VARIATION AND SUBSPECIES OF THE CRAWFISH *ORCONECTES PALMERI* (FAXON) (DECAPODA, ASTACIDAE)[1]

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In a previous study the writer (1952) intimated that a review of the subspecies of *Orconectes palmeri* would be necessary to determine the status of *O. creolanus.* Thus, this research began in 1951. Originally the problem was one of determining the distributional limits and the range of variation of the three subspecies each of which was known from a small number of localities and specimens. *O. p. palmeri* was known from the Obion River in Tennessee and the St. Francis River in Arkansas; *O. p. longimanus* was known from the Arkansas, Red and Ouachita rivers in Oklahoma, Texas and Arkansas; and *O. p. creolanus* was known from the Amite and Little rivers in Louisiana. Plotted geographically, the ranges of these three forms described a rough triangle: *palmeri*—north, *longimanus*—northwest, *creolanus*—south. Gaps in the total range of the species were present between any two of the subspecies in each direction along the sides of the triangle and in the central area, yet clearly all three were closely related. The obvious approach was to obtain materials (by exploration and or from museum collections) which would represent localities between the known ranges of the three subspecies.

Four years of field work has helped to solve this problem; however, the details of variation of the species in the southwest must await further collecting and research in the west-Louisiana east-Texas area.

Historical Statement

Faxon (1884: 124) described *Cambarus palmeri* from 25 specimens (form II males[2] and females) collected from a stream tributary to Reelfoot Lake, Obion County, Tennessee (cotypes: USNM 4872 and MCZ 3564). Later he gave notes (Faxon, 1898: 665) on the form I males based on specimens collected in the St. Francis and Black Rivers in northeastern Arkansas. He noted that these latter specimens agreed "essentially with the Tennessee specimens, differing from them merely in the outline of the rostrum, which is somewhat longer and narrower, with more convergent sides."

Faxon (1898: 655) also described *Cambarus palmeri longimanus*

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[2] Adult male crawfishes of the subfamily Cambarinae pass through two morphological forms in association with the breeding cycle. The terminal processes of the first pair of pleopods of males capable of copulation (form I) are well-defined and usually corneous; those of males incapable of copulation (form II) are usually poorly defined, blunt and never corneous.

(holotype: MCZ 7390) in a few lines which left much to be desired. The complete description is:

> "Similar to *C. palmeri*, but different in the shape of the hand, the body of which (or palm) is thinner (less inflated) and the fingers much longer proportionately. The antennae, too, are longer, and the rostrum as a rule is more deeply excavated."

Faxon's specimens were from northeast Texas (Arthur City, Lamar County) and southeast Oklahoma (Goodland, Choctaw County and Kainister, Pushmataha County). Included also were notes on the color, and figures of the whole crawfish, mesial and lateral views of the first pleopods of both form I and II males, and the annulus ventralis of the female.

Creaser and Ortenburger (1933: 38) stated that *Cambarus longimanus* "exhibits characters in the chelae and sexual appendages which are sufficiently different from those of *palmeri* . . . to warrant specific ranking for *longimanus*."

Creaser (1933: 16) also described *Faxonius creolanus* from "the Amite River, one-half mile north of Ethel, East Feliciana Parish, Louisiana" (holotype: UMMZ 53332). Paratypes were recorded from tributaries of the Little River at Jena, LaSalle Parish, La. and Pollock, Grant Parish, La. In discussing the relationships of creolanus he made the following statements:

> "This species is closely related to *palmeri*. The relationship is manifest in the form of the sexual appendage as well as in the structure of the cephalothroax. The flattened fingers, the spinosity of the inner margin of the palm and outer margin of the moveable finger, and the small tubercles along the opposing margins of the non-gaping fingers are alike in the two species. . . . Doubtless the four species, *longimanus*, *palmeri*, *creolanus*, and *mississippiensis*, are very closely related. The ranges of each of these species, so far as we know do not overlap. The relative lengths of the sexual appendage are sufficient to distinguish *creolanus* from *palmeri*, and *palmeri* from *longimanus*."

However, Creaser did not substantiate the last sentence with any data, nor did he make any statement about distinctions between *creolanus* and *longimanus*.

In 1943, Hobbs and Marchand (p. 28) recorded observations of *O. p. palmeri* in the vicinity of Reelfoot Lake, Obion County, Tennessee and recorded the collection of fourteen form I males from the Obion river drainage in this area.

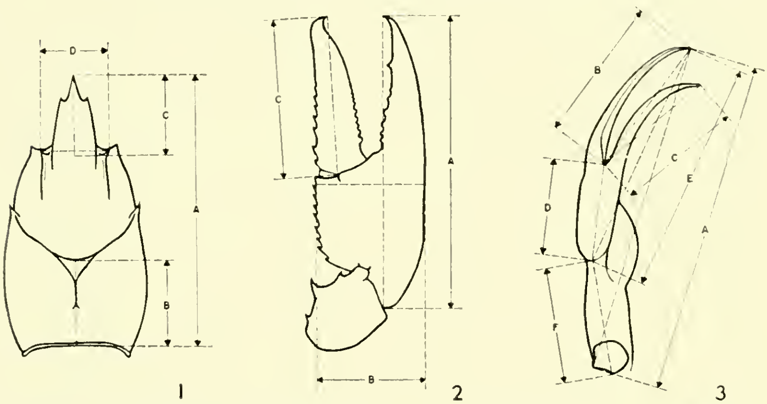
The writer (1952: 744-745) recorded the distribution of what he considered *O. p. creolanus* in Louisiana and stated his belief that *creolanus* should be considered a subspecies of *palmeri*.

Williams (1954: 894-895) studied *O. p. palmeri* and *O. p. longimanus* in the Ozark and adjacent areas of Arkansas and Missouri. He added numerous localities to the known lists of both subspecies, and in particular called attention to a population of what he considered intergrades in the White river drainage of northeastern Arkansas.

Methods

Measurements.—Only inflexible parts of the crawfish were measured. An arbitrary minimum of 23.0 mm cephalothorax length was selected for form II males and females; subsequently, however, smaller form I males (19.0 mm cephalothorax length) were encountered. Calipers and a standard millimeter rule were employed for gross parts. An ocular reticule mounted in an American Optical Co. stereoscopic microscope was used to make all finer measurements.

Routine measurements taken on all specimens utilized in the statis-



Figures 1-3. Basic measurements. **1.** Cephalothorax (A = total length, B = length of areola, C = length of rostrum, D = distance between postorbital spines); **2.** Chela (A = total length, B = width of palm, C = length of dactyl); **3.** Mesial surface of first pleopod of form I male (A = total length, B = length of central projection, C = length of mesial process, D = length of distal mesial shaft, E = length of distal mesial shaft plus central projection, F = length of proximal mesial shaft).

tical analyses were (1) length of cephalothorax, (2) length of areola, (3) distance between apices of postorbital spines, (4) length of rostrum, (5) length of chela, (6) width of palm, and (7) length of dactyl. Each of these measurements was made as shown in figures 1 and 2. Males were subjected to six additional measurements (fig. 3): (1) length of first pleopod, (2) length of central projection, (3) length of mesial process, (4) length of distal mesial shaft, (5) length of distal mesial shaft plus central projection, and (6) length of proximal mesial shaft.

Qualitative characters.—Not subject to the accuracies of linear measurement were three characters: (1) presence or absence of a rostral carina, and, if present, degree of development; (2) fingers of chela gaping or parallel, and, if gaping, to what degree; (3) rostrum with margins convergent or parallel, and, in either case, whether straight or concave.

Statistical procedures.—With the exception of material from the Arkansas, Red and Ouachita rivers all specimens were grouped by river systems for standard statistical analysis. Certain parallel west-east clines (to be noted in detail later) were apparent in the various characters studied in the specimens from each of the Arkansas, Red and Ouachita systems, hence these were finally grouped together by degrees longitude for final analysis (fig. 4). In this grouping, material from these three river systems lying between 92°31′W to 93°30′W was recorded as the "93°" group, 93°31′W to 94°30′W as the "94°" group, etc.

Analyses are presented in graph form following the methods of Hubbs and Hubbs (1953) with the exception of the results of qualitative analyses which were not subject to this type of handling. Standard deviations of small samples (fourteen or less) were computed without grouping according to the method described by Cazier and Bacon (1949). Significance of differences between any two samples for any character was calculated by the Student's t test.

No meristic characters were studied, hence all measurements were reduced to proportional figures. Each proportion is described in detail in the sections that follow.

Materials Examined

Most of the museum specimens previously assigned to any of the

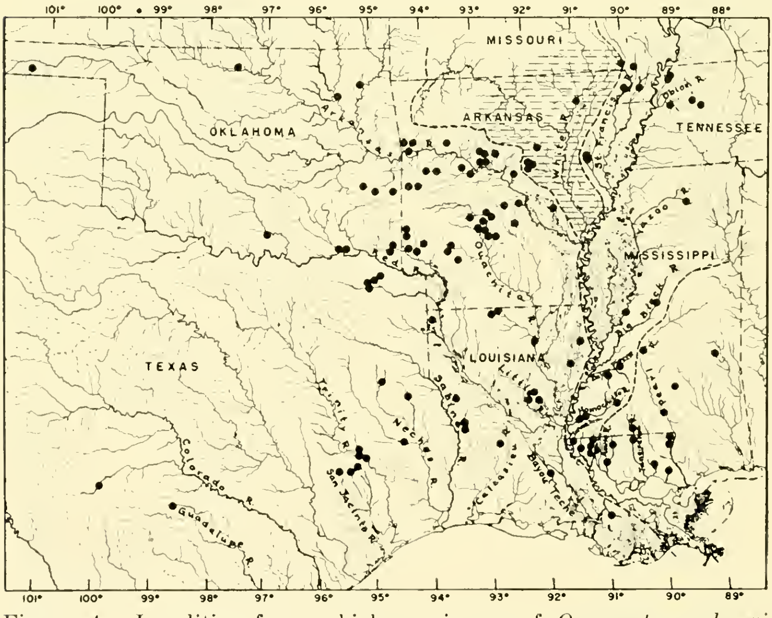


Figure 4. Localities from which specimens of *Orconectes palmeri* were examined. Dashed lines indicate subspecies boundaries; cross-hatched section is White River intergrade area.

subspecies of *Orconectes palmeri* and housed in the invertebrate collections of the United States have been examined in the course of this research. In all, 1,909 specimens were examined; only 746 were used in the statistical analyses (*i.e.*, the majority of the mature individuals), but all were used in assembling the life history data. A detailed list of localities, number of specimens from each and their

TABLE 1.
GEOGRAPHIC DISTRIBUTION OF SPECIMENS INCLUDED IN STATISTICAL ANALYSES

Drainage	State	Grand Total	No. Treated Statistically ♂ I	♂ II	♀
Amite River	La.	211	2	23	17
Arkansas River	Ark.	239	22	67	84
	Okla.	71	8	14	20
Atchafalaya River	La.	1	1	0	0
Bayou Lacombe	La.	1	0	1	0
Bayou Pierre	Miss.	15	0	2	3
Bayou Sara	La.	6	0	2	4
Bayou Teche	La.	16	1	3	4
Big Black River	Miss.	7	0	2	2
Calcasieu River	La.	8	0	0	0
Colorado River	Tex.	3	1	1	1
Guadalupe River	Tex.	6	0	2	2
Homochitto River	Miss.	51	0	11	7
Little River	La.	117	0	6	7
Neches River	Tex.	35	4	0	4
Obion River	Tenn.	60	9	11	20
Ouachita River	La.	5	0	0	1
	Ark.	225	8	59	41
Pascagoula River	Miss.	15	0	0	2
Pearl River	La.	5	0	2	1
	Miss.	18	0	2	7
Red River	La.	1	0	0	0
	Ark.	131	3	34	25
	Okla.	25	5	7	13
	Tex.	152	0	0	0
Sabine River	La.	8	0	0	3
San Jacinto River	Tex.	82	0	0	0
St. Francis River	Ark.	27	5	7	13
	Mo.	13	0	2	4
Tangipahoa River	La.	37	0	1	1
	Miss.	58	1	1	3
Tchefuncta River	La.	1	0	0	1
Tensas River	La.	4	0	0	3
Thompson's Creek	La.	33	0	7	8
Trinity River	Tex.	10	1	0	1
Tunica Bayou	La.	72	0	18	17
White River	Ark.	94	19	6	26
	Mo.	2	0	0	1
Yazoo River	Miss.	44	0	7	12
TOTALS		1,909	90	298	358
				746	

museum locations will be supplied to interested parties on request to the writer. Table 1 will suffice to summarize these data by river systems for specimens used in the systematic analyses (see also fig. 4).

The Palmeri Group

Taxonomists working with the subfamily Cambarinae have found convenient the use of "sections", "groups" and "subgroups" as supra-specific categories instead of other such appellations as "tribe", "subtribe", etc. Although some species appear to be intermediate between certain sections or groups the temporary use of such taxons is desirable in the present state of our knowledge of crawfish phylogeny and variation.

Within the subgenus *Orconectes* three sections (*Limosus*, *Propinquus* and *Virilis*) recognized by Ortmann (1905) are in use. The *Virilis* section, to which *O. palmeri* belongs, was described originally by Ortmann (*op. cit.*) as having "Sexual organs generally quite long (rarely rather stout), reaching about to the second pereiopods, deeply split at the tips, tips slender (rarely shorter) and more or less strongly curved backward, both in the same direction. Always only the third pereiopods bearing hooks (barring freaks)." Ortmann (1931, p. 90) amended this description by substituting "gently recurved" for "strongly curved backward" in the quotation above.

The *Virilis* section is subdivided into three groups: *Virilis*, *Compressus* and *Palmeri*. The latter was characterized by Ortmann (*loc. cit.*) *viz:* "carapace not compressed; lateral spines present; rostrum without keel; areola obliterated in the middle (species: *palmeri*, *difficilis*, *mississippiensis*)."

In view of what we know today the diagnosis for the *Palmeri* group should be revised as follows: "carapace not compressed; lateral spines present; rostrum with or without a carina; areola obliterated in the middle or extremely narrow." The following key for form I males is based on the writer's current concept of the phylogenetic relationships of the species of the group. The last two species in the key were recognized previously (Penn, 1952) as somewhat intermediate between the *Virilis* and *Limosus* sections.

Key to Form I Males of the Palmeri Group

1. Central projection of first pleopod (fig. 3, B) longer than distal mesial shaft (fig. 3, D). 2

   Central projection shorter than distal mesial shaft. 4

2. Rostrum without lateral spines. .... *mississippiensis* (Faxon, 1884: 123) (tributaries of the Tombigbee River in eastern Mississippi)

   Rostrum with lateral spines. 3

3. Areola usually obliterated; quotient of length of first pleopod into cephalothorax usually greater than 3.00 where geographic ranges of *palmeri* and *hobbsi* overlap; cephalothorax length of form I males ranges from 19.0 to 52.0 mm (fig. 5, A). *palmeri* (Faxon, 1884: 124)
(range mapped in figure 4)

   Areola slightly open; quotient of length of first pleopod into cephalothorax usually less than 3.00; cephalothorax length of form I males ranges from 18.0 to 22.5 mm. *hobbsi* Penn (1950: 381)
(streams draining into Lake Pontchartrain)

4. Central projection greater than half the length of the distal mesial shaft; apex of mesial process extending caudad at about a 90° angle to pleopod. *difficilis* (Faxon, 1898: 656)
(tributaries of the Red River in eastern Oklahoma and western Arkansas; tributaries of Bayou Teche and the Calcasieu River in southwestern Louisiana)

   Central projection less than a third the length of the distal mesial shaft; apex of mesial process extending caudad at no greater than a 30° angle to the pleopod. *hathawayi* Penn (1952: 1)
(headwater tributaries of Bayou Teche in Rapides Parish, La.)

Orconectes palmeri (Faxon)

Diagnosis.—With the characters of the genus and of the subgenus *Orconectes.* Rostrum always with a pair of well-developed lateral spines; excavate dorsally, with or without a median carina. Postorbital ridges well-developed and terminating cephalad in strong, divergent lateral spines. Branchiostegal spine present. One strong acute lateral spine projecting anterolaterally from each side of the cephalothorax just caudad of the cervical groove. Upper surface of cephalothorax with numerous setiferous punctations; lateral portions finely granulate.

First pleopod of males terminating in two rami. In form I males the central projection is corneous and curved caudad at less than a 45° angle to shaft of pleopod; the mesial process is usually shorter and similarly curved but non-corneous and somewhat swollen just proximad of the tip and trough-like. In form II males both rami are short, stout, non-corneous and curved caudad at less than a 45° angle.

Annulus ventralis of female sub-elliptical, wider than long; margins bulbous, with sinus lying at the bottom of a narrow, deep transverse fossa.

Other characters and body proportions are variable as described and discussed in the following sections.

Size distribution of samples.—With the exception of a few specimens (4♂♂ I, 7♂♂ II, 7♀♀) from the far western limits of the series (fig. 5-A, 97°), the size ranges and means of geographically combined series were similar (fig. 5). This was a fortunate circumstance for it eliminated the difficulty of using additional tedious

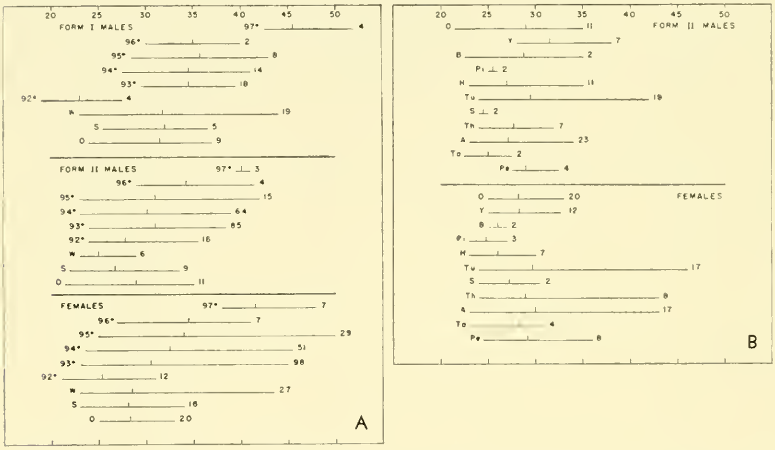


Figure 5. Carapace lengths of specimens examined; range and means in millimeters. **A.** West-east series, **B.** north-south series. Abbreviations: W = White River, S = St. Francis River, O = Obion River, Y = Yazoo River, B = Big Black River, Pi = Bayou Pierre, H = Homochitto River, Tu = Tunica Bayou, S = Bayou Sara, Th = Thompson's Creek, A = Amite River, Ta = Tangipahoa River, Pe = Pearl River. Localities abbreviated at left ends of lines, number of specimens at right ends of lines.

methods for analyzing the geographic variations of those characters which also might show ontogenetic variation.

Sexual dimorphism.—Of the seven characters studied in both sexes dimorphism is marked for only (1) length of chela (shortest in females, longest in form I males, intermediate in form II males) (figs. 6, 15), and (2) width of palm (widest in females) (fig. 14). However, data were calculated separately for the sexes for all characters.

Ontogenetic variation.—Ontogenetic variation is apparent in the length of the chela only (fig. 6). The two other proportions checked: length of areola (fig. 7) and length of the first pleopod of males (fig. 8), do not show significant changes during ontogeny.

Geographic Variation

Length of rostrum.—This is expressed as a ratio of cephalothorax length to length of rostrum (fig. 1, C); lowest figures indicate the longest rostrum.

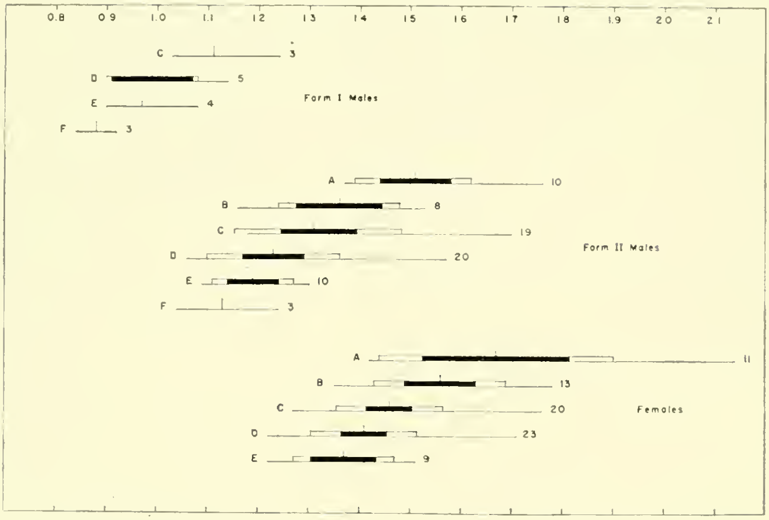


Figure 6. Ontogenetic variation in length of the chela, 93° group. Size groups (cephalothorax length) indicated to left of lines as follows: A = 23.0 to 25.5 mm, B = 26.0 to 28.5 mm, C = 29.0 to 31.5 mm, D = 32.0 to 34.5 mm, E = 35.0 to 37.5 mm, F = 38.0 to 39.5 mm.

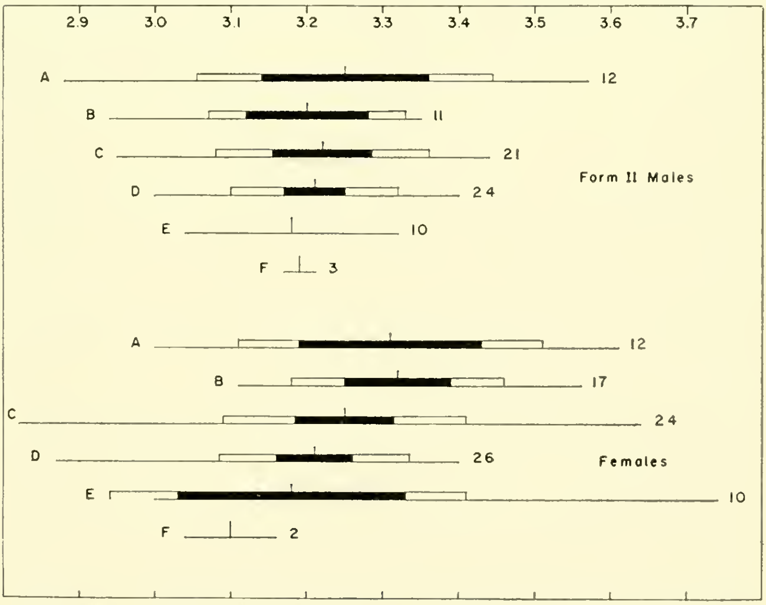


Figure 7. Ontogenetic variation in length of areola, 93° group. Abbreviations same as in fig. 6.

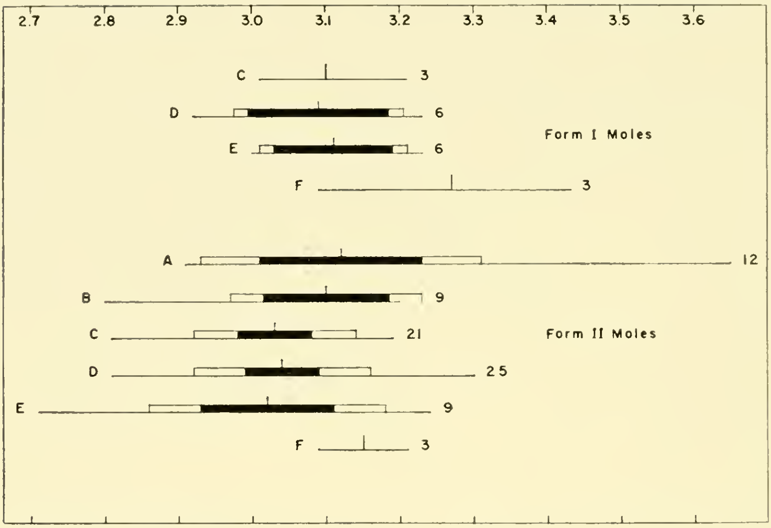


Figure 8. Ontogenetic variation in length of first pleopod of males, 93° group. Abbreviations same as in fig. 6.

There is a slight tendency for a longer rostrum to the west in form I and II males and females (fig. 9-A) but this is a poorly defined cline. The only breaks of significance occur in form II males between the samples from the White River and the 92° group, and between the St. Francis and Obion River samples.

There is a tendency for a slightly longer rostrum in the south (fig. 9-B).

Distance between postorbital spines.—This is expressed as a ratio of the length of the cephalothorax to the distance between the spines (fig. 1, D); lowest figures indicates the greatest distance between spines. This measurement was made in lieu of cephalothorax width, which is difficult to measure accurately, as a means of expressing the relative width of the cephalothorax.

In males of both forms and females there is a definite smooth west-east cline with the least width in the west (fig. 10-A). There are no significant differences between any two groups.

The distance between spines similarly widens toward the south in form II males and females, though this is not as smooth a cline (fig. 10-B). The only significant difference occurs between form II males from the Obion and Yazoo rivers.

Ratio of rostrum length to areola length.—This is expressed as a ratio of rostrum length (fig. 1, C) to areola length (fig. 1, B); figures greater than 1.0 indicate a rostrum longer than the areola.

There are no significant differences between samples of form I males or females in a west-east direction (fig. 11-A). However,

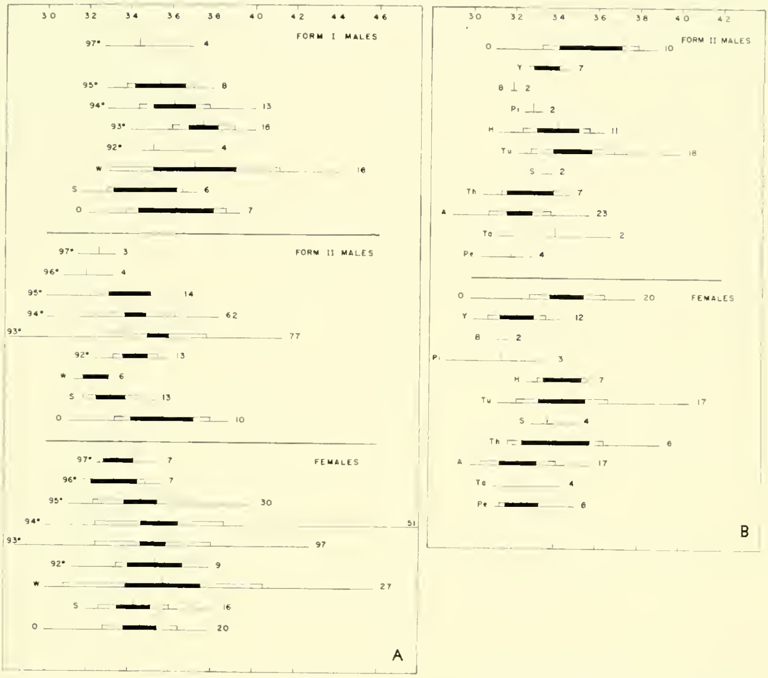


Figure 9. Geographic variation in length of rostrum. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

White river specimens of form II males differ significantly from samples on either side to the west and east.

There is a rough cline from north to south in form II males and females, with the rostrum slightly longer than the areola in the south (fig. 11-B). Significant differences occur between specimens from the Obion and Yazoo rivers in both form II males and females.

Length of areola.—This is expressed as a ratio between the cephalothorax length and the length of the areola; lowest figures indicate the longest areolas.

On the west-east axis (fig. 12-A) there are statistically significant differences seen between form II males and females in the samples from the St. Francis and Obion rivers on the east and samples from the White River. Form I males from the Obion river are significantly different from samples to the west. Also, in form II males only, the White River specimens stand distinct in areola length from specimens to the west. There is no real cline exhibited.

East of the Mississippi river (fig. 12-B) there is an interrupted cline of decreasing areola length from north to south. The only breaks

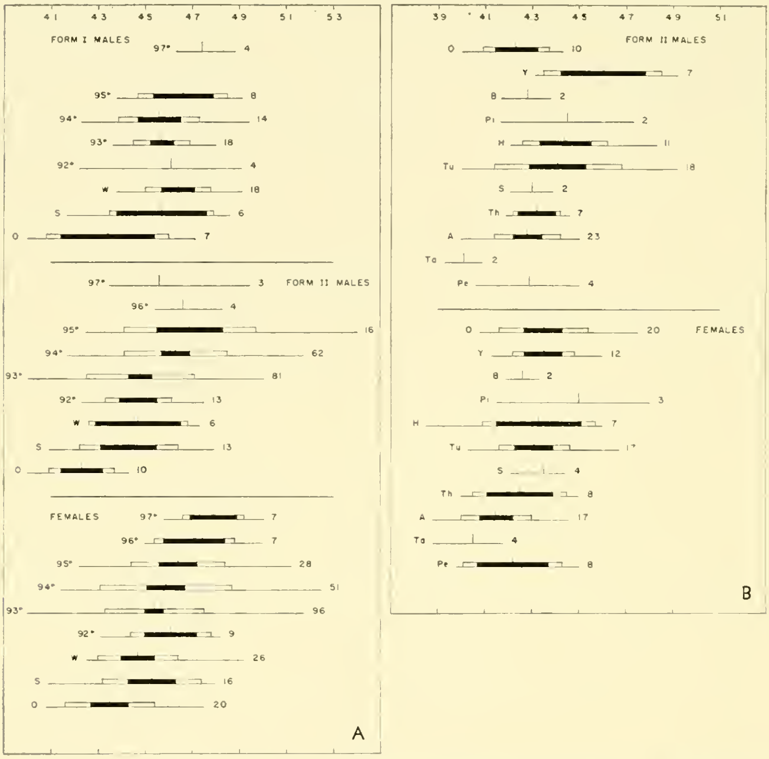


Figure 10. Geographic variation in distance between postorbital spines. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

of significance occur between samples from Tunica Bayou and Thompson's Creek in form II males, and between samples from the Obion and Yazoo rivers in females.

West of the Mississippi river in Gulf drainage systems the means of areola length (Table 2) for the small samples available more nearly correspond to these of specimens from the Red, Arkansas and Ouachita rivers.

An ecocline had been anticipated in this character, for if length of areola is one measure of the size of the branchial chamber, then longer areolas (*i.e.*, larger chambers) would be expected in populations surviving where streams tend to have a lower amount of dissolved oxygen (*i.e.*, streams of either the slow-flowing or intermittent type). Significantly, however, there is no apparent correlation between areola length and the known conditions of the streams sampled.

Length of chela.—This is expressed as a ratio of length of the

TABLE 2.

DATA ON SMALL SAMPLES FROM WEST OF THE MISSISSIPPI RIVER IN GULF DRAINAGE STREAMS AND STREAMS TRIBUTARY TO THE LOWER RED AND OUACHITA RIVERS; RANGE AND (MEAN)

River	State	N	Cephalo thorax Length (mm)	Length of Areola	Length of Chela	Length of Pleopod	Length of Central Projection	DMS PMS[1]	CP MP[2]
					FORM I MALES				
Atchafalaya	La.	1	42.0	3.00	1.01	3.18	1.43	0.76	1.18
Teche	La.	1	44.0	3.08	1.15	3.14	1.58	0.81	1.18
Neches	Tex.	4	38.0 - 41.5	2.96 - 3.12 (3.01)	1.01 - 1.04 (1.02)	2.89 - 3.21 (3.10)	1.43 - 1.59 (1.48)	0.78 - 0.89 (0.82)	1.10 - 1.23 (1.17)
Trinity	Tex.	1	28.5	3.17	1.24	3.13	1.56	0.74	1.03
Colorado	Tex.	1	21.0	3.23	1.27	2.41	1.90	0.71	1.18
					FORM II MALES				
Teche	La.	3	21.5 - 28.5	3.06 - 3.45 (3.27)	1.23 - 1.37 (1.30)	2.87 - 2.95 (2.91)	0.45 - 0.53 (0.50)	1.62 - 2.00 (1.81)	1.50 - 1.62 (1.56)
Little	La.	6	23.0 - 27.0	3.21 - 3.61 (3.38)	1.42 - 1.58 (1.46)	2.90 - 3.19 (3.05)	0.44 - 0.46 (0.45)	1.73 - 1.87 (1.79)	1.46 - 1.78 (1.61)
Colorado	Tex.	1	28.5	3.17	1.43	2.71	0.54	1.67	1.42
Guadalupe	Tex.	2	23.0 - 24.0	3.00 - 3.07 (3.04)	1.28 - 1.31 (1.30)	2.56 - 2.61 (2.59)	0.46 - 0.51 (0.49)	1.80 - 1.92 (1.86)	1.22 - 1.28 (1.25)
					FEMALES				
Teche	La.	4	25.0 - 33.0	3.05 - 3.39 (3.28)	1.38 - 1.67 (1.48)				
Little	La.	7	23.0 - 38.0	3.17 - 3.54 (3.41)	1.33 - 1.55 (1.47)				
Tensas	La.	3	13.7 - 15.5	2.97 - 3.11 (3.06)	1.23 - 1.30 (1.27)				
Sabine	La.	3	29.0 - 32.5	3.00 - 3.25 (3.16)	1.54 - 1.76 (1.62)				
Neches	Tex.	4	35.0 - 47.0	3.04 - 3.18 (3.13)	1.21 - 1.33 (1.30)				
Trinity	Tex.	4	38.5 - 50.0	3.08 - 3.27 (3.20)	1.31 - 1.64 (1.45)				
Colorado	Tex.	1	23.5	3.13	1.57				
Guadalupe	Tex.	2	24.5 - 27.0	2.84 - 3.27 (3.06)	1.35 - 1.58 (1.47)				

[1] Ratio of distal mesial shaft to proximal mesial shaft of first pleopod.

[2] Ratio of central projection to mesial process of first pleopod.

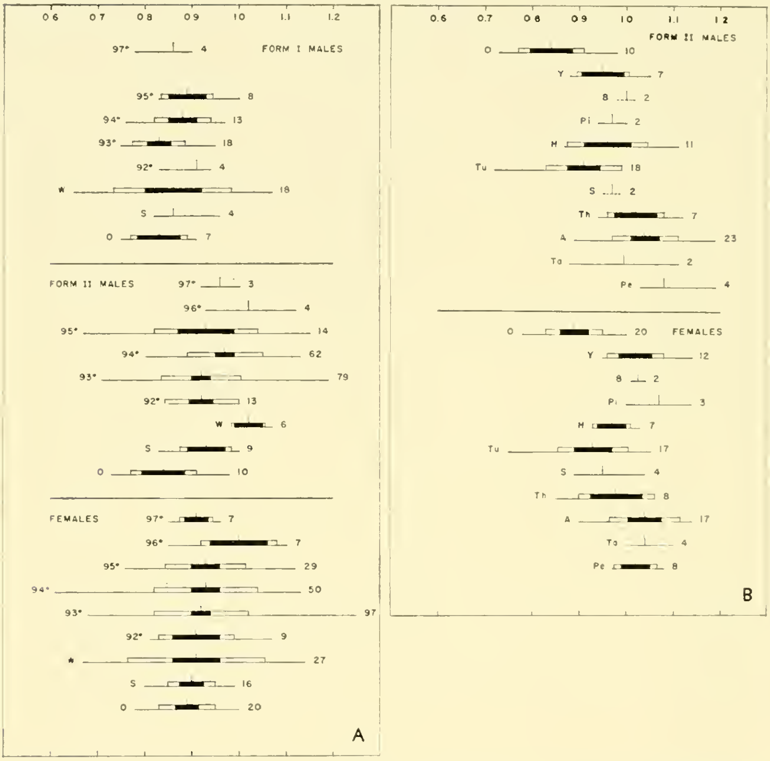


Figure 11. Geographic variation in ratio of rostrum length to areola length. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

cephalothorax to chela length (fig. 2, A); lowest figures indicate the longest chelae.

Length of chela in form I males was one of Faxon's (1898) original diagnostic characters for *O. p. longimanus*. His data indicated that the chela is as long or longer than the cephalothorax in this subspecies.

On a west-east line across Oklahoma and Arkansas (fig. 13-A) the males (both forms) show a decreasing chela length in an interrupted cline toward the White River. This is continued in form I males, but is reversed very significantly from that point in form II males. Females show a continuous west-east cline of decreasing chela length through the same geographic area, but the cline is broken (probably significantly) between the White and St. Francis rivers.

In a north-south line east of the Mississippi River (fig. 13-B) the variation in this character is discordant in both form II males and females, with neither a cline nor significant breaks.

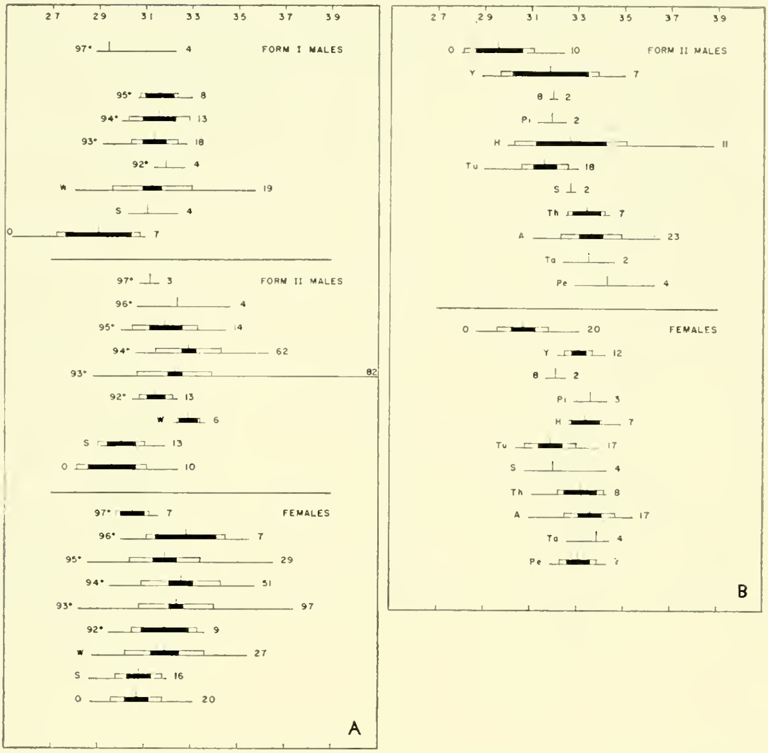


Figure 12. Geographic variation in length of areola. **A,** west-east series; **B,** north-south series east of Mississippi River. Abbreviations same as in fig. 5.

West of the Mississippi River in Gulf drainage streams males of both forms show a tendency toward a chela of decreasing length in the west (Table 2) which is the reverse of the cline across Oklahoma and Arkansas.

Width of palm.—This is expressed as a ratio of the length of the chela to palm width (fig. 2, B); lowest figures indicate the widest palms.

On the west-east axis the widest palms of males (both forms) and females are toward the east (fig. 14-A), however there is not a clearly defined cline. The trend is interrupted by significant reverses in several areas. For example, form II males show the west-east cline of increasing palm width through the 92° group, but the White River specimens have significantly narrower palms; palms of the St. Francis River sample are not significantly wider than those of the White River specimens, but those of Obion River specimens are probably narrower than those of the St. Francis River form II males. Palm

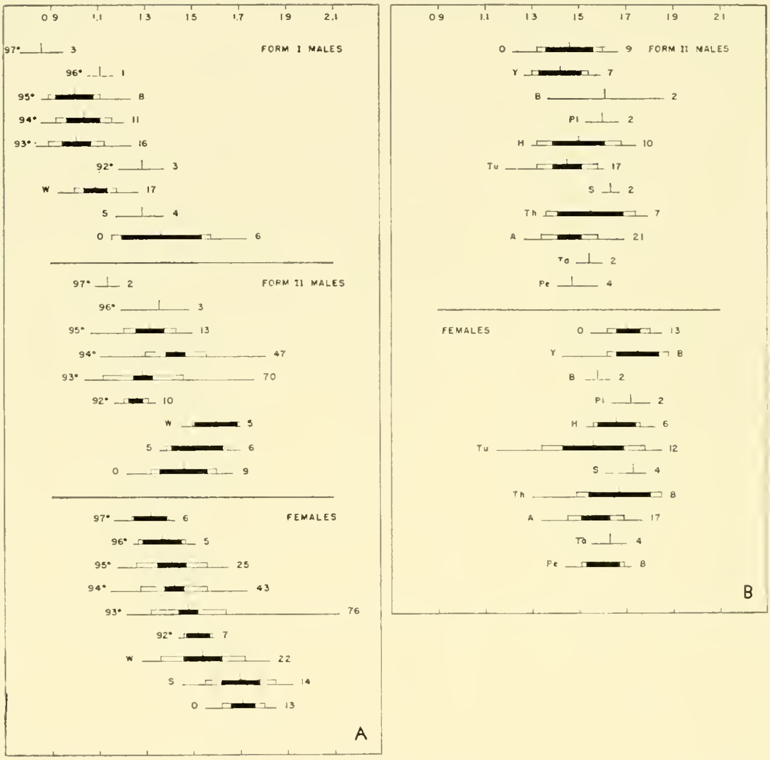


Figure 13. Geographic variation in length of chela. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

width varies in a similar manner among the females with highly significant differences in four areas: (a) 94° samples narrower than 95° specimens, (b) 93° specimens wider than 94° specimens. (c) 92° specimens wider than 93° specimens, and (d) White River specimens narrower than 92° specimens.

On the north-south axis (fig. 14-B) there is no cline in either form II males or females, and the only difference of high significance lies between the palm widths of females from the Obion and Yazoo rivers.

Length of dactyl.—This is expressed as a ratio of length of chela to dactyl length (fig. 2, C); lowest figures indicate the longest dactyl.

In males (both forms) and females the dactyl is longer to the west, forming a definite cline. In form II males and females there is a highly significant difference between samples from the White and St. Francis rivers (fig. 15-A).

On the north-south axis there is no cline shown (fig. 15-B) how-

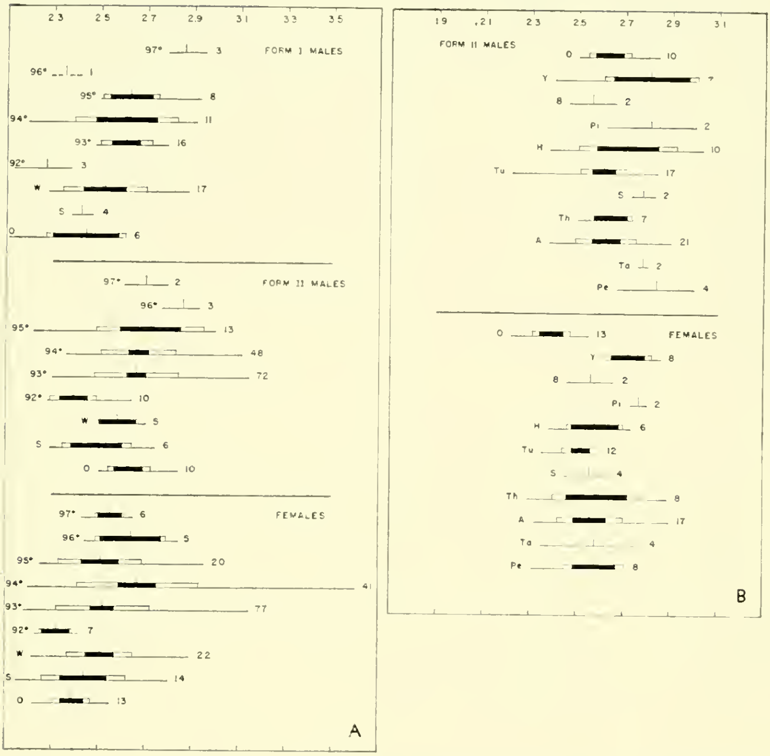


Figure 14. Geographic variation in width of palm. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

ever, significant differences in dactyl length between various samples of form II males do occur: (a) Tunica Bayou specimens have longer dactyls than specimens from Thompson's Creek, (b) Thompson's Creek specimens have shorter dactyls than those from the Amite River. In females there is also no clinal variation shown, but highly significant differences occur at three points: (a) Homochitto River specimens have shorter dactyls than Tunica Bayou samples, (b) Tunica Bayou specimens have longer dactyls than Thompson's Creek specimens, and (c) Thompson's Creek specimens have shorter dactyls than those from the Amite River.

Length of first pleopod of males.—This is expressed as a ratio of length of cephalothorax to pleopod length (fig. 3, A); lowest figures indicate the longest pleopods.

Pleopod length was the most important character cited by Creaser (1933) in distinguishing between *creolanus* and *palmeri*, and between

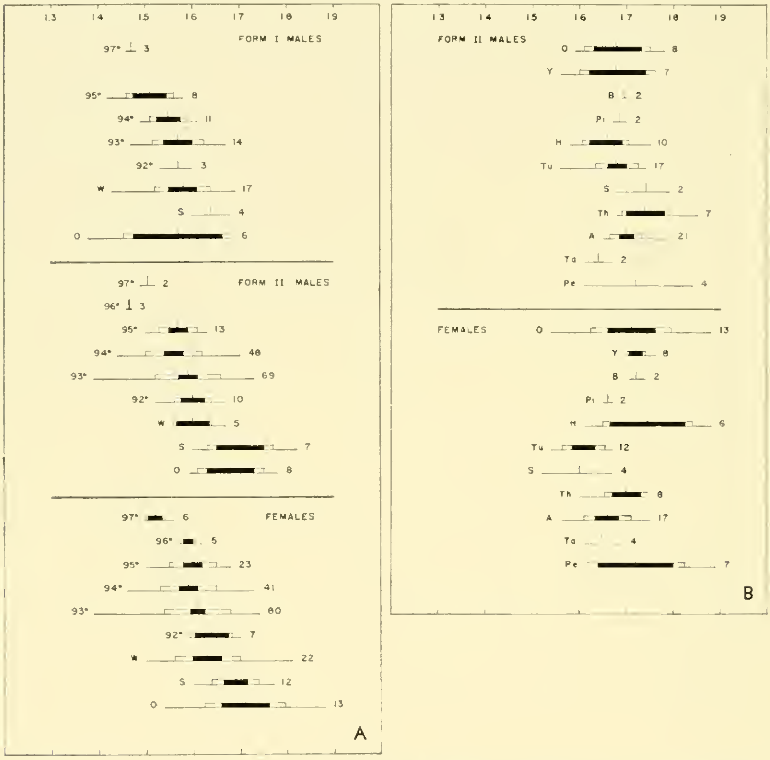


Figure 15. Geographic variation in length of dactyl. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

palmeri and *longimanus*. The data here seem to bear out Creaser's observations as far as he went.

The pleopod is shortest in the west and increases in length in a definite west-east cline in both form I and II males. However, this cline is broken by a highly significant difference between the White and St. Francis river samples (figs. 16, 17), indicating the probable geographic separation between *longimanus* (to the west) and *palmeri* (to the east) in Arkansas.

A north-south cline of decreasing pleopod length in form II males (fig. 17) is reversed by a highly significant difference between samples from Thompson's Creek (the southernmost tributary of the Mississippi River) and Amite River (the westernmost tributary of Lake Pontchartrain). From the Amite River eastward the pleopod increases in length. Perhaps the line between the Amite River and Thompson's Creek should be recognized as the boundary between

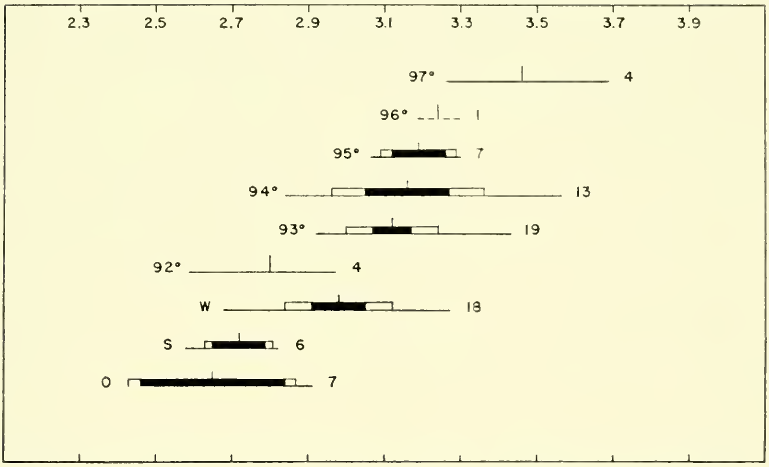


Figure 16. Geographic variation in length of first pleopod of form I males, west-east series. Abbreviations same as in fig. 5.

palmeri (to the north) and *creolanus* (to the south and east) on the east side of the Mississippi valley.

West of the Mississippi River in Gulf drainage streams there is a suggestion of an east-west cline of increasing pleopod length (Table 2) which is the reverse of that shown across Oklahoma and Arkansas.

Length of central projection.—This is expressed as a ratio of the length of central projection (fig. 3, B) to the length of the distal mesial shaft (fig. 3, D); highest figures represent the longest central projection.

The central projection is shortest in the west and increases toward the east in a definite cline in form I males (fig. 18). However, there is a highly significant difference in central projection length between samples from the White and St. Francis rivers as has already been noted for pleopod length. In form II males there is no cline displayed, however there is a highly significant difference in central projection length between samples from the White and St. Francis rivers (fig. 19).

West of the Mississippi River in Gulf drainage streams there is a tendency for a longer central projection to the west in form I males (Table 2), the reverse of the cline shown across Oklahoma and Arkansas. In form II males there is no cline.

A north-south cline of decreasing central projection length occurs in form II males through the Thompson's Creek populations. The cline is reversed in the Amite River sample, the central projection becoming longer toward the southeast (fig. 19). The difference be-

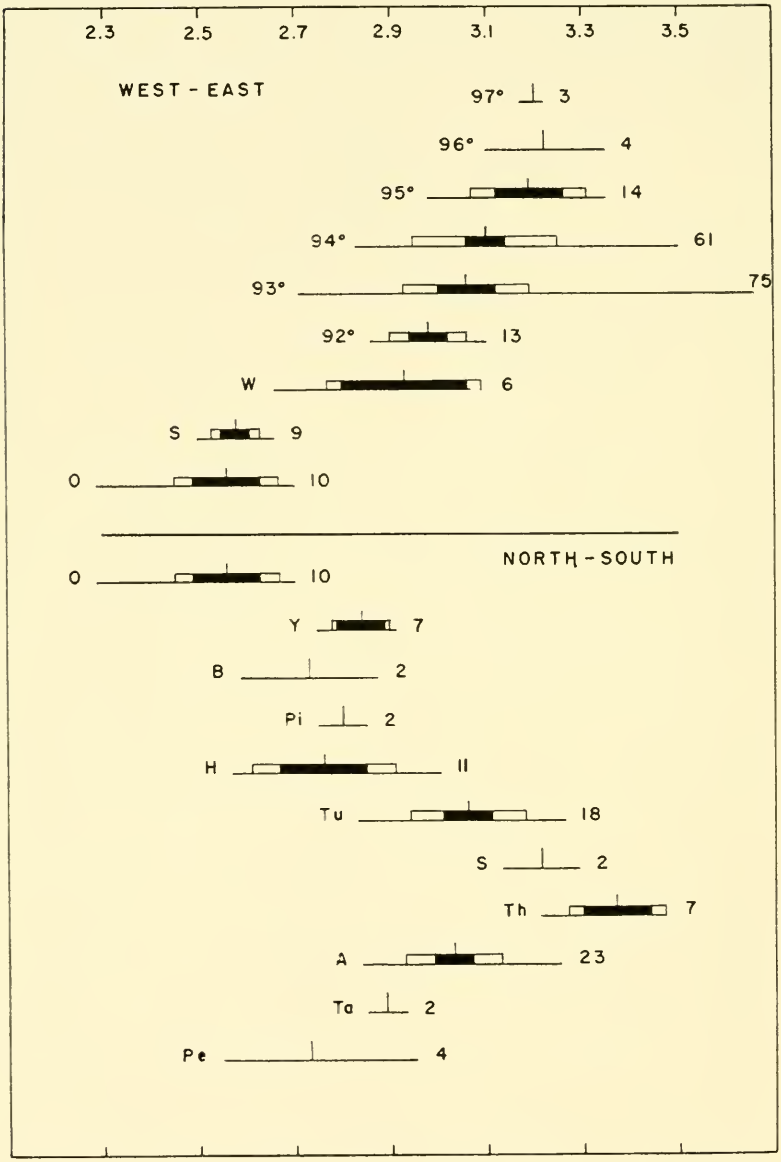


Figure 17. Geographic variation in length of first pleopod of form II males, west-east series and north-south series east of Mississippi River. Abbreviations same as in fig. 5.

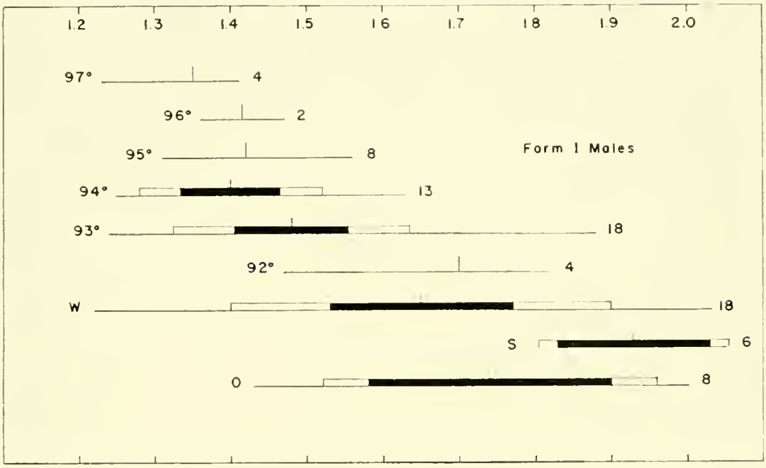


Figure 18. Geographic variation in length of central projection of form I males, west-east series. Abbreviations same as in fig. 5.

tween Thompson's Creek and Amite River specimens is probably significant.

Ratio of central projection length to mesial process length.—In this ratio figures greater than 1.0 indicate that the central projection is longer than the mesial process.

In form I males the variation does not correspond to geographical limits (fig. 20-A), and in all specimens the central projection is longer than the mesial process.

In form II males there is likewise no significant geographical variation either in west-east or north-south directions (fig. 20-B), however, some specimens in the 92° group show a slightly longer mesial process, and the lower limit of the ratio (approaching equality) is seen in a few specimens from Tunica Bayou and the Amite River.

West of the Mississippi River in Gulf drainage streams there is a tendency for an increase in length of the mesial process toward the west in form II males (Table 2). In all specimens the central projection is longer than the mesial process.

Ratio of length of distal mesial shaft to length of proximal mesial shaft.—In this ratio figures greater than 1.0 indicate that the distal mesial shaft (fig. 3, D) is longer than the proximal mesial shaft (fig. 3, F).

In form I males there is no significant geographical variation in this ratio (fig. 21-A) and all specimens show a longer proximal shaft as expected.

In form II males also there is no significant geographical variation in this ratio, but there is a slight tendency for a longer distal mesial

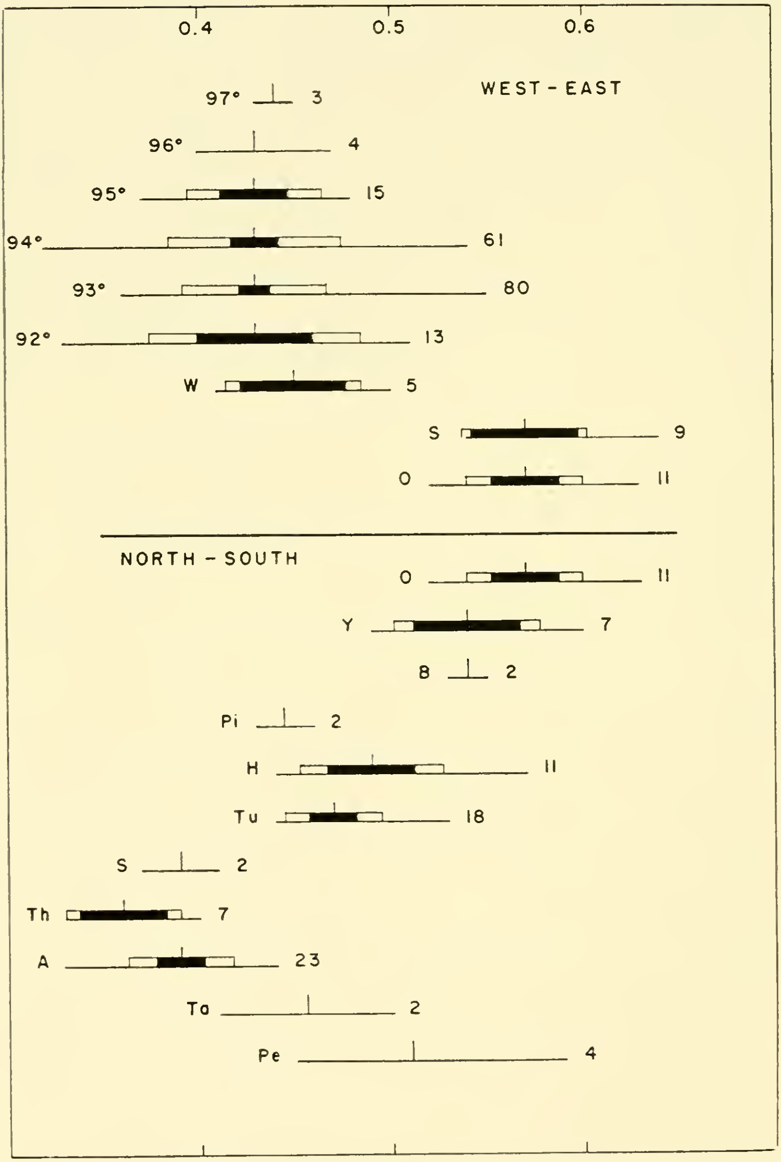


Figure 19. Geographic variation in length of central projection of form II males, west-east series and north-south series east of Mississippi River. Abbreviations same as in fig. 5.

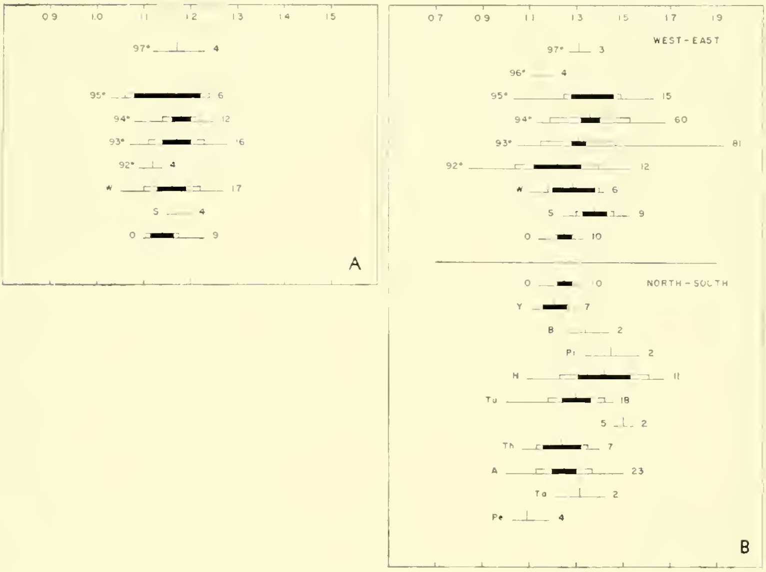


Figure 20. Geographic variation in ratio of central projection length to mesial process length. **A,** west-east series of form I males; **B,** west-east and north-south series of form II males. Abbreviations same as in fig. 5.

shaft to the east (fig. 21-B). As was anticipated, all form II males show a distinctly longer distal mesial shaft.

These same statements apply equally well to the few specimens from Gulf drainage streams west of the Mississippi River (Table 2).

Development of the carina.—In this subjective observation, the rostrum was recorded on an arbitrary scale of carina development of "prominent", "weak", or "absent".

On a west-east axis the carina is absent in the westernmost specimens (97°, 96°) but becomes increasingly more prominent toward the east (fig. 22).

On a north-south axis the prominence of the carina decreases somewhat to the south but is always present in a majority of the specimens (fig. 22).

West of the Mississippi in Gulf drainage streams the carina is present on the majority of specimens examined.

Obliteration of the areola.—Early in the study a number of specimens which otherwise were obviously of the *palmeri* complex were found with slightly open areolas. The percentages of specimens with obliterated (*i.e.*, closed) areolas are plotted in figure 23. All specimens of the 95° group and westward have obliterated areolas, but

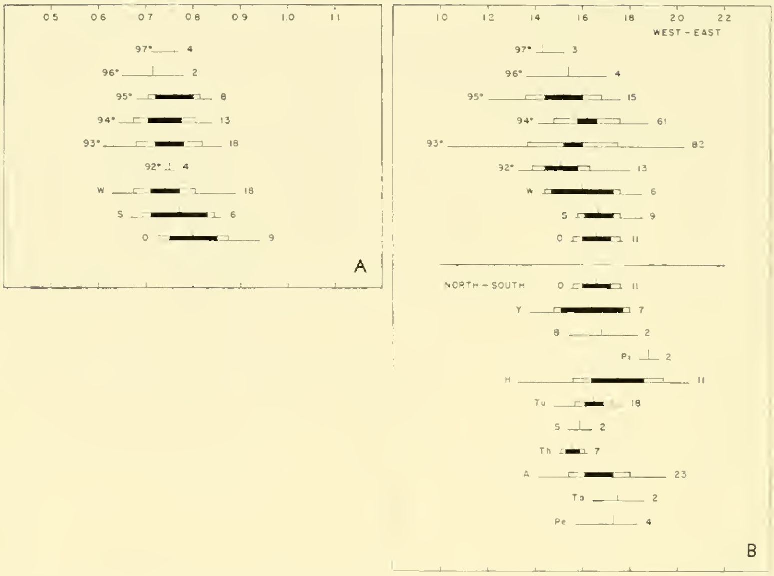


Figure 21. Geographic variation in ratio of length of distal mesial shaft to length of proximal mesial shaft. **A**, west-east series of form I males; **B**, west-east and north-south series of form II males. Abbreviations same as in fig. 5.

from here eastward the number with slightly open areolas increases through the 92° group, and then again increases to the east to reach 100% in the St. Francis and Obion river specimens.

On a north-south axis the percentage of obliterated areolas is quite variable from stream to stream and reaches a low of 17.5% in the Homochitto River specimens (fig. 23).

Shape of the rostrum.—The vast majority of specimens examined showed a rostrum in which the sides were convergent anteriorly and straight (or nearly so). Some individuals from the 93° group (23%), 92° group (8%) and the White River (28%) were the only ones which showed any great variation in rostrum shape. In all variants the sides of the rostrum were convergent anteriorly, but all showed marked concavity of the sides.

Gaping of the fingers of the chela.—As in the shape of the rostrum, the vast majority of specimens agreed in having a small amount of gape between the bases of the fingers of the chela.

On a west-east axis the degree of gape was highest in the westernmost localities. Specimens from the St. Francis and Obion rivers had little or no gape.

On a north-south axis little or no gape is found in specimens from

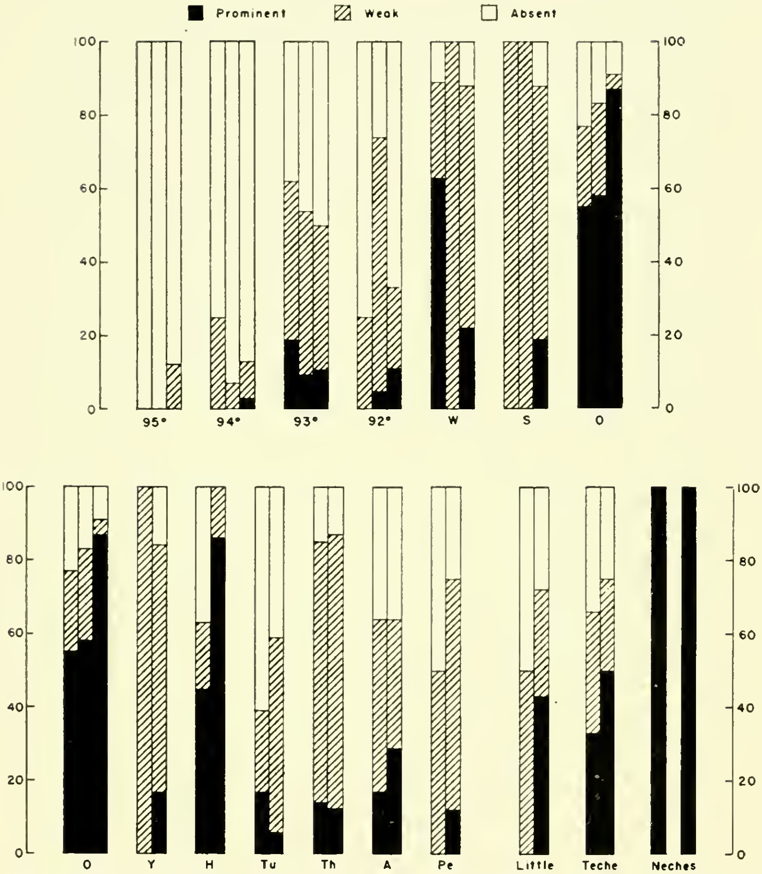


Figure 22. Geographic variation in development of the carina. In each group of three bars, left is form I males, middle is form II males, right is females. In groups of two bars, form I males not present. Abbreviations beneath bars same as in fig. 5.

the Obion River through the Homochitto River, however, the majority of specimens from Tunica Bayou, Thompson's Creek and the Amite River show marked gape. From the Amite eastward the trend is reversed with little or no gape in the Tangipahoa and Pearl rivers.

West of the Mississippi River in Gulf drainage streams the ratio of gape to non-gape is roughly equal, and in only a few specimens from the westernmost rivers is the gape at all marked.

Color.—Brief color notes were given in the original descriptions of *longimanus* and *creolanus* by Faxon (1898) and Creaser (1933) respectively. Creaser and Ortenburger (1933) gave brief color notes

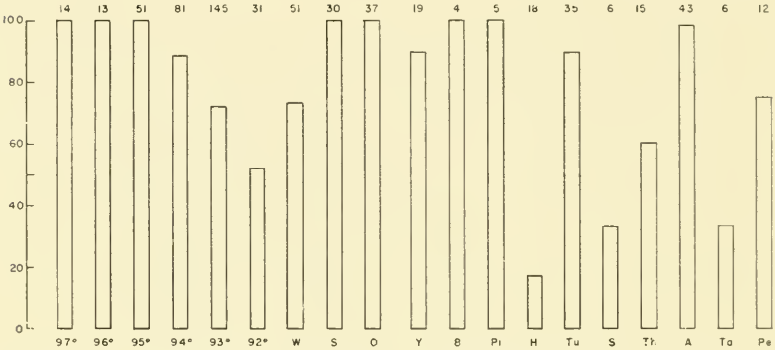


Figure 23. Geographic variation in the obliteration of the areola. Each bar represents the percent of specimens with obliterated areolas. Abbreviations same as in fig. 5, number of specimens at top of each bar.

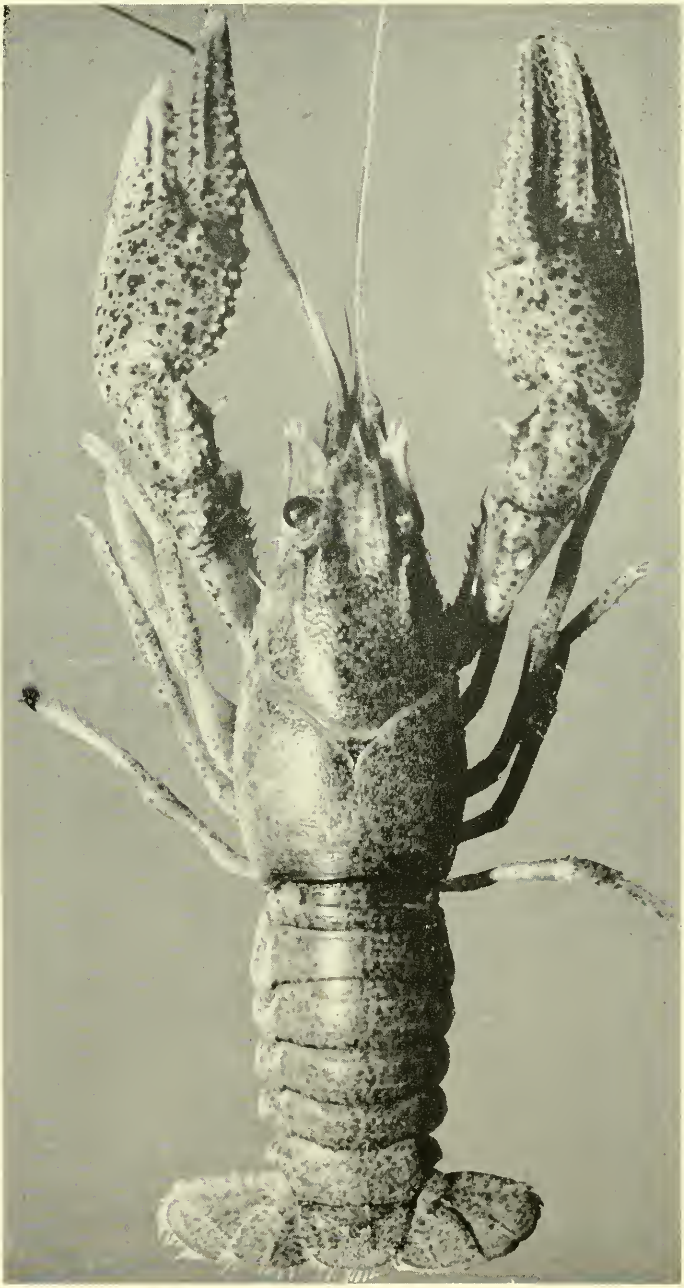
on material from Oklahoma and Hobbs and Marchand (1943) included a rather detailed color description of material from the Reelfoot Lake area.

Color varies considerably even within any given population and since the majority of the specimens examined were not seen alive trends in color variation over the range of the species are not here correlated with geography. The pattern is generally the same for the species. Cephalothorax and abdomen dorsally with irregular-shaped spots of darker color producing a more-or-less mottled appearance (fig. 24). Postorbital ridges red. Abdominal terga each with a thin line of color along posterior margins, and posterior margins of uropods and telson with a similar thin line of color. Chelae generally with the same basic color as the cephalothorax and abdomen and with similar darker mottlings; fingers generally darker than palm and with claws red-tipped; joints between carpus and merus of all five pereiopods red; pereiopods of same basic color, but of a lighter hue.

Specimens from a tributary of the Yocona River (Yazoo drainage) in Lafayette County, Mississippi (TU 3469) have a light olive-tan base color with mottlings of darker olive brown. Posterior margins, abdominal terga, uropods and telson marked by thin bright red line Fingers of chelae darker than palm with apical fourth creamy white and claws bright red. The picture in general agrees with the specimens described by Hobbs and Marchand (1943).

Specimens from a tributary of the Little River in Grant Parish, Louisiana (TU 3159) and the South Fork of the Saline River (Ouachita drainage) in Garland County, Arkansas (TU 2954) agree in

Figure 24. Color pattern of form I male from Redwood Creek (Amite drainage), East Feliciana Parish, Louisiana (TU 3427). (Photograph by Mrs. Fred R. Cagle).



having a base color of olive with a bluish cast and mottlings of darker olive or blue. Posterior margins of abdominal terga edged with dark olive or a bluish-black hue. Posterior margins of telson and uropods edged with dark red. Outer margin of palm and immovable finger dark olive or bluish-black; fingers basally dark olive green with apical fourth bright red or reddish orange.

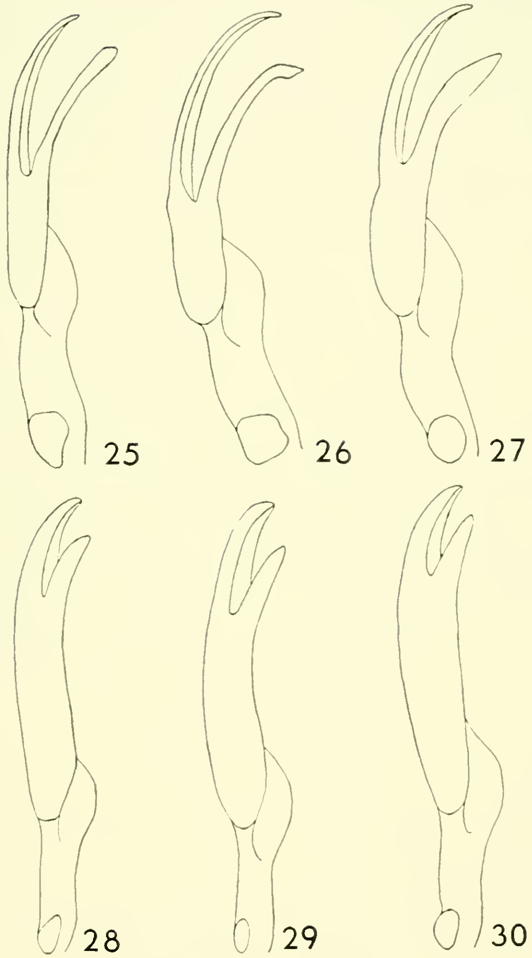
Specimens from Redwood Creek (Amite drainage) in East Feliciana Parish, Louisiana (TU 2801) have a light olive basic color with mottlings of darker olive. Posterior margins of abdominal terga, telson and uropods each with a thin bright red line. Both fingers of chelae darker basally with tip of each claw bright red. Juveniles from the same locality have an area of creamy white between the dark basal color and the bright red tips; in this respect, they resemble the adult specimens from the Yocona River.

The Subspecies of *ORCONECTES PALMERI*

On the basis of data presented here three ill-defined subspecies may be recognized. No one character may be utilized to separate them other than comparative geographic distribution of a number of relatively minor features (see fig. 4), and on inference from their geological history. The three subspecies here recognized are (1) *O. p. palmeri* (Faxon): St. Francis River and all eastern tributaries of the Mississippi River between the Obion River and Thompson's Creek inclusive (figs. 26, 29); (2) *O. p. creolanus* (Creaser): the Lake Pontchartrain drainage area plus the Pearl and Pascagoula rivers (figs. 27, 30); and (3) *O. p. longimanus* (Faxon): all western tributaries of the Mississippi River from the Arkansas River to the Gulf, and Gulf drainage streams from the Mississippi River to the Guadalupe River in Texas (figs. 25, 28). Thus, the specimens recorded as *creolanus* from Claiborne, Franklin, Grant, LaSalle, Madison, Ouachita and St. Landry Parishes in Louisiana by Creaser (1933: 18) and Penn (1952: 745) are *longimanus.*

O. palmeri possibly became differentiated as a species in the late Pleistocene (after the Wisconsin glacial epoch) near the head of the old Mississippi embayment. From this center of distribution it must have spread south in streams flowing into the Mississippi River on both sides. Coincident with reaching its ultimate distribution in a southerly direction it also moved upstream in the rivers already colonized to occupy its westernmost and easternmost limits. Occupation of Gulf drainage streams could have occurred only during periods of flooding of the Mississippi River and its tributaries, for the species is not tolerant to (or, at least does not occur in) parts of streams subject to marine tidal influence. If the Mississippi River's earliest delta was in western Louisiana as suggested by Howe et al. (1935), then occupation of the western Gulf drainage rivers would have been comparatively easy.

Subsequent to the general distribution of *palmeri* westward the Mississippi River moved eastward and laid down most of south Lou-



Figures 25-30. First pleopods of males, mesial views. **25.** *O. p. longimanus* form I, Red River drainage, Polk County, Arkansas (HHH 7-3141-1a); **26.** *O. p. palmeri* form I, Indian Creek at Samburg, Obion River drainage, Obion County, Tennessee (HHH 6-2041-1a); **27.** *O. p. creolanus* form I, Redwood Creek at McManus, Amite River drainage, East Feliciana Parish, Louisiana (TU 2802); **28.** *O. p. longimanus* form II, same data as for fig. 25; **29.** *O. p. palmeri* form II, Indian Creek near Old Samburg, Obion River drainage, Obion County, Tennessee (HHH 7-2541-3a); **30.** *O. p. creolanus* form II, same data as for fig. 27.

isiana. As it reached its present location its floods became more restricted by the topography of the land so that any given population in a stream tended to become isolated. The populations of the subspecies *palmeri* in eastern tributaries of the Mississippi River occur in streams which have remained in relatively close contact through the agency of major floods and this is reflected in the pooled characters of similarity of this subspecies which differ on the one hand from those of the western subspecies (*longimanus*) and the eastern Gulf subspecies (*creolanus*).

Populations of the White River, which lies partially in (*i.e.*, the Black and Cache rivers) and partially out (*i.e.*, the upper White River proper) of the St. Francis basin are in some respects unique, *i.e.* resembling neither of the subspecies to the east or west; in other respects the White River populations are intermediate between *O. p. palmeri* and *longimanus*. I agree, therefore, with Williams (*op. cit.*) that these represent intergrade populations.

Apparently there have been subsequent isolating factors superimposed on the initial three-way geographic distribution of the subspecies. These isolating factors, operating almost stream by stream, have resulted in the formation of north-south ecoclines in the subspecies *palmeri* east of the Mississippi River; definite west-east ecoclines in *longimanus* in both the Arkansas, Red and Ouachita rivers and in the Gulf drainages streams west of the Mississippi River; and in less definite west-east ecoclines in *creolanus*. The infrasubspecific ecoclines correspond remarkably to some of the clinal distributions of meristic characters found by Gibbs (1957) in subspecies of the cyprinid fish *Notropis venustus*.

Life History Data

Although representative numbers of specimens of all size groups for each of the subspecies were examined their seasonal distribution was limited mainly to the warmer months. Hence, accurate predictions of seasonal sequences are not possible. Summaries of the analyses are given, however, as bases for future studies.

O. p. palmeri.—Collections from April through September only. Form I males in June, July and September. Oocytes in mature females show progressive growth from May (average minimum diameter 0.05 mm) through July (average maximum diameter 0.30 mm). Ovigerous females unknown, but on the basis of oocyte development they should be sought in March and April. Collections of small juveniles inadequate (only 38 specimens less than 14 mm cephalothorax length) and equally distributed from May through July.

O. p. creolanus.—Collections from February and March, and May through August. Form I males in June and July only. One ovigerous female (36 mm cephalothorax length) taken on March 29, 1952 in a tributary of the Pearl River in Marion County, Mississippi (TU 2665); 453 eggs carried, average egg diameter 2.0 mm. Oocytes in mature females showed progressive growth from May (average minimum diameter 0.05 mm) through August (average maximum diameter 0.25 mm). Collections of small juveniles (less than 14 mm cephalothorax length) scattered from May through July.

O. p. longimanus.—Collections from January and March, and May through November. Form I males from May through November with the greatest number in July. Ovigerous females unknown; oocyte analysis made only in 18 July specimens, of which sixteen had oocytes in the 0.25 to 0.30 average diameter range (range for all eighteen specimens was 0.17 to 0.40 mm). Small juveniles (less than 14 mm cephalothorax length) most abundant in May and June, perhaps indicating that eggs are laid in April.

Acknowledgements

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Specimens collected in Mississippi by Dr. Royal D. Suttkus of Tulane University have proved invaluable. For help in the field work Messrs. Joe B. Black and Ernest A. Liner are due special thanks.

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ABSTRACT

Orconectes palmeri is distributed in streams in south-central United States from southwestern Tennessee and southeastern Missouri to western Oklahoma and the Guadalupe River, Texas and the Pascagoula River, Mississippi.

The limits of variation of the three previously described subspecies have been studied and the geographic range of each defined. *O. palmeri palmeri* (Faxon) is limited to the St. Francis River in Arkansas and tributaries on the eastern side of the Mississippi River from the Obion River, Tennessee to Thompson's Creek, Louisiana inclusive; *O. p. longimanus* (Faxon) is limited to the Arkansas, Red and Ouachita River drainages in Oklahoma, Arkansas, Texas and Louisiana and Gulf drainage streams west of the Mississippi River; *O. p. creolanus* (Creaser) is limited to the Lake Pontchartrain drainage in Louisiana and Mississippi and the Pearl and Pascagoula River drainages. An intergrade area between *O. p. palmeri* and *O. p. longimanus* occurs in the White River drainage in northeastern Arkansas. Infrasubspecific ecoclines were found for a number of the characteristics studied.

O. palmeri apparently originated in the late Pleistocene near the head of the old Mississippi embayment. Dispersal from this site of origin was in tributaries of the Mississippi River and subsequently into Gulf drainage streams to the west and east.