# GEOGRAPHIC VARIATION IN THE CRAWFISH *FAXONELLA CLYPEATA* (HAY) WITH THE DEFINITION AND DEFENSE OF THE GENUS *FAXONELLA* CREASER (DECAPODA, ASTACIDAE)[1]

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The crawfish *Faxonella clypeata* (Hay) is becoming one of the better studied members of the subfamily Cambarinae. One of the few published life histories of crawfishes is of this species. Its ontogeny has been investigated (Black, 1958), and some phases of its endocrinology and physiology have been explored (Fingerman and Oguro, 1962, etc.). Currently there is a study of its molting cycle being undertaken by Mobberly (Unpubl. data). Taxonomic studies of the animal are primarily of a regional nature, and no one has done a thorough study of the morphological variation of the animal over its geographic range.

Hobbs (1942b: 154) reported that he had examined the ratio of the length of the basal portion of the first pleopod of males of *clypeata* to the length of the central projection and found a significant variation in this character across the geographical range of the animal in a manner suggestive of clinal variation (Fla., 1.23; Ga., 1.26; Ala., 1.36; and La., 2.65). Penn (1952: 746) added that for Louisiana specimens the mesial process was very short in relation to the central projection, one-third to one-half the length. Penn and Hobbs (1958: 481) recorded that the ratio of the mesial process to the central projection of *clypeata* varied from one-half to one-third for Texas specimens. Penn (1959: 8) remarked that the central projection is about three times the length of the mesial process in Louisiana specimens.

In view of the special significance attached to the relative sizes of the two terminal rami in the description of the subgenus *Faxonella* by Creaser (1933: 21) and reports of variation in these parts, a thorough taxonomic study of *F. clypeata* was undertaken. The only other study of variation in the organism is of ontogenetic variation by Black (1958).

[1] The Society of Sigma Xi supported this research in part with a Grant-in-Aid of Research for the year 1960-61.

## Historical Statement

Hay (1899: 122) described *Cambarus clypeatus* on the basis of one female collected by the U. S. Biological Survey in 1892 and deposited in the U. S. National Museum. He designated the type locality as Bay St. Louis, Mississippi. Creaser (1933) described the first and second form males and added that the type specimen was "found in a skiff." This notation appears on the label in the bottle with the holotype. Crawfish of the size of *clypeata* are widely used as fish bait in this section of the country, and frequently are collected at some distance from the place of sale or use. One would be prudent therefore to consider that the type specimen came from the general vicinity of Bay St. Louis or the Mississippi Gulf Coast rather than the restricted locality of Bay St. Louis. Such a thesis can neither be supported nor refuted by my investigation.

Further observations were made on *clypeatus* by Ortmann (1902: 277), Harris (1903: 83), Faxon (1914: 401, 426), and Creaser and Ortenburger (1933: 40). In the redescription of the species by Creaser (1933: 19) *clypeatus* was placed in the newly elevated genus *Faxonius* but recognized as "certainly an orphan among this group of crayfishes." For this reason it was placed in the monotypic new subgenus *Faxonella*. Cope's (1872: 419) genus *Orconectes* was substituted for *Faxonius* by the rule of priority by Hobbs (1942a: 350), and *clypeatus* was redesignated *Orconectes clypeatus* (Hay), but was still distinct from other species of the genus under the subgenus *Faxonella* (Hobbs, 1942b: 28, 154). The subgenus remained monotypic until Penn (1950: 166) described *Orconectes* (*Faxonella*) *beyeri*, recognized its affinities with *clypeatus*, and placed *beyeri* in the subgenus *Faxonella*. Recently, Creaser (1962) challenged the current classification of the Cambarinae and Cambarellinae, contending that *Faxonella* among other taxa is a "natural group" of the same rank as Hobbs' *Cam-*

*barus* (*sensu strictu*). He further contends that *Orconectes* of Hobbs is a grouping of three "natural groups." Fitzpatrick (1962) gave a cursory report of geographic variation in an abstract of a paper presented before the Virginia Academy of Science. This paper is a more complete report of his study of geographic variation.

*Ecology and development.*—Smith (1953) reported on the life cycle of *O. clypeatus.* According to her, seasonal spawning occurred from May until September, with considerable post-seasonal spawning. She observed that ovigerous females retreated into burrows and that this was reflected in the proportionate number of females taken in free-water collections. Although both form I and form II males were present throughout the year, their proportionate numbers varied such that there were relatively more form I males present in the population just prior to oviposition. She further observed that during dry periods the crawfishes burrowed into the mud instead of migrating. Penn (1952: 747) reported the habitat of *O. clypeatus* to be shallow, clear water; temporary; static; and exposed to full sunlight. The habitats have mud bottoms and aquatic plants are present.

Black (1958) determined that the growth increment of *O. clypeatus* averaged 0.41 mm cephalothorax length per molt. The increment is independent of size or sex. The males molted into the first form during the breeding season and reverted to second form following the breeding season. He did not record a form I male of less than 11.5 mm cephalothorax length.

## Materials and Methods

*Materials.*—The materials used in this study were taken from the Tulane University collections and the personal collections of Horton H. Hobbs, Jr., of the University of Virginia. These two collections together comprise what is perhaps the most comprehensive collection of the species available. All collections available were examined, but not all were included in statistical analysis. Excessive redundancies and/or statistically surplus numbers in one population were not used. One of the populations subjected to statistical analysis was used by Black (*loc. cit.*) in his study of ontogeny, and several were used by Smith (*loc. cit.*) for her study of the life history. Both Black and Smith used materials from the Tulane University collections.

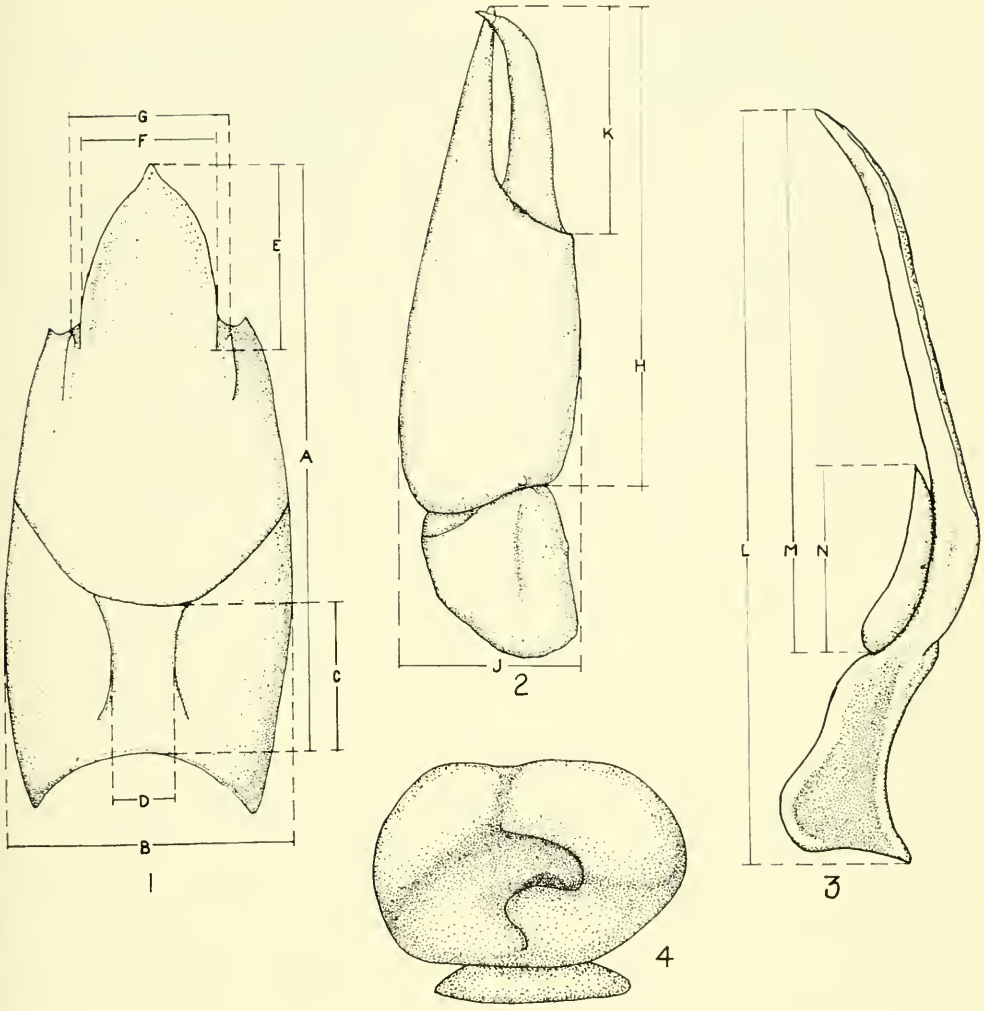
*Measurements.*—The standard measurements of only inflexible parts common to crawfish taxonomy were used. Females and form II males of less than 10.4 mm cephalothorax length were not used because of Black's (*loc. cit.*) observation that pleopod and growth increments were not correlated below this size. All form I males, regardless of size, were included in the data as such animals were regarded as reproductively active and thus mature and contributing to the gene pool. Friction calipers and a standard millimeter rule were used to measure length of cephalothorax, width of cephalothorax, and length of chela. All other measurements were made with an ocular reticule mounted in an American Optical Co. stereoscopic microscope. All measurements were recorded to the nearest 0.1 mm.

Measurements were made on (1) length of cephalothorax, (2) width of cephalothorax, (3) length of rostrum, (4) width of rostrum, (5) distance between postorbital spines, (6) length of areola, (7) width of areola, (8) length of antennal scale, (9) width of antennal scale, (10) length of chela, (11) width of palm, and (12) length of dactyl (figs. 1, 2). Males were subjected to three additional measurements: (1) length of first pleopod, (2) length of central projection, and (3) length of mesial process (fig. 3). On all specimens appendages of the right side were used unless such appendages were damaged or atypical in size and/or morphology.

Because of a misunderstanding on my part of the technique of measurement used by Hobbs (1942b), I did not use his method of measuring the rami of the pleopod and did not evaluate his report. Subsequently I had the opportunity to discuss this matter with him, clarified my thinking, and performed a check of his measurements. My results did not differ significantly from his.

*Qualitative measurements.*—The presence or absence of a sperm plug in the annulus ventralis of females was recorded. This criterion was used in an attempt to determine the reproductive activity of females. I was unable to find plugs in any of the 1500 specimens examined.

Records were kept of the number of each sex category for compilation of life history information. These data are presented in




Figures 1-4. Routine measurements and diagnostic features of *Faxonella clypeata*. **1.** Dorsal aspect of the cephalothorax. **2.** Upper aspect of the left chela. **3.** Caudal aspect of the left first pleopod of the form I male. **4.** Ventral aspect of the annulus ventralis of the female. Key to symbols: A = length of cephalothorax; B = width of the cephalothorax; C = length of areola; D = width of areola; E = length of rostrum; F = width of rostrum; G = distance between postorbital spines; H = length of chela; J = width of palm; K = length of dactyl; L = length of pleopod; M = length of central projection; N = length of mesial process.

tabular form by state and month of collection (Table 2).

*Statistical Procedures.*—After measurement each population was assigned to an appropriate river drainage for further grouping. The grouping of *F. clypeata* by river drainage is totally artificial, and by no means should be interpreted as anything other than convenience in analyzing data. Form I males, form II males, and females of each river drainage were analyzed separately, but where analysis showed no significant difference for a character in all drainages, the males were grouped as a unit for reporting. Analyses are presented in graph form following a modification of the method of Hubbs and Hubbs (1953) with the exception of meristic and qualitative characters which are best expressed in other ways. Appropriate mathematical procedures were per-

formed on an IBM Digital Computer, Model 650, through the courtesy of the Tulane University Computer Center. Significant differences between any two samples for any character were calculated by Student's *t* test.

## The Subgenus *FAXONELLA,* Creaser, 1933.

Creaser (1933) elevated Ortmann's (1905: 97) subgenus *Faxonius* to full generic status, presumably using the same critera used by Ortmann for distinguishing the group: namely, that the first pleopods of the males are never stout, are generally slender or with slightly curved tips which are never truncated, ending always in two more or less elongated spines. The more mesial ramus was termed by Hobbs (1940) as the mesial process and the more lateral the central projection. Because of the extremely short mesial process Creaser (*loc. cit.*) recognized the uniqueness of *clypeatus* and assigned this "orphan" to the new subgenus *Faxonella.* When Penn (1950) described *O.* (*Faxonella*) *beyeri* the subgenus ceased to be monotypic. Hobbs (1942a: 350) placed *Faxonius,* including *clypeatus,* in synonomy with *Orconectes* Cope (1872: 419) by the rule of priority. The monotypic subgenus *Faxonella* was retained for *clypeatus* (Hobbs, 1942b: 28, 154). Creaser (1962) published a defense of the generic ranking of *Faxonius,* contending that in his "Group I" of the Cambarinae there are four "natural groups," "either genera or subgenera": *Faxonius, Faxonella, Orconectes* (restricted to *lancifer, inermis,* and *pellucidus*), and *Cambarus* (*sensu strictu*).

In the same paper Creaser contended that the visible rami of the male first pleopod represent the ancestral endopodite and an accessory process of the basipodite. He equated the cephalic process of Hobbs (1940) with the exopodite, and considered the central projection of Hobbs as the endopodite. However, the work of Hart (1953; 1956) on certain Astacidae and Black (1958) on *clypeata* proved that the visible parts of the distal portion of the first pleopod are in truth derived from the endopodite and must be considered derivatives of it. These works (Hart, *loc. cit.;* Black, *loc. cit.*) also proved that the pleopod is derived from a typical biramous ancestral appendage. The suggested homologies proposed by Hobbs (*loc. cit.*), in the absence of contradictory information, seem reasonable for *Faxonella,* and because of the wealth of literature employing these terms they might well be retained.

In the "Group I" of Creaser (*loc. cit.*), of the four "distinctive subgroups which may be considered either genera or subgenera and which are natural groups", two of his "natural groups" are currently recognized as genera: *Cambarus* (*sensu strictu*) and *Orconectes* (*sensu* Hobbs). *Faxonella* is recognized as a subgenus of *Orconectes* (*sensu* Hobbs), but is considered to be unique with its affinities within the genus obscure. The criterion for the distinction of *Faxonella* exists in the relative lengths of the central projection and the mesial process (Creaser, 1933: 21). In all members of *Faxonella* the mesial process is less than one-half the length of the central projection. Although several species of *Orconectes* (*sensu* Hobbs) have gonopods in which the terminal processes are unequal in length, none approaches the extreme condition found in *Faxonella.* The closest approach to this condition is found perhaps in *O. leptogonopodus* Hobbs in which the mesial process is about 67 per cent the length of the central projection. However, *leptogonopodus* is clearly associated with the Hylas Group of the Propinquus Section and is only remotely related to the two members of the genus *Faxonella.* The annuli ventrales in particular point to the lack of relationship between the two. Examination of the two species of *Faxonella* reveals that they are remarkably similar, with the principal differences being in the relative length of the mesial process, the degree of curvature of the distal portion of the first pleopod, and minor differences in the annulus ventralis. Further, the differences between them are not nearly as great as the differences between the subgenus and the remainder of the species assigned to *Orconectes* (*sensu* Hobbs). Therefore, I propose that the subgenus *Faxonella* be accorded full generic status.

## Key to the Genera of the Subfamily Cambarinae [2]

(Including the species of *Faxonella*)

1. First pleopod of first form male terminating in three or more distinct parts or in two dis-

[2] Based on Villalobos (1955: 45), with modifications.

tinct parts with a strong shoulder on the cephalic margin near the tip ... 2

First pleopod of first form male terminating in only two distinct parts; never with a well developed shoulder on the cephalic margin near the tip ... 4

2. Ischiopodites of third maxilliped with teeth along inner margin ... 3

Ischiopodites of third maxilliped without teeth along inner margin ... *Troglocambarus*

3. Process between the fifth pereiopods of the female present or absent; if present, never compressed in the lateral sense ... *Procambarus*

Process always present between the fifth pereiopods of the female, compressed laterally ... *Paracambarus*

4. Two terminals on first pleopod generally short and strongly recurved. Entire appendage short and heavy ... *Cambarus*

Two terminals on first pleopod short or long, never strongly recurved; if recurved they are slender and in most cases setiform ... 5

5. Mesial process of first pleopod greater than 50% length of central projection ... *Orconectes*

Mesial process of first pleopod less than 50% length of central projection ... *Faxonella* (6)

6. Central projection subcylindrical, more or less straight beyond basal bend, about three times length of mesial process ... *F. clypeata*

Central projection flattened, somewhat sickle-shaped, about twice length of mesial process ... *F. beyeri*

TABLE 1.

*Cephalothorax size ranges of Faxonella clypeata.*

| Length in mm | Locality | Collection no. |
|---|---|---|
| ♀♀ Max. 21.9 | Morehouse Par., La. | TU-P535 |
| Min. 10.4* | Numerous | —— |
| ♂♂ I | | |
| Max. 23.5 | Hancock Co., Miss. | TU3005 |
| Min. 9.7 | Liberty Co., Fla. | HHH19-555-6 |
| ♂♂ II | | |
| Max. 20.8 | Morehouse Par., La. | TU2887 |
| Min. 10.4* | Numerous | —— |

* Females and form II males of less than 10.4 mm cephalothorax length not measured.

## GENUS *FAXONELLA*, Creaser, 1933: 21

*Type*, by monotypy, *Cambarus clypeatus* Hay, 1899: 122.

*Diagnosis.*—First pleopod terminating in two distinct parts; entire pleopod gently curved mesiad distal to proximal one-fourth; mesial process less than 50 per cent the length of central projection; in normal position, pleopods overlap one another (Creaser and Ortenburger, 1933: 29; Penn, 1950: 167). Annulus ventralis of female immovable; subovate, widest in transverse axis; two prominent tuberosities raised ventrally on cephalic margin and separated by a trough; sinus originates in trough and winds either dextrally or sinistrally toward the caudal margin. Male with hooks on the ischiopodies of third pereiopod only. In known species: rostrum lacking marginal spines and spatulate in form with margins entire; areola about three to 3.5 times long as wide, about one-third length of cephalothorax; chela somewhat depressed, palm inflated, no gap between fingers. Maximum known size 23.5 mm cephalothorax length for *F. clypeata; F. beyeri* somewhat smaller.

### *FAXONELLA CLYPEATA* (Hay, 1899)

*Cambarus clypeatus* Hay, 1899.

*Cambarus clypeatus* Hay, Ortmann, 1902; Harris, 1903; Faxon, 1914; Creaser and Ortenburger, 1933.

*Faxonius* (*Faxonella*) *clypeatus* (Hay), Creaser, 1933.

*Orconectes clypeatus* (Hay), Hobbs, 1942a.

*Orconectes* (*Faxonella*) *clypeata* (Hay), Hobbs, 1942b.

*Orconectes* (*Faxonella*) *clypeatus* (Hay), Penn, 1950; Penn, 1952; Penn and Hobbs, 1958; Penn, 1959; Hobbs and Hart, 1959; Fitzpatrick, 1962.

*Faxonella clypeatus* (Hay), Creaser, 1962 (by implication).

*Type locality*, Bay St. Louis, Mississippi.

*Disposition of types*, USNM no. 17277 (one female).

*Localities:* OKLAHOMA, LaFlore Co. (*fide* Creaser and Ortenburger, 1933), McCurtain Co. (USNM no. 96139); TEXAS: Marion Co.; ARKANSAS: Ashley, Columbia, Greene, Hempstead, and Phillips Cos.; LOUISIANA: Allen, Beaureguard, Bossier, Calcasieu, Caldwell, Cameron, Claiborne, East Feliciana, Evangeline, Franklin, Grant,

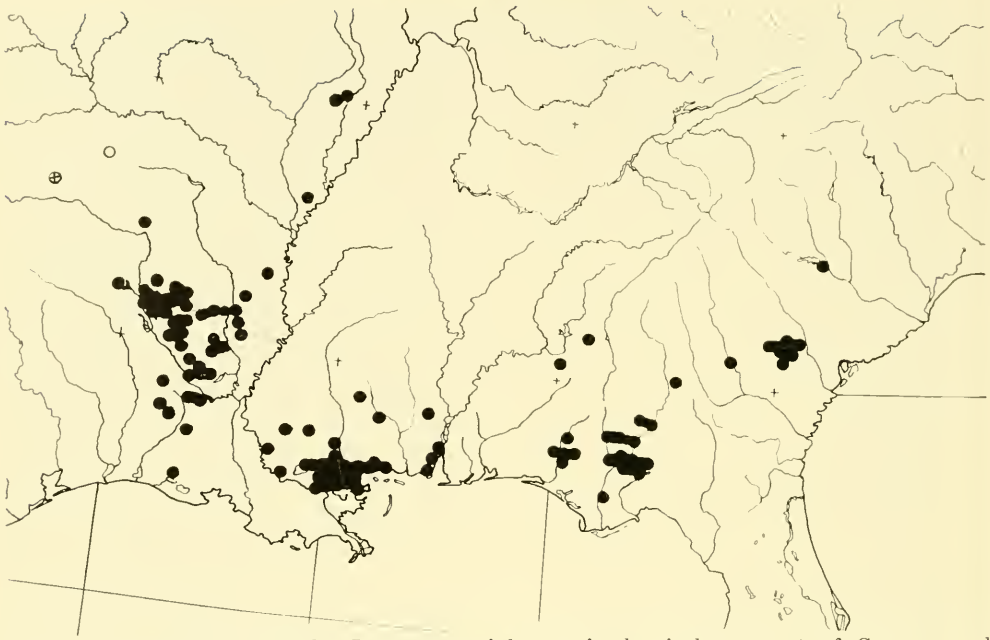


Figure 5. Localities studied. Dots = material examined; circle = report of Creaser and Ortenburger (1933); crossed circle = U.S.N.M. collection referred to in the text.

Jackson, LaSalle, Lincoln, Livingston, Morehouse, Natchitoches, Ouachita, Rapides, Richland, Sabine, St. Helena, St. Tammany, Tangipahoa, Union, Vernon, Washington, Webster, and Winn Parishes; MISSISSIPPI: Forrest, Hancock, Harrison, and Jones Cos.; ALABAMA: Baker, Butler, Burke, Coffee, Dale, Lee, Macon, Mobile, Montgomery, and Washington Cos.; FLORIDA: Gadsden, Holmes, Jackson, and Liberty Cos.; GEORGIA: Baker, Bullock, Burke, Dooley, Dougherty, Early, Emanuel, Jenkins, Johnson, and Seminole Cos.; SOUTH CAROLINA: Richland County. [Interested parties may secure specific information on the localities by consulting a manuscript entitled "A list of the locality records of the crawfish *Faxonella clypeatus* (Hay, 1899) contained in the collections of Horton H. Hobbs, Jr., and of Tulane University of Louisiana as of 1 June, 1961," filed in the Office of the Registrar of the United States National Museum under the number 242747. Information concerning the populations used in statistical analysis can be obtained in detail from Fitzpatrick, J. F., 1961, Geographic Variation in the Crawfish *Orconectes* (*Faxonella*) *clypeatus* (Hay). Unpubl. Master's Thesis, Tulane University, New Orleans.]

*Diagnosis.*—Rostrum with margins entire, usually without marginal spines, spatulate. Postorbital ridges strong, terminating cephalically in strong divergent spines, or spines sometimes absent. Lateral spines absent or greatly reduced. Areola broad (length-width ratio 1.65-4.64, avg. 3.49). Chela with palm inflated and subcylindrical, dactyl shorter than inner margin of palm. First pleopod of male with mesial process less than 40 per cent length of central projection; central projection subcylindrical, more or less straight beyond basal bend. Annulus ventralis as figured (fig. 4). Basic color pattern of Louisiana and Mississippi Gulf Coast specimens olive-tan on cephalothorax and abdomen, two blue black longitudinal lines or stripes extending from behind eyes on either side of areola to end of abdomen.

*FAXONELLA BEYERI* (Penn, 1950)

*Orconectes* (*Faxonella*) *beyeri* Penn, 1950.

*Orconectes* (*Faxonella*) *beyeri* Penn, 1952; Penn, 1959.

*Faxonella beyeri* (Penn), Creaser, 1962 (by implication).

*Type locality,* A roadside ditch on U. S. Route 84, 2 miles northeast of Naborton, DeSoto Parish, Louisiana.

*Disposition of types,* USNM nos. 93061, 93062, 93063 (holotype, allotype, and one paratypic male, respectively).

*Localities,* LOUISIANA: DeSoto and Natchitoches Parishes. The known localities are listed in detail by Penn (1952: 748).

*Diagnosis* (Based on the examination of three paratypes, but mostly from Penn, 1950).—Rostrum with margins entire, without marginal spines, spatulate. Postorbital ridges strong, terminating cephalically in strong divergent spines. Lateral spines absent or greatly reduced. Areola broad (length-width ratio 2.7-3.6, avg. 3.0). Chela

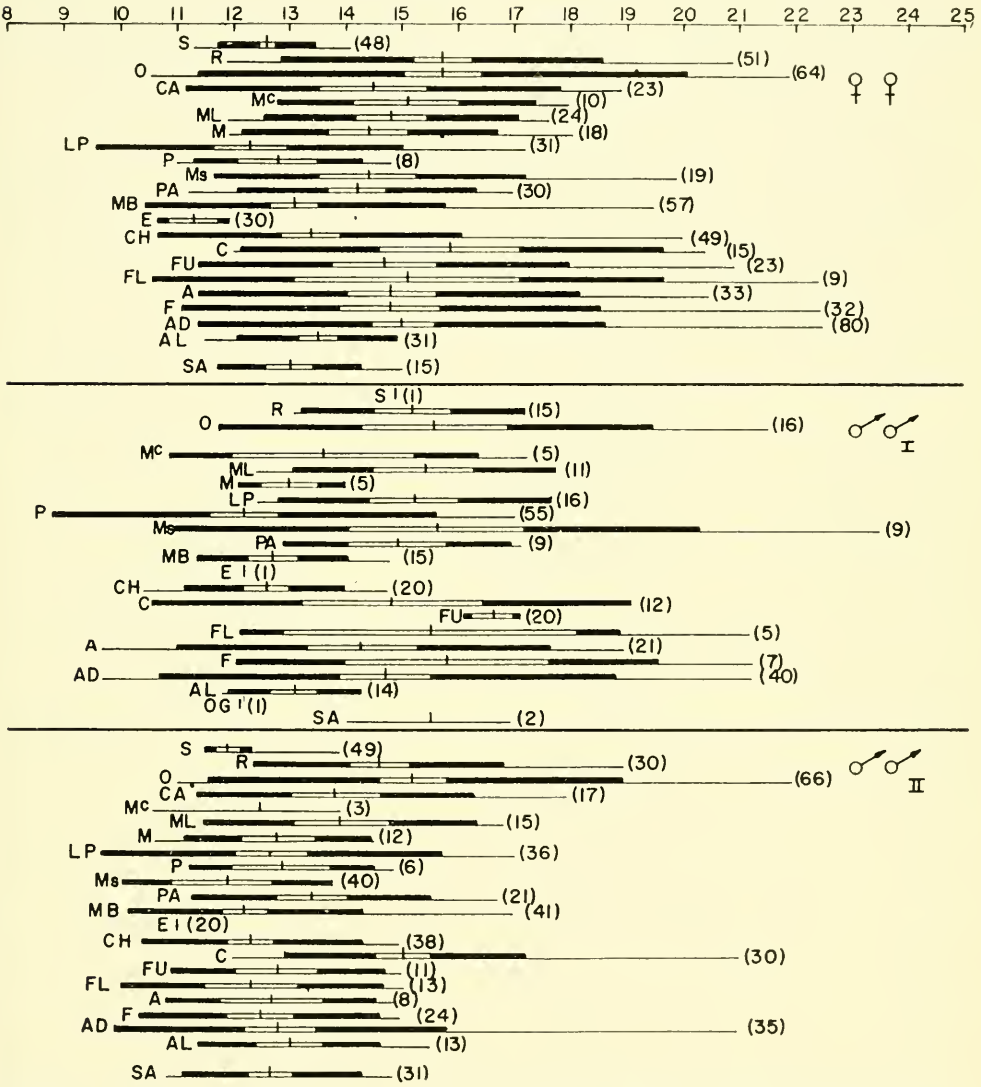



Figure 6. Length of cephalothorax. Numbers in parentheses at right of each bar represent the number of specimens used. Key to symbols at left of bar: S = Sabine River; R = Red River; O = Ouachita River; CA = Calcasieu River; MC = central Mississippi River; ML = lower Mississippi River; M = Mississippi River; LP = Lake Pontchartrain watershed; P = Pearl River; MS = Mississippi Sound drainage; PA = Pascagoula River; MB = Mobile Bay drainage; E = Escambia River; CH = Choctawhatchee River; C = Chattahoochee River; FU = upper Flint River; FL = lower Flint River; F = Flint River; A = Apalachicola River; AD = Apalachicola River drainage; AL = Altamaha River; OG = Ogeechee River; SA = Savannah River; B = Broad River.

with palm inflated and somewhat depressed, surface of palm covered with small tubercles, dactyl subequal in length to inner margin of palm. First pleopod of male with mesial process less than 50 per cent length of central projection, central projection flattened and somewhat sickle-shaped. Annulus ventralis as figured by Penn (1950: 167).

Both the paucity of specimens and known localities of *F. beyeri* make impractical a study of its geographic variation.

## Geographic Variation in *F. clypeata*

*Length of cephalothorax.*—The length of the cephalothorax was taken as the standard of size of the crawfish. It is expressed as an absolute value in Figure 6.

The picture presented was one of a highly variable character with no apparent clines.

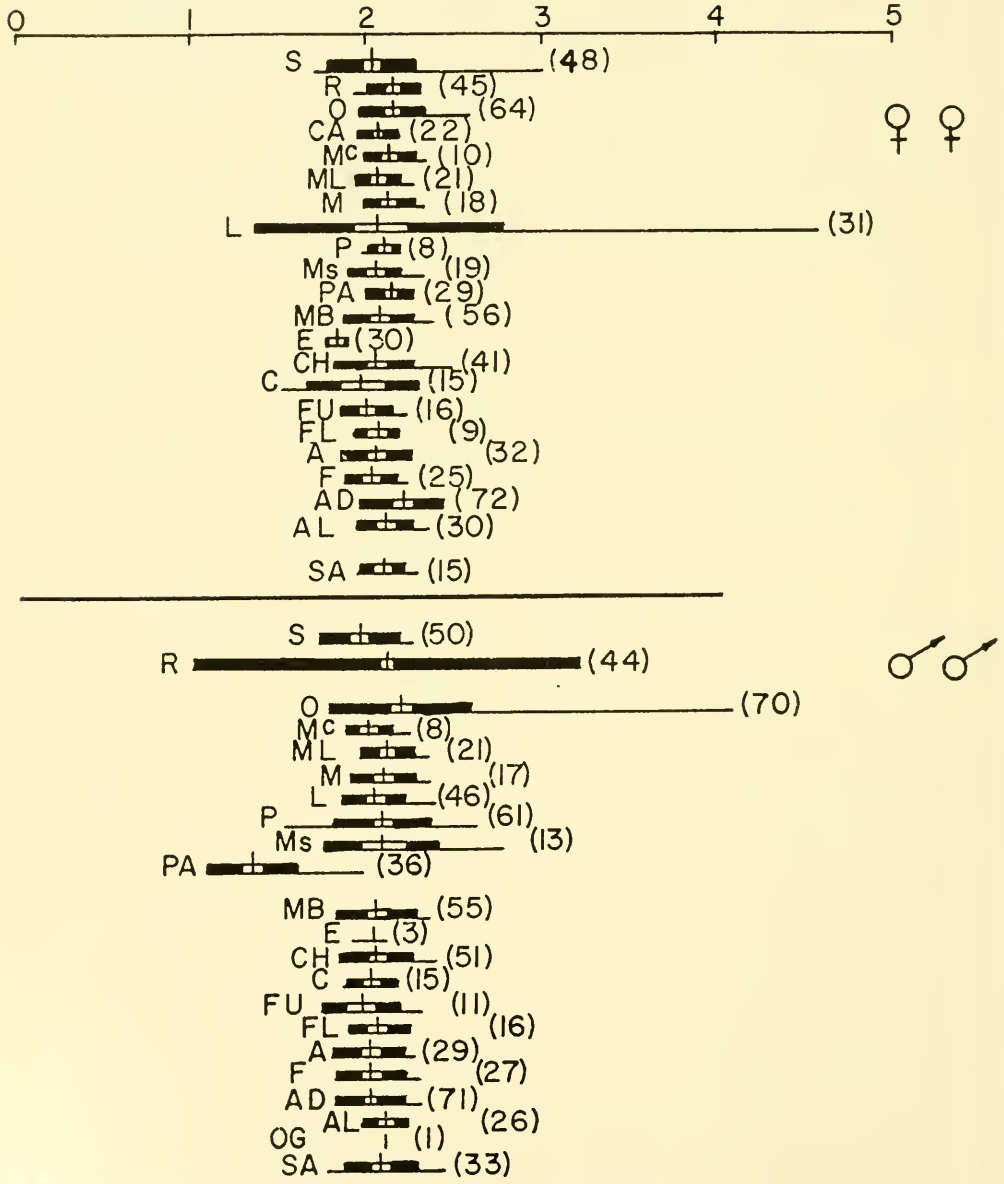



Figure 7. Width of cephalothorax. Symbols same as fig. 6.

There was a faint suggestion that northern areas may be populated by slightly larger individuals. There was no sexual dimorphism.

*Width of cephalothorax.*—The cephalothorax width was expressed as a ratio of the length to width of the cephalothorax (fig. 7). Larger values indicate narrower cephalothoraces.

No clinal variation or sexual dimorphism was evident in this character.

*Distance between postorbital spines.*—Because of the difficulty in obtaining accurate measurements of cephalothorax width in preserved specimens, the ratio of length of cephalothorax to distance between postorbital spines was used as a further check on cephalothorax width (fig. 8). Larger values indicate spines which are closer together.

As was the case in width of the cephalothorax, there was no indication of clinal variation or sexual dimorphism in the distance between the postorbital spines.

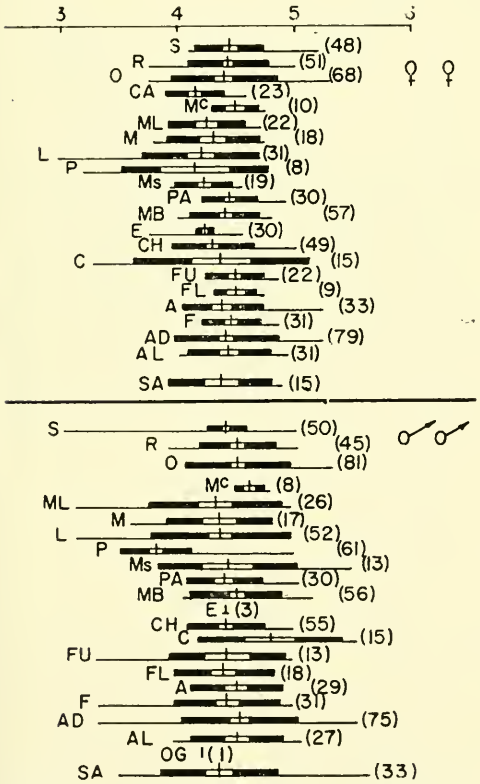



Figure 8. Distance between postorbital spines. Symbols same as fig. 6.

*Length of rostrum.*—The length of the rostrum was expressed as the ratio of the length of the cephalothorax to the length of the rostrum (fig. 9). Larger values indicate shorter rostra.

This character was quite variable, but there was no indication of clinal variation or sexual dimorphism.

*Width of rostrum.*—Rostrum width was expressed as the ratio of length of rostrum to width of rostrum (fig. 10). Larger values indicate narrower rostra.

There appeared to be a slight tendency to wider rostra from west to east. There was an unexplainable narrow rostrum in specimens from the Altamaha River Drainage which I cannot attribute to sampling error. No north-south clines were present, nor was there marked sexual dimorphism.

*Length of antennal scale.*—The ratio of length of cephalothorax to length of antennal scale was used as the value of antennal scale length (fig. 11). Longer antennal scales yield lower values.

The length of antennal scale is another highly variable character, but there was no evidence that an east-west clinal variation occurs. However, specimens from the central Mississippi River area appeared to have shorter antennal scales than did specimens from the lower Mississippi River area. This condition did not seem to be duplicated in the Flint-Apalachicola System, the other area where it is practicable to study north-south variation. In view of this lack of agreement between the two study areas, I am reluctant to interpret the situation found in the Mississippi River Drainage as clinal variation. There was no evidence of sexual dimorphism.

*Width of antennal scale.*—The width of the antennal scale was examined as the ratio of the length of antennal scale to the width of antennal scale at its widest part (fig. 12). Wider antennal scales would yield smaller values.

No evidence of clinal variation or sexual dimorphism was presented by this character.

*Length of areola.*—The length of the areola was expressed as the ratio of length of cephalothorax to length of areola (fig. 13). Larger values indicate shorter areolae. Frequently the length of areola is expressed in the literature as the percentage of the length of the cephalothorax. Such a value may be determined by calculating the reciprocal of the values here reported.

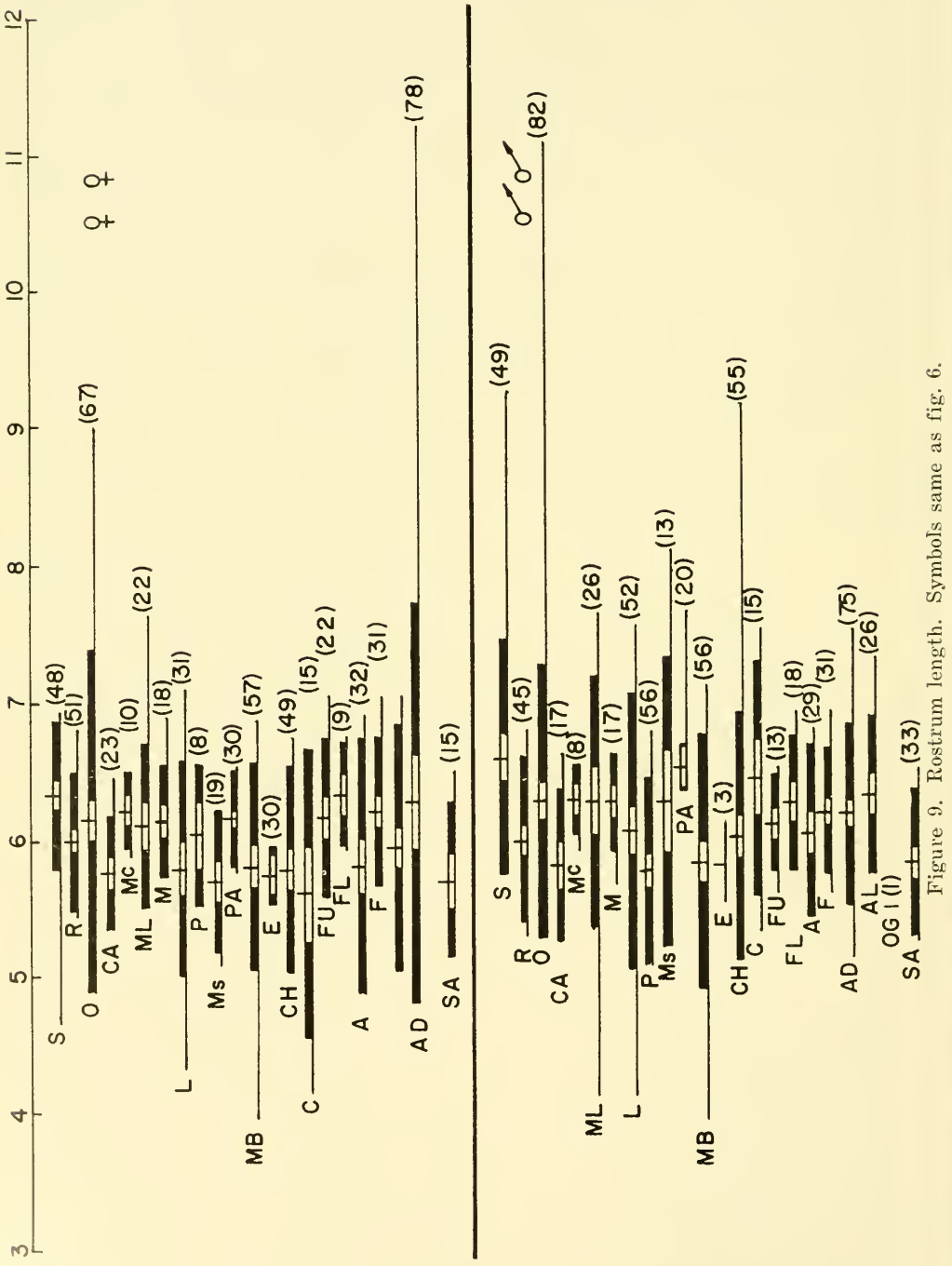



Figure 9. Rostrum length. Symbols same as fig. 6.

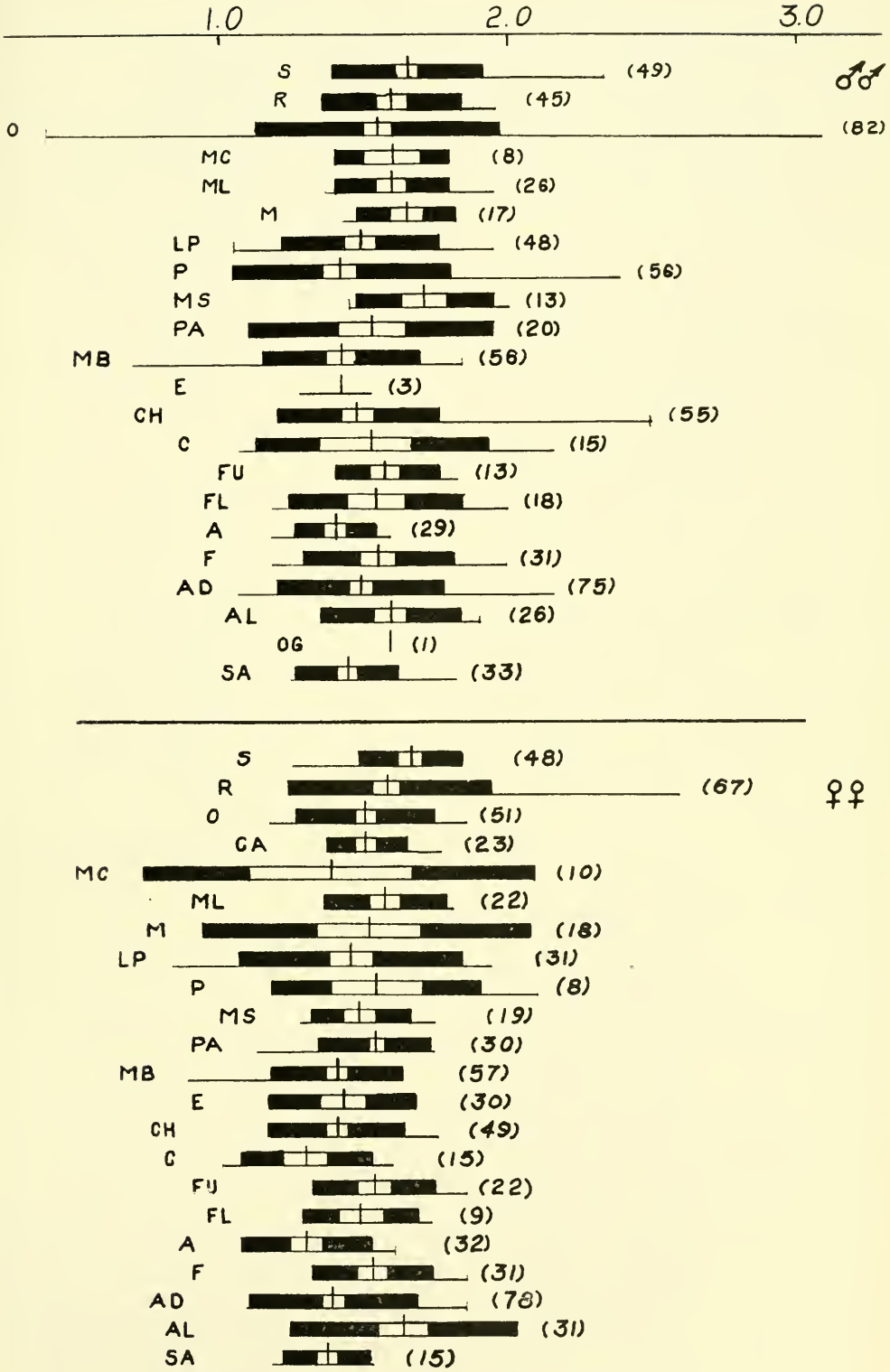



Figure 10. Rostrum width. Symbols same as fig. 6.

No clinal variation was evident, nor was there any evidence of sexual dimorphism.

*Width of areola.*—Areola width was expressed as the ratio of length of areola to width of areola (fig. 14). Wider areolae yield smaller values.

The areolae became wider in a clinal manner as one progressed eastward. This cline was not smooth, nor was it pronounced. A north-south cline seemed to be present in this character, with northern populations having wider areolae. There was no evidence of sexual dimorphism.

*Length of chela.*—The length of chela was measured as the length of the outer margin of the palm, and the character was evaluated as the ratio of length of cephalothorax to this measurement (fig. 15). The values become smaller as the chela becomes longer.

There was no evidence of clinal variation

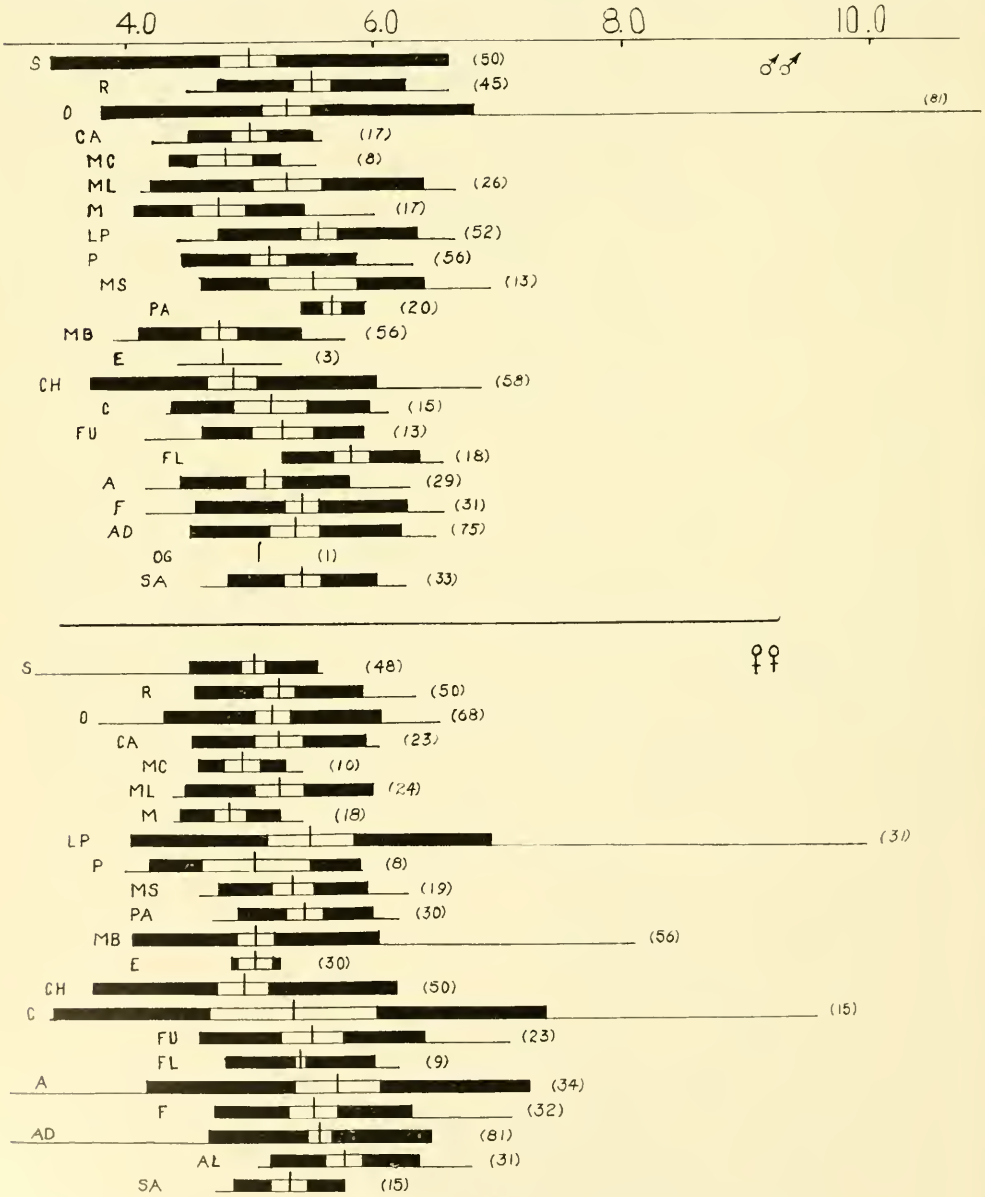



Figure 11. Antennal scale length. Symbols same as fig. 6.

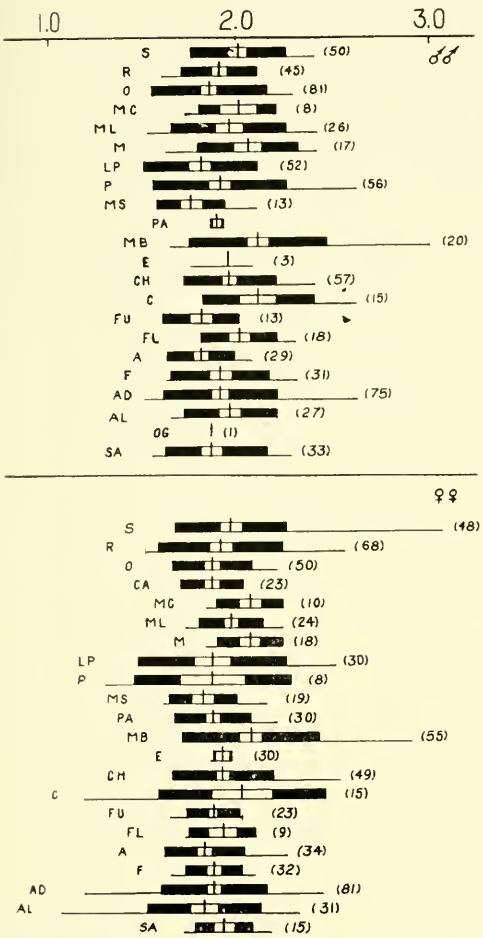



Figure 12. Antennal scale width. Symbols same as fig. 6.

in this character, but it did present a graphic picture of sex-linked variation. As can be seen from the graphs, females were easily separated from form I males, with form II males occupying an intermediate range. Form I males had distinctly longer chela.

*Width of palm.*—The width of the palm was examined as the ratio of the length of chela as recorded to width of palm at its widest part (fig. 16). A wider palm would yield a smaller value.

As in length of chela, there was no evidence of clinal variation, and the same picture of sex-linked variation was seen. The females had proportionately wider palms than did form I males, with form II males occupying an intermediate position.

*Length of dactyl.*—The length of dactyl was examined as the ratio of the length of outer margin of palm to length of dactyl (fig. 17). Longer dactyls yield smaller values.

The length of dactyl appeared to be a highly variable character with no evidence of clinal variation or sexual dimorphism.

*Length of pleopod.*—The ratio of length of cephalothorax to length of pleopod was used to examine the length of pleopod (fig. 18). A larger value is indicative of a shorter pleopod.

There was no evidence of clinal variation or dimorphism in length of pleopod.

*Length of central projection.*—The length of the central projection was examined as the ratio of length of pleopod to length of central projection (fig. 19). A longer central projection yields a smaller value.

There was no evidence of clinal variation in length of central projection, but there was some indication that form I males (as measured) have shorter central projections.

*Length of mesial process.*—The ratio of length of pleopod to length of mesial process was used as the method of evaluating the latter character (fig. 20). Larger values result from shorter mesial processes.

There was indication that eastern specimens tended to have shorter mesial processes than did western specimens with the variation showing a weakly developed cline. Form I males tended to have shorter mesial processes than did form II males.

*Ratio of length of central projection to length of mesial process.*—This important taxonomic character of the genus *Faxonella* was examined to verify its stability across the geographic range of *clypeata* (fig. 21). A larger value is indicative of a relatively shorter mesial process.

Considerable variability was found in this character, but there was no evidence of clinal variation. The variability was expressed in such a way that *clypeata* was easily separable from *beyeri* such that at least 75 per cent of the specimens of *clypeata* may be distinguished with certainty using this character alone. Further, an even higher percentage of individuals belonging to *Faxonella* may be distinguished from *Orconectes* using this character. Form II males have slightly lower ratios than do form I males.

## Life History

Smith (1953) made a thorough study of the life history of *clypeata*. Basing her study on populations of the west bank of the

southern Pearl River drainage, she determined that seasonal breeding of this crawfish occurs from May until September with erratic post-seasonal spawning from November until December. The height of seasonal spawning is in September. Because of the burrowing habit of ovigerous females, freewater collections of *F. clypeata* showed a marked decrease in the relative numbers of females present during the spawning season. At other times the sex ratio of females:males was 1.07. During the seasonal spawning period the percentage of form I males increased. These phenomena were utilized to

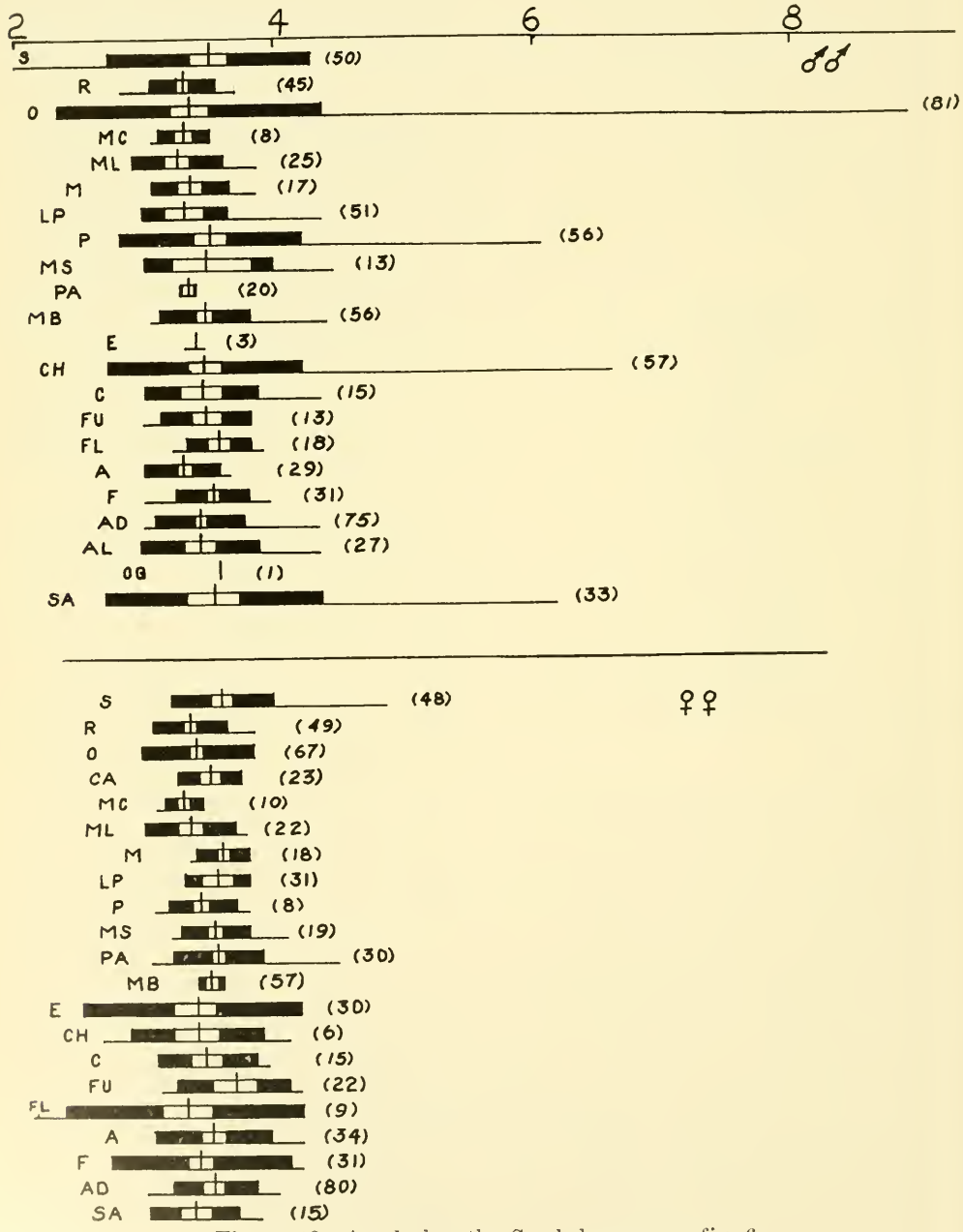



Figure 13. Areola length. Symbols same as fig. 6.

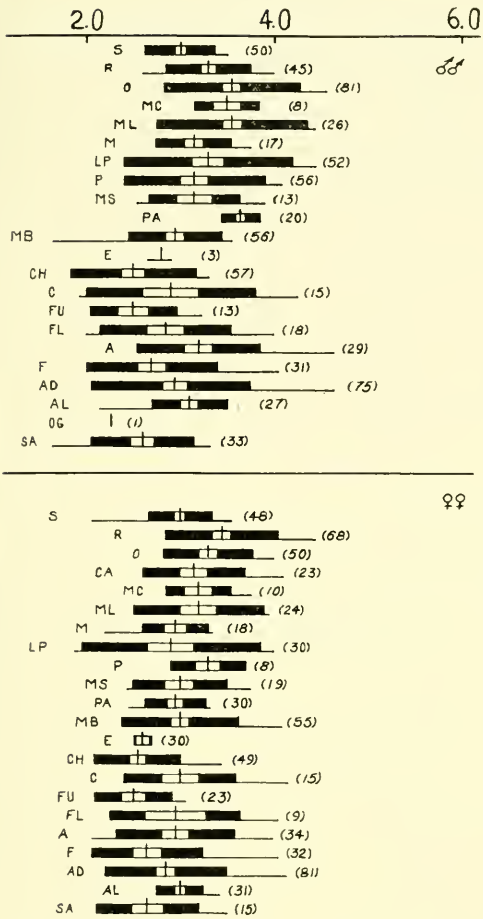



Figure 14. Areola width. Symbols same as fig. 6.

examine the comparative life histories of the crawfish across its geographic range. Total counts of each sex category are presented with corresponding percentages in Table 2. Data were grouped by state and month of collection. Further these data are expressed graphically in Figure 22. Using Louisiana (where Smith, 1953, worked) as a standard, states were arbitrarily separated into an eastern and western range. The Alabama-Mississippi boundary roughly divides the range in half and was used as a crude dividing line between the two ranges. The data available gave no evidence to support an hypothesis that there is any significant deviation from the life history reported by Smith (*op. cit.*) in different geographical locations.

TABLE 2.
*Life History of Faxonella clypeata.**

| State | Month | ♂♂II | ♂♂I | %♂♂I | ♀♀ | %♀♀ |
|---|---|---|---|---|---|---|
| La. | Jan. | 491 | 51 | 4.3 | 643 | 54.3 |
| | Feb. | 405 | 73 | 7.5 | 489 | 50.6 |
| | Mar. | 99 | 22 | 8.2 | 145 | 54.5 |
| | Apr. | 358 | 68 | 8.0 | 424 | 49.9 |
| | May | 169 | 33 | 8.3 | 196 | 49.2 |
| | June | 310 | 42 | 6.4 | 308 | 46.7 |
| | July | 173 | 61 | 13.6 | 216 | 48.0 |
| | Aug. | 13 | 19 | 28.4 | 35 | 52.2 |
| | Sep. | 57 | 144 | 55.2 | 60 | 23.0 |
| | Oct. | 90 | 34 | 23.4 | 21 | 14.5 |
| | Dec. | 179 | 16 | 4.1 | 197 | 50.3 |
| Tex. | Aug. | 0 | 1 | — | 1 | — |
| Ark. | June | 23 | 9 | 15.5 | 26 | 44.8 |
| | July | 3 | 5 | 33.3 | 7 | 46.7 |
| Miss. | Feb. | 2 | 2 | 20.0 | 6 | 60.0 |
| | Mar. | 7 | 5 | 22.7 | 10 | 45.5 |
| | Apr. | 19 | 16 | 21.9 | 38 | 52.1 |
| | June | 26 | 20 | 22.7 | 42 | 47.7 |
| Ala. | Feb. | 8 | 1 | 6.3 | 7 | 43.8 |
| | Apr. | 2 | 0 | — | 2 | — |
| | June | 36 | 14 | 13.7 | 52 | 50.1 |
| Fla. | Mar. | 0 | 2 | — | 1 | — |
| | Apr. | 41 | 35 | 25.9 | 59 | 43.7 |
| | Sep. | 1 | 2 | — | 1 | — |
| Ga. | Feb. | 0 | 1 | — | 2 | — |
| | Mar. | 6 | 2 | 15.4 | 5 | 38.5 |
| | Apr. | 64 | 7 | 5.8 | 49 | 40.8 |
| | May | 0 | 1 | — | 0 | — |
| | June | 2 | 1 | — | 3 | — |
| | Aug. | 3 | 10 | 37.0 | 14 | 51.9 |
| | Sep. | 0 | 3 | — | 0 | — |
| | Dec. | 0 | 0 | — | 1 | — |
| S. C. | Sep. | 1 | 0 | — | 0 | — |

* Percentages calculated only for those groups containing 10 or more individuals.

## DISCUSSION

The impression of Penn (personal communication) is that *Faxonella clypeata* is limited to areas below the Fall Line in the southeastern United States. However, I was unable accurately to delimit its range with any given geographic or geologic location. Several collections occur precisely on the Fall Line, but none (with one exception) occur above the Fall Line. Creaser and Ortenburger (1933) reported that there was one form I male in the Carnegie Museum, the label of which indicated that it was taken from LaFlore County, Oklahoma. They reported that they were unable to re-collect the species. Penn collected in the area in 1956 (personal communication) and also was unable to find the species. I spent one day collecting specifically for this species in Sequoyah and LaFlore Counties in 1960 and was unable to find a specimen. During the period of my collection the area was experiencing drought conditions. Williams (1954) made no mention of the species in his investigation of the crawfishes of the

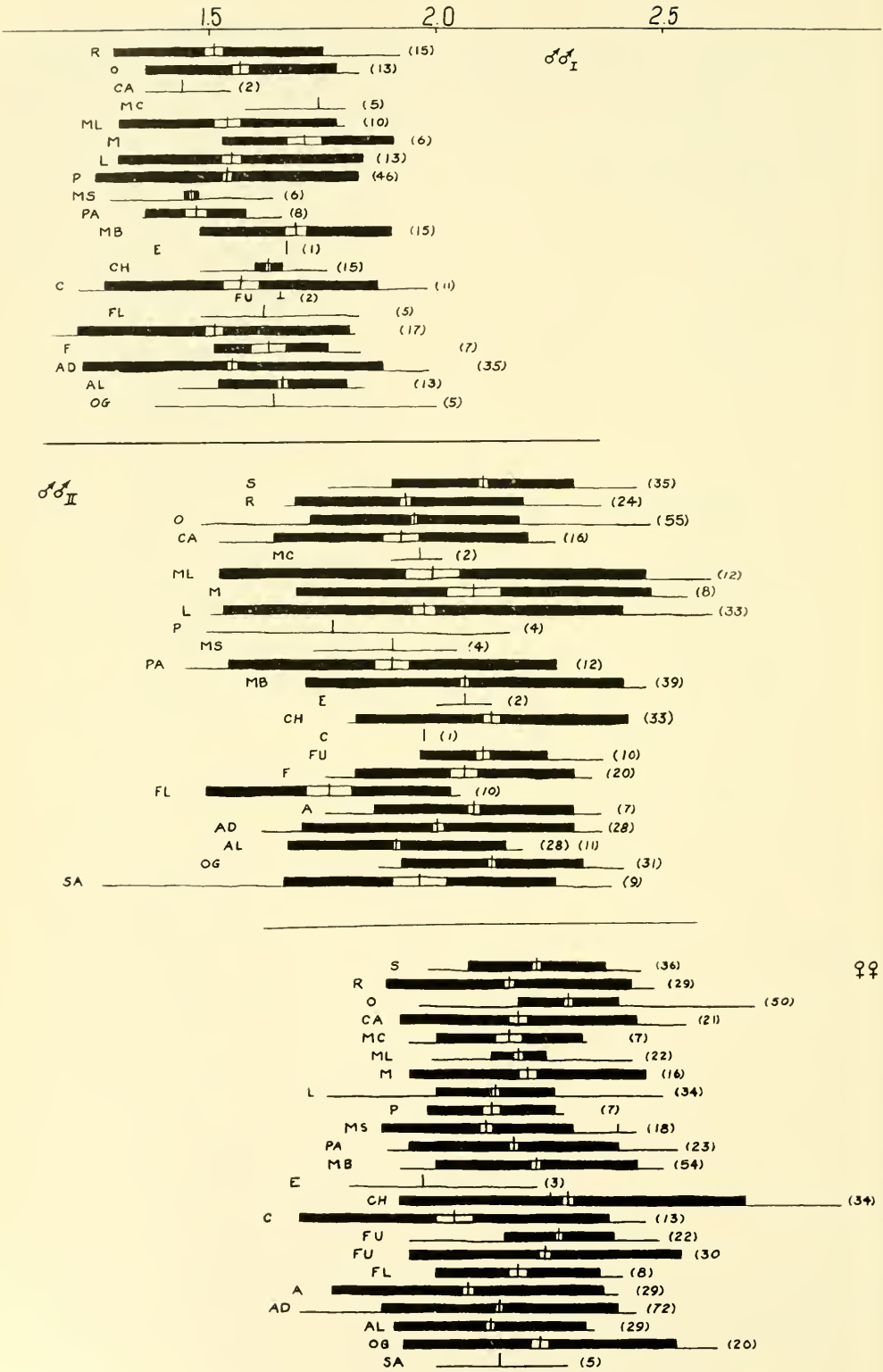



Figure 15. Chela length. Symbols same as fig. 6.

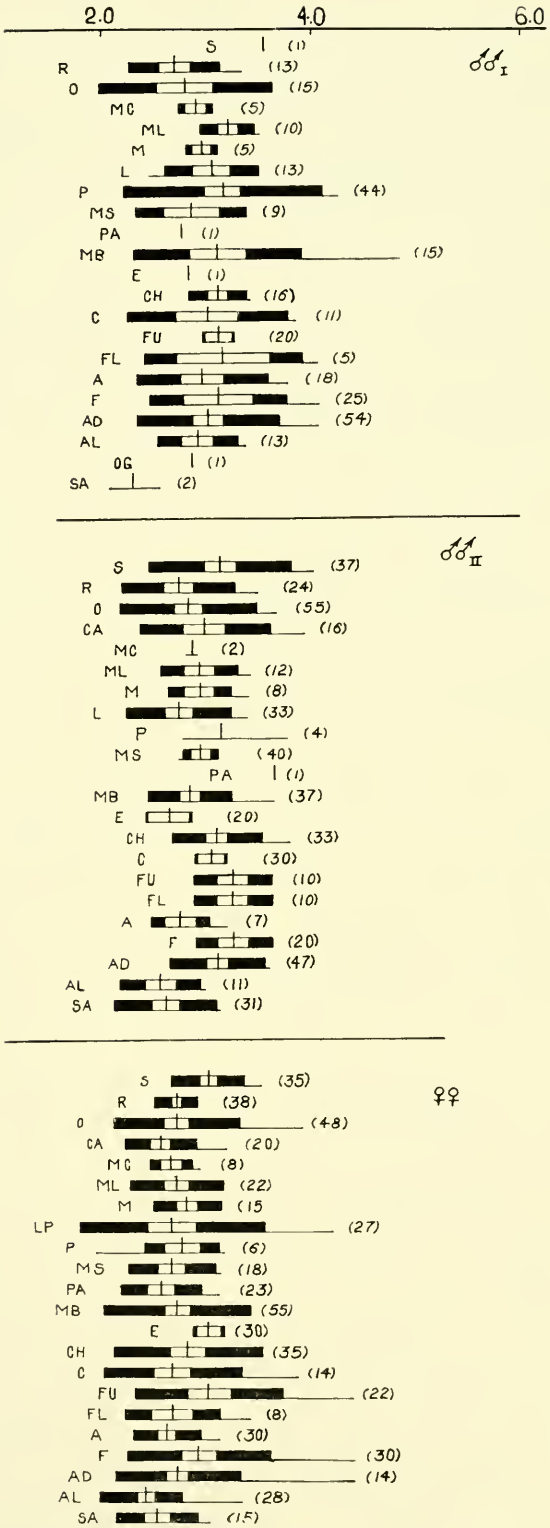



Figure 16. Palm width. Symbols same as fig. 6.


Figure 17. Dactyl length. Symbols same as fig. 6.

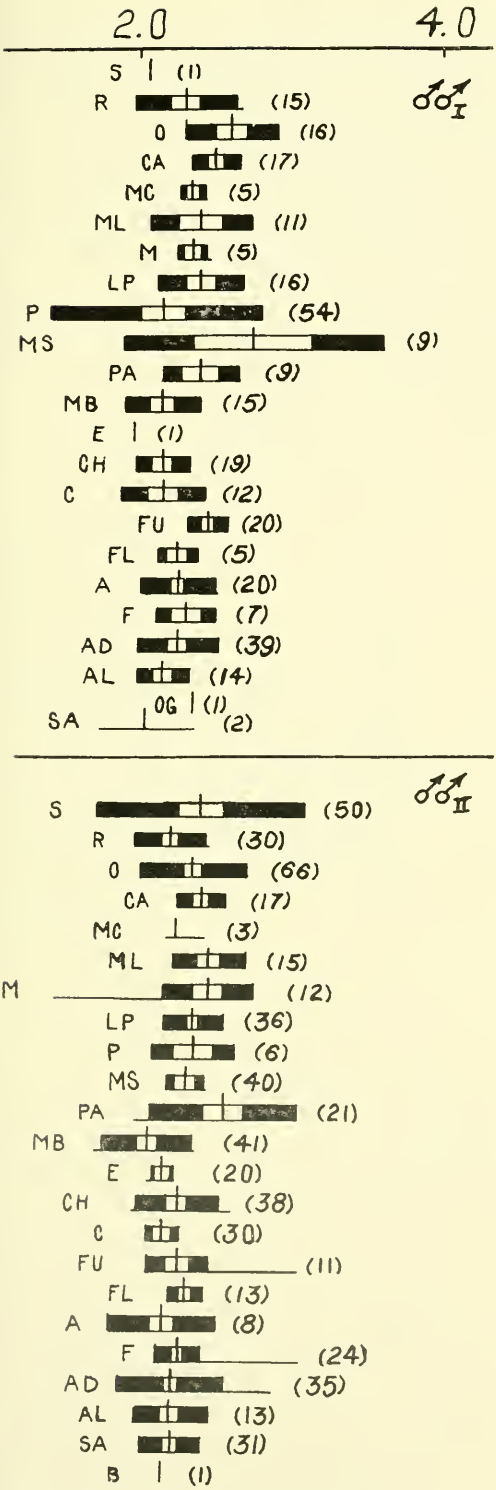



Figure 18. Pleopod length. Symbols same as fig. 6.

Ozark Plateau and Ouachita Province, so one may logically assume that he did not encounter it in his collections. However, there are two females in the United States National Museum which were collected in 1940 near Idabel, McCurtain County, Oklahoma. Another series (Unnumbered) in the Hobbs collections is from the same locality and contains form I males and females. This collection and the one reported by Creaser (*loc. cit.*) represent the westernmost limits of the species. The difficulty in obtaining specimens from this area might indicate a tenuous, and perhaps transient, occupation of the region by *F. clypeata* as is possible at the extreme of the range of any species.

The northernmost collections which I have examined are from the vicinity of Paragould, Greene County, Arkansas. This is in the Mississippi River Valley. The only known locality in Texas is in Marion County, just west of the Louisiana border. In the east the species occurs as far north as the Broad River near Charleston, South Carolina and below the Fall Line. The species occurs south to the Gulf of Mexico but is absent from peninsular Florida, central Mississippi, west-central Alabama and the coastal marshes. There is a possibility that *F. clypeata* occupies a region such that its distribution is complimentary to the Barbatus and Planirostris Groups of the genus *Procambarus*, but the study of such a relationship is beyond the scope of this paper.

Geographic variation is slight in *F. clypeata*. In general, *inter*populational variation is within the limits of *intra*populational variation. The homogeneity of each population (most populations are easily encompassed by two standard deviations) is not remarkable when one considers that the species is non-migratory (Smith, 1953). Such a behavior pattern is compatible with a homogeneous population, although quite conducive to extreme variation between populations should a predisposition to variation exist. Interpopulational variation does not occur. Only three clines were demonstrated and none was marked.

The site or point of origin is indeterminate from the material examined.

Size ranges for each sex category are presented in Table 1. The maximum sizes are recorded here, but one should keep in mind that other areas of the range produced specimens closely approximating the ones re-

corded. Only one form I male—the one reported (Table 1)—was below 10.4 mm cephalothorax length; therefore, this specimen was probably precocious. Fortunately two females with young were present in the Tulane University collections. Because of the difficulty in obtaining such specimens, the cephalothorax measurements of each are included here (12.9 mm, 13.0 mm). Other measurements were typical for the population. Both of these females were included in the statistical analyses. Both are from Pearl River, Louisiana.

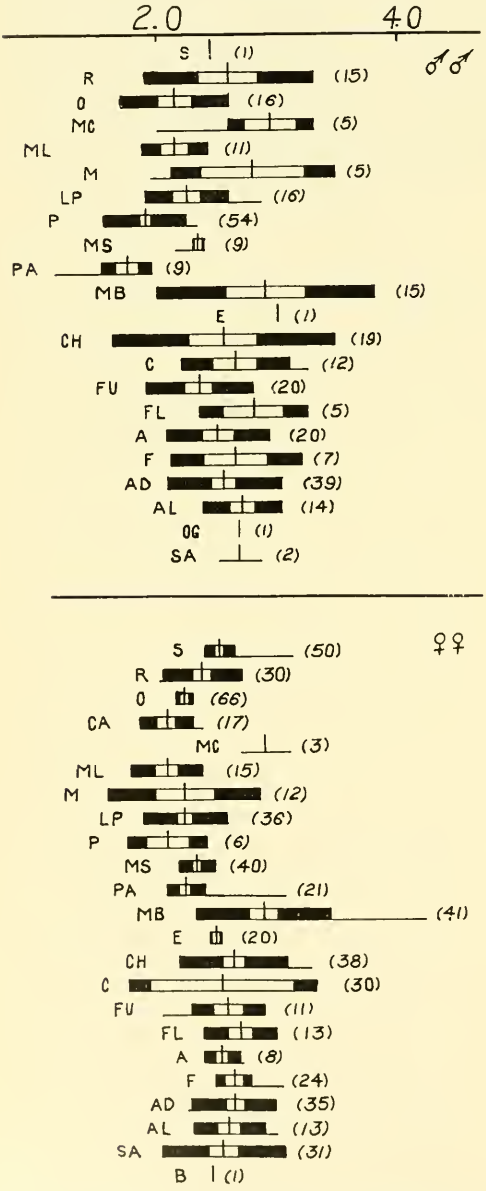



Figure 21. Ratio of length of central projection to length of mesial process. Symbols same as fig. 6.

Life history data are compatible with the overall homogeneity of the populations and further justify the conclusion that there are no significant differences between populations across the geographic range.

Although variations between populations were demonstrated, there was no evidence to support a thesis that subspecies of *F. clypeata* exist.

## Summary

1. The subgenus *Faxonella* Creaser, 1933: 21 is accorded full generic status; the genus was defined and defended.

2. The crawfish *Faxonella clypeata* (Hay) was examined taxonomically.

3. Life history data for *F. clypeata* were accumulated.

4. East-west clines were discovered in three characters: width of rostrum, width of areola, and length of mesial process. None was pronounced.

5. Sexual dimorphism was found in length of chela and width of palm.

6. Differences existed between first and second form males in length of central projection, length of mesial process, and ratio of length of central projection to length of mesial process.

7. Range limits were discussed.

8. No subspecies of *F. clypeata* exist.

## Acknowledgements

The writer is deeply indebted to Dr. George H. Penn under whose direction the majority of this study was made. Not only did Dr. Penn offer many technical assistances, but he also was a constant source of inspiration and encouragement. Dr. Horton H. Hobbs, Jr. generously lent his entire collection of *Faxonella clypeata*, assisted in securing a Society of Sigma Xi Grant-in-Aid of Research, and has offered numerous criticisms and observations during the preparation of the manuscript. To Mr. Joe B. Black and Mrs. Myrna Andersson Wilkens I offer thanks for many helpful criticisms and discussions. I am also indebted to my wife, Sarah E. Fitzpatrick, for assistances far too numerous to enumerate.

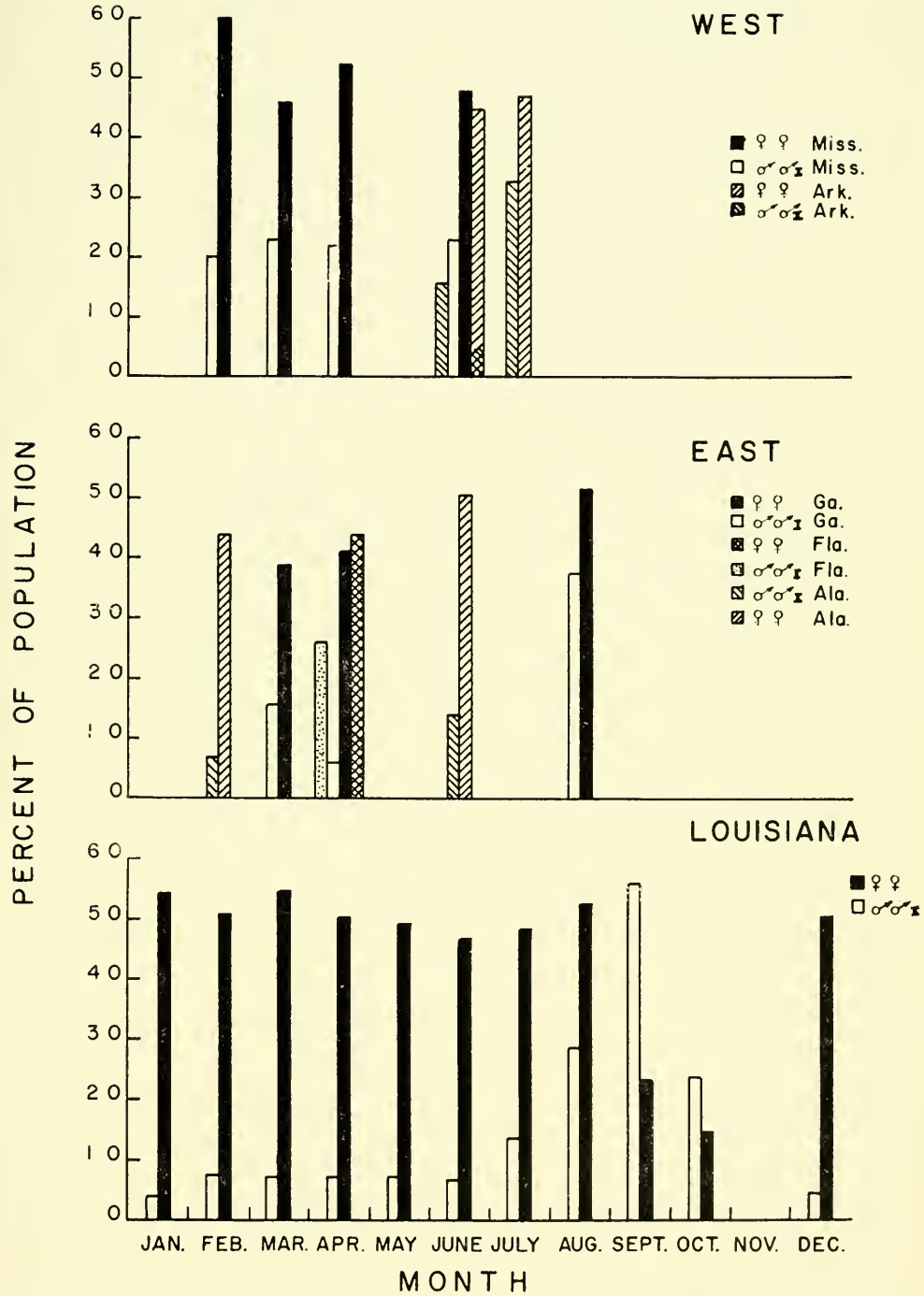



Figure 22. Geographic variation in the life history of *Faxonella clypeata* (Hay).

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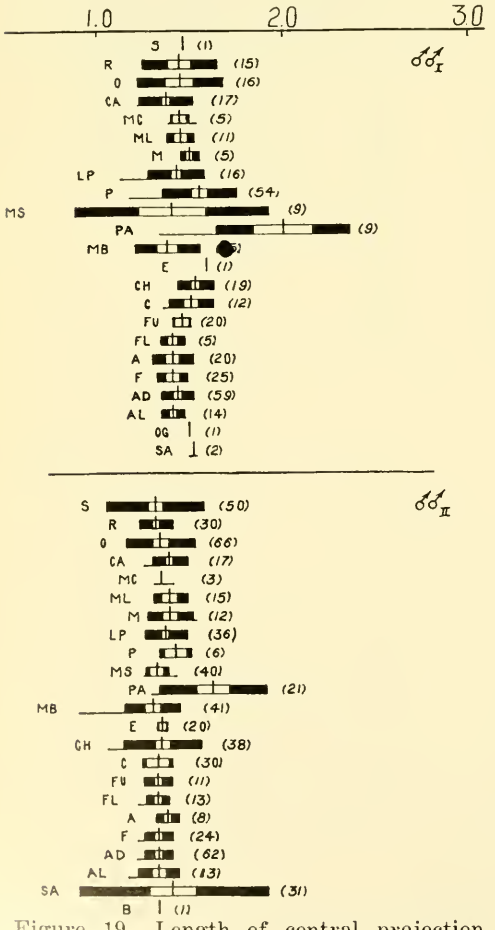


Figure 19. Length of central projection. Symbols same as fig. 6.

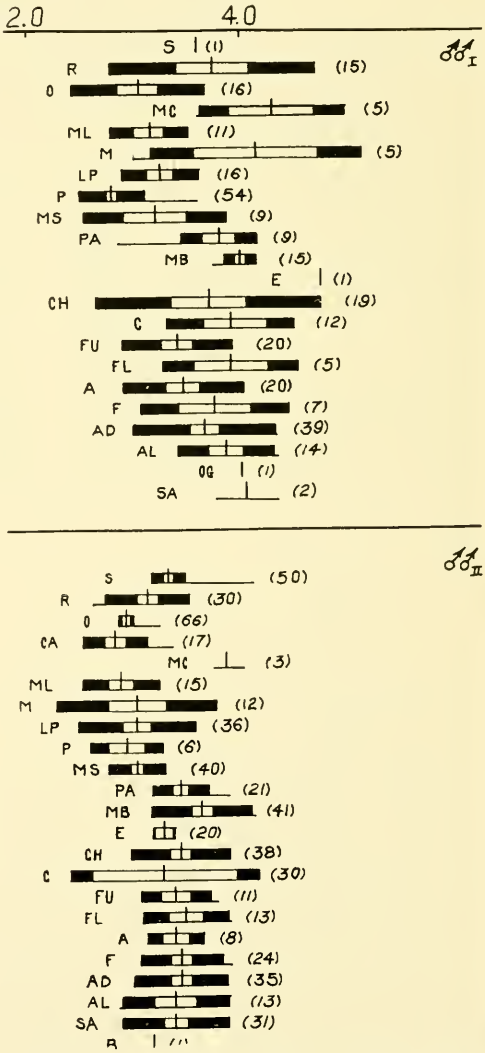


Figure 20. Length of mesial process. Symbols same as fig. 6.

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## ABSTRACT

After an investigation of the geographic variation of the crawfish *Faxonella clypeata* (Hay) and a study of its related species, the writer determined that the two species currently assigned to the subgenus *Faxonella* of the crawfish genus *Orconectes* constitute a distinct group of crawfishes worthy of generic distinction. Therefore the writer proposed that the subgenus *Faxonella* be elevated to full generic status. The new genus was defined and defended. *Faxonella clypeata* was examined taxonomically for geographic variations and three weakly developed clines were demonstrated. There were two instances of sexual dimorphism, and three instances of dimorphism between form I and form II males. The life history of the species was examined across its geographic range, and the writer concluded that there are no significant differences across the range. The range limits of the species were discussed. No subspecies of *Faxonella clypeata* exist.