrapene carolina	(144)	1> (99);	5> (69);	7> (85);	9< (65);	11< (89).
Terrapene ornata	(63)	1> (100);	5> (89);	7> (98);	9< (91);	11< (79).
Emys blandingi	(44)	2< (96);	5< (91);	7> (95);	9> (77);	11< (91).
Clemmys guttata	(33)	1> (49);	5< (57);	7> (66);	9< (74);	11< (91).
Clemmys muhlenbergi	(13)	1> (92);	5< (85);	7< (92);	9< (92);	11< (92).
Clemmys insculpta	(19)	1> (79);	5< (100);	7< (100);	9< (95);	11< (79).
Malaclemmys terrapin	(34)	1> (62);	5< (88);	7< (100);	9< (66);	11< (85).
Graptemys geographica	(25)	1> (56);	5< (100);	7< (100);	9< (100);	11< (92).
Graptemys pseudogeographica	(169)	1> (95);	5< (88);	7< (88);	9< (97);	11< (68).
Graptemys kohni	(158)	1> (91);	5< (85);	7< (94);	9< (99);	11< (88).
Graptemys versa	(64)	1> (83);	5< (41);	7< (97);	9< (100);	11< (91).
Graptemys barbouri	(139)	1> (99);	s5 (39);	7< (98);	9< (94);	11< (94).
Graptemys pulchra	(146)	1> (89);	4> (44);	7< (90);	9< (97);	11< (80).
Graptemys oculifera	(100)	1> (99);	s5 (56);	7< (58);	9< (96);	11< (83).
Graptemys flavimaculata	(64)	1> (100);	5< (58);	s7 (51);	9< (95);	11< (91).
Graptemys nigrinoda	(87)	1> (95);	s5 (47);	6> (60);	9< (94);	11< (87).
Pseudemys scripta	(347)	1> (86);	5< (99);	7< (95);	9< (83);	11< (86).
Pseudemys floridana	(190)	1> (89);	5< (95);	7< (98);	9< (82);	11< (81).
Chrysemys picta	(213)	1> (62);	5< (90);	7> (49);	9< (63);	11< (81).
Deirochelys reticularia	(53)	2< (91);	5< (100);	7< (75);	9< (57);	11< (86).

* Number after the name is the number of specimens examined. The numbers after the contacts are the percentages of individuals of that species with such a contact.

There are two species groups recognizable in the genus *Sternothaerus,* the *carinatus* complex composed of the species *carinatus, minor* and *depressus* and the *odoratus* group consisting of a single recognized species. Seam A contacts (Table 1) reinforce this grouping as do B and C contacts, in general. Contacts of B and C seams show, in addition, a closer relationship between *odoratus* and *minor* than between *odoratus* and other species, a relationship that appears likely for many other reasons (Tinkle, 1958). However, seams C and D do not reinforce our concept of relationships because on the basis of these, *carinatus* and *odoratus* are most closely related to one another. The modal formulae for sternothaerine turtles is no more helpful in indicating the probable relationships of the species.

Terrapene carolina and *Terrapene ornata* have the same modal formulae and there are only minor differences between the two in percentage of contacts at any point.

The genera *Emys* with 96% and *Deirochelys* (92%) are the only emydid turtles with the majority of seam A contacts on the second marginal. This may indicate a close relation between the two or may indicate convergence in shell morphology not necessarily indicative of close taxonomic relationship.

With the exception of seam E contacts, the percentages of individuals of the species of *Clemmys* with a certain contact show a closer relation of *C. muhlenbergi* to *insculpta* than to *guttata.* The modal formulae for all three is very nearly the same with only seam C contacts in *guttata* showing a difference from the other two species.

The species of the genus *Malaclemmys* are probably closely related to those of the genus *Graptemys* and the percentage of each seam contact strengthens this supposition. However, it is impossible to pick one or more species of *Graptemys* to which *Malaclemmys,* on the basis of these contacts alone, can be said to be most closely allied.

The taxonomic arrangement of Cagle (1954) based on examination of large numbers of turtles of the genus *Graptemys* is followed in this paper. The reader is referred to these papers for critical evaluation of relationships. The contacts are not consistent in indicating relationships among the species or even of groups, such as the broad-head complex or the narrow-head species. The modal formulae for members of the genus *Graptemys* are not more instructional.

The two species of *Pseudemys* have the same modal formula and the percentages of contacts at each seam show remarkable similarity and consistency.

Chrysemys has a similar modal formula to that of *Pseudemys* and the percentage contacts in the painted turtles shows close relationship to *Pseudemys* in most instances, although in some contacts, particularly of seam C, the relationship is closer to some of the narrow-head members of the genus *Graptemys*.

It must be concluded that the seam contacts are not consistent in indicating a particular taxonomic relation or in strengthening those established on other bases. With

TABLE 9.

Summary of dominance of a particular seam contact in turtles

Seam	Contacts	No. of species in which dominant	Percentage of species in which dominant
A	1<	3	9
	1>	22	67
	2<	7	21
	2>	1	3
B	4>	2	6
	s5	3	9
	5<	22	69
	5>	4	13
	6<	1	3
C	6<	1	3
	6>	1	3
	s7	1	3
	7<	16	50
	7>	12	38
	8>	1	3
D	8>	1	3
	s9	1	3
	9<	28	85
	9>	1	3
	10>	2	6
E	10>	3	9
	s11	4	12
	11<	24	73
	12>	2	6

TABLE 10.

Variability in seam contacts at different places on the carapace *

Seam	Range of contacts of seam with different areas of marginals or intermarginal seams	Number of units in range of contacts (see text for explanation)	Per cent of contacts at the three most common point of contacts in the range shown at left
A	1< to 2>	4	71, 16, 10
B	3> to 6>	7	74, 15, 7
C	6< to s9	6	50, 40, 3
D	8< to 10>	6	90, 3, 3
E	10> to 12>	5	85, 11, 4

* The three figures in the far right column are the three highest percentages. In seam A, for example, 71% of the species studied had the most frequent contact (modal contact) at one point in the range shown at the left.

the exception of such genera *Chelydra* and *Macroclemmys,* there are seldom contacts that are of diagnostic value at either the specific or generic levels.

The usefulness of this character is in establishing the extent of individual variation in animals with few meristically variable parts and, perhaps, in studying geographic variation as will be discussed later.

Considering all 33 species studied and all the seam contacts, there is obviously strong selection for certain contacts. Coker (1920) has pointed out that the proper adjustment between carapacial laminae may be more important than actual number of laminae because supernumerary laminae are more frequently found than are maladjustments. Table 9 shows the number and percentage of species having a particular seam contact in the majority of individuals.

It is readily seen that with the exception of seam A, most species (50-85%) have contacts in the anterior portions of the marginals. In all except seam C, there is a tendency for all species to have a single dominant contact. In seam C 50% are on 7< while 38% are on 7>.

Some difference appears in the range of variability of contacts in different portions of the carapace. This is seen by assigning each possible contact, with the exception of intermarginal seams, a unit value. Thus, if in a series of specimens seam A contacted marginals one and two at points varying from 1< to 2>, the possible contacts would be between s1 and 1½, between 1½ and s2, between s2 and 2½ and between 2½ and s3, for a total of four units. However, along with this must be considered the fact that in some contacts, the total range of variation in position of contact may be high, but most contacts may still be concentrated at one point. Table 10 shows the ranges in units and the percentage concentration at certain points within the range.

From the table, it appears that considering unit spread only, the most anterior and posterior portions of the carapace are least variable with the mid-section most variable. However, from a consideration of the three largest percentages of contacts, seam C shows the greatest variability because almost one-half of the species examined fall into each of two different contact units. The rank in order of decreasing variability being C-B-A-E-D. This arrangement also takes into consideration the proportion of all turtles examined that fell into the three highest percentages. For example, seam A is considered slightly more variable than seam E because the three contacts in E comprised 100% of all species of turtles examined, while 97% were included in the three highest percentage of A contacts.

Thus, the anterior one-half of the carapace seems more variable than the posterior one-half. The studies of abnormalities in the shells of turtles made by Newman (1906), Coker (1910) and Zangerl and Johnson (1957) indicated that the posterior one-half of the carapace was more variable than the anterior half, but most of the abnormalities considered by the above authors were in the form of supernumerary laminae.

Phylogenetic Aspects of Seam Contacts

Most United States turtles have 12 marginal laminae, but members of the subfamily Kinosterninae (*sensu* Williams, 1950) have only 11. The larger number seems to be primitive and it is characteristic of the relatively primitive forms *Macroclemmys, Chelydra* and *Chelonia.* Newman (1906) pointed out that the more recently a certain scute has been lost phylogenetically, the more common it should be as a supernumerary element in turtles with the reduced number. In turtles studied by him, the frequency of occurence of supernumerary scutes diminished in anterior direction on the carapace. From this he concludes that the earliest losses of scutes occurred at the anterior end of the carapace, the most recent at the posterior end.

It should be instructive then to compare the frequencies of contacts of interlateral seams with the marginal laminae in turtles with 12 marginals with the percentages in turtles with only 11. Also, obviously primitive turtles with 12 marginals (such as *Chelydra*) will be compared with other turtles with 12 marginals, but presumably more recently evolved (such as *Graptemys).* For study, the turtles were divided into three groups—turtles with 11 marginals, those with 12-advanced and those with 12-primitive (*Chelydra, Macroclemmys,* and *Chelonia*). The results are shown in Table 11 which includes all species shown in Tables 1-5 except *Gopherus polyphemus* and *Clemmys marmorata.*

I will first compare the primitive turtles with 12 marginals with advanced ones. With the exception of seam A, the seam contacts for primitive species show a bimodal distribution, which is eliminated by excluding *Chelonia* from consideration. If this exclusion is made, it is clear that compared with the contacts in *Chelydra and Macroclemmys,* the other species with 12 marginals show contacts that are shifted anteriorly. Too, the difference between the contacts in primitive and advanced species increases as one passes from anterior to posterior on the carapace. Thus, in seam A the mode of seam contacts in primitive species is at 2<, in advanced species at 1>; in B the same contacts are 6< and 5<; in C, 8> and 7<; in D, 10> and 9<; in E, 12> and 11<. The unit differences between the modes of primitive and advanced species in seam A contacts is 1; between the two groups in seam B contacts is 1; in C, 2; in D, 3; in E, 3.

If *Chelydra* is assumed to represent the primitive condition of scute arrangement in turtles, and all of the other turtles with 12 marginals are advanced over *Chelydra,* then it is evident that there has been a movement forward of all seam contacts, a movement more pronounced posteriorly. Accordingly, it might be possible to detect primitive members of the other 12-marginal species by considering which of these show the closest approach to the *Chelydra* condition.

In *Chelydra* almost all individuals have seam A contacts at 2< or farther posterior. Other species in which the majority of contacts are at 2< and posterior to this point are *Chelonia mydas, Kinosternon flavescens* and *K. sonoriense, Emys blandingi,* and *Deirochelys reticularia.* In other seam contacts there is no overlap of the other species with *Chelydra* and there is no consistency in which of the other species tend toward the contacts dominant in

TABLE 11.
Average percentage contacts of each interlateral seam and marginal lamina in three groups of turtles *

Seam A Points of Contact	1<	1½	1>	s2	2<	2½	2>
11 (8 species)	27.1	11.0	37.8	4.1	20.3	0.0	0.0
12 primitive (3 species)	0.0	0.0	0.3	0.0	80.0	2.0	18.0
12 advanced (20 species)	2.8	1.9	76.4	7.4	11.4	0.2	0.3

Seam B Points of Contact	3>	s4	4<	4½	4>	s5	5<	5½	5>	s6	6<	6½	6>
11	0.0	0.0	0.0	0.0	0.0	0.0	60.5	14.3	25.4	0.1	0.0	0.0	0.0
12 primitive	1.5	0.0	0.0	0.0	1.5	6.5	38.5	0.0	1.5	0.0	46.5	2.0	2.0
12 advanced	0.0	0.1	0.0	0.0	9.4	15.0	64.1	1.7	10.0	0.0	0.0	0.0	0.0

Seam C Points of Contact	6>	s7	7<	7½	7>	s8	8<	8½	8>
11	0.0	0.0	20.5	11.5	67.0	1.3	0.0	0.0	0.0
12 primitive	1.5	0.0	0.0	0.0	48.5	0.0	2.5	0.5	47.5
12 advanced	3.7	7.8	66.2	1.6	20.7	0.1	0.0	0.0	0.0

Seam D Points of Contact	8>	s9	9<	9½	9>	s10	10<	10½	10>
11	3.3	12.0	82.5	1.3	1.0	0.0	0.0	0.0	0.0
12 primitive	1.0	0.0	24.7	0.0	7.7	0.0	6.3	2.0	58.3
12 advanced	0.3	0.7	82.9	4.6	11.7	0.0	0.0	0.0	0.0

Seam E Points of Contact	10>	s11	11<	11½	11>	s12	12<	12½	12>
11	21.4	47.4	31.0	0.1	0.0	0.0	0.0	0.0	0.0
12 primitive	0.0	0.0	32.3	1.0	0.0	0.0	3.0	2.3	61.3
12 advanced	3.0	6.6	85.7	2.5	2.6	0.1	0.0	0.0	0.0

* Average percentages were obtained by dividing total percentage by all species in each group, not just by those in which some individuals actually had the contact.

Chelydra, so it is doubtful if these contacts are of value as measures of primitiveness in other turtles.

Chelonia, of which only 31 juvenile individuals were studied, is also possibly nearer the ancestral condition of turtles than other species studied. *Chelonia* is more like the advanced 12 marginal species than it is like *Chelydra* or *Macroclemmys* and this may indicate the early establishment of the scute pattern characteristic of recent species, whereas the nearly unique arrangement found in *Chelydra* may be off the main path of evolution.

A comparison of the figures in Table 11 shows that the seam contacts in those species with only 11 marginals are quite different from *Chelydra* with 12, but very similar to other species with 12 marginals. Compared to *Chelydra,* the contacts in species with 11 marginals are shifted far anteriorly, as they are in the advanced 12-marginal species. In fact, there are only slight differences in percentage contacts between species with 11 marginals and those with 12, if the chelydrine turtles are excepted.

Assuming that the eleven marginal condition of kinosternine turtles arose by loss of one marginal from an ancestral type like *Chelydra,* to which the Kinosterninae are most closely related, I attempted to determine from which part of the shell the loss of a marginal occurred by comparing the points of contact in *Chelydra* (tables 1-5) with those in the kinosternine species (table 11). In most individuals of species with eleven marginals the contacts of seams A, B and C are shifted at least one unit anteriorly to the most frequent point of contact in *Chelydra;* in seam D and E, the shift is even further anteriorly. The fact that the shifts in turtles with eleven marginals are toward the anterior portion of the carapace seems to indicate that the phylogenetic loss of a shield was there, forcing a readjustment of seams. If Newman (1906) is correct in his conclusions that the earliest loss of scutes occurred at the anterior end of the carapace, as appears the case here, this loss may have occurred quite early in the evolution of kinosternine turtles.

In *Gopherus polyphemus* in which the last marginal shield in the carapace is common to both sides, most seam contacts are shifted slightly anterior to those seen in most other species of turtles.

In general, it seems that the change in number of marginals has not significantly influenced the positioning of seams between the lateral laminae. In fact, there are greater differences within the group of turtles with 12 marginals (including *Chelonia*) than between those with 11 and those with 12.

Geographic Variation in Seam Contacts

The discussion up to now has been concerned with pooled samples of species from several portions of their range. Tinkle (1958) has shown that in some species of *Sternothaerus* differences exist in these contacts between populations occupying different river drainage systems.

Samples were chosen of *Pseudemys floridana, Terrapene ornata, Pseudemys scripta, Chrysemys picta, Graptemys pulchra, Graptemys nigrinoda* and *Sternothaerus odoratus* from different parts of the range of these species. In some of these, the samples encompass the range of more than one geographic race, in some the samples are widely spaced, in others close together so that variation in species under various conditions can be compared. Each species will be discussed separately with regard to the percentage contacts for each of the interlateral seams.

Pseudemys floridana

Fifty-one specimens from the Black Warrior River of Alabama, 45 from the Flint River in Georgia and 28 from the Pearl River between Louisiana and Mississippi were compared (Table 12).

In seam A, B and C contacts the percentages of the three populations are quite similar, but some contacts do occur in one population that are absent or much less common in another. For example 8% of the Black Warrior turtles have a seam A contact at s2, but this contact does not occur in any of the other population samples. Such situations may indicate genetic divergence of the populations if these contacts are genetically determined, but they might be due to chance. If these contacts are genetically determined, the turtles in the Flint and Black Warrior Rivers should show closer relationship to one another than to those in the Pearl. This

TABLE 12.
Comparison of seam contacts in three populations of Pseudemys floridana *

Seam	Position	Pearl River	Black Warrior River	Flint River
A	1<	3 (11)	1 (2)	0 —
	1½	2 (7)	0 —	2 (4)
	1>	22 (81)	45 (90)	43 (96)
	s2	0 —	4 (8)	0 —
B	s5	3 (11)	1 (2)	2 (4)
	5<	25 (89)	49 (96)	43 (96)
	5½	0 —	1 (2)	0 —
C	s7	1 (4)	0 —	2 (4)
	7<	27 (96)	51 (100)	43 (96)
D	8>	1 (4)	0 —	0 —
	s9	0 —	0 —	0 —
	9<	26 (93)	48 (94)	30 (67)
	9½	1 (4)	1 (2)	6 (13)
	9>	0 —	2 (4)	9 (20)
E	10>	4 (14)	8 (16)	0 —
	s11	4 (14)	8 (16)	0 —
	11<	20 (71)	34 (67)	44 (98)
	11½	0 —	0 —	0 —
	11>	0 —	1 (2)	1 (2)

*Figures in parentheses are percentages; others are number of specimens.

TABLE 13.
Comparison of seam contacts in five populations of Pseudemys scripta *

Seam	Position	Sabine River	Ouachita River	Pearl River	Black Warrior River	Coosa River
A	1<	1 (1)	3 (11)	2 (11)	5 (22)	8 (26)
	1½	1 (1)	1 (4)	0 —	1 (4)	1 (3)
	1>	79 (98)	24 (86)	16 (89)	17 (74)	22 (71)
B	5<	81 (100)	28 (100)	18 (100)	23 (100)	31 (100)
C	7<	70 (86)	28 (100)	18 (100)	23 (100)	29 (100)
	7½	3 (4)	0 —	0 —	0 —	0 —
	7>	8 (10)	0 —	0 —	0 —	0 —
D	9<	58 (72)	25 (96)	16 (89)	22 (96)	28 (90)
	9½	7 (9)	0 —	1 (6)	1 (4)	3 (10)
	9>	16 (20)	1 (4)	1 (6)	0 —	0 —
E	10>	2 (3)	0 —	4 (22)	2 (9)	0 —
	s11	5 (6)	3 (11)	1 (6)	4 (17)	0 —
	11<	73 (90)	25 (89)	13 (72)	17 (74)	28 (100)
	11½	0 —	0 —	0 —	0 —	0 —
	11>	1 (1)	0 —	0 —	0 —	0 —

*Figures in parentheses are percentages; others are number of specimens.

situation is generally true with regard to the first three contacts, but with D and E the closest relationship is between the Pearl and Black Warrior populations.

Clearly there are no consistent clines or indication of relationship in this character in this species.

Pseudyemys scripta

Samples of *Pseudemys scripta* from the Coosa and Black Warrior rivers of Alabama, from the Ouachita in Arkansas, the Pearl between Louisiana and Mississippi, and the Sabine between Louisiana and Texas were examined. These samples included specimens from the ranges of the subspecies *P. s. scripta* and *P. s. elegans.* The zones of intergradation between these two races are apparently wide, but most individuals in the Black Warrior and Coosa populations show predominantly *s. scripta* characteristics, while those in the Ouachita, Sabine and Pearl show mostly *s. elegans* characteristics. It is not uncommon, particularly in the Pearl River, to find individuals showing tendencies in color pattern toward *s. scripta.*

Thirty-one specimens from the Coosa, 23 from the Black Warrior, 28 from the Ouachita, 18 from the Pearl and 81 from the Sabine rivers were compared (Table 13).

As was true in *Pseudemys floridana,* the percentage seam contacts show geographic variation but it is largely non-clinal and probably not indicative of relationships at the subspecies level.

Chrysemys picta

The samples used in this study represent the races *p. picta, p. marginata,* and *p. dorsalis.* Forty specimens were examined from des Allemands and Paradis, Louisiana; 24 from Talladega Co., Alabama; 27 from Monroe Co., Tennessee; 33 from Alexander Co., Illinois; 50 from Lake Geneva, Wisconsin; and 40 from New Haven, Connecticut. Comparative data on these are shown in Table 14.

It is impossible to discern consistent geographic trends, but the data do indicate major differences in the populations. There are no conspicuous differences that are consistent enough to distinguish subspecies on the basis of seam contacts.

Terrapene ornata

Twenty-eight specimens of *Terrapene ornata* from one locality in Colorado and 30 from several in western Texas were

TABLE 14.
Comparison of seam contacts in six populations of Chrysemys picta *

Seam	Position	Louisiana	Tennessee	Alabama	Illinois	Wisconsin	Connecticut
A	1½	0 —	1 (4)	0 —	0 —	0 —	0 —
	1>	5 (13)	22 (81)	13 (54)	24 (73)	30 (61)	38 (95)
	s2	25 (66)	2 (7)	8 (33)	8 (24)	14 (29)	2 (5)
	2<	7 (18)	2 (7)	3 (13)	1 (3)	5 (10)	0 —
	2½	1 (3)	0 —	0 —	0 —	0 —	0 —
B	s5	0 —	0 —	1 (4)	0 —	0 —	1 (3)
	5<	29 (73)	27 (100)	23 (96)	27 (84)	46 (94)	38 (97)
	5½	5 (13)	0 —	0 —	2 (6)	2 (4)	0 —
	5>	6 (15)	0 —	0 —	3 (9)	1 (2)	0 —
C	7<	15 (38)	13 (48)	23 (96)	10 (31)	8 (16)	27 (68)
	7½	4 (10)	1 (4)	0 —	0 —	4 (8)	4 (10)
	7>	21 (53)	13 (48)	1 (4)	22 (69)	37 (76)	9 (23)
D	9<	18 (45)	17 (65)	19 (79)	12 (38)	27 (55)	39 (98)
	9½	6 (15)	3 (12)	2 (8)	3 (9)	1 (2)	0 —
	9>	15 (38)	6 (23)	3 (13)	17 (53)	21 (43)	1 (3)
	s10	1 (3)	0 —	0 —	0 —	0 —	0 —
E	10>	2 (5)	3 (12)	1 (4)	1 (3)	1 (2)	3 (8)
	s11	7 (18)	3 (12)	2 (8)	4 (13)	2 (4)	8 (21)
	11<	29 (73)	20 (77)	21 (88)	27 (84)	45 (92)	28 (72)
	11½	0 —	0 —	0 —	0 —	1 (2)	0 —
	11>	1 (3)	0 —	0 —	0 —	0 —	0 —
	s12	1 (3)	0 —	0 —	0 —	0 —	0 —

*Figures in parentheses are percentages; others are number of specimens.

TABLE 15.
Comparison of seam contacts in Texas and Colorado Terrapene ornata *

Seam	Position	Colorado	Texas
A	1>	28 (100)	30 (100)
B	4>	0 —	1 (3)
	s5	0 —	0 —
	5<	3 (11)	0 —
	5½	2 (7)	1 (3)
	5>	23 (82)	28 (93)
C	7½	1 (4)	0 —
	7>	27 (96)	30 (100)
D	9<	22 (79)	30 (100)
	9½	2 (7)	0 —
	9>	4 (14)	0 —
E	10>	3 (11)	4 (13)
	s11	1 (4)	2 (7)
	11<	23 (82)	24 (80)
	11½	1 (4)	0 —

*Figures in parentheses are percentages; others are number of specimens.

TABLE 16.
Comparison of seam contacts in three river system populations of Graptemys pulchra *

Seam	Position	Pearl River	Pascagoula River	Escambia River
A	1<	3 (7)	2 (7)	3 (4)
	1½	0 —	3 (11)	4 (6)
	1>	42 (93)	23 (82)	64 (90)
B	4>	17 (38)	27 (96)	19 (27)
	s5	21 (47)	0 —	33 (47)
	5<	7 (16)	1 (4)	18 (26)
C	s7	3 (7)	5 (18)	7 (10)
	7<	42 (93)	23 (82)	64 (90)
D	9<	45 (100)	27 (96)	68 (96)
	9½	0 —	0 —	3 (4)
	9>	0 —	1 (4)	0 —
E	10>	1 (2)	0 —	0 —
	s11	15 (33)	1 (4)	5 (7)
	11<	29 (64)	26 (93)	63 (89)
	11½	0 —	0 —	1 (1)
	11>	0 —	1 (4)	2 (3)

*Figures in parentheses are percentages; others are number of specimens.

TABLE 17.
Comparison of seam contacts in Graptemys nigrinoda *from two different localities on the Black Warrior River of Alabama* *

Seam	Position	17 miles ssw of Tuscaloosa	3 miles east of Eutaw
A	1<	0 —	1 (3)
	1½	2 (4)	1 (3)
	1>	45 (96)	38 (95)
B	4>	17 (37)	14 (35)
	s5	25 (54)	16 (40)
	5<	4 (9)	10 (25)
C	6>	28 (62)	22 (58)
	s7	16 (36)	12 (32)
	7<	1 (2)	4 (11)
D	s9	4 (9)	1 (3)
	9<	43 (91)	39 (98)
E	s11	3 (6)	1 (3)
	11<	40 (85)	36 (90)
	11½	2 (4)	0 —
	11>	2 (4)	3 (8)

*Figures in parentheses are percentages; others are number of specimens.

compared (Table 15). With the exception of minor discrepancies in seam B contacts, few differences exist. In the first three seam contacts, Texas specimens show a slightly higher percentage of contacts on the posterior portion of the marginals, while in the last two contacts the reverse is true.

These specimens of *Terrapene ornata* do not represent more than a single recognized geographic race — a fact that may partially explain the greater consistency in these data than in those of the preceding species.

Graptemys pulchra

Forty-five specimens of this turtle from the Pearl River between Louisiana and Mississippi, 28 from the Pascagoula River of eastern Mississippi, and 71 from the Escambia River of western Florida were compared (Table 16).

These data show consistent population relations, although not, perhaps, those that would be expected on a geographic basis. If the modal contact for each interlateral seam is considered, the Escambia populations show in every case closer relation to the Pearl populations than either of these do to the Pascagoula turtles.

Graptemys nigrinoda

Eighty-seven of these turtles from Alabama were studied. The samples were chosen from two areas on the Black Warrior

River with no physiographic or ecological barriers to gene exchange between them. The localities are 17 miles SSW of Tuscaloosa (47 specimens) and 3 miles east of Eutaw (40 specimens). The data appear in Table 17.

The differences between the two populations are obviously minor ones. The largest difference is in seam B contacts in which the s5 and 5< contacts of seam B show differences in percentages of 14% and 16%, respectively. The fact that samples drawn from the same river at different points show such similarities strengthens the idea that these contacts are genetically determined.

Sternothaerus odoratus

This species of turtle occurs in many ecological situations and, unlike most of the species of *Graptemys* studied, is not limited to river drainages. Thus, the possibilities of gene exchange are greater over wide areas. Fifty-five specimens from Texas, 58 from Florida and 72 from Michigan were compared (Table 18).

Seam A and B contacts show greater divergence in the three samples than do the posterior three contacts. The first two show closer relation between Texas and Michigan material. The last three show consistent geographic trends; in each the mode percentage is smallest in the Michigan sample, greatest in the Texas material.

Ontogenetic Changes in Seam Contacts

The failure of most of the seam contact percentages to show consistent differences between populations or to show geographic trends could be due to unequal distribution of size groups in the populations studied if seam contacts were subject to ontogenetic changes, or if there were selection against certain contacts in young turtles which would alter the frequency of these contacts in the adults. Both type changes are included under the term ontogenetic change in the following discussion.

To study such changes, seams B and C were chosen because these contacts generally are representative of the variation in different populations. Large samples for study of geographic variation were compared.

The specimens were arbitrarily divided into size groups. Wherever possible, only individual turtles from the same population were utilized for this study to eliminate possible geographic differences. The same size groups could not be used for comparisons of every species, either because of the nature of the samples or because of the size differences between different species.

Pseudemys floridana (Table 12) shows little difference of seam B and C contacts in three populations studied. There are no ontogenetic changes in this species in these seam contacts. The same is true of *Pseu-*

TABLE 18.

Comparison of Texas, Michigan, and Florida Sternothaerus odoratus *from several localities in those states* *

Seam	Position	Texas	Florida	Michigan
A	1<	18 (33)	4 (7)	18 (25)
	1½	11 (20)	3 (5)	10 (14)
	1>	26 (47)	51 (88)	44 (61)
B	5<	31 (57)	49 (86)	37 (54)
	5½	7 (13)	3 (5)	3 (4)
	5>	16 (30)	5 (9)	29 (42)
C	s8	0 —	0 —	8 (11)
	7<	2 (4)	2 (3)	0 —
	7½	0 —	5 (9)	0 —
	7>	52 (96)	51 (88)	62 (87)
	8<	0 —	0 —	1 (1)
D	s9	1 (2)	3 (5)	1 (1)
	9<	53 (96)	54 (95)	66 (94)
	9½	0 —	0 —	1 (1)
	9>	1 (2)	0 —	2 (3)
E	10>	0 —	2 (4)	0 —
	s11	20 (38)	14 (25)	15 (21)
	11<	33 (62)	41 (72)	55 (79)

*Figures in parentheses are percentages; others are number of specimens.

demys scripta. In *Chrysemys picta* there is considerable variability in seam B and C contacts. The Louisiana specimens are the most divergent from the other five populations studied. In this sample there is a lower percentage of contacts of seam B at 5< and a higher percentage posterior to this point than in other populations. This is precisely what should be expected if a sample contained mostly small individuals. The Louisiana sample is predominently of juvenile individuals under 50 mm in carapace length, a size almost completely absent in other samples. It could be argued that the difference is *still* geographic because most individuals used in a study of ontogenetic differences were from Louisiana. However, if this much difference did exist between Louisiana and other populations, differences of a similar magnitude should occur between some of the other populations since they are from widely separated regions of the United States. It is more reasonable to attribute discrepancies to the difference in size group representation in the six populations.

Seam C contacts in *Chrysemys* show no consistent character. The only strongly evident change is the tendency of larger individuals to have a higher percentage of contacts at 7<. Here the differences existing between populations cannot be correlated directly with differences in size composition of the samples.

In *Terrapene ornata* the two major differences between the two populations studied was a higher percentage of 5> and 9< contacts in the Texas specimens than in those from Colorado. These differences are probably reflective of actual differences between the populations. Differences of the magnitude indicated are not explicable on an ontogentic basis.

The most significant difference between the three populations of *Graptemys pulchra* studied is the high (96%) percentage of contacts at 4> in the Pascagoula River sample. The same population also shows a slightly lower percentage of contacts at 7< than in the other two populations. Both of these differences could be partially explained on an ontogenetic basis if the percentage of individuals in the Pascagoula River sample in the 51-100 and 101-150 mm size classes is greater than in the Pearl or Escambia River samples.

On this basis, too, the Escambia River sample should show closer relation to the Pascagoula than to the Pearl sample. That this is not the case probably indicates that genetic differences, as well as ontogenetic ones are involved.

The differences in *Graptemys nigrinoda* in the two size groups studied are probably negligible. However, almost no large specimens of this little known species are available for study because adults are difficult to capture. Ontogenetic differences may exist and may be shown when more large specimens become available for study. The differences that do exist between the two populations studied are slight and may be genetic or due to chance sampling, but probably not to differences in size distribution of the individuals comprising the samples.

Sternothaerus odoratus, of which the greatest number of specimens was examined, shows very little ontogenetic change in percentage of seam contacts. Contacts at 5< are slightly higher in turtles of a carapace length between 51 and 75 millimeters. The only major geographic difference in the populations studied is the high 5< contacts in Florida samples compared to Texas and Michigan material. This, too, could be partially explained on an ontogenetic basis if a greater percentage of Florida specimens were in the 51-75 mm size group. The percentage of specimens in this group in Texas, Florida, and Michigan samples are 19, 46 and 7 per cent, respectively.

Thus, the difference could be partly accountable to ontogenetic differences. However, Florida *Sternothaerus odoratus* are smaller than those from other areas and the difference in size groups found originally is partly attributable to the smallest size groups being predominantly of Florida turtles, so the differences may still be primarily genetic.

Conclusions

1. The contacts of the seams between the lateral laminae with the marginal laminae or the intermarginal seams vary considerably, but only a few of the variations are divergent enough or consistent enough to be useful as taxonomic

characters. There is obviously strong selection operating for certain shield and seam arrangements.

2. The species most different from all others studied are *Gopherus polyphemus, Chelydra serpentina* and *Macroclemmys temmincki.* Most turtles studied were of the family Emydidae, of which the most divergent were the genera *Deirochelys* and *Emys.*

3. In some instances one or more of the five contacts studied indicate one relationship among species in a large genus, while another contact indicates entirely different relationships.

4. Different portions of the carapace show differing degrees of variability, with the anterior one-half being more variable than the posterior one-half. Studies by other authors show that the posterior one-half of the carapace has a higher number of abnormalities.

5. In the turtles with only 11 marginal shields instead of the typical 12, the contacts are shifted forward when compared to primitive turtles such as *Chelydra.* However, in advanced groups with 12 marginals the same shift has occurred. That the number of marginals has not greatly influenced the position of seam contacts is apparent from the fact that there are greater differences in contacts between species with 12 marginals than between those with 12 and those with 11.

6. The loss of a marginal shield to yield the 11 marginal condition of the kinosternine turtles probably occurred from the anterior part of the carapace.

7. Geographic variation occurs in seam contacts, but this variation is largely nonclinal. This variation is useful in showing divergence at the population level in some species, but not in others.

8. Ontogenetic changes in seam positions must be considered when interpreting geographic differences that do occur, but all differences cannot be explained on an ontogenetic basis, so it is likely that many contacts are genetically determined.

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