THE SYSTEMATICS AND ECOLOGY OF THE *STERNOTHAERUS CARINATUS* COMPLEX

(Testudinata, Chelydridae)

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CONTENTS

Fresh water turtles of the northern coast of the Gulf of Mexico are excellent materials for a study of speciation. Populations of species of several genera occupy approximately the same geographic areas and may have been exposed to the same modifications in drainage systems and geological changes in the Gulf coast.

Turtles of the genus *Sternothaerus* are restricted to the United States and southern Canada. Three species (four forms) are found in the Gulf coastal plain and some adjacent areas, and presumably have undergone the major part of their evolution there. These four forms constitute the *Sternothaerus carinatus* complex. Because of its geographic position, a study of this complex utilizing a field approach with a laboratory analysis was feasible.

Analysis of selected morphological characters as a means of evaluating relationships within the *Sternothaerus carinatus* complex was the first objective. The populations of each major drainage system were considered separately in order to gain a better understanding of geographic variation.

The second objective, to obtain information on behavior, habits and ecology of these turtles, was accomplished primarily in the field, but a few laboratory experiments and observations were made.

The third objective was to correlate the differentiation of the *Sternothaerus carinatus* complex with changes in river systems, stream capture, and changes in coastline elevation. This objective was difficult to attain because the geological history of the Gulf coast is inadequately known.

The last objective was to compare the speciation pattern of the *Sternothaerus carinatus* complex with that discernible in the turtle genera *Pseudemys, Graptemys* and *Trionyx* that occur in the same area. The details of speciation in the last three groups have been worked out by other investigators, and the writer has had considerable field experience with many representatives of these genera.

II. Methodology

Collection of samples.—Collections were made in most Gulf Coast rivers from central Texas to Florida and north into Arkansas and Tennessee (fig. 1). Most collections were made during the summer because this was the only time available for the extensive trips required for this type of study. Supplementary collections were made at other seasons in a few localities.

Traps made of three-quarter inch seine netting yielded the greatest number of specimens. These traps were approximately 30 inches long, 12 to 14 inches in diameter with an open throat at each end. The traps were placed near stumps and brush in shallow, generally quiet-water areas of rivers. Trapping was the most reliable means of obtaining *Sternothaerus.*

A second means of sampling was from brushpiles at night, using the method of Chaney and Smith (1950). This method, the best known for obtaining emydid turtles, is less effective for collecting *Sternothaerus.*

A third method was successfully employed on two occasions. In the Suwannee River near Fannin Springs, Gilchrist County, Florida, *Sternothaerus m. minor* was obtained by backing a 7.5 horsepower outboard motor up to the bank near tangled cypress roots and accelerating the motor to stir up the water. This action attracted the turtles or washed them out of sleeping places under the bank. On June 7 to 8, 1953, 20 *S. m. minor* were taken by this method in about two hours. In the Wacissa River of northern Florida on June 5, 1953, Mr. Robert Webb and I swirled a boat in and out of weed beds in shallow water at night, and collected 34 *Sternothaerus* that came up beside the boat during a three-hour period. Whether the water current from the motor stirred the turtles to the surface or whether they were attracted by the sound of the engine could not be determined. In August 1954, the locality was revisited, the swirling technique employed, but no turtles were seen. Diving in the same area during the day produced 21 *Sternothaerus odoratus* in approximately four hours.

Chaney and Smith (1950) obtained 382 specimens of *Graptemys barbouri* in 13 hours in the Chipola River of Florida by a similar swirling method on July 12 to 14, 1950. A field crew from Tulane University revisited the same locality on June 4, 1953, but collected only two *Graptemys* and saw less than 20. Perhaps faulty technique was partly responsible for the smaller

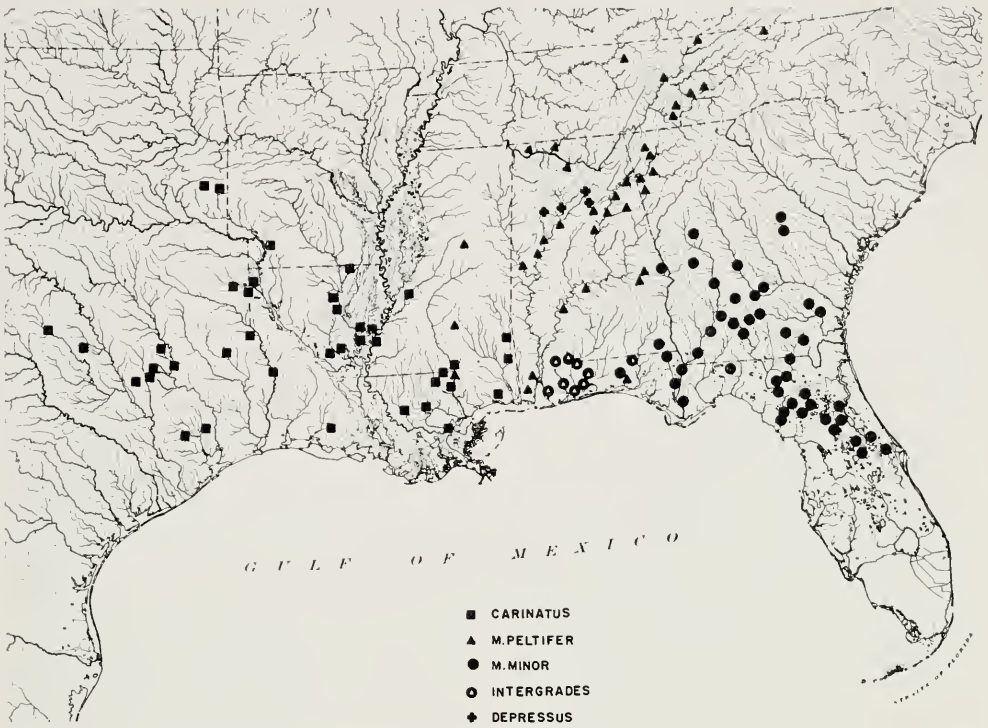


Figure 1. Distribution of members of the *Sternothaerus carinatus* complex. Symbols represent localities from which material has been examined.

catch, but pitch of the motor or seasonal differences in the excitability of turtles may have been influential in this instance and in the Wacissa River. The possibility exists that the *Graptemys* population in this portion of the Chipola River was severely decimated by the collection of 1950 that contained mostly adults.

III. Taxonomic Considerations of Species

The turtles of the genus *Sternothaerus* were placed by Williams (1950) in the subfamily Kinosterninae (*Kinosternon* and *Sternothaerus*) of the family Chelydridae.

Synonymy. — *Testudo* Latreille, 1801; *Testudo* Daudin, 1802; *Terrapene* Merrem, 1820; *Cistuda* Fleming, 1822; *Kinosternon* Spix, 1824; *Cistudo* Say, 1825; *Sternotherus* Gray, 1825; *Sternothaerus* Bell, 1826; *Cinosternon* Wagler, 1830; *Kinosternon* Gray, 1831; *Clemmys* Fitzinger, 1835; *Staurotypus* Duméril and Bibron, 1835; *Kinosternon* LeConte, 1854; *Aromochelys* Gray, 1855; *Cinosternum* Agassiz, 1857; *Ozotheca* Agassiz, 1857; *Goniochelys* Agassiz, 1857; *Kinosternon* Siebenrock, 1907; *Sternothaerus* Lindholm, 1929.

The current spelling of the generic name is incorrect. *Sternothaerus* is the correct transliteration (according to the nomenclatural rules) for the Greek words composing the name, a fact pointed out by Strauch (1862). This was the spelling used by Bell (1826) in his description of the genus, but he was antedated a few weeks by Gray (1825) who described the genus *Sternotherus* with the following notation (p. 211): "3. *Sternotherus,* Bell, MSS - - -". Gray obviously meant to give Bell credit for the generic description. Perhaps Gray had seen Bell's manuscript and had received Bell's permission to include the new genus in his (Gray's) checklist of the genera of reptiles and amphibians.

According to the Copenhagen (Fourteenth International Congress on Zoological Nomenclature) decisions on modifications

of the *Regles Internationales de la Nomenclature Zoologique*, page 45: "An invalid original spelling is to be corrected wherever it occurs, the corrected spelling (*i.e.,* the valid emendation) replacing the invalid original spelling in all respects, including authorship and date." The description of the genus, therefore, should be credited to Bell (in Gray), 1825.

Most authors have followed Gray's spelling and given him credit for the generic description, but some have not. Wright and Funkhouser (1915) listed "*Sternothaerus carinatus* (Gray)" from the Okefinokee Swamp, and Lindholm (1929) gave Bell credit for describing the genus and correctly spelling the generic name.

The genus *Sternothaerus* of Bell also contained pelomedusid turtles and was accordingly associated with the sideneck turtles by later authors. In 1831 Gray placed *Sternothaerus* in the family Chelydae and placed the only musk turtle known at the time (*odoratus*) in the genus *Kinosternon*. Neither Boulenger (1858) nor Siebenrock (1907, 1909) recognized the musk turtles as a separate group, but retained them in the genus *Kinosternon*. Gray (1855) erected the name *Aromochelys*, removed *odoratus* from *Kinosternon*, and placed it (*odoratus*) in the newly created genus. Agassiz (1857) described *Aromochelys carinatus* and placed *odoratus* in the same genus. He also described the genera *Goniochelys* and *Ozotheca*, but later in the same work synonymized them with Gray's *Aromochelys*. Strauch (1862) accepted the name *Aromochelys* for the musk turtles, but pointed out that the name *Sternothaerus* of Bell was earlier and available since the side-neck turtles originally included in it were placed in a different genus by Wagler (1830). The process by which the currently used generic name of the musk turtles became available with *odoratus* as the type species is explained by Stejneger (1902).

If the musk turtles are considered as a group distinct from *Kinosternon* then the spelling must be *ae* in keeping with the rules of nomenclature and the credit for the description should go to Bell, albeit in Gray's publication.

The genus *Sternothaerus* as presently understood contains four species and five forms (Tinkle and Webb, 1955). *Sternothaerus odoratus* is the only species with an extensive range, occurring in "eastern and southern United States from Quebec, Ontario, Michigan, Wisconsin and Minnesota through the tier of states west of the Mississippi to eastern and southern Texas, and southeast to Florida" (Schmidt, 1953). This species is sympatric with the other three in the genus, the taxonomic arrangement of which is that of Tinkle and Webb (1955). The range of the *Sternothaerus carinatus* complex lies almost entirely within the Austroriparian and Texan biotic provinces (Dice, 1943) of the Gulf coastal plain. More exact definition of ranges may be obtained from the distribution map (fig. 1) or from the list of material examined.

The following discussion of species contains primarily new information relative to relationship, distribution and characterization.

Sternothaerus carinatus (Gray), 1855

Synonymy.—*Aromochelys carinatus* Gray, 1855; *Goniochelys triquetra* Agassiz, 1857; *Cinosternum carinatum* Boulenger, 1858; *Sternotherus carinatus* Stejneger, 1923; *Sternotherus carinatus carinatus* Carr, 1952; *Sternotherus carinatus* Tinkle and Webb, 1955.

Type locality.—Louisiana, restricted to vicinity of New Orleans. Cotypes, Museum of Comparative Zoology, Harvard University.

This species is characterized by a high carapace with distinct mid-vertebral keel, by the absence of a gular scute and by presence of a head pattern of dark spots on a light background.

Sternothaerus carinatus extends from the Balcones Escarpment of central Texas (Smith and Buechner, 1947; Brown, 1950), northward through southeastern Oklahoma (Ortenburger, 1927), southern Arkansas, and southward and eastward through all the major rivers of Louisiana and Mississippi. The exact northward limits have not been determined, but this form apparently does not occur far up through the rivers of the alluvial Mississippi Embayment. There is a record from Illinois (Davis and Rice, 1883), but Cahn (1937), in his review of the turtles of Illinois, reported no additional specimens and suggested that this record was based upon a misidentification.

Sternothaerus carinatus and *odoratus* were the only generally recognized species in the genus until 1923, so the following reports were correct considering the taxonomic knowledge available at the time of publication.

Brimley (1910) reported *carinatus* from Mimsville, Georgia, in the Apalachicola River drainage, as did Siebenrock (1907). Mimsville might have been a shipping point for this species, but it is more likely that the specimens were actually *S. m. minor.*

The specimen mentioned by Rhoads (1895) from the Emory River at Harriman, Rhoane County, Tennessee, has elicited much discussion and speculation. Stejneger (1923) examined the specimen and called it *S. minor,* but Smith and Glass (1947) suggested that it was *"S. peltifer"* on the basis of Rhoads' mention of dark stripes on the head. I have seen several specimens from Tennessee and have read Rhoads' description and am in agreement with the allocation of Smith and Glass. Neither *S. carinatus* nor *S. m. minor* is known from Tennessee.

The report of *carinatus* from Arizona by Yarrow (1875) is obviously in error. Loding (1922) reported *carinatus* from Tuscaloosa and Talladega counties, from Sepulga River between Butler and Conecuh counties, and from Saraland, Mobile County, Alabama. These specimens were almost surely *Sternothaerus minor peltifer.*

DeSola and Adams (1933) and Wright and Funkhouser (1915) reported *S. carinatus* from the Okefinokee Swamp of Georgia. The description given by Wright and Funkhouser prove them to be *m. minor.*

The easternmost records are from the Chickasawhay (upper Pascagoula) River of Mississippi. No specimens were seen from the Escatawpa River, but should be interesting as this river, generally speaking, is intermediate between the known ranges of *S. carinatus* and *S. m. peltifer.*

Sternothaerus depressus Tinkle and Webb, 1955

Type locality.—Black Warrior River, 1 mile east of Jasper, Walker County, Alabama. Holotype, Tulane University collections.

This species has a low, flattened carapace without distinct vertebral keel except in young. There is one gular scute and a head pattern of thin, dark reticulae on a greenish-yellow background.

Since the publication of the original description, one juvenile female paratype (TU 16062.2) has been sent to the Museum of Comparative Zoology of Harvard University, and a topotype (TU 16631.4) deposited in the Senchkenberg Museum, Frankfurt, Germany.

This species, the least known of the complex, has been found only in the Mulberry and Locust forks of the Black Warrior River above the Fall Line in Alabama. In this northern area of Alabama, the Tennessee River closely approaches the smaller tributaries of the Black Warrior River. Because of this, Webb and I suggested that further collecting would demonstrate the existence of this species in the Tennessee River. However, all specimens that I have seen from the Tennessee River are *S. m. peltifer,* although some of these approach *depressus* in carapace shape and in color pattern of the head (figs. 2, 3). There is no similar situation of such restricted range among North American turtles with the possible exception of *Kinosternon flavescens spooneri* (Smith, 1951). However, further collecting in western Tennessee may reveal this form and extend its known range farther north and west.

The original description of *S. depressus* was based upon a series containing only one adult. Since then several adults have been secured. The following color description of these was made without reference to a color guide.

Adult female.—Top of head with reticulated pattern of dark lines on a light olive-green background (cream green in some adults). Head with irregular blotches posteriorly which become smaller anteriorly where they are replaced by lines forming the reticulated pattern. The mask reaches midway back on the orbit and is a greenish yellow, distinct from the darker color of the rest of the head. The barbels are red-tinted, and adjoining areas of the chin have a faint tinge of red or orange. Carapace greenish brown or olive drab with numerous dark brown spots and streaks which are particularly prominent on the vertebral shields. No other species of *Sternothaerus* normally has as many or as distinct carapace

markings as *depressus*. Plastron immaculate, yellow-cream in color with light pink cartilage between the scutes. This color description is applicable to other living adults; the color of preserved specimens is like that of living animals except that the light green color of the head is lost and there is a general darkening of the carapace.

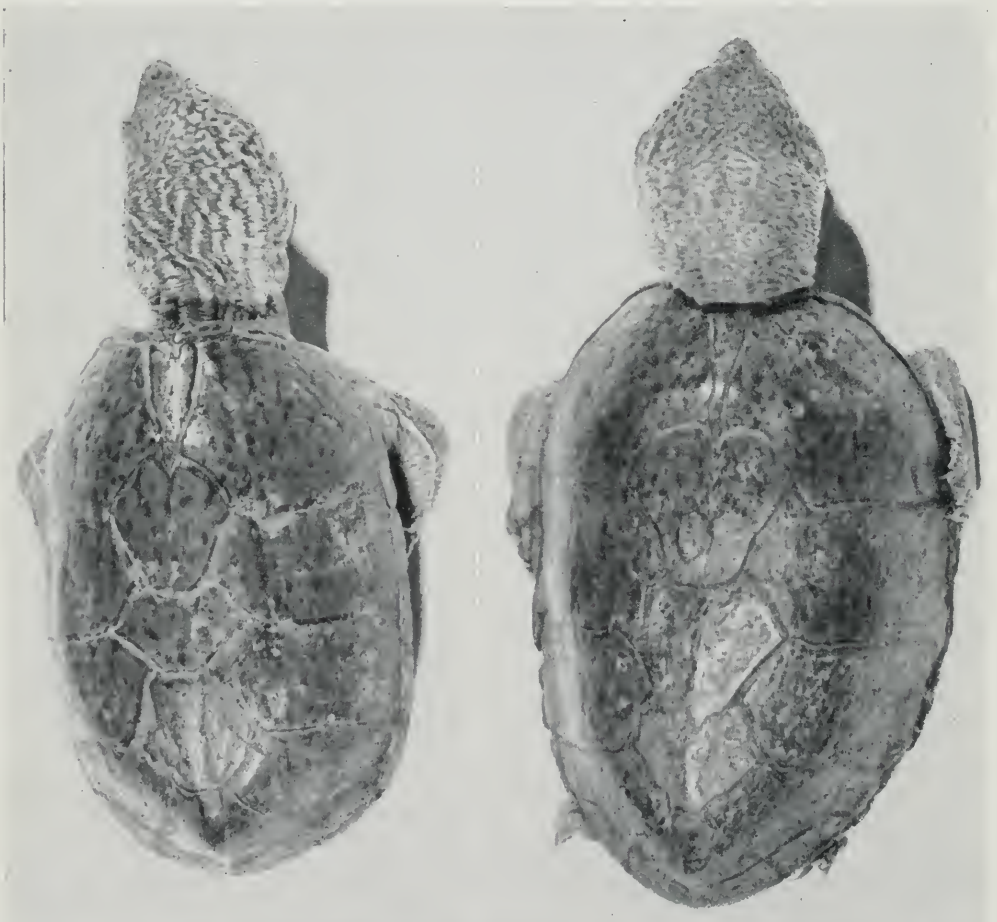
The carapace of adults in outline is a broad oval, made slightly asymmetrical anteriorly by the truncated end. The flattening of the carapace dorsally is characteristic and becomes most pronounced with increasing size, as shown by four specimens at hand. The carapace lengths of these are 91, 99, 100 and 106 mm, and the widths of the flat portion of the carapace are 13, 22, 24 and 30 mm respectively.

Color of juveniles.—Dorsum of head with dark brown to black reticulae on a yellow-green ground color. The yellow-green ground color of the head is unique and diagnostic of living juvenile *S. depressus*. Chin barbels and portions of marginal shields orange-tinted. Plastron an immaculate pinkish-orange color. Carapace light brown to olive drab with dark brown streaks.

Sternothaerus minor peltifer Smith and Glass, 1947

Synonymy. — *Sternotherus peltifer* Smith and Glass, 1947; *Sternotherus carinatus peltifer* Carr, 1952; *Sternotherus minor peltifer* Tinkle and Webb, 1955.

Type locality.—Bassfield, Jefferson Davis County, Mississippi. Holotype, Texas Co-



Figures 2-3. *Sternothaerus m. peltifer*. Both specimens from 5 miles southeast of Cumberland Gap, Tennessee.

operative Wildlife Collection, A & M College of Texas.

This form has a distinct vertebral keel as a juvenile that is lost in the adult. One gular scute is present and the head pattern is primarily one of dark stripes on a light background.

The range of this race embraces most of Alabama, the northwest corner of Georgia, the western tip of Florida, at least the eastern half of Tennessee and an undetermined area in Mississippi and extreme eastern Louisiana.

The holotype is from the Pascagoula River drainage of central Mississippi. I have seen one additional specimen from Mississippi, and one other from the Pearl River boundary of Louisiana and Mississippi. The remaining records are east of the Pascagoula drainage. Both the Pearl and Pascagoula rivers in which *S. carinatus* is common have been extensively investigated so *S. m. peltifer* is almost surely a rarity in these rivers. Perhaps it is expanding its range westward into that of *carinatus*.

Three records in the literature deserve comment. The specimen reported by Rhoads (1895) from the Rhoane River at Harriman, Tennessee was probably *m peltifer*. *Sternothaerus m. peltifer* reported by Neill (1948) from near the Fall Line in Georgia was actually *S. odoratus* (Tinkle and Webb,

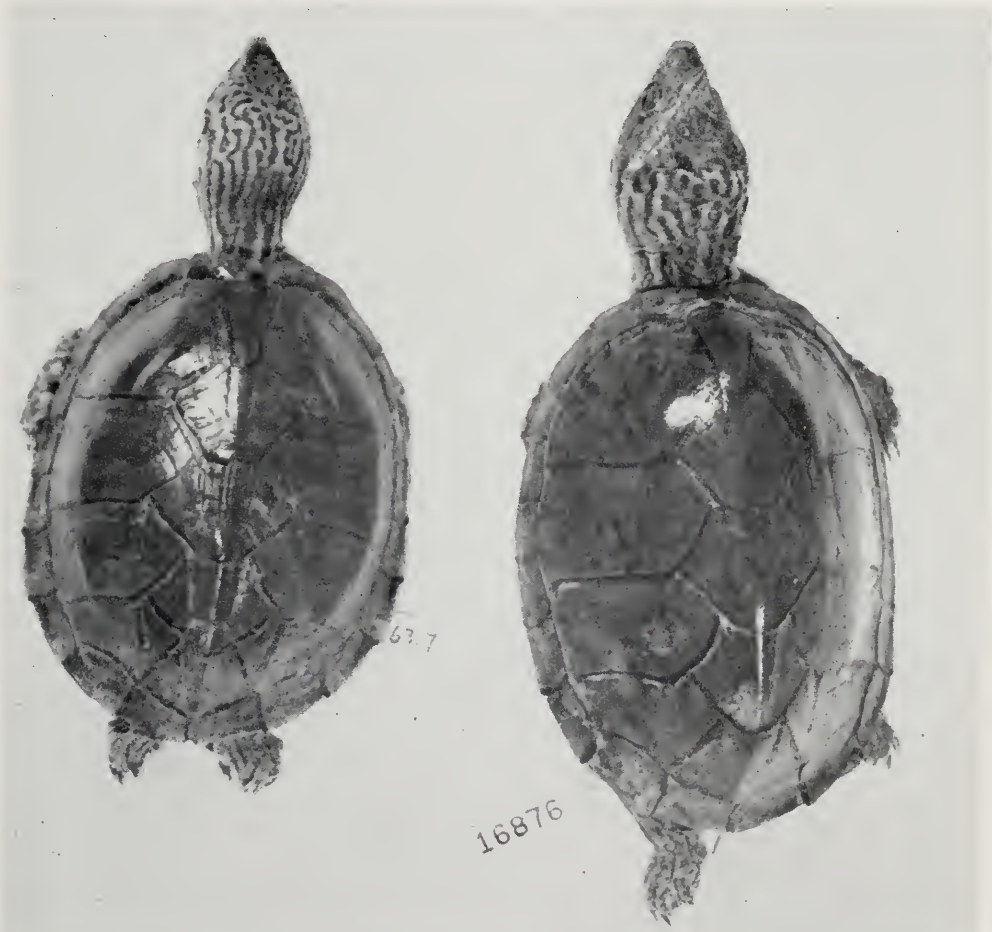


Figure 4. *Sternothaerus m. peltifer*. (Left) specimen from Coosa River, 6 miles east of Pell City, Talladega County, Alabama (No. 16863.7). (Right) specimen from Black Warrior River, 3 miles east of Eutaw, Greene County, Alabama (No. 16876).

1955). King (1939) reported specimens from the Great Smoky Moutain National Park which I have examined and found belong to *m. peltifer.*

Considerable variation exists in this race in different river systems. The specimens from the Tombigbee and Alabama rivers on the coastal plain are most like the holotype. In the Coosa River of northern Alabama, *m. peltifer* develops a rounder carapace with reduced elevation (fig. 4). This same tendency prevails in the Tennessee River drainage where *m. peltifer* specimens are quite flat and the head stripe-spot pattern becomes more diffuse or reticulated (figs. 2, 3).

Since nothing has been published on the coloration of living *m. peltifer,* the following notes on a Coosa River juvenile are pertinent. Plastron dull orange; carapace light to dark brown. Underside of neck reddish, becoming brownish-orange on the lower jaw and cream brown on the upper jaw. Dorsum of head light brown to a point two millimeters posterior to eyes; there this color blends gradually with the yellow-orange ground color of the neck. Dark brown to black stripes pass from the eyes and jaws across the yellow-orange neck. These stripes are also present dorsally, but they break up into spots as they meet the brown ground color.

The plastron of an adult from the same locality is orange-tinted, but the color is not as intense as in the juvenile. Carapace brown. Underside of neck brown to olive. Dorsum of head greenish brown with some yellow; no orange on head. The green and yellow become more obvious posteriorly. Dark brown stripes present as in juveniles, but traversing a brownish-green ground color.

Sternothaerus minor minor (Agassiz), 1857

Synonymy.—*Goniochelys minor* Agassiz, 1857; *Sternotherus minor* Stejneger, 1923; *Sternotherus carinatus minor* Carr, 1952; *Sternotherus minor minor* Tinkle and Webb, 1955.

Type locality.—Restricted to Columbus, Georgia. Cotypes Museum of Comparative

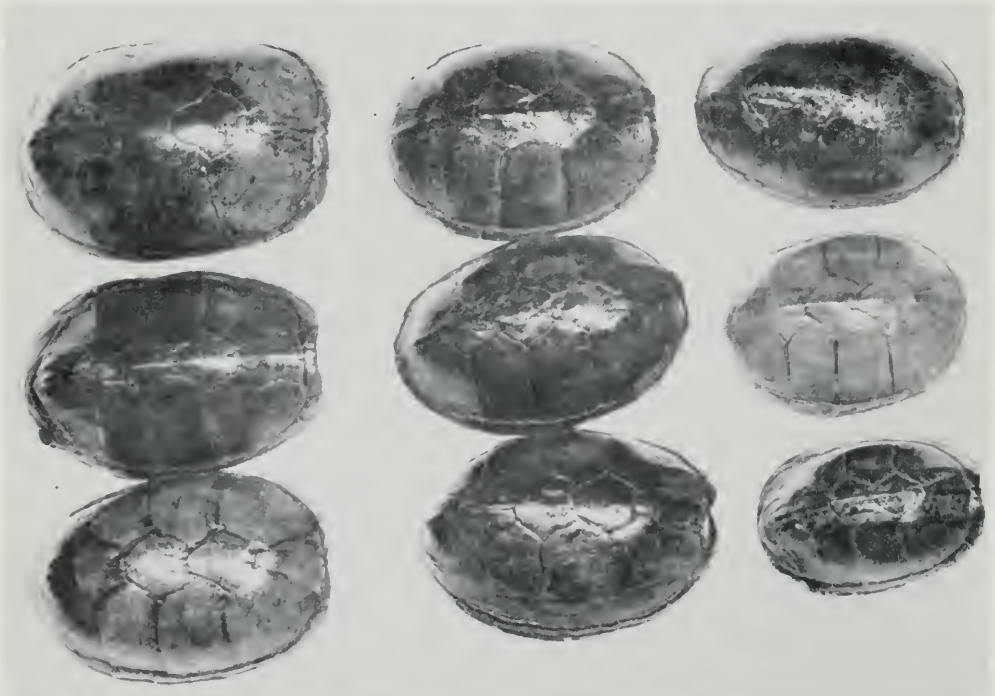


Figure 5. Shells of *Sternothaerus odoratus* from the Savannah River near Price Island, Georgia, showing variation in shape.

Zoology and Museum of Zoology of the University of Michigan.

Juveniles of this race have a mid-vertebral keel as well as a lateral ridge that is absent in other forms except *S. odoratus*. The mid-vertebral keel and lateral ridges are lost in most adults which have a rounded, arched carapace. There is one gular. The head pattern of dark spots on a light background is like that of *S. carinatus*.

I have examined four cotypes. Only one of these is *S. m. minor* (UMMZ 63520) and the locality data on this one (New Orleans, Louisiana) is obviously in error. Two of the cotypes are *S. odoratus* (MCZ 1572 and MCZ 1573) and one is *S. m. peltifer* (MCZ 1570). This mixture of species in the type series calls into question the original description of *m. minor*. However, Agassiz (1857) in his description of *Goniochelys minor* calls attention to the absence of head stripes in that species, stripes which are generally prominent on *odoratus* and *m. peltifer*.

Sternothaerus minor minor extends from Florida (at least as far south as Seminole County) through Georgia at least to Burke County (Neill, 1948b) near the Fall Line which is generally the northern limit of distribution. Westward *m. minor* occurs along the coast as far as the Escambia River drainage in Florida. It occurs in extreme eastern Alabama in the drainages of the Chattahoochee and Choctawhatchee rivers. There are no records of *m. minor* from South Carolina and Albert Schwartz informed me by letter that *m. minor*, to his knowledge, does not occur in that state. Carr (1940) reported it common in north and north central Florida. I did not find *m. minor* in Lithia Springs, Hillsborough County, Florida, although the habitat appeared suitable. The specimens reported as *S. carinatus* from Baker County, Georgia by Siebenrock (1907) and Brimley (1910) were doubtless *S. m. minor*. Wright (1926) described *m. minor* as common in the Okefinokee Swamp.

Although I have not seen *S. m. minor* from further north than the Ogeechee Riv-

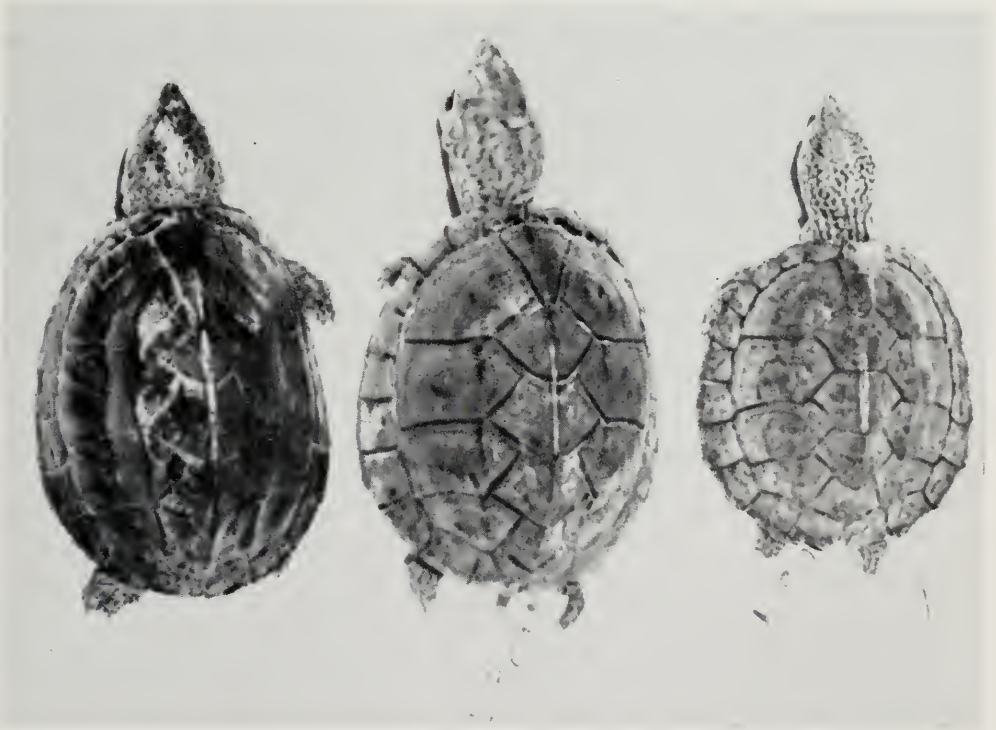


Figure 6. Comparison (left to right) of *Sternothaerus m. minor*, a presumed intergrade between *m. minor* and *m. peltifer*, and a juvenile of *S. m. peltifer*.

er drainage of Georgia, it may occur in the Savannah River. Hayes and Campbell (1900) and Johnson (1907) believed that part of the upper Chattahoochee was directed into the Savannah River. If *S. m. minor* were in the Chattahoochee at the time of this diversion, it could have invaded the Savannah drainage.

I have examined 47 specimens from the Savannah that are represented only by shells and skulls, making specific identification difficult particularly because the series exhibits great individual variation. Most specimens appear to be *S. odoratus*. None has the carapace shape of *S. m. minor*, but some resemble that of *S. m. peltifer* which could also occur in the Savannah River (fig. 5).

The following characters differentiate the turtles in the Savannah River sample from *S. m. peltifer:* 1) first vertebral very wide; the seam between it and the first costal shield contacts the first marginal shield at a point posterior to the midpoint of the marginal; 2) inguinal very wide; 3) keel of carapace greatly reduced; 4) gular large; and 5) shell narrow.

The Savannah River sample was compared with *peltifer* from the Coosa and Tennessee rivers. The turtles from the Savannah River that are most like *m. peltifer* in carapace shape are like *odoratus* in other characters. Twenty-one specimens are shaped like *odoratus*, while 26 have a keeled carapace reminiscent of *m. peltifer*. In *m. peltifer*, the first vertebral overlaps the second, whereas in the Savannah River sample (and generally in *S. odoratus*) this is not so.

Although the characters discussed are somewhat subjective, all specimens were examined at one sitting so that the same relative standards were utilized. The entire series is referable to *odoratus*, but the possibility remains that *m. minor* or *m. peltifer* occurs in the Savannah River (Table 1).

The turtles in the Escambia River and areas immediately east and west appear to be intergrades between *m. minor* and *m. peltifer*. Figure 6 shows a juvenile of *m. peltifer*, *m. minor* and a specimen from the Escambia River. Note the absence of head stripes in the specimen from the Escambia (*m. minor* character) and the absence of lateral ridges (*m. peltifer*) character. The differences are more pronounced in juveniles; the adults may be compared in figures 4, 7 and 8.

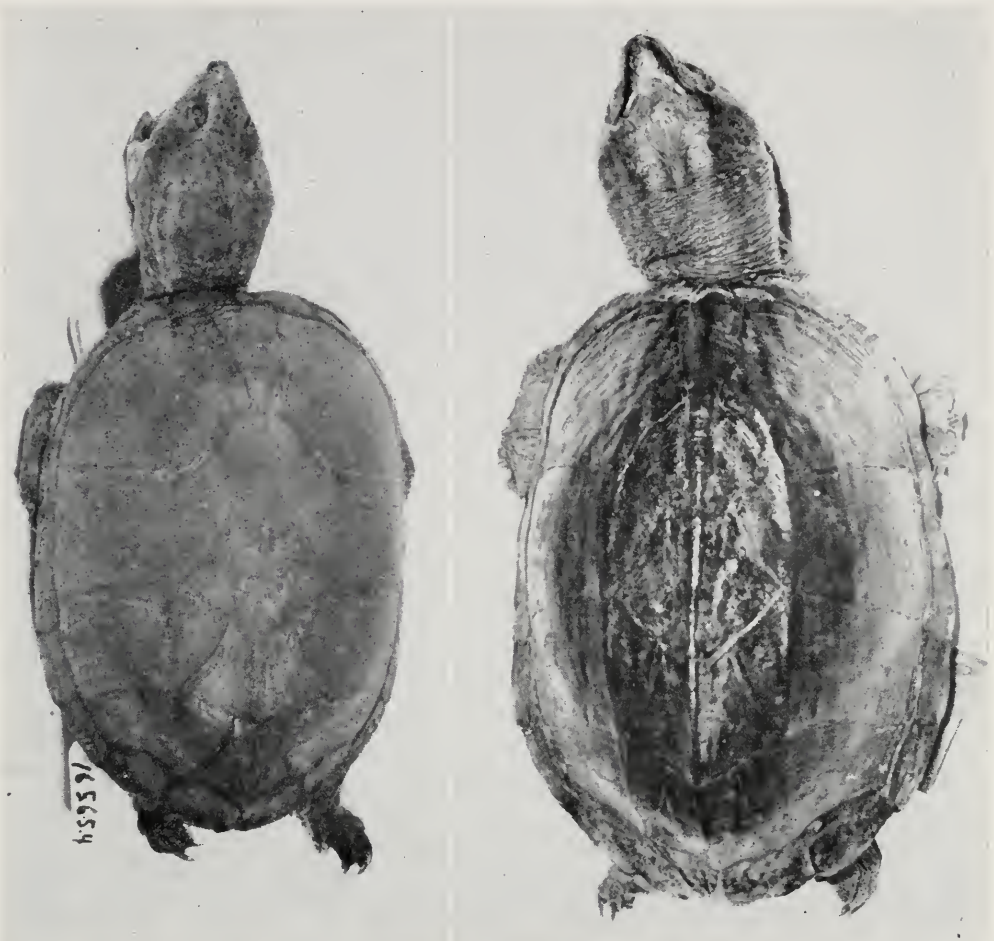
Critical Areas for Collecting

Investigation in the following localities is likely to add significant knowledge concerning the natural ranges of the species.

Sternothaerus carinatus.—The Ouachita, Arkansas and White rivers of Arkansas. I have investigated the White River at Clarendon, Arkansas, and the Ouachita west of Crossett with negative results. The Mississippi River drainage of western Tennes-

TABLE 1. *Distribution of specimens of S. m. peltifer, S. odoratus, and Savannah River material with respect to selected characters*

Character	USNM *peltifer*-like		*odoratus*-like		Tulane *odoratus*		Tulane and PMJ *peltifer*	
Contact of 1st vertebral seam with 1st marginal								
m-1 (<½)	5	19%	4	19%	8	36%	22	92%
m-1 (½)	1	4%	3	14%	1	5%	1	4%
m-1 (>½)	20	76%	14	67%	13	59%	1	4%
Size of inguinal								
wide	16	61%	14	67%	12	54%	4	17%
narrow	10	38%	7	34%	10	45%	20	84%
Size of gular								
large	22	84%	15	72%	17	77%	4	17%
small	4	15%	6	29%	5	23%	20	84%
Shell shape								
long compared with width	21	80%	8	38%	13	59%	9	38%
not so	5	19%	13	62%	9	41%	15	63%



Figures 7-8. **7** (left): adult *Sternothaerus m. minor* X *m. peltifer* intergrade from the Escambia River. **8** (right): typical adult *S. m. minor* from Eureka, Florida.

see. The Escatawpa River in extreme eastern Mississippi.

Sternothaerus minor peltifer.—The western half of Tennessee. Several localities in this area which may be critical also for *carinatus* and *depressus* have been visited but no specimens were obtained.

Sternothaerus depressus.—Further collecting in the upper Black Warrior River and in the Tennessee River is needed.

Sternothaerus minor minor.—The spring runs of southern and southwestern Florida; the Choctawhatchee River; and, the Atlantic coast drainages of Georgia and South Carolina.

IV. Variation

Characters typically used as diagnostic of species are of little value in showing the slight differences between populations of different river systems. Only samples from major rivers are considered in the section on geographic variation. Samples of *S. carinatus* were available from the Pascagoula, Pearl and Tensas Rivers; of *S. depressus* from the Black Warrior River; of *S. m. peltifer* from the Alabama, Tombigbee and Tennessee Rivers; and, of *S. m. minor* from the St. Johns, Suwannee, Apalachicola and Escambia Rivers.

Graphic presentation of data follows the method of Hubbs and Hubbs (1953) and comparable tables were used to assign levels of significance to differences between means. Means were considered significantly different at the one percent level of con-

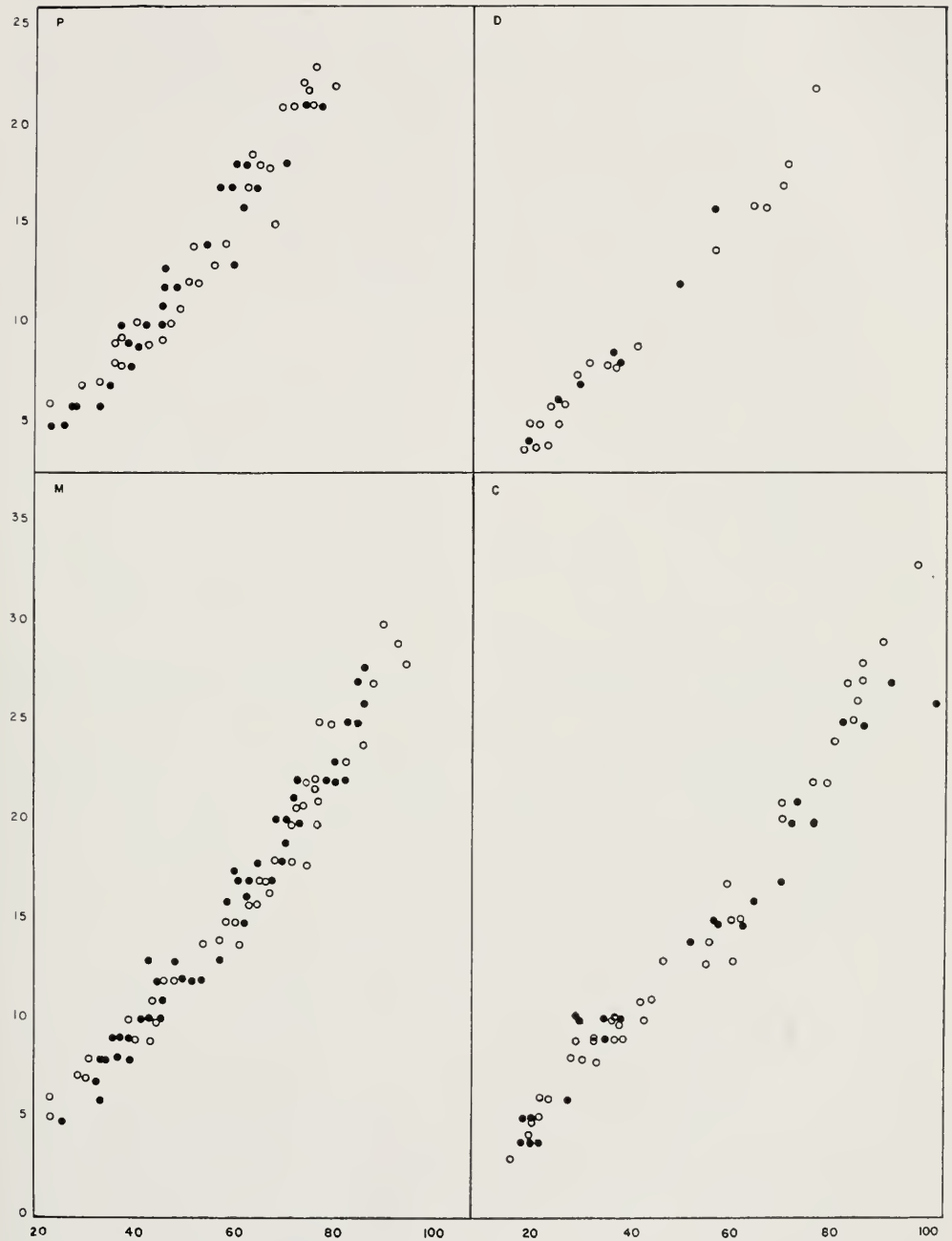
fidence, and were considered marginally significantly different between the one and five percent levels.

The following measurements (to the nearest millimeters) or analyses of characters were used. *Carapace length:* maximum straight line measurement from anterior end of nuchal shield to the seam between the eleventh marginal shields of each side; *carapace width:* at juncture of sixth and seventh marginals; *carapace height:* measured from plastral bridge to juncture of the second and third vertebrals; *carapace angle:* measured at juncture of second and third vertebrals with wire; the angle of the wire when outlined on paper and measured with a protractor actually expresses the acuteness or obtuseness of the angle of the vertebral shield; the general method was developed by Mosimann (1955), and the inherent errors and estimation of them have been discussed previously (Tinkle and Webb, 1955); *plastron length:* measured along the mid-plastral seam; *interhumeral seam:* maximum length; *interpectoral seam:* maximum length; *interabdominal seam:* maximum length; *interfemoral seam:* maximum length; *interanal seam:* maximum length; *length of bridge:* measured from anterior to posterior margin at narrowest point: *length of inguinal:* maximum length from seam to seam: in some instances encroachment of tissue obscured portions, or all of this scute, but the original seams often could be located and accurate measurements obtained; *width of inguinal:* the same pertinent remarks are applicable to this measurement; *head length:* measured from posterior tip of supraoccipital to tip of snout; *head width:* measured across tympanic region; this may or may not be the widest point of the head; *length of dentary symphysis:* measured in a straight line from tip of lower jaw to angle between dentary bones; *length of mask:* in all species there is an ontogenetic development of a cartilaginous or bony mask over the nasal bones, produced apparently by co-ossification of skin and underlying tissues; this mask covers the head anterior to the eyes and sends wing-like projections back to or beyond the eyes; length was measured in the midline and the posterior extent of the wings noted; *tail length:* the tail was straightened as much as possible and then measured from the posterior tip of the plastron to the tip of the tail; *preanal length:* measured from posterior tip of plastron to anterior edge of anus; *number of gular scutes; number of annuli:* only those lines were counted that appeared to be true annual rings; several smaller, sometimes incomplete rings, were usually not included; there is error in this procedure, but no other rapid means of age identification is known; *relative length and width of vertebrals:* ten measurements were made on each turtle; I noted for each of the five vertebrals whether the length and width were equal or one dimension was greater than the other; *seam contacts:* each intercostal seam was lettered anterior to posterior and each of the right marginals was numbered clockwise, then the contact of each costal seam with a marginal or with the seam between marginals was designated; for example, B-m5 (½) signifies that the second intercostal seam contacts the fifth marginal at the midpoint of the latter; *lateral keels:* details of procedure for this measurement are explained in the section on lateral keels (costal ridges) possessed by *Sternothaerus m. minor.*

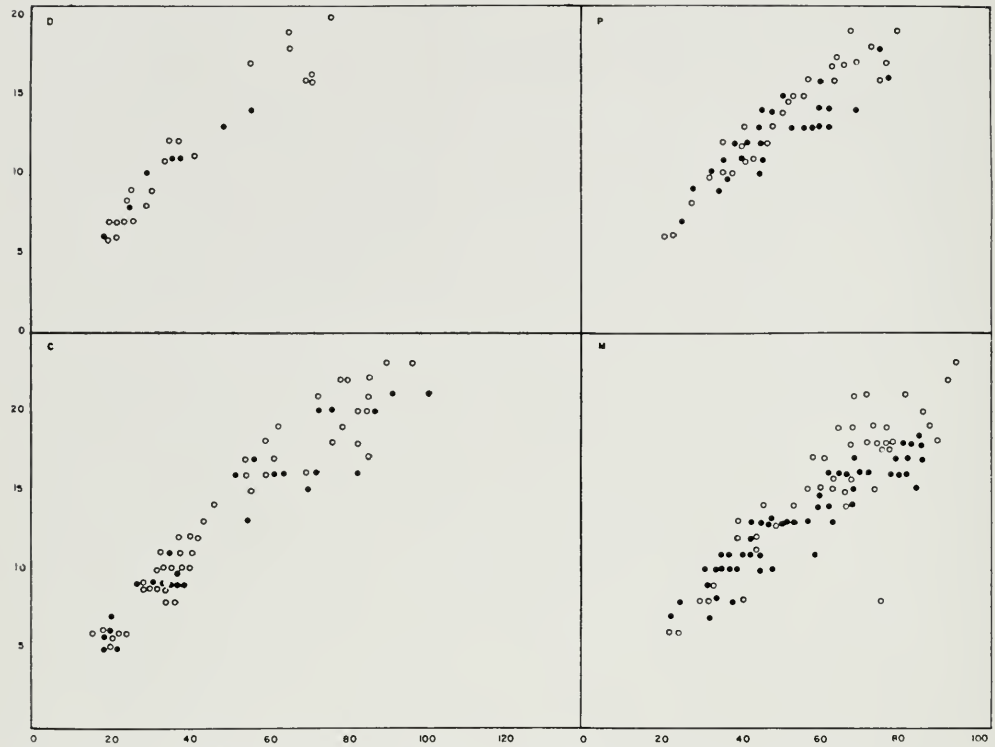
Treatment of measurements.—The following ratios were developed from the measurements and used throughout the study of variation. Reference to these ratios will be made by the abbreviations within the parentheses: Carapace length/carapace width (CL/CW); carapace length/plastron length (CL/PL); carapace angle/carapace height (CA/CH); plastron length/length of bridge (PL/BL); plastron length/length of interhumeral seam (PL/Ih); plastron length/length of interpectoral seam (PL/Ip); plastron length/length of interabdominal seam (PL/Iab); plastron length/length of interfemoral seam (PL/If); plastron length/length of interanal seam (PL/Ian); inguinal length/inguinal width (IL/IW); head length/head width (HL/HW); head length/length of dentary smyphysis (HL/DS); tail length/preanal tail length (TL/PL); preanal tail length/plastron length (PL/PL).

A. *Sexual Dimorphism*

Sex was determined by dissection when possible, by tail length when necessary. The following characters show little or no sexual dimorphism: HL/HW, PL/Iab, HL/DS, CA/CH, PL/Ip, PL/If, PL/Ih, IL/IW,



Figures 9-12. Plastron length (abscissa) plotted against length of interabdominal seam (ordinate). Dots = males, circles = females. Each point may represent one or more specimens. **P.** = *m. peltifer*, **D** = *depressus*, **M** = *m. minor*, **C** = *carinatus*.



Figures 13-16. Plastron length (abscissa) plotted against length of interanal seam (ordinate). Symbols as in figs. 9-12.

CL/CW, vertebral formulae, and seam contacts. The remaining ratios show slight sexual difference in some forms and these will be discussed further.

PL/Ian (figs. 13-16).—The difference between the sexes is most distinct in *S. m. minor* and becomes noticeable at a plastron length of 60 mm which is near the size at sexual maturity. After this point, the increase in length of the interanal does not keep pace with increasing plastron length in males. In females there is almost perfect correlation between the two measurements at all sizes. The same situation exists in *m. peltifer,* although it is less marked. The trend seems to be developing in the graph of *depressus,* but in *carinatus* there is no sexual difference except possibly in very large turtles.

The statistical relationships of this ratio may be seen in figure 17. The differences between the means of males and females were significant in all *m. minor* except those from the Apalachicola and Escambia rivers. The differences in the means of males and females from the Apalachicola are marginally different. The degree of sexual difference diminishes as samples approach the range of *m. peltifer* in which form the mean differences of the sexes are insignificant.

PL/BL (figs. 18-21). — There is no marked divergence of the sexes at a particular size, but, there is an indication, most evident in *m. minor,* that the bridge of the female continues to increase in length after the plastron has reached a definite growth plateau.

CL/PL (figs. 22-25).—The dimorphism in this character begins approximately at sexual maturity and is strongest in *S. m. peltifer.* Apparently the plastron increases at a faster rate than the carapace; a slowing of growth rate of the carapace is not evident. The dimorphism is present in *S. m. minor,* indicated in *depressus,* but absent or weak in *carinatus.* That the differences are not statistically significant may be seen in figure 26.

Risley (1930) found that the plastron

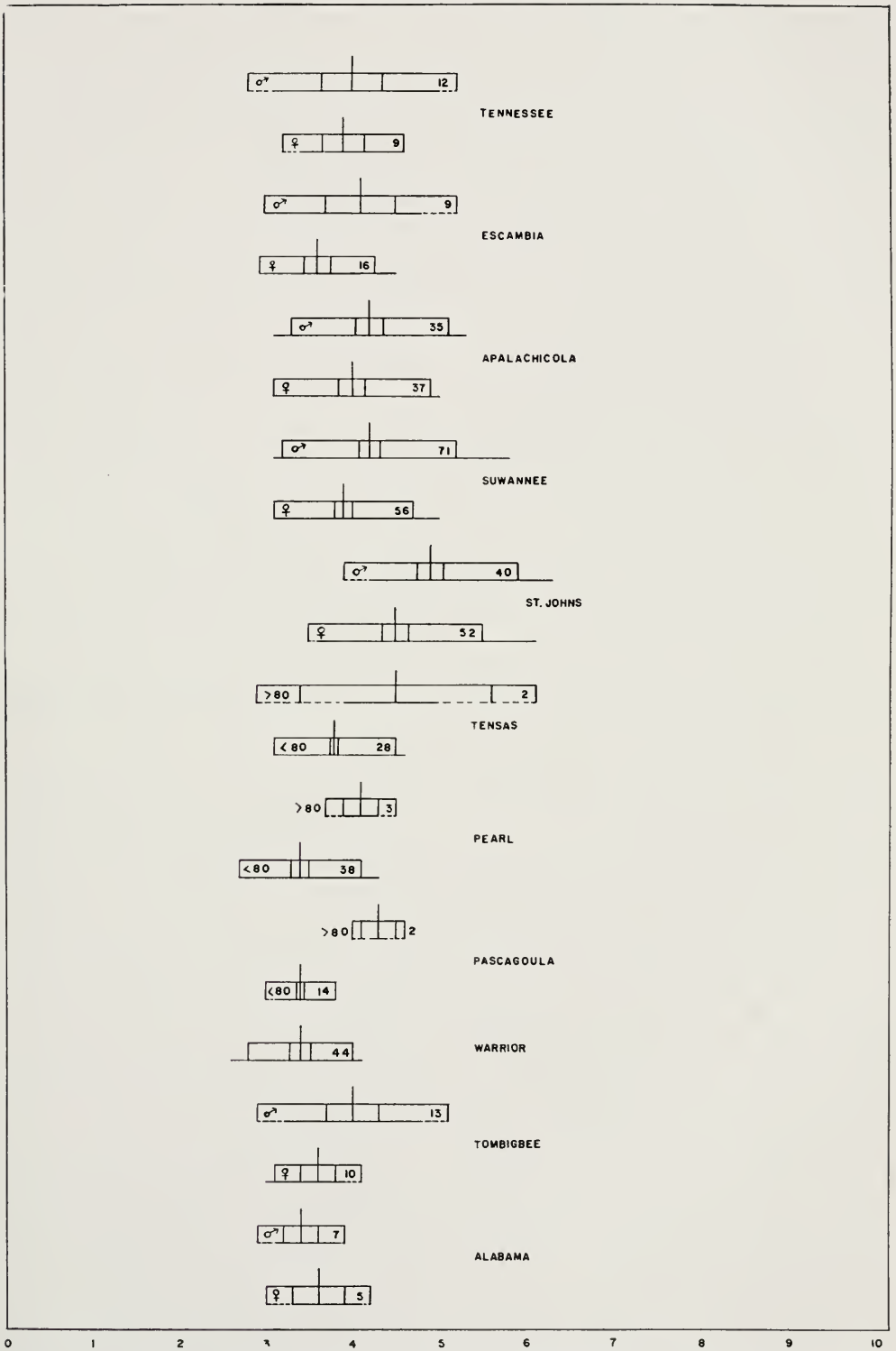
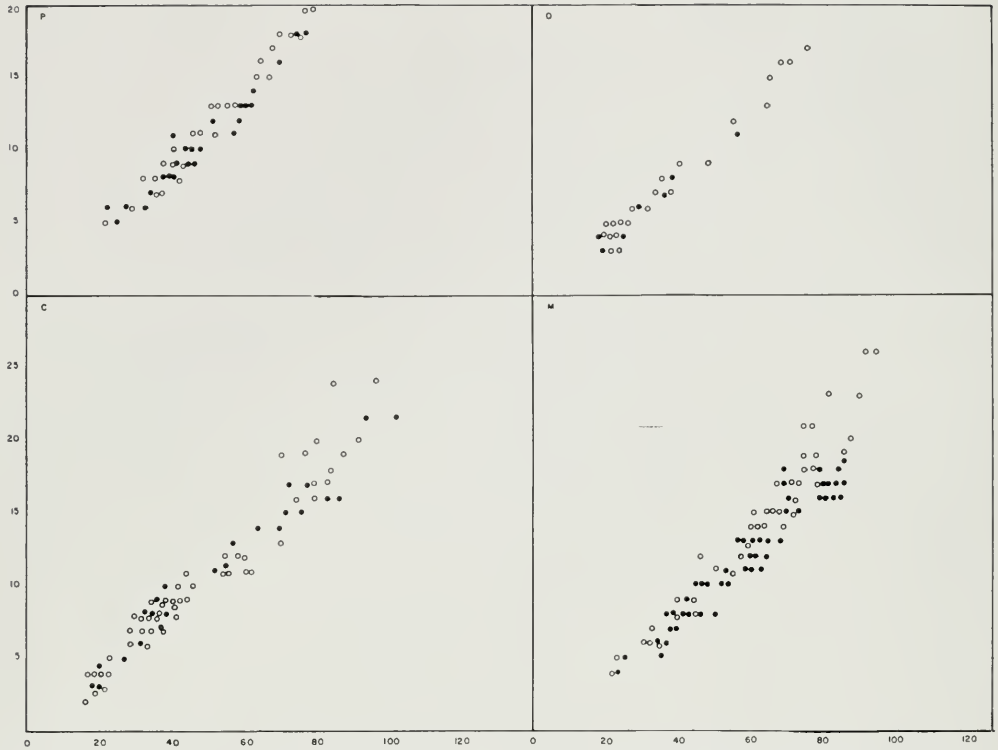


Figure 17. Ratio of plastron length to length of interanal seam. Each bar shows range, two standard errors and two standard deviations of the mean.



Figures 18-21. Plastron length (abscissa) plotted against length of bridge (ordinate). Symbols as in figs. 9-12.

length in female *Sternothaerus odoratus* is greater than that in males. This is true in both races of *Sternothaerus minor.*

TL/PL (figs. 27-30).—In many turtle species, the length of the tail of the male is greater than that of the female. Figures 27 to 30 show that the relative length of the preanal region to the total tail length is approximately the same in both sexes, but the tail of the male in all forms is longer. Thus, in *S. carinatus* the tail of the females did not exceed 34 mm, but in the males a length of 45 mm was attained. In adult or near-adult individuals the length of the tail is 100 percent diagnostic of sex.

Risley (1930) found that the average tail length of male *S. odoratus* is 33.72 mm, that of females 22.31 mm. The average preanal lengths are 16.42 and 10.76 for males and females, respectively. Thus, the ratio of tail length to preanal length of 2:1 is the same for both sexes.

PL/PL (figs. 31-34).—This ratio shows an early separation of males and females and continuing divergence with increasing size of the individual. In *S. m. peltifer* and *m. minor* there is an obvious early differential rate of growth of the preanal tail length in males. Later the rate slows and the growth curves for the two sexes become more parallel. The divergence in *m. peltifer* and *m. minor* takes place at a plastron length of 30 to 35 mm, considerably in advance of attainment of sexual maturity. In *carinatus* the divergence takes place at a plastron length of 40 to 50 mm and is not as marked as in *m. minor.* In *depressus* the dimorphism exists, but the few large specimens available preclude comparisons with the other forms.

B. *Ontogenetic Variation*

Ontogenetic variation was considered to determine whether lumping individuals of different size in comparing various characters in the populations of each river was justified. No regression coefficients were calculated as there was no apparent necessity for doing so. Unless there was a significant change in ratio (as determined by inspection of the graphs), samples were lumped

in further consideration of geographic variation.

There is little change in the following ratios: CL/CW, CL/PL, HL/HW, PL/Ip, PL/If, PL/Ih, IL/IW, CA/CH, and in seam contacts.

The correlation of carapace angle to height is not as close as that of most other ratios, probably because of the greater error involved in measuring the angle. There is little change, however, in the ratio of angle to height with increasing height or widening angle.

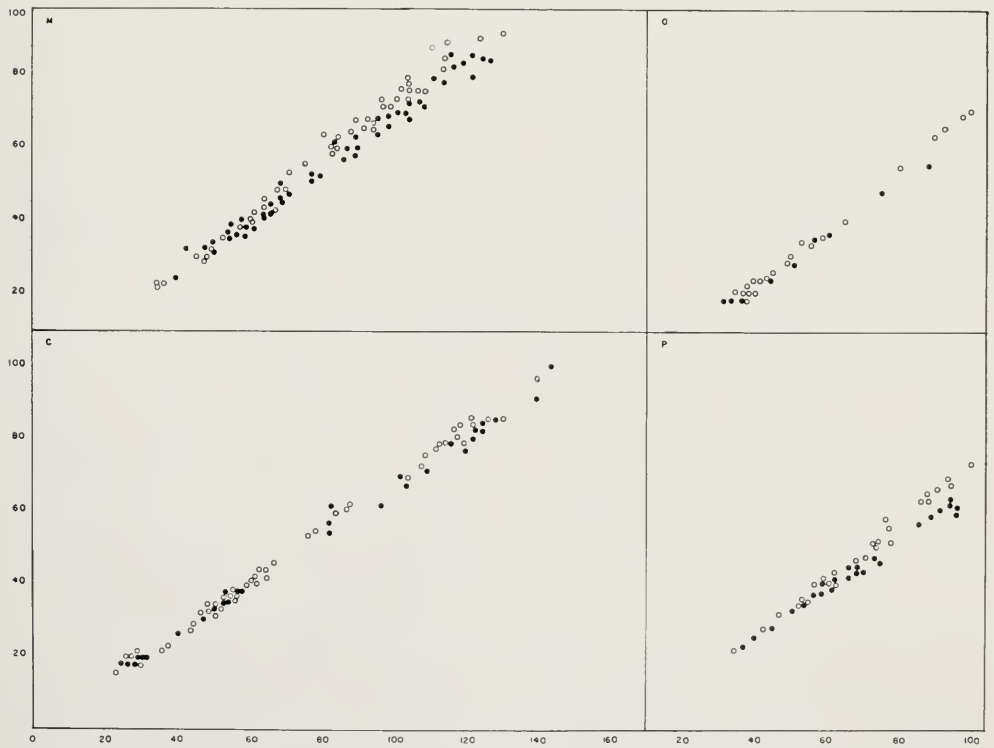
There are few specimens of *S. m. minor* and *m. peltifer* less than 20 mm in carapace height. *Sternothaerus depressus* and *S. carinatus* are represented by many specimens smaller than this, which exhibit a decided difference in the ratio of carapace angle to height. This may be due to a real difference in this ratio in small turtles or to error in obtaining accurate angle measurements of these small turtles because of the thickness of the aluminum wire used and the flexibility of the carapace. Most readings of the angle in turtles less than 20 mm in carapace height are greater than the actual vertebral angle itself.

In *S. depressus, S. m. peltifer* and *S. m. minor* the carapace becomes progressively flatter with increasing size. At a certain point in this flattening process, the carapace angle becomes so wide that it is extremely difficult to measure. Any specimen in which the vertebral angle was 165 degrees or greater was generally considered flat. This explains the absence in the figures of individuals with nearly straight carapace angles.

The following characters or ratios show some ontogenetic changes.

PL/Iab (figs. 9-12).—A slight change in this ratio, particularly evident in *S. m. minor*, appears due to failure of the plastron to continue a rate of growth equal to that of the abdominal scute.

PL/Ian (figs. 13-16).—A change in this ratio is almost non-existent in *S. m. minor*, but is indicated more strongly in males than in females. The change in the ratio, evi-



Figures 22-25. Carapace length (abscissa) plotted against plastron length (ordinate). Symbols as in figs. 9-12.

dent in *S. m. peltifer* is at least indicated in *depressus*. In *S. carinatus* the change is most clearly seen and only in the latter does it require consideration when samples are lumped for study of geographic variation.

PL/BL (figs. 18-21).—There is a change in this ratio, negligible for most purposes, due to failure of the plastron to increase in length at the same rate as the bridge. This change, evident in *m. minor* and *m. peltifer*, is shown more strongly by females than by males and occurs near the size of attainment of sexual maturity.

Vertebral dimensions.—An ontogenetic change in the length/width relationship of the vertebrals occurs only in *carinatus*. Generally, all vertebrals except the first are wider than long in all forms; however, this is generally true only of adults of *carinatus*. Only 13 percent of 124 *carinatus* have all vertebrals longer than wide and only 28 percent have four longer than wide (Table 15).

Length of mask.—The development of the mask begins just posterior to the tip of the snout and proceeds posteriorly as the turtle grows larger. In some old individuals most of the dorsal surface of the head is ossified, but characteristically the mask consists of a basal portion mostly anterior to the orbit with two wings curving backward to a point slightly posterior to the orbit.

The ontogenetic posterior extension of the mask is shown in all forms (Table 2). The mask in the smallest size group of turtles is absent or represented by a rudiment wholly anterior to the orbit in 70 percent of *m. minor*, 96 percent of *m. peltifer*, 100 percent of *depressus*, and 100 percent of *carinatus*. In the 51 to 80 mm size group, the mask reaches the middle of the orbit in 64 percent of *m. minor* and 50 percent of *m. peltifer*. In *depressus* and *carinatus* it reaches mid-orbit in only 20 and 9 percent, respectively, of specimens in the 51 to 80 mm size group. In the 81 to 110 mm size group the mask extends at least to the posterior margin of the orbit in 90 percent of *m. minor*, 67 percent of *m. peltifer*, 50 percent of *depressus* and 67 percent of *carinatus*. The mask in the largest size group of all forms always extends to a point posterior to the orbit.

The fact that the mask in *carinatus* reaches mid-orbit at a carapace length greater than in *m. peltifer* and *m. minor* makes the character of some diagnostic value, and is an additional indication of the uniqueness of *S. carinatus*.

C. *Geographic Variation*

Because the characters must be treated statistically to reveal small differences, I felt obliged to reduce the total number of characters to be analyzed. For the purposes of comparison of the four forms of the *Sternothaerus carinatus* complex, the following ratios were chosen: CL/CW; CA/CH; CL/PL; IL/IW; PL/lh; PL/lf; PL/lan.

In addition to these ratios, geographic variation in seam contacts and in expression

TABLE 2. *Length of mask*

Species	Size groups (mm)	N	Absent	Anterior to orbit	To less than mid-orbit	To mid-orbit	To post-orbit
minor (N=285)	21-50	60	30-50%	12-20%	2-3%	15-25%	1-2%
	51-80	101	0—	4-4%	9-9%	56-55%	32-32%
	81-110	100	0—	0—	1-1%	9-9%	90-90%
	111-140	24	0—	0—	0—	0—	24-100%
peltifer (N=81)	21-50	29	23-79%	5-17%	0—	0—	1-3%
	51-80	32	0—	7-22%	0—	16-50%	9-28%
	81-110	18	0—	0—	0—	6-33%	12-67%
	111-140	2	0—	0—	0—	0—	2-100%
depressus (N=44)	21-50	28	21-75%	7-25%	0—	0—	0—
	51-80	10	1-10%	7-70%	1-10%	1-10%	0—
	81-110	6	0—	0—	1-17%	2-33%	3-50%
carinatus (N=104)	21-50	42	25-60%	17-40%	0—	0—	0—
	51-80	34	2-6%	29-85%	1-3%	2-6%	0—
	81-110	6	0—	1-17%	0—	1-17%	4-67%
	111-140	22	0—	0—	0—	0—	22-100%

TABLE 3. *Treatment of sex and size groups in each species with respect to seven ratios. X's, dashes or explanation under each category show disposition of ratios in calculations*

Character	Lump sexes	Lump sizes	Treat sex separately	Treat sizes separately	Size groups to use	Exceptions
c.l./c.w.	x	x	–	–	–	–
c.h./c.angle	x	x	–	–	–	–
c.l./p.l.	–	x	x	–	–	Lump sexes in *carinatus*
inguinal l./w.	x	x	–	–	–	–
p.l./i.h.	x	x	–	–	–	–
p.l./i.f.	x	x	–	–	–	–
p.l./i.an.	–	–	x in *minor* & *peltifer*	x *carinatus* only	p.l.>80mm p.l.<80mm	–

of the lateral keels of *S. m. minor* are discussed; these latter two characters first.

On the basis of the study of ontogenetic and sexual variation in seven ratios, the statistics for each species were treated as shown in Table 3. In the following discussion, reference may be made to the tables showing the sex ratio of each form (Tables 19-20) and to table 4 which shows the percentage of individuals of each form in various size groups. These tables will help in the interpretations of differences between populations in various river systems.

The fact that the bulk of individuals of *S. depressus* are in the two smallest size groups may tend to exaggerate small ontogenetic differences. The size distributions of *S. m. minor* and *m. peltifer* are comparable. In *S. carinatus* the large percentage of small specimens is balanced by a high percentage of large individuals.

TABLE 4. *Percentage of specimens of each form in four size groups*

carapace length (mm)	21-50	51-80	81-110	111-140
minor	7	36	49	8
peltifer	13	55	29	3
depressus	62	24	14	—
carinatus	33	29	11	25

Seam contacts.—Data pertinent to this discussion are shown in Tables 5 through 7. The modal formula shown is based upon the most frequent points of contact between costal seams and marginal scutes or seams.

In *S. m. minor* of the St. Johns and Suwannee rivers the modal formula is the one most often represented in the populations, but in specimens from the Escambia and Apalachicola rivers other formulae have a greater frequency of occurrence than the modal formula. In the Apalachicola the modal formula occurs second-most, but in the Escambia it is not one of the three most common formulae. The seam contact formula most frequently encountered is dif-

TABLE 5. *Point of contact of costal seams with marginals or marginal scams: S. depressus and S. carinatus*

Contact		*depressus* Warrior (41)	*carinatus* Pascagoula (16)	Pearl (41)	Tensas (30)	Total (87)
m1(<½)	N	26	9	30	14	53
	♂	63♂	56♂	73♂	47♂	61♂
m1(½)	N	13	2	6	9	17
	♂	32♂	13♂	15♂	30♂	20♂
m1(>½)	N	2	5	5	7	17
	♂	5♂	31♂	12♂	23♂	20♂
m5(<½)	N	5	7	15	2	24
	♂	12♂	44♂	37♂	7♂	28♂
m5(½)	N	14	5	18	4	27
	♂	34♂	31♂	44♂	13♂	31♂
m5(>½)	N	22	4	8	24	36
	♂	54♂	25♂	20♂	80♂	41♂
s5	N	0	0	0	0	0
	♂	0♂	0♂	0♂	0♂	0♂
m7(<½)	N	2	2	5	0	7
	♂	5♂	13♂	12♂	0♂	8♂
s8	N	0	0	0	0	0
	♂	0♂	0♂	0♂	0♂	0♂
m7(½)	N	8	2	15	3	20
	♂	20♂	13♂	37♂	10♂	23♂
m7(>½)	N	31	12	21	27	60
	♂	76♂	75♂	51♂	90♂	69♂
m8(>½)	N	10	0	0	0	0
	♂	24♂	0♂	0♂	0♂	0♂
m9(½)	N	0	0	1	0	1
	♂	0♂	0♂	2♂	0♂	1♂
m9(>½)	N	0	0	1	0	1
	♂	0♂	0♂	2♂	0♂	1♂
s9	N	22	1	5	0	6
	♂	54♂	6♂	12♂	0♂	7♂
m9(<½)	N	9	15	34	30	79
	♂	22♂	94♂	83♂	100♂	91♂
s11	N	25	4	8	0	12
	♂	61♂	25♂	20♂	0♂	14♂
m10(>½)	N	2	0	0	0	0
	♂	5♂	0♂	0♂	0♂	0♂
m11(<½)	N	14	12	32	30	74
	♂	34♂	75♂	79♂	100♂	85♂
m11(½)	N	0	0	1	0	1
	♂	0♂	0♂	2♂	0♂	1♂

TABLE 6. *Point of contact of costal seams with marginals or marginal seams: S. m. minor*

Contacts		St. Johns (101)	Suwannee (120)	Apalachicola (83)	Escambia (42)	Total (346)
m1(<½)	N	69	62	42	21	194
	%	68%	52%	51%	50%	56%
m1(½)	N	16	33	24	7	80
	%	16%	28%	29%	17%	23%
m1(>½)	N	16	25	17	14	72
	%	16%	21%	20%	33%	21%
m5(<½)	N	63	83	36	21	203
	%	62%	69%	43%	50%	59%
m5(½)	N	14	24	26	9	73
	%	14%	20%	31%	21%	21%
m5(>½)	N	24	12	21	12	69
	%	24%	10%	25%	29%	20%
s5	N	0	1	0	0	1
	%	0%	1%	0%	0%	0%
m7(<½)	N	0	0	1	3	4
	%	0%	0%	1%	7%	1%
s8	N	3	2	2	0	7
	%	3%	2%	2%	0%	2%
m7(½)	N	3	2	6	2	13
	%	3%	2%	7%	5%	4%
m7(>½)	N	95	116	73	37	321
	%	94%	97%	88%	88%	93%
m8(>½)	N	3	2	1	0	6
	%	3%	2%	1%	0%	2%
m9(½)	N	0	0	0	0	0
	%	0%	0%	0%	0%	0%
m9(>½)	N	1	0	0	0	1
	%	1%	0%	0%	0%	0%
s9	N	23	53	28	11	115
	%	23%	44%	34%	26%	33%
m9(<½)	N	74	65	54	31	224
	%	73%	54%	65%	74%	64%
s11	N	48	79	65	19	211
	%	48%	66%	78%	45%	61%
m10(>½)	N	2	0	0	0	2
	%	2%	0%	0%	0%	1%
m11(<½)	N	51	41	18	23	133
	%	50%	34%	22%	55%	39%
m11(½)	N	0	0	0	0	0
	%	0%	0%	0%	0%	0%

ferent for the samples of *m. minor* from each of four rivers. The situation in *S. m. peltifer* is similar to that in *m. minor,* except that *m. peltifer* in the Alabama and Tennessee rivers have the same formula with the greatest frequency of occurrence. *Sternothaerus depressus* shows extreme variability with 24 different formulae among 41 specimens.

Sternothaerus carinatus shows a definite east to west trend involving a posterior shifting of the point of contact of the second costal seam with the fifth marginal. The formulae most commonly encountered are similar in the Pearl, Pascagoula and Tensas rivers. The specimens from the Tensas River show only nine different formulae, all of which are shared with turtles in either the Pearl or Pascagoula.

Most rivers contain populations showing less than 30 percent unique formulae, *i.e.* formulae not shared with a turtle from any other river system containing turtles of the same form. However, *S. m. peltifer* in the Tennessee River exhibited 65 percent unique formulae, and *S. carinatus* in the Pearl River had 52 percent not shared with turtles in the Pascagoula or Tensas.

In most rivers, the three most common formulae account for less than 35 percent of the total sample from that river. However, *S. m. peltifer* in the Alabama and Tennessee rivers had three formulae accounting for 70 and 64 percent of the specimens, respectively. Seventy percent of the *S. carinatus* from the Tensas River have one of the three most common formulae.

The percentages of contact between the seams and shields show tremendous variation (Table 5-7). The percentages reveal either no trends, east to west trends or un-

TABLE 7. *Point of contact of costal seams with marginals or marginal seams: S. m. peltifer*

Contacts		Alabama (Above Fall Line) (29)	Tennessee (25)	Tombigbee (Below Fall Line) (22)	Total (76)
m1(<½)	N	25	24	17	66
	%	86%	96%	77%	87%
m1(½)	N	4	1	3	8
	%	14%	4%	14%	11%
m1(>½)	N	0	0	2	2
	%	0%	0%	9%	3%
m5(<½)	N	17	23	14	54
	%	59%	92%	64%	71%
m5(½)	N	5	1	4	10
	%	17%	4%	18%	13%
m5(>½)	N	7	1	4	12
	%	24%	4%	18%	16%
s5	N	0	0	0	0
	%	0%	0%	0%	0%
m7(<½)	N	0	1	3	4
	%	0%	4%	14%	5%
s8	N	0	0	0	0
	%	0%	0%	0%	0%
m7(½)	N	0	3	4	7
	%	0%	12%	18%	9%
m7(>½)	N	29	21	15	65
	%	100%	84%	68%	86%
m8(>½)	N	0	1	1	2
	%	0%	4%	5%	3%
m9(½)	N	0	0	0	0
	%	0%	0%	0%	0%
m9(>½)	N	0	0	0	0
	%	0%	0%	0%	0%
s9	N	3	5	9	17
	%	10%	20%	41%	22%
m9(<½)	N	26	19	12	57
	%	90%	76%	55%	75%
s11	N	11	8	14	33
	%	38%	32%	64%	43%
m10(>½)	N	0	0	1	1
	%	0%	0%	5%	1%
m11(<½)	N	17	17	7	41
	%	59%	68%	32%	54%
m11(½)	N	1	0	0	1
	%	3%	0%	0%	1%

correlated variability depending upon which seam contact is considered. The variation in percentages of various seam contacts in each river system makes the mean percentage for each form of little diagnostic value (Table 8). In *S. m. peltifer* and *S. depressus* the frequency of contacts between the first costal seam and the posterior half of the first marginal is low. In *S. depressus* the second costal seam comes in contact with the fifth marginal in 12 percent of the specimens, while this contact occurs in 71 percent of *S. m. peltifer*. Several other instances of this nature could be detailed, but none is diagnostic of a particular form.

TABLE 8. *Percentages of contacts between costal seams and each marginal or marginal seams: summary*

Contact	*m. minor* (346)	*m. peltifer* (76)	*depressus* (41)	*carinatus* (87)
	%	%	%	%
m1 (<½)	56	87	63	61
m1 (½)	23	11	32	20
m1 (>½)	21	3	5	20
m5 (<½)	59	71	12	28
m5 (½)	21	13	34	31
m5 (>½)	20	16	54	41
s5	0	0	0	0
m7 (<½)	1	5	5	8
s8	2	0	0	0
m7 (½)	4	9	20	23
m7 (>½)	93	86	76	69
m8 (>½)	2	3	24	0
m9 (½)	0	0	0	1
m9 (>½)	0	0	0	1
s9	33	22	54	7
m9 (<½)	64	75	22	91
s11	61	43	61	14
m10 (>½)	1	1	5	0
m11 (<½)	39	54	34	85
m11 (½)	0	1	0	1

These formulae and positions of contact between seams and marginal shields (Tables 9-12) serve as additional indicators of divergence of the populations in different rivers. If these contacts are genetically determined, they may serve as useful characters in future studies on transmission of traits in turtles.

Lateral keels of Sternothaerus minor minor.—One distinctive characteristic of *S. m. minor* is the presence of two lateral ridges in addition to the vertebral keel. This character is found elsewhere only in juveniles of *Sternothaerus odoratus.*

These lateral ridges are most distinct in *m. minor* from streams of the Atlantic coast drainage and disappear in specimens from the Escambia River, due probably to gene exchange with *m. peltifer,* a detail for later discussion. Within most drainages in which *m. minor* occurs, there is variability in the degree of expression of the lateral ridges (Table 13). The determination of the relative size of the ridges is subjective, but all examinations were made at the same time without reference to the geographic origin of the turtles.

CL/CW (fig. 35).—The means of *S. m. minor* are the same in the St. Johns, Suwannee and Apalachicola rivers, but there

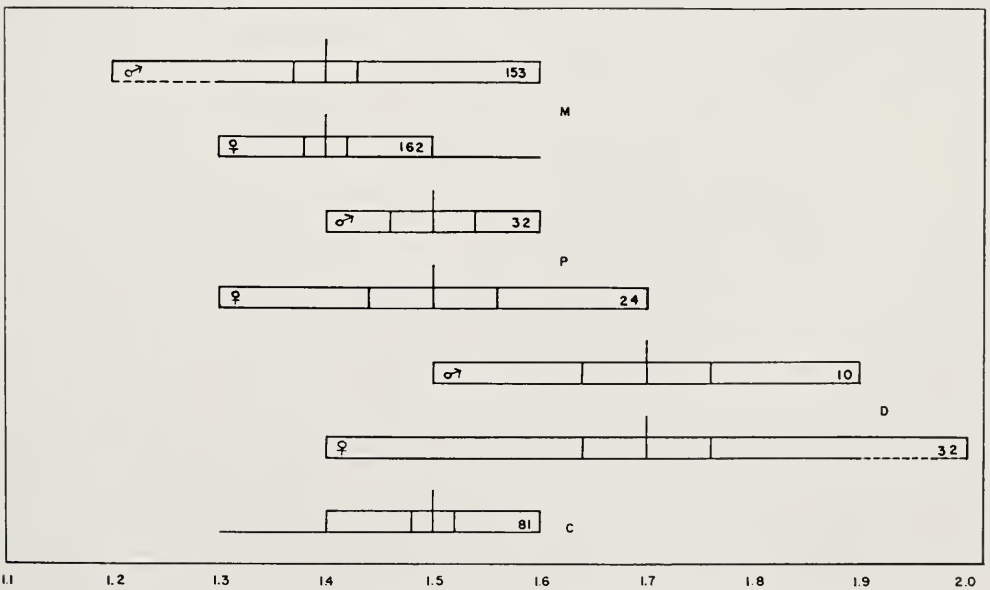


Figure 26. Ratio of carapace length to plastron length. Symbols as in fig. 17.

TABLE 9. *Seam formulae of Sternothaerus m. minor*

		St. Johns	Suwannee	Apalachicola	Escambia
No. of Specimens		101	120	80	42
No. of formulae		34	37	33	26
Spec. per formula		3.4	3.2	2.4	1.6
% shared		71	76	73	85
% unique		29	24	27	15
Modal form		m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)	m1(<½) m5(<½) m7(>½) m9(<½) s11	m1(<½) m5(<½) m7(>½) m9(<½) s11	m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)
% occurrence		18	13	8	2
Most common formulae	1	m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)	m1(<½) m5(<½) m7(>½) m9(<½) s11	m1(<½) m5(<½) m7(>½) s9 s11	m1(<½) m5(>½) m7(>½) m9(<½) s11
	2	m1(<½) m5(>½) m7(>½) m9(<½) m11(<½)	m1(<½) m5(<½) m7(>½) s9 s11	m1(<½) m5(<½) m7(>½) m9(<½) s11	m1(>½) m5(>½) m7(>½) m9(<½) m11(<½)
	3	m1(<½) m5(<½) m7(>½) m9(<½) s11	m1(<½) m5(<½) m7(>½) s9 m11(<½)	m1(>½) m5(>½) m7(>½) m9(<½) s11	m1(>½) m5(<½) m7(>½) m9(<½) s11
Percent occurrence	1	18	13	10	10
	2	10	12	8	10
	3	7	8	8	7

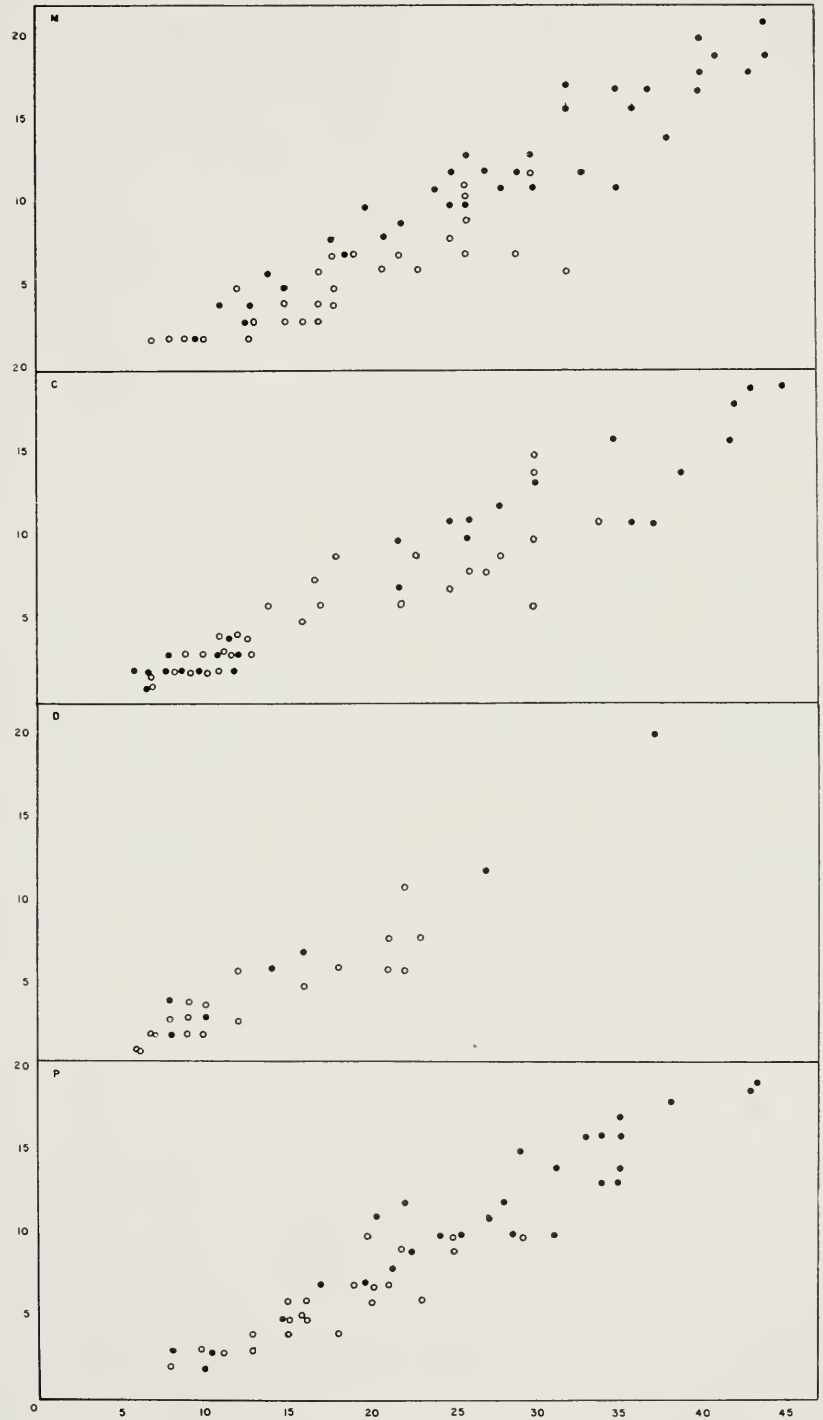
is a significant shift in Escambia River specimens toward the mean of *m. peltifer*. The means of *m. peltifer* are approximately the same in all rivers, and are significantly different from those of *m. minor*. The mean of *depressus* is significantly different from that of the *Sternothaerus* from every other river except that of *S. carinatus* from the Pearl. Because the samples from the Warrior and Pearl rivers contain mostly juvenile individuals, small differences between size groups are accentuated. The means of *carinatus* are significantly different in the Pearl, Pascagoula and Tensas rivers, but little consequence is attached to this because of the difference in proportions of the size groups represented in samples from each river.

CA/CH (fig. 36).—The ratio of carapace angle to carapace height shows a definite longitudinal trend in *S. m. minor*. The mean of the populations in the St. Johns River is significantly different from that of Escambia River samples. In *S. m. peltifer* there is also a longitudinal trend, but the trend is toward a decrease in the ratio of angle to height, whereas in *m. minor* it is toward an increase. The mean of *S. depressus* is significantly different from that of samples from all other rivers, but particularly from the means of *S. carinatus*. The mean differences of *S. carinatus* from different rivers are significant and, generally significantly different from the means of turtles from any other river. The mean of specimens from the Pearl is probably shifted toward a high ratio because of the disproportionate number of young in the sample.

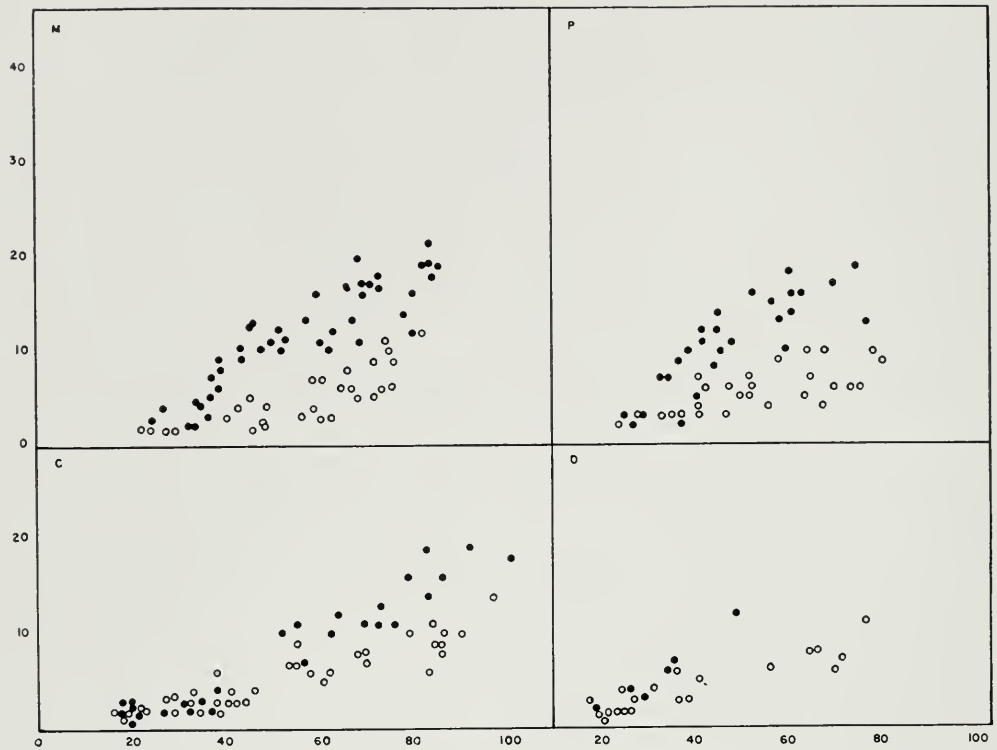
CL/PL (fig. 37).—*Sternothaerus m. minor* shows greater expression of sexual dimorphism in this ratio in the western part of its range. The males and females show little difference in the St. Johns and Suwannee rivers. In the Apalachicola and Escambia rivers the mean of the females remains the same, but the males show a higher mean ratio than do those in the St. Johns or Suwannee rivers. The means of *m. peltifer* are generally slightly different from those of *m. minor*. *Sternothaerus depressus* exhibits the most significant deviation with respect to this ratio. The small plastron size of *depressus* is accentuated by the flared marginal and rounded carapace. The means of *S. carinatus* are significantly different from those of most forms, but similar to *S. m. peltifer* due to convergence in the shape of the carapace and relative size of plastron and carapace.

TABLE 10. *Seam formulae of Sternothaerus m. peltifer*

		Alabama	Tennessee	Tombigbee
No. of specimens		29	25	22
No. of formulae		11	12	17
Spec. per formula		2.6	2.1	1.3
% Shared		64	67	35
% Unique		36	33	5
Modal formula		m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)	m1(<½) m5(<½) m7(>½) m9(<½) s11	m1(<½) m5(<½) m7(>½) m9(<½) s11
% Occurrence		28	20	11
Most common formulae	1	m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)	m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)	m1(<½) m5(<½) m7(>½) m9(<½) s11
	2	m1(<½) m5(>½) m7(<½) m9(<½) m11(<½)	m1(<½) m5(<½) m7(>½) m9(<½) s11	m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)
	3	m1(<½) m5(<½) m7(>½) m9(<½) s11	m1(<½) m5(<½) m7(>½) s9 m11(<½)	m1(<½) m5(<½) m7(½) s9 s11
Percent occurrence	1	28	36	11
	2	21	20	9
	3	21	8	9



Figures 27-30. Tail length (abscissa) plotted against preanal tail length (ordinate). Symbols as in figs. 9-12.



Figures 31-34. Plastron length (abscissa) plotted against preanal tail length (ordinate). Symbols as in figs. 9-12.

IL/IW (fig. 38).—The ratio of samples of *S. m. minor* from the St. Johns and Apalachicola rivers are similar and their means significantly different from those of samples from the Escambia and Suwannee rivers. *Sternothaerus m. peltifer* displays a longitudinal trend toward a nearer equality between the length and width of the inguinal scute, a trend which is carried through *S. carinatus* with slight mean differences in three rivers. *Sternothaerus carinatus* displays the greatest differences in the ratio. The means of samples from the Pearl, Pascagoula and Tensas rivers are significantly different from those of other rivers. The greatest similarity is in the mean of the sample from the Tensas to the mean of *depressus* from the Warrior.

The size of the axillary and inguinal scutes was used by Smith and Glass (1947) to differentiate *"S. peltifer"* from *S carinatus*. My data show that the ratio between the length and width of the inguinal would separate approximately 50 percent of those individuals.

TABLE 11. *Seam formulae of Sternothaerus depressus*

		Black Warrior
No. of specimens		41
No. of formulae		29
Spec. per formula		1.4
% Shared		—
% Unique		—
Modal Formula		m1(<½) m5(>½) m7(>½) s9 s11
% Occurrence		7
Most common formulae		m1(<½) m5(>½)
	1	m7(>½) s9 s11
	2	m1(½) m5(>½) m7(>½) s9 s11
	3	m1(½) m5(½) m7(>½) m9(<½) s11
Percent occurrence	1	7
	2	7
	3	7

PL/Ih (fig. 39).—The St. Johns River sample of *S. m. Minor* has a significantly greater mean ratio than those of samples from the Suwannee and Apalachicola rivers. However, the mean of the St. Johns sample is approached by that of specimens from the Escambia River. The Tennessee River sample of *m. peltifer* shows the widest divergence in this ratio, with a shift of the majority of individuals toward a higher ratio, *i.e.* toward a shorter interhumeral seam. The mean of the Tennessee River samples is significantly different from that of samples from all other rivers. The means of Alabama and Tombigbee river samples are similar to those of *m. minor*. *Sternothaerus carinatus* shows low variability for this character, and the means are all significantly different from those of the *minor* group. The mean of *S. depressus* is approximately intermediate between that of *m. peltifer* and *carinatus*, and is generally different from the means of any of the river samples of these two latter forms.

PL/If (fig. 40).—The mean of the *m. minor* samples from the Suwannee River is

TABLE 12. *Seam formulae of Sternothaerus carinatus*

		Pascagoula	Pearl	Tensas
No. of specimens		16	41	30
No of formulae		14	25	9
Spec. per formula		1.1	1.6	3.3
% Shared		71	48	100
% Unique		29	52	0
Modal formula		m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)	m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)	m1(<½) m5(>½) m7(>½) m9(<½) m11(<½)
% Occurrence		0	22	10
Most common formulae	1	m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)	m1(<½) m5(<½) m7(>½) m9(<½) m11(<½)	m1(<½) m5(>½) m7(>½) m9(<½) m11(<½)
	2	(only 1 specimen)	m1(<½) m5(<½) m7(<½) m9(<½) m11(<½)	m1(>½) m5(>½) m7(>½) m9(<½) m11(<½)
	3	(only 1 specimen)	m1(<½) m5(<½) m7(<½) s9 m11(<½)	m1(<½) m5(>½) m7(>½) m9(<½) m11(<½)
Percent occurrence	1	19	22	27
	2	—	7	23
	3	—	7	20

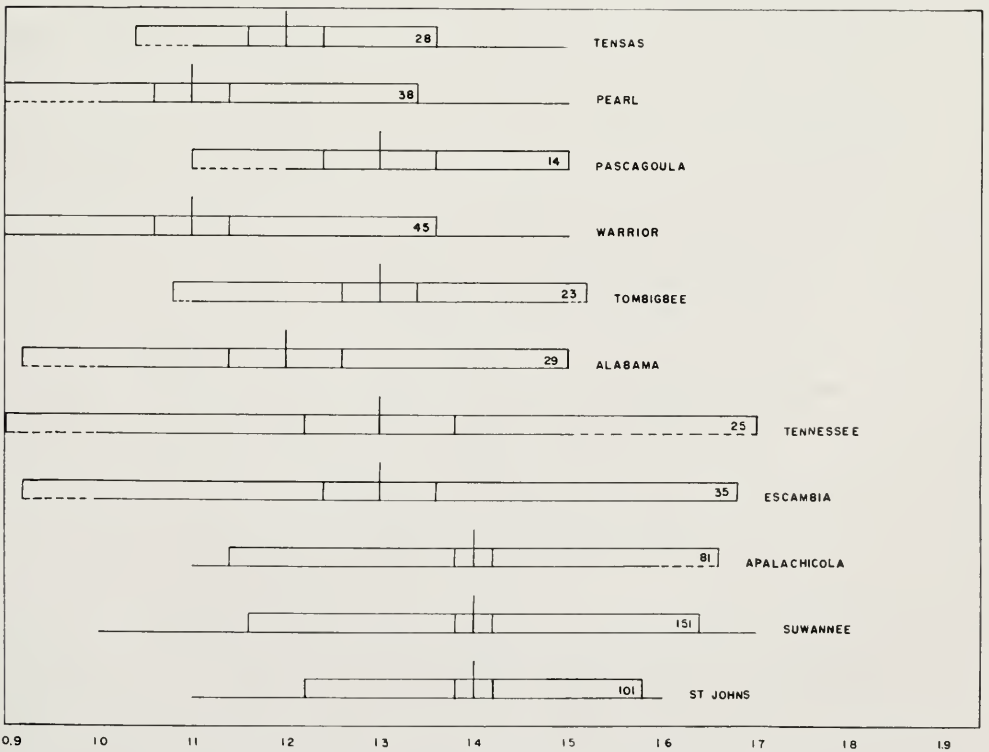


Figure 35. Ratio of carapace length to carapace width. Symbols as in fig. 17.

significantly different from that of the other samples of this race. This difference is more significant because of the narrow range of variation in this ratio in the Suwannee River specimens. The mean of the St. Johns sample is significantly different from that of samples from the Apalachicola and Escambia rivers, but the difference is slight and the ranges of variation overlap considerably. The Apalachicola and Escambia samples have the same mean. The sample of *S. m. peltifer* from the Tennessee River shows tremendous divergence from the samples from the Alabama and Tombigbee rivers. In fact, the extremes of the ratio in the Tennessee River do not overlap the extremes of those from the Alabama and Tombigbee rivers. The means of *S. m. peltifer* from the Alabama and Tombigbee rivers are similar to those of *S. depressus* and *carinatus,* although the Tensas River samples of the latter show a slightly smaller mean ratio than do other samples of this species.

PL/Ian (fig. 17).—The variability in this ratio is less than that encountered in any other. This may reflect the importance to the turtle of having anal plates that do not extend too far posteriorly and interfere with egg deposition or coitus. In general there is a gradual decrease in this ratio from that of *S. m. minor* in the St. Johns River to that of *S. carinatus* in the Pearl River. Small differences exist between the mean ratios of samples from each river system.

D. *Statistical Treatment of Pooled Samples*

The data for each species were combined to facilitate comparison. The figures to be discussed were derived from the data presented in figures 17 and 35 through 40. The mean of means, mean of standard deviation and mean of standard error were calculated by standard procedure.

CL/CW (fig. 41).—The means of all forms are significantly different, but ranges overlap considerably and little significance

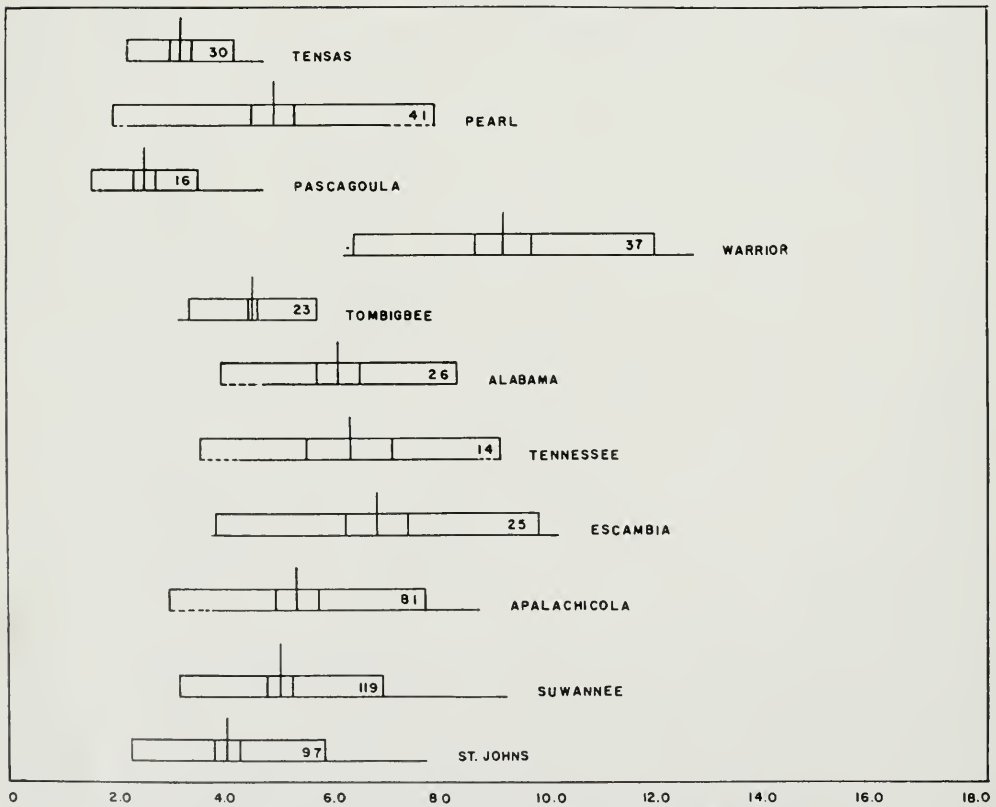


Figure 36. Ratio of carapace angle to carapace height. Symbols as in fig. 17.

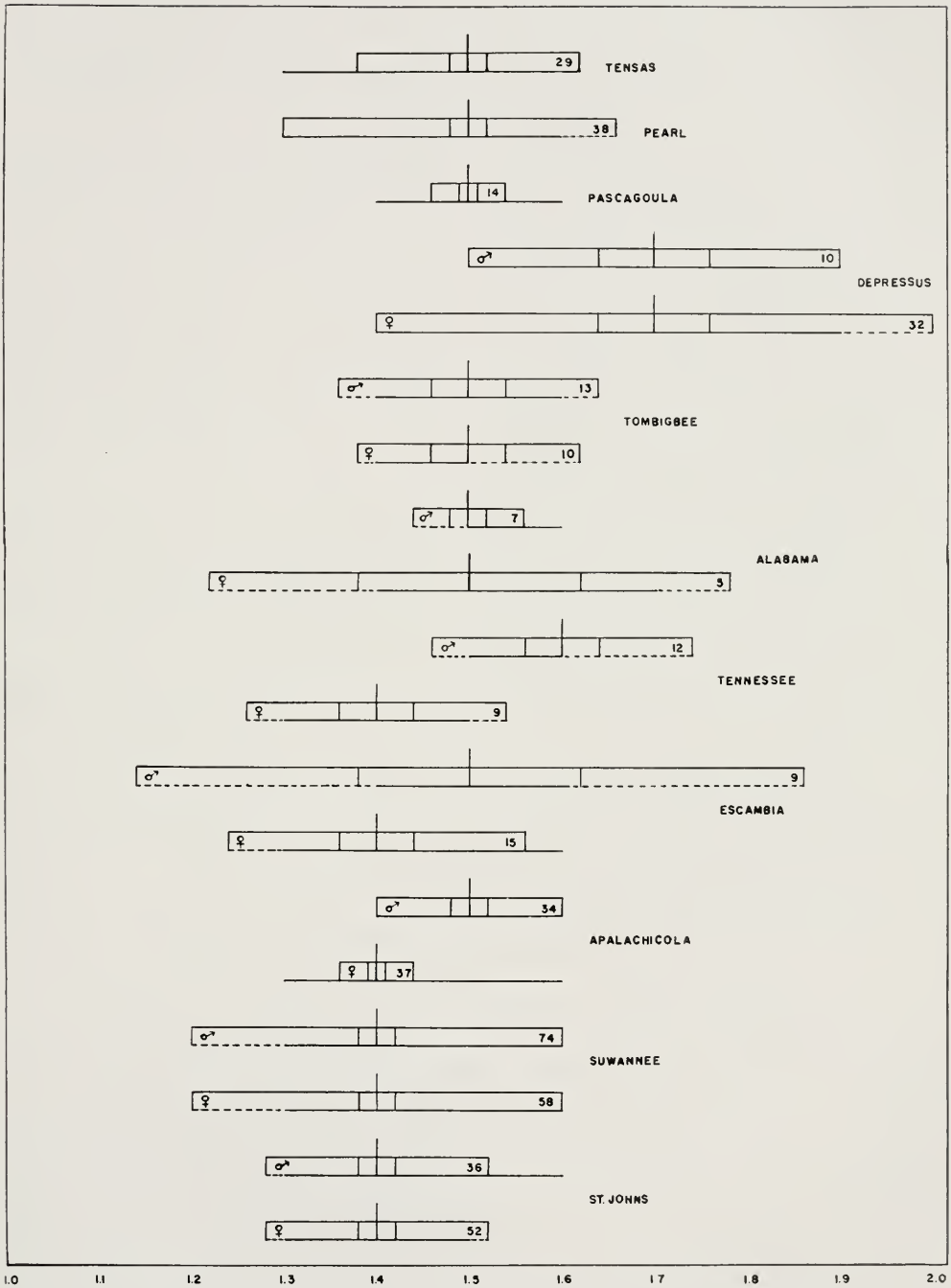


Figure 37. Ratio of carapace length to plastron length. Symbols as in fig. 17.

can be attached to the differences. The carapace shape of *Sternothaerus depressus* is considerably different from that of the other forms. The large numbers of juveniles in the samples of *S. carinatus* shift the mean slightly to a smaller ratio than would a more balanced sample.

CL/PL (fig. 26).—*Sternothaerus depressus* shows the most marked difference in this ratio, but displays considerable overlap with the other forms. *Sternothaerus carinatus* and *S. m. peltifer* are similar, while the mean of *S. m. minor* is significantly different from that of the other three forms.

CA/CH (fig. 42).—The means of the four forms are significantly different from one another, but *Sternothaerus m. peltifer* and *S. m. minor* show close similarity. *Sternothaerus carinatus* shows a significantly smaller ratio because of the acuteness of the vertebral angle, and *Sternothaerus depressus* shows the most significant difference. The ranges of variation of *depressus* and *carinatus* overlap slightly. The standard deviations of the means of *depressus* and *S. m. peltifer* overlap slightly. The majority of individuals of *S. depressus* may be distinguished from all other forms by a high (greater than eight) ratio of carapace angle to height.

IL/IW (fig. 43).—*Sternothaerus carinatus* and *S. depressus* show nearer equality between the length and width of the inguinals than do *S. m. minor* and *m. peltifer.*

TABLE 13. *Geographic trends in expression of lateral keels of S. m. minor*

River	Not Keeled	Faintly Keeled	Fairly Distinct	Prominent	Very Distinct
Altamaha					
Satilla	0	0	1	1	3
Ogeechee					
St. Johns	3	14	26	8	1
Suwannee	1	8	30	5	6
Chipola					
Apalachicola	3	10	7	4	0
Choctawhatchee					
Escambia					
Yellow	27	1	0	0	0

Sternothaerus m. peltifer and *m. minor* show close similarity in this ratio. This character has some diagnostic value for differentiating *S. carinatus* from *S. minor.*

PL/Ih (fig. 44).—*Sternothaerus m. peltifer* shows significant divergence from the other three forms in this character. The means of *carinatus* and *depressus* are similar, while the mean of *S. m. minor* is intermediate between theirs and that of *m. peltifer,* but significantly different from the mean of all three.

PL/IF (fig. 45).—The means of *Sternothaerus carinatus, S. m. peltifer,* and *S. depressus* are strikingly similar, but *S. m. minor* diverges markedly from these three. However, the degree of overlap of the ranges of variation demonstrates the relative uselessness of this character in distinguishing between the members of the complex.

PL/Ian (fig. 46).—The geographic trend from the smaller interanal seam of eastern *minor* to the larger one of western *carinatus*

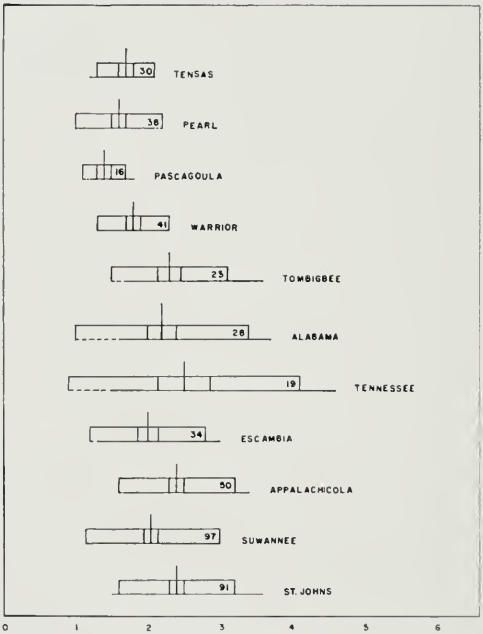


Figure 38. Ratio of inguinal length to inguinal width. Symbols as in fig. 17.

is clearly evident. *Sternothaerus depressus* is significantly different from most of the other forms. There is considerable overlap in the range of variation of *depressus* and that of the other forms, but the ratio differences indicate species divergence. There is a significant ontogenetic shift in the mean ratio of *S. carinatus* in which specimens less than 80 mm in plastron length are similar to *depressus* and different from the other forms.

E. *Uncorrelated Variation*

Vertebrals (Tables 14-16).—The first vertebral is always longer than wide in each form. The second vertebral of *S. m. minor, m. peltifer* and *S. depressus* is wider than long in 90, 98 and 100 percent of the individuals, respectively. In *S. carinatus* the width of the second vertebral is greater than length in only 32 percent of individuals. The width of the third vertebral is greater than the length in 45 percent of *carinatus,* but width is greater than length in 100 percent of individuals of the other three forms. The width of the fourth vertebral is greater than length in 95 percent of *m. minor,* 99 percent of *m. peltifer,* in 100 percent of *depressus,* but in only 28 percent of *carinatus.* The fifth vertebral is wider than long in 69 percent of *m. minor,* 76 percent of *m. peltifer,* 98 percent of *depressus,* and 17 percent of *carinatus.*

TABLE 14. *Relationship between the length and width of each vertebral in each form in the Sternothaerus carinatus complex*

	Vertebrals									
	1		2		3		4		5	
	N	%	N	%	N	%	N	%	N	%
	minor									
L=W	0	—	24	8	1	—	11	4	65	22
L>W	290	100	6	2	0	—	4	1	25	9
L<W	0	—	260	90	289	100	275	95	200	69
	peltifer									
L=W	0	—	1	1	0	—	0	—	17	20
L>W	84	100	1	1	0	—	1	1	3	4
L<W	0	—	82	98	84	100	83	99	64	76
	depressus									
L=W	0	—	0	—	0	—	0	—	1	2
L>W	43	100	0	—	0	—	0	—	0	—
L<W	0	—	43	100	43	100	43	100	42	98
	carinatus									
L=W	0	—	25	20	26	20	35	28	66	52
L>W	127	100	61	48	44	35	57	45	39	31
L<W	0	—	41	32	57	45	35	28	22	17

These data show the tendency for *carinatus* to have all vertebrals longer than wide and the opposing tendency in the other forms to have all vertebrals (except the first) wider than long. Because there is an ontogenetic tendency in *carinatus* for the vertebrals to become longer than wide, we may safely distinguish adults of *carinatus* from the other three forms on the basis of their possession of three or more vertebrals longer than wide.

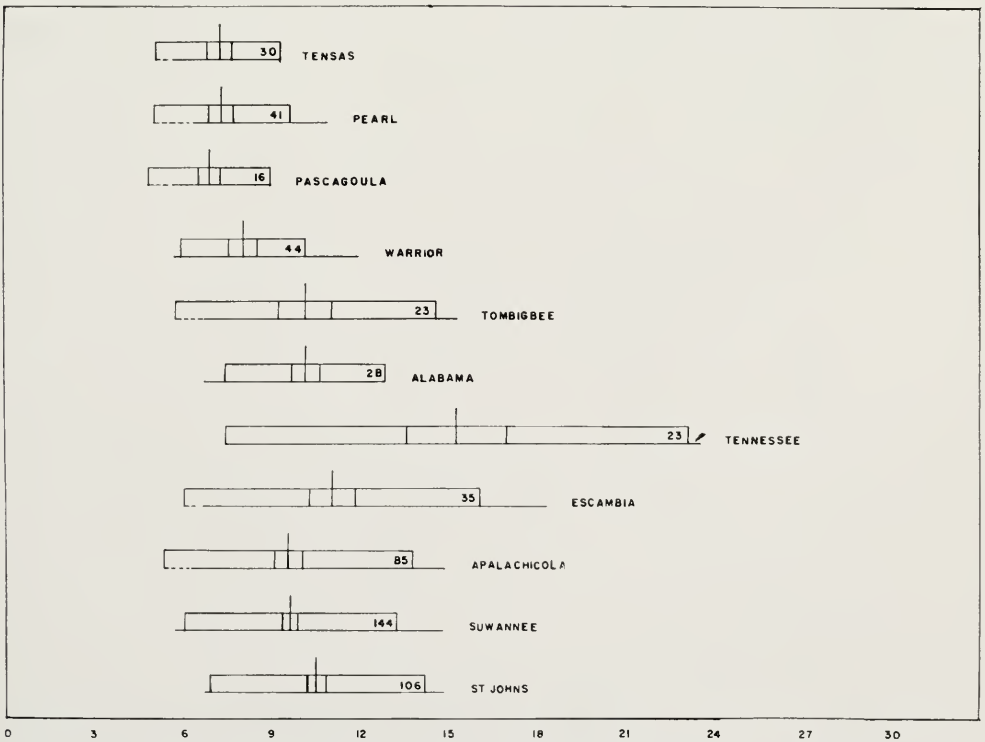


Figure 39. Ratio of plastron length to length of interhumeral seam. Symbols as in fig. 17.

Three or more vertebrals longer than wide are shown by 51 percent of *carinatus*, by one percent of *m. minor* and by no individuals of *m. peltifer* and *depressus*. Two or more vertebrals longer than wide occur in 10 percent of *m. minor*, six percent of *m. peltifer*, in no *depressus*, but in 67 percent of *carinatus*.

Considering another point of view, 89 percent of *m. minor*, 94 percent of *m. peltifer* and 100 percent of *depressus* have only one vertebral in which the length is greater than width, whereas this is true in only 31 percent of *carinatus*.

Smith and Glass (1947) distinguished *peltifer* from *carinatus* on the basis of the second, third and fourth vertebrals of the former being wider than long. This is a good distinguishing feature if juveniles of *carinatus* are excluded.

TABLE 15. *Percent of specimens of each form having 1, 2, 3, 4, or 5 vertebrals longer than wide*

	Number of Vertebrals Longer than Wide									
	1		2		3		4		5	
	N	%	N	%	N	%	N	%	N	%
minor	259	89	27	9	4	1	0	—	0	—
peltifer	79	94	5	6	0	—	0	—	0	—
depressus	43	100	0	—	0	—	0	—	0	—
carinatus	40	31	20	16	29	23	19	15	16	13

Number of gular scutes. — *Sternothaerus m. minor, m. peltifer* and *depressus* usually have one gular scute; *S. carinatus* has none. Of 387 *S. m. minor* examined, 384 had a single gular; one had two, and two had none. One of those without a gular is an embryo in which the scute may not yet have developed. The other specimen appears to have lost the gular scute by wear. Of 87 specimens of *S. m. peltifer*, 85 had one gular and one had none. The two gulars in one specimen resulted from an obvious

TABLE 16. *Percent of specimens of each form having 1, 2, 3, 4, or 5 vertebrals wider than long*

	Number of Vertebrals Wider than Long									
	1		2		3		4		5	
	N	%	N	%	N	%	N	%	N	%
minor	1	—	17	6	100	34	172	59	0	—
peltifer	0	—	1	1	21	25	62	74	0	—
depressus	0	—	0	—	1	2	42	98	0	—
carinatus	28	22	28	22	19	15	2	2	0	—

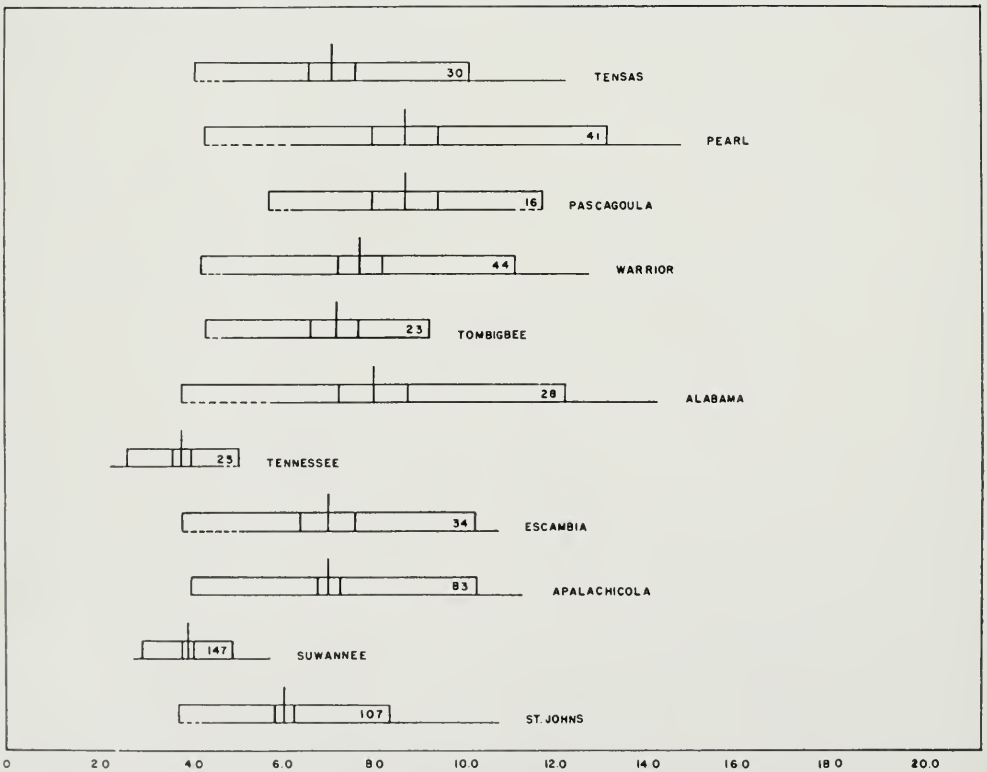


Figure 40. Ratio of plastron length to length of interfemoral seam. Symbols as in fig. 17.

split in a single scute. The 44 specimens of *S. depressus* have one gular. *Sternothaerus carinatus* is usually described as having no gular scute, or an occasional one. Of 135 specimens one had a gular and this one was a cotype (MCZ 15086). Presumably this specimen has been the reason for emphasizing the occasional presence of a gular scute.

Abnormalities. — Abnormalities in the number or arrangement of shields or scutes is uncommon. Three percent of 360 *S. m. minor*, seven percent of 86 *S. m. peltifer*, seven percent of 45 *depressus* and two percent of 123 *carinatus* displayed abnormalities.

The following abnormalities were found in *S. m. minor:* 12 marginals; 12 marginals plus six vertebrals; 12 marginals plus seven vertebrals; six vertebrals plus five pairs of costals; seven vertebrals plus five pairs of costals; two of five vertebrals irregularly divided into four; no seam between abdominal and femoral scutes; no interpectoral seam; split humeral; extra scute between humerals; and a transversely divided anal scute.

Sternothaerus m. peltifer displayed the following abnormalities: supernumerary vertebrals plus an extra costal; split fifth vertebral; 12 marginals; gular in contact with anterior edge of interhumeral beam (2 specimens).

In *Sternothaerus depressus* the following abnormalities were found: seven vertebrals plus five pairs of costals; split fourth vertebral; split tenth marginal.

In *Sternothaerus carinatus* there were two instances of a split first marginal and one of split femoral shields.

Discounting obviously split scutes or shields, there were seven instances of increase in the number of shields or scutes, six of which were accompanied by abnormalities in some other set of shields or scutes. Abnormal development of seams

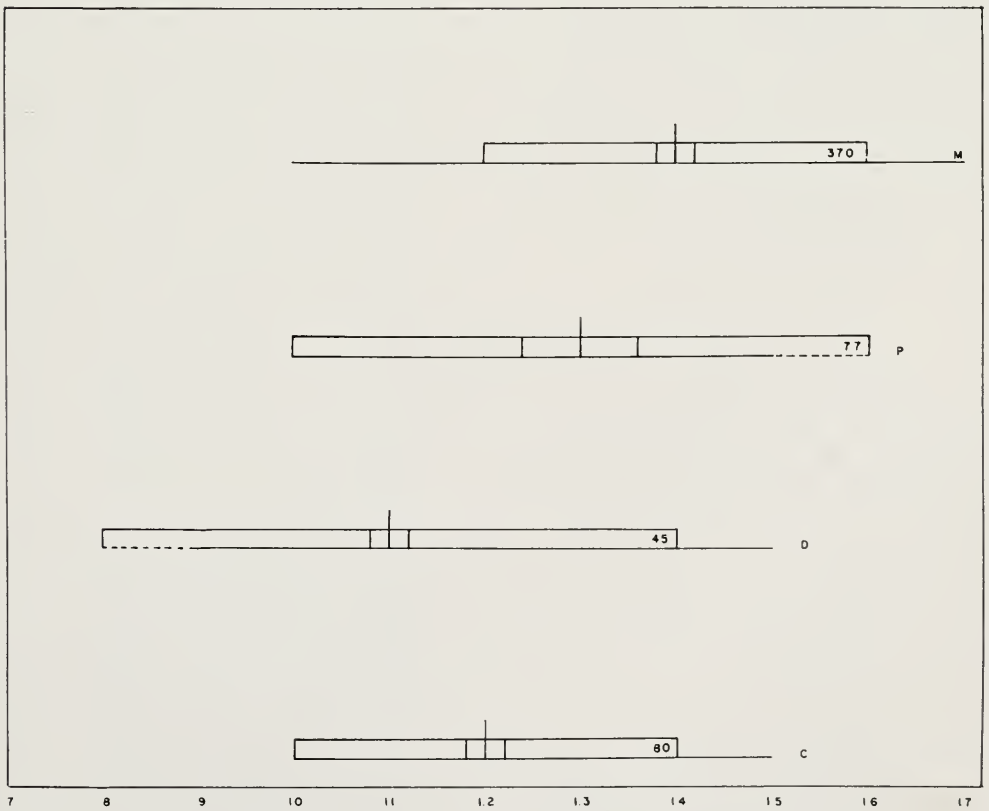


Figure 41. Ratio of carapace length to carapace width. Symbols as in fig. 17.

during early ontogeny in one area of the carapace or plastron may force readjustment and consequent abnormalities in another area.

In *Sternothaerus carinatus*, particularly in the eastern part of its range, some unknown substance erodes the marginal shields and underlying plates, particularly the posterior ones. Many specimens are found in which the posterior marginals and peripheral plates of bone have been eroded completely away. Occasionally lateral marginals have the same fate. Carr (1952) reported a similar observation and said that the "disease" was seen only in Louisiana specimens. I have noticed it most strikingly in specimens from the Pascagoula River drainage of Mississippi.

F. *Intergradation*

Intergradation is definitely indicated between *S. m. minor* and *S. m. peltifer* from the eastern rim of Mobile Bay to the drainage of the Choctawhatchee River. The juveniles in these populations differ from *m. minor* in lacking lateral ridges and from *m. peltifer* by the absence of head stripes. A comparison between juveniles of *m. minor*, *m. peltifer* and a presumed intergrade is shown in figure 6. The adults may be compared in figures 4, 7 and 8.

The area in which intergradation occurs

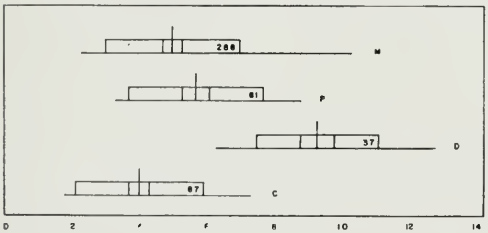


Figure 42. Ratio of carapace angle to carapace height. Symbols as in fig. 17.

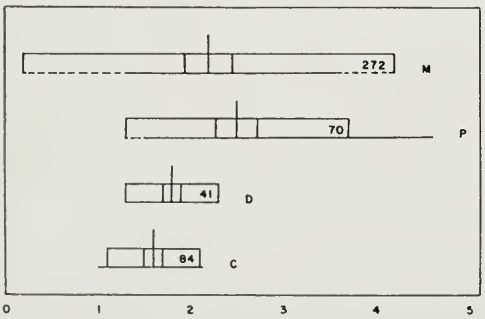


Figure 43. Ratio of inguinal length to inguinal width. Symbols as in fig. 17.

is one of the youngest on the Gulf coast and the overlap of the ranges of *m. minor* and *m. peltifer* may be recent. Most characters studied exhibit intermediacy between these two races in the Escambia River.

V. Key to Species of Sternothaerus

1. Fleshy protuberances on neck in addition to chin barbels; head with light stripes on a dark background; three dorsal keels in juveniles, none in adults; ground color of head dark ..... *odoratus*
   No fleshy protuberances other than chin barbels; stripes, if present, are dark; number of keels variable; ground color of head light ..... *carinatus* complex 2
2. Gular scute absent; lateral ridges never present; carapace high and steep; generally with three or more vertebrals longer than wide (except in many juveniles) ..... *carinatus*
   Gular scute present; lateral ridges present or absent; carapace not high nor steep (except in juveniles of *peltifer*); three or more vertebrals wider than long 3
3. Head with reticulated pattern of narrow lines on a light background; ratio of carapace angle to height greater than eight; adults or near-adults with an extremely low carapace, flat on top; juveniles with flattened carapace and blunt middorsal keel; no distinct lateral ridges ..... *depressus*
   Head with spots, with spots and stripes, or with spots and reticulations on posterior portion of head and neck; ratio of carapace angle to height less than eight; adults with carapace somewhat semicircular in cross-section, seldom completely flat on top; juveniles with pronounced middorsal keel; lateral ridges present or absent 4
4. Dark stripes on sides of head and neck; juveniles and adults without lateral ridges; spots present on dorsum of head in anterior one-half, replaced by stripes or reticulations in posterior region of head ..... *minor peltifer*
   Without dark head stripes (except in occasional juveniles near range of *peltifer*); spots on entire dorsal surface of head; juveniles and some adults with distinct lateral ridge on the carapace ..... *minor minor*

VI. Comparative Skull Osteology

A detailed study of skull structure was not made, but eight skulls of different size of each form were compared and several measurements taken.

The following measurements were taken to the nearest millimeter with dividers. The relationship of these measurements with increasing size of the skull are shown in table 17: 1.) tip to snout to tip of supraoccipital (maximum length); 2.) maximum width; 3) depth of jugal; 4.) anterior edge of prootic to posterior edge of opisthotic; 5.) maximum length of supraoccipital; 6.) maximum depth of supraoccipital; 7.) breadth at waist of pterygoids, *i.e.* at narrowest point; 8.) maximum length of alveolar cartilage in midline; 9.) tip of snout to juncture of parietals and supraoccipitals measured in midline; 10.) width of skull dorsally across the posterior tips of the squamosal bones.

The general appearance of the skulls of adults of each form may be seen in figure 47. The depth of the supraoccipital and the breadth of the skull make *m. minor* outstanding and the low, level skull of *depressus* is also distinctive.

A. *Description of Skulls of Adults*

The skull of *S. m. minor* is short, broad and massive with structural adaptation for accommodation of the powerful jaw musculature. The supraoccipital is deep with broad area for muscle attachment The upper ridge of the parietal is overhanging.

The skull of *S. carinatus* is longer, narrower and lighter than that of *m. minor.* The low, shallow supraoccipital has a strongly developed ridge on the ventrolateral surface. The area for muscle attachment on the supraoccipitals, parietals, quadrates, prootics and paraoccipitals is reduced compared with *m. minor,* but the processes on the basioccipital are more strongly developed than in *m. minor.*

The skull of *S. depressus* is low, neither elongated nor broadened, and similar to *m. minor* in general appearance except that it lacks the auxiliary ridges and excrescences of *m. minor.* One striking feature is the

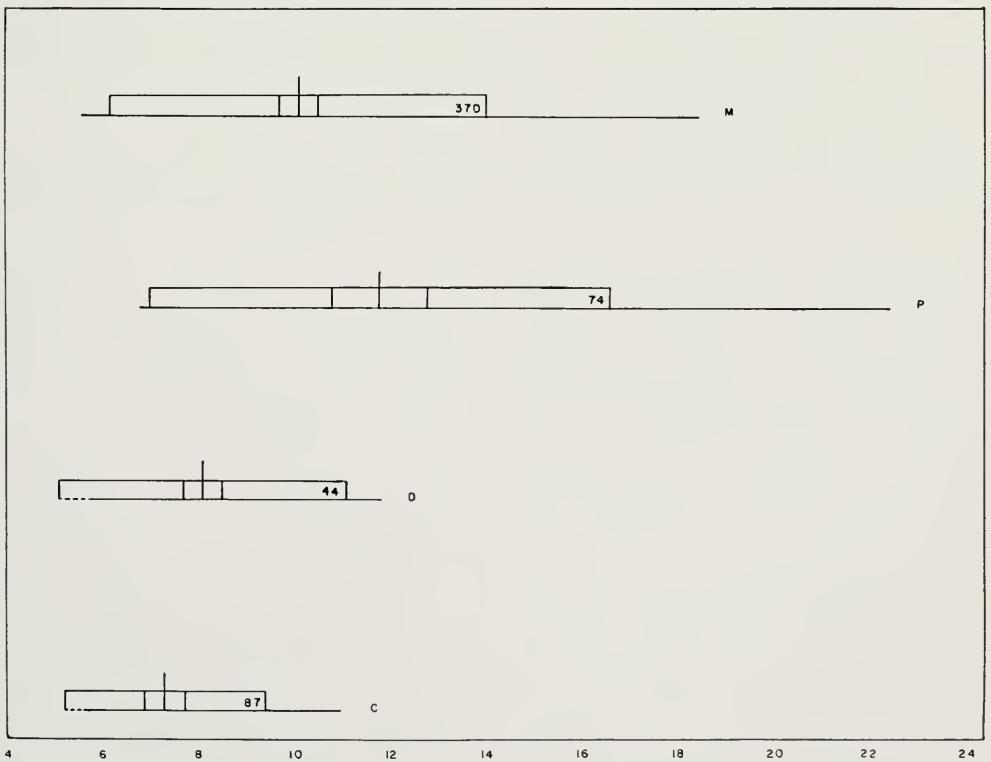


Figure 44. Ratio of plastron length to length of interhumeral seam. Symbols as in fig. 17.

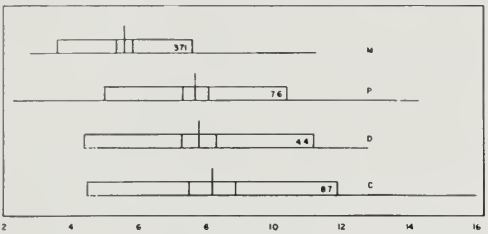


Figure 45. Ratio of plastron length to length of interfemoral seam. Symbols as in fig. 17.

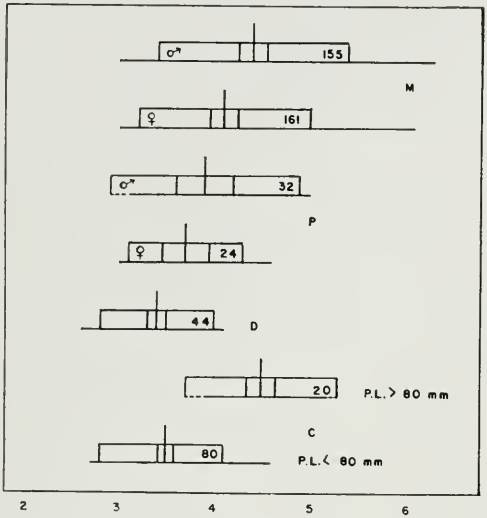


Figure 46. Ratio of plastron length to length of interanal seam. Symbols as in fig. 17.

horizontal slope of the head from the anterior tip of the prefrontal to the posterior tip of the supraoccipital. This condition contrasts with the rather abrupt upward curve in this same region of the skull in *carinatus* and *m. minor*. Another distinctive feature is the trench in the lower surface of the projecting portion of the supraoccipital. The waist of the pterygoid is broad like that of *m. minor* and in contrast to that of *carinatus* and *m. peltifer*.

The skull of *Sternothaerus minor peltifer* is not as broadened, and the supraoccipital is shallower and more elongate than that of *m. minor*. The skull of *m. peltifer* is most like that of *carinatus*. A smooth, rounded ridge along the lateral edge of the pterygoids from the base of the quadrate to the alveolar cartilage is most evident in *m. peltifer*. This ridge is also present in *m. minor*, but extends only about one-half the distance from quadrate to alveolar cartilage.

B. *Possible Diagnostic Characters for Skulls*

The spinous process from the middle of the pterygoid is an ontogenetic development most prominent in adults of *carinatus* in which its size is diagnostic. It is prominent in *m. minor* and *m. peltifer*, but much reduced in *depressus*. In *m. peltifer, carinatus, depressus* and young *m. minor* this process may be seen from a direct dorsal view of the skull, but in adults of *m. minor* this process is obscured from dorsal view by the overthrust of the prootic shelf.

The ventrolateral ridge of the supraoccipital is prominent in adult or near adult turtles. It is distinct in all forms except *m. minor* in which its absence or reduction is diagnostic.

The forward projection of the prootic and parietal develops ontogenetically and is shown by large individuals of all forms except *m. minor* in which its absence is diagnostic.

There is a roughened projection in the anterior temporal fossa which is presumably for muscle attachment. It is absent or scarcely developed in all skulls except those of *m. minor* in which it is diagnostic.

Knob-like projections from the basioccipital are prominent in *carinatus* and *m. minor*, but weak in *m. peltifer* and *depressus*. The skulls of juveniles do not exhibit this characteristic.

A boss on the underside of the squamosal becomes prominent and diagnostic in the skulls of adult *S. carinatus*. In *m. minor* there is a faint elevation, but this feature is absent in *m. peltifer* and *depressus*.

The supraoccipitals (lateral view) in juveniles of all forms taper to a point, but in adults the end of this bone becomes rounded or slightly truncated except in *S. carinatus* in which the tapering point is diagnostic.

The extent of a trench in the ventral surface of the supraoccipital is diagnostic of *depressus* in which this trench is 75 to 100 percent of the length of the projecting portion of that bone. The percentage in *m. peltifer* is always less (highest, 55 percent). In *carinatus* and *m. minor* only the two

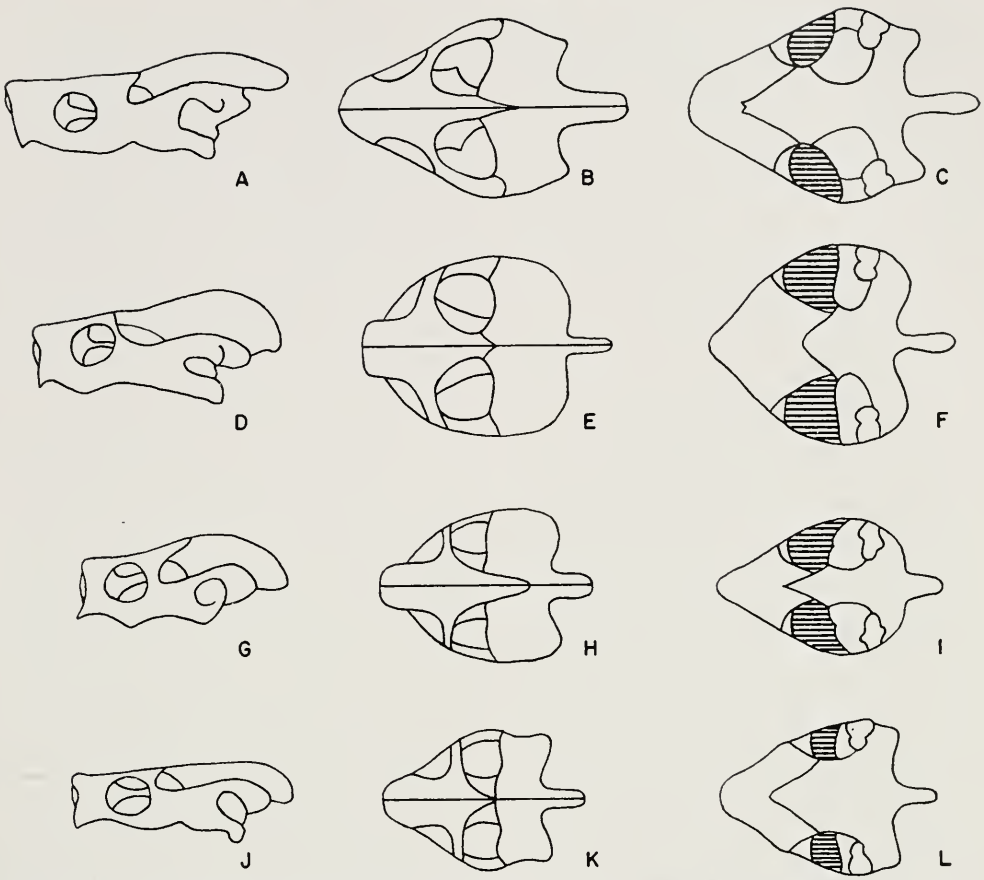


Figure 47. Comparison of skulls of the members of the *Sternothaerus carinatus* complex. Left to right, lateral, dorsal and ventral aspects. **A-C:** *carinatus;* **D-F:** *m. minor;* **G-I:** *m. peltifer;* **J-L:** *depressus.*

smallest skulls examined show any overlap with *depressus* in this characteristic. The percentage of the length of the trench to that of the projecting part of the supraoccipital may be generally stated as follows: *carinatus,* 50 percent; *m. peltifer,* 50 percent or less; *m. minor,* 50-70 percent; *depressus,* 75 to 100 percent.

C. *Discussion of Measurements and Ratios*

The greatest ratio of head length to carapace length is that of *m. minor,* the least that of *depressus.* In *m. minor* there is an abrupt increase in the ratio, indicating continuing growth of the head after cessation of growth in the carapace or a wide differential in rate of increase of head and carapace. The same phenomenon occurs less strikingly in *m. peltifer* and *depressus. Sternothaerus carinatus* shows no abrupt change.

The remaining percentages, all ratios between head measurements, fall into four categories: (a) *no allometry.*—while head length increases, length, etc., of another part increases in proportion; (b) *positive allometry.*—while head length increases, ratio of head length to length, etc., of another part increases; (c) *negative allometry.*—while head length increases, ratio of head length to length, etc., of another part decreases; (d) *no correlation.*—the ratio between two measurements fluctuates.

The distribution of the various measurements with respect to these four categories is shown in table 17.

Only *Sternothaerus m. minor* and *S. carinatus* exhibit definite positive and negative allometry. In *m. minor* this allometry is associated with the disproportionate increase in length of the prootic-opisthotic shelf and

TABLE 17. *Distribution of ratios of skull measurements. Numbers refer to measurements on page 35.*

Species	No Allometry	Positive Allometry	Negative Allometry	No Correlation
carinatus	5	7	2,4,8	3,6,9,10
peltifer			3,9	2,4,5,7,8,10
	(5,6 show weak positive allometry at sexual maturity)			
	(7 exhibits weak and variable negative allometry) except			
minor	4(15915,3) except 6(15915)		3	5,7,9,10
	(2,8 show sudden positive allometry at sexual maturity)			
depressus			2,3,4	7,8,9,10
	(5,6 show weak positive allometry near sexual maturity)			

in depth of the supraoccipital for the head and jaw musculature. The reason for the positive allometry in *S. carinatus* is not clear.

Some characters show rather sudden positive allometry near the size of sexual maturity. The width of the head and the length of the alveolar cartilage of the upper jaw in *m. minor* are examples. In *S. depressus* and *S. m. peltifer,* the length and depth of the supraoccipitals show weak positive allometry near sexual maturity.

Negative allometry is shown clearly only by the breadth of the pterygoid waist in *S. carinatus.* The width of the pterygoid bones increases so little ontogenetically that it does not keep pace with the elongation of the skull. Negative allometry is weakly indicated by the same character in *S. m. peltifer.* The width of the skull across the posterior tips of the squamosal shows negative allometry approximately until sexual maturity, and then positive allometry in all forms except *S. carinatus.*

The difference between no allometry and no correlation is arbitrary and these two categories may be considered as a single one.

The important skull characteristics of *Sternothaerus carinatus* are a prominent pterygoid spinous process in adults; prominent projections from the basioccipital in adults; prominent boss on ventral surface of the squamosal in adults; pointed and tapering supraoccipital in adults; and a long and narrow skull.

The important skull characteristics of *Sternothaerus minor minor* are a spinous pterygoid process that cannot be seen in adults from a direct dorsal view; a weak or absent ventrolateral ridge on the supraoccipital; no forward projection of the prootic or parietal in adults; prominent projections from the parietal in the anterior part of the temporal fossa; and prominent projections from the basioccipital in adults.

The important skull characteristics of *Sternothaerus minor peltifer* are no prominent projections from the basioccipital in adults; a well developed ridge along the lateral surface of the pterygoid bones which extends to the posterior edge of the alveolar cartilage in adults. This is a weak character for diagnostic purposes.

The important skull characteristics of *Sternothaerus depressus* are a small spinous process of the pterygoid; no prominent projections from the basioccipital in adults; length of trench in ventral surface of the supraoccipital is 75 percent or more of the length of the projecting portion of that bone; no overthrust of the parietal in adults; skull level dorsally from a lateral view.

D. *Key to Species Based on Skulls*

1. Supraoccipital pointed and tapering (lateral view); prominent boss on underside of squamosal; prominent projections from basioccipital; prominent spinous process on pterygoids ..... *carinatus*
   Supraoccipital blunt and rounded; boss on underside of squamosal absent or weak; articular projections from basioccipital weak or prominent; spinous process of pterygoids weak or distinct 2
2. Length of trench in ventral surface of supraoccipital 70 percent or more of the length of the projecting portion of the supraoccipital; no overthrust of the dorsal edge of the parietal; spinous process on pterygoid small; no prominent projections from basioccipital; skull low and level from lateral view ..... *depressus*
   Length of trench less than 70 percent (except in some specimens less than 55 mm in carapace length) of length of the projecting portion of the supraoccipital; dorsal edge of parietal overhanging temporal fossa; spinous process of pterygoids larger; size of projections from basioccipital variable 3

3. Ventrolateral ridge of supraoccipital reduced or absent; prominent projections from parietal in anterior part of temporal fossa; spinous process of pterygoid not visible from direct dorsal view of the skull in adults; articular projections from basioccipital prominent; no forward projection of prootic and parietal ..... *minor minor*

Ventrolateral ridge of the supraoccipital distinct; no prominent projection from the parietal (this projection weakly indicated in some skulls); spinous process of pterygoid visible from direct dorsal view of skull; projections from the basioccipital weak; prootic and parietal bones project forward ... *minor peltifer*

VII. Speciation and Phylogeny

Most of the range of the *Sternothaerus carinatus* complex lies within the Gulf coastal plain. In contrast, *Sternothaerus odoratus* is widely distributed over the United States east of the Rocky Mountains. *Sternothaerus odoratus* may have achieved its present distribution since the Pleistocene or it may have survived farther north during this period than members of the *S. carinatus* group. *Sternothaerus odoratus* may be more cold-resistant than most members of the *S. carinatus* complex. The only data available on thermoregulation are the quite inconclusive ones of Edgren and Edgren (1955) on *S. odoratus*.

The relationship between three members of the *Sternothaerus carinatus* complex is clear. *Sternothaerus m. peltifer* is subspecifically related to *S. m. minor*, although the two races are well-differentiated. *Sternothaerus depressus* is obviously related to, and probably derived from the progenitor of *peltifer*. *Sternothaerus carinatus* is distinct and its exact relationship with other members of the complex is not clear, but morphologically it is most like *S. m. peltifer*.

The origin of *Sternothaerus* is not clear. Dunn (1931) said the Kinosternidae were descended from the Central American family Dermatemydidae. Simpson (1943) said the distribution of the Kinosternidae "suggests origin in southern North America or in the ancient part of Central America..."

The only fossils (*i.e.*, Kinosterninae) available are of the genus *Kinosternon* from the Pliocene and Pleistocene of Kansas (Galbreath, 1948) and from the Pleistocene of Arizona (Gilmore, 1922). These fossil species were similar to living ones.

Of all members of the *S. carinatus* complex, the one most closely related to *S. odoratus* is *S. m. minor*. In both species, the juveniles have lateral carapace ridges that are lost completely in older *odoratus* and greatly reduced or lost by most *S. m. minor*. *Sternothaerus odoratus* is possibly the most primitive existing species in the genus. The time or place of origin of *S. m. minor* from *odoratus* is a matter for conjecture, but it seems likely that the differentiation of *m. minor* took place on the Gulf coastal plain in Georgia or Florida. In the clear, calcareous springs of central Florida *m. minor* reaches its greatest abundance.

There is little reason for looking beyond the Pleistocene or Pliocene to explain speciation in the *S. carinatus* complex. The climate of the Pleistocene exerted enough influence to force many species of animals southward (Deevey, 1949, 1950; Richards, 1939). This may have been true especially of river dwelling animals with little means of temperature regulation. The progenitor of *m. minor* was forced into Florida and separated from its western populations by the encroaching Pleistocene sea or by some physiographic rift. Cooke (1939) and Mossom show the sea covering most of Florida during the early Pleistocene.

Sternothaerus carinatus is more differentiated from *S. m. minor* and *S. m. peltifer* than the latter two are from one another. The shape of *carinatus* is approached by *m. peltifer* and little imagination is required to convert *m. peltifer* into *carinatus* by steepening the carapace, eliminating the gular scute and the head stripes of *m. peltifer*.

Therefore, I believe that *carinatus* arose from *m. peltifer* stock just prior to or during the Pleistocene. The separation of the populations in the central Gulf coast was probably caused by the rather sudden entrance of the great mass of water carried by a river in the vicinity of the present Mississippi River (Fisk, 1944) or earlier by encroachment of the sea (Shaw, 1918; Stephenson, 1928). Hobbs (1949) stated that the channel of the Mississippi River south of Cairo, Illinois was tremendously enlarged during the Pleistocene by great

volumes of meltwater during the summers. The range of *carinatus* lies, for the most part, west of the Mississippi embayment, and this species has in comparatively recent times extended its range east of the Mississippi River. *Sternothaerus m. peltifer* has extended its range westward into that of *carinatus*, but only a few specimens have been taken west of the Tombigbee River drainage. There is no evidence of intergradation of these forms, so separation may have been of sufficient duration to allow isolating mechanisms to develop.

The range of *m. peltifer* to the north crosses the Fall Line in the Alabama River and extends into the Tennessee River drainage. The distribution of this form suggests the possibility that this distribution is further evidence of the former connection of the Tennessee and Alabama rivers by way of the Coosa River. This might explain the absence of *m. peltifer* above the Fall Line in the Tombigbee River. The biological evidence for a former connection is good (Simpson, 1900; Van der Schalie, 1938, 1939, 1945; Adams, 1901), but the geological evidence indicates that the Tennessee River has held its present course since Cretaceous time (Johnson, 1905, 1939, 1941). The assumption of a past connection in the present case would require a great amount of geological time which is unnecessary in view of the similarity of *m. peltifer* to *m. minor* and their indicated gene exchange in western Florida. It is more likely that *m. peltifer* migrated into the Tennessee River relatively recently, a supposition borne out by the absence of this form in the Mississippi River drainage. Why *m. peltifer* has been able to cross the Fall Line in the Alabama River, but not in the Tombigbee River is not known. Although the Fall Line is no longer a strong physiographic feature, many costal plain rivers that cross it are interrupted by riffles or rapids that might be a deterrent to upstream movements of turtles. The passage of *m. peltifer* into the Tennessee River may have been facilitated by stream capture, an explanation suggested by Ortmann (1913) to explain the distribution of freshwater molluscs.

The range of *S. m. minor* in Florida occupies primarily the central and western highlands, but not the young (geologically) formations. In Georgia its range, almost entirely south of the Fall Line, indicates the youthfulness of the rivers, recent expansion of the range of *m. minor*, or both.

The work of Campbell (1940) makes it unlikely that *S. m. minor* was in Florida prior to the Pliocene. This is additional evidence for the relatively recent differentiation of *m. minor* in that state. The intergradation between *S. m. minor* and *m. peltifer* is in an area recently reclaimed from the sea (Mac Neil, 1950; Cooke and Mossom, 1939).

The distribution and isolation of *Sternothaerus depressus* is remarkable. Its range and obvious affinities with *m. peltifer* indicate that *depressus* was derived from the

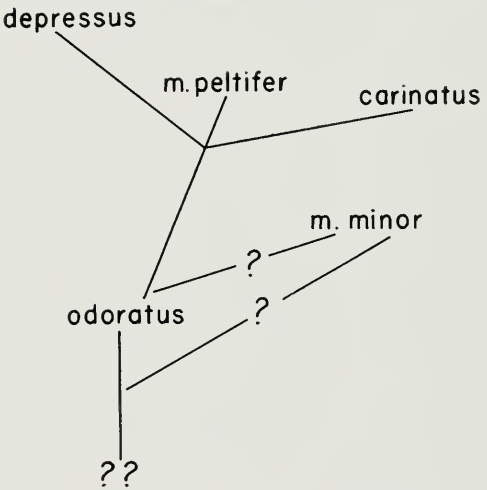
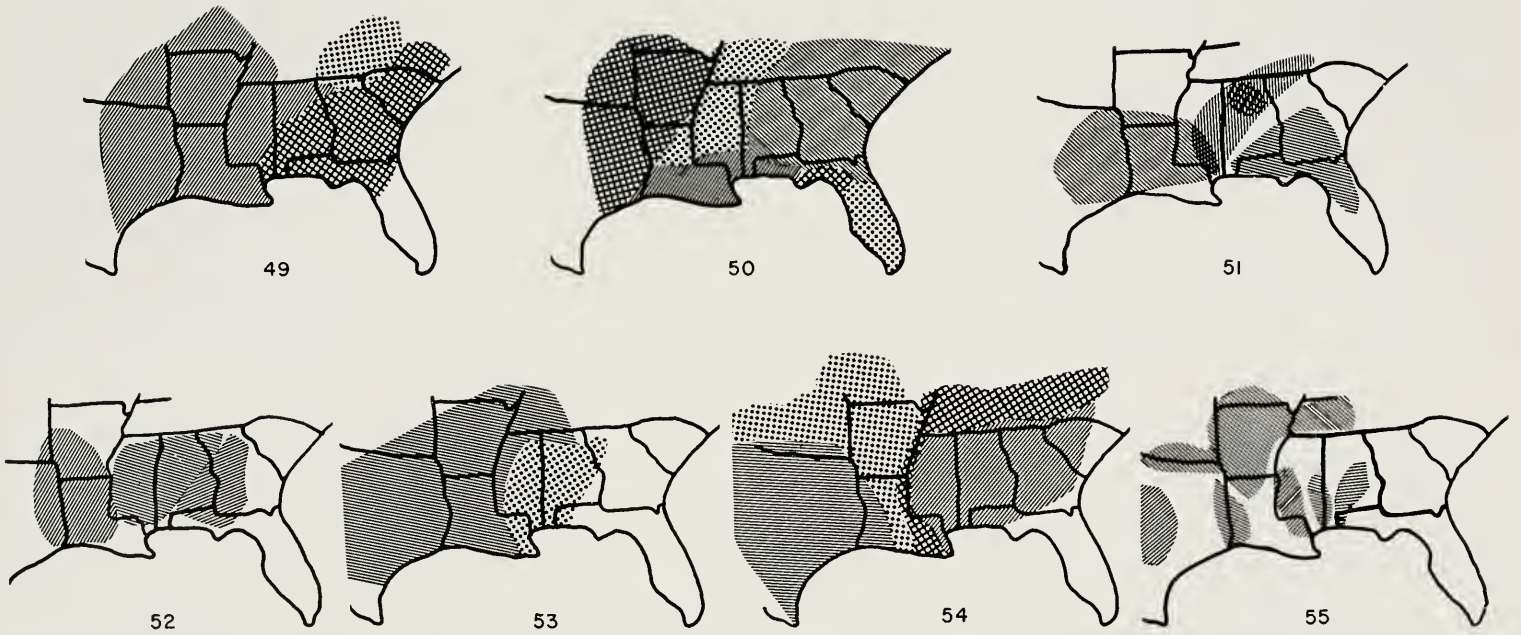


Figure 48. Diagram illustrating phylogeny of *Sternothaerus*.

stock that produced *m. peltifer*, perhaps entering the upper reaches of the Warrior River from the Tennessee River drainage. Its extreme isolation may indicate that it is becoming extinct. Certainly it has not been successful at extending its range as the other members of the complex have done.

Graphically, the phylogeny of the genus *Sternothaerus* appears as shown in figure 48.

The structure of the skull supports this proposed scheme. The external morphology, also in agreement, shows a closer relationship of *carinatus* to *m. peltifer* and *m. minor* than to *depressus*, a close relationship between *m. minor* and *m. peltifer*, and a general similarity of *depressus* to individuals from certain populations of *m. peltifer*.



Figures 49-55. Distribution of races, forms or species of turtles; each pattern represents a different race, form or species. **49.** *Pseudemys scripta* (after Carr, 1952; and Cagle, 1950). **50.** *Pseudemys floridana* (after Carr, 1952). **51.** *Sternothaerus carinatus* complex. **52.** *Graptemys kohni, pulchra* and *barbouri* (after Cagle, 1952, 1953). **53.** *Trionyx muticus* (after Webb, unpublished). **54.** *Trionyx spinifera* (after Crenshaw and Hopkins, 1955; Schwartz, 1956; and Carr, 1952). **55.** Narrow-headed *Graptemys*: *G. versa, pseudogeographica* and *oculifera* (after Cagle, 1954, and unpublished data).

VIII. Patterns of Speciation in Gulf Coast Turtles

Figures 49 to 55 show the distributions of the members of four genera of turtles on the Gulf coastal plain. The data for *Sternothaerus, Graptemys* and *Trionyx* are most reliable. Some distributional data on *Trionyx* were supplied by Mr. Robert Webb from his unpublished records. The distribution of the races of *Pseudemys scripta* is based upon the work of Cagle (1950) and Carr (1952). The distribution and taxonomic status of the races of *Pseudemys floridana* are poorly known, but chiefly I have followed Carr (1952). Dr. John Crenshaw of the University of Missouri is currently investigating the *floridana* group and has furnished me some information on species distribution. I have had considerable field experience with most of the forms of *Graptemys, Pseudemys* and *Sternothaerus*. In the genus *Sternothaerus* I have considered only the *carinatus* complex.

In *Sternothaerus, Pseudemys* and *Trionyx* the patterns are different in detail, but generally similar. These three genera display a pattern of differentiation into several geographic races. This trend is least developed in *Pseudemys scripta,* possibly because its migratory habit and wide range of habitat tolerance facilitates gene exchange. Most other turtles considered show some preference for running water or, at least, for bodies of water associated with lotic situations.

The members of the *Sternothaerus carinatus* complex seem more differentiated than do members of the *Trionyx* and *Pseudemys* groups, but in none of these are great spans of time needed to explain their differentiation. We might conclude that the rates of evolution in these three genera of turtles are essentially the same, assuming that each has had a similar time interval for speciation in the rivers of the Gulf coast.

The genus *Graptemys* exhibits two patterns of speciation. *Graptemys kohni, G. pulchra* and *G. barbouri* (the broad-headed group) form a group displaying slight geographic variation, much like the situation in *Sternothaerus*. An obviously different pattern exists in some narrow-headed *Graptemys; G. oculifera* in the Pearl River, *G. flavimaculata* in the Pascagoula River and *G. nigrinoda* in the Tombigbee-Alabama River are obviously related, but distinct. Yet *Graptemys oculifera* and *flavimaculata* occupy exclusively two of the youngest (geologically) rivers on the Gulf coast, and it is difficult to escape the conclusion that the rate of differentiation in this group has been faster than in the other genera in these same rivers in which no detectable differentiation has occurred. There are no close relatives of the narrow-headed *Graptemys* to the north of their known range, and I conclude that they have differentiated in situ. Cagle's conclusions (1954) concerning speciation in the narrow-headed *Graptemys* are similar to mine.

> "The absence of these three forms in river systems east of the Alabama and west of the Pearl is further evidence that the evolutionary history of this complex is substantially different from that of other turtle species of the Gulf coast—the extent of the Alabama and Tombigbee systems as contrasted with the Pearl and Pascagoula is suggestive of greater age. Perhaps in this situation rests the explanation of the greater divergence in *G. nigrinoda*, it perhaps being the older of the three forms—the relative youth of the Gulf coast streams implies that rapid evolution has occurred in this complex."

The headwaters of the Pearl, Pascagoula and Tombigbee rivers are quite close at present and accelerated stream piracy may soon accomplish or speed the mingling of the narrow-headed *Graptemys*. All three species of the *oculifera* group may have had a common origin from the Tennessee or Tombigbee river systems during the early Pleistocene.

A major difficulty in discussing differences in rates of evolution or in patterns of speciation is that subspecies or species recognized in one genus are not, obviously, at the same level of differentiation as those in another group. For example, the many recognized races of *Pseudemys floridana* are, at best, poorly differentiated with great overlap in most characters. For this reason, the numerous races of *P. floridana* may not have the same significance in terms of evolutionary patterns as the well-differentiated members of the genus *Graptemys*. With this major handicap in mind, plus the knowledge that I have had to rely heavily upon the judgment of other workers, I will attempt further comparisons of the patterns of speciation.

Pseudemys scripta and *Pseudemys floridana* exhibit similar patterns, although fewer races of the former are recognized. *Pseudemys floridana* is more of a river-dwelling turtle than *scripta*, and this may explain its apparent greater raciation. *Pseudemys scripta* shows clearly a correlation of differentiation with the disruption of its range by the Mississippi delta. The wide range of intergradation between *scripta scripta* and *scripta elegans* on recent sediments is a result of the recent expansion of the range of one race into that of the other. *Pseudemys scripta troosti* probably differentiated in the Tennessee River (figs. 49, 50).

The *Sternothaerus carinatus* complex, the broad-headed *Graptemys*, and the *Trionyx muticus* groups show similar patterns of differentiation (figs. 51-53), distinguishable chiefly by the peculiar distribution of *Sternothaerus depressus*. These patterns suggest that similar processes have shaped the course of speciation, and that similar time intervals were involved. The pattern in *Trionyx spinifera* is somewhat different, but is generally similar if allowance is made for the development of two races in an area north of the coastal plain. Considering the coastal plain races, the pattern is similar to the others described (fig. 54).

The pattern of evolution in the narrow-headed *Graptemys*, particularly in the *oculifera* complex, is different. *Graptemys versa* is different from all other members of the genus. *Graptemys pseudogeographica sabinensis* and *G. p. ouachitensis* are related, but well-differentiated. *Graptemys oculifera* is closely related to, but different from *G. flavimaculata* and these two are, in turn, very different from the related *G. nigrinoda*. The conclusion seems inescapable that evolution in the narrow-headed *Graptemys* has been more rapid than that of the genera *Sternothaerus, Pseudemys, Trionyx,* or the broad-headed group of *Graptemys*. In none of the genera, apparently, has the differentiation of recent forms required great expanses of time. The relative youth of Gulf coast rivers inveighs against assumption of antiquity.

IX. Comparative Ecology

A. *Growth*

The rings in the plastral and carapacial shields of some turtles yield accurate age and growth information up to a certain size or age of individual. These rings are seldom as clear in *Sternothaerus* as they are in the emydid turtles, and whether they may be utilized for accurate age determination in the musk turtles has not been established. Risley (1933) used these rings in age and growth studies of *Sternothaerus odoratus*, but pointed out that accurate counts could not be made on turtles more than ten years old, *i.e.*, with more than ten "annuli". This is the age at which counts become difficult or impossible to make in most members of the *S. carinatus* complex.

Counts of rings were made in 205 *S. m. minor*, 82 *S. carinatus*, 63 *S. m. peltifer*, and 30 *S. depressus*. The mean carapace length of the turtles at each age was calculated, and these means used to construct growth curves (fig. 56). The most reliable data are those of *m. minor* because no fewer than three individuals are present in each

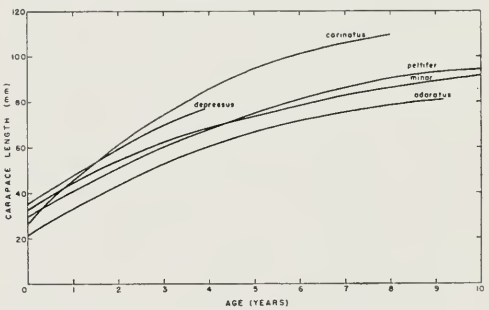


Figure 56. Comparative growth curves of *Sternothaerus*. Ages are based on counts of rings in scutes and shields.

age group and usually 10 or more. In the other forms, plot points represented by a single count which obviously deflected the growth curve in the wrong direction were omitted.

Sternothaerus m. peltifer and *S. m. minor* display almost congruous growth curves, and *S. depressus* may be similar, but specimens of the latter in older age classes are not available. The curves of all forms are similar until three or four years of age is attained and then the rate of growth of *m. minor* and *m. peltifer* declines, while that of *carinatus* continues at the same rate. The growth curve of *S. odoratus* was redrawn from that of Risley (1933). This species differs from the members of the *S. carinatus* complex in exhibiting smaller mean size at each successive age, but the rate in change

of size is similar to that of most other species of *Sternothaerus.*

B. *Size and age at sexual maturity*

The collections lack individuals from some seasons of the year. Most specimens were taken in June, July and August, but a few were available from April and September. Approximately 100 individuals were examined for signs of sexual maturity. Testes were macerated on slides and examined microscopically. Ovaries were removed when necessary for proper examination.

A single large male of *depressus* was available, with a carapace length of 75 mm and with four or five annuli. The testes were enlarged and a few small, possibly immature spermatazoa were present in the smear. The individual was probably subadult. Four large females were available, one a juvenile, the other three at least subadult.

Males may mature at a carapace length of 75 mm and an age of four years; females at a carapace length of 90 to 100 mm and an age exceeding four years.

Twenty large specimens of *S carinatus* were available for dissection. Spermatazoa were not found in any of the smears; the testes of adults were collapsed and obviously out of season. The complete absence of spermatazoa was unusual, as a few generally may be found even in out of season males of other forms. The size of the testes indicates that sexual maturity occurs at a carapace length of 100 to 120 mm and at an age of five to six years. One specimen was apparently a gynandromorph. It possessed the elongate tail of the male, but lacked testes. There were two tubular structures in the body cavity which resembled rudimentary oviducts, but no ovaries were present. Females of *S. carinatus* reach sexual maturity at approximately 100 mm carapace length and at an age of four to five years.

Twenty-five large specimens of *S. m. minor* were examined. Males mature at a carapace length of approximately 80 mm. The age at sexual maturity cannot be accurately stated, but is probably between four and seven years. Females also mature at a carapace length of 80 mm. The youngest sexually mature female had six annuli, another had seven. The age at attainment of sexual maturity is probably five or six years.

Twenty large specimens of *S. m. peltifer* were available for study. Spermatazoa were consistently present in the testes. Sexual maturity in the males is reached at a carapace length of 60 to 70 mm and at an age of three to four years. The data for large females are inadequate. One specimen with a carapace length of 78 mm had ovocytes that were beginning to enlarge and may have been adult or subadult. Two others (C.L. 92 and 95 mm) were subadult, one (C.L. 104 mm) was adult. Sexual maturity in females is reached at a size between 90 and 100 mm and at an age of six to eight years.

TABLE 18. *Summary of sizes and ages at sexual maturity in the four members of the Sternothaerus carinatus complex*

Species	Size		Age	
	Females	Males	Females	Males
carinatus	100 mm	100-120 mm	4-5 years	5-6 years
depressus	90-100	75	>4	4
peltifer	90-100	60-70	6-8	3-4
minor	80	80	5-6	4-7

The data on size and age at maturity are summarized in Table 18. The ages of males and females at sexual maturity are about the same in all forms except in *S. m. peltifer*, in which females are older and males younger than the respective sexes in the other forms. Risley (1933) estimated age at maturity of *Sternothaerus odoratus* as three to four years in males and nine to eleven years in females. The age for females is high compared with females of the other species of *Sternothaerus.*

The sizes at sexual maturity are approximately the same in most forms, but *m. minor* attains sexual maturity at a smaller size than do the other races, although at nearly the same age. The males of *Sternothaerus carinatus* reach sexual maturity at a greater size than any of the other forms. This species, incidentally, reaches the greatest size, *i.e.*, there is a greater percentage of individuals in the largest size class. The time required to reach sexual maturity is approximately the same in *carinatus* as in the other forms. In *carinatus* and *m. minor* the sexes are approximately the same size at attainment of maturity, but in *m. peltifer* and *depressus* the males are smaller than females. Size dimorphism is never so evident as in

TABLE 19. *Sex ratios and percentages of each sex in five arbitrary size groups. Carapace lengths in mm.*

	21-50		51-80		81-110		111-140		141-170	
	Males N %	Females N %	Males N %	Females N %	Males N %	Females N %	Males N %	Females N %	Males N %	
minor	9 39% N=23	14 61%	70 56% N=126	76 44%	76 45% N=170	94 55%	14 50% N=28	14 50%	0 0% N=0	
peltifer	4 50% N=8	4 50%	18 53% N=34	16 47%	8 44% N=18	10 56%	2 100% N=2	0 0%	0 0% N=0	
depressus	6 23% N=26	20 77%	3 30% N=10	7 70%	1 17% N=6	5 83%	0 0% N=0	0 0%	0 0% N=0	
carinatus	20 49% N=41	21 51%	8 22% N=36	28 78%	8 57% N=14	6 43%	3 42% N=31	18 58%	1 100% N=1	

some other turtles (*e.g., Graptemys* and *Trionyx*).

C. *Sex ratios*

The specimens were divided into four arbitrary size groups and the number and percentage of individuals in each group noted (Table 19). This method is not entirely satisfactory because samples taken at different periods of the year at widely scattered localities were combined. However, ratios of pooled samples were compared with those in large samples from a single locality.

The grouped data on sex ratios are shown in Table 20. The differences in *m. minor* and *m. peltifer* are not marked, and the totals show a near 50-50 ratio. In *carinatus* the ratios are approximately 50-50 in the smallest size groups, but fluctuate generally in favor of females in the other groups. The total ratio in *carinatus* differs significantly from a 50-50 one ($X^2 = 4.3$). In *depressus* the female comprises a greater percentage than the male in all size groups. This may be significant since all the specimens are from the same locality, albeit they were not collected at the same time. The differences in *carinatus* and *depressus* may reflect a differential sex ratio, but I am reluctant to attribute differences in the ratios to anything more than chance selection of individuals.

TABLE 20. *Sex ratio obtained from pooled samples of each form in the Sternothaerus carinatus complex*

Species	N	Males		Females	
		N	%	N	%
minor	347	169	49%	178	51%
peltifer	62	32	52%	30	48%
depressus	42	10	24%	32	76%
carinatus	123	50	41%	73	59%

The ratios of sexes in samples from various periods of the year show little consistency in which sex is predominant (Table 21). Likely the distribution and ease with which the two sexes are captured varies with season.

TABLE 21. *Sex ratios in selected samples of each form in the Sternothaerus carinatus complex*

Species	Date	Males N	%	Females N	%
minor	6-7 June 1953	9	50	9	50
	6-10 Aug. 1954	7	41	10	59
peltifer	13-15 Aug. 1955	6	67	3	33
	17-20 Aug. 1955	7	87	1	13
depressus	17 June 1953	4	33	8	67
	11-12 Aug. 1953	1	9	10	91
	9-12 Aug. 1955	1	13	7	87
carinatus	17-18 Aug. 1952	4	40	6	60
	14-21 Apr. 1950	13	57	10	43

Risley (1933) found that the sex ratio in 255 specimens of *Sternothaerus odoratus* was 77 males to 178 females, a ratio similar to that observed in *S. depressus*.

D. *Reproductive potentials*

A small number of specimens was available for estimating reproductive potentials. There were few gravid females, so estimates were based chiefly upon counts of large ovarian follicles.

In *carinatus* the mean number of potentially ovulatory follicles (those in the two largest size groups) is 3.3, if one individual that contained 17 is omitted. This extreme individual affects the mean considerably. The mode is three, and this figure may be the best estimate. The mean for *depressus* is 5.5, that for *m. peltifer* 7.0, but the small size of the sample of these two forms precludes accurate estimate. The largest size group of follicles in *m. minor* does not correspond to the largest in *carinatus*, so the groups used to estimate potential differ.

The mean in six females of *m. minor* is 2.7.

In both *carinatus* and *m. minor,* the probability that there may be two broods during one year is evident, and the same may be true of *m. peltifer* and *depressus.* Both specimens of *carinatus* with oviducal eggs have large follicles approximately equal in number to the oviducal eggs. These large follicles are nearly the same size as the yolk in the oviducal egg and presumably near ovulation. A female with five corpora lutea (the term corpus luteum as used herein neither assumes nor denies an endocrine function of this structure) had four follicles near ovulatory size. One of the females with oviducal eggs had three large lutea obviously representing a recent ovulation and four smaller structures which appear to be old lutea from an earlier ovulation. One female with oviducal eggs was taken in early April, the other in early June. One specimen of *S. m. minor* captured in early June had five corpora lutea and several follicles of ovulatory size.

Corpora lutea should be included in the estimate of potential, but they are not always distinct. Assuming two broods per year, the means given earlier may simply be doubled. However, this procedure introduces error because the original estimate of potential may have been high due to inclusion of follicles that would not contribute to the reproductive pool of the same season. The best estimate is obtained by adding the corpora lutea to the number of potentially ovulatory follicles. The mean number of lutea plus ovulatory follicles in *carinatus* is 7.3. This is more than twice the mean potential calculated previously. The presence of one turtle with 17 enlarged follicles indicates a higher fecundity in some individuals.

The mean number of corpora lutea plus follicles in *S. m. minor* is 6.3. The data indicate that *carinatus* and *m. minor* have approximately the same mean annual reproductive potential. The differences in the size of the largest follicles in *carinatus* and *m. minor* suggest a difference in the size of the eggs at ovulation.

Few data are available on clutch size. Carr (1952) reported finding eggs of *m. minor* in April laid singly or in two's or three's. He also states that eggs "almost certainly of this species", have been found in May and June. Neill (1948a) reported finding two eggs of *S. m. minor* unearthed by a plow in Georgia. I have seen a clutch of two eggs of *carinatus* found half-way up a steep bank on the Pearl River east of Varnado, Louisiana. Data on egg production in relation to potential are needed on all species of *Sternothaerus.*

Risley (1933) reported a variation of two to seven in clutch size of *Sternothaerus odoratus.* The usual number was three to five.

E. *Feeding habits*

General habits.—The stomach and or intestines of 159 *Sternothaerus* were examined, of which 95 were empty. Gut contents were taken when the stomach was empty, but often no food remains were found in the digestive tract. Few specimens were preserved in the field immediately after capture. Most were retained alive for 18 to 36 hours, and many kept indefinitely for laboratory observation.

Samples from the digestive tract of 23 *carinatus,* 7 *depressus,* 17 *m. minor* and 17 *m. peltifer* were examined and the major food categories tabulated (Tables 22-24). The major items in the diet were insects, snails and clams.

There is a clear shift (except in *depressus* from which a sufficient sample is lacking) with increasing size from an insectivorous habit in young turtles to a molluscivorous one in adults.

Sternothaerus m. minor develops heavy musculature associated with the lower jaw and a greatly expanded crushing surface in both jaws. This parallels the development of the crushing apparatus found in *Graptemys pulchra* and *G. barbouri,* and appears to be an adaptation for mollusc eating. *Sternothaerus m. peltifer* also develops a partially expanded, crushing jaw surface, but not to the extent common in *m. minor.* However, *S. m. peltifer* shows the same change in diet to mollusc feeding as does *m. minor. Sternothaerus carinatus* develops the mollusc feeding habit at a smaller size than *m. peltifer* or *m. minor,* but never develops the crushing jaws or hypertrophied head musculature. *Sternothaerus m. minor* may, by virtue of its crushing jaws, have access to larger prey than the other forms. The differences in feeding habits between old and young turtles may reduce compe-

tition and allow for larger populations in a given area.

There is no evidence of a sexual difference in feeding habits and only one instance of a geographic difference. In the Escambia River, most turtle stomachs and intestines examined in large specimens were filled with bottom detritus which was composed chiefly of leaves, seeds, algae and other plant material. It seems unlikely that all of this material was accidentally swallowed by turtles seeking animal food.

Specific items of food.— Adult insects were more commonly encountered than larvae. Coleoptera were the most prevalent with Trichoptera second. Spiders, the most common arachnids, were found in only a few stomachs. The clams encountered were always small and usually represented by fragments. Snails seldom exceeded one-half inch in length.

TABLE 22. *Food items of Sternothaerus m. peltifer and depressus of various sizes*

C.L.	Insecta	Arachnida	Isopoda	Decapoda	Clams	Fish
			peltifer			
40	X					X
43	X			X		
51	X					
						X
					X	
					X	
						X
				X		
				X		
					X	
	X				X	
					X	
	X				X	
	X					
	X				X	
101	X				X	
111					X	
			depressus			
	X					
	X	X				
	X					
	X	X	X			
	X					
	X			X		
50	X	X			X	

In *S. depressus* haliplid beetles were prevalent in the stomachs. This prevalence of shore beetles is correlated with this turtle's habit of frequenting brush and masses of twigs very close to shore. All items in the stomachs and intestines of *depressus* indicate inshore feeding.

Feeding time.—Trapping of *Sternothaerus* is non-selective of sex or size groups and yields information on population density. By analyzing trap records, the time at which turtles feed or are most active may be determined.

Sternothaerus carinatus is difficult to trap. I have had little success at trapping this turtle in the Pearl, Sabine or Pascagoula rivers even though traps were set in areas where basking *carinatus* were abundant. Mr. Paul Anderson obtained only about 12 specimens in several months of trapping in the Pearl River. Cagle and Chaney (1950) reported that *S. carinatus* was reluctant to enter traps or was not attracted by the bait. They captured one specimen in an area where numbers were seen basking.

TABLE 23. *Food items of Sternothaerus carinatus of various sizes*

C.L.	Insecta	Decapoda	Snails	Clams	Plants
					X
	X				
	X				
	X				
	X	X			
	X				
	X				
	X				
	X		X	X	
51	X		X	X	
52	X			X	
			X	X	
	X		X	X	
			X		
			X		
79				X	
116	X				X
128	X				
140			X		
140	X			X	X
144			X	X	

I have attempted to trap *Sternothaerus m. minor* in the Escambia River (intergrades with *peltifer*) and in the Ichtucknee Spring run (Suwannee River drainage) in Florida. *Sternothaerus m. minor* is abundant in the spring run and can be observed easily in the clear water, but no specimens were taken in traps. The clear water may be the factor responsible for trapping failure. At 1330 hours on August 9, 1954, 10 traps were set in quiet eddies out of the main channel of the Escambia River. Six specimens were taken in the traps at 1930 hours, none at 0830, August 10, and three at 2000 hours, August 10. The data are too meager for positive conclusion, but they indicate that these turtles fed in the evening or early night, not during the morning.

More conclusive data are available for *S. m. peltifer*. On August 13, 1955, eight traps were set in shallow water near shore along a 350 yard stretch of the east bank of the Coosa River, six miles east of Pell City, Alabama; five additional traps were set along 150 yards of the west bank. Traps were baited with whiting fish, the most effective bait used throughout the study. From 1930 hours, August 13, until 0600 hours on August 16, 42 *Pseudemys s. scripta*, 19 *Sternothaerus odoratus* and 14 *Sternothaerus minor peltifer* were taken in the 13 traps.

The traps were rebaited each day; when the fish develop a strong odor, turtles avoid them. Traps without bait were used unsuccessfully. At 1200 hours, August 15, the two traps which had been most productive were left unbaited. These traps had accounted for 25 turtles, but yielded none during the next two days.

TABLE 24. *Food items of Sternothaerus m. minor of various sizes*

C.L.	Insecta	Diplopoda	Snails	Clams	Fish	Plants
32	X					
34	X					
35	X					
39	X					
49	X					
69	X					
72				X		X
80					X	
83						X
90				X		X
91				X		
93	X					X
95			X	X	X	
97		X	X	X		
103						X
105			X			
113	X					X

There was a gradual decrease and, finally, a cessation of yield from the traps on the east side of the river. If this indicates that all turtles within feeding range were captured, then the trapping data yield information on relative population density. Continual disturbance of the trapped area causing a decrease in trap efficiency and movement of individuals from outside of the trapped area may produce errors in the census figures. With certain assumptions, the number of individuals of each species in a one-quarter mile stretch of river may be estimated (Table 25).

The traps on the west side of the river were run for two days only, during which time no evidence of decreasing yield was noted. The west bank was shaded for a greater part of the day than the east bank.

TABLE 25. *Numbers of three species of turtles trapped in a one-quarter mile length of the Coosa River during four days*

Species	Aug. 13 E	W	Aug. 14 E	W	Aug. 15 E	W	Aug. 16 E	W	Total E	W
Pseudemys s. scripta	13	—	16	—	8	2	0	3	37	5
Sternothaerus odoratus	5	—	6	—	3	3	0	2	14	5
Sternothaerus m. peltifer	1	—	7	—	1	2	0	3	9	5
					Grand Totals				60	15

Traps were examined at the same time on successive days. The pooled data for different periods of the day reveal patterns of feeding activity which differ in the three species (Table 26). Most *Pseudemys* feed early in the morning and at dusk, but not at night; few are taken during the late afternoon and morning. *Sternothaerus odoratus* is most abundant in the traps early in the morning and later at night than *Pseudemys*. As the traps were not examined throughout the night, it is not clear whether the bulk of individuals taken from the nets in the morning were trapped the previous night or early that morning. In *Pseudemys*, which was not taken at night, it is clear that those in the traps in the morning had most likely been caught that morning. The situation with *Sternothaerus odoratus* is not this clear.

TABLE 26. *Numbers of three species of turtles trapped at five periods of the day during four days of trapping in the Coosa River*

Hours	800	1200	1600	1900	2100
Pseudemys scripta	15	5	6	16	0
Sternothaerus odoratus	7	0	1	3	8
Sternothaerus m. peltifer	6	0	1	7	0
No. of times nets checked	3	2	2	3	3

Sternothaerus m. peltifer displays a morning peak, but none was trapped at night. It is similar to *Pseudemys* in feeding time. The data demonstrate that *Sternothaerus* is inactive during the day, but trapping records from more periods of the night are needed.

Seven traps were set August 17 to 19,

1955, in the Black Warrior River, three miles east of Eutaw, Alabama, covering a combined distance of 200 yards on both sides of the river.

Two *Pseudemys s. scripta* and 12 *Sternothaerus m. peltifer* were collected. The traps were examined at about the same time as those in the Coosa River, and *m. peltifer* shows the same peaks of feeding activity as in the Coosa River. Six *Sternothaerus* were taken during the 0800 hour check and six at 1900. All musk turtles were taken on August 17 and 18, none on the 19th, indicating that most turtles in the area had been trapped. If this is true, the density here was one turtle per 17 linear yards of river bank compared with one per 25 yards in the Coosa River.

TABLE 27. *Numbers of Sternotherus depressus taken during six trapping periods on several visits to the Black Warrior River*

Hours	0500-0600	0700-0800	0900-1000	1500-1600	1800-1900	2100-2200
No. of times nets checked	2	1	1	3	2	2
No. of turtles	7	2	1	0	0	4

Sternothaerus depressus is not so easily trapped as *m. peltifer,* and hand collecting from a boat along the shore at night is as effective as trapping, except that adults are not collected by this method. Table 27 shows during what hours trapping was most successful at the type locality of *depressus* during August, 1954 and 1955. *Sternothaerus depressus* is most active late at night and during the early morning. The exact time of peak activity cannot be determined until trapping experiments are conducted throughout the night.

F. *Basking*

The function of basking in turtles is not clear, but it appears to be thermoregulatory, a means for drying the body, and for disposing of algal, fungal and bacterial growths, or animal parasites.

This habit is poorly developed in *Sternothaerus.* I have never observed basking individuals of *m. minor, m. peltifer* or *depressus.* Occasional instances of basking by specimens of *m. minor* have been reported, but observers who have watched this form for long periods in the field do not find the habit developed in most individuals. In contrast with these forms, individuals of *S. carinatus* habitually bask.

G. *Nocturnal behavior*

Observations around stumps and inshore brushpiles at night often reveal individuals coming to the surface to breathe, or at least extending their snouts to the surface. This habit partly explains the concentrations of turtles around brushpiles where they have immediate access to deep water for rapid escape, but are able by remaining at a shallow level to obtain air during the night with little expenditure of energy.

H. *Habitat preference*

Sternothaerus m. minor, S. m. peltifer and *S. carinatus* are associated with running water or with permanent bodies of water connected with running water, such as oxbow lakes. I have not seen *S. depressus* from enough localities to ascertain its preference. The only habitat from which I have collected this species is sluggish water, but creation of this habitat at the type locality was due to recent damming of the Black Warrior River.

Sternothaerus odoratus is seldom found in equal abundance with any member of the *S. carinatus* complex. *Sternothaerus odoratus* is most abundant in ponds, lakes and other lentic situations and has a habit of overland migration (Cagle, 1944) which in part accounts for its wider range and absence of clear-cut geographic races. The absence of the members of the *S. carinatus* group in most ponds or lakes removed from lotic environments indicates no migration.

In the Coosa River near Pell City, Alabama, *S. odoratus* and *S. m. peltifer* occur in equal abundance. This, I believe, is a secondary phenomenon associated with damming of the river and creation of favorable habitat for *odoratus. Sternothaerus m. peltifer* is common below the Fall Line on the Black Warrior River near Eutaw, Alabama, but I have never collected *S. odoratus* there even though the current is slow.

Lake Concordia, Louisiana, from which I have seen cotypes of *S. carinatus,* is an oxbow lake of the Mississippi River. Extensive collecting and observations in this lake in 1954 revealed no *S. carinatus,* but 25 *S. odoratus* were taken in two days of trapping.

The Wacissa River in Jefferson County, Florida, is an exception to the rule of *odoratus* in quiet water. However, the current there is slow and the clear water channel is bounded by dense lily pads in a mucky bot-

tom, which supports dense weeds in many places. *Sternothaerus odoratus* is common among these plants and the cypress roots near shore. In two trips to this locality, 53 *S. odoratus* and three *S. m. minor* were taken.

Sternothaerus is most abundant around brushpiles, stumps, roots or rocky crevices in quiet areas of rivers, particularly in the inlets behind sand spits. Traps set far from brush or in deep water generally produce no turtles.

I. *Associated Species*

On most trips several techniques were employed to obtain samples of as many turtle species as possible. The emydid turtles are easiest to sample; comparable samples of *Chelydra, Trionyx, Macroclemys* and *Kinosternon* were not obtained. A list of species taken at several localities is of qualitative interest though it sheds little light on relative abundance (Table 28).

X. Behavior of Captive Sternothaerus

A. *Reaction to Light*

Sternothaerus depressus is especially sensitive to light and attempts to burrow in the aquarium when a bright light is turned on. The other forms show a preliminary annoyance with, and movement away from light. When a light is turned on an aquarium in which turtles are quiet, there is a burst of activity as though darker situations were being sought. Most become inactive a short while after the light is removed. Several turtles in a lighted aquarium will generally be at the side away from the highest light intensity. In their behavior, contact with some part of the aquarium or with another turtle appears important.

B. *Reaction to Heat*

Heating coils over a two-gallon aquarium containing juveniles of *Sternothaerus* have a marked effect on activity. At a water

Table 28. *Relative numbers of turtles taken in Gulf Coast rivers. The numbers in parentheses following names of rivers indicate the number of visits to the river. Black Warrior*[a] *is below the Fall Line, Black Warrior*[b] *above the Fall Line*

	Escambia (2)	Suwannee	Wacissa (2)	Flint (2)	Coosa (3)	Pascagoula (2)	Tombigbee	Black Warrior[a] (3)	Black Warrior[b] (4)	Pearl (3)	Teusis	Sabine
S. carinatus						7				8	6	3
S. depressus									48			
S. m. minor	18	21	3	1								
S. m. peltifer					17		6	28				
S. odoratus			53		28				2	2	5	
C. s. serpentina			1						1			
M. temminckii				4								
G. pulchra	78				4	15	13	17	7	57		
G. kohni											30	3
G. barbouri				29								
G. p. ouachitensis											10	
G. p. sabinensis												36
G. oculifera										30		
G. geographica									3			
G. nigrinoda							5	175				
G. flavimaculata						21						
T. f. aspera	4											
T. f. emoryi												3
T. f. ssp.				7	1		1		1			
P. s. scripta	10			7	48	3		26	1			
P. s. elegans										3	23	1
P. f. suwanniensis		3										
P. f. floridana			13	59								
P. f. ssp.	18						1	12	50	12	8	

temperature of 29.5°C, most turtles become active. Repeated efforts were made by two individuals of *S. m. peltifer* to swim to the surface, but they always retreated when about one-half way up, apparently because of the high surface temperature (30°C). The turtles appeared hesitant to extend their heads into this thermal level, and flinched repeatedly when encountering the higher temperature. The juvenile *S. m. minor* remained on the bottom in the sand. When the water surface temperature reached 30° to 31°C, this turtle became active and made one or two attempts to surface, but was repulsed by the high temperature. It returned to the bottom and began to kick up sand in what appeared to be an attempt to cover its body.

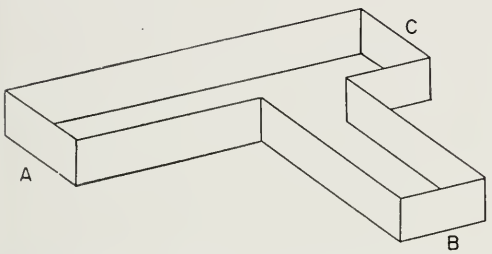


Figure 57. Diagram of trough used in experiments on reaction to current.

C. *Reaction to Current*

Several individuals of each form were placed in a trough shown in figure 57.

Strong currents of water were admitted at A or C, while the water in B remained quiet. Repeated experiments showed that there was little avoidance of the current during movement, but resting places were always chosen out of the main sweep of the current. Only *S. m. minor* avoided the current, moving always into the eddy at B or to the end of the trough opposite the current source.

When the trough was drained, the turtles showed no reaction until the amount of water remaining was insufficient to supply buoyancy to their bodies, at which time there was a sudden scrambling behavior that soon abated. Then the turtles became motionless and partly or wholly withdrew the head and limbs into the shell.

XI. Summary

1. Trapping and hand collecting from a boat are the best means of obtaining *Sternothaerus.*

2. The generic name *Sternotherus* of Gray (1825) is a misspelling and should be replaced by the valid spelling *Sternothaerus* of Bell (in Gray, 1825).

3. The total range of the *Sternothaerus carinatus* complex lies within the Austroriparian and Texan biotic provinces, and almost wholly within the Gulf coastal plain. Several critical areas must be studied before exact range delineation can be made, particularly in the northern limits of distribution.

4. *Sternothaerus minor minor* and *minor peltifer* intergrade in the area between Mobile Bay and the Choctawhatchee River drainage. The other forms show no definite signs of gene exchange.

5. Sexual dimorphism is shown in measurable degree in some forms in the ratios of plastron length/length of bridge, plastron length/length of interanal scute, carapace length/plastron length, and plastron length/preanal tail length. Most characters show no sexual differences.

6. Ontogenetic changes in relative sizes of various structures are shown by the ratios of plastron length/length of interabdominal scute, plastron length/length of interanal scute, and plastron length/length of bridge. In *Sternothaerus carinatus* there is an ontogenetic change in the relationship between the length and width of some of the vertebral shields.

7. Geographic variation occurs in most characters and small differences between populations of the same form in different rivers are apparent. In general, *Sternothaerus depressus* and *carinatus,* which represent the extremes in body shape, show the most striking differences from the other forms.

8. Abnormalities in shields or scutes are rare, averaging five percent in all forms. Abnormalities in one set of shields or scutes is commonly accompanied by abnormalities in another set.

9. The skulls of *Sternothaerus m. minor* and *depressus* are unusual. The former is distinguished by massiveness associated with development of musculature for the crushing jaws, the latter by its nearly level slope from the nasal to the tip of the supraoccipital.

10. The origin and fossil history of *Sternothaerus* is unknown. *Sternothaerus odor-*

atus is possibly the most primitive species in the genus, and is the one most closely related to *S. m. minor.* The differentiation of *m. minor* from *odoratus* or a common stock presumably took place on the coastal plain and probably in Florida, the present area of greatest abundance of *m. minor.*

11. The remarkable isolation of *Sternothaerus depressus* in the upper drainage of the Black Warrior is inexplicable at present, but may indicate imminent extinction. This species is most closely related to *S. m. peltifer* and may have arisen from *m. peltifer* stock, perhaps in the Tennessee River drainage where *depressus* does not now occur.

12. With allowances for small differences, the patterns of race or species differentiation in the *Sternothaerus carinatus* complex, in *Pseudemys, Trionyx* and the broad-headed *Graptemys* group are similar, and apparently the rate of evolution in these groups is nearly the same.

13. The pattern of speciation in the *Graptemys oculifera* complex is different because three well-differentiated species have developed in some of the youngest rivers on the Gulf coast in which turtles of other genera show little or no differences.

14. The growth curves of *Sternothaerus depressus, S. m. peltifer* and *S. m. minor* are almost congruous, and similar in form to that of *S. odoratus.* The growth curve of *carinatus* shows a more rapid rate of growth.

15. Males and females reach sexual maturity at about the same size except in *S. m. peltifer* in which males are smaller than females at sexual maturity. All species reach sexual maturity at about the same size, except females of *m. minor* which are smaller at sexual maturity than the other forms, and in *carinatus,* in which the males are larger.

16. The age at sexual maturity is not very different in males and females, nor between the various forms, except that in *S. m. peltifer* females are generally older at maturity than those of other forms. The age at sexual maturity given in the literature for *S. odoratus* females is twice that of the males at maturity.

17. *Sternothaerus depressus* displays a marked divergence in sex ratio, with females outnumbering males three to one. This ratio is approximately the same as that reported in *S. odoratus.* The sex ratio of other members of the complex is not exactly 50:50, but the divergence is slight.

18. The reproductive potential of all forms in the complex averages between five and seven eggs per female per season. *Sternothaerus carinatus* and *S. m. minor* show potentialities for two broods per year. No data are available on realized egg production.

19. The food habits are similar in all forms. There is a change in food habits from an insectivorous juvenile to molluscivorous adults. *Sternothaerus m. minor* develops hypertrophied jaw musculature and crushing alveolar jaw surface correlated with mollusc-feeding. This is true to a lesser extent in *m. peltifer,* but is not true in *carinatus* and *depressus,* which also become mollusc feeders.

20. Trapping data indicate that *Sternothaerus* is not active during the day. Peak activity, and presumably feeding, occurs in the morning and evening in *m. peltifer* and in the morning and late at night in *depressus,* and probably *m. minor.* Insufficient data are available on *carinatus.* In one locality obvious differences existed in the feeding times of *S. m. peltifer* and *S. odoratus.*

21. The habit of basking is well-developed only in individuals of *S. carinatus,* but basking individuals of *S. m. minor* have been reported.

22. *Sternotherus carinatus, m. minor* and *m. peltifer* are seldom taken outside of rivers, streams or bodies of water connected with lotic environments. Little can be said of *S. depressus* because it has been taken in few localities. *Sternothaerus odoratus* is most abundant in lentic situations. Overland migration, a common habit in *S. odoratus,* has not been observed in other *Sternothaerus.*

23. *Graptemys, Pseudemys* or *Trionyx,* often all three, are generally abundant in the areas where *Sternothaerus* abound.

24. Water current is not shunned during movement (except by *m. minor*) by turtles, but stationary positions are never assumed in the direct sweep of the current.

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XIII. References Cited

Adams, Charles C. 1901. Baseleveling and its faunal significance with illustrations from the southeastern United States. *Amer. Nat.*, 35: 839-852.

Agassiz, Louis 1857. *Contributions to the Natural History of the United States. I, Part II. Testudinata.* Little, Brown and Co., Boston.

Bell, Thomas 1826. A monograph of the tortoises having a movable sternum, with remarks on their arrangement and affinities. *Zool. Jour.* 2: 299-310.

Boulenger, G. A. 1858. *Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History)* Taylor and Francis, London.

Brimley, Clement S. 1910. Records of some reptiles and batrachians from the southeastern United States. *Proc. Biol. Soc. Wash.*, 23: 9-18.

Brown, Bryce C. 1950. *An Annotated Checklist of the Reptiles and Amphibians of Texas.* Baylor University Press, Waco, Texas.

Cagle, Fred R. 1944. Home range, homing behavior and migration in turtles. *Misc. Publ. Mus. Zool. Univ. Mich.*, 61: 1-34.

———— 1950. The life history of the slider turtle *Pseudemys scripta troosti* (Holbrook). *Ecol. Monogr.*, 20: 31-54.

———— 1954. Two new species of the genus *Graptemys*. *Tulane Stud. Zool.*, 1(11): 167-186.

Cagle, Fred R. and A. H. Chaney 1950. Turtle populations in Louisiana. *Amer. Midl. Nat.*, 43(2): 383-388.

Cahn, Alvin 1937. The turtles of Illinois. *Ill. Biol. Monogr.*, 16(1/2): 1-218.

Campbell, Robert B. 1940. Outline of the geological history of peninsular Florida. *Proc. Fla. Acad. Sci.*, 4: 87-105.

Carr, Archie Fairly 1940. A contribution to the herpetology of Florida. *Univ. Fla. Publ., Biol. Sci. Ser.*, 3(1): 1-118.

———— 1952. *Handbook of Turtles.* Comstock Publ. Assoc., Ithaca, New York.

Chaney, Allen and Clarence L. Smith 1950. Methods for collecting mapturtles. *Copeia*, 1950 (4): 323-324.

Cooke, C. Wythe and Stuart Mossom 1939. The geology of Florida. *Ann. Rept. Fla. State Geol. Surv.*, 20: 5-294.

Crenshaw, John W., Jr., and Milton N. Hopkins 1955. The relationships of the soft-shelled turtles *Trionyx ferox ferox* and *Trionyx ferox aspera*. *Copeia*, 1955 (1): 13-22.

Daudin, F. M. 1802 *Histoire Naturelle des Reptiles.* Paris.

Davis, N. S. and F. L. Rice 1883. List of batrachia and reptilia of Illinois. *Bull. Chicago Acad. Sci.*, 1: 25-32.

Deevey, Edward S., Jr. 1949. Biogeography of the Pleistocene. I. Europe and North America. *Bull. Geol. Soc. Amer.*, 60: 1315-1416.

1950. Hydroids from Louisiana and Texas with remarks on the Pleistocene biogeography of the western Gulf of Mexico. *Ecology*, 31(3): 334-367.

DeSola, Ralph and Fredrica Abrams 1933. Testitudinata from southeastern Georgia, including the Okefinokee Swamp. *Copeia*, 1931(1): 10-12.

Dice, Lee R., 1943. *The Biotic Provinces of North America.* Univ. Michigan Press, Ann Arbor.

Duméril, André and G. Bibron 1834-1835. *Erpétologie Générale.* I(1834); II(1835). Librarie Encyclopédique de Roret, Paris.

Dunn, Emmett Reid 1931. The herpetological fauna of the Americas. *Copeia*, 1931(3): 106-119.

Edgren, Richard A. and Margery K. Edgren 1955. Thermo-regulation in the musk turtle, *Sternotherus odoratus* Latr. *Herpetologica*, 11: 213-217.

Fisk, Harold N. 1944. *Geological Investigation of the Alluvial Valley of the Lower Mississippi River.* Mississippi River Commission, Vicksburg.

Fitzinger, L. J. 1835. Entruf einer systematischen Anordnung der Schildkröten nach den Grundsatzen der naturlichen Methode. *Ann. Mus. Wien*, 1: 103-128.

Fleming, John 1822. *The Philosophy of Zoology.* Edinburgh, Archibald Constable and Co.

Galbreath, Edwin C. 1948. Pliocene and Pleistocene records of fossil turtles from western Kansas and Oklahoma. *Univ. Kans. Publ. Mus. Nat. Hist.*, 1(17): 283-284.

Gilmore, C. W. 1923. A new fossil turtle, *Kinosternon arizonense* from Arizona. *Proc. U. S. Nat. Mus.*, 62 (5): 1-8.

Gray, John Edward 1825. A synopsis of the genera of reptiles and amphibians with a description of some new species. *Ann. Phil.*, 10: 193-217.

1831. *Synopsis Reptilium; or Short Prescriptions of the Species of Reptiles. Part I. Cataphracta.* Treuttel, Wurtz and Co., London.

1855. Catalogue of shield reptiles in the collection of the British Museum. Part I. Testudinata (Tortoises). *Proc. Zool. Soc. London*, 1855.

Hayes, C. W. and M. R. Campbell 1900. The relation of biology to physiography. *Science* (N.S.), 12: 131-133.

Hobbs, William Herbert 1949. The Pleistocene history of the Mississippi River. *Ibid.*, 111: 260-262.

Hubbs, Carl L. and Clark Hubbs 1953. An improved graphical analysis and comparison of series of samples. *Systematic Zool.*, 2(2): 50-56.

Johnson, Douglas Wilson 1905. The distribution of freshwater faunas as evidence of drainage modifications. *Science* (N.S.), 21: 588-592.

1907. River capture in the Tallulah district, Georgia. *Ibid.*, 25: 428-432.

1939. Biologic evidence of capture. *In*: Current notes on geomorphology-drainage modifications. *Jour. Geomorph.*, 2: 88-91.

1941. Mussel distribution as evidence of drainage changes. I and II, *Ibid.*, 4: 307-321; III and IV, *Ibid.*, 5: 59-72.

King, Willis 1939. A survey of the herpetology of Great Smoky Mountains National Park. *Amer. Midl. Nat.*, 21(3): 531-582.

LeConte, John 1854. Description of four new species of *Kinosternum*. *Proc. Acad. Nat. Sci. Phil.*, 7: 180-190.

Lindholm, W. A. 1929. Revidiertes Verzeichnis der Gattungen der rezenten Schildkröten nebst Notizen zur Nomenclatur einiger Arten. *Zool. Anz.*, 1929: 275-295.

Loding, H. P. 1922. A preliminary catalogue of Alabama amphibians and reptiles. *Ala. Mus. Nat. Hist., Paper No. 5.*

MacNeil, F. Stearns 1950. Pleistocene shore lines in Florida and Georgia. *U. S. Geol. Surv., Prof. Paper*, 221 F: 95-107.

Merrem, Elasius 1820. *Tentamen Systematis Amphibiorum.* Marburg.

Mosimann, James E. 1955. Methods for measuring cross-section and volume on turtles. *Copeia*, 1955(1): 58-61.

Neill, Wilfred T. 1948a. Use of scent glands by prenatal *Sternotherus minor*. *Herpetologica*, 4: 153-158.

1948b. The musk turtles of Georgia. *Ibid.*, 4(5): 181-183.

Ortenburger, A. I. 1927. Report on the amphibians and reptiles of Oklahoma. *Proc. Okla. Acad. Sci.*, 6: 89-100.

Ortmann, Arnold E. 1913. The Alleghenian Divide and its influence upon the freshwater fauna. *Proc. Amer. Phil. Soc.*, 52: 287-390.

Rhoades, Samuel N. 1895. Contributions to the zoology of Tennessee. *Proc. Acad. Nat. Sci. Phil.*, 1895: 376-407.

Richards, Horace G. 1939. Marine Pleistocene of the Gulf coastal plain; Alabama, Mississippi and Louisiana. *Bull. Geol. Soc. Amer.*, 50: 297-315.

Risley, Paul L. 1929 (1930). Anatomical differences in the sexes of the musk turtle, *Sternotherus odoratus* (Latreille). *Pap. Mich. Acad. Sci., Arts & Letters*, 11: 445-464.

———— 1933. Observations on the natural history of the common musk turtle. *Ibid.*, 17: 687-711.

Say, Thomas 1825. On the fresh water and land tortoises of the United States. *Jour. Acad. Nat. Sci. Phila.*, 4: 203-219.

Schmidt, Karl P. 1953. *A Check List of North American Amphibians and Reptiles*. Sixth edition. Univ. Chicago Press.

Schwartz, Albert 1956. The relationships and nomenclature of the soft-shelled turtles (genus *Trionyx*) of the southeastern United States. *Charleston Mus., Leaflet* No. 26.

Shaw, Eugene Wesley 1918. The Pliocene history of northern and central Mississippi. *U. S. Geol. Surv., Prof. Paper*, 108: 125-163.

Siebenrock, Kustos F. 1907. Die Schildkrötenfamilie Cinosternidae. Sitsberg. *Akad. Wiss. Wien*, 116: 1-73.

———— 1909. Synopsis der rezenten Schildkröten mit Berucksichtigung der in historischer Zeit ausgestorbenen Arten. *Zool. Jahrb.*, Suppl. 10: 427-618.

Simpson, Chas. T. 1900. On the evidence of the Unionidae regarding the former courses of the Tennessee and other southern rivers. *Science* (N.S.), 12: 133-136.

Simpson, George Gaylord 1943. Turtles and the origin of the fauna of Latin America. *Amer. Jour. Sci.*, 241(7): 413-429.

Smith, Hobart M. and Bryan P. Glass 1947. A new musk turtle from the southeastern United States. *Jour. Wash. Acad. Sci.*, 37(1): 22-24.

Smith, Hobart M. and Helmut K. Buechner 1947. The influence of the Balcones Escarpment on the distribution of amphibians and reptiles in Texas. *Bull. Chicago Acad. Sci.*, 8(1): 1-16.

Smith, Philip W. 1951. A new frog and a new turtle from the western Illinois sand prairies. *Bull. Chicago Acad. Sci.*, 9(10): 189-199.

Sonninni, C. S. and P. A. Latreille 1801. *Histoire Naturelle des Reptiles Avec Figures Desinées d'Après Nature*. Deterville, Paris.

Spix, J. 1824. Ranae et Testidunis brasiliensis species novae. *Fol. Min. Monachii*. Fleischer, Leipzig.

Stejneger, Leonhard 1902. Some generic names of turtles. *Proc. Biol. Soc. Wash.*, 15: 235-238.

———— 1923. Rehabilitation of a hitherto overlooked species of musk turtle of the southern states. *Proc. U. S. Nat. Mus.*, 62(6): 1-3.

Stephenson, Lloyd W. 1928. Major marine transgressions and regressions and structural features of the Gulf coastal plain. *Amer. Jour. Sci.*, 16: 281-298.

Strauch, A. 1862. Chelonologische Studien, mit besonderer Beziehung auf die Schildkröten Sammlung der Kaiserlichen Akademie der Wissenschaften zu St. Petersburg. *Mem. Acad. Impériale Sci. St. Petersburg*, VII, serie 5(7):1-196.

Tinkle, Donald W. and Robert G. Webb 1955. A new species of *Sternotherus* with a discussion of the *Sternotherus carinatus* complex. (Chelonia: Kinosternidae). *Tulane Stud. Zool.*, 3(3): 52-67.

Van der Schalie, Henry 1938. The Naiades (fresh-water mussels) of the Cahaba River in northern Alabama. *Occ. Pap. Mus. Zool. Univ. Mich.*, No. 392: 1-29.

———— 1939. Distributional studies of the Naiades as related to geomorphology. *Jour. Geomorph.*, 2: 251-257.

———— 1945. The value of mussel distribution in tracing stream confluence. *Pap. Mich. Acad. Sci., Arts & Letters*, 30: 355-373.

Wagler, Joannes 1830. *Natürliches System der Amphibien*. München.

Williams, Ernest Edward 1950. Variation and selection in the cervical central articulations of living turtles. *Bull. Amer. Mus. Nat. Hist.*, 94(9): 505-561.

Wright, A. H. 1926. The vertebrate life of the Okefinokee Swamp in relation to the Atlantic coastal plain. *Ecology*, 7: 77-85.

Wright, A. H. and W. D. Funkhouser 1915. A biological reconaissance of the Okefinokee Swamp in Georgia, I. Turtles, lizards and alligators. *Proc. Acad. Nat. Sci. Phil.*, 67: 107-139.

Yarrow, Henry C. 1875. Report upon the collections of batrachians and reptiles made in portions of Nevada, Utah, California, Colorado and New Mexico and Arizona, during the years 1871, 1872, 1874. In: *Report upon Geographic and Geological Explorations and Surveys West of the One Hundredth Meridian*, 5: 511-634.

Abstract

The *Sternothaerus carinatus* complex of three species (four forms) is limited primarily to the Gulf coastal plain and has presumably speciated in this area. The present study compares the external morphology, the skull and the ecology of these species to establish the relationships within the group. The pattern of species distribution is compared with that in other turtle genera on the Gulf coast. Samples of *Sternothaerus* were collected from most major rivers of the Gulf coast, and were supplemented by material in many museum collections. The samples from each river

drainage were treated separately to show small differences between populations.

The spelling of the generic name is incorrect and should be changed to *Sternothaerus*.

Geographic, sexual, ontogenetic, or uncorrelated variability exist in each species. Significant differences in certain characters are apparent between populations of the same species in different rivers. Some characters show clear longitudinal trends, while others display the same or fluctuating means between populations in different rivers. Some characters used by previous authors to distinguish between species are not diagnostic and other characters are suggested for use in differentiating species in this complex.

Variability exists in the skulls, but study of these reinforces the ideas of relationship obtained from external characters. The suggested phylogeny within the genus places *S. odoratus* as the oldest form, with *m. minor and m. peltifer* evolving from the same progenitor. *Sternothaerus carinatus* arose from pre-*peltifer* stock. *Sternothaerus depressus* is most closely related to *m. peltifer*, but the path of its differentiation is not clear, nor is the reason for its extreme isolation in northern Alabama. The youth of most Gulf coast rivers and the obvious similarities between members of the *S. carinatus* complex suggests that most of their evolution occurred during the late Pliocene and Pleistocene.

The patterns of speciation in the *Sternothaerus carinatus* complex, in the *Trionyx spinifera* and *T. muticus* groups and in the broad-headed *Graptemys* are grossly similar and may indicate similar rates of evolution. The pattern in the *Graptemys oculifera* complex is one of extreme differentiation in youthful rivers, indicating a more rapid rate of evolution.

The growth curves of all *Sternothaerus* species are similar; growth rate is fastest in *S. carinatus*.

Sex ratios are not markedly divergent from 50:50 except in *S. depressus*, but in this species chance selection of individuals might account for the difference. Generally sexual maturity is reached by individuals of each species at a size of 75 - 100 mm (carapace length) and at four to six years of age. The sexes and species show slight differences in size and/or age at sexual maturity.

The average annual egg production per female is five to seven, but some individuals have a higher potential and may deliver more than one brood per year.

The juveniles in the *S. carinatus* complex are mainly insectivorous, but older individuals and adults become predominantly molluscivorous. Feeding habits vary little geographically or sexually. Feeding takes place in the early morning, late evening or at night; turtles are inactive during the day.

All members of the group are associated with streams, rivers, or bodies of water associated with these lotic environments. In these areas, they occur most abundantly with *Trionyx*, *Pseudemys* and *Graptemys*.

The habit of basking has been reported in several *Sternothaerus*, but is apparently well-developed as a habit only in individuals of *S. carinatus*.