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NEW ORLEANS

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TULANE STUDIES IN ZOOLOGY

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GAMBUSIA HETEROCHIR, A NEW POECILIID FISH FROM TEXAS, WITH AN ACCOUNT OF ITS HYBRIDIZATION WITH *G. AFFINIS*

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Austin, Texas

During the past decade a number of fishes have been described from Texas fresh-waters. Some of them have been known for years, but were not described until recently. Others, such as the new species of *Gambusia* described below, have not been recognized until recently. This new mosquitofish, apparently restricted to the headwaters of Clear Creek, Menard County, Texas, is separated by some 800 miles from the ranges of its nearest relatives.

Many hybrids between this species and *Gambusia affinis* (Baird and Girard) have been collected. The geographic distribution and morphologic variation of the hybrids is discussed.

Material of the new species has been collected by the author, W. Gordon Craig, Theodosius Dobzhansky, Alvin E. Ellington, Sr., James D. French, Murray K. Muston, Kirk Strawn, and John E. Tilton. I also wish to thank Charles Wilkinson and H. Leslie Jones for permission to collect on their ranches. Dr. Billie L. Turner identified the plants. Mr. George G. Henderson, Jr., made the photographs. Miss Nancy Walker and Mrs. Jane Hubby made the drawings. Counts and measurements were made as detailed in Carl L. Hubbs and Lagler (1947). Names for gonopodial structures follow those given by Carl L. Hubbs (1926). The schematic diagrams to determine degree of hybridization are modified from those proposed by Anderson (1949).

GAMBUSIA **HETEROCHIR**, sp. nov.

Fig. 1

Material.—The type material consists of the 24.5 mm holotype (University of Michigan Museum of Zoology No. 170936) and 125 other specimens of 17 to 45 mm (UMMZ No. 170937, Stanford University Nos. 46445 to 46451, United States National Museum No. 164573, Museum of Comparative Zoology, Harvard University No. 39684. Chicago Natural History Museum No. 61805, and Texas Natural History Collection Nos. 3065 and 4652), all of which were seined on two occasions from the headspring of Clear Creek, Menard County, Texas, 10.4 miles west of Menard. The first of these collections was made on February 22, 1953, and the second on February 20, 1956.

Many hybrids with *G. affinis* occur in both collections. Possibly some or all of the specimens designated as *G. heterochir* contain some genes from *G. affinis*. However, as introgression into *G. heterochir* appears to be uncommon and suspected hybrids are excluded from *G. heterochir* collections, I believe that most of the specimens considered to be *G. heterochir* are not contaminated with *G. affinis* genes.

Diagnosis.—A stocky species of *Gambusia*. The deep indentation on the upper margin of the male pectoral fin (fig. 5) distinguishes

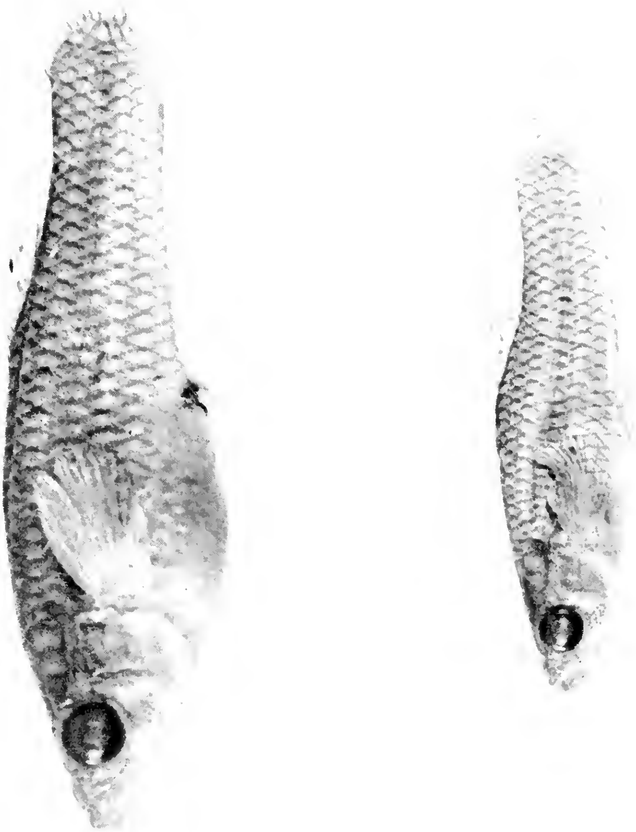

Figure 1. *Gambusia heterochir*, sp. nov. Left: 33 mm female; Right: 23 mm male; both from TNHC 4652.

G. heterochir from all known gambusiine species. It also has the largest gonopodial elbow and bluntest gonopodial tip (fig. 3) when compared with the other known gambusiines.

Description.—A minimum of ten adult males and ten adult females were used for the descriptions. Up to 86 specimens were examined for characters used in the analysis of hybridization. Fin rays: dorsal 7 or 8 (rarely 9); branched caudal 14 (rarely 13 or 15); anal 9 (rarely 10); pelvic 6 (rarely 5); pectoral 13 to 15. Scales: lateral line 30 or 31; caudal peduncle 16; predorsal rows 15 or 16.

The bluntly rounded head enters (step-measurement) standard length 3.7-3.8 times in adult males and 3.3-3.7 times in adult females. The depth at the back of the eye slightly exceeds the width. The gape is equal to or slightly exceeds the snout length. The head is scaled to the anterior margin of the eye. The anterior nostrils open at the posterior lip of the premaxillary groove; the posterior ones open dorsal and anterior to the eye. The lateral line pits on the head are more or less connected: a single large pit mesial and anterior to the posterior nostril; two connected mesial and posterior to the posterior nostril; a crescent shaped series posterior to the upper margin of the eye; a connected row on the posterior margin of the preopercle; an interrupted series of pits on the ventral margin of the preopercle and the mandible; and a connected series of small pits in front of the eye.

The body is deep and rounded. The highest point on the dorsal profile is at or immediately anterior to the anterior dorsal base. The distance between the dorsal insertion and the posterior end of the hypural plate is contained 1.2 to 1.3 and 1.4 to 1.7 times in the predorsal length of males and females respectively.

The dorsal fin is rounded, its depressed length is contained 3.9 to 4.3 and 4.3 to 4.9 times in the standard length of males and females respectively. The caudal is rounded. The anal of females is rounded, that of males modified into a gonopodium. The pelvics are small and the inner ray is bound to the abdomen by a membrane. The pectoral is rounded, the sixth and seventh rays the longest.

The gonopodium of males is distinctive (fig. 3). The anterior branch of ray four reaches almost to the tip of the gonopodium. The two- to four-segmented elbow is longer than the longest modified spine of ray three and often overlaps the adjoining unmodified segments of ray three. The distal serra on the posterior branch of ray four is distal to the elbow. The serrae are numerous and long. The terminal hook is pointed at the distal tip. The terminal hook on the anterior branch of ray five is rounded. The distal segments of that ray meet the main axis of the gonopodium at an angle of more than 45°. Similar to other members of the *G. nicaraguensis* species group, the modified spines on ray three are sharply distinguished from the more proximal undifferentiated segments and the length of the longest spine is much less than the combined basal lengths. One or two of the proximal modified spines have recurved hooks.

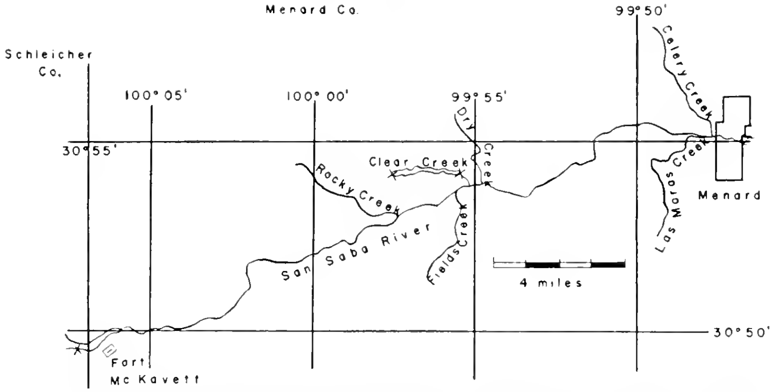

Figure 2. Map of the Clear Creek region. Collection localities designated by "X". *G. heterochir* known only from headwaters of Clear Creek.

Both pectorals of the males are modified. Rays two through five have a flattened region along the ray. The inner half of the ray does not enter into the flattened blade of rays three through five. The upper margin has a deep incision near its tip. Apparently this incision is to steady the gonopodium during intromission.

The color pattern is distinctive. The midorsal coloration is not darker than that of the adjacent area; *i.e.*, there is no middorsal stripe. A fine axial streak extends from the midline above the anus to the caudal base; however, there is no diffuse lateral band surrounding the axial streak. The subterminal dusky markings on the body scales are absent only on the abdominal scales. A large number of the subterminal dusky marks are darker and form black crescents, which are found on all but the predorsal scales. The fine postanal streak is darker than the adjacent subterminal dusky scale marks. In adult females the large black crescents, which extend on each side from in front of the anus to behind the anal origin, do not meet across the midventral line. These anal marks are absent in young and in adult males. The head ground color is similar to that of the body. A black mark at the upper corner of the opercle covers more than one scale. The weak suborbital bar does not reach to the corner of the preopercle. The lips are no darker than the adjoining parts of the head. The dark lateral line pits on the head have light edges. The dorsal has a median row of dark spots and the other fins are dusky to colorless.

Relationships.—In his review of the genus *Gambusia*, Carl L. Hubbs (1926) divided the genus into four subgenera (*Heterophallina* Hubbs, *Gambusia* Poey, *Arthrophallus* Hubbs, and *Schizophallus* Hubbs). Krumholtz (1948) stated that Hubbs and Walker (unpublished ms) consider that two nominal species (*affinis* and *holbrooki*), comprising the nominal subgenera *Arthrophallus* and *Schizophallus* respectively, regularly intergrade in nature and therefore are to be assigned to the same species. Carl L. Hubbs (1929) divided the subgenus *Gambusia* into two species groups, *nobilis* and *nicaraguensis*, and reviewed the former. In his 1926 paper he separated the species comprising the two species groups by key item "h". Members of the *G. nicaraguensis* group differ from those in the *G. nobilis* group in that the former have (1) shorter distal spines on ray three of the gonopodium, (2) the dusky lateral band indistinct or developed only on the trunk, and (3) no dark markings on the anal. *Gambusia heterochir* has the shorter distal spines on the third gonopodial ray and the dusky lateral band indistinct. In both characters it resembles the *G. nicaraguensis* species group. The females have the dark anal markings characteristic of the *G. nobilis* species group. I consider

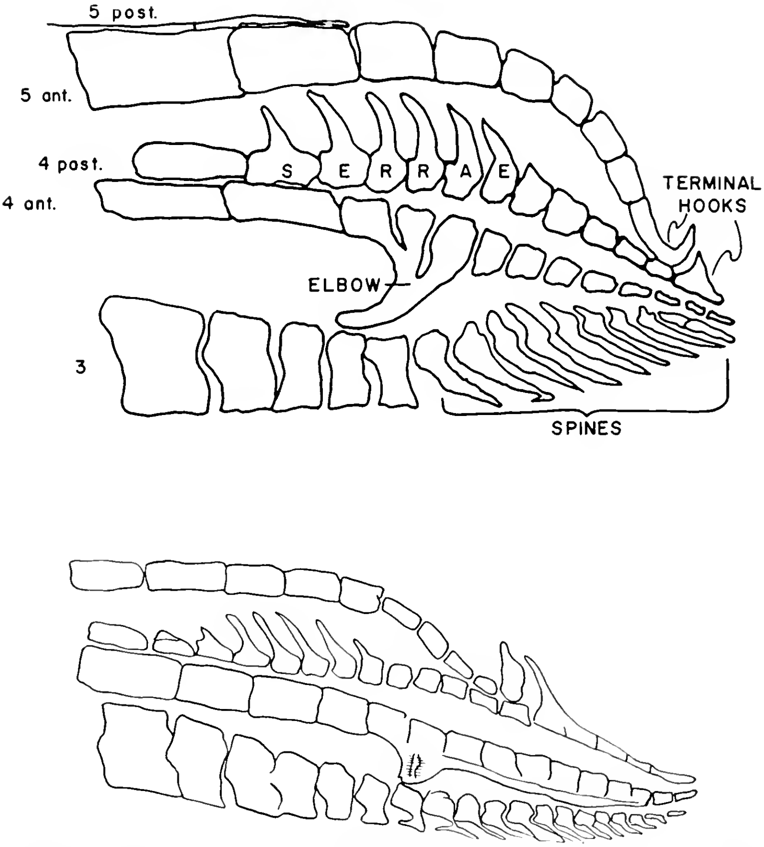

Figure 3. Camera lucida drawings of gonopodial tips: **A** (upper), *G. heterochir* from type locality; **B** (lower), *G. affinis* from Middle Valley Prong of San Saba River.

that *G. heterochir* evolved from the ancestral stock of *G. nicaraguensis* shortly after that stock separated from the ancestral stock of *G. nobilis.*

Range.—Gambusia heterochir is known only from the headsprings of Clear Creek, Menard County, Texas, 10.4 miles west of Menard (fig. 2) and from one locality near the shore 350 yards east of the headsprings. Many other collections have been made in headwaters of the San Saba River in Menard and Schleicher counties, covering all known habitats and concentrating on habitats similar to that of the headsprings of Clear Creek. One of the collections is from the lower part of Clear Creek. None of these collections contains *Gambusia heterochir.* I believe that *G. heterochir* once had a wide distribution in Central Texas. Its range probably has been restricted because this species is unable to compete with *G. affinis.* Clark Hubbs and Springer (ms) suggest that members of the *G. nobilis* species group have restricted ranges for the same reason.

Ecology.—The headsprings of Clear Creek are now impounded. The upper and lower of three dams enclose a small body of water, the middle impounds the bulk of the water. Except for the upper reservoir and the adjacent part of the middle reservoir, the banks are covered with cattails. The collections were made in the cattail-free areas. Submerged and emergent vegetation was prolific in all impounded parts of Clear Creek. A dense growth of *Ceratophyllum* sp. occurred in the headspring. A species of *Ludwigia* was found with the *Ceratophyllum.* Another *Ceratophyllum* bed occurred where the *G. heterochir* was sampled 350 yards east of the headspring. A dense stand of *Jussiaea* sp., *Distichlis* sp., *Typha latifolia,* and *Hydrocotyle umbellata ?* also were found there. Dense growths of *Myriophyllum* sp., *Potomogeton* spp., *Chara* sp., and *Conium maculatum* occurred elsewhere, but no *G. heterochir* specimens were collected. I suspect that *G. heterochir* populations were correlated with factors that were associated with *Ceratophyllum* beds. Daytime surface water temperatures varied between 18.3 and 20.6° C in February and between 27.0 and 31.0° C in July. Although temperatures near 21° C occurred at the bottom (6 inches below the surface) at both seasons, this probably had little effect on the fish as they remained on the surface unless disturbed. Night temperatures were probably lower than those taken during daylight hours.

The name *heterochir* is derived from the Greek *heteros* (= different) and *cheir* (= hand) for the distinctive shape of the pectoral fin.

HYBRIDIZATION WITH *Gambusia affinis*

In his account of natural hybridization in poeciliid fishes, Carl L. Hubbs (1955), listed only two hybrid combinations in the genus *Gambusia:* between two members of the *G. nicaraguensis* species group and between *G. nobilis* and *G. affinis.* The hybrids discussed below constitute a third example, and are the first documented record of natural hybridization amongst gambusiines.

The collections contain specimens of *G. heterochir, G. affinis,* and hybrids. The hybrids do not constitute a discrete intermediate group as described by Carl L. Hubbs, Hubbs, and Johnson (1943) for natural F_1 hybrids, but definitely grade into *G. affinis* and may grade into *G. heterochir*. Thus it appears likely that F_2 and or back crosses occur in the Clear Creek population and gene flow occurs between the two species. However, Clark Hubbs and Strawn (in press) and Clark Hubbs (1956) report F_1 hybrids that are not always intermediate between their parental types. As the two parental species are included in different subgenera, the hybrids are easily recognized and a study of the hybrid swarm may be of value in the study of the selective advantages of hybrids.

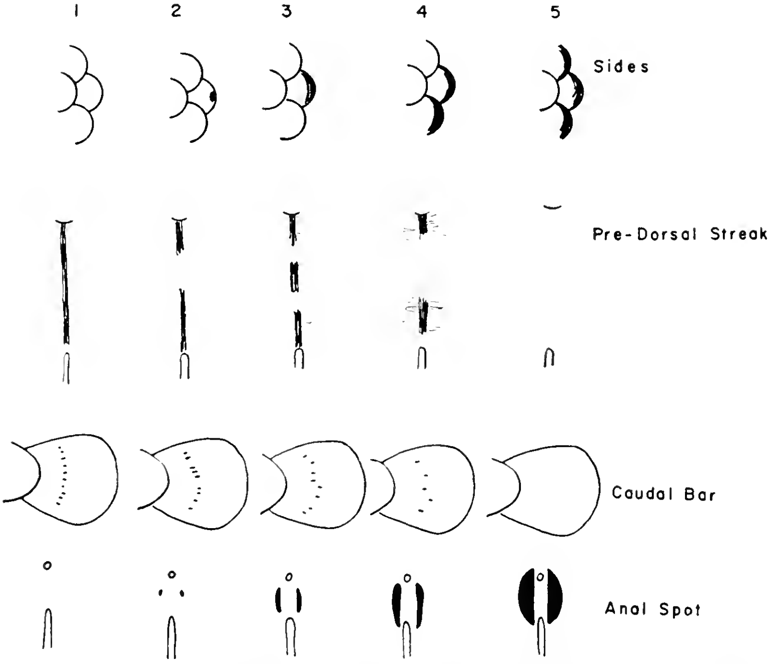

Figure 4. Color codings for individuals in hybrid swarm. Lower numbers for *G. affinis*, higher for *G. heterochir*, intermediate for hybrids.

All of the *Gambusia* specimens in four collections have been analyzed. The collections are: two from the headwaters of Clear Creek; one from the lower part of Clear Creek, 2.4 miles downstream from the hybrid swarm; and one from Middle Valley Prong of the San Saba River, 1 mile west of Ft. McKavett, 17 stream miles from the hybrid swarm. The two collections from the hybrid swarm were selected for obvious reasons. The Middle Valley Prong collection is typical of

G. affinis populations in the area, contains many specimens, and is from a locality ecologically similar to the headwaters of Clear Creek. This collection should show the morphology of uncontaminated *G. affinis.* The collection from the lower reaches of Clear Creek was analyzed to determine if the introgressed population extends downstream.

The data from these four collections have been graphed (figs. 6, 7) following the techniques proposed by Anderson (1949). As poe-

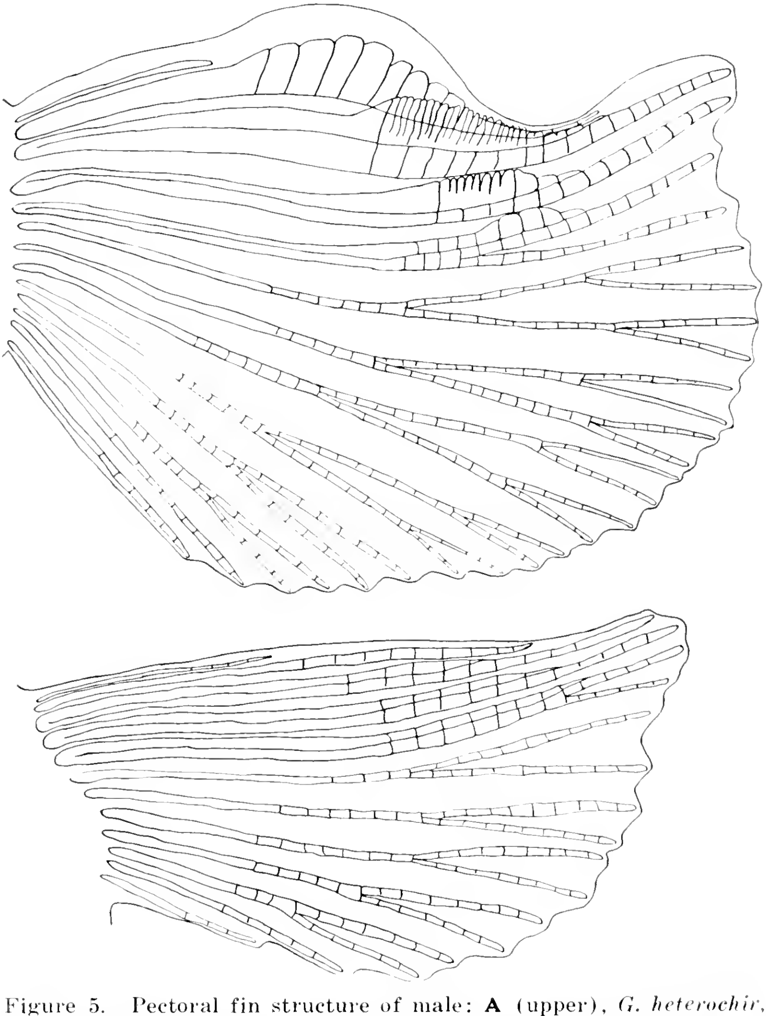

Figure 5. Pectoral fin structure of male: **A** (upper), *G. heterochir,* from a 20 mm specimen from type locality; **B** (lower), *G. affinis,* from a 22 mm specimen from Middle Valley Prong of San Saba River.

ciliids exhibit marked secondary sexual dimorphism the sexes are plotted separately. Only mature males are used since immature males approach females in many characteristics. Only females over 25 mm (standard length) are graphed because some color characteristics are not established until that size. For both sexes the ordinate is the head width added to the head depth (both at the back of the eye) divided by the standard length. The figures do not change appreci-

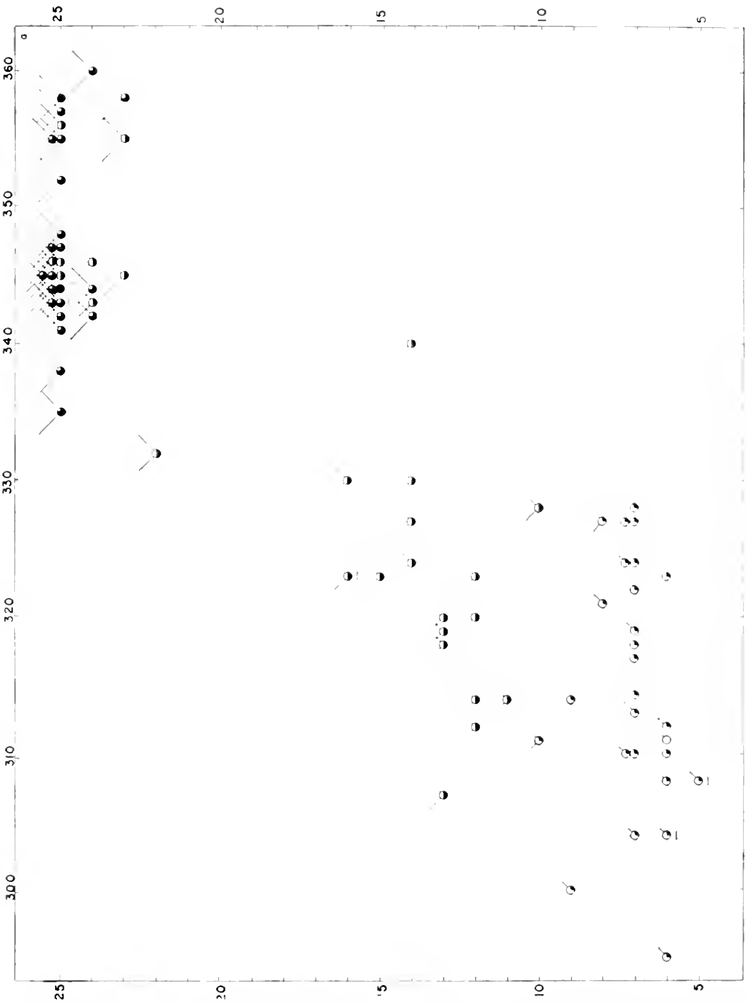

Figure 6a. Pictorialized scatter diagram of *Gambusia* males (see text for explanation of coding). Samples from headwaters of Clear Creek.

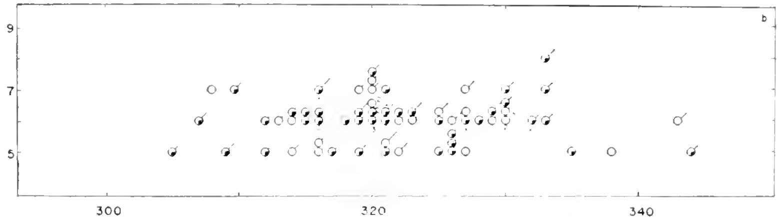

Figure 6b. Pictorialized scatter diagram of *Gambusia* males (see text for explanation of coding). Sample from Middle Valley Prong of San Saba River.

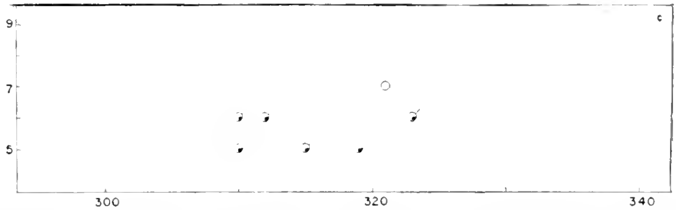

Figure 6c. Pictorialized scatter diagram of *Gambusia* males (see text for explanation of coding). Sample from lower part of Clear Creek.

ably in females over 25 mm standard length. In this index *G. heterochir* figures exceed those of *G. affinis*, and female figures exceed those of males. Environmental factors may effect meristic and morphometric characters of *Gambusia* species during development (Clark Hubbs and Springer, ms.). However, fish from the same locality probably are subjected to similar environmental factors during development. The minor differences between the figures for different populations may in part be due to different environmental factors acting during development; however, in so far as possible sample localities were selected that had similar environments. The abcissa of the graphs for males is made up of the sum of five gonopodial characters that were tabulated from one to five, with the lower numbers for *G. affinis* morphology. The two parental types are shown in Figure 3. The gonopodial characters are: the number of segments in the terminal hook on the posterior branch of ray four; the relative location of the terminal serra of the posterior branch of ray four when compared with the location of the elbow on the anterior branch of ray four; the structure of the elbow; the number and length of the modified spines on ray three; and the angle of contact of the anterior branch of ray five with the main axis of the gonopodium. The abcissa of the graphs for females is made up of the sum of four color characters, that were tabulated from one to five, with the lower numbers for *G. affinis* colors. The color codings are shown by Figure 4. The number of dorsal rays for both sexes is shown by the amount of shading within the circle: no shading = 5 rays; one-quarter shaded

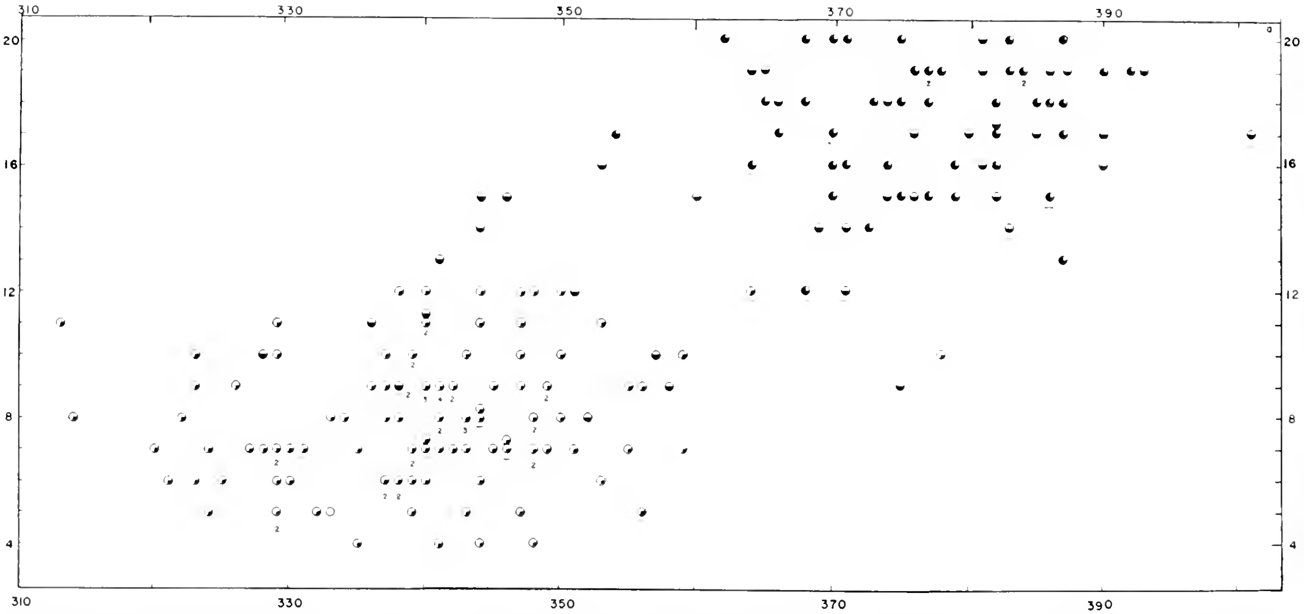

Figure 7a. Pictorialized scatter diagram of *Gambusia* females (see text for explanation of coding). Samples from headwaters of Clear Creek.

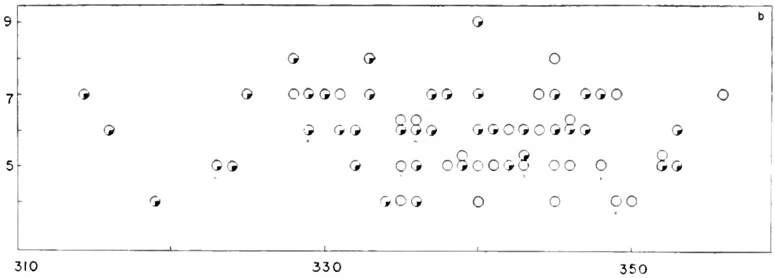

Figure 7b. Pictorialized scatter diagram of *Gambusia* females (see text for explanation of coding). Sample from Middle Valley Prong of San Saba River.

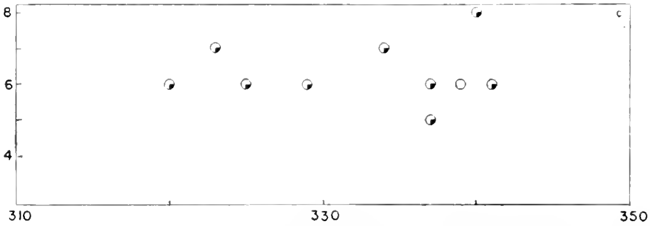

Figure 7c. Pictorialized scatter diagram of *Gambusia* females (see text for explanation of coding). Sample from lower part of Clear Creek.

= 6 rays; one-half shaded = 7 rays; three-quarters shaded = 8 rays; and all shaded = 9 rays. Two of the four color types used to distinguish the females differ in males, caudal fin colors and scale marks. The male colors are coded as in females. The length of the right bar designates the status of the males in regard to color pattern. The pectoral fin of the males differs between the two species (fig. 5). The differences were coded from one to five. The length of the left bar indicates the status of the fish with regard to pectoral fin structure. When some of the figures for individual fish were plotted, they had the same ordinate and abcissa. If other tabulations are the same, the number of examples is indicated beside the circle. If other figures differ, the second type is placed above and adjoining the first. The fishes collected from Clear Creek in 1953 and 1956 are plotted together. The plots of the 1953 specimens lie immediately above a bar. Other plots without bars or above those with bars are for the 1956 specimens.

The distribution plot of males from the headwaters of Clear Creek (fig. 6a) resembles the hybrid swarms discussed by Anderson (1949). Although the plot of the six males in the 1953 collection differs from the plot of the numerous males in the 1956 collection by being in three groups of two males, I feel that the difference is more likely due to chance. Most of the plots fall into two categories, upper right and lower left. Those in the upper right are believed to represent *G.*

heterochir and those in the lower left *G. affinis.* The scattered plots between are considered hybrids. There is a pronounced gap between the plots of the hybrid and the *G. heterochir* males. The plot of only one male definitely falls in this gap. One or two more may represent backcrosses with *G. heterochir.*

The distribution plot of *G. affinis* males from the Middle Valley Prong of the San Saba River (fig. 6b) is similar to that of the assumed *G. affinis* males in the hybrid swarm. The former differs in having more individuals with five dorsal rays (away from *G. heterochir*) and having more individuals with larger heads (toward *G. heterochir*). These differences are believed to result from population or environmental differences such as those shown for members of the related *Gambusia nobilis* species group by Clark Hubbs and Springer (ms). The distribution plot of the males from the lower reaches of Clear Creek (fig. 6c) closely resembles that of both the males from the Middle Valley Prong and the assumed *G. affinis* males from the headspring of Clear Creek. No indication of introgression is noted in the downstream collection.

The pattern of the distribution plots of the females from the headwaters of Clear Creek (fig. 7a) resembles that of the males. There is no significant difference between the collection made in 1953 and that made in 1956. There are two concentrations of plots, one each for females of *G. affinis* and *G. heterochir.* The scattered intermediate plottings are assumed to represent hybrids. The gap is less marked than that found in males. This is probably due to environmental variations of color marking details.

The distribution plot of the females from the Middle Valley Prong of the San Saba River (fig. 7b) is similar to that of the assumed *G. affinis* from the headwaters of Clear Creek. Similar to the males, the females from the Middle Valley Prong differ from those in the hybrid swarm region by having more individuals with five dorsal rays and larger heads. The distribution plot of the females from the lower part of Clear Creek (fig. 7c) resembles that of both the females from the Middle Valley Prong and the assumed *G. affinis* females from the headspring of Clear Creek. No indication of introgression is noted in the downstream collection.

DISCUSSION

A morphological study of the specimens from the headsprings of Clear Creek strongly indicates the presence of a hybrid swarm. The suspected hybrids are intermediate morphologically but definitely grade into *G. affinis* characters. Thus the intermediate hybrids (suspected F_1's) give a hybrid index similar to those given by Carl L. Hubbs, Hubbs, and Johnson (1943) for F_1 sucker hybrids. The correlation between apparently unrelated characters resembles those given by Anderson (1949) for hybrid swarms in plants.

The scarcity of specimens which would be expected to result from backcrosses of hybrids with *G. heterochir* is probably natural. Crosses between hybrids and *G. heterochir* may be inhibited by extrinsic or intrinsic isolative mechanisms. I suspect a sterility mechanism, as the other mechanisms did not prevent crosses between the more distinct parental forms. The few individuals which are morphologically intermediate between the hybrids and *G. heterochir* may represent extreme F_2's or the result of rare backcrosses.

The hybrid swarm was present in February, 1953. In February, 1956, the constitution of the hybrid swarm had not changed noticeably. Other factors being equal, if hybrids are at a selective advantage in the environment, the frequency of hybrids should be more numerous in the later collections. No hybrids have been noted among the 17 plotted individuals from the lower part of Clear Creek or the many unplotted immature individuals from that locality. Although backcrossing with *G. heterochir* appears to be inhibited, morphological evidence indicates potential gene flow into the downstream *G. affinis* populations. Therefore, if introgression is at a selective advantage, some *G. heterochir* influence should be noticeable in downstream collections 36 months after the hybrid swarm was known to have been established.

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ABSTRACT

A new species of poeciliid fishes, *Gambusia heterochir*, restricted to the headwaters of Clear Creek, Menard County, Texas is described. Both pectoral fins have a pronounced groove to steady the gonopodium during intromission. The new species has formed a hybrid swarm with *Gambusia affinis*. Introgression with *G. heterochir* appears negligible. Introgression is not found in near-by populations of *G. affinis*.

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NEW CALANOID COPEPODS OF *PONTELLA* DANA AND *LABIDOCERA* LUBBOCK WITH NOTES ON THE DISTRIBUTION OF THE GENERA IN THE GULF OF MEXICO

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Two previously undescribed species of *Pontella* Dana and one of *Labidocera* Lubbock were found during studies on an extensive collection of plankton samples from the Gulf of Mexico and a small number from the Cape Hatteras region. The plankton tows were made by the vessels ALASKA, ALBATROSS, and FISH HAWK, operating under the supervision of the U. S. Fish and Wildlife Service and its predecessors, the U. S. Commission of Fish and Fisheries and the U. S. Bureau of Fisheries, respectively. The ALBATROSS and the FISH HAWK were engaged in early oceanographic and fishery exploration cruises in the Gulf of Mexico and off Cape Hatteras, whereas the ALASKA recently conducted an oceanographic and biological survey of the Gulf of Mexico.

Notes on the distribution of other species of the two genera found in these collections are presented following the description of the new species. The cruise patterns of the ALASKA, which provided the majority of the records, are available in the Reports of the Texas A. and M. Research Foundation (1952, 1955).

FAMILY PONTELLIDAE

PONTELLA DANA, 1846

PONTELLA **MIMOCERAMI**,[1] sp. nov.

(Figures 1-13)

Localities, Material.—Key West (ALBATROSS, station number and collecting data not available, 1884, 55 males and females; sample taken between April 15-27 or May 7-10 in Key West Harbor according to Townsend's 1901 account of ship's activities; — FISH HAWK, station 7794, 26 December 1912, surface tow, one female). Coastal waters off Galveston, Texas (collected by writer in surface tows, 4 and 17 August 1954, two males). One mile southeast of Port Aransas (collected by Mr. R. J. Kemp, Texas Game and Fish Commission, in surface tow, 18 August 1956, one male). Lat. 34° 20′ N., long. 75° 50′ W., near Lookout Lightship off North Carolina (FISH HAWK, no station number, 3 September 1914, surface tow, one male, one female).

Measurements.—All measurements made from dorsal view; cephalothorax measured along midsagittal plane from anteriormost margin of forehead to posterior margin of intersegmental fold between

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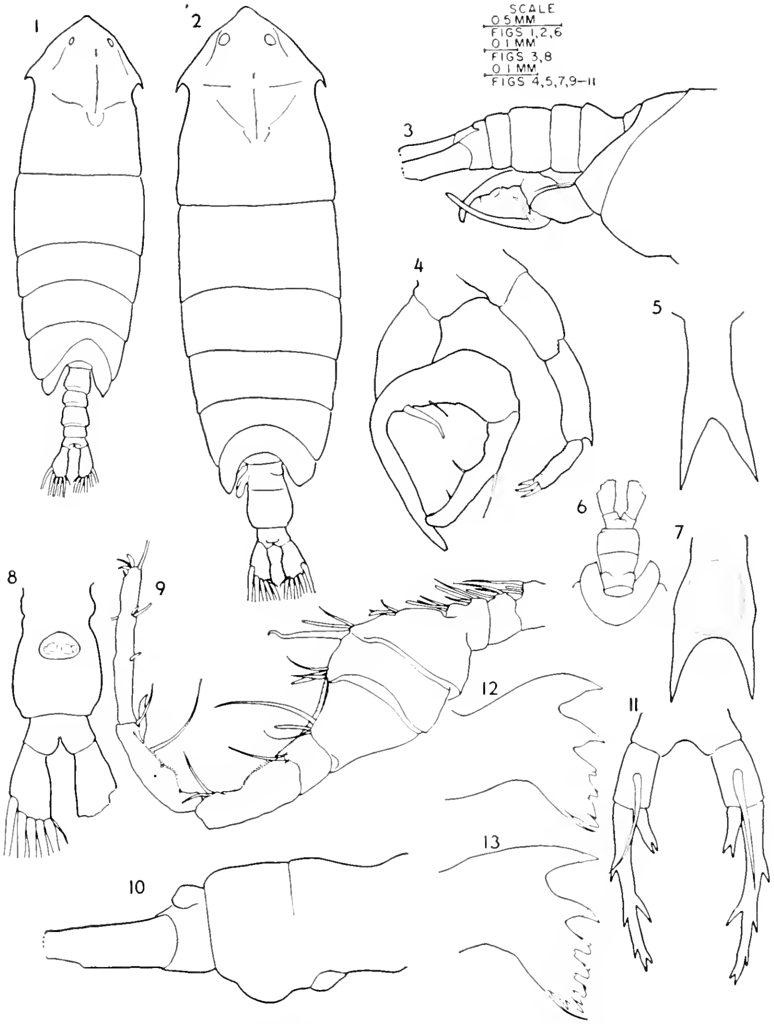
[1] The name *mimocerami* refers to the close relationship between the new species and *P. cerami* Scott.



Figures 1-13. *Pontella mimocerami*, sp. nov.: **1.** male, dorsal view; **2.** female, dorsal view; **3.** male abdomen, lateral view; **4.** male, fifth legs; **5.** female, rostrum; **6.** Female, abdomen, dorsal view; **7.** male, rostrum; **8.** female, abdomen, ventral view; **9.** male, geniculate antenna (less proximal segments); **10.** female, abdomen, lateral view; **11.** female, fifth legs; **12.** mandibular dentition.

Pontella tenuiremis Giesbrecht: **13.** mandibular dentition.

All figures drawn with aid of camera lucida; fig. 2 of holotype, remaining figures, except fig. 13, of paratypes.

thoracic segment V and genital segment; length of abdomen from anterior margin of genital segment to articulation between fifth innermost seta and right furcal ramus. Measurements made at 100x magnification with aid of ocular micrometer; specimen immersed in aqueous solution of 50% glycerine; slender glass rods used to support cephalothorax and abdomen in horizontal position. Measurements include total length (TL) and cephalothorax-abdomen length ratio (CAR).

1. *Adult female:* ALBATROSS; 10 specimens selected at random, TL range 3.18-3.63 mm, mean with standard error 3.29 ± .052 mm, standard deviation 0.156 mm, CAR range 3.5-4.2:1, mean 3.7:1. FISH HAWK, station 7794; TL 3.46 mm, CAR 3.9:1. FISH HAWK, Lookout Lightship; TL 3.40 mm, CAR 4.0:1.
2. *Adult male:* ALBATROSS; 10 specimens selected at random, TL range 2.70-3.18 mm, mean with standard error 2.95 ± .046 mm, standard deviation 0.138 mm, CAR range 2.9-3.5:1, mean 3.3:1. Galveston; two specimens, TL 2.98 mm, CAR 3.7:1; TL 2.46 mm, CAR 3.8:1. FISH HAWK, Lookout Lightship; TL 2.98 mm, CAR 3.6:1.

Diagnosis.—A population inhabiting coastal waters of the Gulf of Mexico and the temperate western North Atlantic Ocean in which the male is close to *P. cerami* Scott and the female is similar to *P. tenuiremis* Giesbrecht.

Adult female: Differs from *tenuiremis* chiefly in details of abdomen, fifth legs, and dentition of mandibular gnathal lobe.

Abdomen with genital segment partially separated from following segment by faint, incomplete suture (figs. 2, 6, 10). Anterior portion of genital segment with latero-dorsal swellings; swelling of left side enlarged in holotype, extending laterad in two lobiform processes (fig. 2); swelling of left side often a single reduced lobe similar to unilobed swelling on right side (fig. 6). Compound genital segment with greatest width posterior to suture, postero-ventral portion with moderate, rounded swelling (fig. 10). Anal segment narrower than preceding segment. Furcal rami normal, not attenuated, about one and one half times longer than maximum width (fig. 8).

Fifth legs (fig. 11) with exopodite bearing total of six spiniform processes, one medial, two terminal, three lateral; all excepting medial process reduced and somewhat equal in length; medial process about twice as long as others. Endopodite typically with bifid apex, bifurcation occasionally lacking; ramus not fused with basal segment 2.

Mandibular gnathal lobe with six teeth, fifth dorsalmost tooth monocuspidate (fig. 12); in *tenuiremis* gnathal lobe with eight teeth, fifth dorsalmost tooth bicuspidate (fig. 13).

Adult male: Differs from *cerami* with respect to thoracic segment V, geniculate antenna, and fifth legs.

Thoracic segment V with terminal portions in both dorsal and lateral views not truncate (figs. 1, 3); processes in dorsal view extending posteriad in triangular lappet somewhat rounded near apex, terminating in reduced spiniform apex.

Segment 17 of geniculate antenna with elongated ridge appressed to segment 16; proximal portion of ridge with low widely-spaced denticles, distal portion with closely-spaced spiniform denticles. Ridge of segment 18 with proximal denticles of uniform size. Proximal ridge of fusion segment 19-21 with single row of denticles. Segments 22-25 perfectly fused (fig. 9).

Chela of fifth legs (fig. 4) slightly different from that in *cerami* (vide Scott 1909: pl. 53, fig. 15); distal segment with blunt apex, irregular margins, and not arcate; proximal segment with small spine medial to large spine.

Types (cf. Localities, Materials).—All deposited in USNM. Female holotype, no. 99193, selected from material of ALBATROSS Key West station. Paratypes: nos. 99194-99196, 99203.

Further Description.—Female: rostrum lacking distinct lens (fig. 5); first antennae with 24 segments; second antennae with endopodal segment 1 separated from basal segment 2; remaining appendages as in genus. *Male:* rostral lens weakly to moderately defined; length of rostral processes about equal to diameter of lens (fig. 7).

Remarks.—Although the new species closely resembles the Indo-West Pacific species, *cerami*, this relationship is evident at present only in the male since the female of *cerami* is undescribed. However, the female of *mimocerami* appears to be similar to the following predominantly Indo-Pacific species of *Pontella*, as described by Giesbrecht (1892: pls. 24, 40): *tenuiremis; chierchiae* Giesbrecht; *fera* Dana.

The new species is distinguished in the male from the four species mentioned above by the following combined characteristics: (1) presence of an elongated, appressed, denticulated ridge on segment 17 of the geniculate antenna, the ridge completely overlapping the anterior margin of the preceding segment; (2) absence of lamellar or triangular processes extending from the proximal segment of the chela; (3) triangular non-truncated condition of the terminal portions of thoracic segment V. In the female it can be separated by (1) the single medial spiniform process on the exopodite of the fifth legs, (2) the pair of lateral swellings on the antero-dorsal portion of the genital segment, (3) the ventral swelling posterior to the genital orifice, and (4) the simple, almost symmetrical, terminal portions of segment V.

PONTELLA **POLYDACTYLA**,[2] sp. nov.

(Figures 14-24)

Localities, Materials.—Key West (ALBATROSS, same tow listed under preceding species, 16 males and females).

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[2] The name *polydactyla* refers to the many processes on the rami of the female's fifth legs.

Measurements.—All measurements made from right lateral view along imaginary straight line between limits; length of cephalothorax from anteriormost limit of forehead to posterior margin of intersegmental fold between thoracic segment V and genital segment; length of abdomen from antero-dorsal margin of genital segment to distalmost margin of right furcal ramus. Otherwise, as already given under preceding species.

1. *Adult female:* 10 specimens; TL range 3.43-4.03 mm, mean with standard error 3.73 ± .062 mm, standard deviation 0.18 mm, CAR range 3.3-3.9:1, mean 3.5:1.
2. *Adult male:* 6 specimens; TL 3.64 mm, CAR 3.5:1; TL 3.76 mm, CAR 3.6:1; TL 3.85 mm, CAR 3.2:1; TL 3.75 mm, CAR 3.6:1; TL 3.54 mm, CAR 3.8:1; TL 3.71 mm, CAR 3.3:1.

Diagnosis.—A robust species closely related to and strongly resembling *P. lobiancoi* (Canu) in dorsal view.

Adult female: Differs from *lobiancoi* primarily in details of thoracic segment V, abdomen, and fifth legs.

Posterior portions of thoracic segment V asymmetrical in dorsal view; right side triangular, left side truncate, each side with terminal styliform process extending posteriad beyond genital segment (figs. 14, 18).

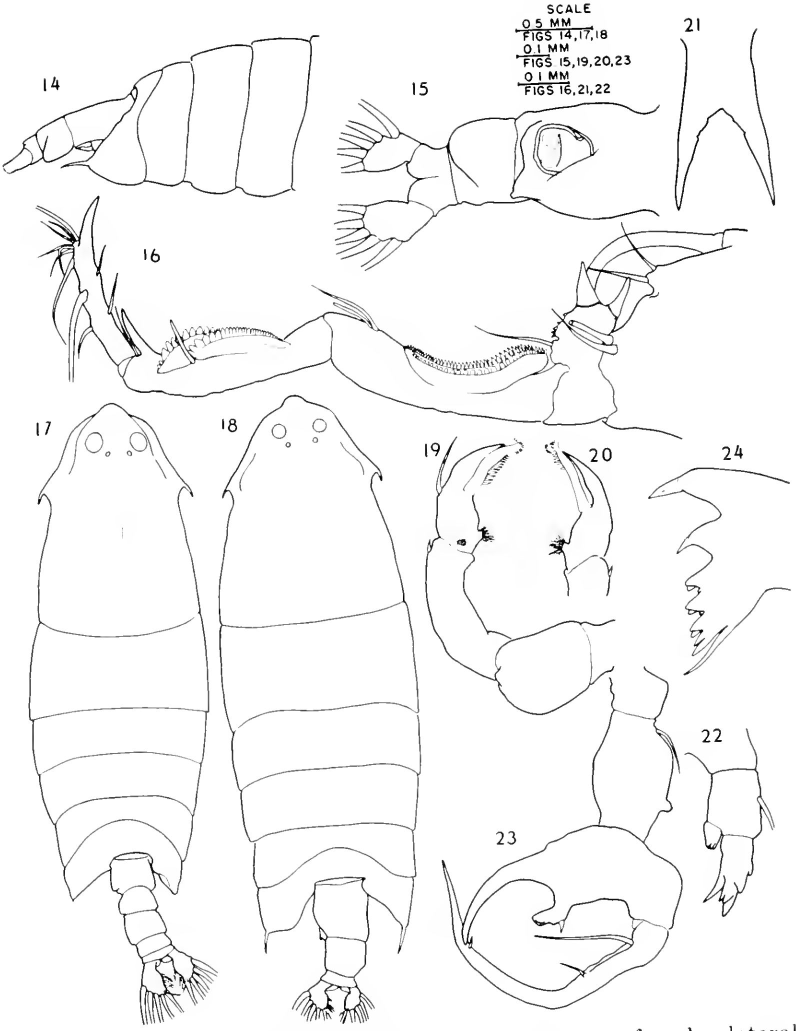
Abdomen with three visible segments as in *lobiancoi.* Genital segment with short ventral process posterior and to left of genital orifice (figs. 15, 18); segment lacking postero-dorsal swelling. Second abdominal segment asymmetrical, right postero-ventral portion bearing a conspicuous swelling (figs. 14, 15); segment's ventral surface smooth, lacking lobules and papillae. Furcal rami in dorsal view somewhat axiniform rather than rectangular.

Fifth legs with short thick rami; exopodite about as long as preceding segment, endopodite about as wide as long (fig. 22). Distal half of exopodite bearing six blunt spiniform processes, four distalmost overlapping. Endopodite terminating in two opposing pairs of short rounded processes.

Adult male: Differs from *lobiancoi* chiefly in details of geniculate antenna and fifth legs.

Geniculate antenna with segment 17 produced anteriad in robust irregular ridge; ridge armed with two, occasionally three, strong spines on proximal half, about six denticles on distal half. Ridge of segment 18 short, not reaching distal setae; denticles of ridge appear to be arranged in two rows, dorsal row with acuminate denticles, ventral row with lamelliform denticles. Two overlapping ridges of fusion segment 19-21 with robust denticles. Fusion segments 19-21 and 22-25 each terminating in a falcate spur (fig. 16).

Terminal segment of left fifth leg with acuminate apex flanked by two elongated lamellae; lamellae with unequal number of spinules on outer margin, unequal number of serrations on distal margin (figs. 19, 20). Chela of right fifth leg with distal segment extending be-



Figures 14-24. *Pontella polydactyla*, sp. nov.: **14.** female, lateral view (less cephalon, thoracic segment I); **15.** female, abdomen, ventral view; **16.** male, geniculate antenna (less proximal segments); **17.** male, dorsal view; **18.** female, dorsal view; **19.** male, left fifth leg, anterior view; **20.** terminal segment of male left fifth leg, posterior view; **21.** female, rostrum; **22.** female, fifth leg; **23.** male, right fifth leg, anterior view; **24.** mandibular dentition.

All figures drawn with aid of camera lucida; figs. 15 and 22 of holotype, remaining figures of paratypes.

yond falcate thumb of proximal segment; proximal segment with a somewhat digitiform process at midlength bearing one short medial spine (fig. 23).

Types (cf. Localities, Material).—All types deposited in USNM. Female holotype, no. 99213, selected from material of ALBATROSS, Key West; paratypes, nos. 99214, 99215.

Further Description.—Both sexes with rostrum lacking distinct lens (fig. 21). Forehead with pair of low rounded swellings just posteromediad to dorsal subcuticular lenses (figs. 17, 18). First antennae except male geniculate antenna with 24 segments; in female antennae extending to anterior margin of thoracic segment V. Second antennae with first segment of exopodite incompletely separated from second basal segment; in female exopodite shorter than first segment of endopodite. Second basal segment of leg 4 lacking distal seta. Male in lateral view with terminal portion of thoracic segment V bearing a short spiniform process on left side, lacking on right side. Remaining appendages as in genus.

Mated females with external lamelliform ornamentation, associated with spermatophore, enveloping genital segment; dorsal lamella with rectangular outline in dorsal view, covering dorsal surface of genital segment and overlapping right half of thoracic segment V; lateral lamellae fused with dorsal lamella, line of fusion sharp-edged; lateral lamellae extending mediad, overlapping ventral surface of genital segment.

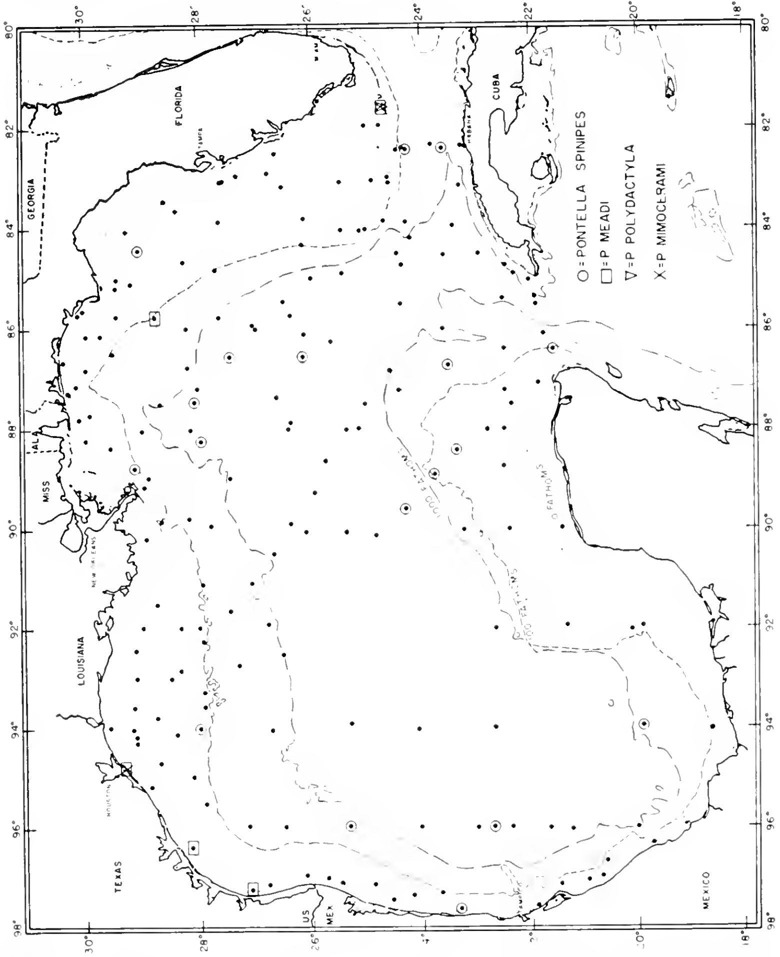
Remarks.—The new species is easily distinguished from all other known species of the genus in the female by the four-pronged endopodite of the fifth legs and the elongated styliform processes terminating thoracic segment V; in the male by the unusual form of the ridge and spines on segment 17 of the geniculate antenna and the pair of serrated lamellae on either side of the distal segment of the left fifth leg.

The similarity between *lobiancoi* and the new species compels reconsideration of the former's records from the Gulf of Mexico and the western Atlantic reported by Wilson (1932, 1942, 1950) and by King (1950). Except for these records, *lobiancoi* is known to occur only in the Mediterranean Sea and in Western European waters, Wimereux (Pas-de-Calais) being the type locality. It is noteworthy that this species was absent in the more than 200 samples collected by the ALASKA in the Gulf of Mexico. Considering the conspicuous, although superficial, resemblance between the two species and the usual occurrence of *lobiancoi* only in western European neritic waters, it seems best to regard Wilson's and King's records with reserve.

THE SPECIES OF *Pontella* IN THE GULF OF MEXICO

A qualitative analysis of more than 200 plankton samples collected by the ALASKA at surface stations scattered throughout the Gulf of Mexico revealed two known species of *Pontella, meadi* Wheeler and *spinipes* Giesbrecht, in addition to those described above. Geographical records of *Pontella* obtained during the present study are presented in Map 1.

P. meadi occurred at six widely scattered neritic localities over the northern shelf between the Florida Keys and Port Isabel. In addition, *P. pennata* Wilson was found together with *meadi* at all but one locality. The latter is not listed separately since there is considerable evidence (unpublished) that *pennata* is synonymous under *meadi*, a detailed account of this synonomy will be presented in a later paper. Previous records of *meadi* in the Gulf list the species from waters off western Florida (King 1950, Wilson 1950).



Map 1. Records of species of the genus *Pontella* collected by the M/V ALASKA in the Gulf of Mexico between April 1951-June 1953. Dots represent stations occupied by ALASKA.

P. spinipes appeared to be the most widespread species of the genus in the Gulf. It was found in 18 samples, occurring most frequently at stations made in slope and oceanic waters. Although there are no previously published Gulf records of *spinipes*, Jones (1952) has listed it from the Florida Straits region. According to T. E. Bowman (personal communication, 1955) the species has also been observed at Dry Tortugas and in the Caribbean Sea. Moreover, I have found *spinipes* together with *P. securifer* Brady in samples taken by the F. W. S. M V OREGON just south of eastern Cuba (unpublished).

Two other species of *Pontella* are purported to occur in the Gulf of Mexico. *P. atlantica* (Milne-Edwards) is questionably reported by Davis (1950), the determination based on a juvenile specimen taken off Rock Island, Florida. In addition, as already mentioned above, Wilson (1950) and King (1950) have listed *lobiancoi* from western Florida waters.

LABIDOCERA LUBBOCK, 1853

LABIDOCERA **MIRABILIS**,[3] sp. nov.

(Figures 25-37)

Localities. Material.—Florida Keys: lat. 24° 43′ N., long. 81° 57′ W. (ALASKA, cruise 11, station 14, 5 June 1953, 10 m. depth of plankton tow); Key West (ALBATROSS, same tow listed under two preceding species); Knight's Key (FISH HAWK, station 7788, 19 December 1912, depth ?); Dry Tortugas (FISH HAWK, station 7794, 24 December 1912, depth ?). Total of 55 specimens including males, females, and immature copepodites found in above samples.

Measurements.—All measurements made at 32x magnification from right lateral view, using methods described above under *Pontella polydactyla.*

1. *Adult female:* 11 specimens selected at random, TL range 2.54-2.95 mm, mean with standard error 2.80 ± .034 mm, standard deviation 0.109 mm, CAR range 3.5-4.2:1, mean 3.8:1.
2. *Adult male:* 18 specimens selected at random, TL range 2.21-2.54 mm, mean with standard error 2.37 ± .026 mm, standard deviation 0.111 mm, CAR range 4.4-5.5:1, mean 5.1:1.

Diagnosis.—A distinctive species of moderate size from the Florida Keys region that resembles *L. detruncata* (Dana).

Adult female: Differs from *detruncata* primarily in details of thoracic segment V, abdomen, and fifth legs.

Thoracic segment IV separated from segment V; terminal portions of V asymmetrical, right side extending farther laterad than left side and bearing larger spiniform process (fig. 28).

Abdomen with two segments. Genital segment asymmetrical, bear-

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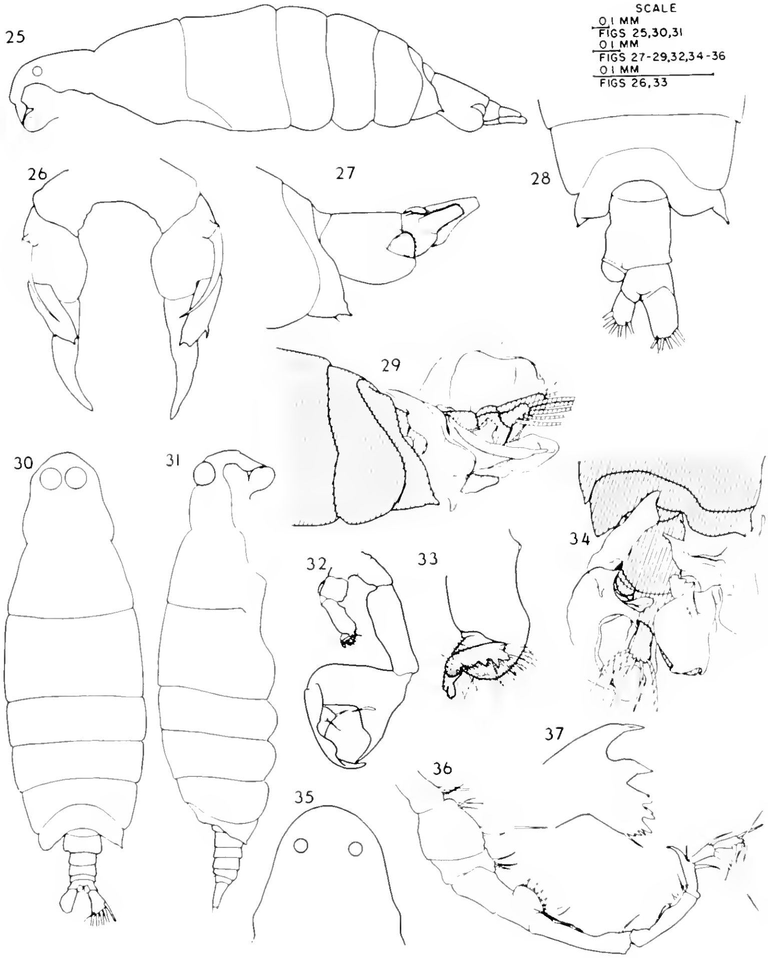
[3] The name *mirabilis* refers to the unique length relationship between the exopodite and endopodite of the female's fifth legs.

ing swelling on left side extending postero-laterad; genital orifice situated on postero-dorsal portion of swelling (figs. 27, 28). Anal segment not reduced. Furcal rami asymmetrical, right ramus longer



Figures 25-37. *Labidocera mirabilis*, sp. nov.: **25.** female, lateral view; **26.** female, fifth legs; **27.** female, abdomen, lateral view; **28.** female abdomen, dorsal view; **29.** female, abdomen with spermatophore and ornamentation, lateral view; **30.** male, dorsal view; **31.** male, lateral view; **32.** male, fifth legs; **33.** male, left fifth leg, terminal segment; **34.** female, abdomen with spermatophore and ornamentation, dorsal view; **35.** female, forehead, dorsal view; **36.** male, geniculate antenna (less proximal segments); **37.** mandibular dentition.

All figures drawn with aid of camera lucida; figs. 25, 26, 29, 34, 35 of holotype, remaining figures of paratypes.

and broader than left (fig. 28).

Fifth legs differ from those of all known species of *Labidocera;* endopodite longer than exopodite, ratio of former to latter about 1.8:1 (fig. 26). Exopodite with total of three shore spiniform processes, one lateral, two apical. Endopodite moderately constricted midway in length, distal half curving mediad.

Adult male: Differs from *detruncata* in details of thoracic segment V, geniculate antenna, and fifth legs.

Thoracic segment V asymmetrical, right side with short spiniform process, left side rounded (figs. 30, 31).

Geniculate antenna (fig. 36) with ridge on segment 17 produced in robust ovate lobe bearing two marginal rows of five to eight denticles; denticles of dorsal row robust, those of ventral row minute. Ridge of segment 18 short, terminating at approximate midlength of segment; ridge armed with about 25 short blunt denticles. Fusion segment 19-21 with two slightly overlapping ridges, each ridge bearing blunt closely-spaced denticles. Segment 22 with distal falcate spur.

Left fifth leg with short ramus superficially unisegmental; short distal segment hirsute, partially fused to proximal segment and extending laterad (fig. 32); distal segment with posterior ridge and short digitiform apex offset laterad; ridge with multilobed distal margin (fig. 33). Chela of right leg with more elongated proximal segment than that in *detruncata;* distal segment with proximal triangular process bearing two spines and distal low lamella (fig. 32).

Types (cf. Localities, Material).—All deposited in USNM. Female holotype, no 99207, selected from material of ALASKA, cruise 11, station 14. Paratypes: nos. 99208-99212.

Further Description.—First antennae in female with 24 segments. Second antennae with basal segment 2 fused with segment 1 of endopodite. Remaining cephalic and thoracic appendages as in genus.

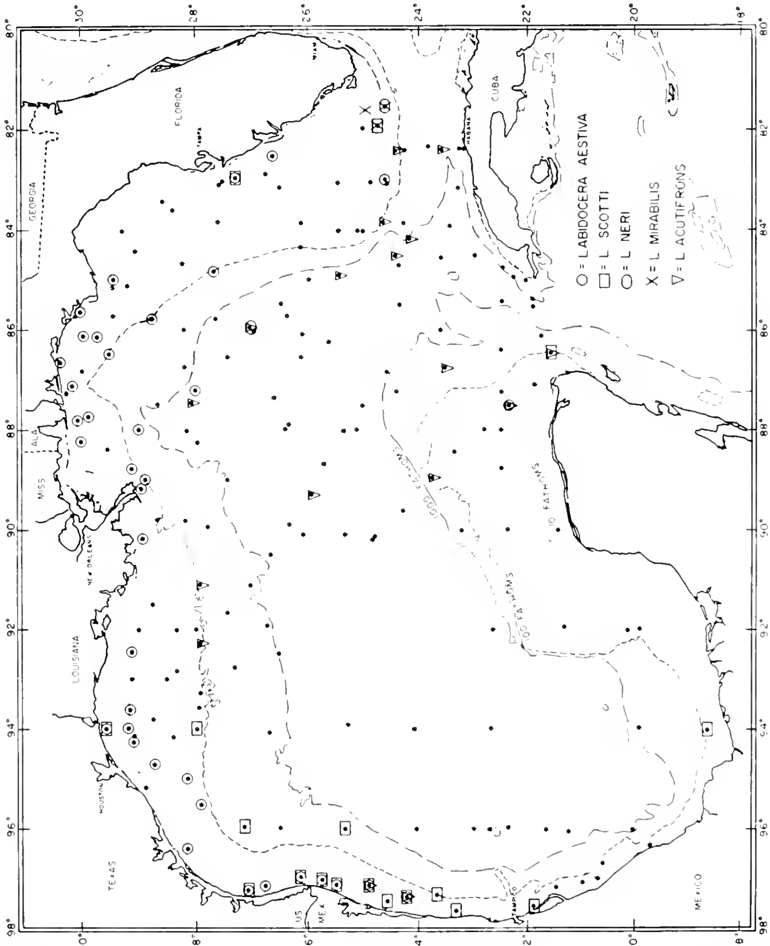
Mated females with abdomen obscured by complex lamelliform ornamentation associated with spermatophore (figs. 29, 34); ornamentation with somewhat rectangular basal plate ventral to genital segment and bearing a short ventral process at each corner; basal plate also supporting lateral lamellae which extend dorsad; those of right side larger, anterior one curving laterad, posterior one curving mediad; left side with two smaller lamellae, anterior one extending mediad, posterior one extending laterad.

Remarks.—The new species is readily distinguished from all other known species of the genus. The female is best characterized by the fifth legs, in which the endopodite is almost twice the length of the exopodite, and by the asymmetrical genital segment, bearing the genital orifice latero-dorsad on a left lateral swelling.

In the male the left fifth leg and the geniculate antenna possess excellent diagnostic features. The left fifth leg is superficially unisegmental with the terminal portion hirsute and turned laterad in a short truncate process. With respect to the geniculate antenna, segment 17 bears two rows of five-eight spines each, the dorsal spines being more than three times the size of the ventral spines, and segment 23 terminates in a robust falcate spur.

THE SPECIES OF *Labidocera* IN THE GULF OF MEXICO

In addition to *mirabilis*, four other species of the genus, *acutifrons* (Dana), *aestiva* Wheeler, *neri* (Krøyer), and *scotti* Giesbrecht, occur in the Gulf of Mexico. The local range of each of these species as determined from the ALASKA plankton collections is presented below (Map. 2).



Map 2. Records of the genus *Labidocera* collected by the M/V ALASKA in the Gulf of Mexico between April 1951-June 1953. Dots represent stations occupied by ALASKA.

L. acutifrons occurred at 13 oceanic localities east of long. 90° W., two oceanic localities south of Atchafalaya Bay, and two outer neritic localities off Laguna Madre. Included in this group are captures made in the mouth of the Yucatan Channel, in the vicinity of the Florida Keys, and off northern Cuba. Previous Gulf localities reported for the species are limited to the coastal waters off the southern half of Florida (King 1950).

L. aestiva, the most abundant species of Pontellidae in the collections, was confined almost exclusively to northern neritic waters between Florida and Laguna Madre. Numerically, the species was highly concentrated between Appalachicola Bay and the East Texas coast. Beyond these limits *aestiva* was taken in very small numbers, often only one or two specimens per standard tow.[1] A single specimen was also obtained from a tow made just off northern Yucatan. Both Davis (1950) and King (1950) have previously listed the species from the waters off western Florida.

L. neri was found at two localities, one in the vicinity of Key West and the other at about lat. 27° N., long. 86° W. The species has not been reported previously from the Gulf region.

L. scotti occurred at 17 ALASKA stations confined to or near neritic waters, including 14 coastal localities between the Lake Charles-Campeche area, one just off northeastern Yucatan, and two in coastal water off Florida, at Tampa and Key West, respectively. In addition, several records from Galveston, southern Florida, and the Florida Keys were established during the present study from collections by the ALBATROSS and the FISH HAWK as well as from material collected off Texas by the writer. The species was not found within the central portion of *aestiva's* range (Cape San Blas-Lake Charles). However, both species broadly overlap in the northeastern and northwestern sections of the Gulf. It is noteworthy that in the western overlap zone the number of *scotti* individuals per standard tow fell off gradually in the more northern samples. Conversely, *aestiva* showed a similar reduction in more southern tows with only single specimens per tow appearing in the Padre Island-Laguna Madre (Mexico) region.

Gradual displacement of *aestiva* by *scotti* also appears to occur proceeding south along the West Florida coast. The ALASKA material presents little evidence of a shift in the numbers of each species because of inadequate coverage of inshore areas in the region. However, Davis (1950) studying the plankton of the entire coast of western and southern Florida found *scotti* to be the most abundant and widespread species of *Labidocera* along the west coast. Around the southern tip of Florida, particularly within Biscayne Bay, extensive sampling both seasonally and geographically by two investigators (Davis 1950, Woodmansee 1949) have firmly established the year-

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[1] A 30 minute horizontal tow at 1 meter depth with one half meter net, No. 10 mesh.

round presence of *scotti*. In contrast, *aestiva* was not found during these studies, nor did it occur in the inshore collections made in Florida Bay by Davis and Williams (1950).

At first glance, King's (1950) plankton survey of the entire west coast of Florida, in which *aestiva* and *acutifrons* are the only species of *Labidocera* listed, would appear to contradict Davis' results. However, *scotti* is not described or mentioned in the literature of those copepod specialists referred to by King as his source for specific identifications. Therefore, it is probable that King was unfamiliar with *scotti* and possibly confused it with *aestiva*.

It is interesting that the distributional patterns outlined by the available data on *aestiva* and *scotti* in the Gulf of Mexico conform closely with the two principle temperature zones of the region. Ekman (1953) and Hedgpeth (1953) have noted that with the exception of the southern half of both Texas and Florida the neritic waters off the Gulf states are characterized by warm temperature conditions (> 10° - ca. 25° C). For example, within the region in which *aestiva* predominates, the molluscan fauna is predominantly Carolinian (Rehder 1954) and *Crassostrea virginica* (Gmelin) occurs as a community dominant (Ekman 1953). The remaining neritic waters of the Gulf, with *scotti* the predominant species of the genus, apparently transcend from subtropical to tropical conditions (ca. 20° - > 25° C), culminating in the presence of coral reefs in the Tampico, Vera Cruz, Campeche, and Yucantan areas (Walton Smith 1954). Thus, in the Gulf the two species appear to be planktonic indicators of the two respective coastal water zones. Since they also fulfill adequately the physical requirements for planktonic indicator species (large size, singular appearance, high relative abundance, etc.), they should be subjected to more detailed study.

Apart from the Gulf, temperatures characteristic of the known range of each species are remarkably similar to conditions within the local Gulf range. *L. aestiva* is a well established inhabitant of temperate coastal waters between northern Florida and the Gulf of St. Lawrence (type locality: Woods Hole, Massachusetts). It has also been recorded from Brazilian coastal waters (Carvalho 1945, 1952; Oliveira 1946), but the existence of three other species in this area (*fluviatilus* Dahl, *darwini* Lubbock, *braziliense* Farran) that are very similar to *aestiva* casts some doubt on the validity of these reports. In contrast, *scotti* is known only from the tropical or near-tropical waters off the African west coast (type locality: Gulf of Guinea).

In summary, at least five species of the genus *Labidocera* are represented in the Gulf of Mexico. Regarding the three most abundant and widespread of these species, each appears to predominate in a different environmental area: *acutifrons* is found throughout the oceanic region, *aestiva* occurs along the northern temperate coastal area, and *scotti* is representative of the tropical or near-tropical coastal area.

Although, admittedly, data on *Pontella* in the Gulf of Mexico are sparse, the available information suggests that, as in *Labidocera*, the species tend to be environmentally separated as follows: *meadi*—warm-temperate neritic, *mimocerami*—tropical neritic, and *spinipes*—tropical oceanic. The remaining species, *P. polydactyla*, *L. neri* and *L. mirabilis*, appear to be infrequent transients in the easternmost portions of the Gulf region.

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ABSTRACT

Descriptions are presented for three new calanoid copepods taken in the Gulf of Mexico during plankton collecting operations of the U. S. Fish and Wildlife Service: *Pontella mimocerami*, n. sp., is related to *P. cerami* Scott; *P. polydactyla*, n. sp., is close to *P. lobiancoi* (Canu); *Labodocera mirabilis*, n. sp., resembles *L. detruncata* (Dana).

Records of previously known species of *Pontella* Dana and *Labidocera* Lubbock that appeared in the numerous plankton samples under consideration are charted. Their distributional patterns in the Gulf of Mexico are discussed. From the available evidence the more abundant and widespread of the species within each genus tend to be separated environmentally from one another. In *Labidocera*, *aestiva* Wheeler is temperate-neritic, *scotti* Giesbrecht is tropical-neritic, and *acutifrons* (Dana) is tropical-oceanic. In *Pontella*, *meadi* Wheeler is temperate-neritic, *mimocerami* is tropical-neritic, and *spinipes* Giesbrecht is tropical-oceanic. The remaining species, *Pontella polydactyla*, *Labidocera neri* (Krøyer), and *L. mirabilis* appear to be transients in the easternmost portions of the Gulf region.

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THREE NEW CRAYFISHES FROM ALABAMA AND MISSISSIPPI

(DECAPODA: ASTACIDAE)

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THREE NEW CRAYFISHES FROM ALABAMA AND MISSISSIPPI

(DECAPODA: ASTACIDAE)

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The three new species of the genus *Procambarus* described here were collected in a small area in the eastern part of Mississippi and western Alabama. The ranges of none of the three are known, and two of the species have been collected only in the type locality. Ecologically they all appear to be secondary burrowers (Hobbs, 1942: 20), associated with temporary pools and roadside ditches.

All are members of the Blandingii Section of the genus, and appear to belong to the Blandingii Group. Two are distinctly related to *Procambarus planirostris* Penn (1953: 71) and are relegated to the Planirostris Subgroup; the third, however, possessing certain characteristics of the Blandingii, Clarkii, and Planirostris subgroups is tentatively assigned to the Clarkii Subgroup.

PROCAMBARUS **HYBUS**,[1] sp. nov.

Diagnosis.—Rostrum without marginal spines and with or without a low median carina; postorbial ridges reduced without spines or tubercles; suborbital angle obtuse or obsolete; lateral tubercles on carapace weak; areola 11.8 to 24.0 times longer than broad and constituting 32.7 to 36.9 per cent of entire length of carapace. Simple hooks present on ischiopodites of third and fourth pereiopods in male. Palm of chela not bearded but with a row of seven to nine tubercles. First pleopod of first form male with a distinct shoulder on cephalic margin just distad of midlength and distal portion of appendage directed at about a 40° to 50° angle to main shaft of pleopod; mesial process non-corneous, usually toothed distally, and directed caudodistad and somewhat mesiad; cephalic process compressed and somewhat hooding the central projection; central projection corneous and directed caudodistad as is the cephalic process (not caudally as in *P. planirostris*); caudal element partially corneous and subtriangular in caudal aspect. Annulus ventralis with a caudally expanded median longitudinal furrow; sinus forming a sinuous line in furrow and terminating caudally on elevated area near mid-caudal margin.

Holotypic Male, Form I.—Body subcylindrical, only slightly compressed laterally; abdomen a little longer than carapace (34.3 and 33.1 mm). Height and width of carapace in region of caudodorsal margin of cervical groove subequal (see measurements); greatest

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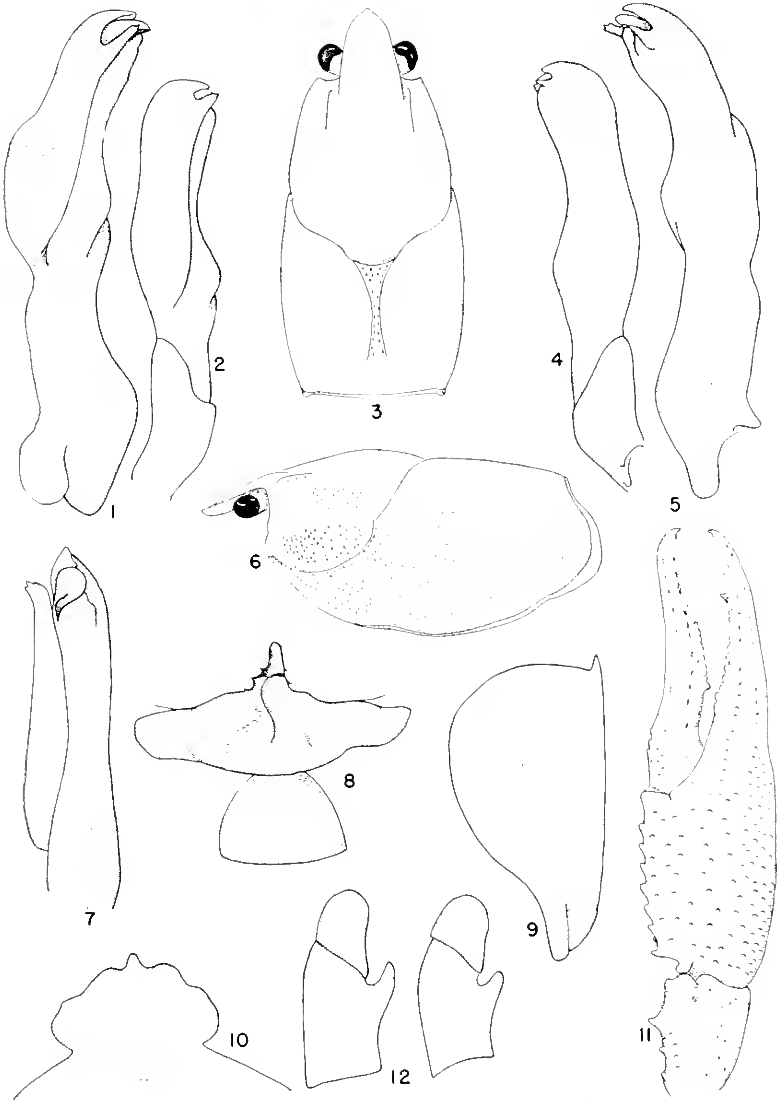
[1] *hybus*: G., humpbacked; referring to the humped first pleopod of the first form male.



Figures 1-12. *Procambarus hybus*, sp. nov.: **1**, mesial view of first pleopod of first form male; **2**, mesial view of first pleopod of second form male; **3**, dorsal view of carapace of first form male; **4**, lateral view of first pleopod of second form male; **5**, lateral view of first pleopod of first form male; **6**, lateral view of carapace of first form male; **7**, caudal view of first pleopod of first form male; **8**, annulus ventralis of female; **9**, antennal scale of first form male; **10**, epistome of first form male; **11**, distal podomeres of cheliped of first form male; **12**, basipodites and ischiopodites of third and fourth pereiopods of first form male.

width of carapace at level of caudodorsal margin of cervical groove.

Areola narrow, about 24 times longer than wide with two punctations in narrowest part. Cephalic section of carapace about 1.8 times as long as areola (length of areola about 35.3 per cent of entire length of carapace).

Rostrum without lateral spines; widest at base; margins distinctly elevated, slightly thickened, and converging to very small, upturned acumen. Upper surface plane, with few punctations basally, a row mesiad of margins and an irregular row along median line. A short, low carina present on upper surface just posterior to apex.

Postorbital ridges not conspicuous, terminating cephalically without spines or tubercles; a shallow ciliated groove on lateral surface of both ridges. Suborbital angle almost obsolete, obtuse. Branchiostegal spine small. Lateral surface of carapace granulate; granulations immediately caudad of cervical groove subequal in size, the usual lateral spines or tubercles not recognizable. Dorsal surface of carapace punctate.

Cephalic section of telson with two spines in each caudolateral angle.

Epistome (fig. 10) broader than long with cephalolateral margins emarginate and with a small cephalomedian projection.

Antennae extend caudad to second abdominal tergum, and of the usual form. Antennal scale (fig. 9) broad; broadest distad of midlength; lateral margin inflated, straight, and terminating in a small spine; total length less than half that of areola (5.7-11.8 mm).

Right chela (fig. 11) with palm inflated and with setiferous squamous tubercles present on all surfaces. Inner margin of palm with a row of seven tubercles; above this row is another consisting of seven tubercles, and below it, a similar one. Both fingers with poorly defined longitudinal ridges on upper and lower surfaces. Opposable margin of immovable finger with a row of 13 rounded tubercles along basal three-fourths of finger, the third from base largest, a large corneous tubercle on same margin, at a lower level, between eleventh and twelfth tubercles of above-mentioned row. Opposable margin of dactylopodite convex with basal fourth bearing a single row of eight small rounded tubercles; distad of this row, two rows of tubercles continue to midlength of finger to be replaced in the third quarter by a single less-well defined row. Crowded minute denticles between and distad of tubercles on opposable margins of both fingers. Setiferous punctations covering both fingers except for a few squamous tubercles at base and on longitudinal ridges. Lower surface of palm with a prominent tubercle at base of dactylopodite.

Carpopodite of first right pereiopod tuberculate mesially and punctate elsewhere. Distal end with four strong tubercles "in a semicircular arrangement extending medioventrally from dorsal to ventral condyles" (Penn, 1953: 72). Only one other tubercle larger than others on mesial surface.

Meropodite tuberculate above, below, and mesiodistally. The usual two rows on lower surface not so sharply defined as in many species. Lower surface of ischiopodite with a row of six tubercles.

Ischiopodites of third and fourth pereiopods with hooks (fig. 12), both simple and neither opposed by a knob-like process on corresponding basipodite. Coxopodite of fourth pereiopod with a caudomesially projecting knob, and coxa of fifth with a small ventrally directed ridge on mesial angle.

First pleopod extending to coxopodite of third pereiopod when abdomen is flexed. Tip terminating in four distinct sclerotized parts (figs. 1, 5, 7). Distal third of appendage directed at about a 50° angle to basal two-thirds. Cephalic margin with a marked shoulder at base of distal third of appendage. Mesial process, arising from mesial face of appendage, subspiculiform, and directed at about a 45° angle to main shaft of appendage; distal portion distinctly tripartate on left pleopod (entire on right). Cephalic process compressed, broader at base than other terminal elements and somewhat hooding the central projection. Central projection composed of the usual two elements, rounded distally and partially hidden in lateral aspect by the caudal process, its distal extremity directed distad and somewhat caudolaterad. Caudal process subtriangular in caudal aspect and consisting of what appears to be two indistinctly separated parts: a more mesial and broader lamellar portion lying immediately caudal to the central projection and a shorter heavier portion that abuts the former along its proximal caudolateral portion.

Morphotypic Male, Form II.—A young animal which is in all probability juvenile, and differs from the holotype in that the rostral surface is more punctate and the carina is not so well defined. One tubercle on lateral surface of carapace larger than others along caudal margin of cervical groove. Antennae extend caudad to fifth abdominal segment. Inner margin of palm of right chela with a row of eight tubercles. Chela and hooks on ischiopodites of third and fourth pereiopods much reduced in size (see measurements). First pleopod (figs. 2, 4) reaches coxopodites of third pereiopods when abdomen is flexed; all terminal elements represented but considerably reduced in size and non-corneous.

Allotypic Female.—Differs from the holotype in the following respects. No carina present on rostrum, suborbital angle obsolete, antennae extend caudad to third abdominal segment. One tubercle on lateral surface of carapace immediately caudad of cervical groove slightly larger than others nearby. Cephalic section of telson with three spines in each caudolateral angle. Inner margin of palm of chela with a row of nine tubercles. Lower margin of ischiopodite of cheliped with a row of only five tubercles. (See measurements).

Annulus ventralis movable, deeply imbedded in sternum and partially covered cephalically by projection from sternum immediately cephalic to it. Subovate in shape with a median longitudinal furrow that is expanded caudally. Sinus a sinuous line extending in furrow from near mid-cephalic margin to elevated area near midcaudal margin; fossa present near midlength of annulus (fig. 8).

Measurements.—As follows (in millimeters):

	Holotype	Allotype	Morphotype
Carapace—			
height	16.6	14.7	10.1
width	16.1	16.0	10.1
length	33.1	32.4	21.2
Areola—			
length	11.8	11.4	7.3
width	0.5	0.8	0.3
Rostrum—			
length	7.5	7.0	4.7
width	5.6	5.3	3.8
Right chela—			
length of inner margin of palm	12.0	7.3	4.6
width of palm	9.1	7.4	4.4
length of outer margin of chela	31.4	20.5	13.5
length of dactyl	17.5	11.8	7.9

Type Locality.—Roadside ditch, 1.7 miles north of Boligee, Greene County, Alabama, on U.S. Highway 11. Here, the ditch, with a clay and muddy bottom, contained clear water which was four to six inches in depth, and the bottom supported a rich growth of grasses, indicating that the water was not permanent. The crayfish were collected with a seine and by hand.

Disposition of types.—The holotypic male, the allotypic female, and the morphotypic male are deposited in the United States National Museum (cat. nos. 99581, 99582, and 99583, respectively). Of the paratypes, one male, form I, one male, form II, and one female are deposited in the collection of Tulane University; three males, form I, 38 males, form II, 32 females, 66 juvenile males, and 63 juvenile females are in the collection of the senior author at the University of Virginia.

Specimens examined.—A total of 238 specimens have been examined from the following localities. ALABAMA—*Greene County:* type locality. MISSISSIPPI—*Kemper County:* 0.2 mi. S. of Noxubee Co. line on Rt. 45; 7.7 mi. N. of Scooba on Rt. 45; 10.5 mi. S. of Scooba on Rt. 45; 1 mi. S. of Scooba on Rt. 45; Scooba Creek, 5.2 mi. S. of Scooba on Rt. 45; *Lowndes County:* 9.1 mi. N. Noxubee Co. line on Rt. 45; *Noxubee County:* 11.3 mi. S. of Macon on Rt. 45. All of these specimens were collected in April of 1951 and 1954 by Jean E. Pugh, Sam R. Telford, and the senior author or by W. R. West and the latter.

Variations.—The following variations from the above descriptions have been noted but none of them appears to be correlated with local populations; rostrum with or without a median carina; seven to nine tubercles along inner margin of palm of chela; suborbital angle weak or obsolete; cephalic section of telson with two to four spines in each caudolateral angle; slight differences in numbers of tubercles on opposable margins of fingers; mesial process of first pleopod simple or with two or three spines at tip; transverse ridge on annulus ventralis may be rounded or crest-like.

Relationships.—Procambarus hybus has its closest affinities with *P. planirostris* Penn (1953) but may be distinguished readily from the latter by the differences in the central projection and caudal element of the first pleopod of the first form males and those between the annuli ventrales of the females.

PROCAMBARUS **MANCUS**,[2] sp. nov.

Diagnosis.—Rostrum without marginal spines; postorbital ridges well developed but without spines or tubercles; suborbital angle obtuse or obsolete; lateral tubercles present on carapace; areola 9.8 to 14.6 times longer than broad and constituting 34.2 to 36.8 per cent of entire length of carapace. Simple hooks present on ischiopodites of third and fourth pereiopods in male. Palm of chela not bearded but with a row of 8 to 10 tubercles. First pleopod of first form male with a distinct shoulder on cephalic margin just distad of midlength and distal portion of appendage directed at about a 35° to 40° angle to the main shaft of the pleopod; mesial process non-corneous, spiculiform, and directed caudad; cephalic process vestigial but vestige lying mesiad of central projection; central projection corneous and beak-like, directed caudad; caudal process partially sclerotized and the more conspicuous part leaf-like with the cephalodistal margin approximating the caudal margin of the central projection. Annulus ventralis subspindle-shaped with a caudomedian prominence flanked laterally by a pair of caudally diverging elevations.

Holotypic Male, Form I.—Body subcylindrical, abdomen longer than carapace (29.1 and 26.5 mm). Carapace broader than high, greatest width of carapace slightly caudal to caudodorsal margin of cervical groove.

Areola narrow (10.4 times longer than wide) with scattered punctations—only two in narrowest portion. Cephalic section of carapace about 1.9 times as long as areola (length of areola 35.1 per cent of entire length of carapace).

Rostrum broadly lanceolate with prominent slightly raised lateral ridges and reaching base of ultimate segment of peduncle of antennule; margins converging to tip, no lateral spines present. Surface of rostrum subplane and with a number of deep punctations; a row of punctations mesiad of margins. Acumen small with upturned corneous tip. Subrostral ridges weak and evident only at base of rostrum.

Postorbital ridges prominent, terminating cephalad without spines or tubercles, and bearing a prominent ciliated groove on lateral surfaces. Suborbital angle weak and obtuse, almost obsolete. Branch-

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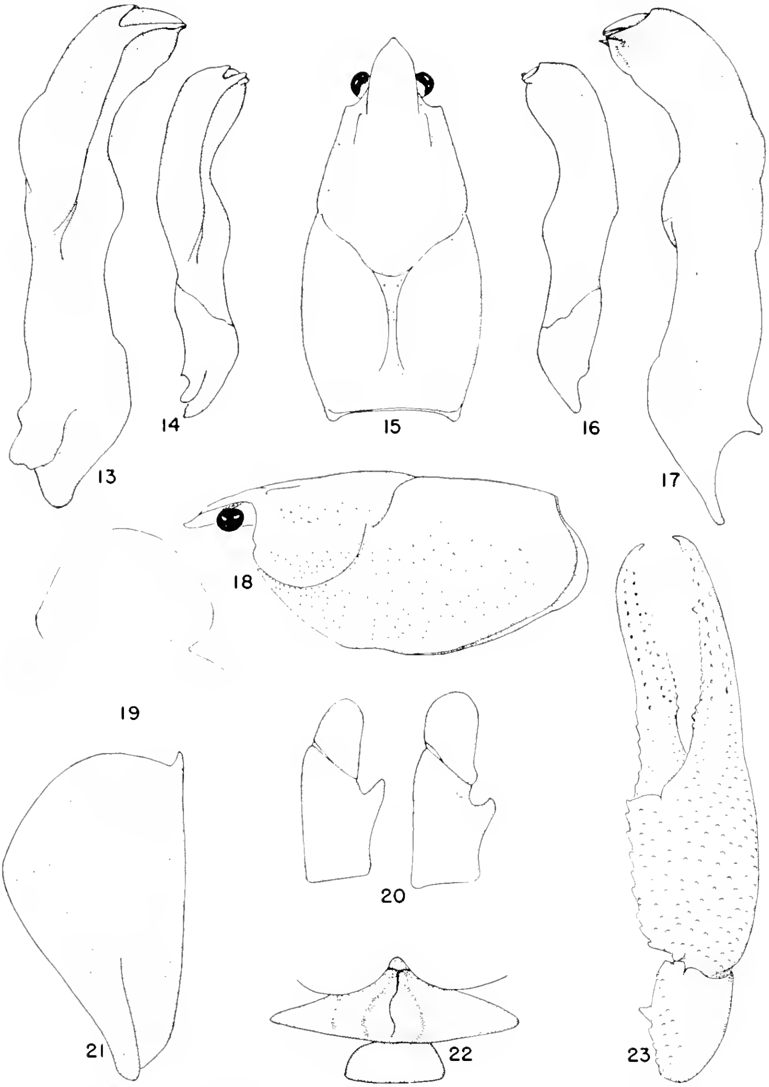
[2] *mancus*: L., maimed, defective; signifying the absence of the cephalic process of the first pleopod of the first form male.



Figures 13-23. *Procambarus mancus*, sp. nov.: **13,** mesial view of first pleopod of first form male; **14,** mesial view of first pleopod of second form male; **15,** dorsal view of carapace of first form male; **16,** lateral view of first pleopod of second form male; **17,** lateral view of first pleopod of first form male; **18,** lateral view of carapace of first form male; **19,** epistome of first form male; **20,** basipodites and ischiopodites of third and fourth pereiopods of first form male; **21,** antennal scale of first form male; **22,** annulus ventralis of female; **23,** distal podomeres of cheliped of first form male.

iostegal spines moderately well developed on the dextral side and lacking on the sinistral one. Lateral surface of carapace granulate; one tubercle somewhat larger than those nearby, on lateral surfaces of carapace immediately caudal to cervical groove.

Cephalic section of telson with two spines in each caudolateral angle.

Epistome (fig. 19) broadly ovate, truncate cephalically, and without a cephalomedian projection. Margins somewhat thickened and elevated.

Antennules of the usual form with a small spine on lower surface of basal segment.

Antennae extend caudad to caudal margin of third abdominal tergum and of the usual form. Antennal scale (fig. 21) broad, broadest slightly distad of midlength; lateral portion inflated and terminating in a small spine; total length greater than one-half that of areola (4.9 and 9.4 mm).

Right chela (fig. 23) with palm inflated and with setiferous tubercles present on all surfaces. Inner margin of palm with a row of nine tubercles; one or two rows of tubercles above and below this row. Both fingers with moderately well defined longitudinal ridge on upper and lower surfaces. Opposable margin of immovable finger with a row of 12 tubercles on proximal four-fifths of finger; third from base largest; one tubercle present at base of distal third of finger below this row. Opposable margin of dactylopodite with a row of 18 tubercles; one large tubercle present at distal end of basal third of finger slightly below aforementioned row. Minute denticles crowded between and beyond tubercles on opposable margins of both fingers. Mesial margin of dactylopodite with a row of nine tubercles on proximal half. Except for a few squamous tubercles at bases, both fingers pitted with somewhat regular rows of setiferous punctations. Lower surface of palm with a prominent tubercle at base of dactylopodite.

Carpopodite of first right pereiopod tuberculate mesially and otherwise punctate. Semicircular arrangement of four larger tubercles between dorsal and ventral condyles on distal end; other tubercles subequal in size.

Meropodite tuberculate above, below, and mesiodistally; one tubercle on upper distal portion larger than others nearby; mesioventral row of 18 tubercles, the lateral row poorly defined and both rows flanked by other small tubercles. Lower surface of ischiopodite with a row of five tubercles.

Ischiopodites of third and fourth pereiopods with simple hooks (fig. 20), neither opposed by a knob-like prominence on corresponding basiopodite. Coxopodite of fourth pereiopod with a caudomesially projecting knob, and coxa of fifth with a small ventrally directed ridge on mesial angle.

First pleopod extending to coxopodite of third pereiopod when abdomen is flexed. Tip terminating in three distinct parts (figs. 13,

17) and a rudiment of a fourth. Distal third of appendage directed at about a 75° to 80° angle to the basal two-thirds. Cephalic margin with a distinct shoulder slightly distad of midlength. Mesial process subspiculiform and directed caudally, evident in lateral aspect only at its tip. Cephalic process vestigial, represented by only a slight prominence on mesial surface above base of mesial process. Central projection a beak-like sclerotized process directed caudally. Caudal process a corneous plate closely applied to the more proximal margin of the central projection, laterally the plate is supported by a small triangular abutment and mesially it is delimited from the basal portion by a low ridge.

Morphotypic Male, Form II.—Differs from the holotype in only a few minor respects; branchiostegal spines are less well developed, the opposable margins of the fingers of the chela bear fewer tubercles, carpus of cheliped with one tubercle proximal to the semicircular row larger than the others nearby. All secondary sexual characters reduced. First pleopod (fig. 14) reaches coxopodite of third pereiopod when abdomen is flexed; all terminal elements represented, and except for the cephalic process, reduced in size and non-corneous.

Allotypic Female.—Differs from the holotype chiefly in the reduced size of the cheliped. Annulus ventralis (fig. 22) movable, and only slightly covered cephalically by the projections from the sternum immediately cephalic to it. Subspindle-shaped in outline with a pair of caudally diverging elevations flanking a swollen caudomedian prominence. Sinus in the form of a sinuous line meandering along median longitudinal line of annulus; fossa not evident.

Measurements.—As follows (in millimeters):

	Holotype	Allotype	Morphotype
Carapace—			
height	13.0	11.0	12.0
width	13.7	11.3	12.0
length	26.5	22.7	23.0
Areola—			
length	9.4	7.7	8.2
width	0.9	0.7	0.9
Rostrum—			
length	5.9	5.1	5.2
width	4.7	4.1	4.2
Chela—	Right	Left	Left
length of inner margin of palm	8.1	4.2	6.4
width of palm	7.5	4.6	5.9
length of outer margin of chela	22.0	12.4	17.0
length of dactyl	12.4	7.4	8.2

Type Locality.—Roadside ditch 5.0 miles south of Meridian, Lauderdale County, Mississippi on U.S. Highway 11. The ditch, some two to three feet wide, contained slightly turbid water about one inch deep that flowed sluggishly over a muddy bottom with a few scattered rocks and a grassy margin. The crayfish were collected with a seine, and a few of the specimens were dug from simple burrows along the margin.

Disposition of types.—The holotypic male, allotypic female, and morphotypic male are deposited in the United States National Museum (cat. nos. 99578, 99579, and 99580, respectively). A paratypic series consisting of a first form male, a second form male, and a juvenile female are in the collection of Tulane University, and the remaining paratypes, one male, form I, one male, form II, one female, 10 juvenile males, and five juvenile females are in the collection of the senior author at the University of Virginia. The type series constitutes all of the specimens available, and all of these were collected in the type locality on April 18, 1954, by Jean E. Pugh, Sam R. Telford, and the senior author.

Variations.—Except for the usual small variations in proportions and in the number of tubercles on the several podomeres, there is remarkable uniformity among the available specimens.

Relationships.—*Procambarus mancus* appears to have its closest affinities with *P. planirostris* and *P. hybus*, but may be distinguished easily from either of these forms by the vestigal cephalic process of the first pleopod of the first form male; in the latter two the cephalic process is well developed.

PROCAMBARUS **JACULUS**,[3] sp. nov.

Diagnosis.—Rostrum without marginal spines; postorbital ridges weak and without spines or tubercles; suborbital angle weak or obsolete; lateral surface of carapace without spines or tubercles; areola 9.9 to 12.2 times longer than broad and constituting 31.9 to 36.5 per cent of entire length of carapace. Simple hooks present on ischiopodites of third and fourth pereiopods in male. Palm of chela not bearded but with a row of eight tubercles. First pleopod of first form male with a weak shoulder on cephalic margin just distad of midlength and distal portion of appendage directed at about a 20° angle to the main shaft of the pleopod; mesial process only slightly sclerotized with a compressed, acute, spear-like tip and directed at about a 30° angle to the main shaft; cephalic process well developed and lying cephalad and slightly laterad of the central projection; the latter heavily sclerotized, somewhat beak-like, and subparallel to mesial process with tip abruptly directed caudad; caudal element consists of a broad leaf-like outer portion and an inner low ridge, both portions sclerotized. Annulus ventralis subcircular in outline with sinus as illustrated (fig. 33).

Holotypic Male, Form I.—Body subcylindrical, abdomen shorter than carapace (29.4 and 30.1 mm). Carapace broader than high, greatest width of carapace slightly caudad of caudodorsal margin of cervical groove.

Areola narrow (12.2 times longer than wide) sparsely punctate

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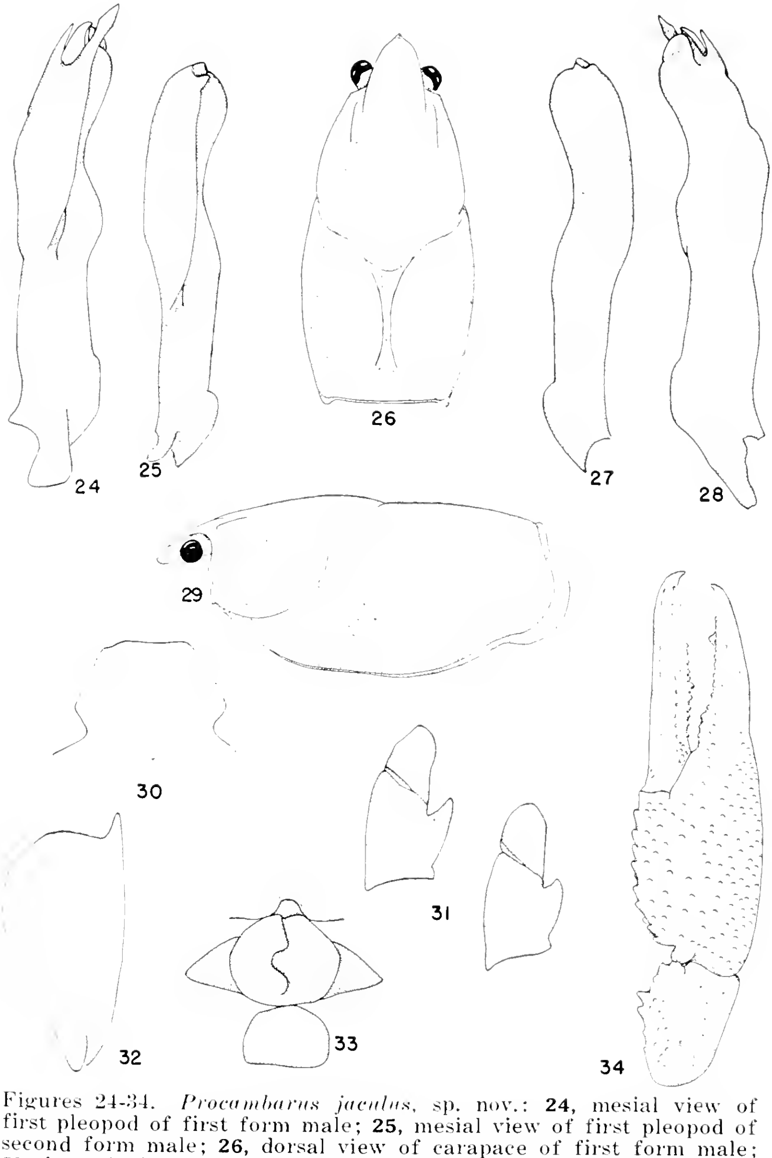
[3] *jaculum*: L., a dart or javelin; denoting the spear-like shape of the mesial process of the first pleopod of the first form male.



Figures 24-34. *Procambarus jaculus*, sp. nov.: **24**, mesial view of first pleopod of first form male; **25**, mesial view of first pleopod of second form male; **26**, dorsal view of carapace of first form male; **27**, lateral view of first pleopod of second form male; **28**, lateral view of first pleopod of first form male; **29**, lateral view of carapace of first form male; **30**, epistome of first form male; **31**, basipodites and ischiopodites of third and fourth pereiopods of first form male; **32**, antennal scale of first form male; **33**, annulus ventralis of female; **34**, distal podomeres of cheliped of first form male.

with only one punctation in narrowest portion. Cephalic section of carapace about 1.7 times as long as areola (length of areola 36.5 per cent of entire length of carapace).

Rostrum broadly ovate, with prominent lateral ridges, and reaching base of ultimate segment of peduncle of antennule; margins converging to tip, no marginal spines present. Surface of rostrum concave and with scattered punctations, a row of them mesial to margins; acumen minute. Subrostral ridges weak and visible for only a short distance at base of rostrum.

Postorbital ridges weak, terminating cephalically without spines or tubercles. A shallow ciliated furrow on lateral surface of each ridge. Suborbital angle extremely weak or obsolete; branchiostegal spines moderately well developed. Lateral surface of carapace granulate with no lateral spine or tubercle present; dorsal surface of carapace punctate.

Cephalic section of telson with three prominent spines in each caudolateral angle.

Epistome (fig. 30) broader than long, angular, and with cephalic margin truncate; margins only slightly elevated.

Antennules of the usual form with a small spine on lower surface of basal segment.

Antennae extend caudad to middle of second abdominal tergum. Antennal scale (fig. 32) broad; broadest distad of midlength; lateral portion slightly inflated and terminating in a small spine; total length about half that of areola (5.1 and 11.0 mm).

Right chela (fig. 34) with palm inflated and with setiferous squamous tubercles present on all surfaces. Inner margin of palm with a row of seven tubercles; rows of tubercles above and below this row somewhat irregular. Both fingers with moderately well defined longitudinal ridges on upper and lower surfaces. Opposable margin of immovable finger with a row of 14 tubercles that extends almost to tip of finger; fourth from base largest; one tubercle present at base of distal fourth of finger below this row. Opposable margin of dactylopodite with a row of 18 tubercles; one large tubercle present at distal end of basal third of finger and slightly below aforementioned row. A single row of minute denticles between and beyond tubercles on opposable margins of both fingers. Except for a few squamous tubercles at bases, both fingers pitted with scattered setiferous punctations. Lower surface of palm with a prominent tubercle at base of dactylopodite.

Carpopodite of first right pereiopod tuberculate mesially and punctate elsewhere. Distal end with four prominent tubercles in a semicircular row extending mesioventrally from dorsal to ventral condyles; only one other tubercle larger than those nearby on mesial surface.

Meropodite tuberculate above, below and mesiodistally. Lower mesial margin with a row of about 15 tubercles and the usual lateral row poorly defined. Additional tubercles between and to the sides of these two rows. Lower surface of ischiopodite with a row of five tubercles.

Ischiopodites of third and fourth pereiopods with simple hooks (fig. 31); neither opposed by a knob-like process on corresponding basipodites. Coxopodite of fourth pereiopod with a caudomesially projecting knob and coxopodite of fifth with a smaller ventrally directed ridge on mesial angle.

First pleopod extending cephalically to coxopodite of third pereiopod when abdomen is flexed. Tip terminating in four distinct parts (figs. 24, 28), all of which are sclerotized. Distal third of appendage directed at about a 20° angle to the basal two-thirds. Cephalic margin with a slight shoulder at base of distal third of appendage. Mesial process slender, lanceolate and directed at about a 30° angle to the main shaft of the appendage. Cephalic process compressed, acute, lying slightly laterad of central projection, its basal portion somewhat hooding the proximal portion of the latter. Central projection compressed, subacute and partially hidden in lateral aspect by the caudal process, and its distal portion beak-like and directed caudad. Caudal process broadly ovate in lateral aspect; consisting of two parts: a lateral plate-like portion, and a low mesial inflated portion with a ridge-like crest.

Morphotypic Male, Form II.—A small juvenile male in which the secondary sexual characteristics, other than the first pleopod, are only slightly evident. Differs from the holotype in the following respects. Height and width of carapace subequal; subrostral ridges evident in dorsal aspect for half the length of rostrum; cephalic section of telson with only two spines in each caudolateral angle. Other differences occur in tubercle numbers and proportions (see measurements). Hooks on ischiopodites of third and fourth pereiopods only slightly indicated, and knobs and ridges on coxopodites of fourth and fifth pereiopods very small. First pleopod (figs. 25, 27) with all terminal elements evident but all reduced and non-corneous.

Allotypic Female.—Differs from the holotype in the following respects. Areola with two or three punctations in narrowest part; rostrum broadly lanceolate and reaching midlength of ultimate segment of peduncle of antennule; cephalic section of telson with only two spines in the dextral caudolateral angle; truncate cephalic margin of epistome very slightly emarginate; opposable margin of immovable finger with a row of six tubercles, the second from base largest; opposable margin of dactyl with a row of 11 tubercles, the fourth from base largest; mesial row of spines on merus with only 11 tubercles; lateral row on merus with six tubercles; lower surface of ischiopodite with a row of four tubercles.

Annulus ventralis (fig. 33) subcircular in outline and traversed by a shallow longitudinal trough bearing the usual sinus which extends from midcephalic margin almost to caudal margin with a dextral loop just caudal to midlength. Fossa disappears below sinistral wall of broad low, transverse ridge. Cephalolateral margin of annulus partially obscured by overhanging sternum immediately anterior to it.

Measurements.—As follows (in millimeters):

	Holotype	Allotype	Morphotype
Carapace—			
height	13.5	14.0	8.5
width	14.8	15.1	8.4
length	30.1	30.9	18.0
Areola—			
length	11.0	10.7	5.9
width	0.9	0.9	0.6
Rostrum—			
length	6.0	7.0	3.8
width	5.1	5.7	3.1
Right chela—			
length of inner margin of palm	9.1	6.2	3.3
width of palm	8.1	6.5	3.4
length of outer margin of chela	24.1	17.0	5.5
length of dactyl	14.5	0.4	5.5

Type Locality.—Roadside ditch 1.0 mile west of Scott-Rankin County line on U.S. Highway 80, Rankin County, Mississippi. The crayfish were taken about 9:00 P.M. with the aid of a head light from a ditch some six to 15 feet in width in which the water was from a few inches to a foot in depth. The terrain was swampy.

Disposition of types.—The holotypic male, allotypic female, and a juvenile morphotypic male are deposited in the United States National Museum (cat. nos. 99584, 99585, and 99586, respectively). One female paratype is in the collection of the senior author at the University of Virginia.

Relationships.—*Procambarus jaculus* is here assigned to the Clarkii Subgroup but its affinities with the members of the Planirostris Subgroup should not be overlooked. The slight hump on the cephalic margin of the first pleopod as well as the well developed plate-like caudal process are characteristics of the Planirostris assemblage whereas the disposition of the other terminal elements of the pleopod resembles that of certain members of the Blandingii Subgroup.

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ABSTRACT

Three new crayfishes of the Blandingii Group are described from Alabama and Mississippi. *Procambarus hybus* was collected from eight localities in Green County, Alabama; Kemper, Lowndes, and Noxubee counties, Mississippi. *P. mancus* and *P. jaculus* are known from single localities in Lauderdale and Rankin counties, Mississippi, respectively. All three of these crayfishes appear to be secondary burrowers, associated with temporary pools and roadside ditches.

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HEAT DEATH AND ASSOCIATED WEIGHT LOSS OF THE OYSTER *CRASSOSTREA VIRGINICA*

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HEAT DEATH AND ASSOCIATED WEIGHT LOSS OF THE OYSTER *CRASSOSTREA VIRGINICA*[1]

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High and low lethal temperatures have been ascertained for many organisms. In general, temperatures for heat death of terrestrial animals (insects, reptiles, birds, and mammals) are high, around 45°C. Temperatures causing heat death in moist air dwellers (earthworms, frogs) are lower than for inhabitants of dry air. Still lower temperatures are lethal for aquatic forms, some normally living in cold waters die of heat shock even below 30°C (Prosser et al., 1950).

Responses of oysters to changes in temperature have been noted by several investigators. The majority have dealt with the effects of temperature upon larval viability (Churchill, 1921; Seno, Hori, and Kusakabe, 1926; Clark, 1933) and spawning (Galtsoff, 1931, 1932; Hopkins, 1931a; Loosanoff, 1939; Nelson, 1928a, b; Stauber, 1950). Stauber (1950) described three physiological types of *Crassostrea virginica* on the basis of differences in minimum spawning temperature. The respective temperatures required for spawning in Long Island Sound, the Bideford River, Price Edward Island, Canada, and Delaware Bay were 16.4°, 20°, and 25°C.

Hopkins (1931b) determined the influence of temperature changes upon shell movements in Olympia oysters, *Ostrea lurida*. He concluded that changes in water temperature were more important than the actual water temperature in determining how long the shells remained open each day. Falling temperatures caused the shells to close while opening followed a temperature rise. Shells of oysters kept at 17°C were open a greater proportion of the day than the shells of oysters at the other temperatures tested. In 1935 Hopkins found *Crassostrea gigas* had an optimum temperature of 27-28°C for pumping activity.

Henderson (1929) determined the upper lethal temperature for several lamellibranchs. The oyster *Crassostrea virginica* survived a higher temperature than any of the other molluscs he used. His experiments showed that 48.5°C was lethal for the oyster when the temperature was raised at the rate of 12° C per hour.

Fingerman and Fairbanks (1956) demonstrated that body fluids were lost by oysters whose valves were kept apart by means of wedges.

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[1] This study was conducted under a contract between Tulane University and the United States Fish and Wildlife Service. It was financed with funds made available under provisions of P. L. 466, 83rd Congress, approved July 1, 1954, commonly called the Saltonstall-Kennedy Act.

These investigators postulated that the oyster has very little ability to control the volume of its body fluids under conditions of stress. They concluded that oysters must be free to open and close their shells in order to control the volume of their body fluid. The present study was undertaken to test the hypothesis presented by Fingerman and Fairbanks (1956). Heat was chosen as the stimulus that would be used to place the oysters under stress.

EXPERIMENTS AND RESULTS

First and second year specimens of the oyster *Crassostrea virginica* grown in Louisiana were maintained in the laboratory in aquaria containing water at a temperature of 22-23° C and with a salinity of 17 ‰. The water was continually recirculated and filtered through cotton, glass wool, and charcoal. An acclimatization period of three to 10 days in the stock aquaria was allowed before the oysters were used in an experiment.

Survival and body fluid loss of oysters heated at different rates.— As stated above, Henderson (1929) determined that 48.5° C was the lethal temperature for oysters heated gradually at the rate of 12 C per hour. The temperature of the water was 15° C at the start of his experiments. The oysters were examined frequently. He assumed that all oysters would gape when they were heated. When an oyster could not close its shells when tapped, it was returned to the 15° C aquarium for three to 12 hours and observed again in order to determine whether or not recovery had occurred, *i.e.* whether the shells would close when tapped. Henderson assumed that the thermal death temperature lay between the highest temperature from which recovery occurred and the lowest point from which no recovery was observed.

In the first series of experiments of the present investigation a technique similar to that employed by Henderson was used. In addition to determining survival of oysters heated gradually, measurements of weight loss upon heating were performed. Weight change was expressed as a percentage of the weight of the oyster body and shell fluid, exclusive of the shells themselves, at the beginning of each experiment. The original weight of the body and fluid in the shell cavity was calculated by shucking the oysters when they were removed from the constant temperature baths, finding the shell weight, and subtracting it from the total weight of shells, oyster body, and shell fluid determined at the start of the experiment. The oyster shells were blotted prior to weighing in order to remove excess moisture. In two experiments that will be described later notches were cut into the shells by means of a carborundum wheel and the shell fluid was shaken out. Weight changes of these oysters were expressed as a percentage of the original body weight.

Henderson's criterion for death was gaping by oysters three to 12 hours after removal from the test tanks. The results of some preliminary experiments revealed that Henderson's criterion for death was not valid because all oysters killed by heat do not necessarily gape at any time during the course of an experiment or during the subsequent 12 hours. The oyster may be killed while the adductor muscle is fully contracted with the result that no gape is evident. According to the criterion of Henderson such oysters would be counted among the survivors. In view of this fact, after a heat exposure the oysters used in the present investigation were returned to the holding tanks for three to seven days to determine accurately the number of oysters that had been killed during the course of an experiment. After this period of time the shells of oysters killed with their adductor muscle contracted gaped because of muscle decay. Oysters with gaping shells were not considered dead until they showed no signs of movement when handled and none of the oysters with closed shells were considered dead until they showed some sign of putrefaction such as gas bubbles and tissue disintegration. In several cases fungal growth was also evident. Oysters that had died with their adductor muscle fully contracted began to gape due to the action of the ligament when the muscle disintegrated.

In each experiment of this series oysters were removed from the stock aquaria, blotted, weighed, and then placed into water baths at 24° C. The water was then gradually heated to 45-55° C. For each experiment a different rate of temperature rise was used. One group was heated at the rate of 0.74° C per hour, another at 4.5° C per hour, and a third at the rate of 13.2° C per hour. At each of the preselected temperatures 10 oysters were removed from the water baths, drained, and weighed in order to determine the weight loss that had occurred during the exposure period, and then replaced in the aquaria for three to seven days when the number of survivors was determined.

Oysters that died as a result of exposure to heat generally did so within five days and almost certainly within seven days after termination of the exposure. The survivors of high sublethal temperatures remained in a weakened condition with shells agape and gave no closing response to shadows but did respond to handling or tapping on the aquarium by closing the shells for a short time. These weakened suvivors apparently regained strength gradually over a period of two to three weeks after exposure because they became better able to close their shells rapidly and to keep them closed for longer periods of time. The gape also became more restricted and definite closing responses to shadows could be observed. Finally the survivors appeared normal.

With two exceptions that will be described later, no attempt was made to exclude the weight of the shell fluid from the oysters prior to their use in these experiments because of the possibility than any physical stimulus necessary to accomplish this would result in compensatory secretion of additional shell fluid by the body that would result in the introduction of another variable. Presumably the shell fluid lost by an oyster would represent a constant percentage of its original body weight, although not necessarily the same percentage for all oysters, and would therefore interfere minimally with the com-

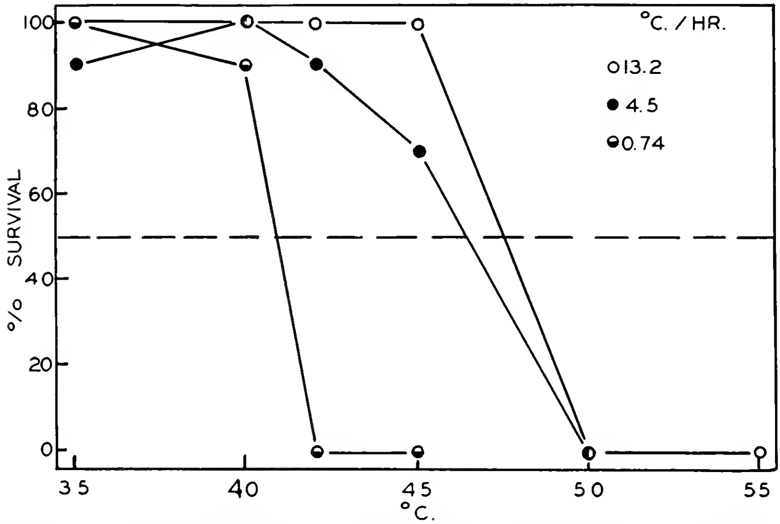

Figure 1. Percentage survival at temperatures reached at three different rates of increase.

parative aspect of the results.

The results of this series of experiments are presented in Figures 1 and 2. Figure 1 represents the percentage survival at temperatures attained by means of three different rates of increase. The dashed horizontal line represents the 50 percent mortality level. In some experiments the time required to kill 50 percent of the oysters was determined from inspection of the figures whereas in others the temperature at which 50 percent of the oysters was killed was determined from inspection of the figures. Fifty percent values served as bases of comparison of the results of different experiments. Use of the time required to kill 50 percent of the organisms in an experiment as determined by inspection of a plot of the data is a standard technique in pharmacology and has been used by several investigators in studies of temperature tolerance in fishes, *e.g.* Brett (1952).

As is evident from Figure 1, the slower the rate of temperature increase, the lower was the temperature required to kill 50 percent of the oysters. With rapid temperature increase (13.2° C per hour) 50 percent were killed at 47.5° C, 100 percent at 50° C; whereas with the slowest temperature rise (0.74° C per hour) 50 percent were killed at 41°, 100 percent at 42° C. With a 4.5° C per hour increase, the 50 percent mortality level was reached at 46.5° C; there was no survival at 50° C.

The computed lethal temperatures are not the temperatures at which the tissues died but are the computed temperatures of the water bath. A time lag in penetration of the heat into the oyster body was evident due to the time required for heat to penetrate the shells. The lag should obviously be greatest with the most rapid rate of increase of temperature, whereas with the slowest rate temperature changes of the oysters should keep pace more readily with temperature changes of the water bath.

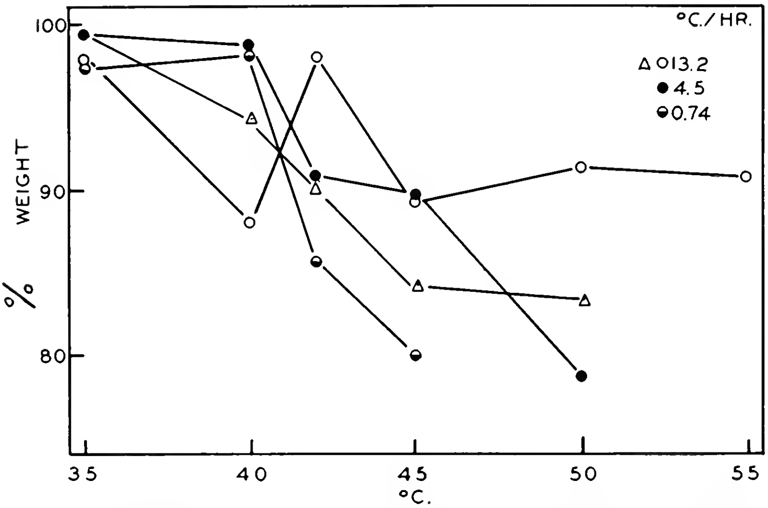

Figure 2. Percentages of original weight remaining after exposure to temperatures reached at three different rates of increase. See text for explanation of "original weight".

In Figure 2 are presented the weight losses of the same oysters represented in Figure 1. The triangles in Figure 2 do not apply to this experiment. Their significance will be described below. Apparently loss of weight is associated with heat death. The critical point in weight loss appears to be about 41° C where the weight loss of the rapidly heated oysters leveled off at approximately 10 percent of the original weight. At about 41° C differences in survival among the three groups of oysters were also manifested. The weight loss was beyond doubt due to loss of body fluid and shell fluid by the oysters. Body fluid must have been the primary source of weight loss. Some mucus and wastes may also have been expelled but in quantities insignificant in comparison with the fluids lost.

The following experiment was performed in support of the contention that most of the weight loss is due to body fluid. Notches were cut into the shells of 40 oysters and the free shell fluid drained. The oysters were then weighed, placed in a water bath, and heated at the rate of 13.2° C per hour. Ten oysters were removed when the temperature reached 40°, 42°, 45°, and 50° C respectively. The free fluid was then shaken out, the shells were blotted, and the oysters were weighed. The oysters were then shucked and the shells were weighed in order to determine the original body weight so that weight changes could be expressed as percentages of the original body weights. The data were presented in Figure 2 (triangles). As is evident from inspection of the figure, the notched oysters lost a greater percentage of weight than the intact oysters heated at the same rate. There is, therefore, no doubt that heating oysters induced a loss of body fluid.

Survival and changes in body fluid volume of oysters placed at constant temperatures.—The second series of experiments utilized an abrupt rather than a gradual thermal change. Oysters that had been in the stock aquaria no less than three days were taken, blotted, weighed, and put into constant temperature baths containing estuarine water at one of a series of constant temperatures for different exposure periods. The water baths were set at 35, 40, 42, and 45° C. At the end of the exposure period the oysters were removed, blotted, and reweighed. After the second weighing the oysters were returned to the stock aquaria. One hour later those that had been in the 42° and 45° C water baths were weighed again and returned to the stock aquaria for three to seven days when the number of survivors was determined. The percentage survival as well as percentage of the original weight was calculated for these oysters also. The term "original weight" refers to the weight of the oyster body and shell fluid at the start of the experiment.

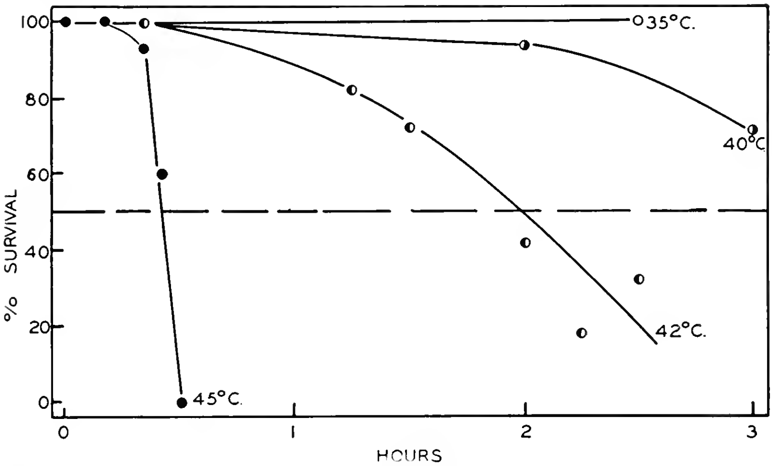

Figure 3. Percentage survival of oysters immersed in water of different temperatures.

Figures 3, 4, and 5 present the results of these experiments. Figure 3 shows the percentage survival in water of different temperatures. Figure 4 presents the weight losses in different temperatures. The triangles in Figure 4 do not refer to this experiment. Figure 5 gives the weight changes of the oysters 60 minutes after they were removed from the water baths and immersed in water at 22-23° C. The percentages in Figure 5 are based upon the weight of the oyster body and shell fluid when the oysters were removed from the water bath. The points in the figures represent from 13 to 43 oysters. The average number in Figure 3 is 24.2; in Figure 4, 27.2; and in Figure 5, 30.3. The 50 percent mortality level is represented in Figure 3 by the dashed horizontal line.

As is evident from Figure 3 no heat death occurred among oysters exposed to 35° C. After three hours of exposure to 40° C 29 percent of the oysters died. At 42° C 50 percent mortality was observed after approximately two hours of exposure; increased exposure duration resulted in progressively higher mortality rates. The 50 percent mortality level was reached after only 25 minutes at 45° C; complete mortality occurring with five additional minutes of exposure to 45° C. Therefore, the higher the temperature of the water bath, the faster the oysters were killed; the time of exposure being important in determining the lethal temperature. The same percentage of the oysters could have been killed by short exposure to high temperature or long exposure to a lower temperature.

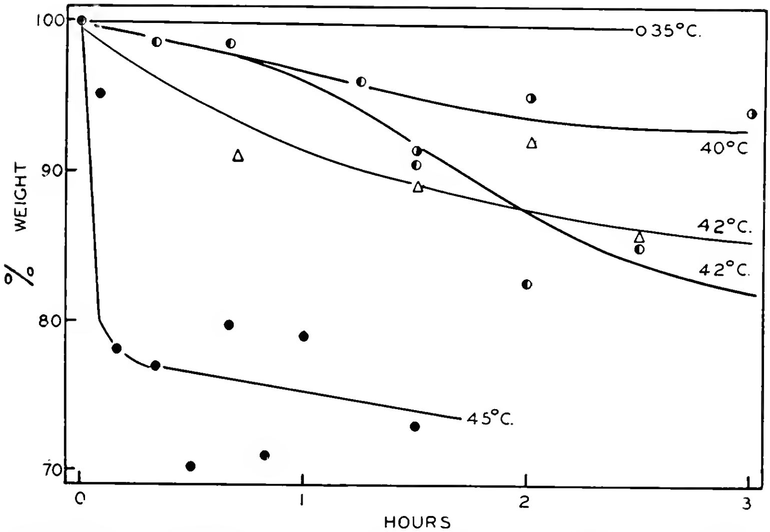

Figure 4. Percentages of original weight remaining after exposure to different temperatures.

The percentage weight loss determined at the time the oysters were removed from the water baths can be determined from Figure 4. Inspection of the families of curves shown in Figures 3 and 4 reveals a striking similarity between them that is highly suggestive of a relationship between exposure time, temperature, survival, and weight loss. Oysters placed in estuarine water at 35° C for 2.5 hours lost only 0.5 percent of their body weight and none died. Oysters kept at 40°C lost six percent of their original body weight after three hours; 29 percent died. Oysters maintained at 42°C lost weight at a still more rapid rate, reaching a 15 percent loss of original body weight after 2.5 hours; the 50 percent mortality level was reached after 117 minutes of exposure. Oysters in 45°C water lost weight very rapidly, approximately 25 percent of the original body weight was lost in five minutes; 50 percent died after 25 minutes of exposure.

The highest temperature used (45°C) in this series of experiments caused the greatest weight losses and the most rapid death. For the same exposure period greater survival and less weight loss were evident at 42°C than at 45°C. For any given percentage survival, *e.g.* 50 percent, oysters that died following exposure to 42°C lost less weight than oysters killed by exposure to 45°C. Therefore, heat was the primary cause of death and not loss of weight because the oysters were killed after losing different amounts of their original weight. Heat death was probably due primarily to heat inactivation of vital enzymatic processes and structural protein denaturation (Prosser et al., 1950). Weight loss was probably merely a secondary cause of death. More weight was lost by oysters kept at 45°C than at 42°C probably because of rapid destruction of membrane semipermeability with a concomitant loss of body fluid; whereas at 42°C death occurred more slowly due to slower inactivation of the vital mechanisms including those whereby tissue fluids are kept within the body.

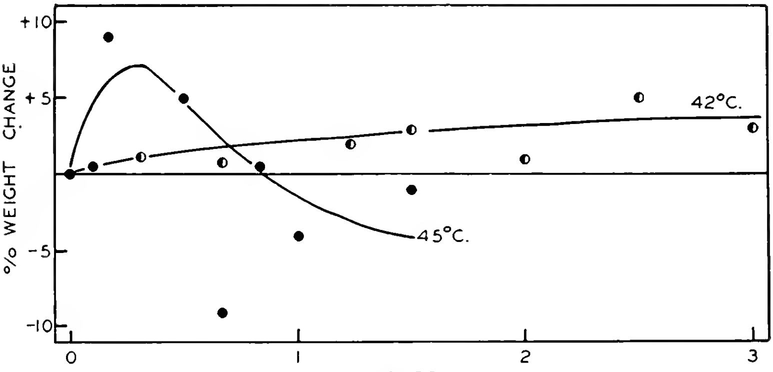

Figure 5. Weight changes of oysters 60 minutes after they were removed from the water baths and immersed in water at 22-23° C. Percentages are based upon the weight of the oyster body plus shell fluid when first removed from the water bath.

As is evident from Figure 5 oysters were able to take back fluids in direct proportion to the amount of weight lost. When oysters were placed in 22-23°C estuarine water after being in 45°C estuarine water for 10 minutes they rapidly regained a large amount of fluid. However, when oysters had been in 45°C water for more than 40 minutes, instead of taking back fluids they continued to lose weight.

At 42°C where death and weight loss were not as rapid as at 45°C, they were able to continue taking back fluids over a considerable period of time. They, however, did not return to their original weight.

To test further the hypothesis presented above that the weight loss was primarily due to escape of body fluids the following experiment was performed. Notches were cut in the shells of 40 oysters, the shell fluid was drained, the shells blotted, and the entire oyster weighed. The oysters were then placed into a water bath maintained at a constant temperature of 42°C. Ten oysters were removed periodically, the shell fluid was drained, shells blotted, and the entire oyster was weighed. The oysters were then shucked and the weight of the shells was determined. Weight changes were calculated as a percentage of the original body weight and presented in Figure 4 (triangles). As evident from inspection of this figure the results obtained with notched and intact oysters maintained at 42°C were comparable. During the first hour of immersion notched oysters lost more weight than intact ones but the difference between the weight loss of the two groups was not as evident during the next 90 minutes of immersion. Obviously, heat induced a loss of body fluids. This

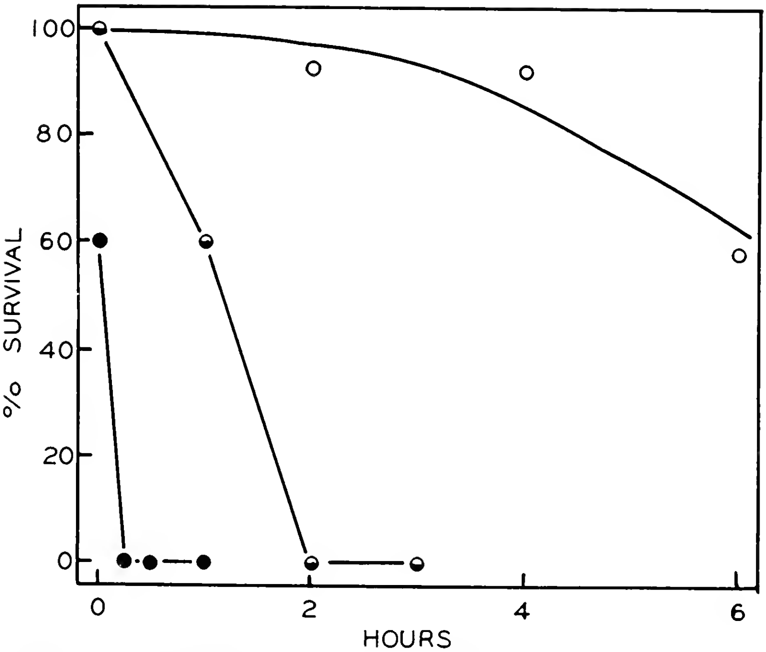

Figure 6. Percentage survival at various temperatures during exposure of oysters to constant temperatures of 40°, 42°, and 45° C. Oysters were immersed in water at 24° C and heated at the rate of 4.5° C per hour to the respective test temperatures. Symbols: circles, 40° C; half-filled circles, 42° C; dots, 45° C.

loss of body fluid must have been responsible for the vast proportion of the weight losses shown in Figures 2 and 4.

Survival of oysters gradually heated and then maintained at a constant temperature.—In the final series of experiments oysters were taken from the stock aquaria and placed in a water bath at 24°C. The water in the bath was then gradually heated at the rate of 4.5°C per hour. When the temperature of the bath reached 40°C the temperature of the water was maintained constant. The experiment was repeated with constant temperatures of 42° and 45°C. Twelve oysters were removed from the water bath when the temperature reached the desired level and at selected intervals thereafter. The oysters were then placed in the stock aquaria for three to 10 days when the number of survivors was determined. The results of this series of experiments are shown in Figure 6. The percentage survival at zero time represents the percentage surviving after the temperature of the water bath had attained the desired level. The results of this series of experiments were essentially the same as shown in Figure 3, *i.e.* oysters were killed more rapidly at higher temperatures. Gradual increase of temperature to 42°C and 45°C, in contrast to direct immersion, caused a more rapid death. For example, in this experiment 50 percent of the oysters were killed approximately three minutes after the water had reached 45°C whereas 50 percent were not killed until after 25 minutes of exposure when oysters were directly immersed in water of 45°C. Evidently much of the lethal effect was produced while the water was heating from 42°C to 45°C since all the oysters survived when removed from the water bath when the temperature had reached 42°C.

GENERAL DISCUSSION

The results of these experiments support the hypothesis of Fingerman and Fairbanks (1956) that bleeding is one of the responses of oysters exposed to injurious stimuli. Apparently oysters have not evolved protective mechanisms whereby they can prevent excessive losses of body fluids when exposed to harmful stimuli inasmuch as under natural conditions they can close their shells and isolate themselves from injurious agents in their environment. However, when they are unable to withstand the harmful stimuli as in the experiments reported above and those of Fingerman and Fairbanks (1956) the generalized response appears to be a loss of body fluids.

Fingerman and Fairbanks (1956) demonstrated that wedging open the valves of an oyster, a mechanical stimulus, caused this generalized bleeding. Likewise heat, a physical stimulus, evokes a generalized loss of body fluids. Presumably noxious chemical stimuli could evoke the same generalized bleeding response.

Henderson (1929) found 48.5°C was the upper thermal death temperature. However, as is evident from the present results, death will occur at lower temperatures if oysters are exposed for long periods of time. Furthermore, Henderson considered the lethal temperature was that temperature between the highest one from which all the oysters recovered and the lowest temperature from which no recovery was observed. He heated his oysters at the rate of 12° C per hour and found 48.5° C was the lethal temperature according to his criteria. The rate of 13.2° C per hour used in the present investigation is comparable to the rate employed by Henderson. Fifty percent of the oysters heated at the rate of 13.2° C per hour were killed at 47.5° C, a value quite similar to the value determined by Henderson. However, oysters from a cooler climate such as those of Henderson would be expected to be killed at a lower temperature than Louisiana oysters. He obtained his specimens from Buctouche, New Brunswick, where the mean water temperature is lower than that of the oyster producing waters of Louisiana, the source of the oysters used in the present investigation. Hathaway (1927) reported that lethal temperatures are lower for organisms from cooler environments. The unexpected result obtained by Henderson is probably due to the criteria for death that he employed. He considered oysters to be dead only if the shells gaped within 12 hours after exposure to high temperatures. However, in the present investigation the observation was made that some oysters will die with their adductor muscles fully contracted. Such oysters do not begin to gape until three to seven days after exposure to high temperature. Furthermore, with a high rate of rise of temperature fewer oysters are killed with their valves agape than with a low rate of temperature rise. According to the criteria of Henderson oysters that had been killed with their valves shut were considered alive giving a higher lethal temperature than the correct one, thus accounting for the unexpectedly high value obtained for the New Brunswick oysters.

Some of the data presented above appeared difficult to interpret and inconclusive without the aid of certain inferential tests. The chi-square test for common distribution seemed to be an appropriate non-parametric test (Walker and Lev, 1953) that could be applied with minimum assumptions to the data of Figure 2 and portions of the data of Figures 1 and 4.

Since the observed weight losses of the four different distributions represented in Figure 2 were all recorded at comparable temperatures and the notched oysters appeared to have lost no more weight than any of the intact oysters it was assumed that the oysters subjected to any one rate of temperature increase would have lost no more at higher temperatures than those recorded. No survival beyond the calculated time of maximum weight loss at these temperatures and rates (fig. 1) supports this assumption in indicating an early death precluded further weight loss. Five hypotheses were tested with the chi-square test at the five percent level of significance. The first hypothesis tested, involving the data of Figure 2, was that the weight losses of intact oysters subjected to different rates of increasing temperature, 0.74° C per hour, 4.5° C per hour, and 13.2° C per hour, all have a common distribution. The hypothesis was rejected ($P < 0.0005$).

The second hypothesis tested, also involving the data of Figure 2, was that the weight losses of intact oysters subjected to two different rates of increasing temperature, 4.5° per hour and 0.74°C per hour, and the weight loss of notched oysters subjected to the rate of 13.2°C per hour all have a common distribution. The hypothesis was accepted ($P = 0.645$).

The third hypothesis tested involved the data of Figure 4 that presented the weight losses of intact oysters subjected to direct immersion in estuarine water at 42°C and notched oysters immersed directly into estuarine water at 42°C. The hypothesis was that the two conditional weight loss distributions are the same. The hypothesis was accepted ($P = 0.081$).

Acceptance of the second and third hypotheses tested shows that the observations do not support a conclusion that the weight losses of notched oysters are different from the weight losses of intact oysters. The variability of weight losses of the notched oysters (fig. 4) appears to be as great as that of the intact oysters. In Figure 2 the data for notched oysters show only slightly less variability in weight loss distribution than do the intact oysters with the exception of the intact oysters subjected to 13.2°C per hour increase in temperature.

Acceptance of the second hypothesis tested shows that the observed weight loss distributions of oysters subjected to the rates of 4.5°C per hour and 0.74°C per hour do not support a conclusion that weight losses associated with these two rates are different from each other or different from weight losses by notched oysters subjected to 13.2°C per hour. Under these circumstances then the conclusion may be reached (from the sample evidence and the inferential tests) that rate of increase in temperature as such has very little influence over extent and rate of weight loss. Apparently, therefore, temperature and time only determine rate and extent of weight loss.

The fourth hypothesis tested involved the three conditional distributions of percentage survival represented in Figure 1. The hypothesis was that oysters subjected to the three different rates of increasing temperature, 13.2°C per hour, 4.5°C per hour, and 0.74°C per hour, have a common conditional distribution of percentages of survival. The hypothesis was rejected ($P < 0.001$).

The fifth hypothesis tested involved the two conditional distributions of percentage survival, 4.5°C per hour and 13.2°C per hour, represented in Figure 1. The hypothesis was that oysters subjected to the two different rates of temperature increase, 13.2°C per hour and 4.5°C per hour, have a common conditional distribution of percentages of survival. The hypothesis was accepted ($P = 0.600$).

SUMMARY

1. Experiments were designed to determine the upper thermal limit for the oyster *Crassostrea virginica* and to determine if loss of body fluid is associated with heat death.

2. All oysters survived temperatures below 35°C with no significant weight loss. Above 41°C appreciable death and weight loss occurred among the oysters. The slower the rate of temperature increase the lower was the temperature at which 50 percent of the oysters were killed. However, no significant correlation was evident between rate of temperature rise and weight loss.

3. Oysters can be killed by short exposure to high temperatures or long exposure to lower temperatures.

4. Oysters exposed to different temperatures for the same period of time lost more weight at higher temperatures than at low temperatures. Weight losses have been interpreted as due primarily to loss of body fluid.

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ABSTRACT

Oysters were taken directly from stock aquaria that contained estuarine water (salinity 17 ‰) at 22-23° C, weighed and placed for different periods of time in constant temperature baths maintained at 35, 40, 42, and 45° C. They were then removed, reweighed, placed in the stock aquaria for one hour, weighed again, and returned to the stock aquaria for several days when the percentage survival was determined. All oysters survived 35° C with no significant weight loss. Twenty-nine percent of the oysters exposed to 40° C for three hours died, 50 percent were killed in 117 minutes at 42° C, and 50 percent were killed in 25 minutes at 45° C. Evidently oysters can be killed by short exposure to high temperature or long exposure to a lower temperature. Oysters exposed for the same interval lost more weight at higher temperatures. Oysters were able to take back fluid in direct proportion to the amount lost during the exposure period. In the second series of experiments oysters were gradually heated from 24° to 45-55° C. The slower the temperature increase, the lower the temperature required to kill 50 percent of the oysters. With rapid temperature increase (13.2° C per hour) 50 percent were killed at 47.5° C, whereas with slow temperature rise (0.74° C per hour) 50 percent were killed at 41° C. Evidently, the lethal temperature varies with the conditions of the experiment.

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THE ODONATA OF LOUISIANA

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TULANE UNIVERSITY
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THE ODONATA OF LOUISIANA [1]

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There is no publication dealing with the Odonata of Louisiana on a statewide basis. Information is scattered in the literature and may be found under the following categories: (1) broad regional works with incidental mention of Louisiana; (2) faunal lists with incidental mention of the Odonata; (3) lists of the Odonata from particular portions of the state; (4) taxonomic studies including Louisiana material.

Hagen (1861) lists 19 species from Louisiana and in 1875 he records 14 as does Banks in 1892. Calvert (1893) lists nine species; Muttkowski (1910) records eight; Needham and Heywood (1929) nine; and Needham and Westfall (1955) list 56. Specific localities are not given for most of these records.

Among the papers which focus on Louisiana but which give only incidental mention to the odonates are those of Shufeldt (1884), Hine (1904, 1906), Glick (1939) and Behre (1950).

Many publications deal with restricted portions of the state. The earliest of this type is the unpublished manuscript of Foster and Smith (1901) which lists 60 species from "Lower Louisiana". Foster (1915), in another unpublished manuscript, lists 14 species from Mound in Madison Parish and Montgomery (1927) records 28 from Madison and Tensas Parishes. The most significant contribution is the work of the late Dr. Mike Wright who published extensively on the Odonata of the Southeastern States. Particularly pertinent to Louisiana are his papers of 1937, 1939, and 1943a, but all are restricted to the southern part of the state.

Primarily because of the Wright collections many recent taxonomic studies include Louisiana material. Among these are contributions by Borror (1942), Gloyd (1940), Walker (1952) and Westfall (1943).

The above sources and a few others list a total of 94 species from Louisiana. Twenty-three of these could not be verified by the writer. One-hundred-and-one species were collected or seen by the writer, 30 of which are new state records.

For areas other than Louisiana important information on the ecology of the Odonata is given by Howe (1921), Kennedy (1915, 1917, 1922b, 1928, 1938), Walker (1941, 1953) and Williamson (1932, 1934). Distribution and seasonal abundance of Indiana species is given by Montgomery (1942, 1944, 1947, 1948). Species composition in relation to physiography, climate and habitat has seldom been undertaken on a state or regional basis. Byers' (1930) analysis

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of the ecology of the Odonata of Florida is perhaps the most comprehensive work of this type.

The present study summarizes data from well over 1,000 collections obtained in all parts of Louisiana during a 20 year period. It presents the first statewide list of species, notes the habitat and behavior of many species, and analyzes distribution in relation to physiography, climate, and habitat.

Many persons assisted in this study. To all of them I extend my sincere thanks. Numerous collections were made by Drs. G. H. Penn and R. D. Suttkus of Tulane University and by my former students J. F. Aycock, L. L. Ellis, L. E. Hornuff and E. N. Lambremont. I was able to study specimens at various institutions in Louisiana because of the interest and cooperation of Drs. J. H. Roberts and O. W. Rosewall of Louisiana State University, Dr. L. T. Graham of Southwestern Louisiana Institute, Dr. J. E. Sublette of Northwestern Louisiana State College and Mr. W. J. Harman of Louisiana Polytechnic Institute. Dr. Sublette and Mr. Harman also personally obtained specimens in their areas. Drs. P. P. Calvert, E. M. Walker, M. J. Westfall and Mr. C. Cook checked certain determinations. I am particularly indebted to Mrs. L. K. Gloyd who not only checked many determinations but also provided unpublished notes which clarified taxonomic difficulties. Drs. T. H. Hubbell and E. J. Kormondy allowed me to study material at the University of Michigan Museum of Zoology, and Dr. Kormondy provided an important file of correspondence between Messrs. E. Foster and E. B. Williamson. Numerous studies of Dr. W. T. Penfound on various plant communities of Louisiana and my personal contact with him furnished an excellent background for this study.

This investigation summarizes collections and observations which began in 1935. Collections were from three sources: (1) those by the writer with detailed notes on habitat and often on behavior; (2) those by members of the Department of Zoology, Tulane University, where the habitat for each collection was described by a checking system and where the extent and accuracy of the information varied somewhat with the collector; (3) collections, from institutions other than Tulane, which gave only locality, date, and collector. It is apparent that information from all sources was not equivalent.

Although each of the state's 64 parishes were represented (fig. 1), collections were most frequent in Orleans and St. Tammany Parishes.[3] The rest of the state was sampled by planning the routes of many trips to include all physiographic areas and a variety of habitats. Collections were from all spots along the line of travel which seemed favorable. Both nymphs and adults were taken. However, many collections of *Libellula*, *Gomphus*, and *Macromia* nymphs and all collections of Zygoptera nymphs are omitted because I was not sure of the species.

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[3] *Parish* is the term used in Louisiana for the unit corresponding to county in all other states.

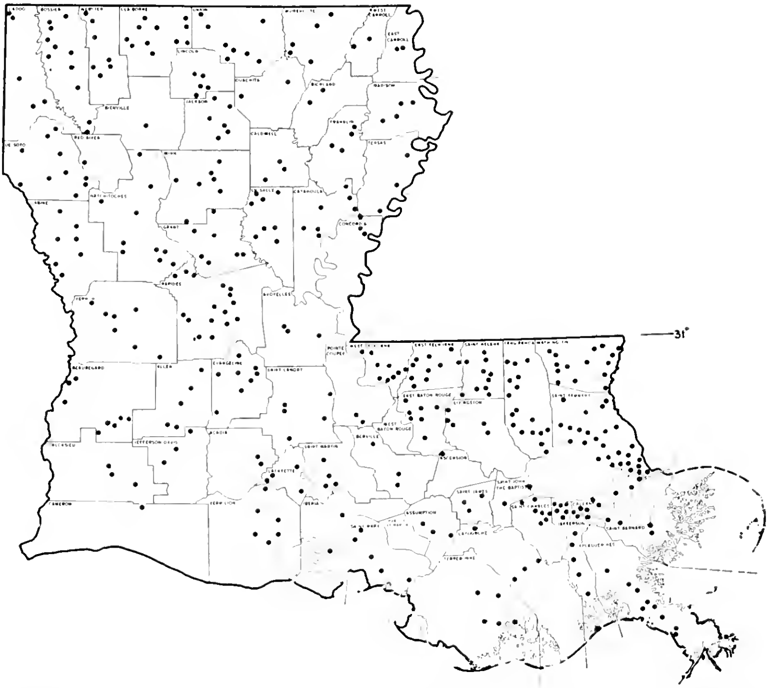

Figure 1. Louisiana parishes and collecting sites. Each of the state's 64 parishes was sampled and 101 species were taken in over 1,000 collections.

Collections were made with traditional net techniques. Original notes were always recorded in the field and are either in the card file of the invertebrate collection of Tulane University or in my notebooks. Adults were papered and nymphs placed in vials of 70% alcohol. Most specimens are in my personal collection, some are in the Tulane collection, and some at other colleges in Louisiana. Representative series were sent to the University of Michigan Museum of Zoology, the Philadelphia Academy of Natural Science, and Cornell University.

CLIMATE

The following salient features of the climate of Louisiana are largely from Dyke (1941). The climate is subtropical because of latitude and proximity to the Gulf. The mean annual temperature is 67° F for the state; 64.1° F in the extreme north and 70.8° F at the mouth of the Mississippi. Mean monthly temperatures (Table 1) vary from 51.8° F in January to 82.3° F in August. The growing season is 220 days in the north and 320 days in the south. From 1950 through 1954 the average January minimum never dropped below 30.9° F anywhere in the state.

TABLE 1.
MEAN MONTHLY TEMPERATURES AND RAINFALL FOR LOUISIANA

Month	Temperature (degrees F)	Rainfall (inches)
January	51.8	4.89
February	54.7	4.54
March	59.8	4.70
April	67.2	4.63
May	73.8	4.46
June	80.4	4.81
July	82.2	6.05
August	82.3	5.07
September	78.0	3.83
October	69.1	3.29
November	58.3	3.78
December	52.9	5.17
	Mean annual—67.0	Average annual—55.22

Rainfall is abundant throughout the state during all months and Visher (1955) states that the average annual precipitation of 55 inches is the highest of any state in the country. The wettest month is July with an average state precipitation of 6.05 inches, and the driest is October with a precipitation of 3.29 inches. Average annual precipitation is 46 inches in the northwest and 62 inches in the southeast.

PHYSIOGRAPHY

All of Louisiana is within the Gulf Coastal Plain. Most of the State is west of the Mississippi and belongs to the West Gulf Coastal Plain. The part of the state east of the Mississippi and north of Lake Pontchartrain is usually called the Florida Parishes and is entirely within the East Gulf Coastal Plain. East and West Coastal Plains are divided by the Mississippi Alluvial Plain with an average width of about 50 miles and a length of 596 miles through the state.

Holland (1944) divides the state into two main physiographic sections, the Tertiary Uplands in the northwest and the Quaternary Lowlands throughout the rest of the state. He further subdivides the Quaternary Lowlands into eight units which include outcrops of each Pleistocene terrace and the alluvial cones of each major river.

A preliminary survey showed little correlation between odonate distribution and the smaller physiographic units given by Holland. There were no species peculiar to the Bentley terrace, the Ouachita alluvial cone, etc. Instead of using these units, four large vegetation types were chosen which correspond in general with the physiographic areas of Holland (1944) and of Viosca (1933). In doing this I wish to stress that I am not proposing a new division of physiographic areas or of major vegetation types, but am merely grouping existing units. These four large areas (fig. 2) are characterized briefly as follows:

1. *Pinelands.* This includes the Tertiary Uplands and all Pleisto-

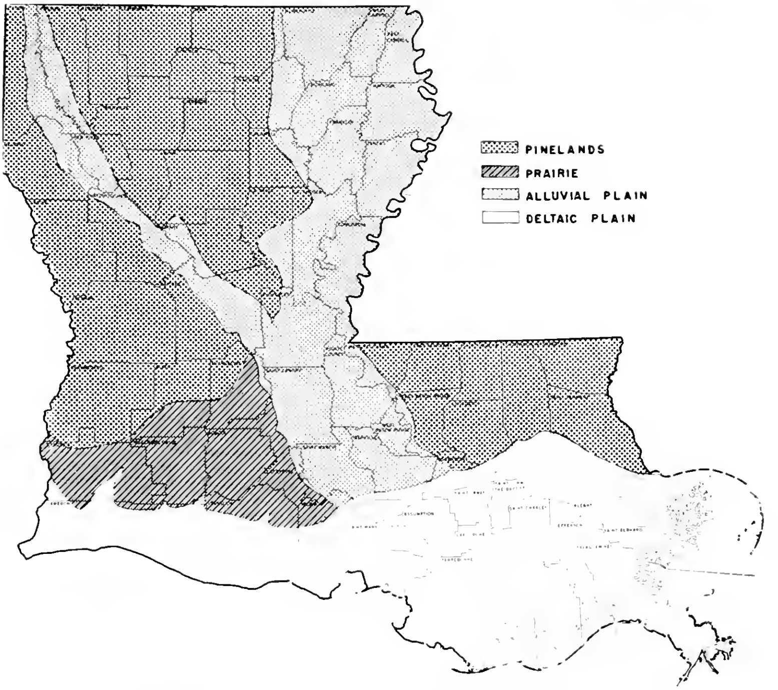

Figure 2. Major physiographic-vegetation areas of Louisiana.

cene terraces except the southwestern Prairie. The Tertiary Uplands of the northwest are primarily shortleaf pine forests. In this area are the highest lands of the state with elevations of approximately 500 feet. The terraces are primarily longleaf or loblolly pine forests. A variety of lentic and lotic habitats are present as a result of the varied topography. The pinelands are the only area in the state where swiftly flowing, clear streams are present. Farms are few and human population density is low. Collecting sites are numerous and varied.

2. *Alluvial.* The alluvial plain of the Mississippi north of Lake Pontchartrain and the alluvial plans of the Red and of the Ouachita Rivers are included here. The forests are primarily mixed hardwood of red gum, oak, elm, and hackberry. Some of the best agricultural lands in Louisiana are along the rivers in this area.

3. *Prairie.* This small area corresponds to Holland's Prairie terrace of southwestern Louisiana. The land is flat with a calcareous hardpan near the surface and the streams are very sluggish. There is a dense human population engaged mainly in rice and cattle growing. Rice cultivation results in extensive wet areas in season and in numerous irrigation canals. All localities are substantially alike and collecting was often impractical because of the dense rural population.

4. *Deltaic.* This area, identical with Holland's Deltaic plain unit, forms a wide band across the southern part of the state. An arbitrary line from the northern shore of Lake Pontchartrain, westward along the northern boundary of Cameron Parish to Texas, forms the northern boundary. The Gulf of Mexico forms the southern boundary. This very recent area was formed by extensions of the deltas of the Mississippi, Atchafalaya, Calcasieu, Sabine, and other rivers. Bordering the streams are the higher front lands which were originally live oak forests but are now mostly cultivated. Elevations are lower away from the streams so that the front lands gradually give way to cypress-tupelo gum swamps and still farther back to fresh water marshes. There are numerous collecting sites in the fresh water swamps, marshes, and borrow pits but most sites are substantially alike. The area is bordered on the south by brackish and salt marshes, but it should be emphasized that abundant fresh water habitats are present in the deltaic plain.

Certain of the habitats recognized in each physiographic unit require description. Borrow pits, very frequent in south Louisiana, are pond-like excavations which provide fill for highways. They may be as wide as 35 feet and extend for miles. Old, well established borrow pits are heavily vegetated and in deltaic areas are often completely covered by dense growths of water hyacinth *(Eichornia crassipes)* and alligator grass *(Alternanthera philoxeroides).*

Lakes in Louisiana never have rocky shores. Many are simply overflow areas of streams and are heavily vegetated with bald cypress *(Taxodium distichum)* and tupelo gum *(Nyssa aquatica).* Locally such areas are called swamps by some, lakes by others. The deep oxbow lakes are always referred to as lakes, but they are often bordered by large swampy areas or by fresh marshes or both so that differences between lake, swamp, and marsh are difficult to define.

Sloughs are small, shallow, static, acid waters in the pinelands with dense stands of black gum *(Nyssa biflora)* and usually with smaller numbers of pond cypress *(Taxodium ascendens).* Sloughs are very different from the extensive swamps of the alluvial and deltaic areas where the waters are invariably alkaline and where the dominant trees are bald cypress *(Taxodium distichum)* and tupelo gum *(Nyssa aquatica).*

Bayou, a term applied to many kinds of streams in the state, is actually a very sluggish stream whose current is reversible. Such streams occur primarily in southern Louisiana where the gradient is very slight. In this study the term bayou is omitted and collections from them are included under the expression sluggish streams.

LIST OF SPECIES

The 101 species collected in Louisiana and seen by the writer are summarized in the following list. The 30 species recorded from the state for the first time are marked with an asterisk.

PETALURIDAE (one species): *1. *Tachopteryx thoreyi.*

CORDULEGASTERIDAE (two species): *2. *Cordulegaster fasciatus*, 3. *C. maculatus*.

GOMPHIDAE (13 species): 4. *Progomphus obscurus*, 5. *Aphylla wiliamsoni*, 6. *Hagenius brevistylus*, *7. *Ophiogomphus mainensis*, *8. *Erpetogomphus designatus*, 9. *Dromogomphus spinosus*, *10. *D. spoliatus*, 11. *Gomphus (Arigomphus) submedianus*, 12. *Gomphus (Gomphus) flavocaudatus*, *13. *G. (G.) hodgesi*, *14. *G. (G.) lividus*, *15. *G. (Stylurus) amnicola*, *16. *G. (S.) plagiatus*.

AESHNIDAE (nine species): 17. *Gomphaeschna antilope*, *18. *G. furciliata*, *19. *Basiaeschna janata*, 20. *Boyeria vinosa*, 21. *Anax junius*, *22. *Anax longipes*, 23. *Coryphaeschna ingens*, 24. *Nasiaeschna pentacantha*, 25. *Epiaeschna heros*.

LIBELLULIDAE (43 species): 26. *Didymops transversa*, *27. *Macromia georgina*, 28. *M. taeniolata*, *29. *Neurocordulia alabamensis*, 30. *N. molesta*, *31. *N. virginiensis*, 32. *Epicordulia princeps*, 33. *Tetragoneuria cynosura*, 34. *Helocordulia uhleri*, 35. *Somatochlora linearis*, 36. *Perithemis tenera*, *37. *Celithemis amanda*, 38. *C. elisa*, 39. *C. eponina*, 40. *C. fasciata*, 41. *C. ornata*, 42. *Macrodiplax balteata*, *43. *Orthemis ferruginea*, 44. *Ladona deplanata*, 45. *Libellula auripennis*, 46. *L. axilena*, *47. *L. flavida*, 48. *L. incesta*, *49. *L. luctuosa*, 50. *L. needhami*, 51. *L. pulchella*, 52. *L. semifasciata*, 53. *L. vibrans*, 54. *Plathemis lydia*, 55. *Erythrodiplax berenice*, 56. *E. connata minuscula*, 57. *E. umbrata*, 58. *Sympetrum ambiguum*, 59. *Tarnetrum corruptum*, 60. *Erythemis simplicicollis*, 61. *Cannacria gravida*, 62. *Pachydiplax longipennis*, 63. *Miathyria marcella*, 64. *Tramea carolina*, 65. *T. lacerata*, 66. *T. onusta*, 67. *Pantala flavescens*, 68. *P. hymenea*.

AGRIONIDAE (four species): 69. *Agrion dimidiatum*, 70. *A. maculatum*, 71. *Hetaerina americana*, 72. *H. titia*.

LESTIDAE (three species): 73. *Lestes disjunctus australis*, *74. *L. inaequalis*, *75. *L. vigilax*.

COENAGRIONIDAE (26 species): 76. *Argia apicalis*, *77. *A. bipunctulata*, 78. *A. fumipennis*, 79. *A. moesta*, 80. *A. sedula*, 81. *A. tibialis*, 82. *A. violacea*, *83. *Nehalennia integricollis*, *84. *Teleallagma daecki*, *85. *Enallagma basidens*, 86. *E. civile*, 87. *E. concisum*, 88. *E. divagans*, *89. *E. dubium*, 90. *E. durum*, 91. *E. exsulans*, 92. *E. geminatum*, 93. *E. signatum*, *94. *E. traviatum*, *95. *E. vesperum*, *96. *E. weewa*, *97. *Ischnura kellicotti*, 98. *I. posita*, 99. *I. prognatha*, 100. *I. ramburi*, 101. *Anomalagrion hastatum*.

Habitat data for each of these 101 species are given in the following section. An additional 23 species reported in the literature are discussed separately under the heading "Records of species not seen by the writer".

Distribution within the state for most species is listed by parishes. Specific locality as well as parish is given for species recorded from Louisiana for the first time and for those with unusual distribution. Literature records are given in the paragraph headed "Louisiana Records", and data on specimens collected or seen by the writer are listed in the paragraph headed "Collections". The total number of collections of each species seen by the author is given in parentheses.

Because ease of capture of the adults varied greatly with the species depending on behavior and flight patterns and because many nymphs were too young to permit species determination, the exact number of individuals collected is not recorded except for scarce species.

Estimates of abundance are given for certain species.

As collecting was neither random nor equivalent in all areas, precise statistical methods are not used to show frequency of occurrence. Instead frequency percentage figures are often used to present comparisons of species composition in relation to physiography and habitat. These figures are recorded only when there are 10 or more collections of a species. Frequency percentages figures do not always total 100 because a listing of infrequent areas and habitats would be too lengthy.

PETALURIDAE

*1. *Tachopteryx thoreyi* (Hagen)

Collections.—St. Tammany. Talisheek, April 3, 1955, 1♂, 1♀; *Union.* Marion, June 24, 1950, 1♂, E. N. Lambremont, ("flying in an open spot in an oak forest").

The Talisheek specimens were from sunny openings in the pine woods. The male perched five feet above ground on the trunk of a pine about 50 feet from the edge of Talisheek Creek; the female was flushed from low weeds and flew a few feet to the trunk of the nearest pine where it was captured at a height of five feet. The female carried a female *Didymops transversa* which had been reduced to a half-eaten thorax, wings, and abdomen.

CORDULEGASTERIDAE

*2. *Cordulegaster fasciatus* Rambur

Collections.—Webster. Caney Lake, January 28, 1950, 1 nymph, A. Chaney.

This collection is a considerable westward extension of the range of this southeastern United States species recorded by Needham and Westfall (1955) from only Georgia, Florida, and North Carolina. The nymph was taken, with *Cordulegaster maculatus,* from a shaded, sand-bottomed creek with clear water.

3. *Cordulegaster maculatus* Selys

Louisiana Records.—Needham and Westfall (1955). *St. Tammany* (Wright, 1939).

Collections.—Webster. Caney Lake, January 28, 1950, 2 nymphs, A. Chaney. These nymphs were part of the collection described above for *C. fasciatus.*

GOMPHIDAE

4. *Progomphus obscurus* (Rambur)

Louisiana Records.—Foster and Smith (1901), Needham and Westfall (1955). Grant (Byers, 1939; Wright, 1939). St. Tammany (Byers, 1939; Wright, 1939; Bick, et al, 1953).

Collections.—Allen, Bossier, Claiborne, East Baton Rouge, East Feliciana, Grant, Livingston, Rapides, St. Tammany, Tangipahoa, Union, Vernon, Washington, West Feliciana (53 collections of nymphs, nine of adults).

P. obscurus was collected only in pinelands along swiftly flowing streams. Adults commonly rested on sunny sand bars and often returned to the same spot, yet were difficult to capture.

The creeks where nymphs were collected were sand (56%) or gravel (22%) bottomed, devoid of vegetation, and less than 15 inches deep. There is a marked discrepancy between 53 collections of nymphs and nine of adults. Byers (1939) discusses this matter and summarizes the ecology of the species.

Adults were collected from April 14 to July 17, but as Needham and Westfall (1955) record a flight season from February (Florida) to September (Texas), I am confident that adults are present in Louisiana earlier than April 14 and later than July 17.

5. *Aphylla williamsoni* Gloyd

Louisiana Records.—Needham and Westfall (1955). Orleans (Wright, 1939, 1943a; Needham, 1940; Bick and Aycock, 1950). St. Charles (Needham, 1940; Wright, 1943a). St. Tammany (Wright, 1939).

Collections.—*Beauregard,* Hollingsworth, September 9, 1952, 1♀; *Jefferson,* Kenner, October 27, 1952, 3 nymphs; *East Baton Rouge,* Baton Rouge, September 27, 1953, 1♀; *Orleans,* New Orleans, July 11, 1949, 1♂.

All collections were from southern Louisiana and the Hollingsworth collection is the westernmost record of the species. Habitat data are based on personal knowledge of the eight collections reported in the literature and on the four detailed above. Nine collections were from the deltaic plain in the vicinity of New Orleans, two from the pinelands and one from an alluvial area.

Seven collections of nymphs were from exposed, mud-bottomed ponds with three to four feet of water where vegetation was scanty or absent and two were from sluggish streams. All nymphs, except those in transformation, were taken by sifting the bottom muck through a Needham scraper.

The writer collected but one adult, a female perched two feet above ground on a small weed adjacent to a pineland pond. In Florida, Mr. Aycock collected 220 nymphs from a limestone pit but no adults except those in transformation. Gloyd (1936) considers the adults shy, restless, and rapid in flight.

Adults were taken in Louisiana during June, July, and September. Hornuff (1950) states that emergence extends from late April to late July. Needham and Westfall (1955) report a flight season from April 14 to November 2 in Florida.

6. *Hagenius brevistylus* Selys

Louisiana Records.—Needham and Westfall (1955). Grant (Wright, 1939, 1944). St. Helena (Wright, 1939). St. Tammany (Bick, et al, 1953).

Collections.—Allen, East Feliciana, Rapides, St. Helena, St. Landry, St. Tammany, Tangipahoa, Vernon, Washington (17 collections of nymphs, two of adults).

This species was limited to swiftly flowing streams in the pinelands of southeastern and central Louisiana. Nymphs were nearly always in the shallow water of sand-bottomed streams among log drifts and accumulated debris. Byers (1930) notes that *brevistylus* is a stream form in Florida but that it occurs in both streams and lakes in Michigan.

Adults were collected on June 4 and July 16.

*7. *Ophiogomphus mainensis* Packard

Collections.—Tangipahoa, Roseland, October 2, 1948, 2 nymphs; *Washington,* Varnado, January 19, 1952, 4 nymphs.

There are no previous Louisiana records of this northeastern United States species but Needham and Westfall (1955) report it from Alabama. The above Louisiana records are the westernmost for the species.

The nymphs from Roseland were in shallow water at the margin of the Amite River at a spot where the river is wide, swiftly flowing and devoid of vegetation or debris. The bottom was covered with gravel which afforded excellent concealment for these brown nymphs. Other odonates were not taken at this distinctive habitat. The nymphs from Varnado were taken with *Erpetogomphus designatus, Progomphus obscurus, Hagenius brevistylus,* and *Macromia* sp. from the swiftly flowing Pushepatapa Creek in darkly stained water, two to 24 inches deep.

*8. *Erpetogomphus designatus* Hagen

Collections.—Washington, Varnado, January 19, 1952, 1 nymph, R. D. Suttkus. This nymph was part of the Washington Parish collection described for *O. mainensis.* It is difficult to account for the apparent scarcity in Louisiana of this widespread eastern United States species which the writer found easy to capture and common at several localities in Oklahoma.

9. *Dromogomphus spinosus* (Selys)

Louisiana Records.—Foster and Smith (1901), Needham and Westfall (1955). Grant and St. Helena (Wright, 1939). St. Tammany (Wright, 1939; Bick, et al, 1953).

Collections.—Allen, East Feliciana, Iberia, Grant, Livingston, Madison, Rapides, St. Helena, St. Tammany (12 collections of nymphs, seven collections of adults).

Sixteen collections were from the pinelands, two from alluvial areas and one from the deltaic plain. Nymphs were taken most often with *Hagenius brevistylus, Progromphus obscurus, Didymops transversa,* and *Macromia* sp. from small, shallow, sandy creeks.

The flight season was from June 8 to September 11.

*10. *Dromogomphus spoliatus* (Hagen)

Collections.—Bossier, East Feliciana, St. Tammany, Tangipahoa, Washington, Webster (ten collections of nymphs).

D. spoliatus was collected only in the pinelands of two widely separated areas, northwestern Louisiana and the Florida Parishes. All collections were from streams, but two were from pools isolated from the flow, and two were from large expanded portions of swamplike streams. *D. spoliatus* was taken with a variety of both lentic and lotic species including *Erythemis simplicicollis, Somatochlora linearis, Tetragoneuria cynosura, Libellula lydia, Progomphus obscurus, Boyeria vinosa.*

11. *Gomphus (Arigomphus) submedianus* Williamson

Louisiana Records.—Needham and Westfall (1955).

Collections.—Morehouse, Perryville, June 25, 1950, 1♀; *Rapides,* Holloway, July 31, 1953, 1♂.

Both collections were from alluvial areas in the northeastern quarter of the state. The individual from Holloway perched on the ground in the extensive flats bordering Catahoula Lake and the Perryville individual perched on weeds in an open field near a sluggish stream.

12. *Gomphus (Gomphus) flavocaudatus* Walker

Louisiana Records.—Needham and Westfall (1955, page 213): "Probably to be considered a variety of *exilis.*" *Tangipahoa,* Hammond, March 26, 1938, seven males (type locality, Walker, 1940).

Collections.—St. Tammany, Tangipahoa, Washington (14 collections of adults including 26 males, 10 females and one tandem pair).

This species was collected only from the pinelands of the Florida Parishes near deeply stained, acid water. Most collections were from lentic water including sloughs, ponds, and borrow pits; two collections were adjacent to swiftly flowing creeks.

The largest number of individuals was taken four miles east of Hammond where six flew low along a roadside ditch having little vegetation and five along a large well established borrow pit almost covered with *Nuphar.* At Slidell, ten individuals were collected as they perched low on vegetation some 50 feet from the margin of a small pond. In spite of careful search of all apparent transformation sites at this pond when teneral adults were present in the immediate area, nymphal skins were not found.

G. flavocaudatus adults were collected between March 3 and May 7, a pair in tandem was taken on April 3, but none were collected during many trips to the above localities between June and September. It seems clear that *flavocaudatus* is an early season form.

*13. *Gomphus (Gomphus) hodgesi* Needham

Collections.—St. Tammany, Talisheek, March 1, 1954, 3♂, teneral; March 12, 1955, 3♂, 1♀, 1 pair in tandem, all teneral; April 3, 1955, 1♀ (three collections of adults).

The three Louisiana collections were in the immediate vicinity of Talisheek Creek which is a swiftly flowing, cold, pineland stream, 10 to 15 feet wide. The bottom is mostly sand and the depth varies from a few inches to three feet. There are scattered patches of

Potomageton in the stream and marginal patches of *Zizaniopsis.* Three teneral males were taken in full sunlight among weeds at the cleared area around the bridge and the others were collected on low shrubs in exposed portions of the pine woods approximately 50 feet from the creek. Adults did not fly along the creek or perch at its immediate edge.

All Louisiana collections were between March 1 and April 3 and in spite of many trips to Talisheek adults were not collected previous and subsequent to these dates. Needham (1950) records adults in Alabama and Mississippi on March 1, April 16, and May 17. Although the total number of collections of *hodgesi* in Louisiana is only three, a brief early flight season is indicated.

*14. *Gomphus (Gomphus) lividus* Selys

Collections.—Lincoln, Ruston, April 19, 1940, 1 ♂; March 31, 1940, 1 ♀ (Louisiana Polytechnic Institute); *Natchitoches,* Provencal, April 10, 1953, 2 ♂; *Tangipahoa,* Natalbany, April 3, 1954, 2 ♂ (four collections of adults).

G. lividus was collected from widely separated localities in the pinelands. Habitat data are available for only the Natalbany and Provencal collections which were from small, shallow, sandy creeks in heavily forested areas. Individuals of *G. lividus* frequently perched on the sand of creek beds and often returned to the same spot when disturbed, yet they were difficult to capture. This behavior pattern is similar to that of *Progomphus obscurus.*

*15. *Gomphus (Stylurus) amnicola* Walsh

Collections.—Washington, Varnado, along Pearl River, June 2, 1948, 1 ♀, L. L. Ellis. This northeastern United States species is reported from Alabama (Needham and Westfall, 1955) but not from any other Gulf State.

*16. *Gomphus (Stylurus) plagiatus* Selys

Collections.—Caldwell, Columbia, August 1, 3, 6, 1948, 2 ♂, 1 ♀, L. L. Ellis; *Catahoula,* Harrisonburg, 1 ♀ ("caught by a robber fly"), June 14, 1950, E. N. Lambremont; *West Carroll,* Wallace Landing, August 29, 1949, 1 ♂, 1 ♀; *St. Tammany,* Indian Village, August 26, 1955, 1 ♀, R. D. Suttkus (six collections of adults).

Five collections were from alluvial areas in the northeastern part of the state and one from the pinelands of the southeast. All specimens were from sunlit areas.

Collections are too few to generalize on the flight season but the collection of *plagiatus* adults on August 29 was the latest for any species of *Gomphus* in Louisiana.

AESHNIDAE

17. *Gomphaeschna antilope* (Hagen)

Louisiana Records.—Needham and Westfall (1955). Orleans (Gloyd, 1940).

Collections.—Orleans. New Orleans, April 11, 1949, 1♂; May 14, 1949, 2♀.

These New Orleans collections are the westernmost for the species. The three specimens were all taken in buildings. Such indoor collections are not unusual as Gloyd (1940) records a female from the ninth floor of a building in a built-up section of Philadelphia and another female from the third story of the U. .S. National Museum in Washington.

All Louisiana collections of *Gomphaeschna* nymphs were from swamps. Martin (1940) records a nymphal skin, believed to be *Gomphaeschna*, from an unspecified locality in Louisiana. The habitat is described as a densely shaded, pineland, black gum swamp, with black, acid water (pH 5.1-5.3), and mud bottom. Needham and Westfall (1955) state that this skin seems to be *Gomphaeschna* by exclusion. Two nymphs in my collection are *Gomphaeschna* but since nymphs of *antilope* and *furcillata* have not been differentiated these specimens can not be placed as to species. One nymph was from a swamp at Kelley's in Jackson Parish, the other from a swamp near Lafayette in Lafayette Parish. Both these swamps have been either drained or dammed and cleared subsequent to collecting the nymphs.

*18. *Gomphaeschna furcillata* (Say)

Collections.—Orleans. New Orleans, February 3, 1950, 1♀; February 10, 1953, 1♀; February 10, 1954, 1♂; February 29, 1956, 1♀; *Jackson.* Eros, April 1, 1950, 1♂; *Madison.* Tallulah, April 7, 1950, 1♀ (six collections of adults).

G. furcillata occurred in widely separated localities in the deltaic plain, pinelands, and in alluvial areas. All collections of adults were early in the season between February 3 and April 7. On the Tulane University campus one adult was collected on almost the same date in early February for each of three years. The flight season in Louisiana is probably longer than these early records show as Needham and Westfall (1955) record adults in Michigan as late as August.

*19. *Basiaeschna janata* Say

Collections.—Washington. Varnado, three miles east, January 19, 1952, 3 nymphs, R. D. Suttkus.

These nymphs were collected with *Hagenius brevistylus* and *Boyeria vinosa* from a small tributary creek of the Pearl River in a heavily wooded area. The brown, flowing water, six to 30 inches deep, covered a bottom of silt and gravel.

20. *Boyeria vinosa* (Say)

Louisiana Records.—Foster and Smith (1901); Needham and Westfall, (1955). Grant (Wright, 1939). St. Tammany (Bick, et al, 1953) .

Collections.—Bossier, Grant, East Feliciana, Livingston, Natchitoches, Rapides, St. Helena, St. Tammany, Tangipahoa, Vernon, Washington, West Feliciana (37 collections of nymphs).

Although widely distributed *Boyeria vinosa* occurred solely in the pinelands. Nymphs were taken from flowing streams, most often in clear water (80%), with sandy (67%) bottoms. Living adults were collected neither by Byers (1930) in Florida nor by the writer in Louisiana. However, on August 10, 1954, a complete set of wings in good condition was collected in a dry creek bed at Provencal in Natchitoches Parish. The situation here appeared similar to that described by Williamson (1932) who surmised that the severed wings which he found were "discarded fragments from a *Hagenius* lunch counter". The absence of adults in Louisiana collections is doubtless due to the limited number of collections at sunset when *vinosa* becomes active.

21. *Anax junius* (Drury)

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955). Cameron (Hine, 1904). Jefferson (Wright, 1944; Behre, 1950). Madison (Foster, 1915; Montgomery, 1927; Glick, 1939). Orleans (Wright, 1944, 1946a; Penn, 1950). Plaquemines (Wright, 1943a). St. Tammany (Bick, et al, 1953).

Collections.—Allen, Beauregard, Calcasieu, Cameron, Claiborne, Concordia, East Baton Rouge, Evangeline, Franklin, Iberia, Iberville, Jefferson, Lafayette, Lafourche, Lincoln, Madison, Natchitoches, Orleans, Ouachita, Plaquemines, Rapides, Richland, St. Bernard, St. Charles, St. Martin, St. Mary, St. Tammany, Tangipahoa, Terrebonne, Vermilion, Vernon, Washington, West Feliciana (73 sight records of adults, 71 collections of adults, 56 collections of nymphs).

A. junius was collected in 33 parishes, was widely distributed in every physiographic area, but was less frequent and abundant than the ubiquitous *Pachydiplax longipennis* and *Erythemis simplicicollis.* The green darner seldom occurred in swarms as did *Libellula needhami* and *Pantala flavescens.* Yet once, on September 27, 1953, over the marshes of Grand Isle in the Gulf I saw more dragonflies than ever before in a limited area and estimated that at least 1,000 adults of *junius* were in a swarm. Hundreds of individuals of *Tramea carolina* and *Pachydiplax longipennis* were also in the swarm. Since prolonged flight in any one direction was not noted this great concentration was probably the result of mass emergence rather than of migration. On the same date, 12 dead but undamaged individuals were collected along the beach near the water's edge and one dead specimen was carried down into the hole of a crab.

On each of two occasions an adult of *A. junius* dove among a swarm of *Pantala flavescens*, captured one and descended swiftly to the ground where both captor and prey were lost from sight.

Nymphs were collected nearly always (92%) in lentic water which was most often ponds (47%) but they were also taken from a variety of other habitats including one collection from a brackish marsh and one from a swiftly flowing pineland stream. The habitats were nearly always (92%) mud bottomed and were usually heavily vegetated.

A. junius was collected during every month of the year and adults were absent only between December 14 and January 19. This is the longest seasonal range of any anisopteran in Louisiana. The flight season for 1948 was from April 1 to December 4, for 1949 from January 22 to October 16, for 1950 from March 10 to December 14, for 1951 from March 3 to December 6, for 1952 from January 19 to October 27, for 1953 from March 22 to November 13, and for 1954 from May 6 to November 21.

*22. *Anax longipes* Hagen

Collections.—St. Tammany, Hickory, May 23, 1954; 1 adult; Indian Village, August 30, 1953, 1 adult (two sight records of adults).

Bick (1953) reports this species from Mississippi and summarizes the United States distribution. The individual at Indian Village flew swiftly over a large, shallow pond and allowed but a brief glimpse; the one at Hickory flew more slowly and followed a fairly regular path in an exposed portion of a slough.

23. *Coryphaeschna ingens* Rambur

Louisiana Records.—Cameron (Hine, 1906). Jefferson (Wright, 1944; Behre, 1950). Orleans (Wright, 1946a). Plaquemines (Wright, 1943a). St. Tammany (Wright, 1943a, 1944; Bick, et al, 1953).

Collections.—Allen, East Baton Rouge, Jefferson, Lafayette, Orleans, St. Bernard, St. Charles, St. Helena, St. James, St. Tammany, Tangipahoa, Terrebonne, Vernon (20 collections of adults, 19 of nymphs).

Although recorded from North Carolina and from northern Mississippi, *C. ingens* was restricted to the southern half of Louisiana where it occurred with equal frequency in the pinelands and in the deltaic plain.

All nymphs were from heavily vegetated ponds or from roadside borrow pits.

A swarm was noted at sunset on May 4 along a road through a swamp and six specimens were captured. Wright (1943a) reports frequent swarms just before dusk, and at Pearl River during September saw a swarm estimated at 200 dashing after gnats and tipulids. He (1944, 1946a) discusses damage to honey bees by *C ingens* in the New Orleans area.

The limits of the flight season were April 15 and October 3.

24. *Nasiaeschna pentacantha* Rambur

Louisiana Records.—Williamson (1899); Foster and Smith (1901); Needham and Westfall (1955). Madison (Montgomery, 1927). Orleans (Hagen, 1875). St. Tammany (Bick, et al, 1953).

Collections.—Ascension, Assumption, De Soto, East Baton Rouge, Jefferson, Iberville, Lafayette, Natchitoches, Orleans, Plaquemines, Richland, St. Charles, St. Tammany, Tangipahoa, Washington (27 collections of nymphs, 17 of adults).

This species was widely distributed but infrequent and never abundant. Fifty-four percent of all collections were from the deltaic plain, 39 percent from pinelands. Eight collections of adults were in buildings. Nymphs occurred in lentic or in very sluggish water, mostly in borrow pits, swamps and ponds.

Adults were collected between March 30 and October 12.

25. *Epiaeschna heros* (Fabricius)

Louisiana Records—Foster and Smith (1901); Needham and Westfall (1955). Cameron (Hine, 1906). Orleans (Shufeldt, 1884; Penn, 1950).

Collections.—Allen, Bossier, Caddo, Cameron, East Baton Rouge, East Feliciana, Evangeline, Grant, Iberville, Jackson, Jefferson, Lafayette, Lafourche, Livingston, Natchitoches, Orleans, St. Charles, St. Landry, St. Tammany, Tangipahoa, Terrebonne, Washington, Webster, West Feliciana, Winn (45 collections of nymphs, 21 of adults).

E. heros occurred in all physiographic areas but was most frequent (60%) in the pinelands. Adults were seldom abundant, but on one occasion along a small, swiftly flowing, pineland creek, approximately ten individuals flew a straight course without perching and seven were easily captured. On July 4, at the edge of an extensive swamp about 20 individuals were observed as they repeatedly flew into a large swarm of *Libellula needhami* and pursued certain individuals. One specimen of *heros* was collected carrying a captured *L. needhami.*

Nymphs occurred almost entirely (96%) in lentic water and 51 percent of all collections of nymphs were from swamps. *E. heros* was one of the few members of the limited odonate fauna of swamps.

Earliest and latest dates for adults were February 22 (1949) and October 28 (1950). The October record was exceptional but adults were collected on March 6, 1940, March 23, 1955, March 26, 1949, and 76 percent of all collections were prior to June.

LIBELLULIDAE

26. *Didymops transversa* (Say)

Louisiana Records.—St. Tammany (Bick, et al, 1953).

Collections.—East Feliciana, Grant, Natchitoches, Rapides, St. Tammany, Tangipahoa, Washington (ten collections of nymphs, three of adults).

Didymops transversa was collected from scattered localities in the pinelands of the Florida Parishes and the central part of the state. All nymphs were from flowing streams; eight collections were from small, shallow, sand-bottomed streams, and two from large rivers. *D. transversa* nymphs were associated with *Progomphus obscurus*, *Hagenius brevistylus*, and *Boyeria vinosa.*

Adults were collected on March 12, April 3, and April 10 near swiftly flowing streams in densely wooded areas.

*27. *Macromia georgina* Selys

Collections.—*La Salle*, Olla, July 29, 1953, 1 ♂; *St. Tammany*, St. Tammany, May 12, 1949, 1 ♂.

Both collections were along creeks in heavily wooded areas in the pinelands. One creek was narrow, shallow, swift, and clear; the other was deeper, more sluggish, and somewhat turbid. Numerous collections of *Macromia* nymphs are not included in this paper because specific identification is not clear to me.

28. *Macromia taeniolata* Rambur

Louisiana Records.—Needham and Westfall (1955). Madison (Montgomery, 1927).

Collections.—Catahoula, Lafayette, Morehouse, Ouachita, St. Tammany, Tangipahoa, Union (eight collections of adults).

M. taeniolata was one of a very few species collected frequently in alluvial areas; it was also present in the pinelands but not in the deltaic plain. There are no obvious habitat differences between the sluggish mud-bottomed streams of the alluvial areas where *taeniolata* was taken and those of the deltaic plain where no species of *Macromia* was seen or collected.

Most collections were along sluggish, mud-bottomed streams but one was along a swiftly flowing, sandy creek and one was from a large pond.

Adults were collected between May 7 and August 11.

*29. *Neurocordulia alabamensis* Hodges

Collections.—*St. Tammany*, Covington, August 10, 1948, 2 nymphs; Talisheek, August 28, 1954, 3 nymphs; *Tangipahoa*, Tangipahoa, August 13, 1948, 2 nymphs; *Washington*, Enon, August 10, 1948, 4 nymphs (four collections of nymphs).

These are the westernmost records for *alabamensis*, previously recorded by Needham and Westfall (1955) from only Alabama, Florida, Georgia, and South Carolina. All Louisiana collections were from the pinelands of the Florida Parishes in clear, flowing creeks with bottoms of sand or of sand and gravel. The nymphs were collected with *Cordulegaster* sp, *Dromogomphus spinosus, Hagenius brevistylus*, and *Progomphus obscurus*.

30. *Neurocordulia molesta* Walsh

Louisiana Records.—Needham and Westfall (1955).

Collections.—*Washington*, Angie, June 3, 1950, 1 nymph; *St. Landry*, Washington, June 22, 1948, 1 nymph.

The Angie collection was from the Pearl River in clear, flowing water with a gravel bottom; the other nymph was from the more sluggish, turbid and mud-bottomed Bayou Courtableau.

*31. *Neurocordulia virginiensis* Davis

Collections.—*St. Tammany*, Talisheek, March 12, 1955, 1 nymph.

This nymph was taken with *Dromogomphus spinosus* from a dense patch of *Potomageton* in a shoal area of a small, swift, shallow, sandy, clear water creek in the pinelands. Collecting was frequent at this locality during all seasons but *Neurocordulia* adults were not taken here or elsewhere in Louisiana. Perhaps this is due to the scarcity of collections at twilight when the adults become active.

32. *Epicordulia princeps* (Hagen)

Louisiana Records.—Needham and Westfall (1955). Madison (Montgomery, 1927).

Collections.—Allen, Avoyelles, Catahoula, Claiborne, Jefferson, Madison, Ouachita, Rapides, St. Landry, Union, West Feliciana (six collections of adults, six sight records of adults, one collection of nymphs).

This species was uncommon and, like *Macromia taeniolata,* was found most often (60%) in alluvial areas. Many years of collecting in the deltaic plain yielded but one nymph from a pond.

Adults were most frequent along large, sluggish streams, with mud bottoms, turbid water, and little or no aquatic vegetation. Wright (1943b) states that *princeps* nymphs always occur on rich mucky bottoms with scanty vegetation and he notes that nymphs were present at one end of a reservoir with a mucky bottom but not at the other end where the bottom was fine sand and gravel.

The flight season was from June 23 to August 19.

33. *Tetragoneuria cynosura* (Say)

Louisiana Records.—Hagen (1875); Calvert (1893); Williamson (1899); Foster and Smith (1901); Martin (1906); Muttkowski (1910); Needham and Heywood (1929); Byers (1930); Needham and Heywood (1929); Byers (1930); Needham and Westfall (1955).

Collections.—De Soto, Jackson, Jefferson, Lincoln, Orleans, Pointe Coupee, Rapides, St. John the Baptist, St. Martin, St. Tammany, Tangipahoa, Washington, Webster, Winn, West Feliciana (37 collections of nymphs, 27 of adults).

T. cynosura was most frequent (74%) in the pinelands but was also found in alluvial and deltaic areas. Nymphs were from lotic (33%) and from varied lentic habitats, including ponds and lakes (33%), borrow pits (22%), and sloughs and swamps (11%). At Bayou Lacombe, Bick, et al (1953) record nymphs as *spinosus,* through typographical error, from stations with practically no flow as well as from others with a definite flow. Nymphs were taken most often (69%) where the bottom was mud and nearly always (92%) among vegetation.

All collections of adults were early in the season between February 17 (1950) and May 3 (1940). The flight season was March 9 to April 8 in 1949, February 17 to April 9 in 1950, and February 21 to March 30 in 1954. Bick (1950) records adults in Mississippi from April to August so it is assumed that they will be taken in Louisiana later than May 3.

34. *Helocordulia uhleri* (Selys)[4]

Louisiana Records.—Needham and Westfall (1955). St. Helena

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[4] After the manuscript of this paper had been put into type I read *Variations in a Local Population of the Dragonfly Helocordulia* (McMahan, E. A. and I. E. Gray, *Ann. Ent. Soc. Amer.*, 50: 62-66, 1957). This caused me to reconsider determinations of *Helocordulia*. A personal communication from Dr. E. J. Kormondy states that legends for male appendages of *uhleri* and of *selysii* (figures 231 and 232) in Needham and Westfall (1955) are reversed and a telegram from Dr. Westfall verifies the reversal. The four males agree with figure 232 which is actually *selysii* and with the McMahan and Gray analysis of *selysii*. However, the immature nymph shows a small but definite spine-like structure dorsally on abdominal segment 6 which indicates that it is *uhleri*. The one female was not available for reexamination.

and St. Tammany (Wright, 1939, 1946b).

Collections.—Lincoln, Ruston, March 30, 1940, 1♀ (Louisiana Polytechnic Institute); *Rapides*, Melder, April 10, 1953, 1 nymph; *St. Tammany*, Talisheek, March 12, 1955, 4♂ (two collections of adults, one of nymphs).

The nymph at Melder was from a clear, shallow, sand-bottomed stream and was the only odonate collected. Adults at Talisheek were from a similar creek where they flew in a straight line four or five feet above the water and were easily captured. *H. uhleri* is usually considered crepuscular but the four adults from Talisheek were collected between 2 and 4 p.m. on a sunny day. Frequent collecting at Talisheek before and after March 12 for many years failed to yield additional specimens.

35. *Somatochlora linearis* (Hagen)

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955). St. Tammany (Wright, 1944; Bick, et al, 1953).

Collections.—Caldwell, Jackson, Lincoln, St. Tammany, Winn (four collections of nymphs, three of adults).

S. linearis occurred in widely scattered localities in the pinelands. All nymphs were from clear, flowing creeks. Adults were collected between June 4 and August 17.

36. *Perithemis tenera* (Say)

Louisiana Records.—Hagen (1861, 1875); Foster and Smith (1901); Calvert (1907); Muttkowski (1910); Needham and Westfall (1955). Madison (Foster, 1915; Montgomery, 1927; Ris. 1930). St. Tammany (Wright, 1937). Tensas (Montgomery, 1927; Ris, 1930).

Collections.—Allen, Ascension, Assumption, Avoyelles, Beauregard, Bossier, Calcasieu, Caldwell, Catahoula, Claiborne, Concordia, De Soto, East Baton Rouge, East Carroll, East Feliciana, Evangeline, Grant, Jefferson, Jefferson Davis, Lafayette, Lafourche, La Salle, Lincoln, Madison, Morehouse, Natchitoches, Orleans, Ouachita, Pointe Coupee, Rapides, Red River, St. Bernard, St. Charles, St. James, St. Martin, St. Mary, St. Tammany, Tangipahoa, Tensas, Union, Vermilion, Vernon, Washington, Webster, West Carroll, West Feliciana, Winn (87 collections of adults 81 sight records of adults, 21 collections of nymphs).

This species was frequent and abundant in all physiographic areas and was collected from 47 of the state's 64 parishes.

Nymphs occurred almost entirely (94%) in lentic water but only 74 percent of the collections of adults were from lentic situations. Most (81%) collections of nymphs were from ponds with mud bottoms and vegetation. Males usually flew low over the water and seldom perched but females perched frequently on low vegetation a short distance from the water.

The long flight season extended from February 1 (1953) to November 6 (1950) yet there was only one collection each in February and March and but two in November. Fifty-two percent of the collections were during July and August. The flight season was April

24 to August 12 in 1948, March 26 to October 24 in 1949, April 16 to October 1 in 1951, February 1 to November 1 in 1953.

*37. *Celithemis amanda* (Hagen)

Collections.—St. Tammany. Florenville, September 9, 1953, 10♂, 1♀.

This is the westernmost record for this Coastal Plain species which is reported by Needham and Westfall (1955) from North Carolina to Mississippi.

The one Louisiana collection was in the pinelands along an old, heavily vegetated roadside borrow pit containing deeply stained acid water. Most individuals perched low on bordering weeds and one was laying eggs. *C. amanda* was collected with *Libellula auripennis, L. vibrans, Celithemis fasciata,* and *C. ornata.* For many years and during all seasons, collecting was frequent and thorough at this site but specimens of *amanda* were taken only once.

38. *Celithemis elisa* (Hagen)

Louisiana Records.—Foster and Smith (1901).

Collections.—Claiborne, Lincoln, Ouachita, St. Tammany, Washington (ten collections of adults).

C. elisa occurred in widely separated localities in pineland (86%) and in alluvial (14%) areas. Habitat data are available for five collections, four from ponds and one from a borrow pit. Adults flew swiftly over the water, perched infrequently and briefly on low twigs, and were more difficult to capture than other species of the genus.

Seasonal limits for adults were March 9 and September 9.

39. *Celithemis eponina* (Drury)

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955). Orleans (Hagen, 1875; Ris, 1912; Wright, 1937; Penn, 1950). Plaquemines (Wright, 1943a). Tensas (Montgomery, 1927).

Collections.—Allen, Claiborne, East Baton Rouge, Jefferson, Lafayette, Natchitoches, Orleans, Ouachita, St. Tammany, Vermilion, Webster (27 collections of adults, five sight records of adults).

This species was collected in all physiographic areas and often in large numbers. All collections were near lentic water where adults were easily captured as they perched frequently in full sunshine. Wright (1943a) records *eponina* from fresh to almost saline areas in the Central Gulf Coast, but I did not obtain a single specimen of this species from saline areas.

The flight season was from April 21 to September 7.

40. *Celithemis fasciata* Kirby

Louisiana Records.—Foster and Smith (1901); Muttkowski (1910); Williamson (1922); Byers (1930); Needham and Westfall (1955). Orleans (Wright, 1937). St. Tammany (Williamson, 1910).

Collections.—Claiborne, East Baton Rouge, Grant, Ouachita, St. Tammany, Vernon, Washington (six collections of adults, seven sight records of adults).

This species occurred in scattered localities in the pinelands (84%)

and alluvial areas (16%) and was never abundant. Wright (1943a) records *fasciata* in fresh or slightly brackish marshes of the Central Gulf Coast but it was not collected by the writer in any part of the deltaic plain. All collections were from ponds, borrow pits, or lakes where the adults perched less frequently than *eponina* and were more difficult to capture.

Adults were collected from June 29 to September 10.

41. *Celithemis ornata* (Rambur)

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955).

Collections.—St. Tammany (six collections of adults, one collection of last instar nymphal skins).

Both *C. amanda* and *C. ornata* are Coastal Plain species which reach their westernmost limits in the Florida Parishes of Louisiana. All collections were near lentic, heavily vegetated, acid water in the pinelands. Two collections of adults were along a well established borrow pit, three from a pond, and one from a slough. Most individuals perched low on weeds a few feet above the water; one female had been captured by an *Erythemis simplicicollis.* The exuviae were one foot above water on stems of *Eriocaulon* at the margin of a slough.

Adults were collected from March 12 to September 9.

42. *Macrodiplax balteata* (Hagen)

Louisiana Records.—St. Tammany (Wright, 1939, 1943a).

Wright (1939, 1943a) reports a single collection of *M. balteata* from the State Fish Hatchery at Lacombe in St. Tammany Parish on July 2, 1938 and states (1943a) he is confident that further collections on the Gulf Coast will show this species to be more common than the single collection indicates. I did not collect *balteata* in Louisiana but, through the kindness of Dr. Kormondy, I examined the two males in the University of Michigan Museum of Zoology collected by M. Wright.

*43. *Orthemis ferruginea* Fabricius

Collections.—Allen, Beauregard, Claiborne, Concordia, De Soto, East Baton Rouge, Jefferson, Lafayette, Orleans, St. Tammany, Vernon, West Carroll (ten collections of adults, ten sight records of adults, three collections of nymphs).

Wright (1937, 1943a) reports this species from the Central Gulf Coast but does not specifically mention Louisiana. *Orthemis ferruginea* was taken in widely scattered localities from Claiborne and West Carroll Parishes in the north to Lafayette and St. Tammany in the south yet was never abundant. Collections were most frequent (75%) in the pinelands and much less so in deltaic and in alluvial areas. Nine of the ten collections of adults were near lentic water including ponds, borrow pits, and sloughs. Two collections of nymphs were from ponds, the other from a ditch choked with vegetation.

Adults of this late season species were collected between July 12 (1950) and December 1 (1953). The flight season was August 29 to October 15 in 1949, July 12 to November 2 in 1950, and July 17 to December 1 in 1953.

44. *Ladona deplanata* (Rambur)

Louisiana Records.—Ris (1910); Needham and Westfall (1955).

Collections.—Lincoln, Rapides, St. Tammany, Union (16 collections of adults, three of nymphs).

L. deplanata occurred in the pinelands at widely separated localities. All collections were near lentic water, including sloughs, ponds, and borrow pits.

Adults were taken early in the season, from February 21 to May 5. This range is one of the briefest for any odonate in Louisiana. In spite of frequent collecting throughout the year in the southeastern part of St. Tammany Parish where *deplanata* was common during early spring, adults were not taken there at any other time of the year. During the 1955 season, adults reached a peak of abundance on April 3 at a heavily vegetated acid pond. Here, they flew swiftly approximately three feet above the water and often perched on the ground not more than 20 feet from the water's edge. On March 12 at this pond two last instar exuviae were collected.

45. *Libellula auripennis* Burmeister

Louisiana Records.—Needham and Westfall (1955). Acadia, Livingston, St. Tammany (all by Westfall, 1943). There are numerous other records of *auripennis* from Louisiana prior to the recognition of *needhami* as a distinct species by Westfall (1943). Because most of these include *needhami* they are not listed.

Collections.—Claiborne, Orleans, St. Tammany, Vernon (seven collections of adults).

This species was collected from a few scattered localities and was neither frequent nor abundant anywhere in the state. The penes of hundreds of the golden wing *Libellula* from the New Orleans area were studied and only one specimen was *auripennis.* It was never taken from the coastal marshes where at the height of the season *needhami* occurred in large swarms.

Six collections were from pinelands; one from the deltaic plain. All were near lentic water and three of the seven collections were from sloughs.

Adults were collected between June 29 and September 9.

46. *Libellula axilena* Westwood

Louisiana Records.—Hagen (1875); Calvert (1893); Foster and Smith (1901); Muttkowski (1910); Kennedy 1922a); Needham and Heywood (1929); Byers (1930); Needham and Westfall (1955). Orleans and St. Tammany (Wright, 1939).

Collections.—St. Tammany, Washington (11 collections of adults).

L. axilena is a Coastal Plain species which reaches its western limit in the Florida Parishes. All collections were from the pinelands of the eastern halves of St. Tammany and Washington Parishes in the southeastern part of the state. In this area the ranges of *axilena, incesta,* and *vibrans* overlap and *axilena* and *vibrans* were taken at the same spot on three occasions. *L. axilena* was one of the few species whose range in Louisiana was restricted. It has not crossed the wide alluvial plain of the Mississippi into the pinelands of central and northern Louisiana. In spite of the fact that *axilena* was common in a pineland area at the eastern end of Lake Pontchartrain, it has not crossed the four miles of slightly brackish marsh at the eastern edge of the Lake to enter the deltaic plain near New Orleans. *L. axilena* was not taken in this part of the deltaic plain during 20 years of frequent collecting. For this reason I doubt the validity of the Wright (1939) record from New Orleans.

Most collections were associated with lentic or with very sluggish water and half were from pineland sloughs where *axilena* perched on the branches of small gum trees. This species was more difficult to capture than either *vibrans* or *incesta.* Byers (1930) states that *axilena* is shy and difficult to capture and that it is found deep in hardwood forests, in small open glades, usually near black gum swamps.

The flight season was from May 23 to September 9.

*47. *Libellula flavida* Rambur

Collections.—East Feliciana, Jackson, July 8, 1953, 1♀; *Lincoln,* Dubach, June 26, 1951, 1♀ (Louisiana Polytechnic Institute); *Sabine,* Negreet, July 8, 1953, 1♂; *Tangipahoa,* Robert, September 6, 1950, 1♀; *Union,* Marion, June 24, 1950, 1♂, 2♀; Randolph, July 1, 1950, 1♀ (six collections of adults).

L. flavida was scarce and occurred in widely scattered localities in the pinelands. Habitat notes are available only for the individual from Jackson which perched low on weeds along a small creek in an exposed portion of a densely wooded beech-magnolia area.

48. *Libellula incesta* Hagen

Louisiana Records.—Needham and Westfall (1955). Madison (Montgomery, 1927).

Collections.—Allen, Ascension, Avoyelles, Beauregard, Bossier, Caddo, Calcasieu, Catahoula, Claiborne, Evangeline, East Feliciana, Grant, Jackson, Lafayette, La Salle, Lincoln, Morehouse, Natchitoches, Ouachita, Rapides, Sabine, St. Helena, St. Tammany, Union, Vernon, Washington, Webster, West Carroll, West Feliciana, Winn (67 collections of adults).

L. incesta was frequent and abundant north of the deltaic plain, in pinelands (76%) and in alluvial areas (24%). The southernmost Louisiana records from Slidell, Gonzales, Lafayette and Sulfur coincide with the northern limits of the deltaic plain. North of these points *incesta* occurred with *vibrans,* south of these points *vibrans* was present but neither *incesta* nor *axilena,* and in the eastern halves of St. Tammany and Washington Parishes all three species were present.

L. incesta was taken with equal frequency along sluggish streams and at varied lentic habitats. During July and August, almost any pineland habitat provided many specimens. Most collections were in full sunlight but Wright (1943a) considers *incesta* a shade loving species. Adults perched low and often returned to the same spot but they were more difficult to capture than the sluggish *vibrans*.

Adults were collected between May 17 (1937) and September 11 (1952). The flight season was June 5 to August 6 in 1948, May 29 to August 30 in 1949, June 18 to September 11 in 1952, and June 23 to September 10 in 1953.

*49. *Libellula luctuosa* Burmeister

Collections.—Bossier, Ninock, August 10, 1954, 2♀; *Ouachita*, Monroe, August 16, 1953, 1♂.

This distinctive and easily captured species was seen and collected at only two localities in northern Louisiana, and was neither seen nor collected southward. I am confident that *luctuosa* occurs sporadically in the northernmost parts of the state and that it is absent southward.

Although *luctuosa* occurs in parts of Mexico and in most of eastern United States including northern Mississippi, it is absent in the southern part of that state (Bick, 1950) and in Florida (Needham and Westfall, 1955). Since the only record from the Gulf Coast is that of Williamson (1914a) from Bay City, Texas, it seems that *luctuosa* is absent or rare in a wide coastal band across the Gulf States. Factors responsible for this restriction are not clear but absences in coastal parts of the Gulf States were noted for other widely distributed eastern species such as *Libellula cyanea*, *Argia violacea*, and *Enallagma basidens*.

50. *Libellula needhami* Westfall

Louisiana Records.—Needham and Westfall (1955). Acadia, Calcasieu, Cameron, East Baton Rouge, St. Tammany (all by Westfall, 1943). Jefferson (Westfall, 1943; Behre, 1950). Orleans (Westfall, 1943; Bick, 1949; Penn, 1950).

Collections.—Acadia, Assumption, Bossier, Calcasieu, Cameron, East Baton Rouge, Iberia, Jefferson, Lafayette, Lafourche, Orleans, Ouachita, Plaquemines, St. Bernard, St. Charles, St. Mary, St. Tammany, Tangipahoa, Terrebonne, Vermilion (76 collections of adults).

L. needhami was present in every physiographic area but was frequent in the southern part of the State and very scarce north of Baton Rouge. Westfall (1943), considering the general distribution of *needhami* and *auripennis*, states that the latter extends farther inland. In Louisiana, both species were rare north of Baton Rouge, but *auripennis* was also rare in the deltaic plain, an area where *needhami* was both frequent and abundant.

Wright (1943a) states that because of the tremendous concentration of individuals, *L. needhami* forms the most conspicuous component of the fauna of the lower Mississippi delta and that adults congregate in vast swarms and penetrate into New Orleans in clouds. I was equally impressed with the great numbers of this species in the deltaic plain during July and August. Large numbers often perched on shrubbery at night at the well lighted Pontchartrain Beach in New Orleans. Just outside the city limits of New Orleans, by using a flashlight for one half hour each night, Bick (1949) collected twenty apparently sleeping individuals on May 4, and eighteen on May 24. In July a swarm of approximately 700 individuals was seen at the edge of an extensive swamp. Adults were also present in large numbers in the brackish marshes. Most roads through the marshes are bordered by dense stands of *Phragmites* and on any sunny day in July or August individuals of *needhami* perched on the top of nearly every cane.

Nearly all (97%) collections were associated with lentic water which was most often (42%) ponds, and less frequently borrow pits, fresh and brackish marshes, swamps, and rice fields.

Adults were collected between April 24 (1948) and September 10 (1952). The flight season was April 24 to August 6 in 1948, April 30 to September 3 in 1949, May 1 to September 10 in 1952, and July 3 to September 7 in 1953.

51. *Libellula pulchella* Drury

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955). Orleans (Ris, 1910). West side of Lake Pontchartrain (Wright, 1943a).

Collections.—Catahoula, East Baton Rouge, Lincoln, Ouachita, St. Tammany, Tangipahoa, Washington, West Carroll (seven collections of adults, three sight records of adults).

This transcontinental species was neither frequent nor abundant and neither Wright (1943a) nor the writer collected the distinctive nymph in Louisiana. Adults were taken in pinelands, alluvial areas, and in the deltaic plain. All collections were near lentic water which included ponds, sloughs, and borrow pits. Numerous adults were noted only once as they flew high and constantly over a large pineland pond.

Adults were taken in Louisiana late in the season, between August 29 and November 7, and oviposition was noted as late as September 10, but since Needham and Westfall (1955) record adults in Ohio as early as May 9, earlier collections in Louisiana are anticipated.

52. *Libellula semifasciata* Burmeister

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955). St. Tammany (Wright, 1939, 1943a; Bick, et al, 1953).

Collections.—Allen, Claiborne, Lincoln, St. Tammany, Washington (15 collections of adults, one reared nymph on which the writer's (1951a) description is based, one additional reared nymph).

This species was collected from a few scattered localities in the pinelands. In shaded portions of a pineland slough at Hickory in St. Tammany Parish, adults were often numerous and were easily captured as they frequently perched on dry clumps of grass or on twigs of small gum trees. Both reared nymphs were from the deeply stained acid water of this heavily vegetated slough.

Adults were collected between March 6 and July 26, but 10 of the 14 collections were in March and April. Eggs were attached to a female taken on March 26 and egg laying was noted on April 25. Needham and Heywood (1929) state that *semifasciata* is the earliest of the genus to be abroad in the spring and that it appears in the north before May. Needham and Westfall (1955) record adults from April 1 in South Carolina to August 16 in New England. Kennedy (1922a) states that the primitiveness of *semifasciata* seems confirmed by its spring and early summer season and perhaps by its retiring habit of life in woods-swamps. In Louisiana, adults were always collected early in the season and always in shaded situations.

53. *Libellula vibrans* Fabricius

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955). Madison (Foster, 1915; Montgomery, 1927; Glick, 1939). Orleans (Ris, 1910; Ferguson, 1942; Penn, 1950). Plaquemines (Wright, 1943a).

Collections.—Allen, Avoyelles, Bossier, Calcasieu, Catahoula, Concordia, East Baton Rouge, East Feliciana, Evangeline, Grant, Iberia, Jefferson, Jefferson Davis, Lafayette, Lafourche, La Salle, Lincoln, Livingston, Morehouse, Orleans, Ouachita, Rapides, Sabine, St. Bernard, St. Charles, St. John the Baptist, St. Helena, St. Landry, St. Mary, St. Tammany, Tangipahoa, Terrebonne, Vernon, Washington (133 collections of adults).

Unlike *L. axilena* and *incesta* whose ranges in Louisiana were limited, *vibrans* occurred throughout the State and was one of the most frequent and abundant odonates, particularly in the deltaic plain where the other two species were absent. *L. vibrans* was one of a very few species abundant in swamps of the deltaic plain. Most (67%) collections were near lentic water including ponds, swamps, and borrow pits.

Wright (1943a) considers *vibrans* the most sluggish of the libellulids and states that it was only occasional in open areas. *L. vibrans* was very sluggish; but although it occurred most often in the shade, collections were frequent in exposed situations.

Adults were collected between March 26 (1949) and September 11 (1952). The flight season was April 15 to August 16 in 1948, March 26 to August 30 in 1949, May 4 to August 15 in 1950, May 4 to September 11 in 1952, April 3 to September 9 in 1953, and April 18 to August 30 in 1954. Adults appeared late in March, approximately two months earlier than the late May appearance of *axilena* and *incesta.* Since adults of the three species were present until the first week of September, the flight season for *vibrans* was approximately two months longer than for *axilena* and *incesta.*

54. *Plathemis lydia* (Drury)

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955). Lafayette (Liner, 1949). Madison (Foster, 1915; Montgomery, 1927). Orleans (Hagen, 1875). Tensas (Montgomery, 1927).

Collections.—Allen, Beauregard, Bienville, Bossier, Catahoula, Claiborne, Concordia, De Soto, East Baton Rouge, East Carroll, East Feliciana, Evangeline, Grant, Jackson, Lafayette, La Salle, Lincoln, Madison, Natchitoches, Ouachita, Rapides, Red River, Richland, St. Tammany, Tangipahoa, Tensas, Washington, Webster, West Carroll, West

Feliciana (41 collections of adults, 37 sight records of adults, 13 collections of nymphs).

P. lydia was widely distributed in all parts of the state except the deltaic plain. Hagen (1875) reports *lydia* from New Orleans but because this distinctive species was neither seen nor collected during 20 years of frequent and thorough collecting in the New Orleans area, I doubt its presence there or anywhere in the deltaic plain. I cannot at present explain the absence of *lydia*, as well as other species, from this extensive area which provides many apparently suitable habitats.

Collections were most frequent (69%) in the pinelands. Adults were taken almost equally near lotic and near lentic water but 11 of the 13 collections of nymphs were from lentic water. Males were more abundant at all sites than females. Individuals of both sexes perched frequently on the ground or on fallen logs but were captured with difficulty.

Adults were collected between March 3 (1951) and November 24 (1939). The flight season was March 15 to August 16 in 1948, May 29 to October 21 in 1949, March 3 to October 1 in 1951, March 28 to September 10 in 1953, and April 3 to August 10 in 1954. Many tenerals were collected as late as August 20.

55. *Erythrodiplax berenice* (Drury)

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955). Cameron (Hine, 1904). Jefferson (Borror, 1942; Behre, 1950). Orleans (Penn, 1950). Plaquemines (Borror, 1942; Wright, 1943a). St. Tammany (Borror, 1942; Wright, 1943a). Terrebonne (Borror, 1942).

Collections.—Jefferson, Orleans, Lafourche, Plaquemines, St. Bernard, St. Tammany, Terrebonne (22 collections of adults, one of nymphs).

Wright (1943a) states that adults were restricted to brackish and salt marshes where they were abundant and that they increase in numbers with increasing salinity, but he did not collect the nymphs. I also found *berenice* adults abundant in and restricted to brackish and salt marshes of the deltaic plain but collected a single nymph in Louisiana from the salt marshes at Buras.

The flight season was from April 11 to November 4.

56. *Erythrodiplax connata minuscula* (Rambur)

Louisiana Records.—Needham and Westfall (1955). St. Tammany (Borror, 1942; Wright, 1943a). Terrebonne (Borror, 1942).

Collections.—Allen, Assumption, Bienville, Calcasieu, Claiborne, East Baton Rouge, Jefferson Davis, Lincoln, Natchitoches, Orleans, Ouachita, Rapides, St. Tammany, Washington (37 collections of adults, five of nymphs).

E. c. minuscula was much more widely distributed than *berenice* and occurred in scattered localities in all physiographic areas. Thirty-seven collections were from pinelands, three from the prairie, and one each from alluvial and from deltaic areas. Wright (1943a) considers *minuscula* rare in the marshes of the Central Gulf Coast and in the present study no adults and but a single nymph were obtained from the entire deltaic plain. In the Slidell area of St. Tammany Parish where pinelands are adjacent to brackish marshes, *minuscula* was regularly collected in the pinelands but never in the marshes, whereas the reverse was true for b*erenice.* The five collections of nymphs were from sloughs or borrow pits.

Adults were collected from April 9 (1950) to November 18 (1953). The flight season was May 12 to October 15 in 1949, April 9 to November 5 in 1950, and May 23 to October 26 in 1954.

57. *Erythrodiplax umbrata* (L.)

Louisiana Records.—Needham and Westfall (1955). St. Tammany (Foster and Smith, 1901).

Collections.—Jefferson. Grand Isle, September 27, 1953, 1 ♂, 1 ♀. These individuals flew over a small area of standing water along a road about 50 yards from the open Gulf.

58. *Sympetrum ambiguum* (Rambur)

Louisiana Records.—Foster and Smith (1901).

Collections.—East Baton Rouge, Richland, St. Tammany (ten collections of adults, one of nymphs).

S. ambiguum was most frequent in shaded swamps and sloughs in the pinelands. Adults were collected between June 27 and November 27 but 77 percent of the collections were in November. Pairs in tandem were taken on November 15. Wright (1943a) reports *ambiguum* as a late summer species in the Central Gulf Coast, rarely found other than in shaded areas.

59. *Tarnetrum corruptum* (Hagen)

Louisiana Records.—Banks (1892); Williamson (1899); Foster and Smith (1901); Calvert (1907); Muttkowski (1910); Needham and Heywood (1929); Byers (1930); Needham and Westfall (1955). Orleans (Wright, 1946c).

Collections.—East Baton Rouge, East Feliciana, Jefferson, Lafayette, Lincoln, Natchitoches, Orleans, Plaquemines, St. Charles, St. Tammany, Tangipahoa, Terrebonne (36 collections of adults, three of nymphs).

This species occurred in scattered localities throughout the state but was most frequent in the deltaic plain, an area where *S. ambiguum* was absent. All collections were near or in lentic water.

The seasonal occurrence was unusual inasmuch as adults were collected as early as March 23 and as late as December 10 but not between May 1 and September 14. One of the 36 collections of adults was in March, five in April, two in September, 14 in October, 11 in November, and three in December. In contrast, Wright (1943a) states that adults appeared in April and lasted throughout the summer.

60. *Erythemis simplicicollis* Say

Louisiana Records.—Hagen (1875); Foster and Smith (1901); Needham and Westfall (1955). Cameron (Hine, 1906). Jefferson (Behre, 1950). Madison (Foster, 1915; Montgomery, 1927). Orleans (Bick, 1941; Wright, 1944; Penn, 1950). Plaquemines (Wright, 1943a). St. Bernard (Hinman, 1933). St. Tammany (Bick, et al, 1953). Tensas (Montgomery, 1927).

Collections.—Acadia, Allen, Ascension, Avoyelles, Beauregard, Bienville, Bossier, Caddo, Calcasieu, Caldwell, Catahoula, Claiborne, De Soto, East Baton Rouge, Evangeline, Franklin, Grant, Iberia, Iberville, Jackson, Jefferson, Jefferson Davis, Lafayette, Lafourche, La Salle, Lincoln, Livingston, Madison, Morehouse, Natchitoches, Orleans, Ouachita, Plaquemines, Pointe Coupee, Rapides, Sabine, St. Bernard, St. Charles, St. Helena, St. James, St. Landry, St. Martin, St. Mary, St. Tammany, Tangipahoa, Tensas, Terrebonne, Vermilion, Vernon, Washington, Webster, West Baton Rouge, West Carroll, West Feliciana, Winn (146 collections of adults, 103 sight records of adults, 151 collections of nymphs).

E. simplicicollis was the second most frequent and abundant odonate in the state and with *Pachydiplax longipennis* was common in all physiographic areas and was represented in 55 of the state's 64 parishes. Wright (1943a) considers these two species similar in habits and abundance and states that at times *Erythemis* almost reached the abundance of *L. needhami.* Although numbers of individuals were not recorded, the writer's opinion is that *P. longipennis* was more abundant than *E. simplicicollis* at nearly every site and that neither rivaled the number of *L. needhami* in the deltaic plain during midsummer.

Seventy-four percent of all collections of adults and 89 percent of the nymphs were associated with lentic water which included ponds, lakes, borrow pits, fresh water marshes, swamps, and sloughs. Twenty-six percent of the collections of adults and 11 of nymphs were from lotic waters. These percentages from lotic waters, like those for *Pachydiplax*, are much greater than is commonly assumed. Nearly all collections of nymphs were associated with mud and with dense vegetation.

Adults were collected between February 18 (1950) and November 18 (1953). The flight season was February 28 to November 7 in 1948, March 8 to October 24 in 1949. February 18 to November 2 in 1950, March 1 to October 1 in 1951, and March 10 to November 18 in 1953. Bick (1941) states that the flight season extends from March 4 to November 2 and records oviposition on April 10 and on September 24. The present more extensive data require little modification of the earlier statement.

61. *Cannacria gravida* (Calvert)

Louisiana Records.—Needham and Westfall (1955). Cameron (Hine, 1906). Jefferson (Behre, 1950). Orleans (Foster and Smith, 1901). Plaquemines (Wright, 1943a). St. Bernard and St. Tammany (Foster and Smith, 1901). Tensas (Montgomery, 1927).

Collections.—Allen, East Baton Rouge, Jefferson, Lafayette, Lafourche, Natchitoches, Orleans, Ouachita, Plaquemines, Pointe Coupee, St. Bernard, St. Charles, St. Tammany, Terrebonne, Vermilion (32 collections of adults, 12 sight records of adults, four collections of nymphs).

Wright (1943a) lists *gravida* as one of the five most common species in the Central Gulf Coast in all types of marshes but predominant in brackish marshes. I, too, found *gravida* abundant in brackish areas and collected it only in the deltaic plain prior to 1953. I considered it restricted to that part of the state until 1953 when it was collected occasionally in all other physiographic areas as far north as Natchitoches and Ouachita Parishes.

C. gravida was taken most often (86%) in the deltaic plain and was by no means restricted to marshes since 71 percent of the collections of adults were from ponds and all nymphs were either from ponds or borrow pits.

The flight season was from April 27 (1954) to October 24 (1949). The season was May 6 to August 17 in 1948, June 10 to October 24 in 1949, May 15 to September 7 in 1952, May 16 to October 16 in 1953, and April 27 to October 15 in 1954.

At the edge of a lagoon in City Park in New Orleans on September 5, individuals of *gravida* were observed in tandem and laying eggs. The male clasped the female and they flew low over the water for about 15 seconds. Then the female broke away and flew low over the water, rapidly dipping her abdomen among submerged *Ceratophyllum*. During egg laying the male circled above her and at times disrupted her flight, but she eluded him and continued oviposition for at least three minutes. Then they paired again, the female broke away and again oviposited. Three such periods of pairing and ovipositing were observed. While ovipositing, the female never soared or dove but flew parallel to the shore in one direction. After three minutes she circled back and repeated the egg laying in the same direction.

62. *Pachydiplax longipennis* (Burmeister)

Louisiana Records.—Hagen (1875); Foster and Smith (1901); Needham and Westfall (1955). Cameron (Hine, 1906). Jefferson (Behre, 1950). Lincoln (Ferguson, 1942). Madison (Foster, 1915; Glick, 1939; Montgomery, 1927). Orleans (Shufeldt, 1884; Ris. 1911; Bick, 1949; Penn, 1950). Plaquemines (Wright, 1943a). St. Tammany (Bick, et al, 1953).

Collections.—Penn (1951) reported *longipennis* from the parishes marked with an asterisk. Allen,* Ascension,* Assumption,* Avoyelles,* Beauregard, Bossier,* Caddo,* Calcasieu, Cameron, Catahoula, Claiborne, De Soto,* East Baton Rouge, East Feliciana, Evangeline, Franklin, Grant, Iberia, Iberville, Jackson, Jefferson,* Jefferson Davis, Lafayette,* Lafourche,* La Salle, Lincoln, Livingston,* Madison, Natchitoches, Orleans,* Ouachita, Plaquemines, Rapides,* Richland, Sabine,* St. Bernard,* St. Charles,* St. Helena, St. John the Baptist, St. Landry,* St. Martin, St. Mary,* St. Tammany,* Tangipahoa,* Tensas, Terrebonne, Union, Vermilion, Vernon, Washington,* Webster,* West Baton Rouge, West Carroll, West Feliciana, Winn (215 collections of adults, 147 collections of nymphs, 141 sight records of adults).

Pachydiplax longipennis was the most frequent and abundant odonate in Louisiana. It occurred in the greatest number of collections, is represented by the largest number of individuals, and, along with *Erythemis simplicicollis*, was present in 55 of the state's 64 parishes in all physiographic areas. There was scarcely a collecting spot where five or six individuals were not encountered at any given time, but *longipennis* was noted only once in a swarm.

Most (66%) collections of adults were associated with a variety of lentic habitats, primarily ponds, but a surprisingly large percentage (34%) was along flowing streams. Eighteen percent of all collections of nymphs were from streams. Because *longipennis* is so generally reported as strictly lentic, these percentages from lotic waters are significant. Almost all collections of nymphs were from habitats with mud bottoms and abundant vegetation.

The long flight season extended from March 9 (1949) to December 2 (1948). The season was March 18 to December 2 in 1948, March 9 to October 24 in 1949, March 24 to November 2 in 1950, March 26 to October 27 in 1952, March 22 to November 18 in 1953, and March 13 to October 26 in 1954. Ovipositing was recorded as late as December 2 and tenerals were taken on September 10.

63. *Miathyria marcella* (Selys)

Louisiana Records.—Orleans and St. Tammany (Bick, et al, 1950).

Collections.—*East Baton Rouge*, Baton Rouge, June 14, 1950, 1♀; October 2, 1950, 1♀; October 10, 1950, 1♀; October 14, 1950, 1♀; exact date unknown, 1950, 1♀; October 1953, 1♂, 1♀ (all in collection of Louisiana State University); *Orleans*, New Orleans, October 27, 1950, 1♀; *St. Tammany*, Hickory, September 29, 1950, 1♂; Indian Village, October 22, 1955, 1♂, 1♀; *West Feliciana*, St. Francisville, July 9, 1953, 1♀ (10 collections of adults).

Bick, et al (1950) judge that this neotropical species is well established along the Gulf Coast and subsequent collecting verified this for Louisiana. *Miathyria marcella* occurred in pineland, alluvial and deltaic areas in southern Louisiana north to St. Francisville which is about 96 air miles from the Gulf. Six collections were obtained by the writer; five were near lentic water and one was near a shallow, clear, swiftly flowing, sandy creek.

Adults were collected between June 14 (1950) and October 27 (1950) and since nine of the ten collections were in October, *marcella* is primarily a late season form.

64. *Tramea carolina* (L.)

Louisiana Records.—Foster and Smith (1901); Muttkowski (1910); Needham and Heywood (1929); Needham and Westfall (1955). Cameron (Hine, 1904). Lincoln (Ferguson, 1942). Madison (Foster, 1915). Plaquemines (Wright, 1943a).

Collections.—Allen, Beauregard, Caddo, Caldwell, East Baton Rouge, Grant, Jackson, Jefferson Davis, Lafayette, Livingston, Natchitoches, Orleans, St. Charles, St. John the Baptist, St. Helena, St. Tammany, Tangipahoa, Terrebonne, Washington, Winn (49 collections of adults, 15 of nymphs).

Tramea carolina was collected from all physiographic areas and was more widely distributed and abundant than *onusta.* Eighty-three percent of the collections of adults were associated with lentic water. Adults were from a variety of habitats including vacant lots in New Orleans, pineland sloughs, and brackish marshes. Like *onusta, carolina* was very abundant in prairie rice fields. Byers (1930) also reports *carolina* as common in fields in Florida. Nymphs were from lentic or from sluggish water, nearly always among vegetation.

The flight season extended from February 24 to November 15 but 59 percent of the collections were between August and October. On September 27, 1953, along the beaches at Grand Isle in the Gulf, ten individuals were captured and hundreds were seen among a huge swarm of *Anax junius* and lesser numbers of *Pachydiplax longipennis* in the greatest concentration of odonates I have ever seen.

65. *Tramea lacerata* Hagen

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955). Cameron (Hine, 1906). Lincoln (Ferguson, 1942). Orleans (Penn, 1950; Bick, 1951b). Madison and Tensas (Montgomery, 1927).

Collections.—Allen, Avoyelles, Beauregard, Calcasieu, Claiborne, Evangeline, Jefferson, Jefferson Davis, Lafayette, Lafourche, Lincoln, Natchitoches, Orleans, Ouachita, Plaquemines, Rapides, St. Charles, St. Mary, St. Tammany, Tensas, Terrebonne, Union, Vermilion, Washington, Webster, West Feliciana (28 collections of adults, 33 sight records of adults, one reared nymph).

Tramea lacerata was widely distributed and was collected in all physiographic areas but was never as abundant as *carolina.* Ninety percent of the collections of adults were near exposed lentic water which was most often ponds or lakes. The reared nymph was from a pond with abundant vegetation.

Adults were collected between March 30 and November 5, but 58 of the 61 collections were between July 1 and October 31.

66. *Tramea onusta* Hagen

Louisiana Records.—Foster and Smith (1901); Needham and Westfall (1955); Cameron (Hine, 1906). Madison (Montgomery, 1927).

Collections.—Allen, Beauregard, Caddo, Calcasieu, Cameron, Iberia, Lafayette, St. Mary, St. Tammany, Vermilion, Winn (13 collections of adults).

T. onusta was more localized than either *carolina* or *lacerata* and was taken in the prairie more frequently than either of these species. Unlike all other Louisiana odonates, most (69%) collections were from the southwestern part of the state and there was but a single collection east of the Mississippi. In contrast, 73 percent of the collections of *carolina* were east of the Mississippi and but 22 percent were from the southwestern parishes. This corresponds with unpublished observations in eastern Oklahoma where during five summers there were numerous collections of *onusta* and only two of *carolina.* I surmise that *onusta* is more common than *carolina* west of the Mississippi and that the reverse is true for the eastern states. In spite of difference in frequency, both were taken together at three separate localities in the Louisiana prairie.

The flight season of *onusta* was from March 31 to September 10.

67. *Pantala flavescens* (Fabricius)

Louisiana Records.—Needham and Westfall (1955). Cameron (Hine, 1904). Madison (Montgomery, 1927).

Collections.—Allen, Avoyelles, Assumption, Beauregard, Bossier, Calcasieu, Caldwell, Cameron, Catahoula, Claiborne, Concordia, East Baton Rouge, East Carroll, East Feliciana, Franklin, Grant, Iberia, Jackson, Jefferson, Jefferson Davis, Lafayette, Lafourche, La Salle, Lincoln, Morehouse, Natchitoches, Orleans, Ouachita, Plaquemines, Pointe Coupee, Rapides, St. Charles, St. James, St. Landry, St. Martin, St. Mary, St. Tammany, Tangipahoa, Tensas, Terrebonne, Union, Vermilion, West Carroll, West Feliciana, Winn (71 collections of adults, 67 sight records of adults).

Collections were from 45 of the state's 64 parishes and in every physiographic area. *P. flavescens* was outranked in number of parishes by only *Pachydiplax longipennis, Erythemis simplicicollis,* and *Perithemis tenera* but unlike these, *flavescens* often occurred in large swarms. These swarms, always in open areas in full sunlight, were noted in the pine barrens at considerable distance from water, above rice fields in the prairie, over sugar cane fields in the deltaic unit, in lesser numbers near brackish marshes, and in the city of New Orleans. *P. flavescens* and the three species of *Tramea* were at times the most abundant odonates in the prairie.

Adults were recorded between April 13 (1954) and December 5 (1949). The season was June 23 to November 1 in 1948, August 4 to December 5 in 1949, July 8 to November 13 in 1953, and April 13 to October 26 in 1954. The April 13 record was unusually early. All swarms occurred in July and August and adults were common in New Orleans throughout October. Oviposition was observed as late as November 15.

68. *Pantala hymenea* (Say)

Louisiana Records.—Needham and Westfall (1955). Cameron (Hine, 1906). Madison (Montgomery, 1927).

Collections.—Caddo, Caldwell, Grant, Jackson, Lafayette, Lafourche, Ouachita, Pointe Coupee, St. Tammany, Union (five collections of adults, six sight records of adults).

P. hymenea occurred in scattered localities in all physiographic areas but was less frequent and abundant than *flavescens.* Adults of *P. hymenea,* unlike those of *flavescens,* were never noted in swarms and were seldom far from water. One or two individuals of *hymenea* were observed on several occasions among swarms of *flavescens.*

Adults of *hymenea* were collected between June 6 and September 9.

AGRIONIDAE

69. *Agrion dimidiatum* (Burmeister)

Louisiana Records.—Foster and Smith (1901).

Collections.—Beauregard, Rapides, St. Helena, St. Tammany, Union, Washington (27 collections of adults).

Wright (1946d) considers *maculatum* common along the Gulf Coast but reports only three collections of *dimidiatum* over a four year period. *Agrion dimidiatum* was not as frequent as *maculatum*, but the author does not consider *dimidiatum* as limited in Louisiana as the Wright comparison indicates.

A. dimidiatum was collected from widely scattered localities in the pinelands, always along small, swift, clear, shaded creeks. *A. maculatum* occurred in the same type of habitat, but since the two species were seldom taken together (never by Wright, 1946d, and three times by the writer), there must be minor differences in habitat requirements which were not detected.

Adults were collected between March 1, (1953, 1954) and September 10 (1952, 1953). Other early dates were March 19, 1949, and March 12, 1955. Adults were often associated with *Argia moesta, A. tibialis, A. fumipennis* and *A. sedula.*

70. *Agrion maculatum* Beauvois

Louisiana Records.—Foster and Smith (1901); Wright (1943a).

Collections.—Beauregard, Bossier, Claiborne, East Baton Rouge, East Feliciana, Jackson, La Salle, Lincoln, Natchitoches, Ouachita, Rapides, St. Tammany, Tangipahoa, Washington, Winn (46 collections of adults).

Agrion maculatum was more common and more widely distributed than *dimidiatum.* Both occurred along small, swiftly flowing, clear, shaded creeks in the pinelands. At times, *maculatum* was the sole odonate present along very small, heavily shaded, and almost dry creeks. *A. maculatum* was collected with a large number of species but most frequently with *Argia tibialis.*

Adults were collected between March 1 (1954) and October 25 (1940). The flight season was May 9 to October 25 in 1940, May 7 to October 2 in 1948, March 29 to August 6 in 1949, March 28 to September 10 in 1953, and March 1 to October 6 in 1954.

71. *Hetaerina americana* (Fabricius)

Louisiana Records.—Foster and Smith (1901).

Collections.—East Baton Rouge, East Feliciana, St. Helena, Tangipahoa, Washington (nine collections of adults).

H. americana is common throughout the United States but in Louisiana was collected only in the Florida Parishes. This area, as well as the rest of the pinelands of the state, provides many apparently suitable habitats where *americana* was not found. The nine collections obtained during years of effort in Louisiana contrasts with an equal number obtained in southern Oklahoma during eight weeks.

Adults were most frequent along swift, wide, sunlit, sand or gravel bottomed streams where they often perched on twigs or fallen logs well out in the stream. *H. americana* occurred along wider and more exposed streams than either species of *Agrion.* Williamson (1923) states that *americana* frequents streams 15 feet or more in width.

Adults were collected between April 3 and October 2 and were often taken with *Argia moesta.*

72. *Hetaerina titia* (Drury)

Louisiana Records.—Foster and Smith (1901). Madison (Montgomery, 1927). St. Tammany (Wright, 1943a).

Collections.—Allen, East Baton Rouge, East Feliciana, Evangeline, Rapides, St. Helena, St. Tammany, Tangipahoa, Vernon, Washington (20 collections of adults).

H. titia was present in 20 collections from scattered localities in the pinelands of the southern half of the state whereas *americana* was limited to nine collections in the Florida Parishes.

All collections were from pinelands, mostly along swift, shallow streams with clear water and with sand or gravel bottoms. Well defined habitat differences between *titia* and *americana* could not be detected yet the two were collected together only twice. Wilson (1928) considers *titia* almost identical with *americana* in habitat and the writer shares Wilsons' opinion that *titia* was more diffcult to capture. Williamson (1923, 1932) considers *titia* more of a shade dweller than *americana,* otherwise he finds it difficult to explain the abundance of one and the absence of the other on some streams.

Adults of *titia* were collected later in the season (June 24 to November 15) than those of *americana* (April 3 to October 2). In contrast, both Williamson (1932) for Missouri and Montgomery (1947) for Indiana give later records for *americana* than for *titia.*

LESTIDAE

73. *Lestes disjunctus australis* Walker

Louisiana Records.—Walker (1953). Terrebonne (Walker, 1952).

Collections.—Ascension, East Baton Rouge, Lincoln, Ouachita, Sabine, St. Tammany (26 collections of adults).

This species was widespread in the pinelands but abundant in few localities. Adults were equally frequent in sloughs and around ponds. *L. d. australis* was most often in sunlight whereas *L. vigilax* was always in the deep shade of black gum sloughs or woods.

Walker (1952) reports adults from March 8 to November 21 in Florida. In Louisiana the flight season was longer, February 19 to December 16, but adults were not collected during April, May, June, and July at localities where they were common in early spring and in late autumn. This indicates a possibility of two emergence peaks in Louisiana.

*74. *Lestes inaequalis* Walsh

Collections.—*Webster,* Sibley, August 18, 1953, 1♀.

This collection from northwestern Louisiana is a significant extension of the range of this species which Walker (1953) records south to Oklahoma, Tennessee, and North Carolina. The female perched low on matted roots and vegetative debris above deeply stained water of an extensive swampy area where the underbrush was dense and the entire area heavily shaded. *Enallagma geminatum* and *E. signtum* were also collected at this locality.

*75. *Lestes vigilax* Hagen

Collections.—Bossier, Claiborne, Lincoln, St. Tammany, Tangipahoa (13 collections of adults).

This species was widespread but neither frequent nor abundant. Adults were always in dense shade in acid, pineland sloughs or ponds, never in the numerous alluvial or deltaic swamps of the Mississippi drainage. At one locality, a thick stand of shrubs provided complete cover and was so dense that walking was impossible. Here, numerous individuals perched on trunks, twigs, and moss, just above the saturated soil, and were captured by crawling and using a very unorthodox swing of the net. Only once, at twilight, was *L. vigilax* seen flying from the shade out into the open. These observations agree with Byers' (1930) notes, "Appears in March and is usually associated with the luxuriant mass of low vegetation found around the mucky edges of black gum swamps in heavily wooded areas. Shuns sunlight and companionship, usually occurring alone, in areas singularly free from other Odonata".

The flight season was from April 25 to October 19.

COENAGRIONIDAE

76. *Argia apicalis* (Say)

Louisiana Records.—Banks (1892). Madison and Tensas (Montgomery, 1927).

Collections.—Ascension, Avoyelles, Beauregard, Bienville, Catahoula, East Baton Rouge, East Feliciana, Grant, Lafayette, La Salle, Lincoln, Madison, Natchitoches, St. Helena, Tangipahoa, Tensas, Washington, West Feliciana (31 collections of adults).

This widely distributed species was most often (53%) in pinelands but was one of the few species frequent (43%) in alluvial areas. *Argia apicalis* and *A. tibialis* were the only members of the genus collected in the prairie, and no species of *Argia* was collected in the deltaic plain. *A apicalis* occurred most often (66%) along streams which were either swift or sluggish.

The limits of the flight season were April 17 (1954) and November 24 (1951). Other early and late dates were April 24, 1951, November 15, 1936, October 2, 1948, October 19, 1950, October 4, 1953, October 20, 1954.

*77. *Argia bipunctulata* (Hagen)

Collections.—*Caldwell*, Columbia, August 4, 1948, 2♂; *De Soto,* Keachie, August 2, 1949, 1♂; *Lincoln*, Ruston, May 20, 1938, 1♀; May 5, 1940, 1♂ (Louisiana Polytechnic Institute) (four collections of adults).

All collections were from northern parishes, three from the pinelands and one from an alluvial area.

78. *Argia fumipennis* (Burmeister)

Louisiana Records.—Foster and Smith (1901); Wright (1943a).

Collections.—East Baton Rouge, East Feliciana, St. Helena, St. Tammany, Tangipahoa, Washington (20 collections of adults).

This Coastal Plain species reaches its western limit in the Florida Parishes. The wide Mississippi alluvial plain is apparently a barrier to its westward extension.

A. fumipennis was always in pinelands, most often (89%) in the shade along small, swiftly flowing, sandy creeks with acid water. Associates were recorded for eight collections and seven of these included either *Agrion dimidiatum* or *maculatum.* Unlike these species which were always at the creeks, *fumipennis* was found twice, without associates, more than 200 yards from water.

The limits of the flight season were March 28 (1953) and October 4 (1948). Other early and late records are April 26, 1939, April 21, 1951, April 25, 1954, April 3, 1955; September 8, 1950, September 10, 1953.

79. *Argia moesta* (Hagen)

Louisiana Records.—Foster and Smith (1901).

Collections.—Allen, Beauregard, Claiborne, East Baton Rouge, East Feliciana, Grant, La Salle, Livingston, Morehouse, Rapides, St. Helena, St. Tammany, Tangipahoa, Vernon, Washington, Winn (45 collections of adults).

Williamson (1932) states that *moesta* is a river species, but Borror (1944) and Walker (1941, 1953) note that it occurs along rocky shores of lakes as well as along streams. Kennedy (1922) reports *moesta* abundant along the rocky, wave-swept shores of the Bass Islands in Lake Erie. None of the 45 Louisiana collections of adults were from lentic water; all were from pineland streams. However, fresh water lakes in Louisiana are rarely wind-swept and turbulent. Apparently moving water of either streams or wave-washed lakes is required by *moesta.*

Wright (1943a) states that *A. moesta* occurs in the same areas as *A. fumipennis.* The present study records both species along flowing water in the pinelands, but *fumipennis* was restricted to small, very swift creeks whereas *moesta* was found along both small, swift creeks and large, slow streeams. The two were collected together only twice. *A. moesta* was taken most often with *Argia tibialis* and *A. sedula.*

The flight season was from April 3 (1955) to September 11 (1952). Other early and late records are April 29, 1948, April 3, 1954, and September 10, 1953.

80. *Argia sedula* (Hagen)

Louisiana Records.—Madison and Tensas (Montgomery, 1927).

Collections.—East Baton Rouge, East Feliciana, La Salle, Livingston, St. Helena, St. Tammany, Tangipahoa, Washington, West Feliciana (26 collections of adults).

Argia sedula occurred along small, swift, sandy creeks in the pinelands. It was less widely distributed and less abundant locally than either *Argia moesta* or *A. tibialis* with which it was frequently associated.

The flight season was from April 17 to September 10.

81. *Argia tibialis* (Rambur)

Louisiana Records.—Foster and Smith (1901). Madison (Montgomery, 1927). St. Tammany (Wright, 1943a).

Collections.—Allen, Ascension, Beauregard, Bossier, Caddo, Catahoula, Claiborne, De Soto, East Baton Rouge, East Feliciana, Evangeline, Jackson, Jefferson Davis, Grant, La Salle, Lincoln, Livingston, Madison, Morehouse, Natchitoches, Rapides, St. Helena, St. Landry, St. Tammany, Tangipahoa, Union, Vernon, Washington, Webster, West Carroll, Winn (83 collections of adults).

A. tibialis, the most frequent and widely distributed species of *Argia* in Louisiana, was absent in the deltaic plain. It occurred most often (87%) in the pinelands, seldom (11%) in alluvial areas, and rarely (2%) in the prairie.

This species was collected from a wider range of habitats than any other *Argia*. In the pinelands, *A. tibialis* occurred along swift creeks (73%), along sluggish streams (9%), and near sloughs, swamps, or ponds (5%). In alluvial areas it was taken near sluggish streams (9%) and at an oxbow lake. There was one collection from a sluggish stream in the prairie. The wide range of habitats is reflected in the list of associates which included both lentic and lotic species: *Agrion maculatum, Argia moesta, Libellula incesta, Erythemis simplicicollis, Pachydiplax longipennis* and *Ischnura posita*.

Adults were collected between March 13 (1954) and September 16 (1948). The flight season was April 29 to September 16 in 1948, March 26 to August 30 in 1949, and April 10 to September 10 in 1953.

82. *Argia violacea* (Hagen)

Louisiana Records.—Foster and Smith (1901).

Collections.—*Claiborne*, Homer, August 17, 1953, 1♂; *Vernon*, Cravens, July 17, 1953, 5♂.

A. violacea, a common and widespread eastern United States species reported as far south as Guatemala, was present in but two of the writer's collections. Both were from ponds. The pond at Homer was small, shaded, and in a wooded area; the one at Cravens was large, exposed and in barren, cut-over pineland. Other writers (Williamson, 1932; Wright, 1946a; Walker, 1953) record *violacea* from streams.

*83. *Nehalennia integricollis* Calvert

Collections.—Seven collections of adults were obtained from three different sites all within a 20 mile radius in *St. Tammany* Parish: St. Joe, July 12, 1953, 6♂, 3♀; July 26, 1953, 2♂; May 23, 1954, 12♂, 3♀; August 30, 1954, 2♂, 3♀. Slidell, May 25, 1954, 3♂, 1♀. Florenville, August 31, 1953, 2♂; September 10, 1953, 3♂, 2♀.

N. integricollis is recorded from just three states, New Jersey

(Calvert, 1913; Beatty, 1946); Florida (Byers, 1930; Wright, 1943c); and Oklahoma (Pritchard, 1935). In Louisiana, it was collected from a single area in the pinelands and occurred among abundant low vegetation growing in deeply stained, shallow, acid water. Four collections were from a slough, two along a roadside borrow pit, and one at the edge of a pond. *N. integricollis* was collected with *Enallagma concisum* and *Ischnura kellicotti* at Florenville but, unlike these species, did not perch on the abundant lily pads.

The flight season was from April 25 to September 10.

*84. *Teleallagma daecki* (Calvert)

Collections.—St. Tammany, Slidell, April 25, 1954, 2♂; St. Joe, May 23, 1954, 1♂.

This species is recorded from New Jersey to Florida (Needham and Heywood, 1929), from southeastern Oklahoma (Pritchard, 1935), and from Indiana (Montgomery, 1951). There are no published records from any Gulf State west of Florida.

Both collections were in the pinelands within a three mile radius, one from a pond, the other from a slough. At the margins of these deeply stained, acid waters *T. daecki* flew low among dense vegetation and was collected with *Erythrodiplax connata minuscula, Nehalennia integricollis* and *Lestes vigilax.*

*85. *Enallagma basidens* Calvert

Collections.—Natchitoches, Natchitoches, October 5, 1954, 1♂, 1♀, (Northwestern State College); *Tensas*, Lake Bruin, August 15, 1953, 3♂, 1 tandem pair.

E. basidens occurs in eastern United States from Texas and Kansas to New York and South Carolina but is not reported from any Gulf State east of Texas. Montgomery (1942) states that when first found in Indiana in 1929, *basidens* had been reported from Kansas and Texas, and that subsequent to 1929 it has increased in Indiana and spread through many states to the Atlantic Coast. Because many years of collecting in Louisiana yielded but three recent records from the northern part of the State, I believe that *basidens* has recently entered Louisiana.

At Lake Bruin, a large oxbow of the Mississippi with abundant marginal vegetation, *basidens* was taken with *Argia apicalis, Enallagma vesperum, E. signatum* and *Ischnura posita.*

86. *Enallagma civile* (Hagen)

Louisiana Records.—Madison and Tensas (Montgomery, 1927).

Collections.—Caldwell, East Baton Rouge, Jackson, Jefferson, La Salle, Lincoln, Natchitoches, Ouachita, Webster, West Feliciana (22 collections of adults).

E. civile was widely distributed yet neither frequent nor abundant.

The five collections obtained by the writer were from diverse situations. The three pineland collections included one along a moderately flowing stream and two adjacent to ponds. One collection was from an alluvial pond and one from a brackish marsh about 50 yards from the open waters of the Gulf at Grand Isle. Wright (1943a) does not record *civile* from the Gulf Coast marshes, but Walker (1953) reports it from several stations on Cape Breton Island near the ocean, and Osburn (1906) states that it breeds to some extent in brackish water.

The flight season was from April 4 to November 8.

87. *Enallagma concisum* Williamson

Louisiana Records.—St. Tammany (Wright, 1943a).

Collections.—*Jefferson.* Grand Isle, September 27, 1953, 1♂; *St. Tammany.* Florenville, August 31, 1953, 10♂, 7♀, 1 tandem pair; September 10, 1953, 4♂, 2♀; Slidell, March 6, 1955, 1♂; St. Joe, March 12, 1955, 1♂ (five collections of adults).

This species, recorded from Georgia (Williamson, 1934), Florida (Byers, 1930; Westfall, 1941), and Louisiana (Wright, 1943a), was restricted to southeastern Louisiana, and the record from Grand Isle is the westernmost for the species.

Collections were from two different kinds of habitats. The Grand Isle specimen was taken with *E. civile* as both flew low among grass in a brackish marsh about 50 yards from the Gulf. These are the only species of *Enallagma* which I found in brackish areas in Louisiana. Other collections were from pinelands. Both Florenville collections were at the margin of a borrow pit of stained, acid water covered with pads of *Nuphar.* Here *E. concisum* was associated with *Nehalennia integricollis, Enallagma dubium* and *Ischnura kellicotti* The Slidell and St. Joe specimens were from margins of heavily vegetated acid ponds and were associated with *Enallagma signatum, Ischnura posita, I. ramburi* and *Anomalagrion hastatum.* Individuals of *concisum* were taken both from *Nuphar* pads and among marginal vegetation, both at dusk and in full sunlight.

88. *Enallagma divagans* Selys

Louisiana Records.—Foster and Smith (1901).

Collections.—Natchitoches, St. Helena, St. Tammany, Tangipahoa (11 collections of adults).

This species was collected from pinelands in the eastern and central parts of the state. Nine of the 11 collections were along small, swift creeks; two were from lentic waters. Williamson (1932) reports *divagans* from glacial lakes, pools in spring fed brooks, and from sloughs along steep hills.

E. divagans was one of the few early season species and was not collected later than May. Specimens were taken between March 14 and May 7, but not later in the season in spite of repeated collecting at the same localities. Tenerals were numerous on April 10 and 17. In Indiana, Montgomery (1942) records *divagans* from May to early July.

At the creeks, *divagans* was associated with *Agrion dimidiatum, Argia fumipennis* and *A. tibialis;* at a pond with *Argia apicalis, Enallagma traviatum, E. signatum* and *Ischnura posita.*

*89. *Enallagma dobium* Root

Collections.—St. Tammany, Florenville, September 10, 1953, 2♂; Hickory, May 23, 1954, 1♂; Folsom, September 10, 1953, 2♂.

E. dubium is reported previously from only Georgia (Root, 1924; Williamson, 1934), Florida (Byers, 1930; Westfall, 1941), Mississippi (Wright, 1943a), and southeastern Oklahoma (Pritchard, 1935). The three Louisiana collections were from lentic, stained, acid water in the pinelands; two from borrow pits, one from a slough. *E. dubium* did not perch on the *Nuphar* pads abundant at one site but on small dead twigs in the water or on marginal vegetation. Associated species were *Enallagma concisum*, *Nehalennia integricollis* and *Anomalagrion hastatum*.

90. *Enallagma durum* Hagen

Louisiana Records.—Banks (1892); Calvert (1893); Foster and Smith (1901); Muttkowski (1910); Needham and Heywood (1929); Byers (1930). Madison (Foster, 1915). Jefferson (Behre, 1950).

Collections.—Orleans, New Orleans, June 9, 1923, 1♀, T. H. Hubbell, (University of Michigan, Museum of Zoology); *Orleans*, New Orleans, April 25, 1954, 2♂, 1♀; April 27, 1954, 1♀; May 10, 1954, 2♂, 2♀ (four collections of adults).

Although frequently reported from Louisiana and considered widespread and common in the Central Gulf Coast by Wright (1943a), *durum* was not collected in Louisiana by the writer until 1954 when it was found within the city limits of New Orleans. All specimens were from artificial ponds and were taken with *Ischnura ramburi* and *I. posita*. Wright (1943a) finds *durum* abundant in brackish areas of the Central Gulf Coast but the writer's collections were from fresh water habitats.

91. *Enallagma exsulans* (Hagen)

Louisiana Records.—Walker (1953). Madison (Montgomery, 1927).

Collections.—Madison, Tendal, August 16, 1953, 5♂, 3♀; *Washington*, Franklinton, September 10, 1953, 3♂.

E. exsulans is recorded throughout eastern United States west to North Dakota and Texas but was scarce in Louisiana and restricted to the eastern part of the state. In the pinelands at Franklinton, *exsulans* hovered over the deeper holes in a swift, clear, sand-bottomed stream and was collected with *Agrion maculatum*, *A. dimidiatum* and *Argia tibialis*. At Tendal, in an alluvial area, *exsulans* was among dense stands of *Zizaniopsis* and *Cephalanthus* at the margin of the sluggish Tensas River and was collected with *Argia apicalis*, *A. tibialis* and *Ischnura posita*.

92. *Enallagma geminatum* Kellicott

Louisiana Records.—Needham and Heywood (1929); Byers (1930). Madison and Tensas (Montgomery, 1927).

Collections.—Webster, Sibley, August 18, 1953, 2♂, 1♀.

This collection was from a densely shaded swamp where *geminatum* either perched on lily pads or hovered low over the darkly stained water. *Lestes inaequalis* and *Enallagma signatum* were also collected at this habitat.

93. *Enallagma signatum* (Hagen)

Louisiana Records.—Calvert (1893); Williamson (1899); Foster and Smith (1901); Muttkowski (1910). Cameron (Hine, 1906). Madison and Tensas (Montgomery, 1927).

Collections.—Ascension, Caldwell, Catahoula, Claiborne, East Baton Rouge, Evangeline, Jefferson, Lafourche, Lincoln, Madison, Natchitoches, Orleans, Rapides, St. Martin, St. Tammany, Tangipahoa, Tensas, Webster, West Feliciana (34 collections of adults).

Enallagma signatum and *E. durum* were the sole members of the genus collected in the deltaic plain. *E. signatum* was the most frequent and widespread *Enallagma* in the state and occurred from the Arkansas border to New Orleans, in pinelands (50%), alluvial areas (25%) and in the deltaic plain (25%). Most (72%) collections were from lentic habitats including ponds, lakes, and sloughs but 20 percent were along swift, pineland streams and eight percent along sluggish streams. Walker (1953) also records *signatum* from both lentic and lotic habitats.

The limits of the flight season were February 13 (1954) and October 3 (1954). *E. signatum* was also taken in February, 1955, and in March, 1938, 1948, 1950, and 1953 but only once in October. Numerous pairs in tandem were noted on March 5, 1955.

*94. *Enallagma traviatum* Selys

Collections.—Tangipahoa, Amite, April 17, 1954, 8♂, 2♀, all teneral.

These specimens were taken with *Argia apicalis, Enallagma divagans, E. signatum* and *Ischnura posita* among dense shrubs and vines adjacent to a deep, clear pond in the pine woods.

*95. *Enallagma vesperum* Calvert

Collections.—Claiborne, Summerfield, August 17, 1953, 1♀; *Tensas,* Lake Bruin, August 15, 1953, 3♂, 2♀. All specimens were teneral. These identifications are tentative pending clarification of the *vesperum-laurenti* difficulty. Mrs. L. K. Gloyd concurs with the determination until more material is available.

The Lake Bruin individuals perched on dense vegetation at the margin of this large oxbow lake and were collected with *Enallagma basidens* and *E. signatum.* The Summerfield collection was from a large artificial pond in an extensive wet area in the pinelands. Walker (1953) states that *vesperum* is semi-crepuscular and flies in the late afternoon and evening. Both Louisiana collections were on sunny days at approximately 3 p.m.

*96. *Enallagma weewa* Byers

Collections.—St. Tammany, Abita Springs, August 31, 1953, 1♂; September 9, 1953, 5♂, 2 tandem pairs; September 10, 1953, 7♂; Talisheek, April 25, 1954, 1♂, 1 tandem pair (four collections of adults).

These Louisiana collections are the westernmost for this species recorded along the Atlantic Coast from New Jersey (Montgomery, 1933; Beatty, 1946) to Florida (Westfall, 1941) and on the Gulf Coast from only Gulf County, Florida (Byers, 1930).

All Louisiana collections were from pinelands along small, shallow, swiftly flowing streams with partly sandy bottoms and very darkly stained acid water. *E. weewa* hovered low over pools and was difficult to see because the dark bodies offered little contrast with the almost black water. Westfall (1941) records this species as abundant at similar habitats in Florida.

In New Jersey, Montgomery (1933) collected 88 males and only one female and Beatty (1946) collected 96 males but no uncoupled females. Uncoupled females were not taken in Louisiana.

The long flight season in Louisiana lasted from April 25 to September 9.

*97. *Ischnura kellicotti* Williamson

Collections.—*Claiborne*, Randolph, August 17, 1953, 1♀; *Ouachita*, Calhoun, April 1, 1950, 1♀; *Lincoln*, Ruston, October 1, 1954, 2♂, (Louisiana Polytechnic Institute); *St. Tammany*, Florenville, August 31, 1953, 6♀ (four collections of adults).

The only previous record of *kellicotti* from any Gulf State is that of Westfall (1941) for Florida.

Habitat data are available for the widely separated Florenville and Randolph localities; both habitats were similar lentic, acid, pineland waters with abundant pads of *Nuphar*. Individuals perched on the pads and were collected by scooping up both pads and water in the air net. Williamson (1899, 1914a) discusses this method of collecting *kellicotti*. At Florenville *kellicotti* was taken with *Enallagma concisum;* at Randolph with *E. signatum*.

98. *Ischnura posita* (Hagen)

Louisiana Records.—Foster and Smith (1901). Madison (Foster, 1915; Montgomery, 1927). Plaquemines (Wright, 1943a). Tensas (Montgomery, 1927).

Collections.—Acadia, Ascension, Caldwell, Catahoula, Claiborne, East Baton Rouge, East Feliciana, Evangeline, Franklin, Grant, Jackson, Jefferson, Lafayette, Lafourche, La Salle, Lincoln, Livingston, Madison, Morehouse, Natchitoches, Orleans, Ouachita, Rapides, Richland, Sabine, St. Charles, St. Martin, St. Tammany, Tangipahoa, Tensas, Terrebonne, Vernon, Washington, Webster, West Feliciana (112 collections of adults).

With the exception of *I. ramburi*, *posita* was the most common damselfly in Louisiana and was recorded from 36 of the state's 64 parishes. *I. posita* occurred from Webster parish in the northwest to Terrebonne, near the Gulf, but was less frequent than *ramburi* in the southern half of the state and particularly so in the New Orleans area.

I. posita was in all physiographic areas, pinelands (60%), deltaic (23%), alluvial (16%), and prairie (1%). It occurred at both lentic (61%) and lotic (39%) habitats. Lentic habitats were most often well vegetated ponds and lotic ones mostly swift pineland streams. Walker (1953) reports *posita* from both lentic and lotic situations in Canada.

The limits of the flight season were February 13 (1954) and November 30 (1954). These dates were not exceptional for *posita* was taken on February 17, 1949, February 18, 1950, February 15, 1955, November 1, 1949, November 20, 1952.

A total of 184 males and 248 females were collected but pairs in tandem were never observed. Walker (1953) states that he has no data on mating or oviposition. On March 12, 1955, I watched a female oviposit on a small succulent plant, at the edge of a pineland pond. Unaccompanied by the male she clasped the stem with her legs about six inches above the water surface with head upward and abdomen arched. For a minute she gently probed the stem with her ovipositor, remained motionless in the same position for four minutes, and then flew away and was captured.

99. *Ischnura prognatha* Hagen

Louisiana Records.—Cameron (Hine, 1906). Orleans (Wright, 1943a).

Collections.—Jefferson, Orleans, St. Tammany, Tangipahoa (14 collections of adults).

This species was infrequent and was limited to southeastern Louisiana. I did not collect *prognatha* in Louisiana prior to 1953 and even though five collections were from my own yard, none was obtained there until 1954.

Fifty-seven percent of the collections were from the deltaic unit, 43 percent from pinelands. Most collections were from lentic situations but five were at least a mile from the nearest water. Byers (1930) states that *prognatha* shuns sunlight and companionship; 12 of the 14 collections were in shade and *prognatha* occurred alone on seven occasions.

Adults were collected between February 15 and September 9.

100. *Ischnura ramburi* Selys

Louisiana Records.—Banks (1892); Calvert (1893, 1902); Foster and Smith (1901). Cameron (Hine, 1904). *Madison* (Foster, 1915; Montgomery, 1927). Plaquemines (Wright, 1943a). Tensas (Montgomery, 1927).

Collections.—Allen, Ascension, Avoyelles, Beauregard, Bienville, Bossier, Calcasieu, Cameron, Claiborne, East Baton Rouge, East Carroll, East Feliciana, Franklin, Iberia, Jackson, Jefferson, Jefferson Davis, Lafayette, Lafourche, Lincoln, Livingston, Natchitoches, Orleans, Ouachita, Plaquemines, Rapides, St. Mary, St. Tammany, Tangipahoa, Tensas, Terrebonne, Vermilion, West Feliciana (153 collections of adults).

This species was the most common damselfly in Louisiana and was rivaled only by *I. posita*. *I. ramburi* was collected in 33 of the state's 64 parishes from Webster in the northwest to Grand Isle in the Gulf. Ninety-four percent of the collections of *ramburi* were from the southern half of the state, whereas 61 percent of the collections of *posita* were from this area, and in the New Orleans area there were twice as many collections of *ramburi* as of *posita*. This contrast reflects the continental distribution of the two species. *I. posita* is nearctic and is found throughout eastern United States and Canada; *ramburi* is tropical and in the United States occurs primarily in the southern states.

I. ramburi was in every physiographic area but, unlike *posita*, was much less common (34%) in the pinelands and much more frequent in the deltaic plain (46%) and in the prairie (10%). Seventy-six percent of all collections were at the margins of lentic waters which were most often heavily vegetated ponds.

Adults were collected between January 2 (1949) and December 2 (1948). *I. ramburi* is the only zygopteran collected in Louisiana during every month of the year. The flight season was January 2 to October 4 in 1949, February 18 to November 7 in 1950, March 10 to November 11 in 1953, February 20 to November 30 in 1954.

101. *Anomalagrion hastatum* (Say)

Louisiana Records.—Banks (1892); Williamson (1899); Calvert (1893); Walker (1953). Cameron (Hine, 1904). Madison and Tensas (Montgomery, 1927). Plaquemines (Wright, 1943a).

Collections.—Allen, Caldwell, Claiborne, East Baton Rouge, Franklin, Grant, Iberia, Jackson, Jefferson, Lafayette, La Salle, Lincoln, Madison, Morehouse, Natchitoches, Ouachita, Orleans, Rapides, Richland, St. Helena, St. Martin, St. Tammany, Sabine, Tangipahoa, Vernon, Vermilion, Washington, Webster, Winn (99 collections of adults).

A. hastatum was outranked in frequency by *I. ramburi* and *I. posita*. Both *hastatum* and *posita* were much more frequent in the pinelands (each 60%) than in the deltaic plain (each 23%) whereas the reverse was true for *ramburi*.

Most (87%) collections were near lentic water which included ponds, borrow pits, sloughs, swamps, fresh and brackish marshes. (Wright (1943a) collected adults from the salt marshes of Louisiana and Alabama but does not accept it as a true salt marsh form. Several collections were approximately one mile from water. *I. ramburi* was collected once carrying a partly eaten *hastatum*.

Adults were taken between February 17 (1949) and November 18 (1953). The flight season was March 3 to October 2 in 1948, February 17 to November 7 in 1949, February 18 to September 8 in 1950, and March 28 to November 18 in 1953.

RECORDS OF SPECIES NOT SEEN BY THE WRITER

Most species included here were first recorded in an unpublished manuscript by Foster and Smith (1901) from "Lower Louisiana", an area in the southeastern part of the state embracing Orleans, Jefferson, St. Bernard, St. Tammany and Tangipahoa parishes. The writer collected more frequently in this part of the state than any other, yet many species listed by Foster and Smith were not collected. While serving with the Louisiana State University Sugar Experiment Station, the Federal Horticultural Board, and the Louisiana State Department of Agriculture, Mr. Edward Foster collected dragonflies in "Lower Louisiana" for many years, corresponded with E. B. Williamson from 1899 to 1923, and sent at least some specimens to Williamson. The Foster letters to Williamson are available at the University of Michigan but none of Foster's specimens could be located there. Wright (1939) suggests that the odonates in the Louisiana State Museum, all but one without data, are probably Foster's specimens.

1. *Gomphus (Arigomphus) lentulus* Needham

Recorded from Louisiana by Needham and Westfall (1955). Westfall (personal communication) states that this record was based on a reared female in the Cornell University collection taken at Des Allemands (St. Charles Parish) on June 6, 1937 and that the specimens can no longer be located. Dr. Westfall, who did not see the specimens, suggests that the original determination was probably in error and that the specimens are possibly *submedianus*.

2. *Gomphus (Arigomphus) pallidus* Rambur

Recorded from New Orleans by Hagen (1875) as *Gomphus pilipes* Selys. Williamson (1899) lists *pallidus* from Louisiana and records one male from New Orleans (1914b). Foster and Smith (1901) include *pallidus* from "Lower Louisiana". On April 9, 1917, Foster sent to Williamson several jars of specimens which were broken in transit and at least some of the specimens damaged. On the back of an April 7, 1917 letter from Foster to Williamson is a list of determinations of these specimens in Williamson's handwriting; included in a vertical column are [sic] "Gom. abbreviatus, " minutus, " pallidus(?)." Needham and Westfall (1955) record *pallidus* from Illinois, Indiana, Louisiana, Massachusetts, Michigan, Mississippi, Oklahoma, and Texas. Records of *pallidus* from Louisiana are probably valid but I doubt that it now occurs in New Orleans for no species of *Gomphus* was taken in the city during 20 years of collecting.

3. *Gomphus (Gomphurus) dilatatus* Rambur

Recorded by Foster and Smith (1901) from "Lower Louisiana". On June 24, 1922, Foster wrote Williamson, "The *Gomphus* you noted in the bottle of fragments we ran down to *dilatatus*. That I distinctly remember and it is recorded on my list as from Amite River, May 28, 1899." Calvert (1921) states, "After this paper had been put into type Mr. Williamson sent me a male and a female *Gomphus* labelled 'Amite River, L[ouisian]a, 5.28.99, Ed. Foster. Fragments received in bottle years ago'." Calvert then states that in some characteristics these two specimens resemble *lineatifrons* but that in most features they resemble *dilatatus*. Calvert (1923) lists fragments of *dilatatus* from Amite River, Louisiana. Needham and Westfall (1955) record *dilatatus* from Alabama, Florida, Georgia, Louisiana, and South Carolina.

4. *Gomphus (Gomphus) minutus* Rambur

Reported from "Lower Louisiana" by Foster and Smith (1901). Foster's specimens were studied and determined as *minutus* by Williamson in 1917 as mentioned for *pallidus.* The range given by Needham and Westfall (1955) is primarily southern and includes Florida, Georgia, Louisiana and Mississippi.

5. *Gomphus (Gomphus) spicatus* Hagen

Recorded from "Lower Louisiana" by Foster and Smith (1901). This species is not mentioned in the correspondence between Foster and Williamson. Louisiana is far south of the southernmost states, Illinois, Indiana and Ohio, listed by Needham and Westfall (1955). I judge that the Foster and Smith record is based on a misidentification.

6. *Gomphus (Hylogomphus) abbreviatus* Hagen

Recorded from "Lower Louisiana" by Foster and Smith (1901). Foster's specimens, though probably damaged, were studied and determined as *abbreviatus* by Williamson in 1917 as has been mentioned for *pallidus. G. abbreviatus* is recorded south to Ohio and South Carolina but not from Louisiana by Needham and Westfall (1955).

7. *Anax amazili* (Burmeister)

Calvert (1927) reports Ris' 1918 record of two females from New Orleans and Calvert (1934) gives the range as Louisiana to Rio de Janeiro and the Galapagos. *A. amazili* is listed for Louisiana by Needham and Heywood (1929) and by Needham and Westfall (1955).

8. *Neurocordulia obsoleta* (Say)

Byers (1937) states that Burmeister's 1839 New Orleans record places this species in the far south and out of its continuous range. All Louisiana records are apparently based on the Burmeister record: Hagen (1875), Calvert (1893), Williamson (1899), Muttkowski (1910), Needham and Heywood (1929), Byers (1930), Needham and Westfall (1955). If the Burmeister specimen was *obsoleta,* I surmise that it was actually collected in the nearby pinelands of St. Tammany Parish and not in New Orleans proper. All *Neurocordulia* nymphs collected by the writer were from flowing creeks in the pinelands; none were from the lentic waters of the New Orleans area.

9. *Tetragoneuria spinigera* Selys

Recorded from Louisiana by Foster and Smith (1901). Wright (1937) states that specimens of *T. spinigera,* without locality data, are in the Louisiana State Museum. These specimens cannot be safely assigned to Louisiana because northern species such as *Leucorrhinia intacta* are also in the museum without data. Louisiana is included in the Needham and Westfall (1955) list but is far south of the other states in their list. Dr. E. J. Kormondy (personal communication) states, "There is no question in my mind that *spinigera* does not occur that far south."

10. *Tetragoneuria stella* Williamson

Williamson (1911), in describing *T. stella* states, "It is interesting to note that Dr. Ris found *stella* in the de Selys collection under the label *cynosura.* One of these specimens is from Louisiana (Morrison)." *T. stella* is listed from Louisiana by Muttkowski (1915), Byers (1930), and Davis (1933). Needham and Westfall (1955) record it from Florida, Georgia, and Louisiana.

11. *Nannothemis bella* Uhler

Recorded from Louisiana by Foster and Smith (1901) and by Needham and Westfall (1955). Wright (1937) states that this species is in the Louisiana State Museum without data. Westfall (1952) reports *bella* from Lucedale (George County), Mississippi, which is approximately 75 miles east of the Louisiana-Mississippi state line.

12. *Libellula cyanea* Fabricius

The sight record of Foster (1915) from Mound in Madison Parish is the only Louisiana record of this species. Bick (1950) records *cyanea* from Coahoma County, Mississippi, approximately 95 miles north of Mound. I surmise that this species occurs in northern Louisiana.

13. *Ladona exusta* (Say)

Foster and Smith (1901) record *exusta* from "Lower Louisiana". Wright (1937) states that specimens of *exusta* without data are in the Louisiana State Museum. The range of *exusta* in Needham and Westfall (1955) is primarily northern; that of *deplanata* primarily southern. The writer did not collect *exusta* in Louisiana but found *deplanata* common in St. Tammany Parish in "Lower Louisiana". For these reasons, I believe that Louisiana records of *exusta* should be referred to *deplanata.*

14. *Lestes forcipatus* Rambur

Recorded by Foster and Smith (1901) from "Lower Louisiana" and by Foster (1915) from Mound, Louisiana. Walker's 1952 description of *L. disjunctus australis* differentiates it from *forcipatus,* and on page 66 he states, "The general distribution of *L. d. australis* is thus the eastern United States, from Pennsylvania, northern Ohio and Indiana, Iowa, Nebraska and Kansas, south to Florida and west to Texas and Oklahoma." On page 70 he states, "The distributional range of *L. forcipatus* thus centers around the Great Lakes and the St. Lawrence River and from this region it extends northward to the Hudson Bay watershed in Quebec and Ontario, westward to middle Saskatchewan, and southward to Tennessee and Missouri." It seems that Louisiana records of *forcipatus* should be referred to *disjunctus* australis.

15. *Lestes rectangularis* Say

Recorded from "Lower Louisiana" by Foster and Smith (1901). Walker (1953) records *rectangularis* from Nova Scotia to western Ontario and North Dakota to Connecticut, South Carolina, Florida, and Alabama, and west to Kansas and Oklahoma. Based on this distribution, *rectangularis* probably does occur in Louisiana.

16. *Lestes unguiculatus* Hagen

Hine (1906) lists this species from the Gulf Biologic Station in Cameron Parish and states that the determination was by E. B. Williamson. The occurrence of *unguiculatus* in the coastal marshes of Louisiana is considerably farther south than the range given by Walker (1953), Nova Scotia to British Columbia, south to New Jersey, Tennessee, Missouri, Oklahoma, and California.

17. *Lestes vidua* Hagen

Hagen (1861) describes *vidua* from a New Orleans collection. Both Williamson and Foster were apparently concerned about this record for in a 1922 letter to Williamson, Foster writes, "In regard to *Lestes vidua* my notes fail to show that we collected this species, the only record being the original of Hagen, who seems to have described it from the Pfeiffer collection, the whereabouts of which I do not know." Muttkowski (1910) and Wright (1943a) record this species from New Orleans, and Banks (1892), Needham and Heywood (1929), and Byers (1930) list it from Louisiana. The only other records of *vidua* known to the author are from Florida (Byers, 1930) and South Carolina (Montgomery, 1940).

18. *Enallagma aspersum* (Hagen)

Recorded from "Lower Louisiana" by Foster and Smith (1901). Louisiana is a considerable distance south of the range of *aspersum*, recorded by Walker (1953) from South Carolina, Tennessee, and Oklahoma, north to Maine, New Hampshire, and southern Canada.

19. *Enallagma pollutum* (Hagen)

Reported from "Lower Louisiana" by Foster and Smith (1901) in a handwritten addition to their typed manuscript. This note was probably prior to Calvert's (1919) description of *vesperum*. The only other records of *pollutum* known to the writer are from Florida (Byers, 1930; Westfall, 1941).

20. *Enallagma praevarum* (Hagen)

Calvert (1902) mentions Selys' 1876 record of *praevarum* from New Orleans; Banks (1892), Muttkowski (1910), and Needham and Heywood (1929) list it from Louisiana. Montgomery (1942) states that *praevarum* is a western species. There are no records east of Kansas and Oklahoma (Bird, 1932), other than those which seem to be based on the 1876 listing from New Orleans by Selys, therefore I seriously doubt the validity of all records of *praevarum* from Louisiana.

21. *Nehalennia irene* Hagen

Recorded from "Lower Louisiana" by Foster and Smith (1901) and from Madison Parish by Foster (1915), probably before they were aware of Calvert's (1913) description of *integricollis*. Montgomery (1944) gives the range of *irene* as transcontinental in Canada, and in eastern United States as far south as South Carolina. Walker (1953) reports *irene* south only to northern Ohio, Indiana, and Illinois. The writer found *integricollis* locally abundant in St. Tammany

Parish but did not collect *irene* anywhere in Louisiana. For these reasons I doubt the validity of Louisiana records of *irene.*

22. *Nehalennia pallidula* Calvert

Reported from Grand Isle in Jefferson Parish by Behre (1950). Mr. George Beatty informs me in correspondence that he has one female in his collection from Grand Isle, Louisiana.

23. *Ischnura verticalis* Say

Recorded from Louisiana by Calvert (1893), Williamson (1899), and Foster and Smith (1901), and from Madison Parish by Foster (1915). Walker (1953) reports *verticalis* south to South Carolina, Tennessee, and Texas.

GEOGRAPHIC DISTRIBUTION

North American distribution patterns of the 101 species seen by the writer were determined primarily from Needham and Heywood (1929), Montgomery (1942, 1947, 1948), Walker (1953), and Needham and Westfall (1955). Based on area of primary occurrence each species was placed in one of these categories: Eastern, Coastal Plain, Tropical and Eastern, Transcontinental, Tropical and Transcontinental.

Eastern species (59) extend from the Atlantic Coast to a line from North Dakota south through Texas with very few records west of this line. A few included here occur also in Mexico and many are recorded from Canada. These species are *Progomphus obscurus, Tachopteryx thoreyi, Cordulegaster maculatus, Ophiogomphus mainensis, Hagenius brevistylus, Erpetogomphus designatus, Dromogomphus spinosus, D. spoliatus, Gomphus amnicola, G. lividus, G. plagiatus, G. submedianus, Gomphaeschna antilope, G. furcillata, Basiaeschna janata, Boyeria vinosa, Nasiaeschna pentacantha, Epiaeschna heros, Macromia georgina, M. taeniolata, Didymops transversa, Neurocordulia molesta, N. virginiensis, Epicordulia princeps, Tetragoneuria cynosura, Helocordulia uhleri, Somatochlora linearis, Perithemis tenera, Celithemis elisa, C. eponina, C. fasciata, Libellula auripennis, L. flavida, L. incesta, L. luctuosa, L. semifasciata, L. vibrans, Erythrodiplax c. minuscula, Sympetrum ambiguum, Cannacria gravida, Tramea carolina, Agrion dimidiatum, A. maculatum, Lestes d. australis, L. inaequalis, L. vigilax, Argia apicalis, A. bipunctulata, A. tibialis, Enallagma basidens, E. divagans, E. exsulans, E. geminatum, E. signatum, E. traviatum, E. vesperum, Ischnura kellicotti, I. posita and I. prognatha.*

Coastal Plain species (17) occur primarily in the area designated as Coastal Plain by Fenneman (1930) and extend along the Atlantic and Gulf Coasts from New Jersey to Texas. A few of these species have been recorded beyond the limits of the Coastal Plain: *L. deplanata* and *T. daecki* are recorded from Indiana, *L. needhami* from Cuba and Mexico, and *E. berenice* from the Bahamas and Mexico. Coastal Plain species are *Cordulegaster fasciatus, Gomphus flavocaudatus, G. hodgesi, Neurocordulia alabamensis, Celithemis amanda, C. ornata, Ladona deplanata, Libellula axilena, L. needhami, Ery-*

throdiplax berenice, Argia fumipennis, Teleallagma daecki, Enallagma concisum, E. dubium, E. durum, E. weewa and *Nehalennia integricollis.*

Tropical and Eastern species (10) occur in the tropics south of Mexico as well as in Eastern North America. Some are widely distributed in eastern United States, others are restricted to the Gulf Coast. Species in this category are *Aphylla williamsoni, Anax longipes, Coryphaeschna ingens, Macrodiplax balteata* (Antilles, but not south of Mexico), *Erythrodiplax umbrata, Miathyria marcella, Hetaerina titia, Argia violacea, Ischnura ramburi* and *Anomalagrion hastatum.*

Transcontinental species (5) cross the United States and/or Canada and may or may not be reported from Mexico. Species included here are *Libellula pulchella, Plathemis lydia, Tramea lacerata, Argia moesta* and *A. sedula.*

Tropical and Transcontinental species (10) occur in the tropics south of Mexico and also cross the United States and/or Canada; some occur also in other regions of the world. These species are *Anax junius, Tarnetrum corruptum, Orthemis ferruginea, Pachydiplax longipennis, Erythemis simplicicollis, Pantala flavescens, P. hymenea, Tramea onusta, Hetaerina americana* and *Enallagma civile.*

Fifty-nine species are listed under Eastern but those in all other categories occur at least somewhere in Eastern United States hence all Louisiana species were shared with this area. None was restricted to Louisiana and none was western.

Fourteen species reach their western limits in Louisiana: *Cordulegaster fasciatus, Aphylla williamsoni, Gomphaeschna antilope, Coryphaeschna ingens, Enallagma concisum, Ophiogomphus mainensis, Gomphus flavocaudatus, G. hodgesi, Neurocordulia alabamensis, Celithemis amanda, C. ornata, Libellula axilena, Argia fumipennis* and *Enallagma weewa.* The last eight do not extend west of the Florida Parishes.

Nineteen of the 101 Louisiana species occur also in the tropics south of Mexico; 23 of the 126 species recorded from Oklahoma (Bick, unpublished) are tropical. Eight of the 46 genera collected in Louisiana are listed by Tillyard (1917) as entogenic to Neotropica alone whereas 11 of the 48 genera recorded from Oklahoma are in this category. Because southern Louisiana is semitropical one might anticipate that a greater number of tropical species and genera would be present in Louisiana than in Oklahoma. However, there are apparently two main routes of migration of South American species into the United States: (1) via Central America, Mexico, and Texas; (2) via Central America and the West Indies to Florida. Oklahoma is at the head of the first route but Louisiana is distant from either route.

Eleven species were restricted within the state; 90 were in a geographic sense statewide. This does not mean that 90 species were collected in every parish or even in every physiographic area but rather that United States and Louisiana records suggest that these will be found eventually throughout the state wherever the habitat is suitable. Because all of the state is within the range of an overwhelmingly eastern fauna, an east-west statewide distribution of most species would be anticipated.

Further, a north-south statewide distribution for most species would be expected because of the slight north-south variation in climate. The average annual rainfall decreases from 60 inches in the southeast to 46 inches in the northwest; even the minimum is sufficient for a mesophytic flora and fauna. Insufficient rainfall is certainly not a critical factor limiting odonate distribution in Louisiana. Byers (1930) considers average January temperatures as the factor that controls odonate distribution and accounts for their zonation in Florida. The average January temperature in north and south Florida differs by 17 degrees. In Louisiana, average annual temperatures vary from 64° F in the north to 70° F in the south, and average January temperatures also differ by but six degrees, 48° in the north and 54° in the south. This six degree temperature difference in Louisiana could scarcely be a major factor in odonate distribution. The minor role of temperature was shown by the few species limited in a north-south direction. *Aphylla williamsoni* and *Miathyria marcella*, tropical species which did not extend north of 31° latitude in Louisiana, were limited perhaps by the slightly colder temperatures of northern Louisiana. *Lestes inaequalis*, found only in the northern part of the state, is northern in United States distribution and was limited possibly by the warmer temperatures of southern Louisiana.

The other eight species restricted within the state did not extend beyond the western limits of the Florida Parishes: *Gomphus flavocaudatus*, *G. hodgesi*, *Neurocordulia alabamensis*, *Celithemis amanda*, *C. ornata*, *Libellula axilena*, *Argia fumipennis* and *Enallagma weewa*. Viosca (1926) lists several cold blooded vertebrates common to the Atlantic and the East Gulf Coastal Plains which occur at least as far west as the Florida Parishes but whose extension westward is limited by the broad Mississippi alluvial plain. The above odonates occur primarily in the Coastal Plain and in Louisiana primarily in the pinelands. Because climate and habitats are similar in the pinelands of the western part of the State and in the Florida Parishes, the 50-mile wide alluvial plain seems to be a barrier to the extension of at least eight species. I consider it the only physical feature causing geographical restrictions of odonates in Louisiana.

Physiography and Species Composition

Odonate distribution could not be correlated with small physiographic units as the Bentley Terrace, the Red River Alluvial Cone, etc., but there was some correlation between major physiographic areas (fig. 2) and certain groups of species.

Table 2 gives the percentage of the total collections of each species in each physiographic area. Species are arranged in a sequence depending on their frequencies in each area. Since species present in

TABLE 2.

THE PERCENTAGE OF THE TOTAL NUMBER OF COLLECTIONS OF EACH SPECIES (PRESENT IN FIVE OR MORE COLLECTIONS) FOR EACH PHYSIOGRAPHIC AREA

	Total No. Collections	Pineland	Alluvial	Deltaic	Prairie
Progomphus obscurus	62	100			
Hagenius brevistylus	19	100			
Dromogomphus spoliatus	10	100			
Gomphus flavocaudatus	14	100			
Boyeria vinosa	37	100			
Didymops transversa	13	100			
Somatochlora linearis	7	100			
Celithemis ornata	7	100			
Ladona deplanata	19	100			
Libellula axilena	11	100			
Libellula flavida	6	100			
Libellula semifasciata	17	100			
Agrion dimidiatum	27	100			
Agrion maculatum	46	100			
Hetaerina americana	9	100			
Hetaerina titia	20	100			
Lestes vigilax	13	100			
Argia fumipennis	20	100			
Argia moesta	45	100			
Argia sedula	26	100			
Nehalennia integricollis	7	100			
Enallagma divagans	11	100			
Lestes d. australis	26	97	3		
Argia tibialis	83	87	11	0	2
Celithemis elisa	10	86	14	0	0
Dromogomphus spinosus	19	85	10	5	0
Libellula auripennis	7	85	0	15	0
Erythrodiplax c. minuscula	42	85	3	3	8
Celithemis fasciata	13	84	16	0	0
Enallagma concisum	5	80	0	20	0
Orthemis ferruginea	23	75	10	15	0
Tetragoneuria cynosura	64	74	5	21	0
Libellula incesta	67	76	24	0	0
Plathemis lydia	91	69	31	0	0
Sympetrum ambiguum	11	60	40	0	0
Enallagma civile	22	55	40	5	0
Argia apicalis	31	53	43	0	4
Enallagma signatum	34	50	25	25	0
Macromia taeniolata	8	50	50	0	0
Epicordulia princeps	13	30	60	10	0
Miathyria marcella	10	33	50	17	0
Libellula pulchella	10	37	50	13	0
Gomphus plagiatus	6	17	83	0	0
Tarnetrum corruptum	39	26	24	50	0
Nasiaeschna pentacantha	44	39	7	51	0
Ischnura prognatha	14	43	0	57	0
Coryphaeschna ingens	39	42	0	58	0
Gomphaeschna furcillata	5	20	20	60	0
Libellula needhami	76	15	6	77	2
Aphylla williamsoni	12	14	7	78	0
Cannacria gravida	48	2	10	86	2
Erythrodiplax berenice	23	0	0	100	0
Anax junius	200	37	3	56	3
Epiaeschna heros	66	60	19	19	2
Perithemis tenera	189	49	20	29	2
Libellula vibrans	133	52	11	34	2
Erythemis simplicicollis	400	45	19	34	1
Pachydiplax longipennis	503	45	11	39	4
Ischnura posita	112	60	16	23	1
Anomalagrion hastatum	99	60	10	23	7
Pantala flavescens	138	48	22	21	8
Tramea carolina	64	47	9	34	9
Celithemis eponina	32	31	22	38	9
Pantala hymenea	11	40	30	20	10
Ischnura ramburi	153	34	19	46	10
Tramea lacerata	62	32	18	40	10
Tramea onusta	13	46	8	23	23

less than five collections are excluded from the table, the following discussion is based on the remaining 67 unless otherwise stated.

Fifteen species were recorded from all physiographic areas and 11 of these, *Anax junius, Perithemis tenera, Libellula vibrans, Erythemis simplicicollis, Pachydiplax longipennis, Ischnura posita, Anomalagrion hastatum, Pantala flavescens, Tramea carolina, Tramea lacerata* and *Ischnura ramburi,* were frequent and abundant in all areas.

Most species were associated primarily or entirely with one physiographic area, 38 with pinelands, nine with deltaic, five with alluvial. The greatest number of species occurred in the pinelands and 22 were restricted to this area. When species present in less than five collections are considered, a total of 96 was taken in pinelands whereas the number from deltaic, alluvial, and prairie combined was 54. *Gomphus submedianus, Gomphaeschna antilope, Erythrodiplax berenice, Erythrodiplax umbrata* and *Enallagma durum* were the only species not collected in pinelands. No species was restricted to prairie or to alluvial areas; only *Erythrodiplax berenice* was restricted to the deltaic plain.

Prairie, alluvial, and deltaic areas presented little variation in habitat and shared many species; collecting in any one was representative of the three. Collections from these areas nearly always lacked surprises, but almost every trip to the pinelands added species or important distribution notes. The pineland fauna contrasted markedly with that of the other three areas. Because collecting was more frequent in pineland and deltaic areas, the species composition of the major physiographic areas may be reduced to a contrast between pineland and deltaic faunas.

Thirty-two species absent in the deltaic plain are listed in Table 2. The dropping out of species in this area is more striking when species present in less than five collections are considered. Sixty two of the 101 species were absent in the deltaic plain, 24 of the state's 46 genera were absent, but no genus was restricted to this area. The very minor temperature differences between deltaic and adjoining areas could hardly be responsible for the absence of so many species and genera.

Four species, *Libellula incesta, Plathemis lydia, Argia apicalis* and *Argia tibialis,* well illustrate absences in the deltaic plain. They were widespread and frequent throughout most of the state and were taken from both lentic and lotic habitats, yet were absent in the deltaic plain. A common misconception is that the deltaic plain consists solely of brackish marsh which precludes the occurrence of fresh water species. There are large brackish areas, but there are also numerous fresh marshes, ponds, and borrow pits which these four species and others seemingly could utilize but did not.

A comparison of the distribution of two closely related species, *Libellula vibrans* and *L. incesta* further emphasizes absences in the deltaic plain. The former was widely distributed throughout the state and was abundant in the deltaic plain; the latter was also widespread but was never taken in that area. Since the two species are similar in so many respects, no tenable hypothesis can be offered to account for the exclusion of *incesta* from the deltaic plain.

Three important conclusions regarding Louisiana distribution are given by Foster and Smith (1901) and repeated by Wright (1939): (1) the Odonata of the low lying deltaic lands in which there are no rapid or clear streams are limited as regards the number of species and genera but are remarkably rich in individuals; (2) all the deltaic species are distributed over higher lands, while numerous genera never seek the bottoms; (3) no species of the subfamily Gomphinae was ever seen on deltaic soil.

As a test of these conclusions I compared the total number of species in St. Tammany (pineland) with Orleans, Jefferson, and St. Charles (deltaic) parishes combined. Collecting in these contrasting areas was approximately equal and they correspond closely to those studied by Foster and Smith. Sixty-five species were found in St. Tammany, 30 in Orleans, Jefferson, and St. Charles combined. Forty-two species were in the St. Tammany area but not the deltaic, whereas six were collected in the three deltaic parishes but not in St. Tammany. *Aphylla williamsoni* was the only gomphine collected in the deltaic plain. These comparisons definitely support Foster and Smith's conclusions.

Viosca (1944) points out the association of the frog, *Acris crepitans,* with alkaline water and of *Acris gryllus* with acid water in Louisiana. There is a great difference in pH between the acid waters of the Florida Parishes and the alkaline waters of the deltaic plain. It could be assumed that this pH difference accounts for the differences in species of odonates present in the two areas. However this assumption is not valid as illustrated by the occurrence of the following lentic and or lotic species in wide pH ranges. *Progomphus obscurus, Hagenius bravistylus, Boyeria vinosa, Libellula incesta, Plathemis lydia, Argia apicalis* and *Argia tibialis* were frequently taken in pinelands of the Florida Parishes at pH 5.0 and in southern Oklahoma at values as high as 8.2. They were never found in the deltaic plain where pH values average 8.0. I therefore do not consider pH a factor responsible for the contrast in species composition between the pinelands and the deltaic plain.

Topography seems to be the most important factor responsible for the contrast in species composition between pinelands and deltaic plain. All waters in the deltaic areas are lentic or very sluggish with mud bottoms. There are lentic waters such as ponds and sloughs in the pinelands, but there are also swiftly flowing creeks, wide shallow rivers, springs, and even a small waterfall, each with sand, gravel, clay, or mixed bottoms. Varying topography and the resulting variety of habitats in the pinelands seems to account for the large number of lotic species there which are absent in the deltaic plain. On the other hand, neither topography nor pH can account for the many lentic species present in the pinelands but absent in the deltaic plain.

Kennedy (1922b) states that the more primitive forms are adapted to well aerated water and are true stream species. Observations in Louisiana were similar to those of Kennedy in that most genera characteristic of lotic water are placed low in phylogeny by systematists. Moreover a greater proportion of more recently evolved genera occurred in the most recent land in the state, the deltaic plain, where all habitats are essentially lentic. For example, *Aphylla* was the only genus in the primitive families Petaluridae, Cordulegasteridae and Gomphidae present in the deltaic plain; seven genera in these families, characteristic of lotic water and present elsewhere in the state, were absent. The more primitive Zygoptera, Agrionidae and Lestidae, were entirely absent in the deltaic plain. There are 14 genera of the highly evolved Libellulinae in Louisiana; ten of these were present and four absent in the deltaic plain. The fauna of the deltaic area was predominantly libelluline because of numbers of genera and of individuals in this group. There was a greater proportion of recent than of primitive genera in the lentic and geologically recent waters of southern Louisiana.

HABITAT AND SPECIES COMPOSITION

Most species could easily be divided into those characteristic of lentic and those characteristic of lotic waters. However I could not prepare a different list of species for each minor habitat within the lentic or the lotic series, because these habitats were similar in physical characteristics and species composition. For example, it was impossible to give contrasting species lists for ponds, lakes, or swamps and contrasting lists for creeks, rivers, etc.

In the pinelands where both lentic and lotic habitats are present, two contrasting lists of common species can be given. The following were sufficiently frequent to be considered characteristic of clear, running, pineland streams: *Progomphus obscurus, Hagenius brevistylus, Dromogomphus* spp., *Boyeria vinosa, Agrion dimidiatum, Agrion maculatum, Hetaerina titia, Argia fumipennis, Argia moesta, Argia sedula* and *Argia tibialis*.

Exposed lentic habitats in the pinelands shared the following species: *Tetragoneuria cynosura, Orthemis ferruginea, Ladona deplanata, Plathemus lydia, Libellula incesta, Erythrodiplax c. minuscula* and *Lestes d. australis. Libellula axilena, Libellula semifasciata, Lestes vigilax* and *Nehalennia intergricollis*, though local and not frequent, were characteristic of shaded sloughs in pinelands.

Since no species was associated primarily with prairie and none was closely associated with the alluvial area, species lists are not given for habitats in these areas. The deltaic plain does not have a characteristic fauna except for the three species common in brackish situations, *Erythrodiplax berenice, Cannacria gravida* and *Libellula needhami*.

SEASONAL DISTRIBUTION

There was a long flight season for most species in Louisiana because of the mild climate. Two species, *Anax junius* and *Ischnura ramburi*, were collected as adults during every month of the year and many common forms were abundant from March to October. There was, however, a definite seasonal succession in the percentage of the total number of species flying during each month. These percentages closely parallel mean monthly temperatures (Table 1): January (4%), February (20%), March (50%), April (80%), May (80%), June (92%), July (94%), August (92%), September (86%), Octo-

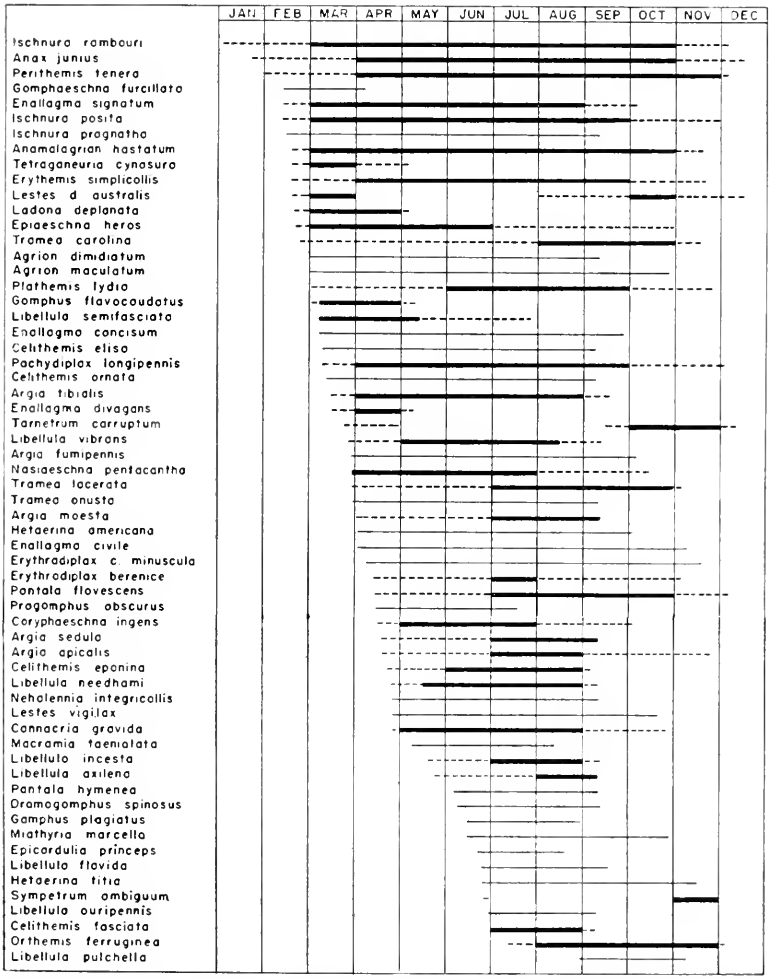

Figure 3. Limits of the flight season for species present in five or more collections. For many species, the periods of greatest frequency and/or abundance could be detected. These periods are shown by thickened lines and the extremes of the flight season by dotted lines. Other species showed little variation in frequency or abundance and this is indicated by thinner unbroken lines.

ber (52%), November (36%), December (10%).

Figure 3 shows seasonal succession of adults of species present in five or more collections. The sequence for the more common species in the New Orleans area was as follows. The season began in January with the occasional appearance of *Ischnura ramburi* and *Anax junius*. In February *Perithemis tenera, Erythemis simplicicollis, Enallagma signatum* and *Ischnura posita* appeared. March was the earliest month when any species was considered common and *Pachydiplax longipennis* and *Libellula vibrans* were added. April added *Libellula needhami. Cannacria gravida* and *Celithemis eponina;* by the close of this month all common species were flying and nearly all were abundant. In July *Tramea carolina, T. lacerata* and *Pantala flavescens* became abundant. The season waned in September; by the end of the month *Libellula vibrans* and *L. needhami* were no longer found and *Pachydiplax longipennis* and *Erythemis simplicicollis* were scarce. Many forms dropped out in October but *Pantala flavescens* was still frequent. After October no species was abundant, but *Ischnura ramburi, Anax junius, Ischnura posita, Erythemis simplicicollis, Tramea carolina, Pachydiplax longipennis* and *Pantala flavescens* were still present in November. *I. ramburi, A. junius, P. longipennis* and *P. flavescens* were the only species taken in December.

The seasonal range for most species was long but a few were more sharply limited. *Gomphaeschna furcillata, Gomphus flavocaudatus, Tetragoneuria cynosura, Ladona deplanata* and *Enallagma divagans* were not collected later than May 7. *Epicordulia princeps, Hetaerina titia, Sympetrum ambiguum, Celithemis fasciata, Orthemis ferruginea, Libellula pulchella* and *Miathyria marcella* were late season species not collected earlier than June 30. *Tramea carolina, T. lacerata* and *Pantala flavescens* appeared in March but were very scarce until July. *Lestes d. australis* and *Tarnetrum corruptum* were common in April and October but were not collected during May, June, and July suggesting the possibility of two emergence peaks.

Species which appeared early in the season were also found very late. For example, the adults of most species taken in February were also taken in November, whereas most species which first appeared in late April or May were not collected later than September. If a brief adult life of several months is assumed, it seems that species which transform in early spring when temperatures are low also transform during the low autumn temperatures and are therefore present as adults for a long period of the year.

Kennedy (1928) states that there is a tendency for primitive species to be early season forms. Byers (1930) states that, in general, neotropical species of restricted range become dominant in the fall months and that those with wider ranges emerge earlier and last longer. These relationships could not be verified in this study.

SUMMARY

Each of Louisiana's 64 parishes was sampled during 20 years of collecting. One-hundred-and-one species were collected or seen by

the writer and 30 of these are recorded from Louisiana for the first time.

Twenty-three species recorded in the literature from Louisiana were neither collected nor seen by the writer. The validity of these records is discussed.

Each of the 101 species seen by the writer is discussed in regard to distribution, physiography, habitat, and seasonal occurrence. Frequency percentage figures are often used to present comparisons of species composition in relation to physiography and habitat.

Based on area of primary occurrence, 59 species were Eastern, 17 Coastal Plain, 10 Tropical and Eastern, five Transcontinental, and 10 Tropical and Transcontinental. All categories include Eastern United States, hence all Louisiana species were shared with this area. None was restricted to Louisiana and none was western.

Within the state, 90 species were in a geographical sense statewide. Insufficient rainfall is not a factor limiting distribution in the state. The small average annual and January temperature differences between northern and southern Louisiana preclude temperature as a major factor limiting distribution. The minor role of temperature was shown by the fact that only three species were limited in a north-south direction.

Eight species extended no farther west than the Florida Parishes. The 50-mile wide alluvial plain of the Mississippi prevents their westward extension and is apparently the only major physical barrier causing geographical restrictions in Louisiana.

Louisiana was divided into four large physiographic-vegetation areas: pinelands, alluvial, deltaic, and prairie. Of 67 species present in five or more collections, 15 occurred in each of these four areas, 38 were associated primarily or entirely with pinelands, nine with deltaic, and five with alluvial. None was found primarily in the prairie.

The total number of species from deltaic, alluvial, and prairie areas combined was 54. These areas, with only sluggish or static water, presented but little variation in habitat and shared many species. In contrast, 96 species were collected in the pinelands. The more varied topography and the greater variety of lentic and lotic habitats probably accounted for the large number of species in the pinelands.

Many species, common elsewhere in the state, were absent from the deltaic plain; 24 genera and 62 species were absent from this area. Most primitive genera in the state were absent in the deltaic plain and a greater proportion of recently evolved genera were present in the lentic waters of the geologically recent deltaic plain.

Most species could be grouped easily into those characteristic of lentic and those characteristic of lotic waters. However I could not prepare a contrasting list of species for each minor habitat within the lentic or lotic series because those habitats were similar in physical characteristics and species composition.

The flight season was long as a result of the mild climate but there was a definite seasonal succession in the percentage of the total number of species flying during each month.

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ABSTRACT

Each of Louisiana's 64 parishes was sampled during 20 years of collecting. One-hundred-and-one species were recorded, 30 of which are new state records. Each species is discussed in relation to distribution, physiography, habitat, and seasonal occurrence. All species were shared with eastern United States; none was restricted to Louisiana and none was western. Ninety species were in a geographical sense statewide, three were restricted in a north-south direction, and eight did not extend west of the Florida Parishes. Rainfall and temperature differences between north and south Louisiana are not sufficient to be considered controlling factors. The Mississippi alluvial plain apparently is the only physical barrier causing geographical restrictions in the state. The state was divided into four physiographic-vegetation areas. Of 67 common species, 15 occurred in each of the four areas but 38 were associated primarily or entirely with pinelands, nine with deltaic, five with alluvial, and none was primarily in the prairie. Fifty-four species were collected in, and but one was restricted to, alluvial, deltaic, and prairie areas which lacked distinctive faunas. In contrast, 96 species were collected in the pinelands. Varying topog-

raphy and the resulting variety of habitats probably accounted for the large number of species in the pinelands. Twenty-four genera, mostly phylogenetically primitive, and 62 species were absent in the lentic waters of the geologically recent deltaic plain but were present elsewhere in the state. A greater proportion of recently evolved genera were present in the deltaic plain. Species characteristic of lentic and of lotic waters are given but those closely associated with each minor habitat within the lentic or lotic series could not be listed because these habitats were similar in physical characteristics and species composition. The flight season was long but there was a seasonal succession in the percentage of the total number flying during each month.

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ENDOCRINE CONTROL OF THE RED AND WHITE CHROMATOPHORES OF THE DWARF CRAWFISH, *CAMBARELLUS SHUFELDTI*

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ENDOCRINE CONTROL OF THE RED AND WHITE CHROMATOPHORES OF THE DWARF CRAWFISH, *CAMBARELLUS SHUFELDTI* [1]

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Evidence that color changes in crustaceans are mediated by endocrines rather than nerves was first supplied by Koller (1925, 1927) who showed that blood from a shrimp, *Crago vulgaris*, dark as a result of having been maintained on a black background, darkened a light animal kept on a white background. Blood from a yellow-adapted *Crago* caused yellowing of a light specimen. Perkins (1928) was the first investigator to describe an endocrine source in a crustacean. He found that eyestalk extracts of the prawn *Palaemonetes vulgaris* caused body lightening after injection into dark specimens. The first evidence that central nervous organs produce chromatophorotropins was supplied by Brown (1933) who showed that sea water extracts of central nervous organs of the prawn *Palaemonetes vulgaris* caused body lightening. Additional investigations of several species of crustaceans have revealed that the eyestalks and central nervous organs are each a source of at least two chromatophorotropins (Brown and Scudamore, 1940; Brown and Saigh, 1946). Since the early work of Koller (1925, 1927, Perkins (1928), and Brown (1933) the literature concerning the endocrine control of color change in crustaceans has increased extensively. A comprehensive review of the subject has been prepared by Brown (1952).

Although the endocrine control of chromatophore systems of several crustaceans has been investigated in detail, *Orconectes immunis* is the only crawfish in which the action of chromatophorotropins has been described. Brown and Meglitsch (1940) found that the sinus gland in the eyestalk of *Orconectes immunis* is a source of at least two chromatophorotropins, one disperses white pigment and the other concentrates red pigment. McVay (1942) investigated the physiological effects of extracts of the central nervous system upon chromatophores of *Orconectes immunis*. She found that central nervous organs are potent sources of chromatophorotropins capable of concentrating red and white pigments.

The eyestalks and central nervous organs of the dwarf crawfish, *Cambarellus shufeldti*, the species used in the investigation described herein, are endocrine sources. Removal of the eyestalks of *Cambarellus shufeldti* resulted in an increased metabolic rate. Eyestalk extracts injected into *Cambarellus* reversed the metabolic effect of eyestalk ablation (Fingerman, 1955). The eyestalks and central nervous organs of *Cambarellus* are also sources of a light-adapting

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hormone that affects the distal retinal pigment (Fingerman, 1956a, 1957). In addition to the light-adapting hormone, a dark-adapting hormone affecting retinal pigments was probably produced by *Cambarellus.*

In view of the scarcity of information available concerning the endocrine control of chromatophores in crawfishes, some preliminary experiments were performed with the dwarf crawfish, *Cambarellus shufeldti.* The results indicated that chromatophorotropins of the eyestalk act differently from those found in *Orconectes immunis* by Brown and Meglitsch (1940). The investigation described herein was, therefore, undertaken to determine in detail the sources and actions of the hormones controlling pigment migration within the red and white chromatophores of the dwarf crawfish.

Materials and Methods

Adult specimens of the dwarf crawfish, *Cambarellus shufeldti,* collected at frequent intervals near Crown Point, Louisiana, were used in the experiments described herein. Specimens were maintained at 22-24°C under normal day-night conditions in aquaria that contained aerated tap water one inch deep. Crawfish were selected from the stocks for use in experiments without regard to sex. Adults of *Cambarellus* are generally about 22 mm long. The females are slightly larger than the males. The average wet weights are approximately 0.20 grams for adult males and 0.25 grams for adult females. Enameled pans containing aerated tap water about one inch deep and with a bottom diameter of 14 cm were used as containers for the crawfish in all experiments.

Extracts of eyestalks and central nervous organs were prepared in the following manner. The organs were removed from the crawfish with the aid of a stereoscopic dissecting microscope and placed in van Harreveld's solution. When the desired number of each organ had been dissected, the organs were transferred with a minimum of saline to a glass mortar and triturated. The organs were then resuspended in a volume of van Harreveld's solution such that the final concentration was one-third of an organ per 0.02 ml of extract. Each crawfish received a dose of 0.02 ml of extract.

Extracts were injected into one-eyed crawfish; one eyestalk was removed at least 24 hours previous to the use of the crawfish in an experiment. Extracts were injected into one-eyed rather than normal crawfish because Brown, Webb, and Sandeen (1952) had demonstrated that eyestalk and central nervous organ extracts, when injected into one-eyed *Palaemonetes vulgaris,* evoked a greater chromatophore response than when injected into normal prawns. One-eyed prawns probably show a greater response to chromatophorotropins than do intact prawns because the former lack a major source of chromatophorotropins that may antagonize the injected hormones. Preliminary experiments have shown that one-eyed *Cambarellus* are also more responsive to eyestalk chromatophorotropins than are normal dwarf crawfish. Removal of both eyestalks of the crawfishes *Orconectes* and *Cambarellus* resulted in permanent, maximal dispersion of red and white pigments.

The exoskeleton of *Orconectes immunis* is opaque. Brown and Meglitsch (1940) and McVay (1942) were forced, therefore, to use chromatophores on portions of the carapace removed from the body in order to assay the organ extracts. *Cambarellus* has a carapace sufficiently transparent to allow accurate, direct observation of the underlying red and white chromatophores.

Throughout the experiments described herein, observations were made on the amount of pigment dispersion in the red and white chromatophores of the portion of the carapace dorsal to the heart. The chromatophore staging system of Hogben and Slome (1931) was used. According to their scheme, stage 1 represents maximal concentration of pigments, stage 5 maximal dispersion, and stages 2, 3, and 4 the intermediate conditions.

Activity (potency) values of organ extracts were calculated from the data of several experiments in order to facilitate comparison of extracts with one another. The method of calculation was similar to that described by Sandeen (1950). The average red and white chromatophore stages of specimens injected with organ extract or with van Harreveld's solution as a control were determined prior to injection and 15, 30, 60, 90, and 120 minutes following injection of the extract or saline. The average red and white chromatophore indices, determined after the injections has been administered, were summed. The product of five times the initial stage of the red and white chromatophores of each group was then calculated. If in the course of the experiment the pigments had concentrated, the sum was subtracted from the product. If the pigment had dispersed, the product was subtracted from the sum. The differences calculated in this manner for the red and white chromatophores of the crawfish that had been injected with van Harreveld's solution were then subtracted from the differences calculated for the red and white chromatophores of the crawfish that had been injected with organ extract. The final differences obtained in this fashion constitute the activity values of the red and white pigments in response to each extract and were a measure of the dispersing and or concentrating potencies of the extract with respect to the red and white pigments.

Two types of red chromatophores, light red and deep red, are present in the carapace of specimens of *Cambarellus*. The former are generally smaller and more dispersed than the latter. The two types were not staged separately because they showed qualitatively similar responses to tissue extracts. Instead the average stage of all the red chromatophores was determined. Brown and Meglitsch (1940) followed the same procedure with the crawfish *Orconectes immunis*.

EXPERIMENTS AND RESULTS

Background responses of Cambarellus shufeldti.—Twenty specimens of *Cambarellus shufeldti* were selected from the stock aquaria and separated into two lots of ten individuals each. One group was placed in a white enameled pan and the second group in a black one. At noon both pans were placed under an illumination of 40 ft. c. light intensity. At 2:00 P.M. the average chromatophore index of the individuals in each pan was determined and the backgrounds were exchanged with the result that the *Cambarellus* that had been on a white background were placed on a black background and vice versa. The chromatophore stage of the individuals in each pan was then determined 15, 30, 45, and 60 minutes after the backgrounds had been interchanged.

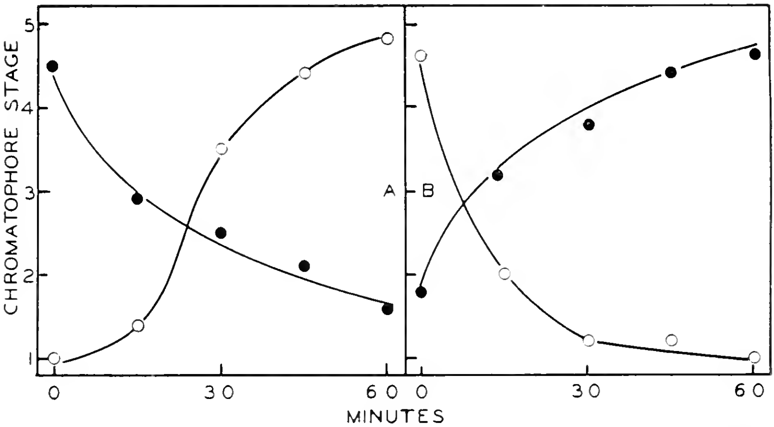

Figure 1. Responses of red and white chromatophores of *Cambarellus* to background changes. **A**, crawfish on a black background changed to a white background; **B**, crawfish on a white background changed to a black background. Dots, red chromatophores; circles, white chromatophores.

The data were used in the preparation of Figure 1. As evident from the figure the red pigment of crawfish on a black background became maximally dispersed and the white pigment maximally concentrated. On a white background the situation was reversed. The white pigment of crawfish on a white background dispersed maximally and the red pigment concentrated. Background adaptation was completed in 60 minutes. No evidence of a 24-hour rhythm of pigment migration was noted.

Chromatophorotropins in the central nervous organs and eyestalks of Cambarellus.—Eyestalks were removed from several specimens of *Cambarellus.* The entire central nervous system was then dissected from these specimens of *Cambarellus* and divided into four portions, the supraesophageal ganglia, circumesophageal connectives, thoracic nerve cord, and abdominal nerve cord. The eyestalks and each portion of the central nervous system were extracted as described above so that the final concentration was one-third of a structure per 0.02 ml of extract.

Five one-eyed crawfish were placed into each of six white enameled pans that contained aerated tap water. The crawfish had been on a white background for at least one hour in order to obtain dispersed white pigment and concentrated red pigment. In like manner five crawfish were placed into each of six black enameled pans. The latter crawfish had been on a black background for at least one hour with the result that their red pigment was dispersed and their white pigment was concentrated.

The crawfish in one black and one white pan were injected with 0.02 ml of each of the central nervous organ and eyestalk extracts. The crawfish in the sixth black pan and sixth white pan were each injected with 0.02 ml of van Harreveld's solution as a control. The average red and white chromatophore stages of the crawfish on the black and white backgrounds were determined at the time of injection of the extracts and 15, 30, 60, 90, and 120 minutes thereafter. The experiment was repeated once.

The results are presented in Figures 2 (red chromatophores) and 3 (white chromatophores). Each point in the figures represents the average of 10 crawfish. As is evident from both figures, all portions of the central nervous system contained principles that dispersed and concentrated red and white pigment. Red and white pigment concentrating hormones of the central nervous organs exhibited their

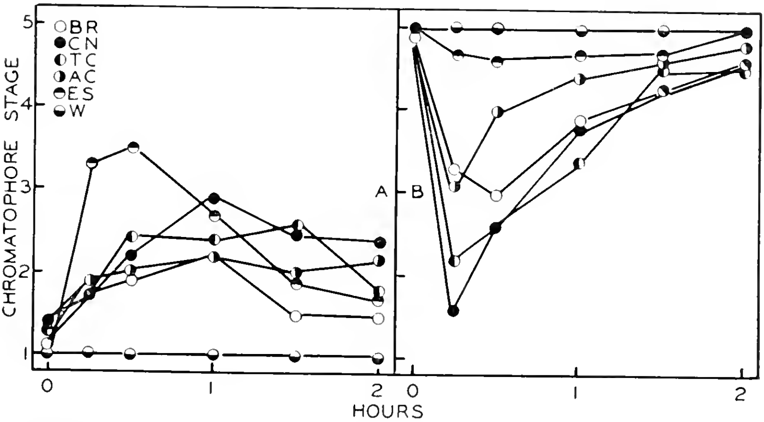

Figure 2. Responses of red chromatophores of one-eyed *Cambarellus* on a white background (**A**) and on a black background (**B**) to extracts of central nervous organs and eyestalks. BR, supraesophageal ganglia; CN, circumesophageal connectives; TC, thoracic nerve cord; AC, abdominal nerve cord; ES, eyestalk; W, control (van Harreveld's solution).

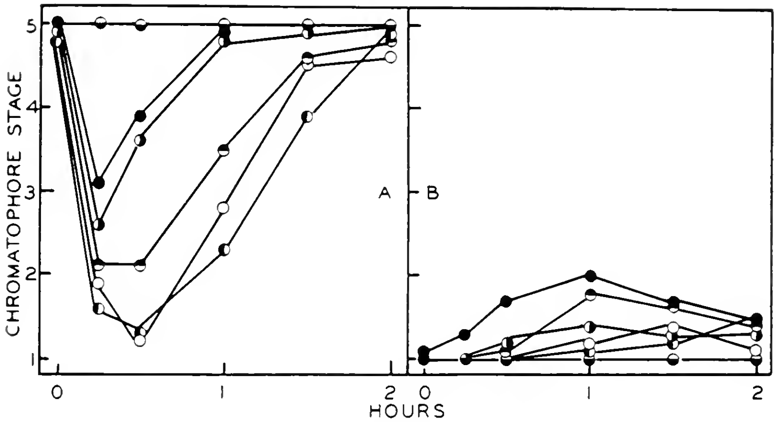

Figure 3. Responses of white chromatophores of one-eyed *Cambarellus* on a white background (**A**) and on a black background (**B**) to extracts of central nervous organs and eyestalks. Symbols same as in figure 2.

maximal effect more rapidly than the red and white pigment dispersing hormones. Maximal pigment concentration occurred 15-30 minutes after injection of the extracts whereas maximal pigment dispersion was not apparent until 60-90 minutes after the extracts had been administered. Apparently, pigment dispersing hormones of the central nervous system were not able to express themselves maximally until the predominant red and white pigment concentrating effects had begun to diminish.

Table 1 was prepared to facilitate comparison and discussion of the data presented in Figures 2 and 3. In the table, activity values which indicate the extent to which the red and white pigments were

TABLE 1.

ACTIVITY VALUES OBTAINED WITH EXTRACTS OF CENTRAL NERVOUS ORGANS

Tissue	Red pigment dispersing activity	Red pigment concentrating activity	White pigment dispersing activity	White pigment concentrating activity
Supra-esophageal ganglia	3.5	5.4	0.7	9.5
Circum-esophageal connectives	6.1	8.1	2.6	3.1
Thoracic nerve cord	4.4	7.3	0.7	10.0
Abdominal nerve cord	3.8	3.6	1.2	3.6

dispersed or concentrated, are presented for each tissue of the central nervous system. In order of decreasing activity for the dispersion of red pigment are: circumesophageal connectives > thoracic nerve cord > abdominal nerve cord > supraesophageal ganglia. In order of decreasing activity for the concentration of red pigment are: circumesophageal connectives > thoracic nerve cord > supraesophageal ganglia > abdominal nerve cord. The decreasing orders of red pigment dispersing and concentrating activities were practically identical. In both series the circumesophageal connectives were the most potent source followed by the thoracic nerve cord.

In order of decreasing activity for the dispersion of white pigment are: circumesophageal connectives > abdominal nerve cord > supraesophageal ganglia = thoracic nerve cord. In order of decreasing activity for the concentration of white pigment are: thoracic nerve cord > supraesophageal ganglia > abdominal nerve cord > circumesophageal connectives. The decreasing order of white pigment dispersing activity was practically the reverse of the decreasing order of white pigment concentrating activity, *e.g.* the circumesophageal connectives had the least white pigment concentrating activity but were the most potent source of white pigment dispersing hormone. In contrast, the organ with the most red pigment dispersing hormone also had the most concentrating hormone. The circumesophageal connectives were the most potent source of three of the four hormones.

The order of decreasing activity for a white pigment activator was not the same as that for a red pigment chromatophorotropin (Table 1). Therefore, the four chromatophorotropins must be distinct entities.

The eyestalks contained appreciable quantities of red pigment dispersing and white pigment concentrating and dispersing hormones, plus a small quantity of red pigment concentrating hormone. As observed with extracts of central nervous organs, maximal white pigment concentration appeared before (15-30 minutes) maximal white pigment dispersion (60-90 minutes). Maximal red pigment dispersion due to eyestalk extract occurred more rapidly than maximal red pigment dispersion due to nervous tissue extracts, presumably because of the relatively small amount of antagonistic red pigment concentrating hormone in the eyestalk.

GENERAL DISCUSSION

The hormonal mechanisms involved in control of the chromatophore system of the dwarf crawfish, *Cambarellus shufeldti*, differ considerably from those of *Orconectes immunis*, the only other crawfish in which the action of chromatophorotropins has been investigated in detail. All portions of the central nervous system and the eyestalks of *Cambarellus shufeldti* produce four hormones, red pigment concentrating, red pigment dispersing, white pigment concentrating, and white pigment dispersing.

Brown and Meglitsch (1940) showed that sinus gland extracts of *Orconectes* disperse white pigment and concentrate red pigment. In contrast the predominant effects of eyestalk extracts of *Cambarellus* are dispersion of red pigments and concentration of white pigment. McVay (1942) found that extracts of central nervous organs of *Orconectes* contained red and white pigment concentrating hormones only. Extracts of central nervous organs of *Cambarellus* caused both concentration and dispersion of red and white pigments.

Red and white pigments of *Orconectes* and *Cambarellus* disperse maximally following eyestalk ablation. The stage that chromatophores attain after eyestalk removal has been generally assumed to be a function of the action of the hormones produced by the eyestalk. If the predominant hormone in the eyestalk disperses pigment, then the pigment will concentrate after eyestalk removal and vice versa. For example, after the eyestalks are removed from the blue crab, *Callinectes sapidus*, the black pigment concentrates and the red pigment disperses (Fingerman, 1956b). Injection of eyestalk extract counteracted the effects of eyestalk ablation, the red pigment concentrated and the black pigment dispersed. In view of the fact that the eyestalks of *Cambarellus* produce a red pigment dispersing hormone that predominates over the red pigment concentrating hormone, concentration of red pigment rather than dispersion might be anticipated after eyestalk removal. A corresponding situation was noted in the crawfish *Orconectes*, whose eyestalks produce a white pigment dispersing hormone yet white pigment disperses following eyestalk ablation. The red and white pigments of eyestalkless specimens of both *Cambarellus* and *Orconectes* are probably maintained in the dispersed state by means of pigment dispersing hormones secreted by central nervous organs.

Knowles and Carlisle (1956) have reviewed the literature concerning neurosecretion and chromactivating hormones. The current hypothesis is that chromatophorotropins originate in neurosecretory cells, are transported via nerve fibers to storage centers such as the sinus gland, and from there are released into the blood on appropriate stimulation.

SUMMARY AND CONCLUSIONS

1. Red and white chromatophores of the dwarf crawfish, *Cambarellus shufeldti*, exhibited specific background responses. In crawfish on a black background the white pigment concentrated and the red pigment dispersed. The pigmentary states reversed themselves in crawfish on a white background.

2. Central nervous organs and eyestalks produce red and white pigment dispersing and concentrating hormones. The four hormones are distinct entities. The order of decreasing hormonal content of central nervous organs is practically the same for red pigment concentrating and dispersing hormones whereas the decreasing order of

white pigment concentrating hormone content is practically the reverse of that of white pigment dispersing hormone.

3. Endocrine control of crawfish chromatophores is discussed.

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ABSTRACT

Red and white chromatophores of the dwarf crawfish, *Cambarellus shufeldti*, exhibit background adaptations. In crawfish on a black background the white pigment concentrates and the red pigment disperses. The pigmentary states reverse themselves in crawfish on a white background. The central nervous organs produce red and white pigment concentrating and dispersing hormones. The four hormones are distinct entities. The order of decreasing hormonal content of central nervous organs is practically the same for red pigment concentrating and dispersing hormones whereas the decreasing order of white pigment concentrating hormone is practically the reverse of that of white pigment dispersing hormone. The eyestalks of *Cambarellus* produce appreciable quantities of red pigment dispersing hormone and white pigment dispersing and concentrating hormones and a small quantity of red pigment concentrating hormone. The endocrine control of crawfish chromatophores is discussed. The chromatophore system of *Cambarellus* is different from the the chromatophore system of *Orconectes immunis*, the only other crawfish investigated in this respect.

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HORMONES CONTROLLING THE CHROMATOPHORES OF THE DWARF CRAWFISH, *CAMBARELLUS SHUFELDTI*: THEIR SECRETION, STABILITY, AND SEPARATION BY FILTER PAPER ELECTROPHORESIS

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HORMONES CONTROLLING THE CHROMATOPHORES OF THE DWARF CRAWFISH, *CAMBARELLUS SHUFELDTI*: THEIR SECRETION, STABILITY, AND SEPARATION BY FILTER PAPER ELECTROPHORESIS[1]

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The chromatophore system of the dwarf crawfish, *Cambarellus shufeldti*, has been the subject of previous investigations (Fingerman, 1957a, b; Fingerman and Lowe, 1957). Red pigment concentrates and white pigment disperses when specimens are put on a white background. The pigmentary states reverse themselves when crawfish are put on a black background. Central nervous organs of *Cambarellus* were sources of red and white pigment concentrating and dispersing hormones. Of all the central nervous organs, the circumesophageal connectives were the most potent source of white pigment dispersing, red pigment dispersing, and red pigment concentrating hormones. The thoracic nerve cord contained the most white pigment concentrating hormone. Eyestalks produced appreciable quantities of white pigment dispersing and concentrating hormones and a red pigment dispersing factor. A red pigment concentrating hormone was present in small quantity (Fingerman, 1957a).

Behavior of red and white chromatophores on isolated portions of the carapace of dwarf crawfish that had been on black and on white backgrounds was also investigated (Fingerman, 1957b). Red pigment had an inherent tendency to concentrate nearly maximally and white pigment to disperse nearly maximally when the chromatophores were no longer controlled by hormones. Reciprocal blood transfusions between *Cambarellus* that had been on black and on white backgrounds for two hours revealed that the blood always contained pigment dispersing and concentrating hormones. The degree of pigment dispersion at any time appeared to be determined by the relative quantity of each antagonistic factor in the blood (Fingerman, 1957b). Investigation of the control of the chromatophores of the crawfish *Orconectes clypeatus* likewise revealed the simultaneous presence of red and white pigment dispersing and concentrating hormones in the blood (Fingerman, 1957c).

Fingerman and Lowe (1957) determined the effects of maintenance

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[1] This investigation was supported by Grant No. B-838 from the National Institutes of Health.

of *Cambarellus* on black and on white backgrounds for periods up to three weeks. Rates of red and white pigment dispersion and concentration in intact crawfish progressively decreased. Red and white pigments gradually lost their inherent abilities to concentrate and disperse respectively after isolation.

The titers of chromatophorotropins in the circumesophageal connectives also changed during the time the crawfish were on the backgrounds. After the crawfish had been on the backgrounds for two hours the titers of hormones in the circumesophageal connectives required for proper background adaptation increased. For example, circumesophageal connectives of crawfish on a black background contained more red pigment dispersing hormone than circumesophageal connectives of crawfish on a white background. However, after the crawfish were on the black and the white backgrounds two weeks the relationship between synthesis, storage, and release of the hormones required for background adaptation changed; the hormones not required for proper background adaptation, *e.g.* red pigment dispersing hormone of crawfish on a white background, were stored. The quantities of chromatophorotropins in the blood also changed. The factors stored in the circumesophageal connectives of crawfish that were on a background for two weeks decreased and the hormones needed for proper background adaptation increased.

The present investigation was undertaken to obtain further information concerning control of the chromatophores of the dwarf crawfish, *Cambarellus shufeldti.* Changes of blood titers of red pigment dispersing and of white pigment dispersing hormones as well as effects of eyestalk removal upon the chromatophore system were considered. Filter paper electrophoresis of central nervous organ extracts was also attempted.

MATERIALS AND METHODS

Adult specimens of the dwarf crawfish, *Cambarellus shufeldti,* collected at Crown Point, Louisiana, were used in the experiments reported below. The crawfish were kept in the air-conditioned laboratory, 23-24° C, where the experiments were performed, in aquaria containing aerated tap water approximately one inch deep. Red and white chromatophores in the portion of the carapace dorsal to the heart were staged according to the system of Hogben and Slome (1931). Stage 1 represented maximal pigment concentration, stage 5 maximal dispersion and stages 2, 3, and 4 the intermediate conditions.

Cambarellus that received injections of blood or tissue extracts had had one eyestalk removed at least 24 hours prior to the experiment. Brown, Webb, and Sandeen (1952) and Fingerman (1957a) found that responses of one-eyed individuals to chromatophorotropins were greater than responses of intact specimens, presumably because the presence of both eyestalks made the organisms more capable of antagonizing injected hormones.

Two types of red chromatophores, deep red and light red, are present in the carapace of *Cambarellus.* The former are generally smaller and more dispersed than the latter. The two types were not staged separately because they showed qualitatively similar responses to tissue extracts. Instead the average stage of all the red chromatophores was determined. Brown and Meglitsch (1940) followed the same procedure with the crawfish *Orconectes immunis.*

Knowles, Carlisle, and Dupont-Raabe (1955) used filter paper electrophoresis to separate red pigment dispersing and concentrating chromatophorotropins from the sinus gland and postcommissure organs of the prawn *Leander serratus.* Electrophoresis of extracts of central nervous organs of *Cambarellus* was performed with a Research Equipment Corporation Filter Paper Electrophoresis Apparatus, Model E-800-2. The voltage was held constant at 500 volts and the current varied between 0.5 and 1.0 milliampere. For any one experiment the supraesophageal ganglia plus the circumesophageal connectives of 15 *Cambarellus* were dissected out, triturated, and resuspended in 0.1 ml of distilled water. The extract was then gradually applied to a filter paper strip 0.5 inch wide. A hot air blower was used to evaporate the water as the extract was applied to prevent spread of the extract more than one-quarter inch along the strip in either direction from the point of application. The entire strip was then wetted with the appropriate buffer and placed in the electrophoresis migration chamber. Tap water flowed through the chamber to minimize heating of the paper due to current flow. After electrophoresis had proceeded for three hours the filter paper strip was removed from the chamber and cut into three portions, the center portion about 0.5 inch long where the extract had been applied originally and two pieces three inches long on either side of the center portion. The three pieces were not allowed to dry. Instead each piece was placed into 0.35 ml of van Harreveld's solution for 30 minutes. The resulting extracts were then taken up in syringes and injected into one-eyed crawfish that had been on a black or a white background for two hours.

EXPERIMENTS AND DISCUSSION

Titers of red and white pigment dispersing hormones in the blood of dwarf crawfish following a background change.—The following experiments were performed to determine the changes in blood titer of red and white pigment dispersing hormones following background changes of the dwarf crawfish. *Cambarellus* were placed on black and on white background at 7 A.M. At 9 A.M. the backgrounds were interchanged and blood of the crawfish was assayed for red and white pigment dispersing hormones after these crawfish had been on the new backgrounds 15, 30, 60, and 120 minutes. From 0.01 to 0.04 ml of blood was taken from the region of the heart of one crawfish. A crawfish on a black or a white background was injected with 0.02 ml of blood as rapidly as possible to minimize clotting in the syringes.

Changes in amount of red and white pigment concentrating hormones could not be determined with accuracy because of the small quantities of these hormones normally present in the blood of *Cambarellus* (Fingerman, 1957b; Fingerman and Lowe,1957).

The stages of the red and white chromatophores of assay crawfish were determined at the time of injection of blood and 15, 30, 60, 90, and 120 minutes thereafter. Crawfish used for assay were inspected prior to injection of blood to certify that their red and white pigments had attained the proper degree of concentration on the particular background. Activity (potency) values for blood were determined as measures of titers of red and white pigment dispersing hormones as follows. In experiments designed to test pigment dispersion red and white pigments were in stage one at the outset. The average chromatophore stages determined 15, 30, 60, 90, and 120 minutes after the blood had been administered were summed. Five was then subtracted from the sum because if no pigment dispersing hormone was present, the sum would have been five.

Activity values were plotted against the time following the background change that the crawfish had been on a black or white background prior to taking blood from them (fig. 1). Each point represents the average of 20 assay crawfish. The first time the experiment was performed 10 assay crawfish were used. However, in view of the surprising results obtained with white chromatophores that will be described below, the experiment was repeated. The results of both experiments were the same and were averaged.

As evident from inspection of the left half of Figure 1, the amount of red pigment dispersing hormone decreased in the blood of crawfish

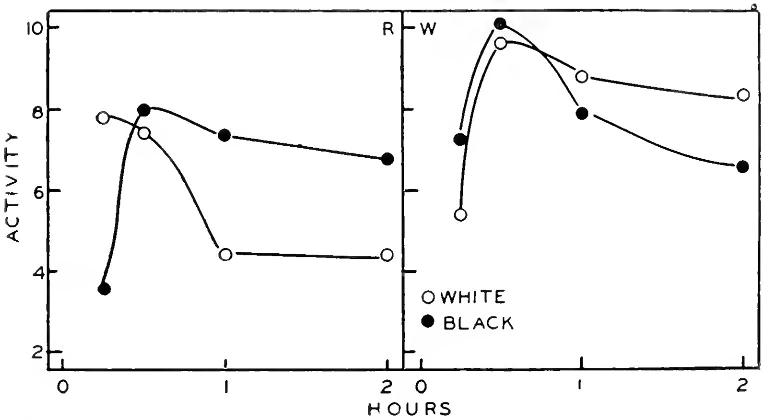

Figure 1. Blood titer changes of red pigment dispersing hormone (**R**) and white pigment dispersing hormone (**W**) of *Cambarellus* on black (dots) and on white (circles) backgrounds for different periods of time.

placed on a white background and increased in the blood of *Cambarellus* put on a black background. The red pigment dispersing hormone was still present in the blood of crawfish kept on the white background for two hours as observed previously by Fingerman (1957b). More red pigment dispersing hormone was present in the blood of crawfish that had been on the black background for 30 minutes than in the blood of *Cambarellus* that had been on a black background 15, 60, or 120 minutes.

Red pigment of *Cambarellus* migrated from a maximally concentrated condition to maximal dispersion 60 minutes after transfer of crawfish from a white to a black background (Fingerman, 1957a; Fingerman and Lowe, 1957). Evidently, after transfer from a white to a black background *Cambarellus* secreted more red pigment dispersing hormone than was necessary to maintain the red pigment at maximal dispersion. This phenomenon may be explained in several ways. (1) More red pigment dispersing hormone was required to disperse the pigment than was needed to keep it dispersed. (2) An overabundance of red pigment dispersing hormone was secreted to disperse the pigment rapidly, and once the pigment was dispersed the excess was excreted or inactivated. (3) Both (1) and (2) apply. (4) The excess might be needed to antagonize pigment concentrating hormone.

Consideration of the results obtained with the white pigment dispersing hormone (fig. 1, right half) revealed that upon transfer of *Cambarellus* from a black to a white background more white pigment dispersing hormone was present in the blood of crawfish 30 minutes after transfer to the white background than at any other time. The same interpretation may be applied here as was used with the red pigment dispersing hormone in the blood of crawfish put on a black background.

Blood titer changes of white pigment dispersing hormone of crawfish transferred from a white background to a black background were different from those observed with red pigment dispersing hormone of crawfish transferred from a black to a white background. Instead of a gradual decrease of the titer of white pigment dispersing hormone, an increase was observed prior to the decrease. Evidently more pigment dispersing hormone was secreted when the crawfish were taken from a white background and placed on a black background.

Analysis of effects of eyestalk removal upon the red and white chromatophores.—This series of experiments was designed to yield further information about the behavior of red and white pigments after removal of both eyestalks from specimens on black and on white backgrounds in an effort to determine why these pigments disperse maximally in eyestalkless crawfish. The first experiment was designed to determine the effects of darkness upon the red and white chromatophores. For the first series of observations intact crawfish were maintained on black and on white backgrounds for two hours and then placed in darkness. The stages of the red and white chromatophores were determined at the time the crawfish were placed in the darkroom and 15, 30, 60, 90, and 120 minutes thereafter. The results have been presented in Figure 2 where each point represents the average of 10 crawfish. Each point in the individual curves of Figures 2-9 represents the same crawfish but each curve in these figures represents a separate group of crawfish. White pigment of specimens that had been on a white background remained maximally dispersed and white pigment of specimens from a black background dispersed rapidly when the crawfish were placed in darkness. Red pigment of speci-

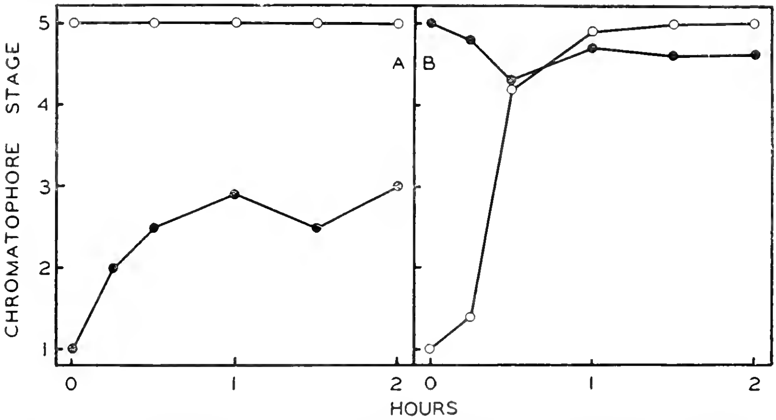

Figure 2. Responses of red (dots) and white (circles) chromatophores of *Cambarellus* taken from white (**A**) and black (**B**) backgrounds and placed in darkness.

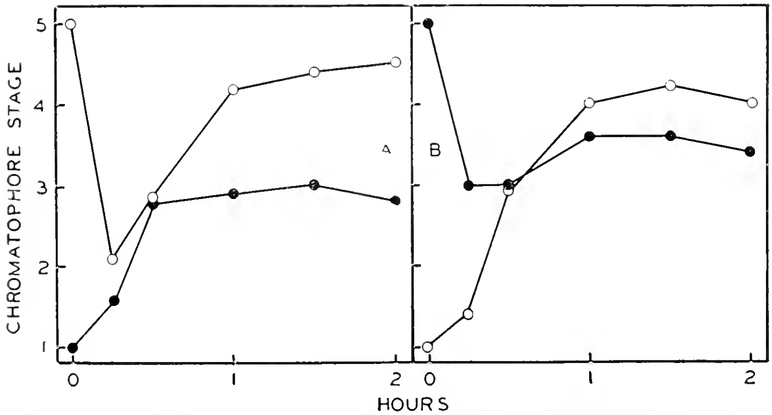

Figure 3. Responses of red (dots) and white (circles) chromatophores of *Cambarellus* taken from white (**A**) and black (**B**) backgrounds, destalked, and placed in darkness.

mens that had been on a white background attained an intermediate degree of dispersion after the crawfish were in darkness one hour whereas dispersed red pigment of specimens that had been on a black background merely concentrated slightly.

Both groups of crawfish were kept in the darkroom for 18 hours when the average stages of the red and white chromatophores were again determined. For specimens that had been on a white background prior to being put in darkness, the average stages of the red and white chromatophores were 3.4 and 5.0 respectively. The corresponding stages for crawfish originally on a black background were 4.0 and 4.8.

In the second experiment of this series the effects of destalking, followed by darkness, upon the red and white chromatophores were determined. Intact crawfish were placed in black and in white enameled pans for two hours. Crawfish whose red and white chromatophores were in the proper stages of adaptation to the backgrounds were selected, the eyestalks were removed, and the red and white chromatophore stages of the crawfish that had been on the black and the white backgrounds were determined 15, 30, 60, 90, and 120 minutes after the eyestalkless crawfish had been placed in darkness. The results are presented in Figure 3 where each point represents the average of 10 individuals.

As evident from comparison of Figures 2 and 3 the behavior in darkness of red and white chromatophores of intact *Cambarellus* differed in some respects from the behavior of the chromatophores of eyestalkless crawfish. Red chromatophores of intact and eyestalkless specimens that had been on a white background became intermediately dispersed after two hours in darkness. Responses of white pigment of intact and eyestalkless specimens that had been in a white pan differed. No concentration of white pigment was observed when intact individuals adapted to a white background were placed in darkness, but considerable white pigment concentration was evident when eyestalkless specimens were placed in darkness. Evidently, the stimulus of eyestalk removal resulted in release of white pigment concentrating hormone from the neurosecretory cells of the central nervous system.

Differences between the behavior in darkness of red and white chromatophores of intact specimens that had been in a black pan (fig. 2B) and of crawfish that had been in a black pan before their eyestalks had been removed (fig. 3B) were evident. Very little red pigment concentration was evident in intact crawfish (fig. 2B), but considerable red pigment concentration was evident in eyestalkless specimens. Apparently, as postulated for the white pigment, eyestalk removal stimulated release of red and white pigment concentrating hormones. Maximally concentrated white pigment of crawfish on a black background dispersed after eyestalk removal but at a slower rate than observed in intact *Cambarellus*, probably because of white pigment concentrating hormone released into the blood when the eyestalks were removed.

Red and white pigments of crawfish placed in darkness immediately after destalking ultimately dispersed maximally. The eyestalkless crawfish used in the experiment described above were kept in the darkroom for 24 hours when the chromatophores of each group were again examined. The average red and white chromatophore stages for the crawfish that had been on a white background were both five. The corresponding values for eyestalkless crawfish that had been on a black background were 4.9 and five. Rates of red and white pigment dispersion following eyestalk removal appeared to be slower in specimens placed in darkness (fig. 3) than in crawfish kept in light after eyestalk removal (figs. 6B, 7A, and 8A). Light may aid in inactivating red and white pigment concentrating hormones that are released when eyestalks are removed.

Stimulation of eyestalk stubs of eyestalkless crawfish with an electric cautery resulted in red and white pigment concentration. The stimulus of the cautery must have caused secretion of red and white pigment concentrating hormones by central nervous organs. Removal of eyestalks is probably a sufficient stimulus to elicit the same response.

Fingerman (1957b) showed that after removal of the eyestalks of *Cambarellus* a shift of the hormonal titers in the blood occurred. Blood of eyestalkless *Cambarellus* had (1) less red pigment dispersing and more red pigment concentrating hormone than blood of crawfish on a black background and (2) more white pigment concentrating and less white pigment dispersing hormone than blood of crawfish on a white background. Apparently, eyestalk removal caused a shift of the hormonal titers in the blood toward a more neutral condition. In view of the data of Fingerman (1957b) and the results presented in Figures 2 and 3 comparison of the hormonal titers of the blood of intact and eyestalkless crawfish in darkness seemed desirable.

Blood was removed from *Cambarellus* that had been taken from the stock aquaria and placed in darkness for 24 hours. One-eyed crawfish that had been on a black or white background for two hours under an illumination of 20 ft. c. light intensity were each injected with 0.02 ml of blood. The same procedure was followed with blood taken from crawfish both of whose eyestalks had been removed 12 to 24 hours previously. The eyestalkless crawfish were kept under an illumination of 20 ft. c. from the time of eyestalk removal.

The results are presented in Figures 4 (intact crawfish) and 5 (eyestalkless crawfish) where each point represents the average of 10 crawfish. As evident from inspection of the figures, blood of both groups contained red and white pigment dispersing and concentrating hormones. However, blood of eyestalkless individuals contained more of each hormone than did blood of intact specimens kept in darkness

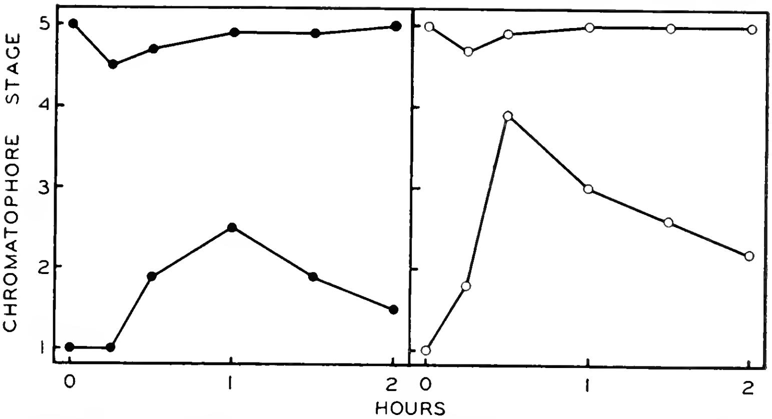

Figure 4. Responses of red (dots) and white (circles) chromatophores of dwarf crawfish on black and on white backgrounds to blood from crawfish that had been in darkness 24 hours.

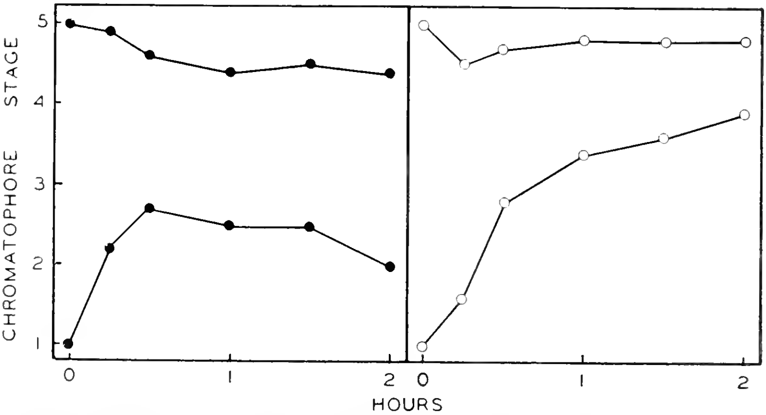

Figure 5. Responses of the red (dots) and white (circles) chromatophores of dwarf crawfish on black and on white backgrounds to blood from crawfish whose eyestalks had been removed 12 to 24 hours previously.

for 24 hours. Maximal dispersion of red and white pigments of *Cambarellus* can not be due merely to the absence of photic stimuli via the optic nerves.

The following set of experiments was designed to analyze the responses of red chromatophores of crawfish subjected to a background change at the time of blinding or eyestalk removal. In the first group of experiments crawfish were kept on black and white backgrounds under an illumination of 20 ft. c. light intensity for two hours before the average red chromatophore stage of each group was determined.

Their eyestalks were then covered with an opaque black cloth. Half of the blindfolded crawfish that had been in a white pan were kept on a white background, the remainder were placed in a black pan. In like manner half of the crawfish that had been on a black background were kept in a black pan, the remainder were put into a white pan. The average red chromatophore stages of the crawfish in each of the four pans were then determined 15, 30, 60, 90, and 120 minutes after blindfolding. The first time the experiment was performed 10 crawfish were used in each of the four pans. The experiment was repeated with 40 more crawfish blindfolded with a different material, Plaster of Paris, to assure that the results abtained were due to blindfolding and not to the nature of the opaque material. The results were the same in both experiments, were averaged, and presented in Figure 6A where each point represents the mean of 20 crawfish. As evident from inspection of the figure, transitory concentration of the red pigment of crawfish that had been on a black background prior to blindfolding occurred. The red pigment of crawfish that were on a white background when blindfolded dispersed slightly. No significant difference was apparent between red chromatophore stages of crawfish that had their background changed and those that did not. Changes of degree of dispersion or concentration of the red pigment of blindfolded individuals were not as large as those of intact specimens placed in darkness (fig. 2). Light impinging on *Cambarellus* appears to influence the chromatophores when the eyes are non-operative.

The next experiment, also performed twice, was similar to the one described above with the exception that instead of blindfolding the

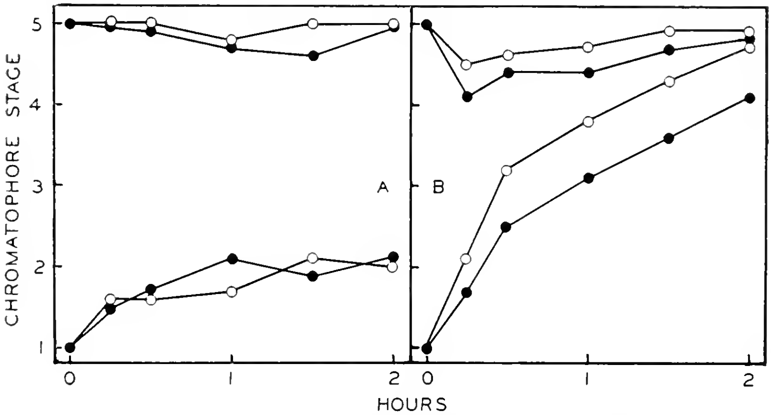

Figure 6. Responses of the red chromatophores of dwarf crawfish on black and on white backgrounds to background change. **A**, eyes covered with an opaque material prior to background change; **B**, eyestalks removed prior to background change. Circles, control on same background; dots, background changed.

crawfish both eyestalks were removed. The results are presented in Figure 6B where each point represents the average of 20 crawfish. As evident from inspection of the figure, the responses of crawfish whose background was changed differed from the responses of crawfish kept on their original background. Red pigment of crawfish that had been changed from a white to a black pan at the time of eyestalk removal did not disperse as rapidly as red pigment of crawfish kept on a white background. Red pigment of specimens that had been in a black pan prior to removal of eyestalks concentrated transitorily after eyestalk ablation. Red pigment of crawfish transferred to a white pan from a black pan at the time of eyestalk removal concentrated more than red pigment of crawfish kept in black pans and returned more slowly to the original maximally dispersed condition. The stimulus of eyestalk removal probably resulted in release of red pigment concentrating hormone. The differences observed between crawfish kept on the same background and those changed appeared to be due to slower removal of red pigment concentrating hormone from the blood of the changed group. The difference in rates of pigment dispersion did not depend directly upon the nature of the background since in one instance the crawfish were transferred from white pans to black ones and in the second case from black pans to white ones. In both instances rates of pigment dispersion decreased. Since no differences due to changes of background were evident in intact blindfolded crawfish whereas differences showed up in eyestalkless crawfish, the eyes must predominate in photic responses when photoreceptors are present.

Fingerman (1957d) demonstrated that the degree of light adaptation of the distal retinal pigment of *Cambarellus shufeldti* depended upon the brightness of the visual field and was not a true albedo response. A black background acted simply to reduce the amount of light striking the major portion of the eye.

Welsh (1934) observed that eyestalkless specimens of the crawfishes *Orconectes virilis* and *Procambarus clarki* avoided light through random movements and use of their caudal photoreceptor. To determine if a caudal photoreceptor were responsible at least in part for the results reported above the following experiments were performed.

In the first experiment 20 eyestalkless crawfish were placed under an illumination of 20 ft. c. in an enameled pan with the bottom half white and half black. The percentage of the crawfish on the black half was determined after 1, 2, 18, 24, 42, 48, and 70 hours. The respective percentages were 40, 55, 50, 40, 65, 50, and 55, an average of 50.7. Intact *Cambarellus* will avoid light by congregating on the black half. In 30 minutes 16 of 20 of one group of intact crawfish and 19 of 20 of another group went to the black half of the pan, an average of 87.5 percent. The caudal photoreceptor evidently played no role since eyestalkless *Cambarellus* did not congregate on the black side of the pan.

In another experiment the abdomens of 40 crawfish were completely covered with opaque black cloth to prevent light from exciting the caudal photoreceptor. The crawfish were then divided into two equal sized groups; one group was placed on a white background and the other on a black background. After the red chromatophores of the crawfish had adapted to their respective backgrounds, the eyestalks were removed and the background of 10 crawfish from each group was changed.

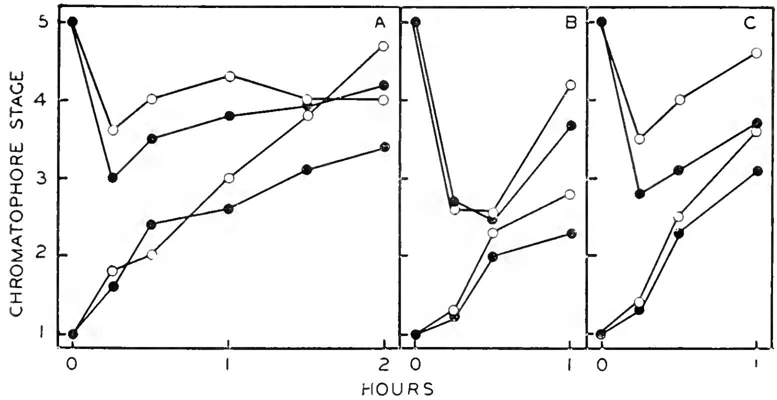

Figure 7. Responses of the red chromatophores of dwarf crawfish on black and on white backgrounds to background change at the time of eyestalk removal. **A**, abdomen covered with an opaque material; **B**, cephalothorax from the base of the eyestalks to the abdomen covered with an opaque material; **C**, abdominal nerve transected. Circles, control on same background; dots, background changed.

The red chromatophores were then observed at intervals for two hours (fig. 7A). The results were qualitatively the same as reported in Figure 6B. Changing the background slowed the rate of red pigment dispersion as compared with the rate of pigment dispersion of crawfish whose background had not been changed. The response must have been partly endocrine and not a direct response of the exposed red chromatophores to light for when the opaque material was removed from the abdomen the red chromatophores from the posterodorsal portion of the crawfish were in the same average stage as those on the anterodorsal portion. The caudal photoreceptor must not have had a role in determining the results shown in Figure 6B since the same results were apparent in Figure 7A when the caudal photoreceptor was covered with an opaque material.

The next experiment was the same as reported above (fig. 7A) with the exception that the cephalothorax from the base of the eyestalks to the abdomen was enclosed instead of the abdomen (Figure 7B). The results were the same as presented in Figure 7A. No specialized photoreceptor in the cephalothorax was responsible for the differences in rate of red pigment dispersion.

For still another experiment, prior to placing the crawfish on the black and the white backgrounds the abdominal nerve cord was transected between the fifth and sixth ganglia to eliminate in another fashion any possible role of the caudal photoreceptor. After the crawfish had adapted, the eyestalks were removed and the backgrounds of one-half changed (fig. 7C). The results were the same as shown in Figures 6B, 7A and 7B. The experiments described above have shown that the caudal photoreceptor was not responsible for the decreased rate of dispersion of red pigment of specimens whose background had been changed at the time of eyestalk removal.

The following experiments were designed to elucidate the role of light intensity changes in the results presented above (figs. 6B, 7A, 7B, 7C). For one experiment crawfish were placed in a white pan under an illumination of 65 ft. c. for two hours. The red chromatophore stage of the crawfish was then determined. Thirty crawfish were selected for use in the experiment because their red pigment had concentrated maximally. The eyestalks were then removed and the crawfish divided into three groups. Ten crawfish were kept on the white background under an illumination of 65 ft. c., 10 were placed in a white pan under an illumination of 1 ft. c., and the remaining 10 were placed in a black pan under an illumination of 65 ft. c. The stages of the red chromatophores were then determined at intervals during the next two hours. The experiment was repeated once. The results of the two experiments were averaged and presented in Figure 8A where each point represents the mean of 20 crawfish. Red pigment of each group dispersed after eyestalk removal, but red pigment of crawfish kept on a white background under an illumination of 65 ft. c. dispersed most rapidly. Little difference was noted between the rates of dispersion of red pigment of crawfish transferred to a black background at 65 ft. c. and those on a white background under an illumination of 1 ft. c. Since the black background reflected 1/65 of the light reflected by a white background, the amount of reflected light striking the crawfish in a black pan under an illumination of 65 ft. c. and in white pans under an illumination of 1 ft. c. was the same, accounting for the similar rates of pigment dispersion.

The final experiment of the series was similar to the experiment just described. Crawfish were placed on a black background for two hours under an illumination of 20 ft. c. The stage of the red chromatophores was then determined and three groups of 10 crawfish each were selected because their red pigment was maximally dispersed. The eyestalks of the 30 were then removed. Ten crawfish were kept on a black background under an illumination of 20 ft. c., 10 others were placed on a white background under the illumination of 20 ft. c. The remaining 10 crawfish were kept on a black background but were

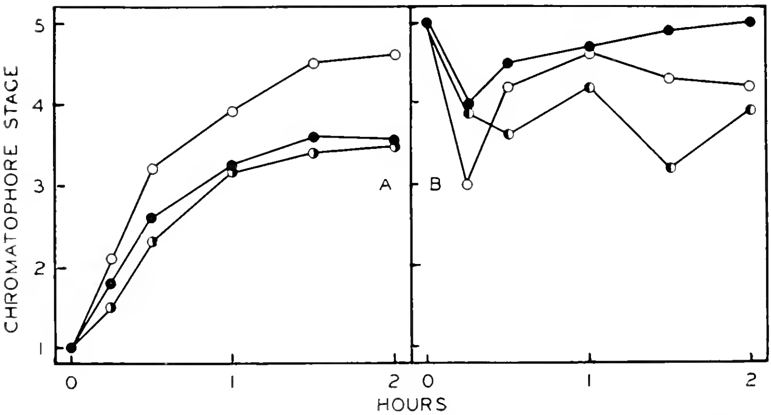

Figure 8. Responses of the red chromatophores of dwarf crawfish on white (**A**) and on black (**B**) backgrounds to background and illumination changes at the time of eyestalk removal. In **A** circles represent crawfish kept on a white background at an illumination of 65 ft. c.; dots, transferred to a black background at 65 ft. c.; half-filled circles, kept on a white background but at one ft. c. In **B** circles represent crawfish transferred to a white background at 20 ft. c.; dots, kept on a black background at 20 ft. c; half-filled circles, kept on a black background but at 2000 ft. c.

placed under an illumination of about 2000 ft. c. The latter light intensity was obtained with sunlight. The water in the pan in sunlight was changed frequently to eliminate effect of heat on red chromatophores. The experiment was repeated once. The results of the two experiments were averaged and presented in Figure 8B where each point represents the mean of 20 crawfish.

Red pigment of crawfish kept on a black background under an illumination of 20 ft. c. concentrated after eyestalk removal and returned most rapidly to the original state of maximal dispersion. Red pigment of crawfish transferred to a white background under an illumination of 20 ft. c. was next to return to the original condition. Red pigment of crawfish kept on a black background but placed under an illumination of about 2000 ft. c. was the slowest to return to the original maximally dispersed state.

The reflected light intensity in the black pan under the illumination of about 2000 ft. c. was calculated to be about 1.5 times brighter than in the white pan at 20 ft. c., based on the fact that the black background reflected 1 65 of the light reflected from a white background. The 1.5-fold greater reflected light intensity in the pans in sunlight may explain why the red pigment of crawfish on a black background under the approximate light intensity of 2000 ft. c. was the last to return to the original state. With a greater increase of reflected light intensity the slower would be the return of the pigment to the original condition.

These experiments demonstrated that differences observed in rates of red pigment dispersion of eyestalkless crawfish on black and on white backgrounds were not an albedo response but were due to changes in reflected light intensity from the backgrounds. The exoskeleton may contain photosensitive free nerve endings, a dermal light sense, sensitive to changes of light intensity resulting in the same chromatophoric response whether light intensity increases or decreases. In some manner a change of reflected light intensity is translated into decreased rate of inactivation of red pigment concentrating hormone in the blood of dwarf crawfish whose eyestalks have been removed. Wells (1952) hypothesized that the brain of the eyeless white cave crawfish *Cambarus ayersi* is photosensitive. The brain of *Cambarellus* likewise may be photosensitive.

Electrophoresis of extracts of supraesophageal ganglia plus circumesophageal connectives.—Extracts of supraesophageal ganglia plus the circumesophageal connectives of dwarf crawfish were subjected to filter paper electrophoresis performed at pH 7.4 with N/30 phosphate buffer and at pH 7.8 with N/10 borate buffer. After electrophoresis each fraction obtained from the filter paper strips was injected into one-eyed crawfish kept on black and on white backgrounds to determine if red pigment dispersing and concentrating hormones had been separated from one another. Electrophoresis at each pH was performed three times. Results obtained from the three experiments at each pH were averaged and presented in Figure 9 where each point represents the mean of 15 crawfish. As a control, 0.02 ml of van Harreveld's solution was injected into individual crawfish. The saline neither dispersed nor concentrated the red pigment.

As is evident from inspection of Figure 9, separation of red pigment dispersing and concentrating hormones was achieved. Red pigment concentrating hormone migrated toward the negative pole whereas red pigment dispersing hormone remained at the point of application on the filter paper strip or migrated toward the positive pole. The fraction that had the most red pigment concentrating hormone had the least red pigment dispersing hormone.

Fingerman (1957a) demonstrated the presence of red pigment dispersing and concentrating hormones in the central nervous organs of *Cambarellus* by simultaneous injection of the same extract into crawfish on black and on white backgrounds. Maximal red pigment concentration occurred 15 to 30 minutes after injection of extract but maximal red pigment dispersion did not occur until 60 to 90 minutes after extract had been administered. Presumably, the red pigment dispersing hormone could not run its full course until red pigment concentrating hormone began to disappear. In the current experiment the difference in time of maximal effect was negligible. Maximal red

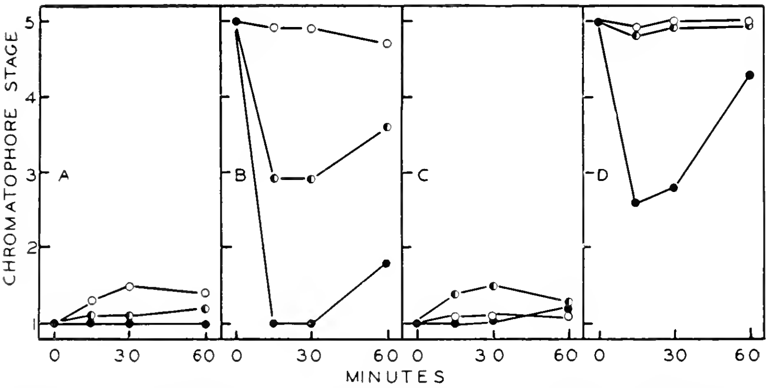

Figure 9. Responses of red chromatophores of dwarf crawfish on white (**A** and **C**) and on black (**B** and **D**) backgrounds to extracts of supraesophageal ganglia plus circumesophageal connectives. Electrophoresis of the extracts was carried out at pH 7.4 (**A** and **B**) and at pH 7.8 (**C** and **D**) for three hours. Circles, positive pole; dots, negative pole; half-filled circles, region of application of extract to filter paper strip.

pigment concentration occurred 15 to 30 minutes after injection of extract and maximal red pigment dispersion occurred 30 minutes after injection of extract. Evidently, in the absence of red pigment concentrating hormone, red pigment dispersing hormone can cause rapid red pigment dispersion and the delay observed in the results of Fingerman (1957a) must have been due to the presence of red pigment concentrating hormone in the extracts.

Rate of inactivation of chromatophorotropins of dwarf crawfish.—The final group of experiments was designed to yield information concerning the rates of inactivation of red and white chromatophorotropins of eyestalks and circumesophageal connectives of *Cambarellus.* The experiments were suggested by the results of preliminary experiments on electrophoresis in which migration was allowed to proceed for 18 hours. After this period of time little or no chromatophorotropin was present in the extracts from filter paper strips, presumably due to inactivation of the hormones. Extracts were prepared that contained one pair of eyestalks or one pair of circumesophageal connectives per 0.1 ml of van Harreveld's solution. Each crawfish received a dose of 0.02 ml of extract. Freshly prepared extract was assayed in five one-eyed crawfish on a black background and five on a white background to determine the amount of red and white pigment concentrating and dispersing hormones in the extract. Into depressions on glass slides were placed 0.15 ml of the original extract. Onto one-half of the depressions containing extract were placed squares of carapace with attached hypodermis, about 3 mm on a side. Extracts that had been on glass depression slides one and two hours were likewise injected into one-eyed dwarf crawfish that had been on black and on white backgrounds for two hours. Depression slides were covered to minimize evaporation. Stages of the red and white chromatophores of the one-eyed assay animals were determined at the time of injection of the extracts and 15, 30, 60, 90, and 120 minutes thereafter. To facilitate discussion of the results, activity (potency) values were calculated for extracts. The method was described above for calculations of pigment dispersing potency. However, if the pigment had been maximally dispersed at the start of the experiment (stage 5), the sum of the average chromatophore stages determined 15, 30, 60, 90, and 120 minutes after the extracts had been administered was subtracted from 25 because if no pigment concentration had occurred the sum would have been 25.

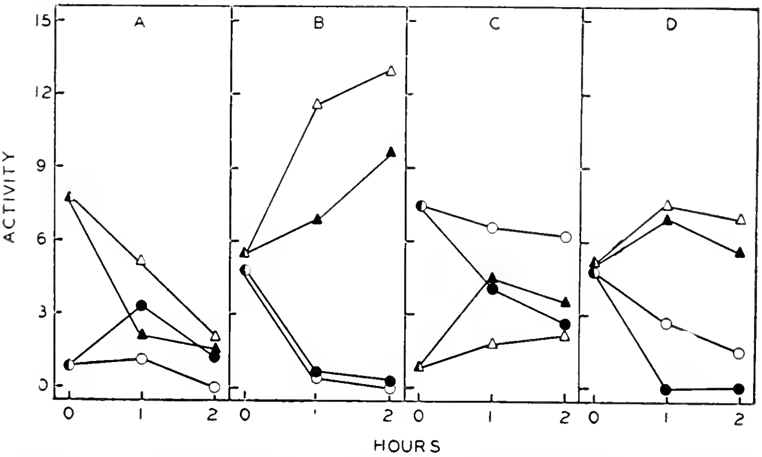

Figure 10. Potency changes of red and white pigment concentrating and dispersing hormones in extracts of eyestalks (**A** and **B**) and circumesophageal connectives (**C** and **D**) kept at room temperature. **A** and **C**, red chromatophores; **B** and **D**, white chromatophores. Circles and dots, concentrating hormone; open and filled triangles, dispersing hormone. Solid symbols represent extracts exposed to pieces of carapace; open symbols represent extracts kept on glass depression slides in the absence of pieces of carapace.

The experiment was repeated once. Results were averaged and presented in Figure 10 where each point represents the mean of 10 crawfish. Activities obtained with eyestalk extracts are shown in Figures 10A and 10B. Fingerman (1957a) demonstrated that eyestalks of *Cambarellus* produce red and white pigment dispersing hormones, white pigment concentrating hormone, and an extremely small amount of red pigment concentrating hormone. Red pigment dispersing hormone disappeared more rapidly in the presence of hypodermis than in its absence presumably due to the action of the chromatrophorotropin inactivating enzyme of the hypodermis as described by Carstam (1951) for the prawn *Leander adspersus.* As the red pigment dispersing hormone disappeared red pigment concentrating effect increased. Red pigment dispersing hormone began to disappear from extracts that had been on glass slides for two hours.

Rapid inactivation of red pigment dispersing hormone due to carapace fragments allowed greater expression of the antagonistic red pigment concentrating hormone than observed in extracts not exposed to hypodermis. White pigment concentrating hormone of eyestalk disappeared at a rapid rate, faster than white pigment dispersing hormone. The latter increased in activity as its antagonist disappeared.

Red pigment dispersing and white pigment concentrating hormones are the predominant ones in the eyestalk (Fingerman, 1957a) and are the first to disappear from extracts. Perhaps more of these hormones are found in the eyestalk because they are more labile than their antagonists.

Red and white pigment concentrating hormones of the circumesophageal connectives disappeared more rapidly than the red and white pigment dispersing hormones. As a result of rapid disappearance of antagonistic pigment concentrating hormones, red and white pigment dispersing effects increased. Fingerman (1957a) demonstrated that red and white pigment concentrating hormones were the predominant ones in the central nervous organs. Just as with the eyestalk, the predominant chromatophorotropins disappeared more rapidly than their antagonists.

GENERAL DISCUSSION

Whether the pigments in chromatophores of crustaceans become concentrated or dispersed after eyestalk removal was thought to depend upon the chromatophorotropins produced by the eyestalks. For example, after removal of the eyestalks of the fiddler crab *Uca pugilator* black pigment becomes maximally concentrated and white pigment maximally dispersed (Sandeen, 1950). The conditions of the black and the white pigments of eyestalkless fiddler crabs were thought to be due to removal of sources of black pigment dispersing and white pigment concentrating hormones in the eyestalk.

Results obtained with dwarf crawfish, *Cambarellus shufeldti*, do not support this concept. Red and white pigments of eyestalkless *Cambarellus* are maximally dispersed yet the predominant chromatophorotropins produced by the eyestalk are the red pigment dispersing and white pigment concentrating hormones (Fingerman, 1957a). Similarly, red and white pigments of the crawfish *Orconectes immunis* disperse maximally after eyestalk removal but the predominant hormones produced by the sinus gland in the eyestalk of this species are red pigment concentrating and white pigment dispersing (Brown and Meglitsch, 1940).

The ultimate stage of the chromatophores of eyestalkless individuals is probably determined by hormones released from central nervous organs and not primarily to absence of chromatophorotropins from the eyestalk. Two lines of evidence support this concept. Firstly, a shift of hormonal balance in the blood after eyestalk removal results in the blood having (1) less pigment dispersing hormone than the blood of specimens with maximally dispersed pigment due to background and (2) more pigment concentrating hormone than the blood of specimens with maximally concentrated pigment due to background (Fingerman, 1957b). Secondly, data presented above lead to the conclusion that the hormonal content of blood of eyestalkless crawfish differs from that of intact crawfish in darkness. In *Orconectes* and *Cambarellus* the predominant hormones in the central nervous organs are red and white pigment concentrating ones (McVay, 1942; Fingerman, 1957a, c). Hormones that are not predominant quantitatively in the central nervous organs but are relatively stable molecules probably determine the final stage of the chromatophores of eyestalkless crawfishes.

SUMMARY AND CONCLUSIONS

1. Endocrine control of red and white chromatophores of the dwarf crawfish, *Cambarellus shufeldti*, was investigated further. Changes in blood titers of red pigment dispersing and white pigment dispersing hormones were followed in crawfish placed on black and on white backgrounds.

2. Rates of dispersion of red pigment after eyestalks of crawfish were removed were investigated. The rate of degredation of red pigment concentrating hormone from the blood appeared to be altered by changes of reflected light intensity, but was not an albedo response.

3. Separation of red pigment dispersing and concentrating hormones in extracts of supraesophageal ganglia plus circumesophageal connectives was accomplished by filter paper electrophoresis. At pH 7.4 and 7.8 red pigment dispersing hormone remained at the point of application to the filter paper strip or migrated toward the positive pole and the red pigment concentrating hormone migrated toward the negative pole.

4. Rates of disappearance of red and white pigment dispersing and concentrating hormones from extracts of eyestalks and circumesophageal connectives were determined. When fresh extracts were injected into crawfish, the hormone that expressed itself maximally before its antagonist disappeared first. Hypodermis hastened inactivation of the chromatophorotropins, presumably by enzymatic action.

5. Dispersion of the pigments of eyestalkless crawfish appeared to be due to hormones secreted by the central nervous organs after eyestalk removal and not to the absence of hormones from the eyestalk.

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ABSTRACT

Endocrine control of the red and white chromatophores of the dwarf crawfish, *Cambarellus shufeldti*, was investigated further. Crawfish were adapted to black and to white backgrounds. Their background was then changed and changes in the blood titers of red and white pigment dispersing hormones were followed. For example, red pigment dispersing hormone decreased in the blood of crawfish changed from a black to white background, and increased in the blood of crawfish changed from a white to a black background. Separation of red pigment dispersing and concentrating hormones in extracts of supraesophageal ganglia plus circumesophageal connectives was accomplished by filter paper electrophoresis. At pH 7.4 and 7.8 red pigment dispersing hormone stayed at the point of application to the filter paper strip or migrated toward the positive pole; red pigment concentrating hormone migrated toward the negative pole. Rates of disappearance

from extracts of the red and white chromatophorotropins of the eyestalks and central nervous organs were determined. When fresh extracts were injected into crawfish, the hormone that expressed itself before its antagonist disappeared first. Hypodermis hastened inactivation of the chromatophorotropins, presumably by enzymatic action. The degree of dispersion or concentration of the pigments of crustaceans whose eyestalks have been removed is probably due to hormones secreted by the central nervous organs after eyestalk removal and not to the absence of hormones from the eyestalks.

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CYPRINID FISHES OF THE SUBGENUS *CYPRINELLA* OF *NOTROPIS*. III. VARIATION AND SUBSPECIES OF *NOTROPIS VENUSTUS* (GIRARD)

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The cuts for figure 6 (page 188) and figure 7 (page 193) were inadvertently reversed in printing this issue.

CYPRINID FISHES OF THE SUBGENUS *CYPRINELLA* OF *NOTROPIS*. III. VARIATION AND SUBSPECIES OF *NOTROPIS VENUSTUS* (GIRARD)

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The complex of forms which are here considered as a single species, *Notropis venustus*, has been treated rather superficially for many years, resulting in differential usage of nomenclature, as well as confusion with regard to species status. In one hundred years since the original description of *Cyprinella venusta* (Girard, 1856), ten additional names have been bestowed on populations of this minnow, in spite of (or perhaps because of) a relative scarcity of collections from the southeastern United States. Until recently, four of these names represented nominal species to many workers (*venustus, cercostigma, stigmaturus, eurystomus*), or at least subspecies, one was never certain which. Bailey, Winn and Smith (1954) were the first to express in print their doubt concerning the status of the four names, and they recognized only one species, *Notropis venustus*, pending investigation.

Following the 1948 decision of the International Commission on Zoological Nomenclature, which temporarily formalized the rule of line priority, the name *notatus*, which preceded *venustus* in Girard, 1856 (p. 198), was used for this species, but fortunately did not find its way into print. In 1952, the Commission reversed itself, and Clark Hubbs, as first reviser (1954b), placed *notatus* in the synonymy of *venustus*.

Although its caudal spot makes *Notropis venustus* one of the most easily recognized species of *Notropis*, the variation in shape and intensity of this spot, together with considerable variation in body proportions, has led to confusion and the unwarranted naming of species. This paper clarifies the situation by pointing out the patterns of variation and by indicating rather precisely the validity of the acceptable subspecies. Three subspecies with five races are recognized.

MATERIALS AND METHODS

The writer is grateful to the following institutions and their respective staffs for making available materials under their care: Dr. Edward C. Raney, Cornell University; Dr. Reeve M. Bailey, Museum of Zoology, University of Michigan; Dr. Leonard P. Schultz, Dr. Ernest A. Lachner and Mr. Robert H. Kanazawa, United States National Museum; Dr. Royal D. Suttkus, Tulane University.

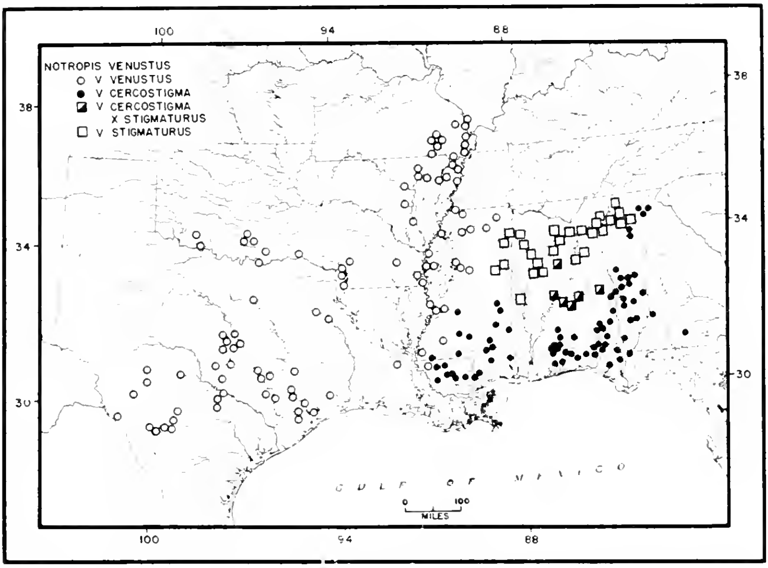
Counts and measurements were made as described by Hubbs and Lagler (1947), with the exception of postdorsal length (dorsal origin to caudal base) and the distance from dorsal origin to lateral line. Only specimens of between 50 and 60 mm were used for proportional measurements. As in my study of *Notropis spilopterus* (Gibbs, in press), when adequate samples were available, no more than ten specimens were counted from any single collection.

Because of the healthy skepticism which exists at present, it is necessary to comment on the terms "subspecies" and "race" as they are used here. Because of the ample evidence, which need not be cited here, that characters may be affected directly by the environment, any designation of an infraspecific category must be subject to doubt unless genetic evidence is available. If this sort of evidence is not forthcoming, then it is necessary to choose between two expedients: (1) merely giving the data for what it is worth, letting the reader decide whether the results are due to genotypic or to phenotypic variation or both; (2) calling attention to the major segments of a species by giving them categorical recognition on the assumption (perhaps wrong) that the differences have a genetic basis. The latter is followed here due to the conviction that the subspecies is a real and important category, and that the naming of these has value in the fact of pronouncement, if nothing else. That individual cases prove to be judged wrongly is not sufficient reason for eliminating the whole procedure.

The *defining* of the infraspecific categories is another matter. In particular it is difficult to say what is to be a subspecies and what a lesser category. It is this writer's tendency to feel that, if a meristic character has the same mode and distribution in samples from a number of adjacent river systems and those are different from the modes and distributions of another homogeneous-appearing group of samples, then the two are subspecies. This is exemplified in this paper by *Notropis v. venustus* and *N. v. cercostigma* (see Table 4) in which homogeneity of eastern and western Gulf populations is evident, as is the *difference* in the mode and distribution of each. When a single river system varies rather widely from the rest, then the actual separation must be relatively larger. In such instances, the criteria of Ginsburg (1938) are as near an approach to objectivity as any, although some personal judgment should be exercised. I draw my lines slightly higher than does Ginsburg. The subspecies *N. v. stigmaturus*, found only in the upper Alabama and Tombigbee rivers of the Apalachicola system, typifies this procedure (see Tables and Figures).

Below what I judge to be the subspecies category, I use somewhat less restraint. If a single river system varies noticeably in one or more characters, it may be called a "race" if the separation falls below an average of about 80 per cent and the modes are distinct and different. Thus the Upper Chattahoochee Race of *N. v. cercostigma* is rather distinctive in the number of lateral-line scales and pectoral rays, and in having 8 or 9 anal rays in almost equal numbers. The Red-Lower Miss. Race, however, differs most in body depth and related characters from the others of the western Gulf subspecies and is less well-defined meristically. Both of these differ considerably more from the others of the particular subspecies than these do among themselves (see Tables and Figures).

This incomplete discussion, then, should indicate the reasons for my formalized recognition of certain segments of *Notropis venustus*. Had there been any convincing suggestions of gradients, no particular status would have been applied to these segments other than to recognize clines. Thus the view is held that these segments have a genetic basis, even if this should be disproved eventually.



Map 1. Distribution of collections examined of *Notropis venustus*.

NOTROPIS VENUSTUS (GIRARD)

Diagnosis.—A species of *Cyprinella* (Gibbs, 1957) with a pronounced dark basicaudal spot; a terminal or subterminal mouth; 1,4-4,1 teeth; 8 anal rays (often 9 in the upper Chattahoochee River); 15-2-11 predorsal circumferential scales; usually with no contrastingly darker pigment in the posterior dorsal membranes, the melanophores gradually increasing in density to the rear (except *N. v. stigmaturus*, which lacks the melanophores on the first three membranes and has a pronounced concentration in the last two). Comparisons will be made under each subspecies.

Description.—Teeth 1,4-4,1, hooked, the cutting surfaces narrow and concave, with or without serrations. Anal rays 8; pectoral rays usually 14 or 15. Dorsal fin moderate in size, the first or second ray longest; anterior and posterior rays almost even in the depressed fin; origin nearer caudal base than snout.

Lateral-line scales variable in races and subspecies, usually 36 to 43. Predorsal circumferential scales usually 15-2-11; caudal peduncle scales 7-2-5. Scales not crowded before dorsal. Exposed edges of lateral scales higher than wide, especially just above and below the lateral line.

Head triangular, snout rather sharp. Orbit usually 7-8% of standard length, very slightly shorter than snout, about $3\frac{1}{2}$ to 4 in head. Mouth terminal or subterminal, oblique, moderately large, end of upper jaw reaches about to anterior margin of orbit, slightly longer than orbit.

Body form slender to moderately deep, subterete, caudal peduncle depth varies similarly to body depth. Lateral line slightly decurved from opercular margin to below dorsal fin.

Tubercles in breeding males (fig. 6) not enlarged, crowded on top of head, on end of snout, and between eye and upper jaw, a hiatus between those of head and snout. More than one row of tubercles on each chin ramus. Tubercles of notal ridge crowded and about similar in size to those of head, becoming less dense and smaller toward dorsal origin. Small tubercles on all body scales except belly, commonly in a row on exposed margins. A row of tubercles on each ray of all fins, following branchings, less prominent on dorsal and caudal.

Coloration.—The most prominent character in this species is the black basicaudal spot, which is variable in intensity and in dimensions from race to race and from stream to stream, and is probably partially under genetic and partly under environmental control. A leaden lateral band, of distinctly different intensity than the caudal spot, runs forward to below the dorsal, where a narrow line from its upper end extends anterior to the operculum. Between the narrow line and the lateral line the melanophores become thinned out, but are still more dense than on most of the body, suggesting a wide continuation of the lateral stripe. Scales narrowly outlined in black, appearing diamond-shaped. Belly unpigmented except sides of anal fin base, where pigment is most prominent at the posterior edge of the fin and a short distance rearward on the lower part of the caudal peduncle. Dark humeral bar absent. Head darkly pigmented dorsally and laterad to the level of the lower edge of the orbit on the snout, and above eye level behind the eye. Melanophores may be lightly scattered as far as the lower part of the operculum. A narrow, deep-lying dark bar between chin rami. Lips moderately pigmented, the lower less than the upper.

Remaining fins free of pigment except for that part of the basicaudal spot which may extend onto the caudal fin and a narrow line behind each leading pectoral ray. Dorsal fin with scattered melanophores on all membranes in adults, the density becoming gradually greater posteriorly. The pigmentation is, therefore, stronger on the last two membranes, but is not prominent due to the gradual increase in density. This is at variance with the majority of species of the subgenus *Cyprinella*. *N. v. stigmaturus*, however, displays the typical subgeneric form of this character, the posterior membranes being prominently pigmented, while the first three almost never show pigment.

In breeding males, the unpaired fins become yellow, and all fins display the milky pigment characteristic of the species of *Cyprinella*.

Furthermore, these males develop a diffuse spot due to a concentration of dark pigment beneath the scales just above the lateral line and about midway between the dorsal origin and the operculum.

NOTROPIS VENUSTUS VENUSTUS (GIRARD)

Western Blacktail Shiner

Cyprinella venusta—Girard, 1856: 198 (orig. descr., Rio Sabinal, Tex.); 1858b: 54 (char., plate); Jordan and Copeland, 1876: 153; Jordan, 1878 422; Cope, 1880: 38 (Texas); Schrenkeisen, 1938: 131 (char., distr.).

Cliola venusta—Jordan and Gilbert, 1883: 178 (char., distr., syn.).

Erogala venusta—Jordan, Evermann and Clark, 1930: 130 (distr., syn.).

Notropis venustus—Jordan, 1885: 25; 1886: 119 (types examined; comparisons); Jordan and Gilbert, 1887: 14, 15 (Red, Sabine, Brazos, Colorado systems, Tex.); Everman, 1893: 79 (Texas); Evermann and Kendall, 1894: 83, 86, 92, 102 (Texas); Meek, 1895: 77, 82 (Arkansas distr.); Jordan and Evermann, 1896a: 255 (distr., syn.); 1896b: 257, 274 (char., distr., syn.); Meek, 1896: 343 (Red and St. Francis systems); Evermann, 1899: 308 (Neches system, Tex.); Fowler, 1910: 281 (variation); Jordan, 1928: 369 (distr.); Bailey, Winn and Smith, 1954: 128; Hubbs, 1954a: 73 (*texanus* in syn.); 1954b: 280 (*notatus*, *texanus* in syn.); Riggs and Smithpeter, 1954: 53 (L. Texoma, Okla.).

Notropis, venustus venustus—Lamb, 1941: 44 (San Jacinto system, Tex.); Paden, 1948: 38 (Okla., compared with E. Ozark form); Baughman, 1950: 130 (Texas); Hubbs, Kuehne and Ball, 1953: 223, 226, 243 (Guadalupe system, Tex.; habitat, hybridization with *N. lutrensis*); Knapp, 1953: 62 (Texas distr.).

Cyprinella notata—Girard, 1856: 198 (orig. descr., Rio Seco, Tex.); 1858a: 269 (char., plate); Jordan and Copeland, 1876: 153; Jordan, 1878: 422; Schrenkeisen, 1938: 131 (char., distr.).

Cliola notata—Jordan and Gilbert, 1883: 177 (char., distr., syn.).

Erogala notata—Jordan, Evermann and Clark, 1930: 130 (distr., syn.).

Notropis notatus—Jordan, 1885: 25; 1886: 124 (types examined); Call, 1887: 76 (Reynolds, Shannon, Texas cos., Mo.); Jordan and Gilbert, 1887: 20 (Colorado system, Tex.); Evermann and Kendall, 1894: 83, 86, 92, 103 (Tex.); Jordan and Evermann, 1896a: 255 (distr., syn.); 1896b: 257, 274 (char., distr., syn.); Pratt, 1923: 79 (char., distr.); Fowler, 1945: 234 (Tex).

Cyprinella texana (misidentifications)—Girard, 1856: 198 (orig. descr., Rio Salado and Turkey Creek, Tex.); 1858b: 55 (char., plate); Jordan and Copeland, 1876: 153; Jordan, 1878: 422.

Notropis texanus (misidentifications)—Jordan and Gilbert, 1887: 17 (Trinity and Brazos systems, Tex.); Evermann and Kendall, 1894: 86, 92, 103 (Tex.); Jordan and Evermann, 1896a: 255 (distr., syn.); 1896b: 257, 274 (char., distr., syn.); Fowler, 1910: 281 (variation); Pratt, 1923: 79 (char., distr.).

Erogala texana (misidentification)—Jordan, Evermann and Clark, 1930: 130 (distr., syn.).

Luxilus stigmaturus (misidentification)—Hay, 1883: 71 (Big Black R., Miss.).

Cliola urostigma—Jordan and Meek, 1885: 475 (orig. descr.; Colorado and Brazos systems, Tex.).

Notropis cooglei—Hildebrand and Towers, 1928: 18 (orig. descr., Greenwood, Miss.).

Notropis cercostigma (misidentification)—Hubbs and Ortenburger, 1929: 78 (Ark.).

Types.—Girard's original *Cyprinella venusta* is represented by two sets of extant syntypes at the Academy of Natural Sciences of Philadelphia and the Museum of Comparative Zoology at Harvard University. One of the Philadelphia specimens, ANSP 3035, a male, 50.2 mm, is here designated lectotype; another syntype bears the number ANSP 3036. These were labeled as having been collected in the Rio Sabinal, Texas, by Dr. C. B. Kennerly and received from the Smithsonian Institution (No. 140). Both specimens are in rather poor condition, but have the basicaudal spot well-developed. The syntypes at Harvard are catalogued as MCZ 1695 and are accompanied by a replacement label which reads: *Cyprinella venusta*—2 sp., now = *Erogala venusta* (Girard), Rio Sabinal, Texas, C. B. Kennedy probably a misspelling of Kennerly , Smithsonian Institution 1861.

The following types of other nominal species have been checked.

Cyprinella notata Girard. USNM 136. Rio Seco, Texas, 1853. C. B. Kennerly. Jordan (1886) noticed that one of the original three specimens was *Notropis lutrensis* (Baird and Girard), and this was removed as USNM 162720 by Clark Hubbs, who also placed *notatus* in the synonymy of *venustus* (Hubbs, 1954b). The lectotype, which

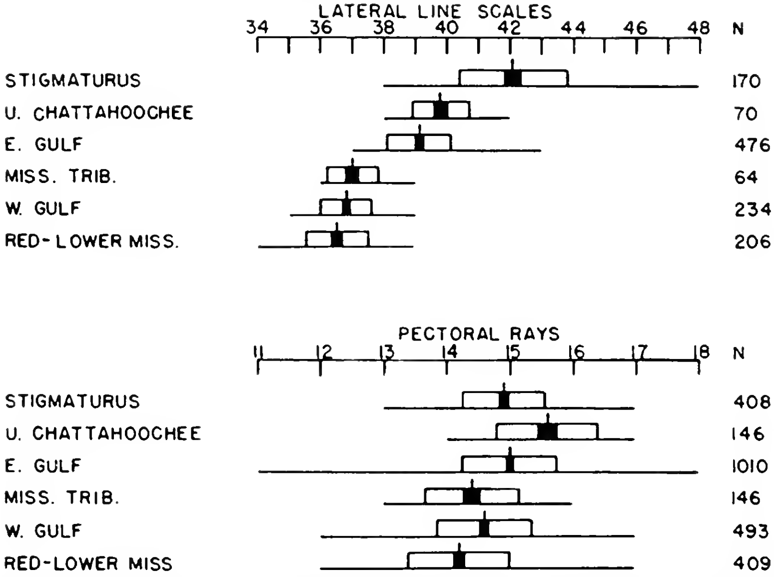


Figure 1. Graphic analysis of some meristic characters of *Notropis venustus*. Horizontal line = range. Vertical line = mean. Open rectangle = one standard deviation on each side of mean. Black rectangle = two standard errors on each side of mean.

is herein designated, retains USNM 136; the other specimen of *notatus* now is *Notropis venustus* USNM 163955.

Cyprinella texana Girard. USNM 128. Rio Salado, Texas. Clark. This name has also been included in the synonymy of *venustus* by Clark Hubbs (1954a). Royal D. Suttkus has studied the available syntypes of this nominal species and has found that none of them is a *Cyprinella* at all. He will discuss this in a forthcoming publication. The name, therefore, is included in the synonymy of *N. v. venustus* only as a misidentification.

Cliola urostigma Jordan and Meek. USNM 20446. Fort McKavit (= McKavett), Texas, W. W. Anderson; and USNM 17812. Clear Creek, Waller Co., Texas, December 14, 1876, Kumlein and Earll. The counts by Jordan and Meek (1885) were apparently made on specimens from USNM 20446. The lectotype here designated, a female, 76.3 mm, will retain this number. The remaining eight syntypes from that collection are recatalogued as USNM 163952.

Notropis cooglei Hilderbrand and Towers. Holotype USNM 88379 (Pelucia Creek, Greenwood, Miss., June 19, 1925, I. L. T. Towers). Numerous paratypes are also present in the U. S. National Museum, and several have been sent to the Museum of Zoology, University of Michigan. The anal ray count in the original description, given as 10, is presumably in error, as the holotype has the typical count of

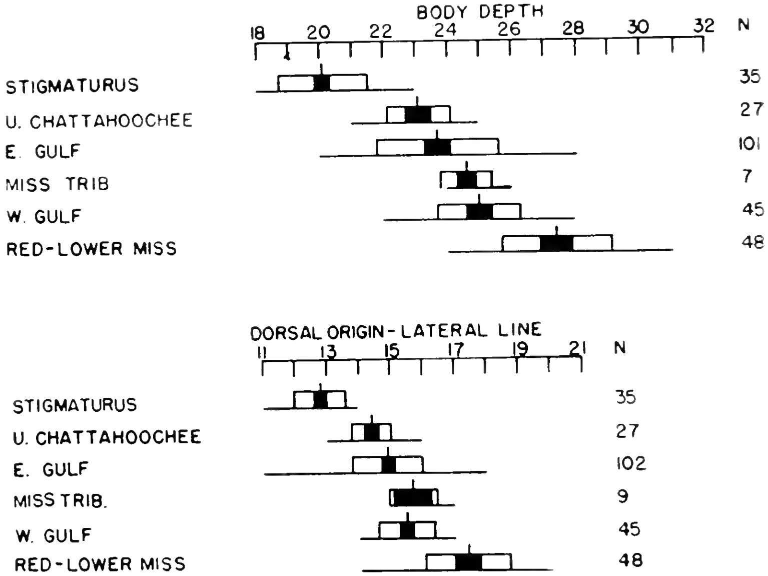


Figure 2. Graphic analysis of some proportional characters of *Notropis venustus*, expressed as percent of standard length. See Figure 1. for explanation.

eight, and since no counts of 10 have been recorded in this study for the species *venustus*. This form is the "Red-Lower Miss. Race" of *Notropis v. venustus*, which is discussed later.

Number of collections examined by river systems.—"Red-Lower Miss. Race": Lower Mississippi tribs. (S. Illinois to Louisiana), 39; Red, 12. Western Gulf Race: Ouachita, 2; White, 23; St. Francis, 12; Sabine, 3; Neches, 1; Trinity, 3; San Jacinto, 8; Brazos, 24; Colorado (of Texas), 8; Guadalupe, 5; Nueces, 6; Rio Grande, 2.

Comparative diagnosis.—Only three species of *Cyprinella* are found in the range of this subspecies. In much of its distribution it occurs adjacent to or with *N. lutrensis*. In tributaries to the lower Mississippi River in Mississippi and Louisiana it is assocated with a race of *N. camurus*, and in the Ouachita, Black, and St. Francis, *N. whipplei* is a cohabitant. *N. v. venustus* may be distinguished from all these by the presence of a black basicaudal spot and eight anal rays, instead of nine. *N. lutrensis* further usually has 4-4 teeth and develops red fin pigment in breeding males. *N. whipplei* is very similar in body form, but usually has 13-2-11 predorsal circumferential scales instead of 15-2-11, and the last two dorsal membranes are prominently pigmented. *N. camurus* has a depigmented area along the caudal base which *venustus* lacks, and also has prominently darkened posterior dorsal membranes. *N. camurus* from the lower Mississippi River also differs from *N. v. venustus* in several proportional characters. The

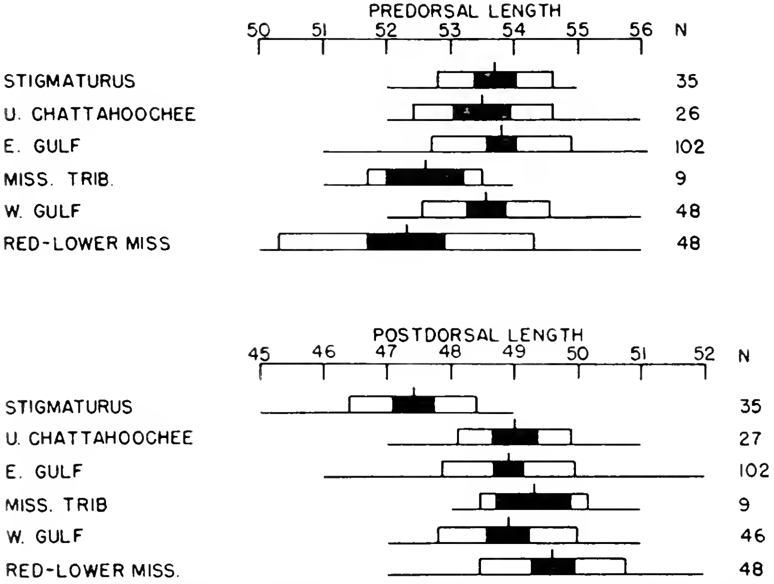


Figure 3. Graphic analysis of some proportional characters of *Notropis venustus*, expressed as percent of standard length. See Figure 1. for explanation.

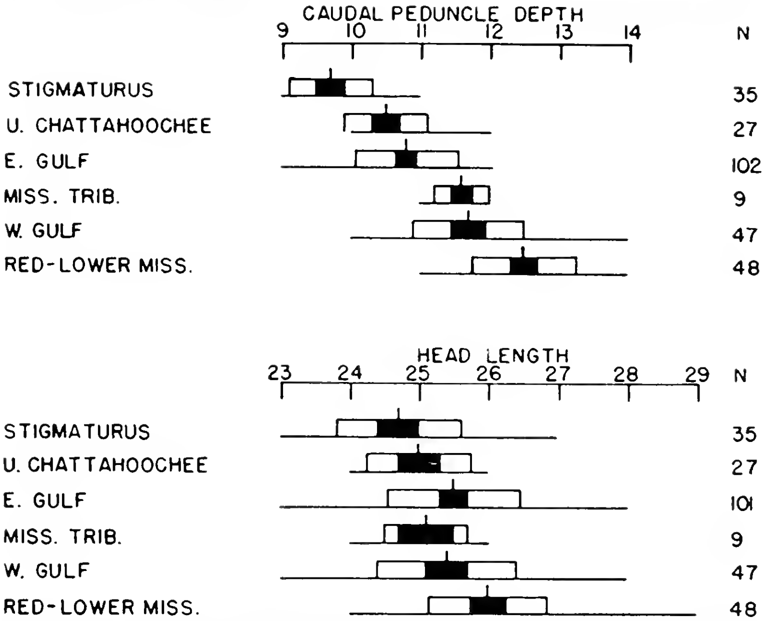


Figure 4. Graphic analysis of some proportional characters of *Notropis venustus*, expressed as percent of standard length. See Figure 1. for explanation.

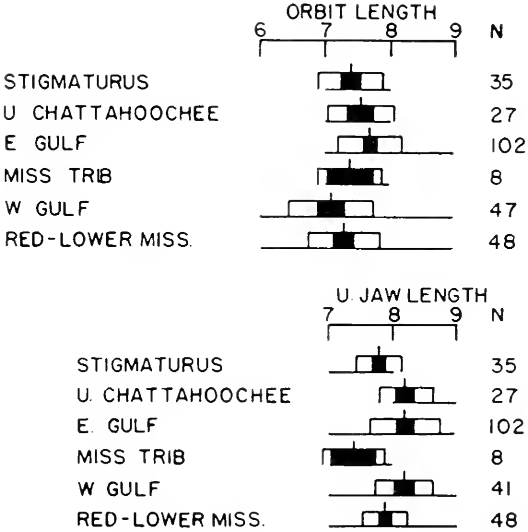


Figure 5. Graphic analysis of some proportional characters of *Notropis venustus*, expressed as percent of standard length.

TABLE 1.

Frequency Distribution of Some Meristic Characters in Subspecies, Races, and Populations of *Notropis venustus*

Lateral Line Scales

Subspecies	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	N	$\bar{X}$	SD	SE
venustus stigmaturus					1	5	21	43	33	41	12	8	4	1	1	170	42.1	1.67	.13
venustus cercostigma																			
E. Gulf Race				1	87	214	134	28	6	3						476	39.1	.96	.04
Upper Chattahoochee Race					2	28	26	12	2							70	39.8	.87	.10
venustus venustus																			
W. Gulf Race																			
W. Gulf population		9	62	112	46	5										234	36.8	.81	.05
Miss. trib. population			17	31	14	2										64	37.0	.79	.10
Red Lower Miss. Race	8	20	71	77	24	6										206	36.5	1.01	.07

Pectoral Rays

	11	12	13	14	15	16	17	18	N	$\bar{X}$	SD	SE
venustus stigmaturus			4	94	257	48	5		408	14.9	.65	.03
venustus cercostigma												
E. Gulf Race	1	1	17	217	558	196	19	1	1010	15.0	.77	.02
Upper Chattahoochee Race				19	36	79	12		146	15.6	.82	.07
venustus venustus												
W. Gulf Race												
W. Gulf population		2	30	152	235	13	1		433	14.6	.76	.03
Miss. trib. population			12	75	50	9			146	14.4	.73	.06
Red Lower Miss. Race		5	64	198	129	12	1		409	14.2	.79	.04

Frequency Distribution of Some Proportional Characters, Expressed as Percent of Standard Length, in Subspecies, Races, and Populations of *Notropis venustus*

Predorsal Length

Subspecies	50	51	52	53	54	55	56	N	$\bar{X}$	SD	SE
venustus stigmaturus			3	11	13	8		35	53.7	.92	.16
venustus cercostigma											
E. Gulf Race		1	12	27	33	24	5	102	53.8	1.11	.11
Upper Chattahoochee Race			6	8	7	4	1	26	53.5	1.14	.22
venustus venustus											
W. Gulf Race											
W. Gulf population			8	13	20	5	2	48	53.6	1.03	.15
Miss. trib. population		1	3	4	1			9	52.6	.88	.29
Red-Lower Miss. Race	1	3	7	15	14	6	2	48	52.3	2.01	.29

Postdorsal Length

	45	46	47	48	49	50	51	52	N	$\bar{X}$	SD	SE
venustus stigmaturus	1	5	13	12	4				35	47.4	.97	.16
venustus cercostigma												
E. Gulf Race		1	7	27	36	26	4	1	102	48.9	1.07	.11
Upper Chattahoochee Race			2	4	14	6	1		27	49.0	.92	.18
venustus venustus												
W. Gulf Race												
W. Gulf population			6	2	13	13	2		46	48.9	1.12	.16
Miss. trib. population				1	5	2	1		9	49.3	.87	.29
Red-Lower Miss. Race			1	7	16	15	6	3	48	49.6	1.14	.17

Head Length

	23	24	25	26	27	28	29	N	$\bar{X}$	SD	SE
venustus stigmaturus	4	8	19	3	1			35	24.7	.90	.15
venustus cercostigma											
E. Gulf Race	1	12	39	35	13	1		101	25.5	.93	.09
Upper Chattahoochee Race		7	12	8				27	25.0	.76	.15
venustus venustus											
W. Gulf Race											
W. Gulf population	1	8	14	20	2	2		47	25.4	1.03	.15
Miss. trib. population		1	6	2				9	25.1	.60	.20
Red-Lower Miss. Race		1	14	25	7		1	48	26.0	.85	.12

Body Depth

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	N	$\bar{X}$	SD	SE
venustus stigmaturus	3	10	9	7	4	2									35	20.1	1.35	.23
venustus cercostigma																		
E. Gulf Race			6	10	8	16	25	21	10	4	1				101	23.7	1.87	.19
Upper Chattahoochee Race				3	7	6	6	5							27	23.1	.97	.19
venustus venustus																		
W. Gulf Race																		
W. Gulf population					1	6	8	13	12	4	1				45	25.0	1.33	.20
Miss. trib. population							4	2	1						7	24.6	.79	.30
Red-Lower Miss. Race							4	1	13	8	7	9	5	1	48	27.4	.74	.11

TABLE 3.

FREQUENCY DISTRIBUTION OF SOME PROPORTIONAL CHARACTERS, EXPRESSED AS PERCENT OF STANDARD LENGTH, IN SUBSPECIES, RACES, AND POPULATIONS OF *Notropis venustus*

Dorsal Origin Lateral Line

Subspecies or Race	11	12	13	14	15	16	17	18	19	20	N	X̄	SD	SE
venustus stigmaturus	1	12	16	6							35	12.8	.77	.13
venustus cercostigma														
E. Gulf Race	1		11	23	38	23	5	1			102	11.9	1.15	.11
Upper Chattahoochee Race			4	10	10	3					27	14.1	.89	.17
venustus venustus														
W. Gulf Race														
W. Gulf population				6	15	18	6				45	15.5	.89	.13
Miss. trib. population					5	2	2				9	15.7	.87	.29
Red Lower Miss. Race				1	1	10	13	13	9	1	48	17.4	1.25	.18

Caudal Peduncle Depth

	9	10	11	12	13	14	N	X̄	SD	SE
venustus stigmaturus	12	20	3				35	9.7	.61	.10
venustus cercostigma										
E. Gulf Race	5	28	53	16			102	10.8	.77	.08
Upper Chattahoochee Race		14	12	1			27	10.5	.58	.11
venustus venustus										
W. Gulf Race										
W. Gulf population		2	19	19	6	1	47	11.7	.80	.12
Miss. trib. population			4	5			9	11.6	.43	.14
Red Lower Miss. Race			3	23	18	4	48	12.5	.71	.11

Orbit Length

	6	7	8	9	N	X̄	SD	SE
venustus stigmaturus		20	15		35	7.4	.50	.09
venustus cercostigma								
E. Gulf Race		29	71	2	102	7.7	.49	.05
Upper Chattahoochee Race		12	15		27	7.6	.51	.10
venustus venustus								
W. Gulf Race								
W. Gulf population	8	29	9	1	47	7.1	.67	.10
Miss. trib. population		5	3		8	7.4	.64	.23
Red Lower Miss. Race	1	32	14	1	48	7.3	.55	.08

Upper Jaw Length

	7	8	9	N	X̄	SD	SE
venustus stigmaturus	8	27		35	7.8	.33	.06
venustus cercostigma							
E. Gulf Race	8	68	26	102	8.2	.55	.06
Upper Chattahoochee Race		22	5	27	8.2	.40	.08
venustus venustus							
W. Gulf Race							
W. Gulf population	1	30	10	41	8.2	.48	.07
Miss. trib. population	5	3		8	7.4	.64	.23
Red-Lower Miss. Race	5	42	1	48	7.9	.35	.05

latter has a shorter postdorsal length, usually 47-51% of standard length, instead of 51-54%; a slightly smaller orbit, usually 7% instead of 8%; and a smaller mouth, upper jaw usually 7-8% instead of 9%.

The subspecies *N. v. venustus* is a deeper, larger-scaled form than any of the other subspecies. Comparisons are shown in Tables 1-3. Its lateral-line scale count seldom exceeds 38, whereas in the other subspecies this count is rarely less than 39. The body depth is usually 24-27% of standard length, compared to 21-25% in *N. v. cercostigma*. In other characters which reflect depth—dorsal origin to lateral line and caudal peduncle depth—*N. v. venustus* shows a difference which is less distinct, but similar. The eye tends to be smaller than in *N. v. cercostigma*, particularly in the Red-Lower Miss. Race, and there is a tendency for a higher proportion of specimens to have 13-2-11 predorsal circumferential scales and 13 pectoral rays.

Even the diagnostic caudal spot follows the proportional trend in *N. v. venustus* (figs. 6, 7). Although it is commonly quite similar to that in *N. v. cercostigma*, it tends to be shorter and wider, and in some specimens, or even whole collections, is almost square. The darkness of the spot is variable, for this is almost certainly dependent upon the turbidity of the water.

In those characters by which *N. v. venustus* differs from *N. v. cercostigma*, it is even more extreme in its separation from *N. v. stigmaturus* (see Tables 1-3).

Races.— Two races of *N. v. venustus* are recognizable. One of these is found in the Red River and the tributaries of the lower Mississippi River, and is hereafter referred to as the "Red-Lower Miss. Race". The other has its range divided by the first. It is found in western affluents of the Gulf of Mexico, from the Rio Grande to the Sabine (W. Gulf population) and again in the Ouachita, Black, and St. Francis Rivers in Missouri and Arkansas (Miss. trib. population). As a unit, it will be called the "Western Gulf Race".

The "Red-Lower Miss. Race" carries the tendencies of the subspecies to the extreme, as may be seen in Tables 1-3 and Figs. 1-5. The body depth averages over 27% of standard length, as compared to means of 24.6% and 25% in the two populations of the Western Gulf Race and 23.1% and 23.7% in the two races of *N. v. cercostigma*. The proportions dorsal origin to lateral line and caudal peduncle depth show similar differences. The tendency is strongest here to have 13-2-11 predorsal circumferential scales, although 15-2-11 remains the mode. Pectoral rays are modally 14 instead of 15, although this is true of the Miss. trib. population of the Western Gulf Race. Lateral-line scales show the greatest tendency to be few in number, and the caudal spot is commonly short and wide. This race is the form which Hildebrand and Towers (1928) described as *Notropis cooglei* from Greenwood, Mississippi.

The "Western Gulf Race" is less extreme than the Red-Lower Miss. Race in its distinctive characters, but is nevertheless quite different from *N. v. cercostigma*, as noted in the comparative diagnosis. Its two geographically separated populations, between which the Red-Lower Miss. Race is interposed, are not significantly different in any of the characters analyzed (Tables 1-3; figs. 1-5).

Range (Map 1).—Tributaries to the Gulf of Mexico in Texas from the Rio Grande to the Sabine; Red River as far west as Oklahoma and Texas; Ouachita, Black, and St. Francis Rivers; Mississippi River tributaries from Mississippi and Louisiana to Missouri and Illinois.

Habitat.—The subspecies seems to prefer rather clear streams, and is apparently not extremely averse to warmth, or to temporary stagnation, which are common conditions in southwestern streams. Hubbs, Kuehne, and Ball (1953: 226) found it commonly in "clearer waters downstream from the spring sources". *N. lutrensis*, on the other hand,

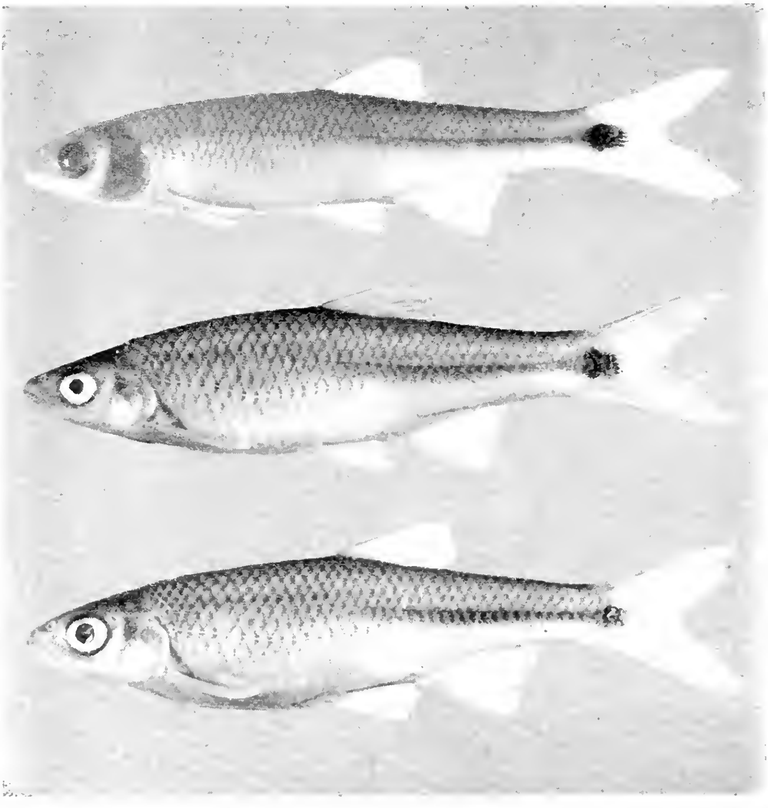


Figure 6. Top. *Notropis v. venustus*. Female, 69.7 mm. USNM 166095. Hays Co., Texas. Guadalupe drainage. Middle. *N. v. venustus*. Nuptial male, 52.9 mm. CU 16297. West Feliciana Co., La. Lower Mississippi drainage. Bottom. Dorsal view of predorsal part of *N. v. cercostigma* showing breeding tubercle pattern. Photographs taken by Douglass M. Payne.

more frequently inhabited murky waters. Where the two were sympatric, *venustus* was "more abundant in swifter water".

Etymology.—The name *venustus* is an adjective derived from the name of the Roman goddess of love, Venus.

NOTROPIS VENUSTUS CERCOSTIGMA (COPE)

Eastern Blacktail Shiner

Cyprinella cercostigma—Cope, 1867: 157 (orig. descr., Pearl R. system, La.); Jordan and Copeland, 1876: 153; Jordan, 1878: 422; Jordan, 1928: 370 (Perdido Bay); Pratt, 1935: 75 (char., distr.); Schrenkeisen, 1938: 130 (char., distr.).

Minnilus cercostigma—Jordan and Gilbert, 1883: 193 (char., distr., syn.).

Notropis cercostigma—Jordan, 1885: 814; Jordan and Evermann, 1896a: 255 (distr., syn.); 1896b: 257, 275 (char., distr., syn.); Pratt, 1923: 79 (char., distr.); Jordan, 1928: 369 (distr.); Fowler, 1941: 4 (*cooglei* believed synonymous); 1945: 363 (Miss. and La.).

Notropis venustus cercostigma—Gilbert, 1891: 158 (in part; Escambia system, Ala.); Kuhne, 1939 (Tenn., doubtful).

Erogala cercostigma—Jordan, Evermann and Clark, 1930: 130 (distr., syn.); Fowler, 1933: 59 (La., bait); Driver, 1942: 274 (char., distr.); 1950: 287 (char., distr.).

Photogenis eurystomus—Jordan, 1877b: 356 (orig. descr.; upper Chattahoochee system, Ga.); 1880: 239 (*leucopus* in syn.).

Cyprinella eurystoma—Jordan and Copeland, 1876: 153 (nom. nud.); Pratt 1935: 75 (char., distr.); Schrenkeisen, 1938: 131 (char., distr.).

Minnilus eurystomus—Jordan, 1877a: 80 (nom. nud.).

Codoma eurystoma—Jordan, 1878: 423; 1879: 111 (distr.); Jordan and Brayton, 1878: 20, 42.

Cliola eurystoma—Jordan and Gilbert, 1883: 180 (char., distr., syn.).

Notropis eurystomus—Jordan, 1885: 814; Jordan and Evermann, 1896a: 255 (distr., syn.); 1896b: 257, 276 (char., distr., syn.); Pratt, 1923: 79 (char., syn.); Jordan, 1928: 369 (distr.); Carr, 1937: 80 (Fla. key); Fowler, 1945: 234 (Ga).

Ergola eurystoma—Jordan, Evermann and Clark, 1930: 130 (distr., syn.).

Photogenis leucopus—Jordan and Brayton, 1878: 41 (orig. descr., upper Chattahoochee system, Ga.).

Luxilus leucopus—Jordan, 1878: 421.

Luxilus chickasavensis—Hay, 1881: 506 (orig. descr., Pascagoula system, Miss.).

Luxilus stigmaturus (misidentification)—Hay, 1883: 71, 74 (Pearl R. at Jackson, Miss.).

Notropis venustus stigmaturus (misidentification)—Bollman, 1887: 462 (Escambia system).

Notropis stigmaturus (misidentification)—Evermann and Kendall, 1900: 52 (Florida).

Types.—No trace has been found of any specimen from Cope's type series of *Cyprinella cercostigma*. The utility of choosing a neotype is not great enough at present to warrant such action. The pharyngeal tooth count given by Cope (1867) of 2,4-4,2 is definitely aberrant, if correct. Types of several synonyms have been studied as follows.

Photogenis leucopus Jordan and Brayton. USNM 31124. Chattahoochee River at Shallow Ford, NW Gainesville, Jordan and Brayton. This has proved to be a composite collection (see Bailey and Gibbs, 1956). Two specimens of *Notropis callitaenia* Bailey and Gibbs have been recatalogued as USNM 163964. The two remaining specimens are of the Upper Chattahoochee Race of *Notropis venustus cercostigma.* One of these, a female, 77.8 mm, has been designated lectotype and retains USNM 31124. The other is recatalogued as USNM 163963. Another syntype is located in the Museum of Comparative Zoology and is MCZ 35935. This bears the notation that it was from USNM 31124. This nominal species has been considered synonymous with *Notropis eurystomus* (= *venustus cercostigma*) by Jordan and Gilbert (1883) and subsequent authors.

Luxilus chickasavensis Hay. USNM 27419. Chickasawha R., Miss., O. P. Hay. Taken in a major tributary of the Pascagoula, these specimens display no essential differences from *N. v. cercostigma.* Their synonymy has been recognized by Jordan (1886) and others. The lectotype here designated, a female, 76.6 mm, retains USNM 27419. Eight syntypes from the same collection have been recatalogued as USNM 163953.

Photogenis eurystomus Jordan. MCZ 24388. Now *Erogala eurystoma* Jordan. Chattahoochee Riv., Atl., Coll. by D. S. Jordan. Rec. 1879. This specimen, 68.3 mm in standard length, is hereby designated lectotype. The remaining specimens of Jordan's type series are apparently no longer extant.

Number of collections examined by river system.—Upper Chattahoochee Race: Upper Chattahoochee, 10. Eastern Gulf Race: Suwannee, 1; Apalachicola (Lower Chattahoochee, Flint), 26; Econfina, 2; Choctawhatchee, 13; Pensacola Bay (Black, Yellow), 13; Escambia, 16; Pascagoula, 14; Pearl, 7; Lake Pontchartrain drainage, 12.

Comparative diagnosis.—*Notropis callitaenia* and *N. leedsi* are the only species of *Cyprinella* known to occur in the range of *N. v. cercostigma.* The occurrence of intergrades between *N. v. cercostigma* and *N. v. stigmaturus* in the lower Alabama system may indicate the necessity for comparison with the three species of *Cyprinella* in the upper Alabama. Since this appears unnecessary at present, these species will be compared with *N. v. stigmaturus* only. Bailey and Gibbs (1956) have compared *N. v. cercostigma* with *callitaenia* and have shown that *callitaenia* has an inferior, rather then terminal or subterminal mouth; 13-2-11 predorsal circumferential scales, instead of 14- or 15-2-11; and an unpigmented lower jaw, which is pigmented at the symphysis in *venustus. N. callitaenia* often lacks pigment in the dorsal fin, whereas this is usually present and scattered on all membranes in *N. venustus,* and *callitaenia* possesses a chain of macromelanophores along the lower edge of the lachrymal bone from the eye to the middle of the upper jaw. The larger basicaudal spot in *N. v. cercostigma* would ordinarily be diagnostic, but in the Chattahoochee and Flint Rivers, where *callitaenia* is found, this spot tends to be reduced. Still, it is larger, usually twice as long as wide, and distinct from the lateral stripe, while in *callitaenia*, the spot is not so large and often contrasts little with the dark lateral stripe. *N. callitaenia* often lacks a tooth in the minor row of one pharyngeal arch, whereas this is rare in *N. v. cercostigma.*

Notropis leedsi has been taken together with *N. v.. cercostigma* only once, by D. C. Scott in the Alapaha River, a tributary to the Suwannee River, in Georgia. *N. leedsi* is a very different fish, in which the mouth is inferior, the scales are not narrowly outlined in black, the dorsal fin is most heavily pigmented in front, the membrane behind the leading rudimentary ray is usually notably dark, and the tooth count is 4-4. The tubercles of breeding males are in rows on the head, notal ridge, and lower caudal peduncle, and none are present on the chin rami. At the same time, the dorsal fin is greatly enlarged These differences are trenchant and need no further elaboration.

Comparison has been made between *N. v. venustus* and *N. v. cercostigma* under the former subspecies. *N. v. venustus* is generally deeper, has usually 37 or less lateral-line scales, and commonly has a more square caudal spot. For comparison with *N. v. stigmaturus* and that subspecies, see Tables 1-3.

Races.—In addition to the typical race of *N. v. cercostigma*, which is widely distributed and will be called the "Eastern Gulf Race", there is a rather well-defined race in the upper Chattahoochee River above the rapids, which was recognized by Jordan (1877b) as *Photogenis eurystomus.* The most unusual difference between this and the remainder of *N. v. cercostigma* is the polymorphism in anal rays—eight and nine occurring in almost equal numbers in any collection (Table 6). The transition from collections which have almost entirely eight anal rays to those which have half-and-half is sudden. The Fall-zone rapids near Columbus are apparently an effective barrier, for all collections examined from above it have been different, with respect to anal rays, from those below. In addition, the pectoral rays are modally 16, although commonly 14 or 15, and the basicaudal spot is usually pale and narrow by comparison to the "Eastern Gulf Race". The latter phenomenon may be attributed to the turbidity of the water in which the fish exists. The same tendency is found, but less constantly, in specimens from the lower Chattahoochee (see fig. 7, bottom), Flint, and Apalachicola Rivers. Perhaps this indicates a genetic basis for caudal spot intensity, but as yet the proof is lacking.

Range (Map 1).—River systems of the eastern Gulf of Mexico from the Lake Pontchartrain drainage in Louisiana and Mississippi to the Suwannee system, Georgia (and probably Florida). Not yet collected in the Ochlockonee, but is probably there.

Habitat.—Clear, sandy-bottomed streams are the most common habitat. In the Chattahoochee the subspecies has been taken over sandy bottom, but in extremely turbid waters as well as clear ones. The turbid condition is probably normal in the larger streams of the system, and may be a major factor in reducing the dimensions and intensity of the basicaudal spot.

Etymology.—The name *cercostigma* is a substantive derived from the Greek *kerkos*, tail, and *stigma*, spot, in allusion to the prominent basicaudal spot.

NOTROPIS VENUSTUS STIGMATURUS (JORDAN)

Slender Blacktail Shiner

Photogenis stigmaturus—Jordan, 1877b: 337 (orig. descr., Etowah R., Ga.).

Cyprinella stigmatura—Jordan and Copeland, 1876: 153 (nom. nud.); Pratt, 1935: 75 (char., distr.); Schrenkeisen, 1938: 130 (char., distr.).

Minnilus stigmaturus—Jordan, 1877a: 80 (nom. nud.).

Codoma stigmatura—Jordan, 1878: 410, 423; Jordan and Brayton, 1878: 20, 50, 52, 92 (char., distr., designated type of the new subgenus *Erogala*); Jordan, 1879: 111 (distr.).

Cliola stigmatura—Jordan and Gilbert, 1883: 182 (char., distr., syn.).

Notropis stigmaturus—Jordan, 1885: 814; Jordan and Evermann, 1896a: 255 (distr., syn.); 1896b: 257, 275 (char., distr., syn.); Fowler, 1910: 281 (variation); 1923a: 25 (paratypes in Acad. Nat. Sci. Phila.); 1923b: 20 (Coosa R., Ga.); Pratt, 1923: 79 (char., distr.).

Erogala stigmatura—Jordan, Evermann and Clark, 1930: 129 (distr., syn.); Fowler, 1935: 72 (Armuchee, Ga.).

Notropis venustus cercostigma (misidentification)—Gilbert, 1891: 154, 158 (in part; Alabama and Tombigbee systems, Ala.).

Types.—*Photogenis stigmaturus* Jordan. USNM 17891. Etowah River, Georgia, July, 1876, D. S. Jordan. The lectotype here designated, a male, 84.4 mm, retains USNM 17891. Ten syntypes bearing the same data have been recatalogued as USNM 163938. Another syntype, with essentially similar data, was found as USNM 20125. Eight further syntypes are located at the Philadelphia Academy and bear the catalogue numbers ANSP 19820 - 19827; and one at the Museum of Comparative Zoology is MCZ 24371.

Cyprinella calliura Jordan. USNM 6865. These specimens are recorded as collected in the Black Warrior River, Selma, Alabama, by Prof. Winchell. Selma is located in the drainage of the lower Alabama system and a good distance from the Black Warrior or any other part of the Tombigbee system. The specimens, therefore, are from an area of intergradation. The lectotype designated here, a male, 89.6 mm, retains USNM 6865; seven syntypes are now catalogued as USNM 163951.

Number of collections examined by river systems—Upper Alabama, 50; Tombigbee, 21.

Comparative diagnosis.—This subspecies is found in only the upper Alabama and Tombigbee rivers. In these systems, there are few species with which it could be confused, all of these belonging to the

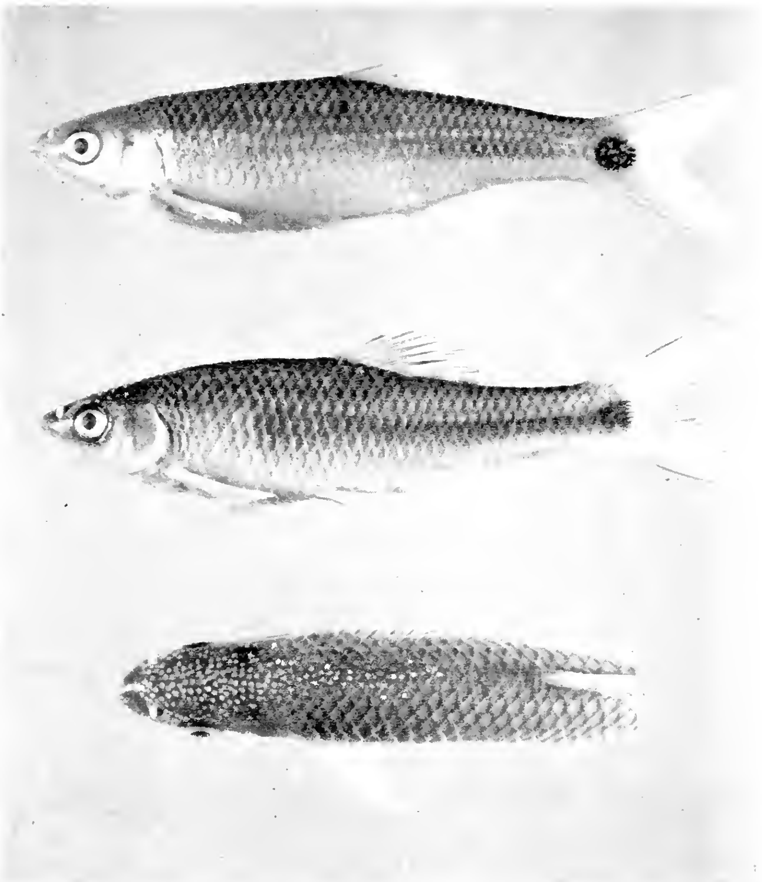


Figure 7. Top. *Notropis v. stigmaturus.* CU 17574. Gordon Co., Ga. Alabama drainage. Negative borrowed from E. C. Raney. Middle. *N. v. cercostigma.* Male, 66.4 mm. CU 16255. Wayne Co., Miss. Pascagoula drainage. Bottom. *N. v. cercostigma.* Female, 58.7 mm. CU 15836. Russell Co., Ala. Lower Chattahoochee drainage. Last two photographs taken by Douglass M. Payne. Notice the three degrees of development of the basicaudal spot.

subgenus *Cyprinella.* *Notropis callistius* and *trichroistius* have a more or less well-developed basicaudal spot. *Notropis caeruleus* lacks this.

N. caeruleus may be eliminated from consideration by its lack of the caudal spot, by its narrow, dark, blue to black lateral stripe which runs the entire length of the body, and its 11-2-9 predorsal circumferential scale count. The species is quite rare.

From *callistius*, *N. v. stigmaturus* may be differentiated by its terminal or subterminal, rather than inferior, mouth; by the narrowly outlined, diamond-shaped scales margins which *callistius* lacks; by the concentration of melanophores in the last two or three dorsal membranes as compared to the scattered pigment in the fin of *callistius* (or a wide band in the middle of the fin in breeding males of the latter); and by the large, very dark basicaudal spot, which in *callistius* is lighter in its anterior half, is rather rounded posteriorly, and does not extend out onto the caudal rays. The species differ in many meristic counts. *N. callistius* usually has 38-40 lateral-line scales, rather than 40-43, 11-2-11 predorsal circumferential scales, instead of 15-2-11, and 7-2-7 caudal peduncle scales, instead of 7-2-5.

Breeding males of *callistius* have red dorsal and caudal fins (those of *N. v. stigmaturus* are yellow) and have large tubercles arranged in rows on the head and notal ridge, but none on the chin rami.

Notropis trichroistius comes nearest to being similar to *N. v. stigmaturus*, but here, too, the differences are trenchant. The lateral scales of *trichroistius*, except those just below the lateral line, are not narrowly edged in black, the pigment of the posterior dorsal rays is very dark, often jet black, and the caudal spot usually represents an expansion posterior to a constriction of the lateral stripe (i.e., continuous with the lateral stripe). Meristically there is much overlap, but *trichroistius* has predominantly 39-41 lateral-line scales, rather than 40-43, and usually 13-2-11 predorsal circumferential scales, instead of 15-2-11. Dorsal origin to lateral line in *trichroistius* is usually 14-16% of standard length, instead of 12-14%, the orbit 8-9%, instead of 7-8%, the upper jaw 9-10%, instead of 7-8%.

Breeding males of *trichroistius* have brilliant orange fins, and large tubercles in rows on the head, notal ridge, and lower caudal peduncle.

There is apparent intergradation between *N. v. stigmaturus* and *N. v. cercostigma* in the lower Alabama and, presumably, the Mobile rivers. These presumed intergrades have been analyzed meristically, but not proportionally. The comparisons between subspecies do not take cognizance of these intergrades.

N. v. stigmaturus is in every respect a long, slender fish, the extreme for the species *venustus*. The postdorsal length is slightly less than in *N. v. cercostigma*, indicating a less-declivitous profile. The head averages the shortest of all the populations. Body depth is usually 19-22% of standard length, compared to 21-26% in *cercostigma*, dorsal origin to lateral line 12-14%, rather than 13-16%, and caudal peduncle depth averages less than any other. Lateral-line scales are usually 40-43, but range as high as 48.

N. v. stigmaturus alone, of all the subspecies of *venustus*, has the pigmentation of the last two dorsal membranes quite prominent, and usually lacks melanophores in the anterior three membranes. The basicaudal spot is the best developed, but this is difficult to measure and is an average phenomenon, many *N. v. cercostigma* approaching closely.

Tables 1-3 and Figs. 1-5 give comparisons with other subspecies and races.

Range (Map 1).—Upper Alabama and Tombigbee systems in Mississippi, Alabama, and Georgia.

Habitat.—Clear, cool streams, commonly with gravel to pebble bottoms. The subspecies has been taken in turbid water, but this may be presumed to have been a temporary condition.

Etymology.—The name *stigmaturus* is an adjective derived from the Greek *stigma*, spot, and *oura*, tail, in reference to the prominent tail spot.

NOTROPIS VENUSTUS: CERCOSTIGMA X STIGMATURUS
Intergrades

Cyprinella calliura—Jordan, 1877b: 61 (orig. descr., locality partly in error. Selma, Ala. is in Alabama R. drainage).

Luxilus calliurus—Jordan, 1878: 421; 1879: 110 (distr.).

Cliola calliura—Jordan and Gilbert, 1883: 178 (char., distr., syn.).

Notropis venustus cercostigma—Gilbert, 1891: 154 (in part; Alabama system, Ala.).

Discussion.—Principally on the basis of intermediacy in lateral-line scale counts, specimens from the lower Alabama system are considered intergrades. No collections of *Notropis venustus* have been seen from the lower Tombigbee, the lowest portion of the Alabama, or the Mobile River. Future collecting in this area may turn up proof either for or against the present contention.

The status of the types of *Cyprinella calliura* has been discussed with the types of *N. v. stigmaturus*.

Number of collections examined.—Lower Alabama system, Dallas, Lowndes, and Macon cos., Ala., 17.

INFRARACIAL VARIATION

The variation among river systems which is obvious in Tables 4-6 may be attributed to sampling error or to slight genetic drift, for no consistent pattern is shown. Perhaps the effects of slightly different environments have evoked phenotypic responses, but much more work will have to be done on this subject before the answer is forthcoming.

DISPERSAL AND SPECIATION

Notropis venustus seems closest related to *N. spilopterus* on a morphological basis. Both species have yellow fins in breeding males, have a similar tubercle pattern, and display a tendency toward reduction in pigmentation of the dorsal fin. Both have similar body forms, although this could easily be due to convergence. The basic pigmentation patterns are quite alike. Although *spilopterus* usually lacks a caudal spot, specimens have been seen in which a definite spot was present. Both have a rather prominent and wide lateral stripe. The dark side patch of breeding males of *N. venustus* has been noticed on occasion in *spilopterus*. This postulated relationship may not be extremely close, but it probably represents the nearest observable approach.

TABLE 1.

FREQUENCY DISTRIBUTION OF LATERAL-LINE SCALES OF *Notropis venustus* BY RIVER SYSTEMS

River System	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	N	$\bar{x}$	SD	SE
Suwannee	—	—	—	—	2	4	1	—	—	—	—	—	—	—	—	7	38.9	.69	.26
Apalachicola	—	—	—	—	—	5	13	1	—	—	—	—	—	—	—	19	39.8	.54	.12
Flint	—	—	—	1	11	22	4	1	—	—	—	—	—	—	—	39	38.8	.76	.12
Lower Chattahoochee	—	—	—	—	18	49	19	2	1	—	—	—	—	—	—	89	39.1	.78	.08
Upper Chattahoochee	—	—	—	—	2	28	26	12	2	—	—	—	—	—	—	70	39.8	.87	.10
Econfina	—	—	—	—	—	5	9	2	1	1	—	—	—	—	—	18	40.1	1.08	.25
Choctawhatchee	—	—	—	—	9	22	8	—	—	—	—	—	—	—	—	39	39.0	.67	.11
Pensacola Bay	—	—	—	—	4	37	35	4	—	—	—	—	—	—	—	80	39.5	.68	.08
Lower Alabama	—	—	—	—	1	5	11	5	2	1	—	—	—	—	—	25	40.2	1.12	.22
Tombigbee	—	—	—	—	1	4	16	21	10	11	1	5	1	—	1	71	41.6	1.80	.22
Upper Alabama	—	—	—	—	—	1	5	22	23	30	11	3	3	1	—	99	42.4	1.50	.15
Pascagoula	—	—	—	—	16	27	9	5	—	—	—	—	—	—	—	57	39.1	.89	.12
Pearl	—	—	—	2	15	10	5	2	—	—	—	—	—	—	—	34	38.7	1.00	.17
Pontchartrain	—	—	—	1	11	28	20	6	2	1	—	—	—	—	—	69	39.4	1.09	.13
Lower Mississippi	7	13	41	67	21	6	—	—	—	—	—	—	—	—	—	155	36.7	1.09	.09
Red	1	7	30	10	3	—	—	—	—	—	—	—	—	—	—	51	36.1	.80	.11
Ouachita	—	—	—	4	1	—	—	—	—	—	—	—	—	—	—	5	37.2	.45	.20
White	—	—	7	26	6	2	—	—	—	—	—	—	—	—	—	41	37.1	.72	.11
St. Francis	—	—	10	5	8	—	—	—	—	—	—	—	—	—	—	23	36.9	.79	.17
Sabine Lake	—	—	5	16	6	—	—	—	—	—	—	—	—	—	—	27	37.0	.65	.13
Galveston Bay	—	1	10	24	14	2	—	—	—	—	—	—	—	—	—	51	37.1	.84	.12
Brazos	—	5	29	46	11	—	—	—	—	—	—	—	—	—	—	91	36.7	.76	.08
Colorado	—	1	16	12	6	3	—	—	—	—	—	—	—	—	—	38	36.8	1.00	.16
Guadalupe	—	1	1	5	3	—	—	—	—	—	—	—	—	—	—	10	37.0	.94	.30
Nueces	—	1	1	8	5	—	—	—	—	—	—	—	—	—	—	15	37.1	.83	.22
Rio Grande	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	2	37.5	—	—

TABLE 5.
FREQUENCY DISTRIBUTION OF PECTORAL RAY COUNTS OF *Notropis venustus* BY RIVER SYSTEMS

River System	11	12	13	14	15	16	17	18	N	$\bar{x}$	SD	SE
Suwannee	—	—	—	4	7	3	—	—	14	14.9	.73	.20
Apalachicola	—	—	—	4	16	18	—	—	38	15.4	.68	.11
Flint	—	—	2	20	43	16	3	—	84	15.0	.82	.09
Lower Chattahoochee	—	1	1	38	94	38	4	1	177	15.0	.80	.06
Upper Chattahoochee	—	—	—	19	36	79	12	—	146	15.6	.82	.07
Econfina	—	—	—	6	31	3	—	—	40	14.9	.47	.07
Choctawhatchee	—	—	1	17	62	27	3	—	110	15.1	.73	.07
Pensacola Bay	—	—	1	29	103	30	3	—	166	15.0	.67	.05
Lower Alabama	—	—	4	14	22	10	—	—	50	14.8	.87	.12
Tombigbee	—	—	1	30	99	19	3	—	152	15.0	.65	.05
Upper Alabama	—	—	3	64	148	29	2	—	246	14.9	.66	.04
Pascagoula	1	—	7	31	69	16	2	—	126	14.8	.86	.08
Pearl	—	—	—	24	32	10	—	—	66	14.8	.69	.09
Pontchartrain	—	—	2	30	79	25	4	—	140	15.0	.75	.06
Lower Mississippi	—	5	39	147	108	9	1	—	309	14.3	.79	.04
Red	—	—	25	51	21	3	—	—	100	14.0	.77	.08
Ouachita	—	—	—	5	3	2	—	—	10	14.7	.82	.26
White	—	—	6	44	34	4	—	—	88	14.4	1.27	.14
St. Francis	—	—	6	26	13	3	—	—	48	14.3	.77	.11
Sabine Lake	—	—	1	16	40	4	—	—	61	14.8	.59	.08
Galveston Bay	—	—	—	41	50	13	—	—	104	14.7	.67	.07
Brazos	—	1	15	62	88	15	1	—	182	14.6	.80	.06
Colorado	—	—	9	32	36	7	—	—	84	14.5	.80	.09
Guadalupe	—	—	2	9	9	4	—	—	24	14.6	.88	.18
Nueces		1	3	22	8	—	—	—	34	14.1	.67	.11
Rio Grande	—	—	—	—	4	—	—	—	4	15.0	—	—

TABLE 6.
FREQUENCY DISTRIBUTION OF SOME MERISTIC CHARACTERS OF *Notropis venustus* BY RIVER SYSTEMS

	Anal Rays				Pred. Circumf. Scales above LL					
River System	7	8	9	N	13	14	15	16	17	N
Suwannee	—	7	—	7	—	—	6	—	1	7
Apalachicola	—	17	2	19	—	4	11	1	3	19
Flint	—	38	4	42	2	5	31	1	1	39
Lower Chattahoochee		80	9	89	18	7	61	3	—	89
Upper Chattahoochee	—	38	44	82	7	9	56	1	—	73
Econfina	—	20	—	20	—		16	1	1	18
Choctawhatchee	—	53	3	56	2	4	31	—	4	41
Pensacola Bay		79	1	83	5	8	60	4	2	79
Lower Alabama		23	2	25	2	4	16	2	1	25
Tombigbee	3	71	3	77		1	57	7	2	70
Upper Alabama	—	116	8	124	2	4	75	5	11	100
Pascagoula	—	62	1	63	6	9	37	3	3	58
Pearl	—	32	2	34	1	1	29	1	2	34
Pontchartrain		67	3	70	6	3	54	1	5	69
Lower Mississippi	1	116	9	156	56	23	73	2	1	155
Red	1	50		51	16	7	27	1		51
Ouachita	—	4	1	5	1	—	4	—	—	5
White		12	2	44	17	5	19	—	—	41
St. Francis	—	22	2	24	8	4	11	—	—	23
Sabine Lake		28	3	31	3	—	23	—	1	27
Galveston Bay	—	50	2	52	6	3	41	—	2	52
Brazos	1	86	4	91	30	11	45	2	2	90
Colorado	—	39	3	42	10	4	4		—	38
Guadalupe	—	7	3	10	5	1	4			10
Nueces		16	1	17	8	1	7	—	—	16
Rio Grande		2		2		—	2	—	—	2

The following paragraphs must be taken in the proper perspective. They represent conjecture as to the possible sequence of events in the history of the species, the evidence for which is little more than the present pattern of distribution of the subspecies and races. Admittedly alternative explanations might be possible.

From the present distribution of the species *venustus*, it seems logical to assume a center of origin somewhere in the Gulf coast drainages. With the abundance of bays and estuaries, the distribution to the east and west is not difficult to explain. Jordan (1928: 370) reports seeing *Cyprinella cercostigma* (= *N. v. cercostigma*) in Perdido Bay, along with a marine goby and a sea eel; and Bailey, Winn and Smith (1954: 160) have recorded it in the tidal portion of the Escambia River, where the salinity was recorded as 1.8 ‰ at the surface and 22.6 at the bottom. The species, then, can tolerate brackish water, through which it has dispersed.

The precise sequence of origin of the subspecies (presuming their genetic validity) is indefinite. Gene flow between *N. v. venustus* and *N. v. cercostigma* must have been rather long restricted, for when the Mississippi River, which presently demarcates their respective ranges, did not extend for its present length, there was an embayment in which coastal plain sediments were laid down as far north as southern Illinois and up the Red River valley to Texas and Oklahoma. Which of the two subspecies was the ancestral form is uncertain.

Following the differentiation of the two subspecies, *N. v. venustus* was apparently able to disperse up the west side of the Mississippi and become established in its western river systems. At some time during the repeated inundations of the Mississippi basin, a stock presumably became at least partially isolated in the Red River and differentiated to a racial level. The Red River is postulated as the place of origin because it seems more likely to have been suitable habitat and at the same time fairly well isolated during the Pleistocene than do the tributaries of the lower Mississippi, which would have been non-existent at the same time and seem to offer poor opportunity for isolation and later dispersal. The resultant deep-bodied form has since occupied most of the lower Mississippi tributaries and is interposed between two segments of the Western Gulf Race. The isolated populations of the "Western Gulf Race" in the Ouachita, Black, and St. Francis rivers have apparently not been swamped because of their habitat in the Ozark Plateau and the Ouachita Mountains, to which the "Red-Lower Miss. Race" is less well-adapted.

Of the affluents of the eastern Gulf, only two systems, the Alabama and the Chattahoochee, reach to any extent out of the Coastal Plain. In the upper portions of each of these systems a distinctive form has evolved. The Fall Zone, therefore, apparently acts as a partial barrier. The upper "Chattahoochee Race" of *N. v. cercostigma* is differentiated on a fairly low level, but, as has been pointed out, the presence of an almost equal number of specimens having eight and nine anal rays is noteworthy. The Alabama River is well-known as the habitat of a number of distinctive forms. There are three species of *Cyprinella*, in addition to *N. v. stigmaturus*, which are found only there or also in the Tombigbee. Probably the high water levels of the Pleistocene were directly responsible for the isolation and speciation of *stigmaturus*.

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ABSTRACT

Notropis venustus is redescribed and its three subspecies are characterized and their synonymies given. *N. v. venustus* consists of two races, one in the affluents of the Gulf of Mexico west of the Mississippi to the Rio Grande and in certain Ozarkian drainages, the other interposed in the Red River and tributaries to the lower Mississippi. *N. v. cercostigma* has a typical race occupying Gulf of Mexico drainages east of the Mississippi to the Suwannee and another restricted to the upper Chattahoochee River above the Fall Zone. *N. v. stigmaturus* is found only in the Alabama and Tombigbee rivers. Apparent intergrades, *N. v. : cercostigma* x *stigmaturus* are found in the lower part of the Alabama system.

The closest relative of *N. venustus* appears to be *N. spilopterus*. *N. venustus* is believed to have originated somewhere in the Gulf of Mexico tributary system, and to have dispersed through the more or less brackish estuaries and embayments. Where populations have reached above a zone of rapids, differentiation has been accelerated, giving rise to *N. v. stigmaturus* and the Upper Chattahoochee Race of *N. v. cercostigma*.

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THE EARLY DEVELOPMENT OF *RANA CAPITO SEVOSA*

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THE EARLY DEVELOPMENT OF *RANA CAPITO SEVOSA*

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The geographic range of the dusky gopher frog, *Rana capito sevosa*, was recorded by Netting and Goin (1942) as limited to the Gulf Coast region between Saint Tammany Parish, Louisiana and Baldwin County, Alabama. A wider distribution of the dusky gopher frog in Mississippi and Alabama was reported recently by Neill (1957). *R. capito sevosa* apparently intergrades with the northern crawfish frog, *R. areolata circulosa*, in Mississippi, as well as with the Florida gopher frog, *R. capito capito*, in the region between Mobile Bay, Alabama and the Apalachicola drainage in Florida. Neill (*op. cit.*) proposed that the dusky gopher frog and the Florida gopher frog be listed as subspecies of *R. areolata*, namely, *R. a. sevosa* and *R. a. aesopus* respectively. He recommended also that the gopher frog from the lower Atlantic Coastal Plain (Carolinas and Georgia), described by Schwartz and Harrison (1956) as a new subspecies, *R. capito stertens*, be designated as *R. areolata capito*. The nomenclature used herein follows the more familiar terminology found in Schmidt's 1953 check list. This does not necessarily imply a rejection of Neill's revisions.

Continual efforts have been made by members of the field crews of Tulane University to accumulate data on the habits and life history of the dusky gopher frog in Louisiana. This elusive frog has been collected from several localities in Saint Tammany Parish. Adult specimens are represented in the Tulane University Vertebrate Collections from Slidell[1] (11 ♂♂, 2 ♀♀, TU 4883, 4919), Covington, (1 ♀, TU 4901), Talisheek (1 ♂, TU 4888), and Pearl River (6 ♂♂, 4 ♀♀, TU 1352, 4902, -05, -07, 5461).

Breeding aggregations of *R. capito sevosa* have been encountered in clear, woodland pools located three miles north of Pearl River, off state highway 41. Preliminary observations indicate that the peak of breeding activity is during the early part of February. *Rana pipiens* (= *R. pipiens sphenocephala*) commonly has been observed participating in the congregations. The mating call of the dusky gopher frog may be likened to the roar of an outboard motor, more continuous and hoarser than the guttural croaks of the leopard frog. The voice is stated (Goin and Netting, 1940) to be less "snore-like" than that of the Florida gopher frog, *R. capito capito*.

The dusky gopher frog reacts quickly to slight disturbances in the water, diving to, and swimming rapidly along, the bottom of the pool. Efforts to capture mated pairs have not been successful. However, egg masses and tadpoles have been collected on several occasions.

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[1] The locality at Slidell, La. is the source of the type specimen of the dusky gopher frog (Carnegie Museum No. 16809), an adult male collected by Percy Viosca, Jr. on April 11, 1926 and described by Goin and Netting (1940).

Those masses containing large-sized eggs, assumed not to be those of *R. pipiens*, were assigned with reservation to *R. capito sevosa.* Likewise, the tadpoles of the dusky gopher frog and the leopard frog could not be separated with absolute assurance. Precise identification of the eggs and tadpoles of *R. capito sevosa* awaited the opportunity when eggs could be obtained from known parents, or when larvae collected in the field could be reared through metamorphosis.

On the evening of February 9, 1955, an egg mass containing approximately 6,000 eggs was taken from a temporary pool in the pine-oak woodland at Pearl River by a Tulane University party of Liner, Tinkle, and Lubritz. The plinthlike, submerged egg mass was collected shortly after 7:00 p.m. and apparently had been recently deposited. The eggs were examined by the writer the following morning (11:00 a.m.), at which time they were in the late cleavage stage (stage 9, defined in Shumway, 1940). The eggs appeared to be larger than those of the southern leopard frog. This impression was confirmed by measurements of the vitellus diameter. The diameter of 100 eggs ranged from 1.67 to 2.18 mm, the mean being 1.84 mm and the standard deviation, 0.11. Eggs of *R. pipiens* from three localities in eastern Louisiana (Boutte, New Orleans, and Slidell) varied from 1.44 - 1.76 mm, with a mean of 1.62 mm and a standard deviation, 0.09. The difference in egg sizes in significant (the difference between the means is greater than three times the standard error of the difference).

Most of the eggs were preserved (TU 16999); approximately 400 eggs were distributed in groups of twenty into white enamel pans containing pond water. The embryos were reared in an air-conditioned laboratory, in which the temperature was maintained at 20 C ± 3 . All stages of development through and beyond metamorphosis were obtained. The transformed frogs were *R. capito sevosa.*

The purpose of this paper is to describe the early development, heretofore unrecorded, of the dusky gopher frog. The phrase "early development" encompasses both embryonic and larval periods. An embryo is designated here as the prefeeding individual, beginning with the cleavage of the egg and continuing until the external gills are lost. Larva and tadpole are considered synonymous terms, each referring to the individual that feeds and passes through a period of metamorphosis before assuming the adult shape.[2] Following the scheme proposed by Taylor and Kollros (1946), the embryonic stages are designated by arabic numerals; the larval stages, by Roman numerals (except for practical considerations in fig. 5).

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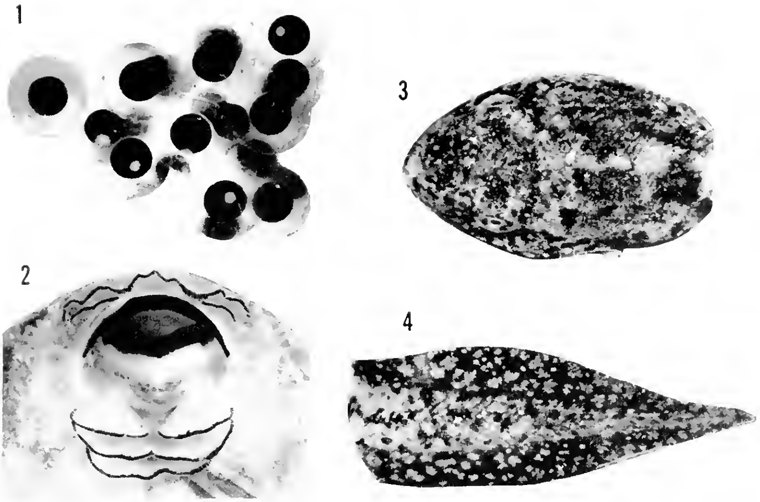
[2] The time of hatching is generally considered as the transition period from embryonic to larval development. However, since hatching occurs at different stages of development in anurans, then that which constitutes an embryo in a late-hatching species would be a tadpole in an early-hatching species. This difficulty is circumvented by the terminology employed in this paper.



Figures 1-4. *Rana capito sevosa.* **1** Late gastrula stage; **2, 3, 4** features of a tadpole at stage VI.

EMBRYONIC DEVELOPMENT

As previously mentioned, the embryos were in the late cleavage stage (stage 9) when examined at 11:00 a.m. of February 10. The dorsal lip of the blastopore (stage 10) was evident at 7:00 p.m. The embryos exhibited a circular blastopore (stage 12) at 10:00 a.m. the following day, at which time the photograph shown in figure 1 was taken. Two gelatinous envelopes are present; the inner one is not visible in the figure. The diameter of the outer envelope of 100 eggs averaged 4.00 mm (standard deviation: 0.24, range: 3.44 - 4.48 mm); the inner, 2.37 mm (standard deviation: 0.15, range: 2.06 - 2.75). The embryos were observed at close intervals thereafter; the data are recorded in Table 1. The age, in hours, accompanying a given stage refers to the time that had elapsed since fertilization (stage 1). It is estimated that the eggs were fertilized at 7:00 p.m. of the evening they were collected. Based on this estimate, the onset of stage 25, the last of the embryonic stages, occurred 259 hours after fertilization. Total length of twenty embryos measured at stage 25 averaged 13.30 mm (range: 12.02 - 14.46 mm).

The embryos hatch in the tail bud stage (stage 17). No active muscular movements or contractions are involved in the hatching process. The activity of cilia on the ectodermal surface apparently plays an important role. The embryo begins to rotate slowly by means of ciliary action during the closure of the neural tube (stage 15). Just prior to hatching, the embryo comes to rest with its head pressed against the vitelline membrane ("vitelline capsule", "fertilization membrane", "chorion"). The membrane bulges at its point of con-

TABLE 1.
THE EMBRYONIC DEVELOPMENT OF *Rana capito sevosa*

Age in Hours	Stage	Age of Hours	Stage
0	1[a]	110.5	19M
16.0	9	115.0	19L
22.0	10	120.0	20E
37.0	12L	133.2	20L
46.5	14E	138.0	21
61.0	16E	156.5	22
68.2	16M	169.0	22
77.7	17E	193.0	23
86.0	17L (Hatching)	216.7	23
92.5	18E	236.5	24
98.0	18L	259.0	25

[a] The stages are described in Shumway, 1940; the letters E, M, and L signify early, middle and late.

tact with the head and then ruptures. The rate of ciliary beat increases and the embryo, without bending or twitching its body, slides slowly through the aperture. The rupture of the membrane or the emergence of the embryo is not abrupt or explosive, suggesting no mechanical effects of vitelline fluid pressure. Noble (1926) claims that a group of eosinophilic cells ("frontal gland") in the head ectoderm of anuran embryos secretes a dissolving factor. This secretion may be instrumental also in softening or dissolving the jelly in the path of the emerging embryo, although other factors must be operative since the outer jelly coat appears to soften or liquify prior to the inner jelly coat. After hatching, the embryo clings to the jelly mass by means of its V-shaped mucous gland ("suckers"). Active spontaneous swimming begins at stage 23.

The mouthparts begin to differentiate in late embryonic development. Horny beaks, pigmented at the inner edges, appear in the mouth at stage 24. Marginal papillary fringes are also present in a rudimentary condition at this stage. At stage 25, the greater part of the horny beaks are pigmented, the lateral papillary fringes contain small papillae, and the first upper and three lower labial ridges are present. Labial teeth appear in late stage 25 embryos. The first upper ridge is invariably the first to possess teeth, followed shortly thereafter by the differentiation of teeth on the three lower ridges. As discussed below, labial teeth do not appear on the second upper row until larval stage II.

LARVAL DEVELOPMENT

Commencing with the larval period (stage I), the tadpoles were fed boiled spinach. When the tadpoles approached metamorphosis, they were transferred to terraria containing pond water at one end. Juvenile frogs were fed vestigial-winged fruit flies, meal worm larvae, and pieces of liver.

The larvae were preserved at intervals, and staged according to the

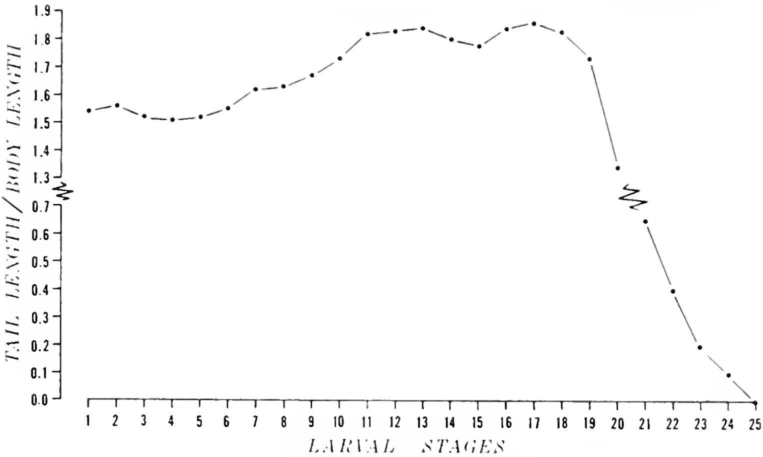


Figure 5. Mean body ratios of *R. capito sevosa* during larval development.

system of Taylor and Kollros (1946). Two measurements were taken: (1) body length, measured from the tip of the snout to the curvature of the body at the point of insertion of the tail, in line with the lateral axis; and (2) tail length, measured from the tip of the tail to the point of its insertion on the body. A third dimension, total length, was computed by adding the values of body length and tail length. Tadpoles in an early stage of development were measured to the nearest 0.01 mm with the aid of a Filar micrometer eyepiece inserted into a stereoscopic microscope; those too large to be handled satisfactorily under a microscope were measured with a dial caliper.

Measurements.—The linear dimensions of the tadpoles at each stage of development are recorded in Table 2. The body dimensions are expressed in terms of ratios in figure 5. The tail length body length ratios were calculated from the data of Table 2 and plotted against stages of development. The tail is approximately 1.5 times as long as the body during the early stages (I-VI). The ratios are higher in the mid-period of larval development; the highest value is 1.84 for stage XVII. The ratios decrease rapidly during the metamorphic period (stages XVIII-XXV).

Length of larval period.—No attempt was made to ascertain precisely the extent of variation in growth rates of the tadpoles. Critical observations were made during four periods, namely, when the majority of the tadpoles reached stages V, X, XVII, XXV. At stage V, the hind limb is a small, undifferentiated bud, reaching a maximum size of one millimeter. The majority of the tadpoles entered stage V at 34 days after the onset of larval development (stage I). Thirty-two days elapsed between stage V and stage X, the latter being characterized by the presence of five interdigital indentations on the distal part of

TABLE 2.

MEASUREMENTS (IN MILLIMETERS) OF TADPOLES OF *Rana capito sevosa*

Stage	Number of Tadpoles	Total Length Mean (Range)	Body Length Mean (Range)	Tail Length Mean (Range)
I	14	17.5 (16.4 - 18.5)	6.9 (6.1 - 7.5)	10.6 (9.6 - 11.4)
II	20	20.0 (18.3 - 21.8)	7.8 (7.1 - 8.6)	12.2 (11.3 - 14.0)
III	21	26.7 (22.8 - 29.0)	10.6 (9.4 - 11.6)	16.1 (13.4 - 17.6)
IV	14	32.6 (31.6 - 34.6)	13.0 (12.4 - 13.7)	19.6 (18.4 - 20.4)
V	11	40.1 (35.1 - 43.8)	15.9 (14.3 - 17.1)	24.2 (20.7 - 27.4)
VI	11	47.6 (44.7 - 53.8)	18.3 (16.4 - 20.5)	28.3 (26.4 - 30.9)
VII	13	53.0 (49.4 - 55.9)	20.2 (18.5 - 22.4)	32.8 (30.1 - 35.8)
VIII	3[a]	58.1 (57.0 - 59.4)	22.1 (22.0 - 22.4)	36.0 (36.0 - 37.0)
IX	2	59.5 (58.5 - 60.4)	22.3 (21.7 - 22.8)	37.2 (36.6 - 37.7)
X	2	60.8 (60.2 - 61.4)	22.3 (22.0 - 22.6)	38.5 (38.2 - 38.8)
XI	1	62.2 (59.0 - 65.0)	22.1 (21.0 - 23.5)	40.1 (38.0 - 42.5)
XII	4	63.4 (62.0 - 64.5)	22.4 (21.5 - 23.5)	41.0 (40.5 - 42.0)
XIII	6	63.7 (61.5 - 66.0)	22.4 (22.0 - 23.5)	41.3 (39.5 - 42.5)
XIV	3	63.8 (62.5 - 66.5)	22.8 (22.0 - 24.0)	41.0 (40.0 - 42.5)
XV	1	63.0	22.7	40.5
XVI	3	66.2 (64.0 - 69.5)	23.3 (22.5 - 24.5)	42.8 (41.5 - 45.0)
XVII	4	71.2 (69.5 - 74.0)	24.9 (24.0 - 26.5)	46.3 (45.5 - 47.5)
XVIII	2	70.8 (68.5 - 72.0)	25.0 (24.0 - 26.0)	45.8 (44.5 - 47.0)
XIX	2	67.8 (67.0 - 68.5)	24.8 (24.0 - 25.5)	43.0 (41.5 - 44.5)
XX	5	57.5 (49.5 - 63.5)	24.5 (23.0 - 27.5)	32.9 (25.5 - 39.5)
XXI	3	43.0 (40.5 - 46.5)	26.0 (25.0 - 27.5)	17.0 (15.5 - 19.0)
XXII	2	36.3 (33.0 - 39.5)	26.0 (25.0 - 27.0)	10.3 (6.0 - 14.5)
XXIII	4	31.3 (30.0 - 33.0)	26.0 (24.5 - 27.5)	5.3 (4.0 - 7.0)
XIV	2	30.3 (27.5 - 33.0)	27.5 (25.5 - 29.5)	2.8 (2.0 - 3.5)
XV	10	28.2 (26.5 - 30.1)	28.2 (26.5 - 30.1)	——

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[a] Considerable mortality among the tadpoles necessitated reducing the sample size.

the hind limb bud. The majority of the tadpoles entered stage XVII, when the foot of the hind limb is differentiated, 40 days after stage V. The first tadpole transformed (stage XXV) 35 days later, or 141 days after the onset of larval development. Thirty-one tadpoles metamorphosed within a two-week period; consequently, the length of the larval period under laboratory conditions may be placed at 141-155 days or approximately 5 months.

Mouthparts.—The mouthparts contain a full complement of teeth at stage V. Teeth differentiate on the first upper and three lower labial ridges during the last of the embryonic stages (stage 25) and increase in number up to larval stage V. Teeth first appear on the second upper labial ridge at stage II.

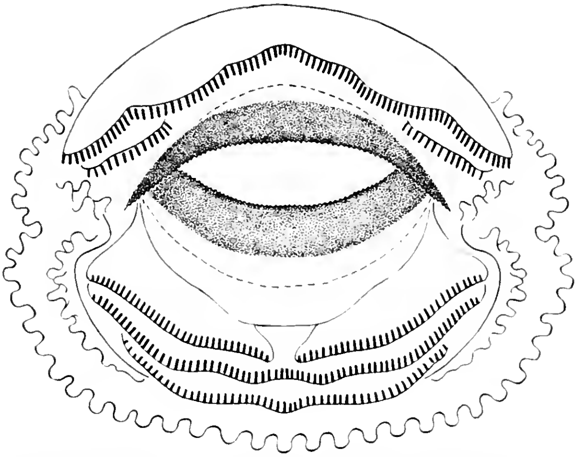


Figure 6. Mouthparts of a formalin-preserved tadpole of *R. capito sevosa* at stage XVII.

A photograph was taken of the mouthparts of a tadpole at stage VI (fig. 2). The labial tooth formula is 2/3. The first upper tooth row is divided medially; the median space is 1.0 to 2.5 times the length of either lateral segment. Each lateral segment of the second upper tooth row is equal to one fourth to one third of the first upper row.

The first lower tooth row is interrupted medially by a short space; the second and third lower rows are continuous. The first and second lower rows are equal in length. The third is 0.2 to 0.4 shorter than either the first or the second lower rows. Marginal papillae are present along the sides of the upper and lower labia and continue uninterrupted along the bottom of the lower labium. A well-defined row of submarginal papillae is present (not conspicuous in fig. 2, but shown in fig. 6). Each lateral fringe bearing the papillae is slightly emarginate.

With the emergence of the forelimbs (stage XX), the rows of teeth disappear, the papillary fringes become resorbed, and the horny beaks are lost, the lower beak generally before the upper.

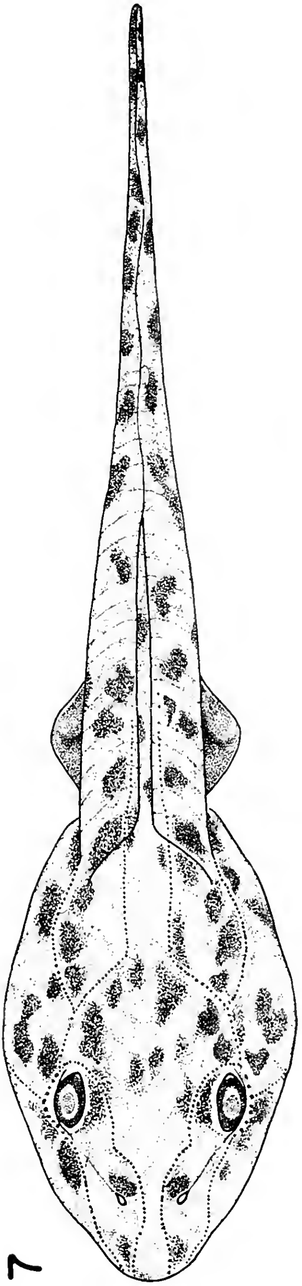
General appearance of tadpole.—A conspicuous feature of the living tadpole is its metallic yellow cast, due to the abundance of yellow chromatophores. The distribution of yellow chromatophores is shown in figures 3 and 4. The photographs were taken of a living tadpole at stage VI narcotized in M.S. 222 (Sandoz Chemical Co., N.Y.C.). The pattern is evident in tadpoles between stages IV and XVII. The yellow chromatophores are found throughout the epidermis of the head and tail, and tend to obscure the subepidermal melanophores. The distribution of subepidermal melanophores is shown in figures 7 and 8, which illustrate a formalin-preserved tadpole at stage XVII. The large clusters of melanophores on the head, tail musculature, and dorsal fin serve to characterize preserved tadpoles of the species. The belly surface is strongly pigmented, a lustrous opaque yellow. The viscera do not show through in the living tadpole, but are faintly visible in formalin-preserved specimens.

The closely spaced muciferous crypts are distinct in both living and preserved tadpoles (figs. 7 and 8). The dorsal row of pits on either side of the dorsal fin extends forward to join the main dorsolateral row of crypts. The latter courses from the tip of the tail to the back of the eye, where it bifurcates to form supraorbital and infraorbital branches, both of which extend to the tip of the snout. Beneath the eye, the infraorbital branch sends a loop ventrally, which meets the mandibular branch to the mouth region. On the ventrolateral surface of the body may be seen a row of crypts extending to the spiracle.

The spiracle is a circular aperture at the end of a short spiracular tube located on the left ventrolateral surface midway between the tip of the snout and the cloaca. The cloaca is dextral, opening on a level with the edge of the ventral fin. The dorsal fin is highly arched, rising above the level of the head and reaching its highest point midway between the tail tip and the insertion of the tail on the body. The tip of the tail is a blunt point.

The eyes are above the lateral axis and nearer the lateral outline in dorsal view than the mid-dorsal line. The eyes are not visible when the tadpole is viewed from the ventral surface.

Transformation.—The pattern of dorsal spots appears when one or both forelimbs protrude (fig. 9). The spots are dark green against a pale green background; in formalin-preserved specimens, the spots and ground color are dark brown and light brown respectively. The spots are irregular in shape and are not light-margined. The dorsolateral folds are delimited as slightly raised surfaces. The legs are conspicuously marked with bands that are equal to or greater than the width of the interspaces. The ventral surface has a white lustre in life and is unspotted.



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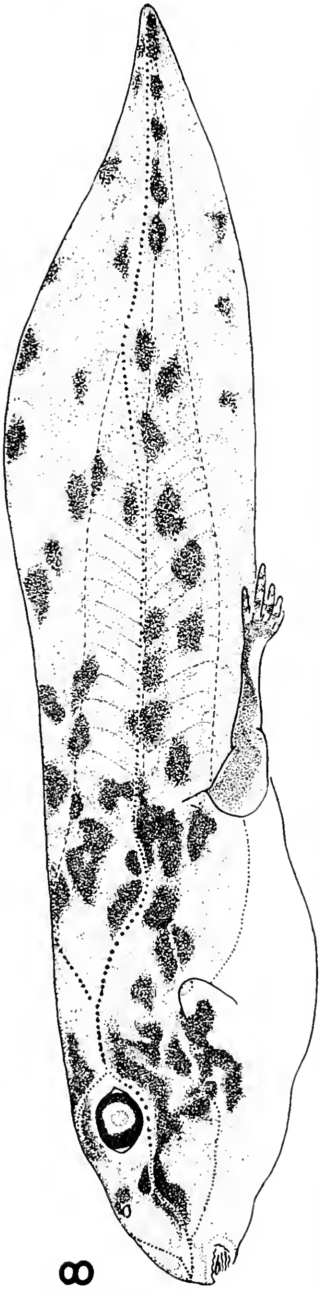

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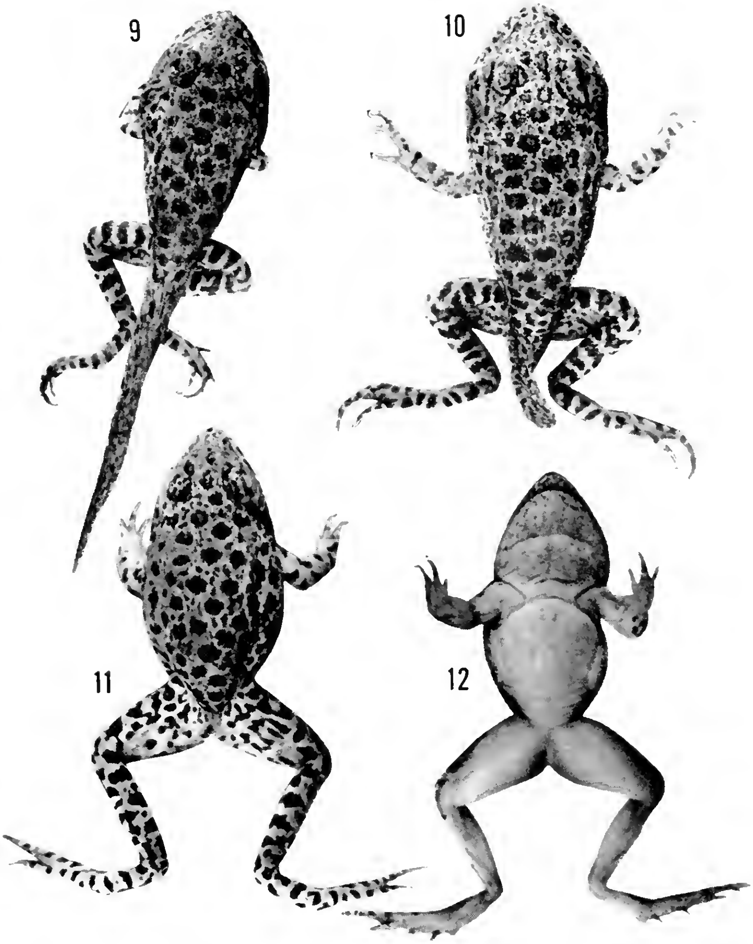
Figures 7-8. **7** Dorsal and **8** lateral view of a formalin-preserved tadpole of *R. capito sevosa* at stage XVII.



Figures 9-12. Stages in the metamorphosis of *R. capito sevosa*. **9** stage XX; **10** stage XXIII; **11, 12** stage XXV.

During the period (stages XXI-XXV) that the tail is resorbed (fig. 10), the dorsolateral folds thicken and brown spots appear on the throat surface. At the end of metamorphosis (stage XXV, figs. 11 and 12), small dark green spots are present in the interspaces between the larger spots on the dorsum and the throat region contains scattered brown pigment spots. Unlike the adult, the dorsolateral folds are not conspicuously elevated, the dorsal skin is smooth, the head is subtriangular, the belly and the undersurface of the thighs are unspotted, and the tympana and post-tympanic folds are undifferentiated. The body length (snout to vent) of ten frogs preserved at transformation averaged 28.2 mm (range: 26.5 - 30.1 mm); the tibia (tibiofibula) length, 12.5 mm (range: 11.3 - 13.2 mm).

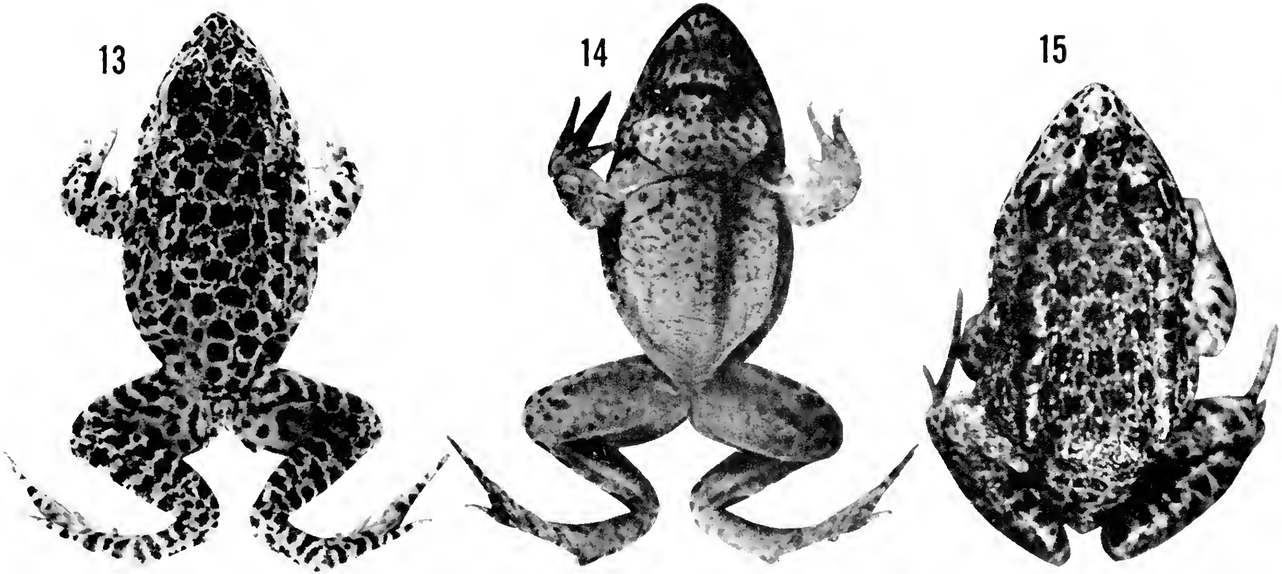
POSTMETAMORPHOSIS

External changes.—Twenty-one frogs were reared beyond metamorphosis. One was reared for a period of one month after transformation, two for 2.5 months (± 3 days), one for 3.5 months, four for 7.2 months (± 5 days), and five for 9.7 months (± 4 days). Eight others died and underwent post-mortem changes before they could be preserved, rendering them useless for analyses. The five frogs preserved at 9.7 months averaged: in body length, 49.1 mm (range: 48.2 - 50.4 mm); in tibia length, 21.1 (range: 20.5 - 22.4 mm).

The most conspicuous changes in postmetamorphic growth were the formation of wartlike elevations on the dorsal skin, the thickening of the dorsolateral folds, and the appearance of brown spots on the venter and inner surfaces of the thighs. Figures 13 and 14 show a 7.2-month old dusky gopher frog. The overall appearance of the frog is brown-green; the ground color dorsally is brown-green containing dark-green spots. Characteristics of the adult are evident: a narrow, triangular head, a broad body, a warty dorsum, a heavily spotted venter, irregularly shaped, unbordered spots, and dark hindlimb bands that are wider than the interspaces. The dorsolateral folds are conspicuously elevated in the 9.7-month old frog (fig. 15).

Analysis of growth.—Measurements were taken of the body lengths and tibia lengths of the ten recently metamorphosed frogs, the thirteen postmetamorphic frogs, and the twenty-five adults contained in the Tulane University Veterbrate Collections (mentioned in the introduction). The adults possess relatively longer legs, as indicated by the significantly lower value of the mean ratio between body length and tibia length (B.L./T.L. = 2.16, range: 2.04 - 2.24) of the adults as compared to that of the recently metamorphosed frogs (B.L./T.L. = 2.26, range: 2.15 - 2.39). The ratios do not vary significantly in the laboratory-raised frogs at the various periods of growth.

The relation between body length and tibia length may be translated into a mathematical expression that reveals more precisely the rate of change of the two body components. If the tibia length is designated as y, and the body length as x, the relation between them may be expressed by the formula for heterogonic growth, $y = b \cdot x^k$ (or $\log y = k \log x + \log b$), in which b and k are constants, with k representing the coefficient of heterogony. The magnitude of k indicates the amount of discrepancy between the growth processes of the two body parts. In figure 16, the logarithms of the tibia lengths of the laboratory-raised frogs are plotted against the logarithms of the body lengths, and the resulting straight line reveals k as the tangent of its angle of incidence. The calculated value of k is 1.013. The relation between the two body components in the laboratory-



Figures 13-15. Postmetamorphic stages of *R. capito sevosa.* **13, 14** 7.2-month old frog; **15** 9.7-month old frog.

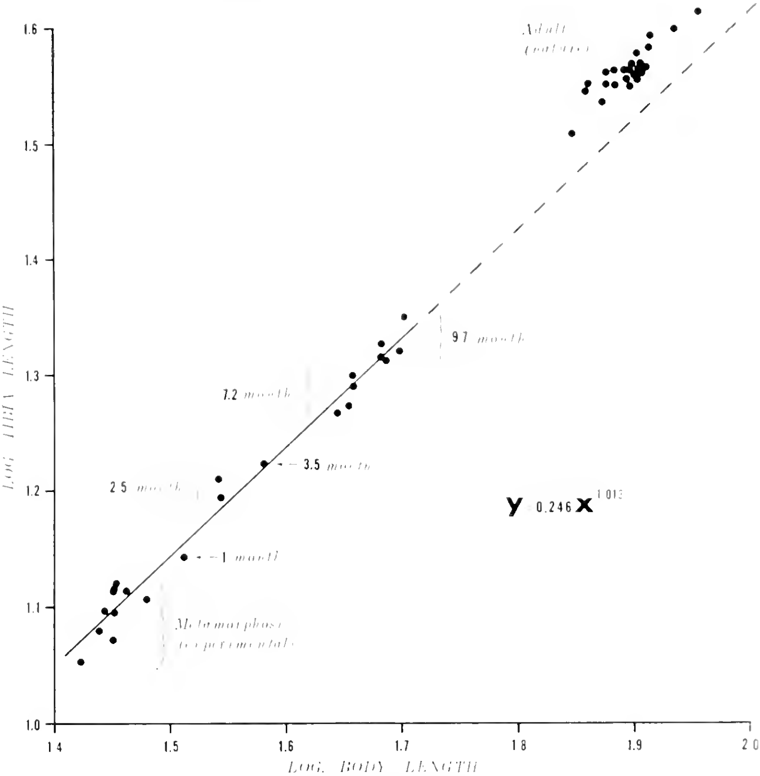


Figure 16. Log-log plot of tibia length (Y) and body length (X) of laboratory-raised *R. capito sevosa* (metamorphosis to 9.7 months) and of adults of natural populations.

raised frogs is essentially isogonic; as the body increases the tibia increases slightly more rapidly. When the values for the two body components of the adults are plotted on the same log-log graph (fig. 16), a striking fact is revealed. The values do not fit on the straight line, but fall above it. Assuming that the heterogonic formula expresses accurately the growth relations of the two body components during early growth, then either a sharp change in rate occurs as the frog approaches adulthood, or environmental factors in nature have disturbed the growth relations.

COMPARISONS

The early development of *R. capito sevosa* is strikingly similar to that of the Florida gopher frog, *R. capito capito*, as described by Wright (1929, 1932). The early stages of the dusky gopher frog resemble in certain aspects those of the crawfish frog (*R. areolata*) and the leopard frog (*R. pipiens*). The discussion below is an attempt to bring forth the similarities and differences in the eggs, tadpoles, and transformed stages of the gopher, crawfish and leopard frogs. The author is familiar with the early stages of development of only the dusky gopher frog and the leopard frog. Consequently, the reliability of the comparisons reflects to a large extent the adequacy of the descriptions in the literature.

Eggs.—The eggs of *R. capito sevosa* are smaller than those of *R. capito capito*, *R. areolata circulosa*, and *R. areolata areolata*. The number of eggs per mass, as well as the size of the eggs, distinguish the dusky gopher from the leopard frog of Louisiana. Other comparative data are given in Table 3.

In a cluster, the eggs of the dusky gopher frog appear to be larger in diameter than actual measurements reveal. Bragg (1953) reports the same phenomenon for eggs of crawfish frogs, and infers that the jelly surrounding the eggs has a particularly effective lens action.

Mouthparts.—The larval mouthparts of the dusky and Florida gopher frogs are characterized by a wide median space in the second upper labial row of teeth. Wright (1929) states for larvae of *R. capito capito:* " . . . median space between the second upper labial row 1.0 - 2.0 times the length of either lateral part of this row; third lower row 0.33 - 0.66 shorter than the first or second rows . . . ". The median space in the larval mouthparts of *R. capito sevosa* is 1.0 to 2.5 times either lateral segment of the second upper row, and the third lower row is 0.2 to 0.4 shorter than the first or second lower rows. The differences in the relative length of the third lower labial row may be significant.

The second upper tooth row is interrupted in the midline by a narrow space in tadpoles of both northern and southern crawfish frogs. The illustration by Smith, Nixon and Smith (1948) of the mouth disc of larvae of *R. areolata circulosa* from central Illinois shows a median space that is less than one half of the length of either lateral row. Bragg (1953) reports a similar condition in tadpoles of *R. areolata areolata* from Oklahoma.

Wright (1914, 1929, 1932) states that the median space in the second upper tooth row is 0.5 to 1.0 times either lateral segment in tadpoles of southern leopard frogs, whereas it is 1.0 to 1.5 times either lateral part in larvae of northern leopard frogs. Wright's descriptions of "northern" and "southern" leopard frogs are based on tadpoles from the vicinity of Ithaca, New York, and Okefinokee swamp, Georgia, respectively. The description of larval mouthparts of *R. pipiens* from eastern Wisconsin (Volpe, 1955) fits Wright's account of northern *R. pipiens*. However, the mouthparts of tadpoles of leopard frogs from eastern Louisiana (Boutte, New Orleans, and Slidell) differ considerably from those of larvae of leopard frogs from Georgia. The median space in the larval mouthparts of leopard frogs from eastern Louisiana is 1.0 to 2.0 times either lateral segment

TABLE 3.
COMPARISONS OF EGGS OF GOPHER, CRAWFISH AND LEOPARD FROGS
(Measurements in Millimeters)

Taxon	Locality	Vitellus	Inner Membrane	Outer Membrane	Egg Complement	Authority
		Mean Diameter (Range in Parenthesis)				
R. areolata circulosa	Eastern Kansas	— (2.46 - 2.50)	— (3.15 -)	— (4.5 - 5.0)	7,000	Smith (1934)
	Central Illinois	2.05 (1.91 - 2.18)	2.53 (2.3 - 3.1)	4.03 (3.9 - 4.3)	3,192 - 6,807	Smith, Nixon and Smith (1947, 1948)
	Eastern Oklahoma	2.2 (1.8 - 3.8)	3.2 (2.9 - 3.2)	4.3 (4.0 - 4.5)	7,000	Bragg (1953)
R. areolata areloata	Eastern Oklahoma: Sample 1	2.1 (1.7 - 2.4)	2.8 (1.00 - 3.3)	4.0 (3.3 - 5.0)	3,000 - 4,500	Bragg (1953)
	Sample 2	2.1 (1.0 - 2.2)	2.8 (2.5 - 3.0)	4.1 (4.0 - 4.1)		
R. capito capito	Okefinokee Swamp, Georgia	2.0 (1.8 - 2.4)	3.9 (3.4 - 4.4)	5.3 (4.4 - 6.0)	5,000	Wright (1932)
R. capito sevosa	Pearl River, Louisiana	1.84 (1.67 - 2.18)	2.37 (2.06 - 2.75)	4.00 (3.44 - 4.48)	6,000	Present Report
R. pipiens (*R. pipiens pipiens*)	Ithaca, New York	1.7 (1.6 - 2.0)	2.4 (2.3 - 3.0)	5.1 (4.2 - 6.0)	3,500 - 4,500	Wright (1914)
R. pipiens (*R. pipiens pipiens*)	Wisconsin	1.73 (1.60 - 1.95)	2.15 (2.10 - 2.72)	4.15 (3.24 - 4.95)		Volpe (1954)
R. pipiens (*R. pipiens sphenocephala*)	Okefinokee Swamp, Georgia	1.6 (1.1 - 1.8)	2.6 (2.4 - 3.0)	3.8 (3.4 - 4.0)	1,054 - 1,500	Wright (1932)
	Eastern Louisiana	1.62 (1.44 - 1.76)	2.30 (2.06 - 2.46)	3.66 (3.18 - 4.04)	2,000	Volpe (unpublished)

of the second upper labial row, a condition similar to that in tadpoles of the dusky gopher frog. The relative length of the third lower row of teeth constitutes the best criterion for distinguishing the larval mouthparts of the dusky gopher frog and the leopard frog of eastern Louisiana. The third lower row in the latter larvae is generally half as long (range: 0.3 - 0.7) as the first or second lower tooth rows. Smith (1934) reports that the third lower row is approximately one half of the length of the second lower row in tadpoles of the leopard frog from Kansas.

General appearance of tadpole.—The distinctive features of the tadpoles of the dusky gopher frog are: (1) the yellow lustre, an effect created by numerous yellow chromatophores, (2) the large clusters of melanophores on the head, tail musculature, and dorsal fin, (3) the conspicuous pattern of muciferous crypts, and (4) the high arc of the dorsal fin. As far as can be determined from Wrights' description (1929, 1932), these features are found also in larvae of *R. capito capito.*

The dorsal fin is highly arched in the tadpole of *R. areolata areolata*, whereas in *R. areolata circulosa*, it is "more evenly rounded from one end to the other" (Bragg, 1953). The tail fins of northern and southern crawfish frogs are not as heavily mottled with black pigment, as judged by Bragg's illustrations (*op. cit.*).

Melanophores are present in the tail fins of larvae of leopard frogs, but they are not typically grouped in large clusters. The "spots" or aggregations of melanophores are more pronounced in southern than in northern leopard frogs. Wright (1932) describes the tail fins of the latter as "marked with scattered fine spots and pencilings"; those of the former as "usually with quite prominent dark spots".

Larval dimensions.—Data on absolute body dimensions of tadpoles must be interpreted with caution, since tadpoles vary in size at different developmental stages and under different environmental conditions. Knowledge of the potential range of sizes that may be realized by tadpoles of a particular species is lacking. Most investigators, however, present data on the largest tadpole in their sample, with the view, I presume, that the largest tadpole represents the maximum size that can be achieved by the larvae of a particular species. This approach may be valid only if the samples are large and are taken from various populations throughout the geographic range of the species. The following maximum sizes have been reported for the larvae of the species under consideration: *R. capito capito*, 84 mm (Wright, 1929, 1932), *R. pipiens pipiens,* 84 mm (Wright, 1914), *R. pipiens sphenocephala*, 74 mm (Wright, 1929, 1932), *R. areolata circulosa*, 65 and 76 mm (Smith, Nixon, and Smith, 1948, and Bragg, 1953, respectively), and *R. areolata areolata*, 63 mm (Bragg, 1953). The largest size achieved by a tadpole of the dusky gopher frog under the growth conditions described herein was 74 mm. The significance of these values is questionable; one certainly would be hesitant to consider a given value as characteristic of a particular species.

Transformation.—The newly metamorphosed dusky gopher frog lacks the warty dorsum, conspicuously elevated dorsolateral folds, and the heavily mottled venter of the adult. At this stage the dusky gopher frog simulates the appearance of the Florida gopher frog but may be distinguished from it by its broad leg bands and associated narrow interspaces (*cf.*, fig. 9 or 10 with Wright's plate XXXV, 1932). It may be further distinguished from a recently metamorphosed crawfish frog by the absence of light margins around the dorsal spots. There is no difficulty in differentiating recently transformed gopher frogs and leopard frogs. Among other distinguishing features, the dorsal spots of the latter are generally larger, fewer in number, and more regularly shaped.

The following ranges of body lengths (snout to vent) of newly metamorphosed frogs have been reported: *R. pipiens pipiens*, 18-31 mm (Wright, 1914), *R. pipiens sphenocephala*, 18-33 mm (Wright, 1932), *R. capito capito*, 27-35 mm (Wright, 1932), and *R. areolata circulosa*, 22.2 - 24.2 mm (Smith and List, 1955). The last mentioned authors record a snout-to-vent length of 31 mm for one transformed dusky gopher frog collected in Jackson County, Mississippi. The dusky gopher frogs reared in the present study averaged 28.2 mm at transformation (range: 26.5 - 30.1).

SUMMARY

1. Embryos of the dusky gopher frog, *Rana capito sevosa*, collected at Pearl River, Saint Tammany Parish, Louisiana, were reared through metamorphosis in the laboratory.

2. The dimensions of the egg and its two gelatinous coats are: mean diameter of vitellus, 1.84 mm (range: 1.67 - 2.18); mean diameter of inner envelope, 2.37 mm (range: 2.06 - 2.75); mean diameter of outer envelope, 4.00 mm (range: 3.44 - 4.48).

3. The embryos hatch at stage 17, just prior to the onset of muscular activity, approximately 3.5 days after fertilization. The operculum covers the gills (stage 25), marking the end of the embryonic period, approximately 7 days later. The embryos at stage 25 averaged, in total length, 13.3 mm.

4. The duration of the larval period (stages I-XXV, defined in Taylor and Kollros, 1946) was approximately 5 months. The mouthparts contain a full complement of teeth at stage V. The mouthparts are characterized by a wide median space in the second upper tooth row (1.0 to 2.5 times the length of either lateral segment) and a third lower tooth row that is 0.2 to 0.4 shorter than either the first or second lower rows. Conspicuous features of the tadpole are its metallic yellow lustre, the large clusters of melanophores on the head, tail musculature, and dorsal fin, the pattern of well-defined muciferous

crypts, and the high arc of the dorsal fin. The largest size (snout-to-tail tip length) attained by the tadpoles was 74 mm.

5. Metamorphosed frogs averaged 28.2 mm in snout-to-vent length. The leg bands are equal to or greater than the width of the interspaces and the irregular spots on the back are not light-margined. However, the transformed frogs lack the warty dorsum, elevated dorsolateral folds, and mottled venter that are characteristic of the adult. Frogs reared for a period of approximately 10 months after metamorphosis resemble the adult.

6. The body length tibia length ratios are significantly lower in young laboratory-raised frogs than in adults from natural populations. Either the growth rates of the two body components change as the frog approaches adulthood, or the growth relations are different in frogs developing in nature than in the laboratory.

7. The early stages of development of the dusky gopher frog are compared with those of the Florida gopher frog, northern and southern crawfish frogs, and northern and southern leopard frogs. The early development of *R. capito sevosa* is strikingly similar to that of *R. capito capito.*

ACKNOWLEDGMENT

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ABSTRACT

The eggs, tadpoles, and recently metamorphosed forms of the dusky gopher frog, *Rana capito sevosa*, from Saint Tammany Parish, Louisiana have been described. The near-identity of the early stages of development of the dusky gopher frog to the Florida gopher frog, *Rana capito capito*, attests to their close affinity.

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

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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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[1] This investigation was supported in part by grants NSF-G947 and NSF-G2330 from the National Science Foundation.

[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.

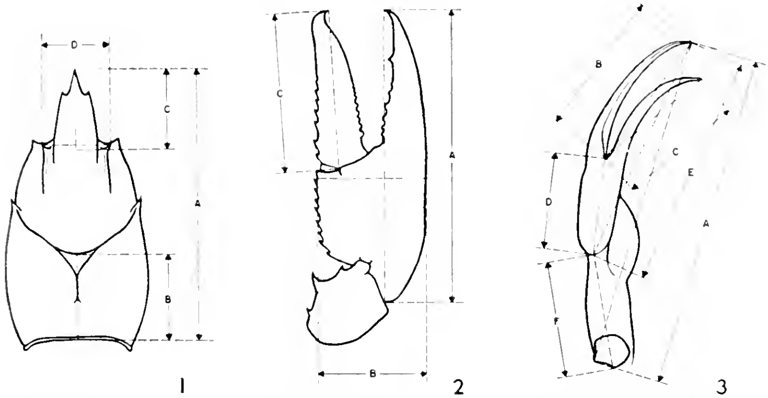
The writer (1952: 744-745) recorded the distribution of what he considered *O. p. creolanus* in Louisiana and stated his belief that *creolanus* should be considered a subspecies of *palmeri*.

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 statistical 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.



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).

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

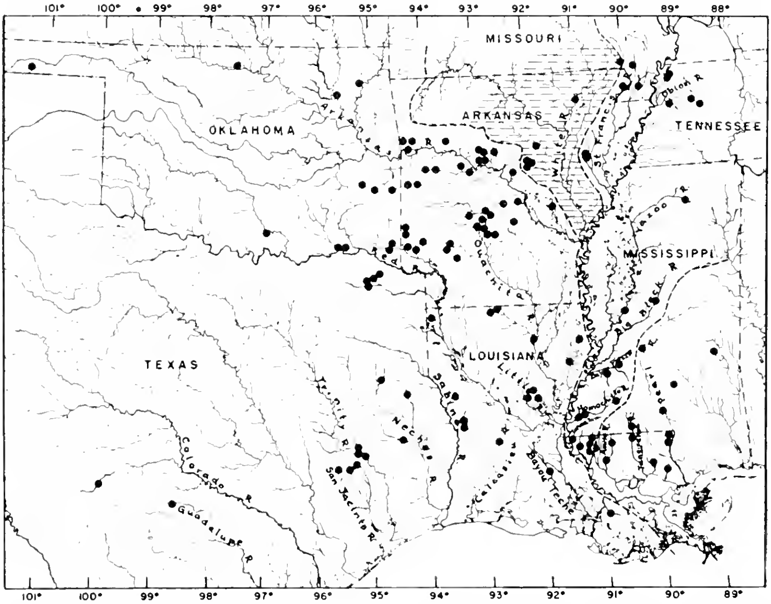


Figure 4. Localities from which specimens of *Orconectes palmeri* were examined. Dashed lines indicate subspecies boundaries; cross-hatched section is White River intergrade area.

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

			No. Treated Statistically		
Drainage	State	Grand Total	♂ 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	1
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.	91	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 I 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 supraspecific 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: 121)
(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 methods for analyzing the geographic variations of those characters which also might show ontogenetic variation.

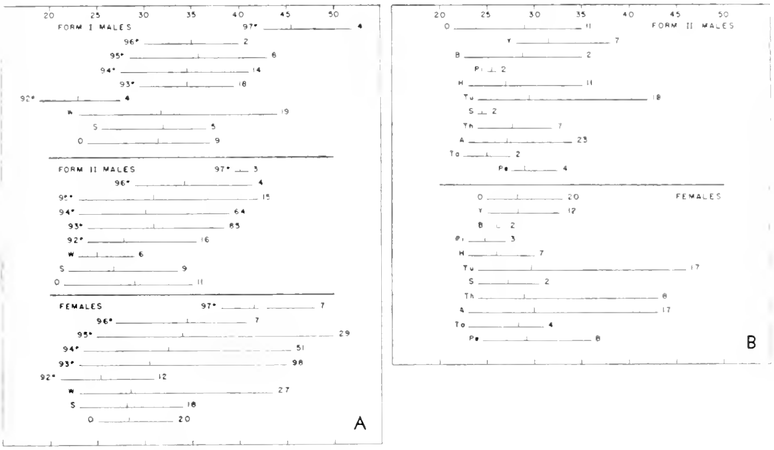


Figure 5. Carapace lengths of specimens examined; range and means in millimeters. **A.** West-east series, **B.** north-south series. Abbreviations: W = White River, S = St. Francis River, O = Obion River, Y = Yazoo River, B = Big Black River, Pi = Bayou Pierre, H = Homochitto River, Tu = Tunica Bayou, 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.

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.

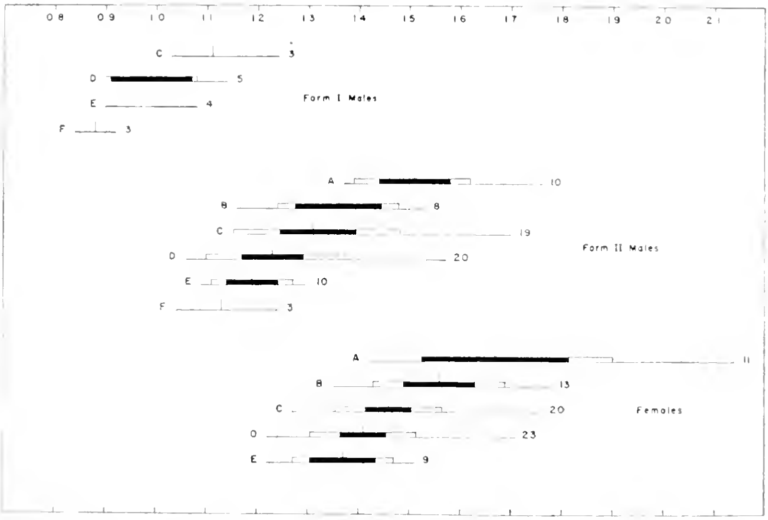


Figure 6. Ontogenetic variation in length of the chela, 93 group. Size groups (cephalothorax length) indicated to left of lines as follows: A = 23.0 to 25.5 mm, B = 26.0 to 28.5 mm, C = 29.0 to 31.5 mm, D = 32.0 to 34.5 mm, E = 35.0 to 37.5 mm, F = 38.0 to 39.5 mm.

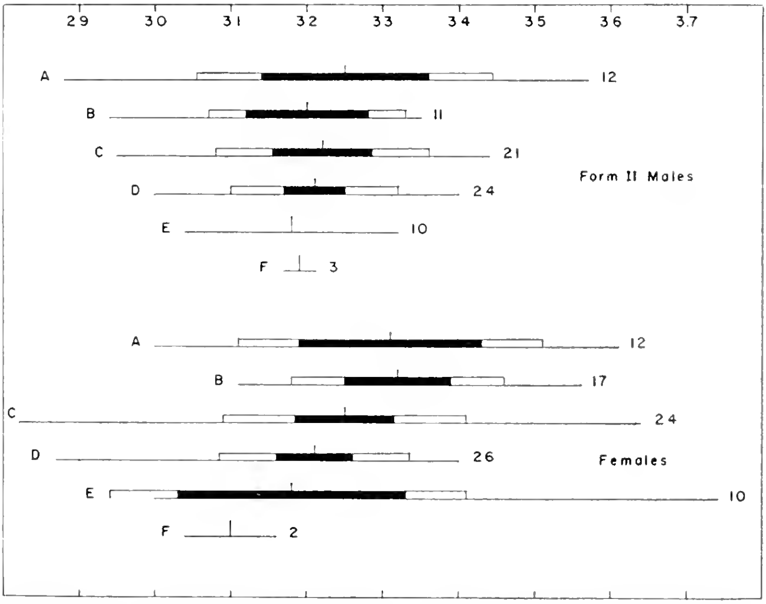


Figure 7. Ontogenetic variation in length of areola, 93 group. Abbreviations same as in fig. 6.

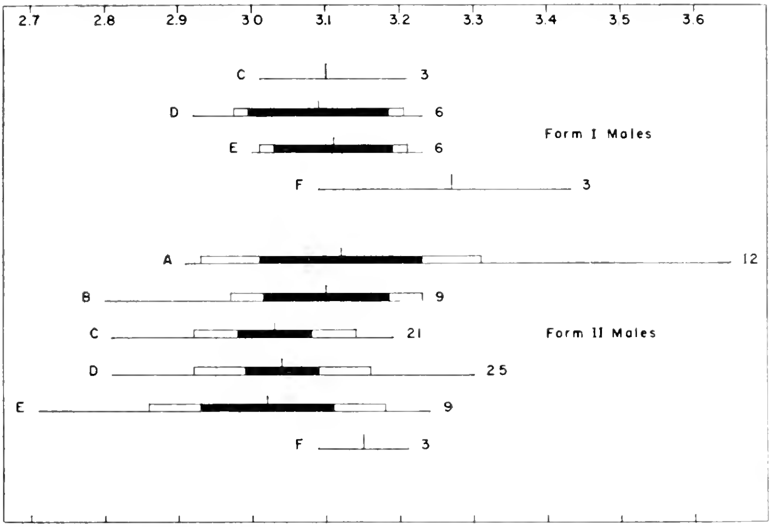


Figure 8. Ontogenetic variation in length of first pleopod of males, 93° group. Abbreviations same as in fig. 6.

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,

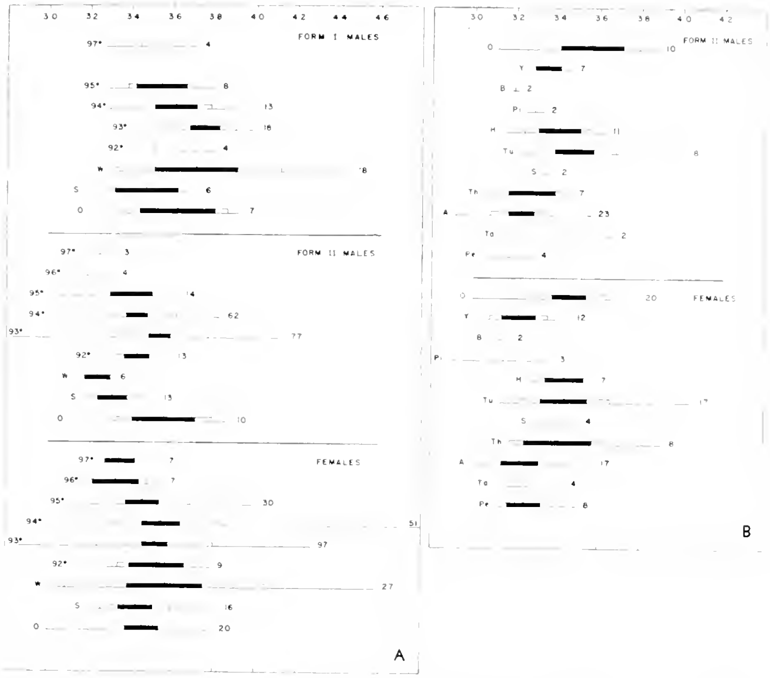


Figure 9. Geographic variation in length of rostrum. **A,** west-east series; **B,** north-south series east of Mississippi River. Abbreviations same as in fig. 5.

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

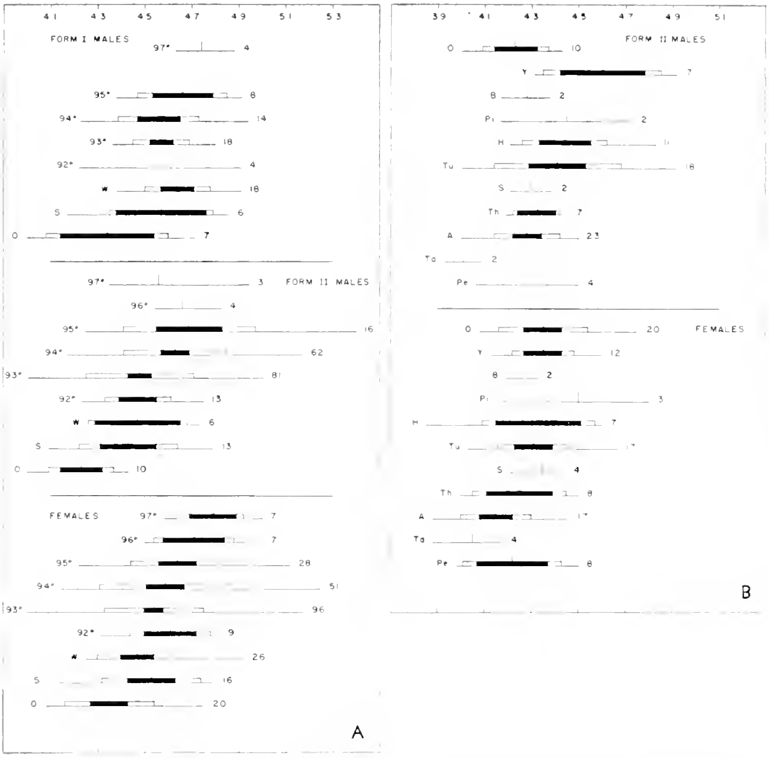


Figure 10. Geographic variation in distance between postorbital spines. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

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	Cephalothorax 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	41.0	3.08	1.15	3.11	1.58	0.81	1.18
Neches	Tex.	4	38.0 – 41.5	2.96 – 3.12 (3.04)	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	1.21	3.13	1.56	0.74	1.03
Colorado	Tex.	1	21.0	3.23	1.27	2.11	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 – 3.64 (3.38)	1.42 – 1.58 (1.46)	2.90 – 3.19 (3.05)	0.41 – 0.46 (0.45)	1.73 – 1.87 (1.79)	1.16 – 1.78 (1.61)
Colorado	Tex.	1	28.5	3.17	1.43	2.71	0.51	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.	1	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	43.7 – 45.5	2.97 – 3.14 (3.06)	1.23 – 1.30 (1.27)				
Sabine	La.	3	29.0 – 32.5	3.00 – 3.25 (3.16)	1.51 – 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	21.5 – 27.0	2.81 – 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.

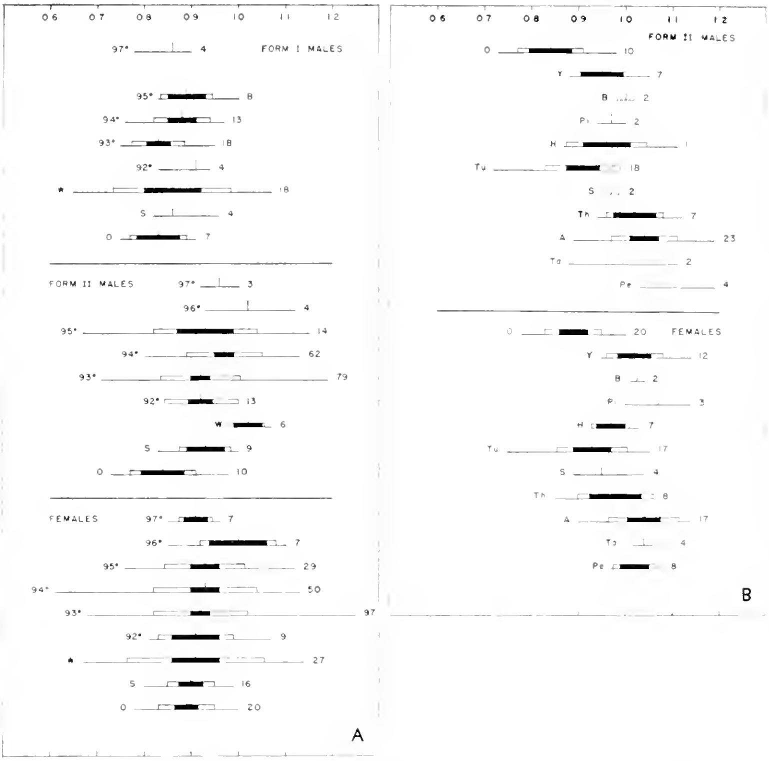


Figure 11. Geographic variation in ratio of rostrum length to areola length. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

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.

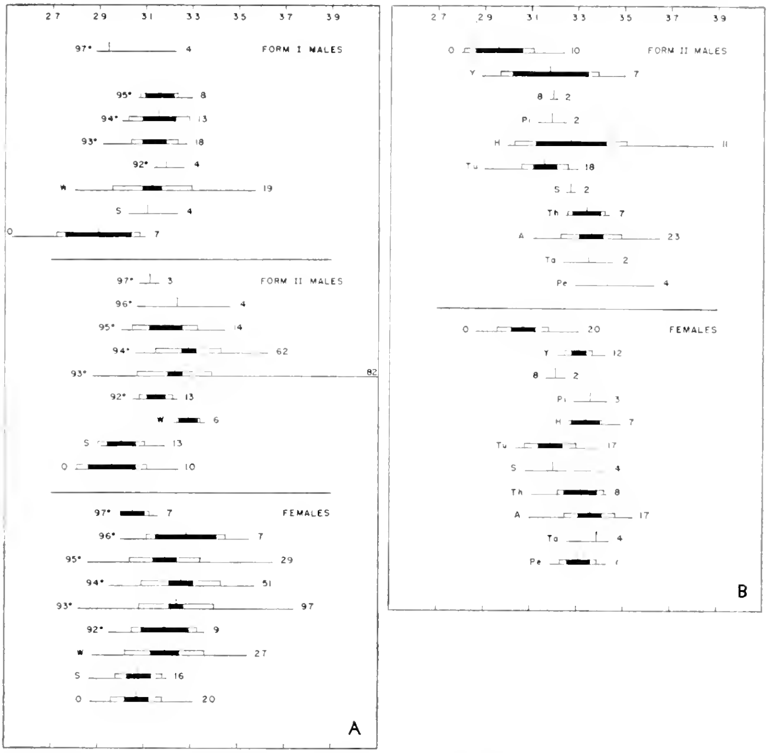


Figure 12. Geographic variation in length of areola. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

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

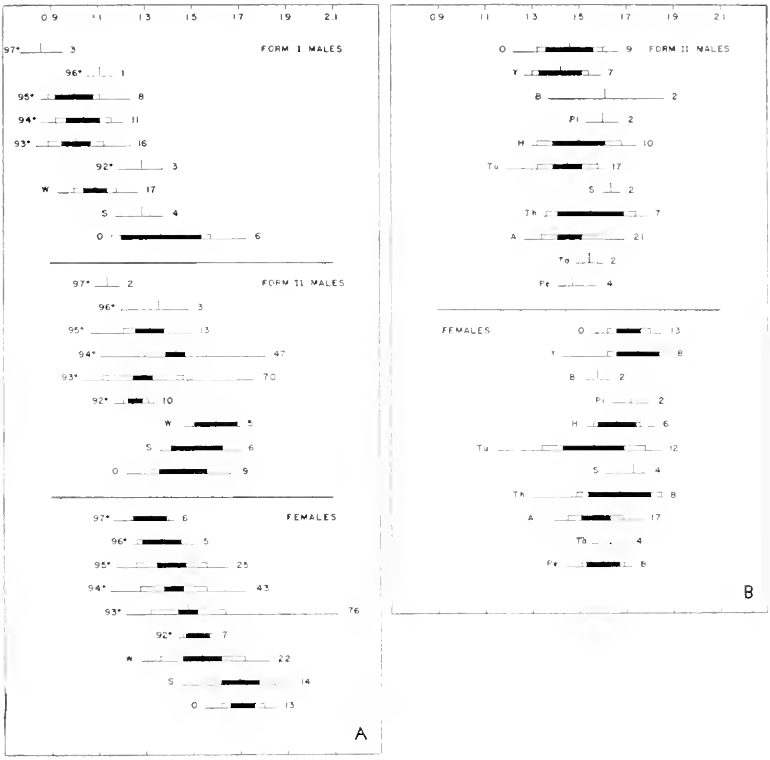


Figure 13. Geographic variation in length of chela. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

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-

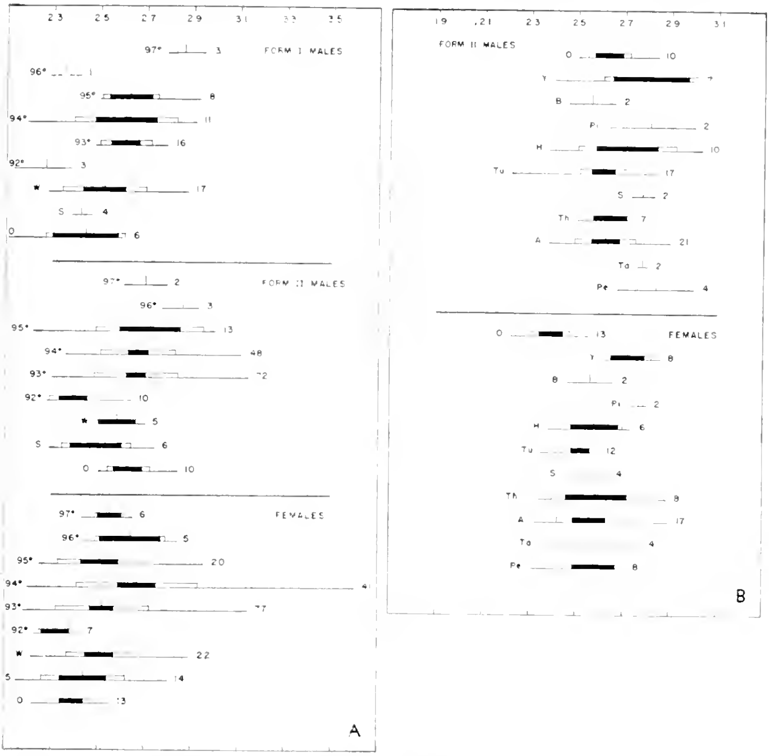


Figure 14. Geographic variation in width of palm. **A,** west-east series; **B,** north-south series east of Mississippi River. Abbreviations same as in fig. 5.

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

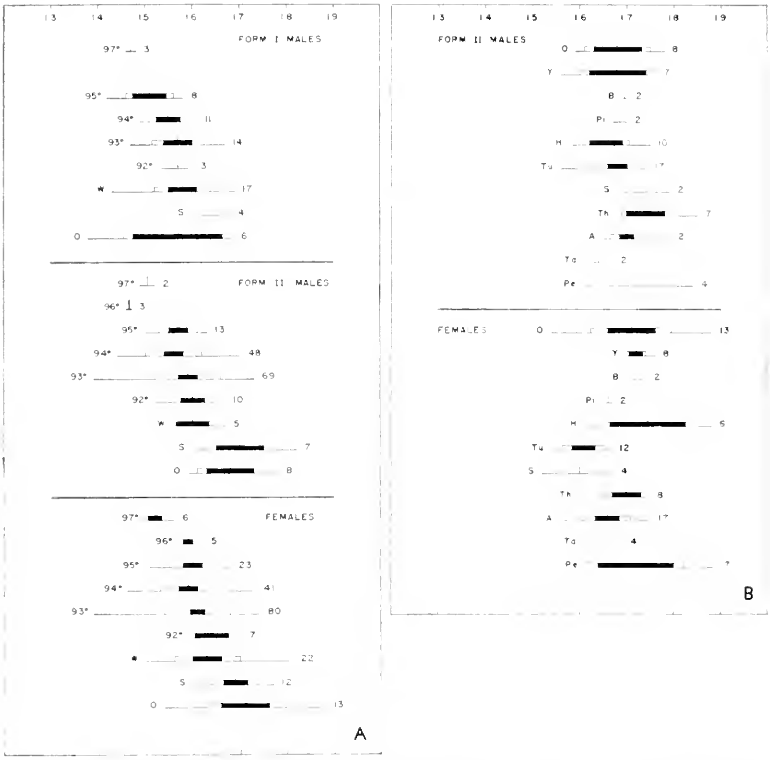


Figure 15. Geographic variation in length of dactyl. **A**, west-east series; **B**, north-south series east of Mississippi River. Abbreviations same as in fig. 5.

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

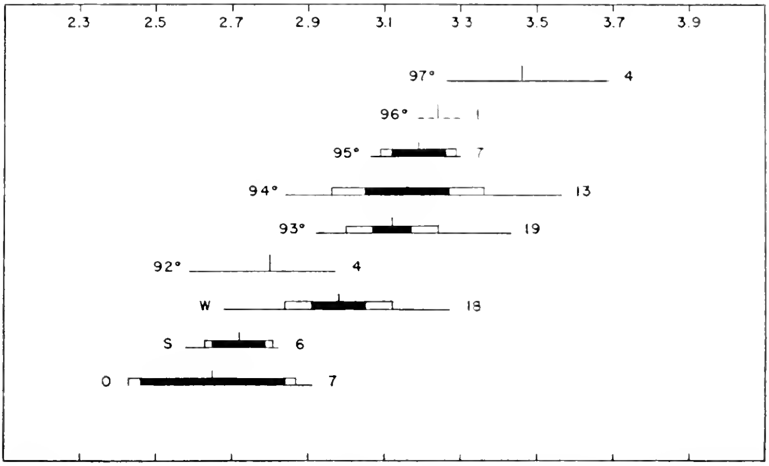


Figure 16. Geographic variation in length of first pleopod of form I males, west-east series. Abbreviations same as in fig. 5.

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-

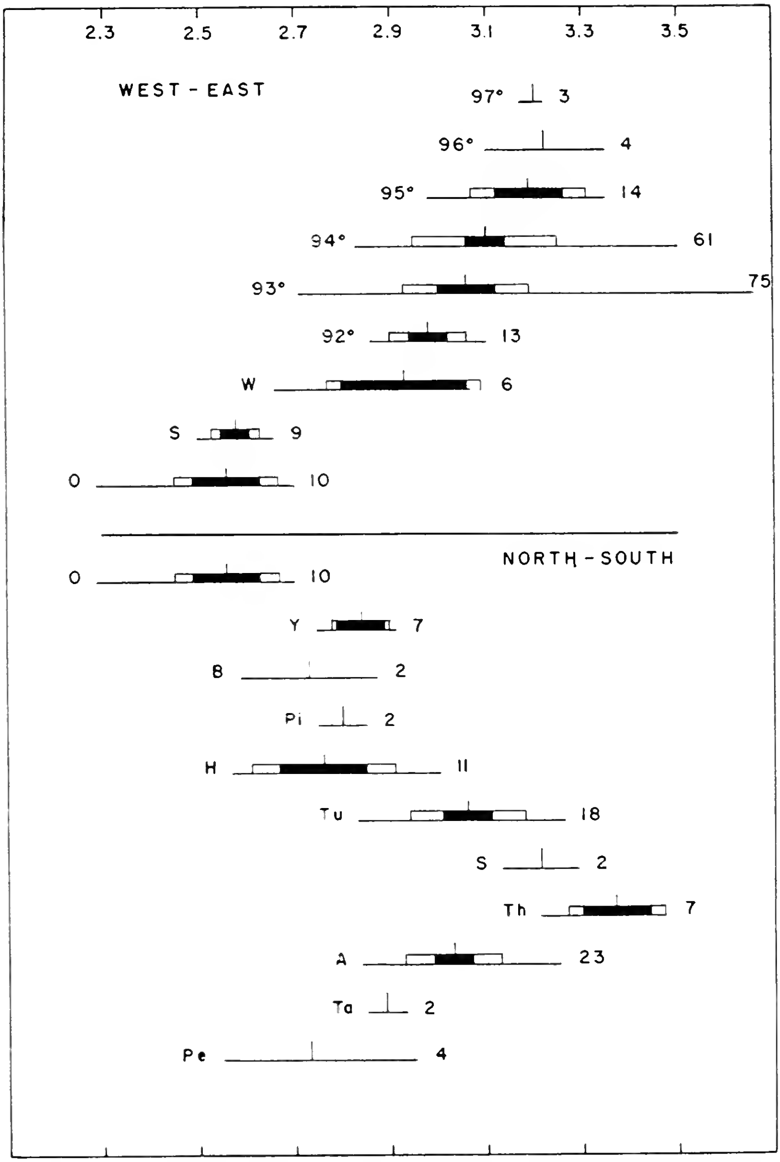


Figure 17. Geographic variation in length of first pleopod of form II males, west-east series and north-south series east of Mississippi River. Abbreviations same as in fig. 5.

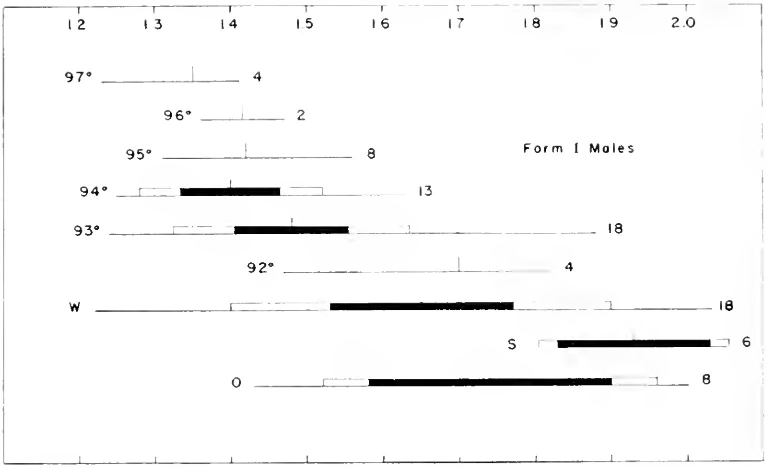


Figure 18. Geographic variation in length of central projection of form I males, west-east series. Abbreviations same as in fig. 5.

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

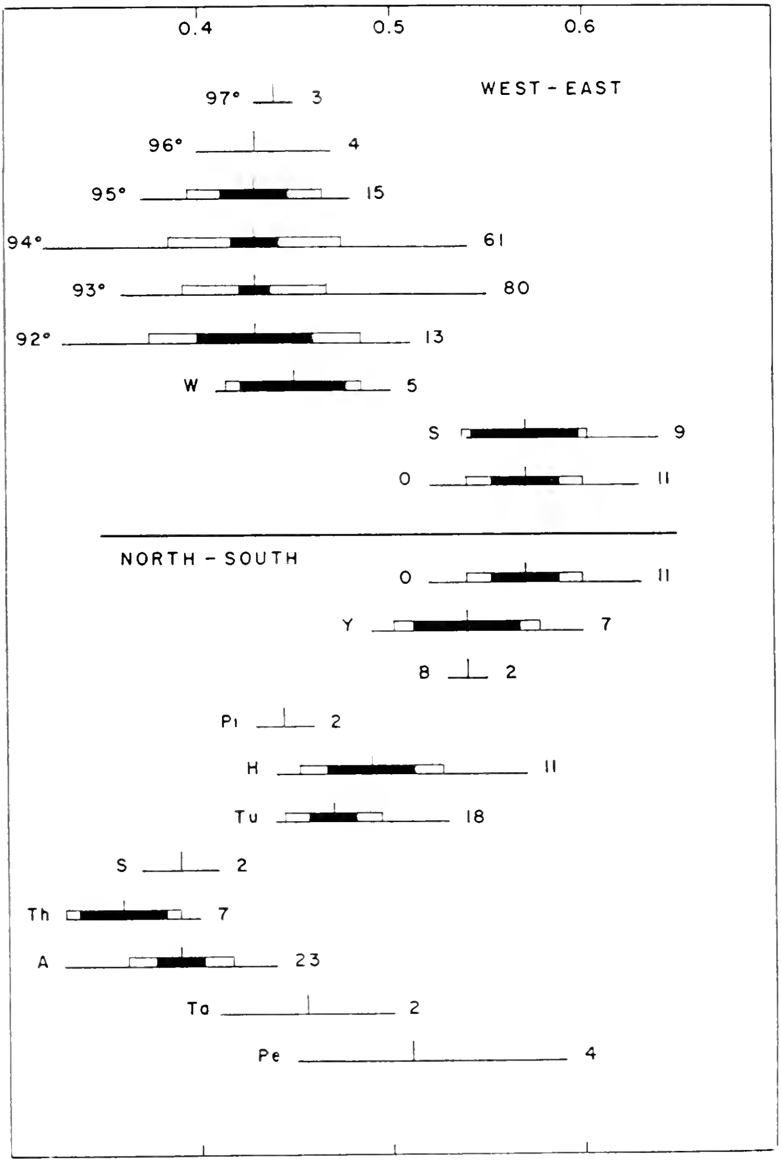


Figure 19. Geographic variation in length of central projection of form II males, west-east series and north-south series east of Mississippi River. Abbreviations same as in fig. 5.

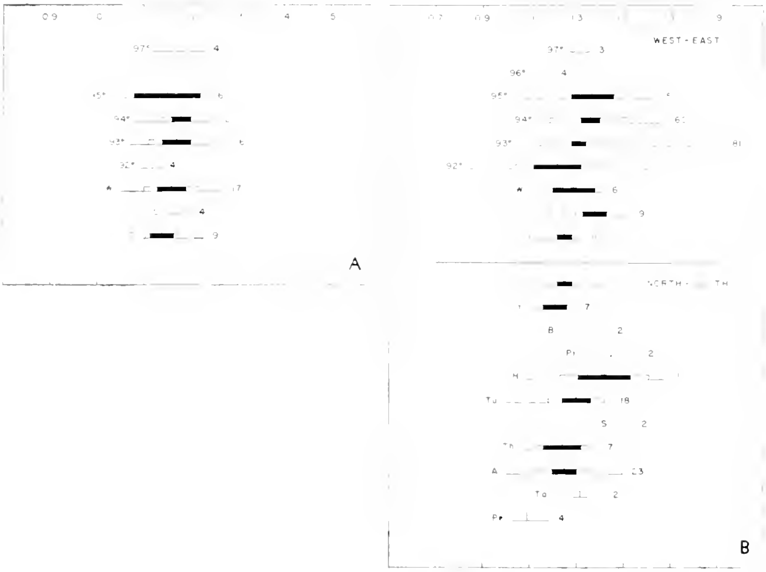


Figure 20. Geographic variation in ratio of central projection length to mesial process length. **A**, west-east series of form I males; **B**, west-east and north-south series of form II males. Abbreviations same as in fig. 5.

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

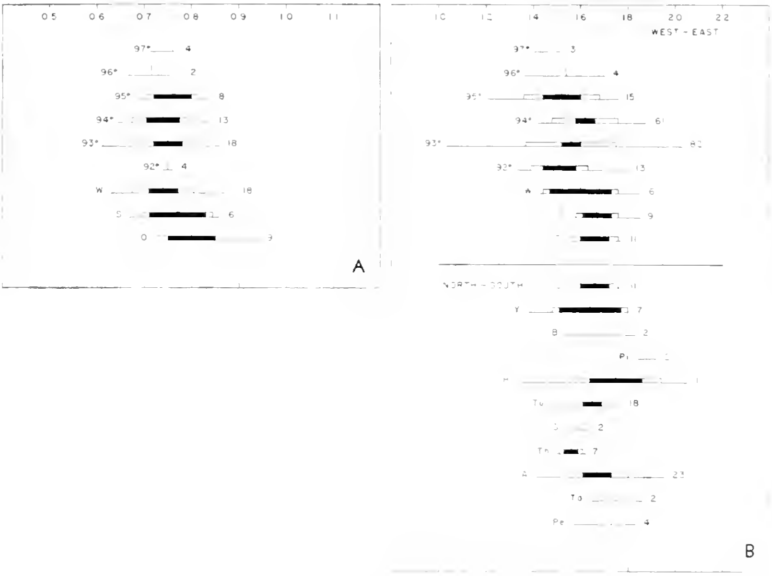


Figure 21. Geographic variation in ratio of length of distal mesial shaft to length of proximal mesial shaft. **A**, west-east series of form I males; **B**, west-east and north-south series of form II males. Abbreviations same as in fig. 5.

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

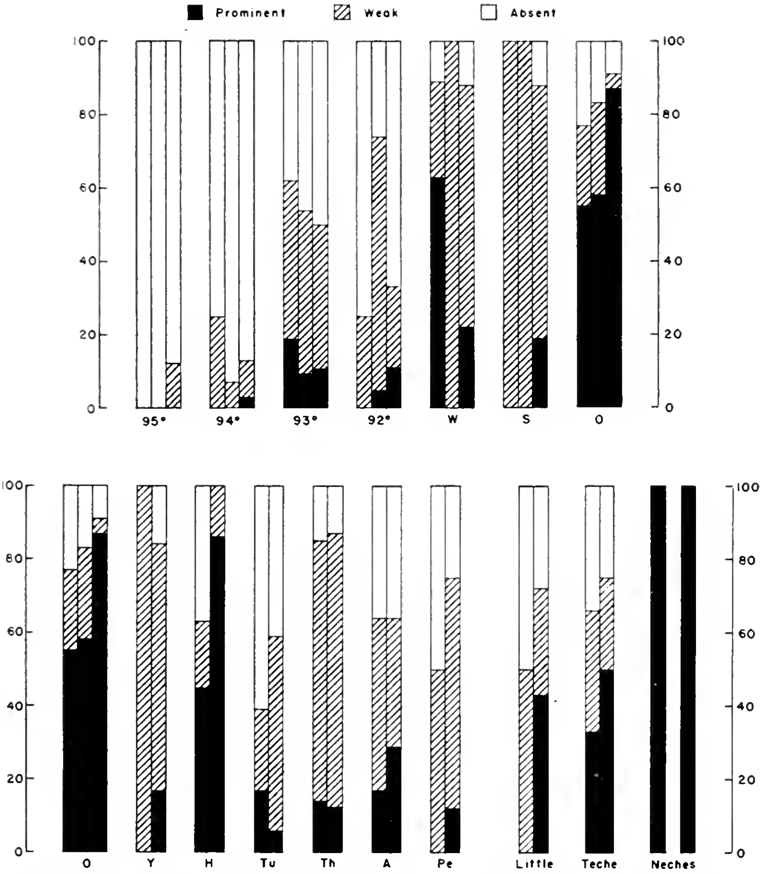


Figure 22. Geographic variation in development of the carina. In each group of three bars, left is form I males, middle is form II males, right is females. In groups of two bars, form I males not present. Abbreviations beneath bars same as in fig. 5.

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

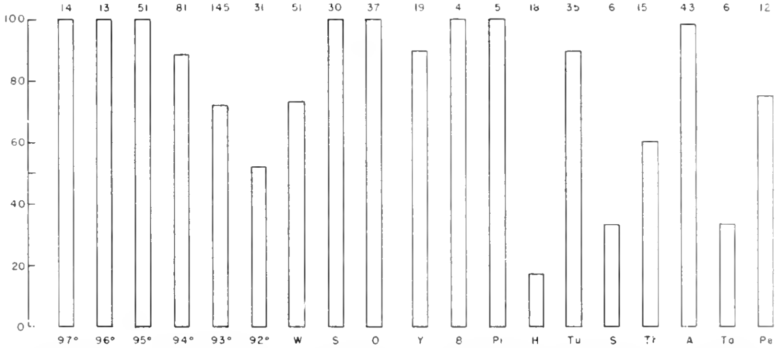


Figure 23. Geographic variation in the obliteration of the areola. Each bar represents the percent of specimens with obliterated areolas. Abbreviations same as in fig. 5, number of specimens at top of each bar.

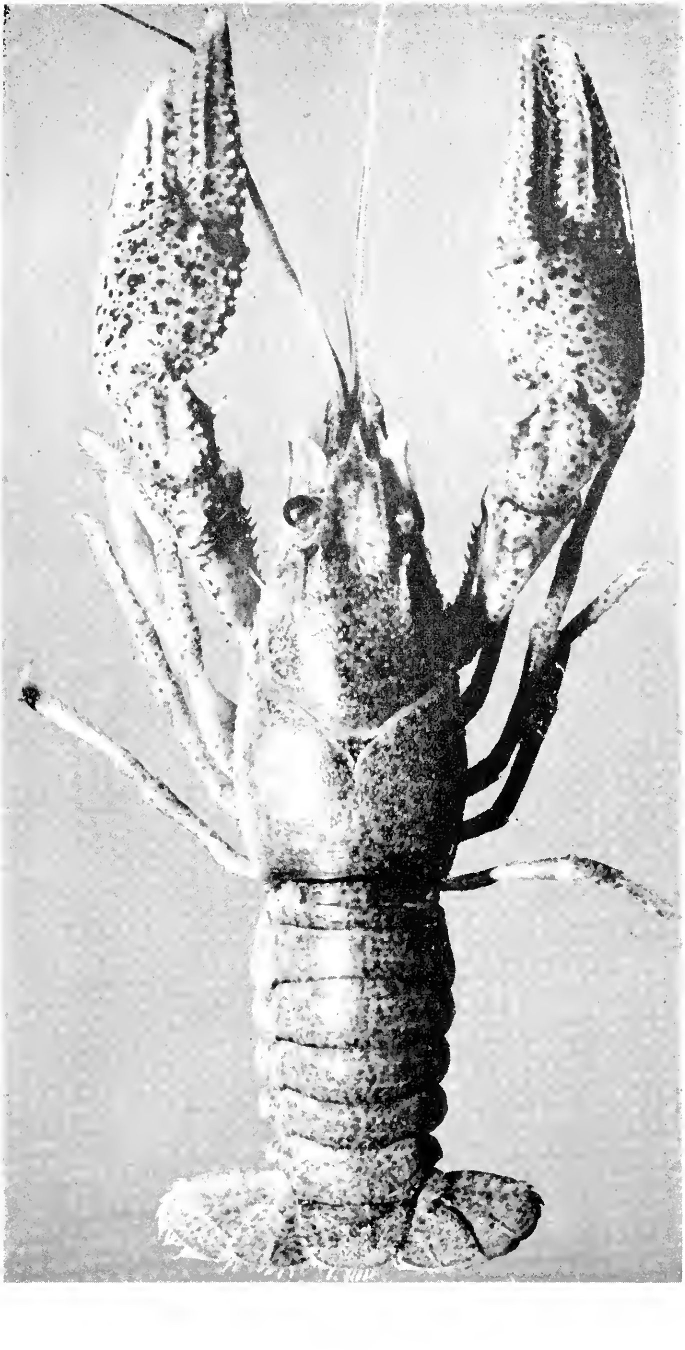
on material from Oklahoma and Hobbs and Marchand (1943) included a rather detailed color description of material from the Reelfoot Lake area.

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.

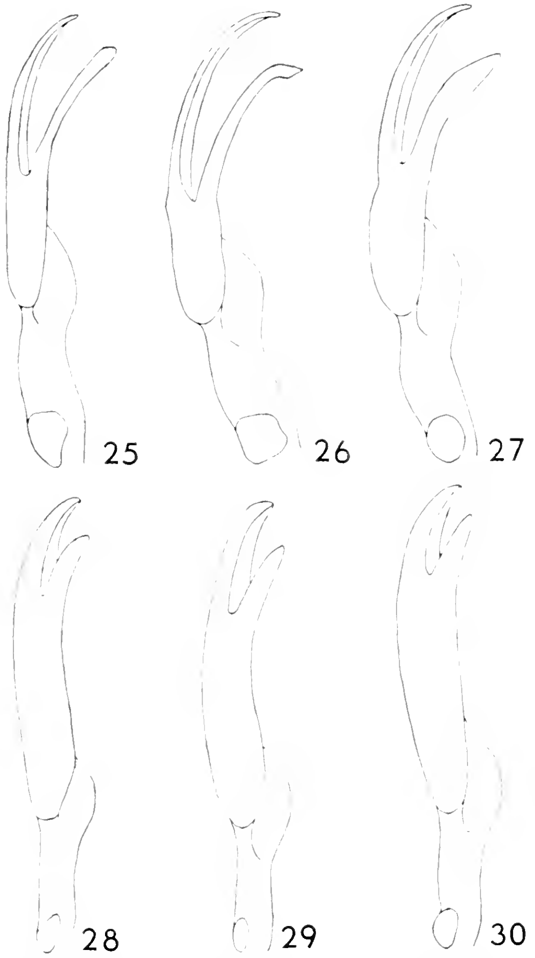
Specimens from Redwood Creek (Amite drainage) in East Feliciana Parish, Louisiana (TU 2801) have a light olive basic color with mottlings of darker olive. Posterior margins of abdominal terga, telson and uropods each with a thin bright red line. Both fingers of chelae darker basally with tip of each 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 (HHHH 7-3141-1a); **26.** *O. p. palmeri* form I, Indian Creek at Samburg, Obion River drainage, Obion County, Tennessee (HHHH 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 (HHHH 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

For museum materials used in this study I am indebted to Dr. Horton H. Hobbs, Jr. for the loan of all the specimens in his personal collection (including topotypic *palmeri*) at the University of Virginia; to the late Dr. J. Speed Rogers for the loan of Creaser's entire series of *creolanus* (including the types) from the University of Michigan Museum of Zoology; to Dr. Fenner A. Chace, Jr. for the loan of all three subspecies from the United States National Museum; to Drs. A. I. Ortenburger and Howard P. Clemens for the loan of *longimanus* materials from the University of Oklahoma Museum of Zoology; and to Dr. A. Byron Leonard for the loan of selected series of Arkansas *palmeri* and *longimanus* from the University of Kansas Museum of Natural History.

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.

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THE SKELETON SHRIMPS (CRUSTACEA: CAPRELLIDAE) OF THE GULF OF MEXICO

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THE SKELETON SHRIMPS (CRUSTACEA: CAPRELLIDAE) OF THE GULF OF MEXICO[1]

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To our knowledge, the only published records of skeleton shrimps, or caprellids—amphipods of the suborder Caprellina (or Caprellidea)—from the Gulf of Mexico are: 1) in a paper by Pearse (1908), in which he described as new *Protellopsis stebbingii* (=[better] *stebbingi*) on the basis of specimens collected in the Gulf off Key West, Florida (24°44′50″ N; 81°55′50″ W);[2] 2) in a second paper by Pearse (1913), in which he listed *Caprella geometrica* Say, 1818, from this same locality, as well as *P. stebbingi* and a female of a *Caprella* sp. collected together at 25-27 fathoms between the delta of the Mississippi (29°0-20′ N; 89°0-40′ W) and Cedar Keys, Florida (29°10′ N; 83°2′ W); 3) in a pamphlet by Reed (1941: 43), who mentioned "*Caprella acutifrons*" as occurring on "elk's hair alga" found on rocks—near jetties, for example; 4) in a paper by Whitten, Rosene, and Hedgpeth (1950: 59, 61) and in an appendix to this paper by Hedgpeth (1950: 77-78), in both of which an unidentified "green" *Caprella* sp. and what was identified as "probably *Caprella acutifrons*" Latreille, 1816, were reported from jetties along the Texas coast; and 5) in a drawing by Hedgpeth (1953, fig. 46) of the faunal association of a sargassum bladder.

As regards the species reported in the first two of the foregoing papers, we believe that *Protellopsis stebbingi* is in reality *Deutella incerta* (Mayer, 1903) comb. nov., the status of which is treated later in this paper (*viz.*, in the discussion under *Deutella californica* Mayer, 1890) and that *C. geometrica* should properly be known as *Caprella carolinensis* Mayer, 1890, grad. nov.;[3] it has not been possible to identify Pearse's "*Caprella* sp.". As regards the third paper we assume that, by "*Caprella acutifrons*", *C. carolinensis* was meant, for we have so identified the "*Caprella acutifrons*" of the fourth paper; we also believe that the "*Caprella* sp." of the latter paper was most probably *Paracaprella pusilla* Mayer, 1890, which we have ourselves identified

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[1] Contribution No. 8 from the Laboratory of Comparative Physiology and Morphology of the Kaiser Foundation.

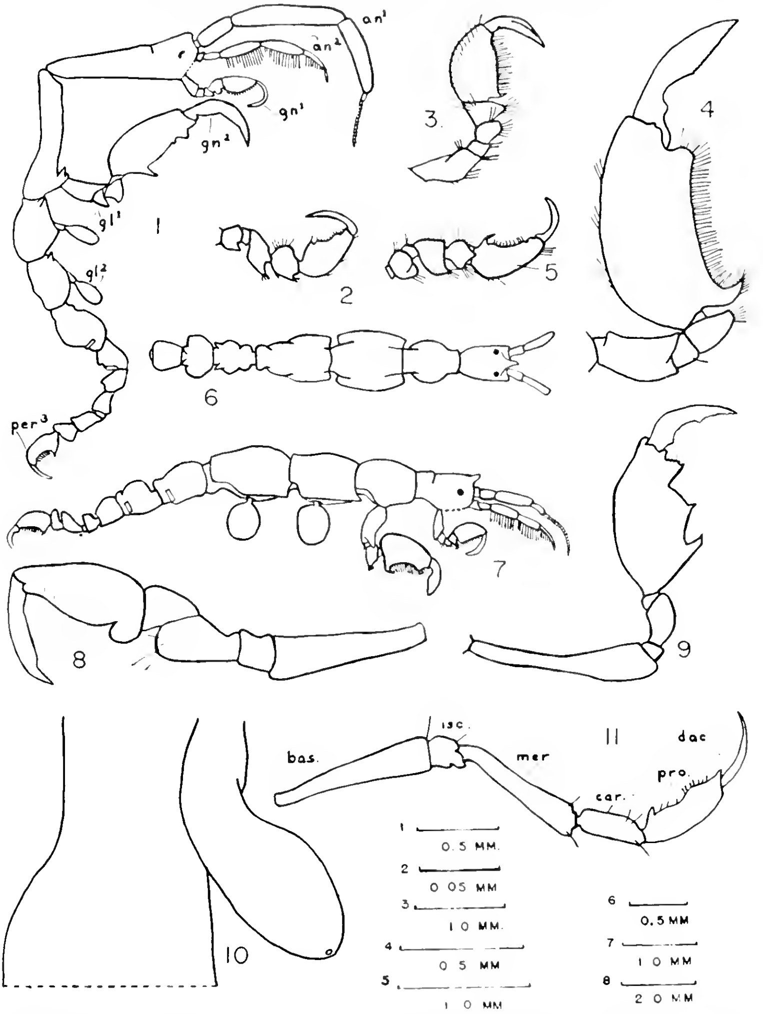
[2] For those latitude and longitude figures, given in this paper, that apply to specimens now in, or on loan from, the U. S. National Museum, Washington, D. C., we are indebted to Dr. Thomas E. Bowman, Associate Curator in charge of lower Crustacea, Division of Marine Invertebrates.

[3] Grad. nov. = *gradus novus;* = new rank.

from specimens submitted to us as occurring together with *C. carolinensis* on the fishing pier at Port Aransas. The small caprellid figured in the fifth paper is not identifiable with certainty, but apparently represents *Hemiaegina minuta* Mayer, 1890. Therefore, there have been records, so far published, of at least four, probably five, caprellids from the Gulf of Mexico.

Some years ago Dr. Joel W. Hedgpeth (now of the Pacific Marine Station, Dillon Beach, California) kindly made available to one of us (E.C.D.) a small collection of skeleton shrimps from Port Aransas (27°50′ N; 97°3′ W) and Port Isabel (26°4′ N; 97°12′ W) on the Texas coast. Already at hand at that time were two vials included in a collection on loan from the U. S. National Museum by Dr. Waldo L. Schmitt and largely comprised of specimens from the Pacific coast of North America; the vials in question derived, however, from the Gulf and bore Albatross station numbers 2387 (29°24′0″ N; 88°4′0″ W) and 2389 (29°28′0″ N; 87°6′0″ W)— between the delta of the Mississippi and Cedar Keys, Florida. In addition, we have more recently received specimens collected: 1) in Alligator Harbor, Florida (29°54-55′ N; 84°22-25′ W), from Dr. Harold J. Humm (now of Duke University, Durham, North Carolina); 2) off Ship Island, Mississippi (30°14′ N; 88°50′ W), from Dr. Ellinor H. Behre (of the Louisiana State University, Baton Rouge; 3) from a fishing pier at Port Aransas, Texas 27°50′ N; 97°3′ W), from Dr. Henry Hildebrand (formerly of the Institute of Marine Science, University of Texas, Port Aransas); and 4) from two localities at Port Aransas, from C. E. Dawson (now of Bears Bluff Laboratories, Wadmalaw Island, South Carolina). We have also had specimens from other areas for comparative purposes—those already mentioned as loaned from the U. S. National Museum and others collected for us by Dr. Thomas E. Bowman (then of the Narragansett Marine Laboratory, University of Rhode Island, Kingston) in the vicinity of his laboratory. These collections have been studied and constitute the basis upon which the present paper has been written. We wish to express our appreciation to the foregoing workers for their generous assistance.

We have identified seven species in the material available to us, but, of these, only three (*C. carolinensis, H. minuta,* and *P. pusilla*) are among the four or five species already indicated as occurring in the Gulf of Mexico. It is possible that *Caprella* sp. of Pearse is also represented in our collection, but for the present there is no way of determining this point. We have not found *Deutella incerta.* [See Addendum.] Of the four species found by us, but not hitherto reported (either as such or under a name that we recognize as a synonym) from the Gulf, two have been described previously from other areas; one appears new to science, but is represented by inadequate material (a species of *Caprella*); and one is here described and named as new. There accordingly appear to be at least eight species of



Figures 1-11. Adult males, or appendages thereof. **1.** *Caprella equilibra* (1st and 2nd pereopods missing): an^1—antennula; an^2—antenna; gl^1, gl^2—1st and 2nd gills; gn^1, gn^2—1st and 2nd gnathopods; per^3—3rd pereopod (7th pereod); **2.** *C. equilibra*, 1st pereopod (*i.e.*, of 5th pereod); **3.** *C. carolinensis*, 1st gnathopod; **4.** *C. carolinensis*, 2nd gnathopod; **5.** *C. carolinensis*, 1st pereopod (*i.e.*, of 5th pereod); **6.** *C. carolinensis*, dorsal view; **7.** *C. carolinensis*, lateral view (1st and 2nd pereopods missing); **8.** *Hemiaegina minuta*, 1st gnathopod; **9.** *H. minuta*, 2nd gnathopod; **10.** *H. minuta*, vestigial appendage of 3rd pereod attached at top of 1st gill (cut at dotted line); **11.** *H. minuta*, 1st complete pereopod (*i.e.*, of 5th pereod): *bas.*—basis; *car.*—carpus; *dac.*—dactylus; *isc.*—ischium; *mer.*—merus; *pro.*—propodus. (Figs. 1, 6, and 7, scale 8; fig. 2, scale 7; figs. 3 and 4, scale 6; fig. 5, scale 3; fig. 8, scale 1; fig. 9, scale 5; fig. 10, scale 2; fig. 11, scale 4.)

Caprellidae now known in the Gulf of Mexico, and there can be little doubt that systematic collecting will reveal others.

CAPRELLA CAROLINENSIS MAYER, 1890, loc. nov.

(Figures 3-7)

Synonymy.—*Caprella acutifrons* var. *carolinensis* Mayer, 1890; *Caprella geometrica*, of Pearse, 1913 (*non* Say, 1818); *Caprella acutifrons*, of Whitten, Rosene, and Hedgpeth, 1950 (*non* Latreille 1816).

Diagnosis.—*Caprella:* cephalon bearing a median, anteriorly directed spine; rest of body (figs. 6, 7) smooth except for a pair of spines located at posterior end of pereods[4] 5 and 6; third and fourth pereods of equal length, with pleura rather well developed and somewhat thickened; fifth, sixth, and seventh pereods successively smaller and approximately as long as cephalon and second pereod combined; gills oval to round in outline.

Antennule (first antenna) about one-fourth length of body; flagellum slightly shorter than peduncle and composed of 12 segments. Antenna proper (second antenna) nearly as long as antennule and bearing natatory hairs on its inner surface.

First gnathopod small (fig. 3) palm of propodus straight and

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[4] The word *pereod* (then spelled "peraeod") was introduced by us (Dougherty and Steinberg, 1953) without our realizing that we were creating—so far as we can now determine—a new term. The meaning is implicit in our 1953 paper and later (Dougherty and Steinberg, 1954, p. 167) explicitly given as a "segment [of the *peraeon*]." It can be construed as derived from the Greek words περαιοῦν (*to bring across*—thence the combining form περαιο-) and εἶδος (*figure, thing*—contracted to the suffix—ωδης, with its declensional ending dropped).

The familiar words *pereion* (or *peraeon*) and *pereiopod* (or *peraeopod*) are here rendered as *pereon* and *perepod*, along with *pereod*, in accordance with the general tendency in American English to reduce the classic diphthongs "æ" and "œ" of Latin (= αι and οι of Greek) to "e". It may be remarked that the spelling *pereion*, etc., are defective transcriptions, originating with Spence Bate (1856—who misused words of Greek origin in a number of curious ways); the Greek combining form περαιο- should be Anglicized as *peraeo-* (British) or *pereo-* (American), not as *perei-* or *pereio-*. (Spence Bate actually used the plural spelling *pereipoda* [sic] and only later—1857—corrected it to *pereiopoda* [sic], the singular form *pereiopodos* [!] being then employed by Spence Bate and Westwood—1861. Amusingly enough, in several places Spence Bate—*e.g.*, 1859—used the singular form *pereiopod* along with the plural form *pereiopoda*. His usage was a hopeless mishmash of imperfectly Latinized Greek and vernacular English!) Smith (1880) appears to have been the first to correct Spence Bate's erroneous transcription, although without specifying that he was so doing. The spellings *pereon* and *pereopoda* (as respective Latin equivalents of the Russian переон and of переопод—sing., переоподы—pl.) have already been used by Gur'ianova (1951, p. 24).

By analogy with *pereod*, one can form *pleod* for individual segments of the *pleon*. These two forms (*pereod* and *pleod*) commend themselves to us as short and euphonious.

bearing a pair of spines at base (only one can be shown in view depicted in fig. 3) and hairs along entire edge; dactylus only slightly curved and minutely denticulate on inner surface with lateral surface also bearing a longitudinal line of denticulations distally. Second gnathopod[5] (fig. 4) a little longer than cephalon and second pereod combined and attached to middle of segment in both sexes; first segment (basis[6]) slightly longer than second (ischium[6]) and third (merus) combined and bearing a single anterior ridge on outer edge—merus bearing a small tuft of hairs on posterodistal aspect; fourth segment (carpus) a narrow wedge-shaped connecting piece between third and fifth segments; fifth segment (propodus) comprising about two-thirds length of entire appendage[7]—palm slightly concave in outline, bearing a "poison tooth" at base and a rectangular projection distally; sixth segment (dactylus) curved, crocked, and denticulate on distal half of inner edge.

Pereopods on pereods 5 (fig. 5), 6, and 7 set with spine-like hairs; palm of propodus of each bearing a pair of grasping spines proximally and two rows of spine-like hairs, each row consisting of 10-12 hairs (only one spine and one row of hairs can be shown in view depicted in fig. 5).

A large male measured 10 mm in length; a large female, 9.5 mm.

Occurrence.—Type locality: Charleston, South Carolina—on *Tubularia* (Mayer, 1890, as *C. acutifrons* var. *carolinensis*). *Other previous records:* 10.5 fathoms at Fish Hawk station 7292 off Northwest Channel (Key West), Gulf of Mexico (Pearse, 1913—as *C. geometrica*); north jetty at Galveston, Texas, and northeast jetty at Freeport, Texas—on algae (*e.g., Cladophora*) in association with *Carinogammarus* (Whitten, Rosene, and Hedgpeth, 1950—as *C. acutifrons*). *New records:* north jetty at Port Isabel, Texas—10 males and 2 females, collected Mar. 20, 1947 (Dr. Joel W. Hedgpeth); "probably Port Aransas," Texas—1 female (Dr. Hedgpeth); Gulf Beach, Port Aransas—4 males and 6 females (together with 9 males and 7 females of *Paracaprella pusilla*) from fouling organisms on fishing pier, collected Sept. 19, 1954 (Dr. Henry Hildebrand); Alligator Harbor,

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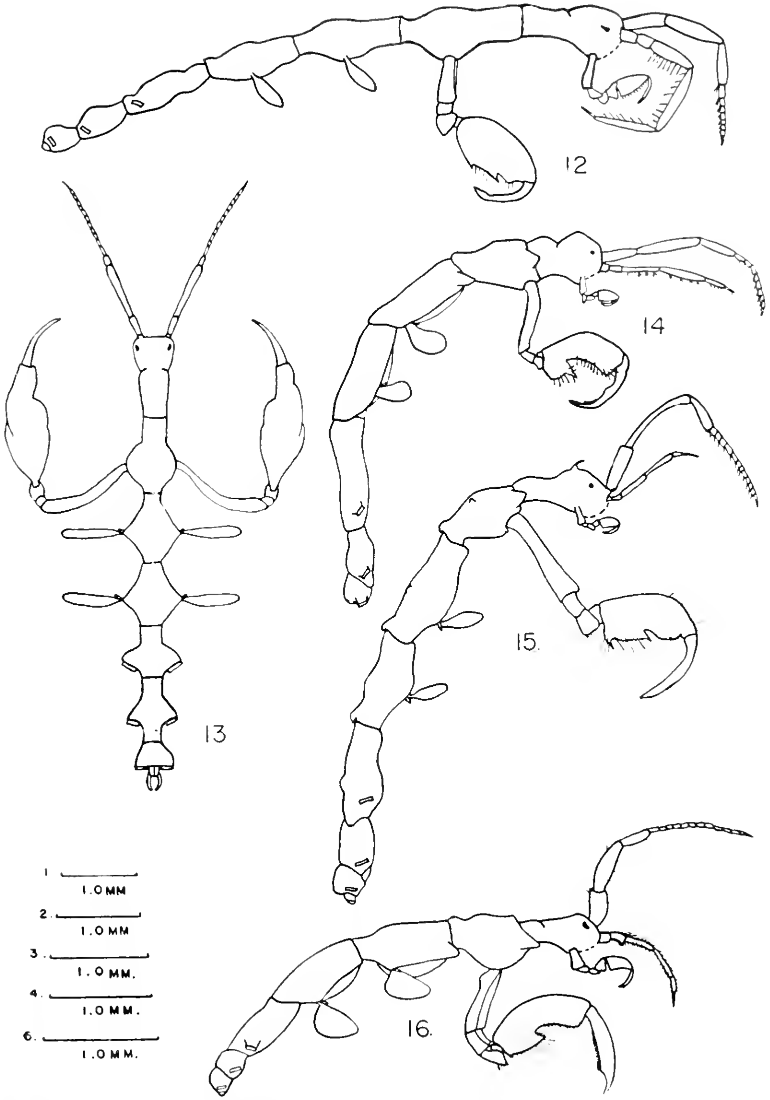
[5] Here and in all subsequent descriptions in which the length of gnathopods (either first or second) is reckoned and compared with that of other anatomical parts, the length of the dactylus has been omitted by reason of the confusion that might arise from the fact that the dactylus may be extended or closed.

[6] In our earliest paper (Dougherty and Steinberg, 1953) we referred to these segments as the "coxa" and "basis", respectively, and subsequently in a key (Dougherty and Steinberg, 1954) used the term "coxa" in this manner. In accordance with the usage of Snodgrass (1952, p. 185) these should, however, be known as the "basipodite" (or basis) and "ischiopodite" (or ischium) respectively, the true "coxopodite" (or coxa) of thoracic limbs having become fused with their respective body segments (pereods) in most of these peracaridan Crustacea.

[7] See footnote 5.



Figures 12-16. Adult males (with pereopods of pereods 5-7 missing). **12.** *Caprella* sp.; **13.** *Hemiaegina minuta* (antennae not shown; palms of propodi of 2nd gnathopods directed downward); **14.** *Deutella abracadabra;* **15.** *D. californica;* **16.** *Paracaprella pusilla.* (Fig. 12, scale 4; fig. 13, scale 5; fig. 14, scale 1; fig. 15, scale 3; fig. 16, scale 2.)

Franklin County, Florida—1 female on *Bugula neritina*, dredged Mar. 13, 1954 (Dr. Harold J. Humm); at South Pier, Mustang Island Beach, Port Aransas, from fouling on dorsum of dead *Caretta*—approximately 2500 specimens, collected Mar. 21, 1955 (Mr. C. E. Dawson).

Discussion.—Our specimens differ from Mayer's description of *Caprella acutifrons* var. *carolinensis* only in the number of spine-like hairs on the palm of the propodus of the appendages on the fifth pereod. Mayer's specimens had seven; ours have 10-12.

Two other members of the *Caprella "acutifrons"* group have been described from the East coast of the United States: *Caprella geometrica* Say, 1818, from "salt water bays" and *Caprella acutifrons* var. *virginia* Mayer, 1890, from Old Point Comfort, Virginia. Mayer (1882) did not consider *C. geometrica* a separate species, but synonymized it with *Caprella acutifrons* Latreille, 1816.[8] Later (1890, 1903), however, he neither recognized it as a distinct variety, nor placed it in one of this named varieties. (He began the naming of varieties in *C. acutifrons* in his second monograph—1890.) We are of the opinion that it merits full specific rank. Therefore, the problem arises as to which of Mayer's "varieties", if any, is synonymous with *C. geometrica.* Having examined material from Woods Hole, Massachusetts, loaned by Dr. Waldo L. Schmitt from the U. S. National Museum, and from the vicinity of the Narragansett Marine Laboratory, Rhode Island, collected for us by Dr. Thomas E. Bowman, we have come to the conclusion that animals of the *C. "acutifrons"* type from these areas belong to *C. geometrica* as described by Say and differ from *C. carolinensis*, especially in the form of the propodus of the second gnathopod. The palm thereof in *C. geometrica* lacks a distal rectangular projection, which is present in *C. carolinensis*.

Unfortunately we have no specimens of *C. acutifrons* var. *virginia* and so are unable at this time to make any statements regarding its relationships and taxonomic position. It may be that the three forms under consideration represent variation within a single species of wide distribution along the East coast and into the Gulf. However, until such a condition can be shown to exist, we prefer to recognize at least *C. geometrica* and *C. carolinensis* as separate species.

CAPRELLA EQUILIBRA Say, 1818

(Figures 1, 2)

Synonymy.—See Stebbing (1888: 1254-1255); *Caprella mendax* Mayer, 1903.

Diagnosis.—*Caprella:* cephalon smooth; pereods 2-5 smooth dorsally (fig. 1), pereod 2 bearing an anteriorly directed spine at base of each second gnathopod and a median ventral spine between these appendages; pereods 3 and 4 each bearing a spine at the anterior,

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[8] The specific name "*acutifrons*" is, we feel, invalid; but an analysis of this point is beyond the scope of the present paper.

ventrolateral edge of the segment; pereods 6 and 7 each bearing a pair of low dorsal tubercles. Cephalon and second pereod subequal; pereods 3-5 all approximately of equal length and, combined, slightly longer than cephalon; pereods 6 and 7, combined, as long as fifth pereod. Gills elliptical and somewhat elongate.

Antennule one-half length of body; flagellum composed of 9-14 segments and comprising one-fourth or less of entire antennule. Antenna approximately one-half length of antennule and bearing natatory hairs.

First gnathopod small. Second gnathopod a little less than one-third length of entire body and attached to posterior part of second pereod in male and at anterior end in female; basis comprising about one-fourth entire appendage and bearing an anterior ridge ending in a sharp projection on both outer and inner edges; ischium and merus each bearing a smaller projection posteriorly; propodus comprising about one-half entire appendage, with palm nearly straight in outline and bearing a "poison tooth" just distally to base and, more distally still, a triangular projection, proximally to which is a small spine; dactylus curved and crooked.

Pereopods on pereods 5 (fig. 2), 6, and 7 progressively larger posteriorly; palm of propodus of each bearing a pair of small spines (only one shown in fig. 2) one-third of way distally from base; distal two-thirds concave and bearing numerous small hairs.

Largest male measured 19 mm in length; largest female, 11 mm.

Occurrence.—Type locality: around Charleston, South Carolina (Say, 1818). *Other records:* cosmopolitan. *New records:* Port Aransas, Texas— 14 males and 6 females from buoy, collected Apr. 14, 1948, and 1 male, collected Mar. 15, 1948 (Dr. Hedgpeth); on dock at Institute of Marine Science, Port Aransas, Texas—about 700 individuals from fouling on oyster shell bags, collected Apr. 5, 1953 (Mr. C. E. Dawson).

Discussion.—This cosmopolitan species was originally described by Say (1818) from specimens collected as indicated. It was recorded from this region again by Mayer (1890), who also found it in Bermuda (1903). It has, in addition, been listed by Kunkel (1910) as occurring in Bermuda. It has not hitherto been recorded from the Gulf of Mexico.

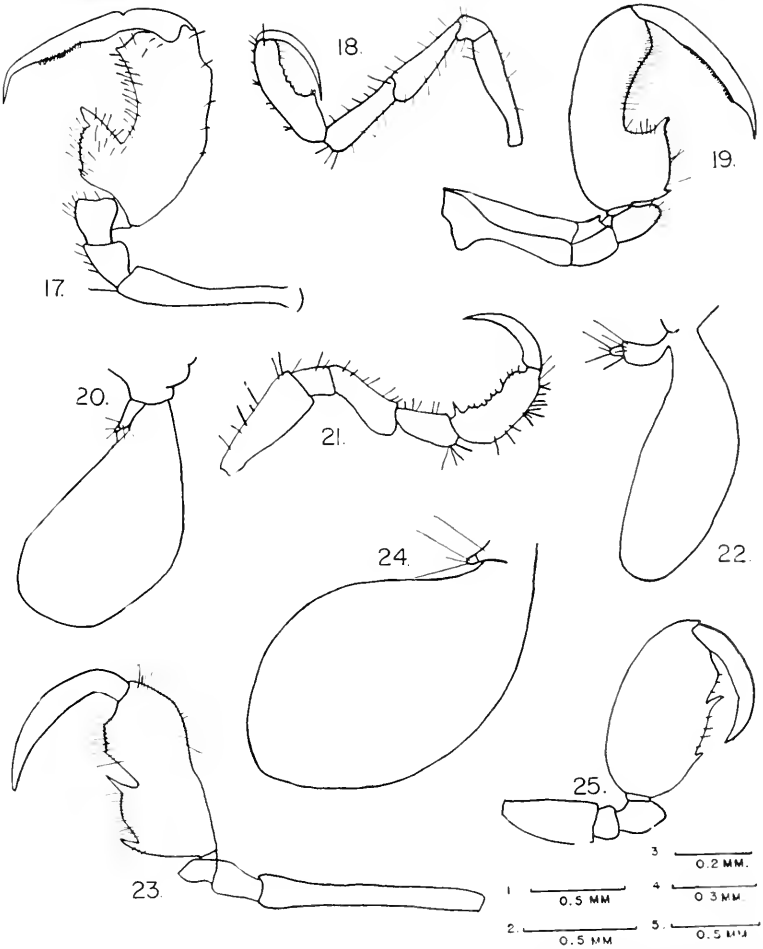
The males collected from the buoy at Port Aransas in April, 1948, are smaller than the single male collected from Port Aransas (location not noted) in March of the same year. The largest in the April collection measures only 10 mm. However, except for size, these animals are all morphologically similar.

CAPRELLA sp.

(Figures 12, 25, 26)

Synonymy.—?Caprella sp., of Pearse, 1913.

Diagnosis.—Caprella: entire body smooth, slender (fig. 12). Cephalon and pereods 4 and 5 of equal length and slightly shorter than



Figures 17-25. Appendages of adult males. **17.** *Deutella abracadabra*, 2nd gnathopod; **18.** *D. abracadabra*, 1st complete pereopod (*i.e.*, of 5th pereod); **19.** *Paracaprella pusilla*, 2nd gnathopod; **20.** *Deutella abracadabra*, 1st gill and associated vestigial appendage (*i.e.*, of 3rd pereod); **21.** *D. californica*, 1st complete pereopod (*i.e.*, of 5th pereod); **22.** *D. californica*, as in fig. 20; **23.** *D. californica*, 2nd gnathopod; **24.** *Paracaprella pusilla*, as in fig. 20; **25.** *Caprella sp.*, 2nd gnathopod. (Figs. 17 and 25, scale 1; fig. 18, scale 4; figs. 19 and 23, scale 5; figs. 20, 22, 24, scale 3; fig. 21, scale 2.)

pereod 3; pereods 2 and 3 of nearly equal length; pereods 6 and 7, combined, equal to pereod 5 in length. Gills lanceolate in outline and somewhat elongate.

Antennule about one-third length of body; flagellum composed of seven segments and comprising one-third length of entire antennule. Antenna slightly longer than antennule and bearing natatory hairs on inner surface, except for first two segments of peduncle; flagellum composed of two segments. Mandible without palp.

First gnathopod about as long as cephalon. Second gnathopod (fig. 25) roughtly one-fourth length of body and attached just posteriorly to middle of second pereod in male; basis comprising one-third length of entire appendage and bearing an outer anterior ridge; propodus a little over one-half length of appendage with palm slightly convex in outline and bearing a proximal tooth one-third, and a "poison tooth" two-thirds, of way distally from base—latter separated from distal third of palm by shallow cleft; dactylus slightly curved, with tip tapered.

As characteristic of *Caprella*, no appendages (other than gills) on pereods 3 and 4. Pereopods on pereods 5-7 missing in our specimens.

Abdomen in male bearing "1½ pairs" of appendages (vestigial uropods—*i.e.*, a rudimentary, one-segmented, ventrally located pair followed posteriorly by a pair of lappets [= "½ pair" of Mayer], representing an almost vanished second pair; see fig. 26).

Both males measured 6 mm in length.

Occurrence.—Between delta of Mississippi and Cedar Keys, Florida; Albatross station 2387—1 juvenile male at 32 fathoms, and Albatross station 2389—1 juvenile female at 27 fathoms, both collected Mar. 4, 1885 (U. S. National Museum collection); "probably Port Aransas", Texas—1 juvenile male (Dr. Hedgpeth).

Discussion.—Only the three specimens indicated in the foregoing paragraph have been available to us—two juvenile males, which fit the foregoing description, and one juvenile female, which we tentatively refer to the same species. All undoubtedly belong to the genus *Caprella* and somewhat resemble *C. bermudia* Kunkel, 1910. However, the antennae are slightly longer than the antennules in our specimens, and somewhat shorter in *C. bermudia.* Also the males of the former lack the ventral process between the 2nd gnathopods and the serrations on the anterior ridges of the bases of these appendages as described for *C. bermudia.* Until more specimens, including definite adults, are available, we feel it best to designate these animals as *Caprella* sp.

Pearse (1913) reported a female of a *Caprella* sp.? collected from "Albatross stations 2369-2374" between the delta of the Mississippi and Cedar Keys, Florida, at 25-27 fathoms. This specimen could belong to the same species as ours inasmuch as the collecting stations are very close and as the specimens were recovered by dredging in both cases; but, since Pearse published no description and since we have not (at least as yet) studied his specimen, we cannot be certain for the present.

DEUTELLA **ABRACADABRA**[9] sp. nov.

(Figures 14, 17, 18, 20, 27)

Diagnosis.—Deutella: entire body smooth (fig. 14). Second pereod bearing an anteriorly directed, triangular projection laterally on anterior edge; third pereod bearing a similar projection on anterior, ventrolateral edge. Cephalon and second pereod of nearly equal length; third, fourth and fifth pereods all approximately of equal length; sixth and seventh pereods, combined, two-third of fifth pereod. Gills oval (fig. 20), those on pereod 3 larger than those on pereod 4.

Antennule little more than one-third length of body; flagellum just less than one-half length of peduncle and composed of 8-10 segments in male and 5-8 segments in female. Antenna two-thirds length of antennule and bearing sensory hairs. Mandibular palp three-segmented.

First gnathopod as long as peduncle (first three segments) of antenna. Second gnathopod (fig. 17) about one-third length of body and attached at anterior end of pereod in both sexes; basis about equal in length to propodus; carpus set anteriorly to merus so that propodus appears to be resting on both; propodus in male about one-half length of entire appendage, with palm bearing long hairs—"poison tooth" located on shelf about one-third of way distally along palm—a single grasping spine located at base of palm, and area between it and "poison tooth" denticulate—middle of palm deeply concave and distal part bearing a triangular projection, the anterior edge of which is minutely denticulate (in female, palm of propodus slightly convex and lined with small hairs bearing a single grasping spine at base and a very small spine near distal end); dactylus curved, irregular on inner surface, and bearing a row of short, stiff hairs distally.

Appendages on pereods 3 and 4 each two-segmented and attached at bases of gills in males (fig. 20), each segment bearing three hairs; gills on pereod 4 in females attached to posterior brood pouch below attachment of appendages. Pereopods on pereods 5 (fig 18), 6, and 7 progressively smaller in size; palmar surface of each concave with a pair of grasping spines proximally.

Abdomen in male (fig. 27) bearing "1½ pairs" of appendages; female abdomen bearing "½ pair" (*i.e.*, a pair of lappets only). Posterior brood pouch of female with no hairs.

A large male measured 6 mm in length; a female, 5 mm.

Type specimen.—Adult male: U.S. National Museum catalog number 97624.

Occurrence.—Type locality: Alligator Harbor, Franklin County, Florida—10 males and 1 female on *Bugula neritina*, dredged Mar. 13, 1954 (Dr. Harold J. Humm). *Other record:* off Ship Island, Mississippi—6 males and 7 females from *?Crisia* in surf, collected May 10, 1954 (Dr. Ellinor H. Behre).

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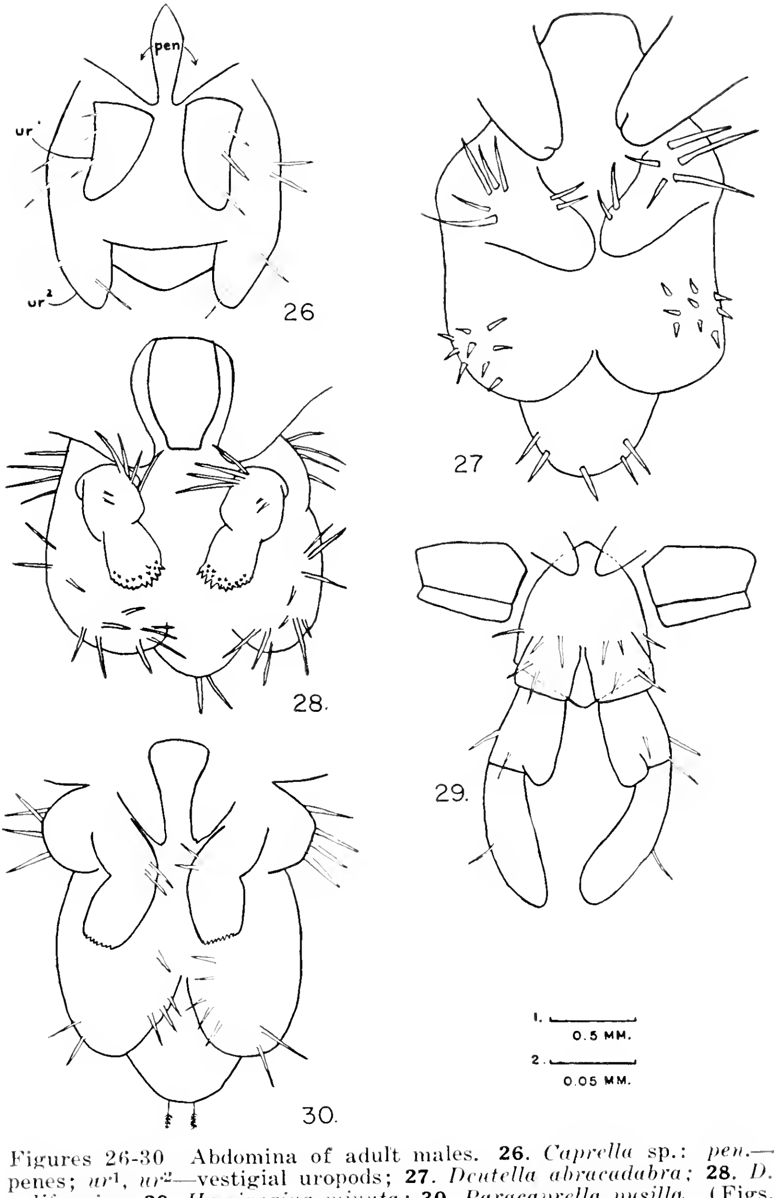
[9] Specific name selected because it is bizarre, in keeping with the bizarre nature of the skeleton shrimps.



Figures 26-30 Abdomina of adult males. **26**. *Caprella* sp.: *pen*.—penes; *ur*^{1}, *ur*^{2}—vestigial uropods; **27**. *Deutella abracadabra*; **28**. *D. californica*; **29**. *Hemiaegina minuta*; **30**. *Paracaprella pusilla*. (Figs. 26, 27, 28, and 30, scale 1; fig. 29, scale 2.)

Discussion.—See under *Deutella californica*, the description of which follows immediately.

DEUTELLA CALIFORNICA MAYER, 1890

(Figures 15, 21-23, 28)

Diagnosis.—*Deutella:* cephalon bearing a small, pointed erect spine in male and a low blunt tubercle in female; rest of body (fig 15) smooth except for a pair of low, bluntly pointed tubercles located on either side of dorsal median line above second gnathopods; a rudimentary median pair of tubercles may or may not be present above gills on pereods 3 and 4; posterodorsal regions of pereods 2, 3, and 4 each projecting upwards in median line; female bearing a single low tubercle in median line dorsally in middle of third pereod; second pereod bearing an anteriorly directed triangular projection on anterior edge of segment; third and fourth pereods approximately equal in length, with pleura weakly developed; fifth, sixth, and seventh pereods progressively shorter—sixth and seventh combined, about two-thirds length of fifth. Gills elliptical and somewhat elongate (fig. 22).

Antennule one-half as long as body; middle segment of peduncle curved; flagellum almost two-thirds length of peduncle and composed of 8-12 (usually 11) segments in male and 7-10 (usually 9) segments in female. Antenna a little less than one-half as long as antennule and bearing a few sensory hairs; second segment of flagellum teardrop-shaped. Mandibular palp three-segmented.

First gnathopod a little longer than 1st segment of antennule. Second gnathopod (fig. 23) two-fifths length of body and attached anteriorly to middle of second pereod in males and at anterior end in females; ischium and merus short, and carpus very short and wedge-shaped; propodus about twice as long as broad and bearing a "poison tooth" halfway along palmar surface, separated from distal part of palm by a deep cleft—another small tooth at base of palm and separated from rest of palm by a very small cleft in which dactylus rests when closed—palmar surface just distal to large cleft coarsely denticulate for one-half distance from cleft to articulation of dactylus—entire palmar surface (and also distal region of propodus) bearing many long hairs (in female, palm of propodus nearly straight and bearing a small tooth at base—palmar surface lined with short hairs); dactylus sharply bent near proximal end and distally thereafter almost straight, with minute denticulations on inner surface.

Appendages on pereods 3 and 4 each consisting of two segments attached to bases of gills in males (fig. 22); in females, gills on pereod 4 attached to posterior brood pouch below attachment of appendages; pereopods on pereods 5 (fig. 21), 6, and 7 all normal (six-segmented); palmar surface concave, with a proximal tooth.

Abdomen in male (fig. 28) bearing "1½ pairs" of appendages and having a chitinous plate between penes; female abdomen bearing "½ pair" of appendages. Leaves of posterior brood pouch of females sparsely haired.

A large male measured 8 mm in length; a female, 5½ mm

Occurrence.—Type locality: Cape Mendocino, California (Mayer, 1890). *Other previous records:* Monterey wharf in Monterey Bay, California—on campanulariid hydroids; also at Mussel Point, ?substrate (Dougherty and Steinberg, 1953). *New record:* "probably Port Aransas, Texas"—8 males and 7 females (Dr. Hedgpeth).

Discussion.—Deutella abracadabra differs from *D. californica* (type species of *Deutella* Mayer, 1890, as selected by Dougherty and Steinberg, 1953, p. 48) in being entirely smooth and in having a different form to the palm of the propodus of the second gnathopod, as may be seen by comparing figs. 17 (*D. abracadabra*) and 23 (*D. californica*). The abdomen of the male of *D. abracadabra* (fig. 27) lacks the chitinous plate found between the penes of *D. californica* (fig. 28); the first pair of vestigial uropods are incipiently two-segmented in the latter, clearly one-segmented in the former.

Another species of *Deutella, D. mayeri,* was described by Stebbing (1895) from Antigua in the West Indies. *D. abracadabra* resembles this species in being entirely smooth, but differs from it esepcially in the form of the propodus of the second gnathopod. The palm of *D. abracadabra* bears a large proximal shelf comprising about one-third of the palmar surface and one triangular tooth at the distal end, whereas that of *D. mayeri* has what amounts to only a large tooth proximally and bears two triangular teeth distally, the more proximal one being acute, the other obtuse. The number of segments in the flagellum of the antennule also differs, there being six in the male and five in the female of *D. mayeri,* whereas the male of *D. abracadabra* has 8-10, the female, 5-8. *D. mayeri l*acks the anteriorly directed triangular projections that occur laterally on the anterior edges of pereods 2 and 3 in *D. abracadadra.*

The remaining named species already referred to this genus (*Deutella venenosa* Mayer, 1890, from Coquimbo, Chile) bears a forward directed spine on the cephalon, as does *D. californica,* but the spination of the rest of the body differs markedly between the two, as does the form of the palm of the second gnathopod. The form of this palm in *D. venenosa* is quite similar to that in *D. mayeri,* but the two species otherwise differ importantly in that the former is spinous and the latter, as already noted, is entirely smooth. The abdomen of the male of *D. abracadabra* (fig. 27) resembles that of *D. venenosa* in general, but differs in details (see Mayer, 1890, Taf. 5, fig. 19).

Mayer (1890) described a single female, which he referred to *Deutella,* from one of the Pontine Islands in the Mediterranean Sea. It was quite smooth dorsally and had five segments in the flagellum of the first antenna. In these two respects it differs from *D. californica* and *D. venenosa,* but resembles *D. mayeri* and *D. abracadabra.* Until the male of this *Deutella* sp. is found, however, no conclusions may be made as to its relationship to the latter two species.

In addition to the foregoing four named and one unnamed species already referred to *Deutella*, we believe that the species *Luconacia incerta* Mayer, 1903, only (hence type) species of the genus *Luconacia* Mayer, 1903, also belongs in that genus—as *Deutella incerta* (Mayer, 1903) comb. nov., of which, as we state in the introduction, we consider *Protellopsis stebbingi* Pearse, 1908, to be a synonym.

The abdomen of *Protellopsis stebbingi* Pearse, 1908, is significantly different from that of *Protellopsis kergueleni* Stebbing, 1888—only (hence type) species of the genus *Protellopsis* as established by Stebbing (1888). In the male of the latter, there are two clearly evident pairs of vestigial appendages, plus, apparently, a pair of lappets representing a third pair, whereas in the male of the former there is but one pair of distinct vestigial appendages, plus a definite pair of lappets. However, when compared to the illustration of the abdomen of *Luconacia incerta* given by Mayer (1903), it is obvious that *Protellopsis stebbingi* is closely allied to *Luconacia*, and further comparison of Pearse's illustrations and descriptions with Mayer's reveal that *P. stebbingi* is definitely synonymous with *Luconacia incerta*.

The genus *Luconacia* as set up by Mayer differs from *Deutella* in the form of the propodus of the appendage on the fifth pereod. In the former, this segment lacks a definitive palmar surface and is not unlike the carpus, but, in the latter, has a concave palmar surface, on which denticulations are borne. Mayer includes the presence of swimming hairs on the antennae (as are characteristic of *Caprella*) as one of the distinguishing features of the genus, but neither Pearse's nor Kunkel's figures show them to be greatly developed. These are not present in the species heretofore placed in *Deutella*. All of these differences seem minor to us and thus not to justify the separation of *Deutella* and *Luconacia*, the latter therefore falling as a subjective junior synonym of the former.

Deutella abracadabra sp. nov. is accordingly the first species of the genus *Deutella* Mayer, 1890, to be described since *D. incerta* and makes a total of five named and one unnamed species in the genus.

HEMIAEGINA MINUTA Mayer, 1890

(Figures 8-11, 13, 29)

Synonymy.—Hemiaegina quadripunctata Sundara Raj, 1927; *Hemiaegina ?minuta*, of Barnard, 1937.

Diagnosis.—Hemiaegina: entire body smooth (fig. 13) except for a pair of spines ventrally between second gnathopods; pereods 2-6 appear from above somewhat hexagonal in outline; second and third pereods equal in length; third, fourth and fifth pereods progressively shorter; sixth as long as fourth pereod, and seventh shortest of all. Gills oval and quite elongate.

Antennule about two-fifths length of body; second segment of peduncle extremely long, first and third quite short; flagellum of approximately same length as peduncle and composed of 11-13 segments in both sexes. Antenna as long as peduncle of antennule and bearing a few sensory hairs; flagellum two-segmented. Mandibular palp absent.

First gnathopod (fig. 8) one-half length of antenna; palm of propodus nearly straight and bearing a proximal lobe. Second gnathopod (fig. 9) about two-thirds length of body and attached to middle of second pereod; basis long and club-shaped; propodus comprising slightly over one-half length of entire appendage and almost twice as long as broad, with palm bearing "poison tooth" one-third of way distally from base, convex in middle third, and there bearing a small tooth in adult males (more distally in females and sometimes absent in juveniles)—distal third of palm bearing a shelf, which is separated from rest of palm by a cleft and bears two small teeth and a few short hairs; dactylus crooked and finely denticulate on inner surface.

Appendages on pereods 3 and 4 very small; each consisting of one segment and attached to bases of gills (fig. 10). Appendages on pereods 5-7 normal (six-segmented), increasing in size from 5 to 7; palm of propodus of appendage on pereod 5 (fig. 11) and 6 irregular and bearing a single tooth proximally; palm of propodus of appendage on pereod 7 more concave and bearing a large proximal tooth in addition to smaller ones.

Abdomen of male bearing one pair of two-segmented appendages (fig. 29); abdomen of female similar to that of male.

A large male measured 4 mm in length; a female, also 4 mm.

Occurrence.—Type locality: 8-25 fathoms, rocky ground, 15 miles outside of Amoy, China (Mayer, 1890). *Other previous records:* Station 164, Siboga Expedition (Mayer, 1903); 1°42′5″ S; 130°47′5″ E—at 32 meters (Mayer, 1903); Pamban Bridge, Krusadai Island, Gulf of Manaar, India (Sundara Raj, 1927—as *Hemiaegina quadripunctata*); Station 51, South Channel, Cockburn Sound,[10] region of Fremantle, Australia—at 6½-8 meters (Mayer, 1912); Waikiki Reef, Oahu, Hawaii—on a plumularian hydroid in shallow water (Edmondson and Mansfield, 1948); South Arabian coast (Barnard, 1937—as *Hemiaegina ?minuta*). *New record:* Port Aransas, Texas—10 males and 9 females on sargassum floating by dock, collected in July and Aug. 1948 (Dr. Hedgpeth).

Discussion.—These specimens agree with *Hemiaegina minuta* as described by Mayer (1890) and also with specimens as described by Edmondson and Mansfield (1948) from Hawaii.

Sundara Raj (1927) described a species of *Hemiaegina* from India, *H. quadripunctata*, which he claimed differed from the type of the genus in the form of the cleft on the palm of the second gnathopod,

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[10] 32° 10′ S; 115° 45′ E.

his specimens having what he termed a "squarish" rather than an angular one, and in the number of segments in the flagellum of the antennule, his having only 11 as compared to the 13 of *H. minuta.* However, he stated that his "species" might be only a variety of H. *minuta.* Our specimens from the Gulf of Mexico show a variation in the number of segments of this appendage from 11 to 13, thus lending support to this opinion. We believe that *H. quadripunctata* Sundara Raj, 1927, should fall as a synonym of *H. minuta.* In keeping with this, the locality for the former has been included in the above list of occurrences of *H. minuta.*

Barnard (1937) recorded a male of "*Hemiaegina ?minuta*", which he stated was lacking the second gnathopods and therefore could not be differentiated from *H. quadripunctata.* Since we have submerged the latter nominal species as a synonym of *H. minuta,* we have included Barnard's record as applying to *H. minuta.*

PARACAPRELLA PUSILLA MAYER, 1890

(Figures 16, 19, 24, 30)

Synonymy.—?Caprella sp., of Hedgpeth, 1950.

Diagnosis.—Paracaprella: entire body smooth (fig. 16); second pereod in male bearing an anteriorly directed, triangular projection on anterolateral edge; pleura on pereod 3 weakly developed anteriorly. Cephalon and second pereod nearly equal in length, latter three-fifths length of pereod 3; pereods 3, 4, and 5 approximately equal in length; pereods 6 and 7, combined, two-thirds as long as pereod 2. Gills oval to elliptical and directed anteriorly (fig. 24).

Antennule one-half length of body; flagellum composed of 12 segments in male and 8-10 segments in female; flagellum comprising one-half length of entire antennule. Antenna one-half length of antennule, second segment bearing a small, downward directed projection anteriorly; flagellum composed of two segments and bearing many sensory hairs. Mandibular palp absent.

First gnathopod nearly as long as antennule. Second gnathopod (fig. 19) slightly less than one-half length of body and attached at middle of second pereod; basis almost as long as propodus and triangular in cross section, bearing a rounded projection on posterior edge near point of proximal attachment; ischium bearing two low, lateral, longitudinal ridges; propodus about one-half length of entire appendage, with "poison tooth" located on shelf nearly half way distally from base of palm and with distal palmar surface concave—all of palm covered with hairs; dactylus with nearly straight inner border, latter hairy in middle two fourths and quite narrow in distal fourth.

Rudimentary appendages on pereods 3 and 4 each two-segmented and attached to bases of gills (fig. 24), with proximal segment bearing stiff hair and distal segment bearing three terminal hairs. Pereopods on pereods 5-7 missing in our specimens.

Abdomen bearing "1½ pairs" of appendages in male (fig. 30) and "½ pair" in female.

The largest male measured 6 mm in length; a female, 4 mm.

Occurrence.—Type locality: Rio de Janeiro—on ascidians (Mayer, 1890). *Other previous records:* Desterro, Brazil; Fort de France and St. Anne, Martinique; Kingston, Jamaica—from the sides of a lighter six weeks within the harbor ((all records of Mayer, 1903). Dar es Salaam[11] (Schellenberg, 1928); Suez Canal: Kantara, Station Km. 46; Kabret Signal Station, Station K.O; Port Taufiq bathing place, Station PT.3 (all records of Schellenberg, 1928—see Munro Fox, 1929, for description of collecting stations). Honolulu Harbor, Hawaii—from screen of an intake water pipe of Hawaiian Electric Co. and on *Pennaria* sp. (Edmondson and Mansfield, 1948). *New records:* Port Aransas, Texas—2 males and 3 females collected Nov. 20, 1947 (Dr. Hedgpeth) and 9 males and 7 females (together with 4 males and 6 females of *Caprella carolinensis*) from fouling organisms of Gulf Beach fishing pier, collected Sept. 19, 1954 (Dr. Hildebrand).

Discussion.—The specimens from the Gulf of Mexico agree with Mayer's description of *Paracaprella pusilla* in body outline as he described it in his "Nachtrag" (1890), but are slightly larger and bear more segments in the flagellum of the antennule. In size and in the number of segments of this appendage they are identical with the animals he described in his 1903 paper. They differ from these, however, in lacking a small tubercle on the anterodorsal part of the second pereod, but this feature was apparently absent in the specimens that he described in the "Nachtrag", since he made no mention of it.

As already mentioned in the introduction, Whitten, Rosene, and Hedgpeth (1950) and Hedgpeth (1950) spoke of an unidentified "green" Caprella sp., which occurred together with "*C. acutifrons*" (= *C. carolinensis*), but was less common and apparently smaller than the latter. Unfortunately we have so far been unable to obtain specimens from the Gulf whose color description in the living state has been recorded as green. However, since the specimens of *C. carolinensis* and *P. pusilla* received by us from Dr. Hildebrand were collected together and are not inconsistent with Dr. Hedgpeth's account, we believe by the process of elimination that the latter's "*Caprella* sp." was most probably *P. pusilla*.

KEY TO THE CAPRELLIDAE OF THE GULF OF MEXICO

1.	Vestigial appendages on pereods 3 and 4	2
	No vestigial appendages on pereods 3 and 4 (*Caprella*)	6
2.	Appendages on pereods 3 and 4 one-segmented	*Hemiaegina minuta*

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[11] 6°50′ S; 39°17′ E.

	Appendages on pereods 3 and 4 two-segmented	3
3.	Mandibular palp absent	*Paracaprella pusilla*
	Mandibular palp present *(Deutella)*	4
4.	Palm of propodus of appendage on pereod 5 straight and lacking denticulations, two spines on cephalon	*Deutella incerta*
	Palm of propodus of appendage on pereod 5 concave and bearing denticulations; one or no spine on cephalon	5
5.	One spine on cephalon	*Deutella californica*
	No spine on cephalon	*Deutella abracadabra* sp. nov.
6.	With spine ventrally between second gnathopods	*Caprella equilibra*
	Without spine ventrally between second gnathopods	7
7.	With spine on cephalon	*Caprella carolinensis*
	Without spine on cephalon	*Caprella* sp.

SUMMARY

1. Descriptions based on original material are herein given for seven species of skeleton shrimps found in various parts of the Gulf of Mexico. Study of earlier reports has revealed that two of these seven have previously been recorded: *Caprella carolinensis* Mayer, 1890 (as *Caprella acutifrons*) and *Hemiaegina minuta* Mayer, 1890 (figured but not named); a third, *Paracaprella pusilla* Mayer, 1890, is probably the same as *Caprella* sp. of Hedgpeth, 1950, a form reported from the Gulf, but described merely as "green" and smaller than *C. carolinensis;* and the remaining four are new records. Of the last group, two (*Caprella equilibra* Say, 1818, and *Deutella californica*, Mayer, 1890) are known from other areas; and descriptions of two (*Deutella abracadabra* sp. nov. and *Caprella* sp.) are new to science, the latter species being left unnamed, however, because of inadequate material.

2. An eighth species, hitherto known as *Luconacia incerta* Mayer, 1903, was not found among our specimens. [See Addendum.] Nevertheless, it is herein transferred on the basis of its original description to the genus *Deutella* Mayer, 1890. *Protellopsis stebbingii* [sic] Pearse, 1908, is here synonymized with *Deutella incerta* (Mayer, 1903) comb. nov. on the basis of comparison of Pearse's and Mayer's descriptions and figures.

3. *Hemiaegina quadripunctata* Sundara Raj, 1927, originally described from India, is herein suppressed as a synonym of *Hemiaegina minuta* Mayer, 1890—one of the seven species here treated.

4. A key to the eight described species of caprellids found in the Gulf of Mexico is provided.

ADDENDUM

Since the completion of this paper, reëxamination of the material from Alligator Harbor, Franklin Co., Florida, has revealed an immature female belonging to the genus *Deutella*, but not to the species

D. *abracadabra;* it bears a pair of minute spines on the cephalon and one slender spine dorsolaterally on the left side of the second pereod—no corresponding spine is evident on the right side, but may have been knocked off. The appendages on the fifth and subsequent pereods are missing.

The vestigial appendages on pereods three and four are larger than in *Deutella abracadabra,* but the palmar surface of the propodus of the second gnathopod is nearly identical with that of a female *D. abracadabra,* being slightly convex and set with hairs, with a small grasping spine proximally. The specimen is 4 mm long.

We are reasonably sure that this represents an immature female of *Deutella incerta.* It thus appears that all named species hitherto recorded from the Gulf are represented in our collection.

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ABSTRACT

Descriptions are given for eight, and illustrations for seven, species of skeleton shrimps from various parts of the Gulf of Mexico. *Deutella abracadabra*, sp. nov., is described and one new species of *Caprella* is described but unnamed because of inadequate material. Two species, *Caprella equilibra* Say, 1818, and *Deutella californica* Mayer, 1890, are new records for the Gulf. *Hemiaegina minuta* Mayer, 1890, and *Paracaprella pusilla* Mayer, 1890, are believed to have been collected in the Gulf previously, but were not recorded from there by name. *Protellopsis stebbingii* [sic] Pearse, 1908, originally reported under that name from the Gulf, is synonymized with *Deutella incerta* (Mayer, 1903), which was described by Mayer as *Luconacia incerta*. The genus *Luconacia* Mayer, 1903, is treated as a synonym of *Deutalla* Mayer, 1890. *Hemiaegina quadripunctata* Sundara Raj, 1927, originally described from India, is suppressed as a synonym of *Hemiaegina minuta* Mayer, 1890.

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THE SYSTEMATIC STATUS OF THE SUCKERS OF THE GENUS *MOXOSTOMA* FROM TEXAS, NEW MEXICO AND MEXICO

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THE SYSTEMATIC STATUS OF THE SUCKERS OF THE GENUS *MOXOSTOMA* FROM TEXAS, NEW MEXICO AND MEXICO

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The occurrence on the Pacific slope of Mexico of *Moxostoma*, a genus of suckers widespread in eastern and central United States, was first noted by Bean (1880). Regan (1907) treated more fully the southwestern representatives of this genus and presented a key to the identification of the nominal forms. Aside from scattered distributional records, the Mexican forms have not been reviewed since that time. DeBuen (1940: 11) and Alvarez (1950: 42-43) relied entirely on Regan's paper in their treatment of *Moxostoma*.

The lack of attention to the Mexican forms is not surprising in view of the confusion that has attended studies of the more northern and better sampled species. Three subgenera, *Moxostoma* Rafinesque, *Megapharynx* Legendre, and *Scartomyzon* Fowler were recognized by Robins and Raney (1956) who noted that the nominal Mexican species clearly belong to *Scartomyzon*. Very little material of nominal Texan and Mexican forms was at hand when we treated this subgenus and only brief mention was made of them. The close relationship of *congestum* and *austrinum* with the geographically distant *robustum* was noted. This tentative assignment has been verified in the current study.

Through the efforts of Robert R. Miller and John T. Greenbank, considerable material is now available from Mexico and more extended comment is possible. We are especially indebted to Dr. Miller who has freely made available his extended knowledge of the relations of the river systems and their faunas. We also acknowledge the assistance of Reeve M. Bailey, Museum of Zoology, University of Michigan, for the loan of specimens under his care. Leonard P. Schultz, Ernest A. Lachner, and Robert H. Kanazawa of the United States National Museum have been helpful in many ways including making available working space, literature, and specimens, and in arranging shipments of material. George S. Myers and Margaret H. Storey have similarly aided us at the Stanford Natural History Museum.

A gazetteer of localities and a map of Mexico is given by Meek (1904: xxviii-xxx and opposite page xlvii). The National Geographic Society's map of Mexico and Central America (edition of March,

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1953) shows the river systems and many of the localities mentioned below. Counts and measurements were taken as explained in Robins and Raney (1956: 4). Abbreviations used are: CU = Cornell University, SNHM = Stanford Natural History Museum, UMMZ = University of Michigan Museum of Zoology, USNM = United States National Museum.

Six nominal forms are considered here: *Ptychostomus congestus* Baird and Girard (1854), *Ptychostomus albidus* Girard (1856), *Myxostoma austrina* Bean (1880), *Moxostoma mascotae* Regan (1907), and *Moxostoma parvidens* Regan (1907). Of these only *austrina* and *mascotae* apply to populations on the Pacific slope. An examination of all extant material has shown that three species are included.

The following key summarizes our concept of the species involved.

KEY TO THE SPECIES AND SUBSPECIES OF *Moxostoma (Scartomyzon)* FROM TEXAS, NEW MEXICO AND MEXICO

(based on adults and large juveniles)

1\. Pectoral fin short; its length is much less than depth of head at occiput and enters standard length 5.5 or more times in adults. Intestine coiled in rather open loops, no tight spiral on the right side. Depth of head at occiput greater than its width *(Moxostoma austrinum)* 4

Pectoral fin long; its length is greater than depth of head at occiput and enters standard length 5 or fewer times. Intestine coiled in a tight spiral situated ventrally on the right side. Depth of head at occiput equal to the head width *(M. congestum)* or greater *(M. mascotae)* 2

2\. Lacks keel on dorsum. Head subconical in lateral view; U-shaped in dorsal view. Mouth moderate in size and slightly oblique. Upper lip is overhung by the conical snout. Infraorbital canal lacks lateral canals and has numerous large pores. Occipital line curved and anteriorly does not reach the vertical extension of the posterior border of cheek. Pharyngeal shelf is wider than height of largest tooth. Body stout. *(Moxostoma congestum)* 3

Hard bony keel present under skin on mid-dorsum between occiput and origin of dorsal fin. Head subquadrate in lateral view; V-shaped in dorsal view except for truncate tip. Mouth large, horizontal, and located far forward. The upper lip extends as far anteriorly as the snout tip. Infraorbital canal with few but well developed lateral canals which terminate in small pores. Midsection of occipital line truncate; reaches anteriorly to the posterior border of cheek. Pharyngeal shelf narrower than height of largest tooth. Body elongate and compressed *Moxostoma mascotae* Regan

3. Dorsal rays usually 12. The hind margin of lower lip curved, the two halves meet at an obtuse angle. Lower lips restricted laterally and circumscribed by folds of skin. Canal and pores of lateral line often inconspicuous and reduced or absent in many juveniles. *Moxostoma congestum congestum* (Baird and Girard)

Dorsal rays usually 11. Lower lip full, its hind margin quite straight and its outer corners often squarish. Lower lips lack surrounding folds of skin. Lateral-line canal well developed even in young *Moxostoma congestum albidum* (Girard)

4. Dorsal ray usually 11. Plicae of lower lip number fewer (approximately 20) and are entire. Pectoral and anal fins rounded. Distance from hypural to pelvic base when measured forward reaches the upper lip. *Moxostoma austrinum austrinum* (Bean)

Dorsal rays usually 12. Plicae of the lower lip are greater in number (approximately 25) and the posterior half of some tend to break up and are semipapillose. Pectoral and anal fins pointed. Distance from mid base of hypural to pelvic base when measured forward reaches to (rarely) or behind the lower lip. *Moxostoma austrinum milleri*, new subsp.

MOXOSTOMA CONGESTUM (BAIRD AND GIRARD)

Description.—A moderate sized species; the largest specimen examined was 274 mm in standard length. The dorsal profile is strongly convex from the origin of the dorsal fin, the highest point on the body, to the tip of the snout. Posterior to this point the dorsal contour is gently concave; the steepest portion of the slope is along the base of the dorsal fin. The ventral contour is flat anterior to the anus and along the caudal peduncle whereas the body deepens distinctly from the posterior base of the anal fin to the anus.

The body is variable in width. Specimens from the Llano River are especially robust; their greatest width nearly equals the greatest depth. In most specimens, however, the body is more compressed, much less wide than deep, a feature which emphasizes the considerable depth of body.

In lateral view the head is subconical. The head depth at the occiput slightly exceeds the head width. Viewed from above the snout is U-shaped whereas, laterally, its profile forms a smooth curve with the predorsal profile. The eye is somewhat forward of the midpoint of the head. The mouth is included; it is moderate in size and the gape forms a broad arc. Differences exist between the subspecies *albidum* and *congestum* in the detailed configuration of the lips although both are basically plicate. They will be described later.

The occipital line at its most forward point generally does not reach the vertical extension from posterior margin of the cheek.

The origin of the dorsal fin is slightly in advance of the midpoint of the body, and lies directly over the tip of the depressed pectoral fin. The pelvic insertion is under the anterior half of the dorsal fin.

Berner (1948: 140-141) noted differences between the genera *Ictiobus* and *Carpiodes* in the shape and number of intestinal convolutions. The amount of inter- and intra-specific variation in this feature and its reliability in general as a systematic tool has been little studied and should be investigated. In *congestum* a large spiral of intestine is situated ventrally on the right side. This is similar to the condition found in *mascotae* but quite different from the open looping seen in *austrinum* which resembles Berner's (*loc. cit.*, figs. 1-2) illustration of *Ictiobus*. Interestingly, *robustum* exhibits a somewhat intermediate condition between *congestum* and *austrinum* in this feature. The peritoneum is silvery.

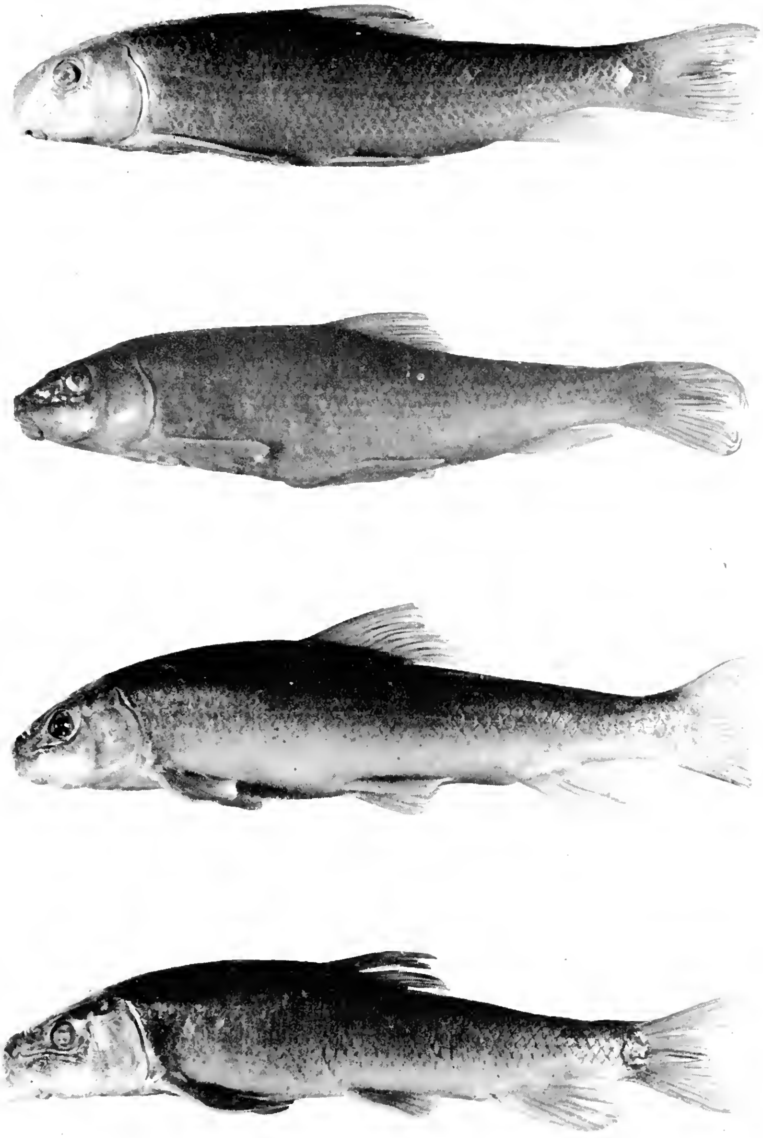
The pharyngeal arch is scythe-shaped. The third or fourth tooth is largest; the other teeth gradually diminish in size toward the tip of the arch. The teeth are compressed, numerous, and somewhat hooked at the tip. The lateral shelf is broad; the distance from the base of the tooth row to the margin of the shelf at its widest point is greater than the height of the teeth. The fontanelle is rectangular.

The features of the tripus are noted under relationships and comparisons. In this character *congestum* is closest to *robustum* whereas *mascotae* and *austrinum* are similar. Fin-ray and lateral-line scale counts, and proportional measurements are given in tables 1 and 2.

Coloration.—The body is not sharply bicolored; alternate dark and light colored streaks extend to the venter. The under parts of the head, body, pectoral and pelvic fins are light colored.

The lateral scales are outlined in dark but the conspicuously paler central region of each scale appears to join the next to form the light longitudinal streaks on the body. The contrast between center and edge of scale is less obvious on the dorsum. The head is bicolored; the lower half of the cheek and snout is light. Melanophores are scattered on the upper half of the inner surface of the opercle. The occipital line is not much darker than the nape and is inconspicuous; nor is the continuation of this line very evident on the shoulder.

The pectoral fins are not heavily pigmented on their dorsal surfaces.



Figures 1-4. **1.** (top) *Moxostoma congestum albidum*, adult female, 194 mm in standard length, from Rio San Juan near Monterey, Nuevo Leon, Mexico (Rio Grande Drainage), UMMZ 97382; **2.** (second) *Moxostoma austrinum milleri*, holotype, female, 138 mm from the Rio Mezquital at Rayar, about 5 miles south of Durango City, Durango, Mexico, USNM 132446; **3.** (third) *Moxostoma austrinum austrinum*, adult male, 171 mm, from a tributary of Rio San Pedro at bridge 9 miles northeast of Autlán, Jalisco, Mexico (Rio Armeria Drainage), UMMZ 172206; **4.** (bottom) *Moxostoma mascotae*, adult male, 188.5 mm, from Rio Ameca, 25 miles east (by highway 70) of Ameca, Jalisco, Mexico. UMMZ 172125. (All photographs by Douglass M. Payne)

However, the first ray is pale, and the darker coloration extends from the second ray where it is most intense over the remainder of the fin, a common pattern in the subgenus. The surfaces of the pelvic fin are light except for scattered melanophores on the upper side of the second to third rays in occasional specimens.

The dark interradial membranes are a conspicuous feature of the dorsal fin and mid-caudal region. This feature is shared by the related species; *robustum, mascotae* and *austrinum.* The interradial membranes of the anal fin are often similarly pigmented although this is not evident in young and juvenile specimens.

Sexual dimorphism.—The edge of the dorsal fin in males is sigmoidal, due to the expansion of the hind portion of the fin. In females the posterior edge of the dorsal fin is straight.

The pelvic fins do not show sexual dimorphism to the extent noted by us in other *Scartomyzon* including *austrinum* and *mascotae.* The outer pelvic rays in our specimens of *congestum* are generally longer in both sexes. The anal fin is slightly longer in the male but the fin is not more expanded than in the female. No nuptial tubercles are present. Apparently none of the specimens examined were taken in the breeding season.

Distribution and ecology.—*M. congestum* is distributed from the Rio Soto la Marina of Tamaulipas in northeastern Mexico and the Rio Conchos of Chihuahau (drainage of the Rio Grande) northward to the valley of the Brazos River in Texas. It extends westward to the Rio Florido of Durango, in the Rio Grande proper at least to El Paso and in the Pecos River to the vicinity of the Roswell, New Mexico. Hubbs, Kuehne and Ball (1953: 225) note that *M. c. congestum* is found (in the Guadalupe River of Texas) most abundantly in pools with silt bottom and that young are often found in moving water. Woolman (1894: 56) records the species as abundant in a rocky area in the Rio Grande near El Paso. Bonham (1941: 360-361) reported specimens up to 9 inches long from the stomachs of the longnose gar, *Lepisosteus osseus,* in the Guadalupe River in Kerr County, Texas. This seems to indicate that even fairly small individuals will enter quiet-water situations. Lachner collected specimens in the Brazos Drainage from pools below a dam. The vegetation here was abundant and the water was white and clear.

Relationships and comparisons.—There is no doubt about the close relation of the four species, *robustum, congestum, austrinum* and *mascotae.* However, within this species group, the similarity of *mascotae* and *congestum* in possessing a long pectoral fin (see key above) is clearly due to convergence. The differences between *robustum* and *congestum* were treated in Robins and Raney (1956). *M. robustum* lines up closely with *congestum* and differs from *austrinum* and *mascotae* in the characters considered below. It was noted by Robins and Raney (1956) that the tripus of *austrinum* differed from that of *congestum* in having the medial edge of the anterior shelf projecting dorsally; the tripus of *mascotae* is similar to that of *austrinum*. This feature is best seen from the medial aspects. We believe that this character is indicative of the natural relationships. Other characters strengthen this view although convergence in some, such as the length of the pectoral rays, make them less useful.

Other characters that separate *congestum* from *austrinum* and *mascotae* are as follows. *M. congestum* is a stouter fish. Viewed from above the head is primarily V-shaped in *austrinum* and *mascotae* whereas it is broadly U-shaped in *congestum*. The head is broader throughout in *congestum*. The depth of the head at the occiput is about equal to the head width while in *austrinum* and *mascotae* it is deeper than wide due in part to the fact that the nape extends further forward in *austrinum*. This gives a different appearance to the temporal region where the middle third of the occipital line is truncate in *austrinum* and *mascotae* but in *congestum* it is evenly curved. The lips and gape are wide in *congestum* but elongate in *austrinum* and *mascotae*. In *mascotae* the mouth is especially large. One of the best differences lies in the nature of the lateral tubes and cephalic pores of the infraorbital canal in adults. In *austrinum* and *mascotae* the pores are small and are located at the end of small but well developed side canals whereas in *congestum* the lateral canals are wanting or poorly developed and the large pores are on the infraorbital canal proper. In *congestum* the preopercular mandibular canal is usually not connected to the suborbital branch. In *austrinum* and *mascotae* the connection may or may not be present. Considerable individual variation exists in the pathways of the cephalic canals on the top of the head in all forms.

The pectoral fin is long in *congestum*; its length considerably exceeds the distance from the snout tip to the occipital line and enters the standard length less than five times. It is shorter in *austrinum* but *mascotae* converges with *congestum* in this character.

SUBSPECIES OF MOXOSTOMA CONGESTUM

Our material of *congestum* is separable into two allopatric units. While there is little evidence of intergradation we feel that these two units are best considered as subspecies. *M. c. congestum* and *M. c. albidum* are north-south representatives which differ most trenchantly in the numbers of dorsal rays and in the configuration of the lips.

MOXOSTOMA CONGESTUM CONGESTUM (BAIRD AND GIRARD)

Catostomus congestus.—Baird and Girard, 1854: 27 (description; type locality: Rio Salado, Texas). Gunther, 1868: 19 (compiled). Jordan and Gilbert, 1883: 138 (erroneously associated, fide Cope, with *M. macrolepidotum*).

Ptychostomus congestus.—Girard, 1856: 172 (compiled). Girard, 1859: 36, pl. 21, figs. 5-8 (description given in detail for first time).

Teretulus congestus.—Jordan and Copeland, 1876: 157 (name only).

Myxostoma congesta.—Jordan, 1878a: 317 (compiled). Jordan, 1884: 317 (in part, compiled; *M. bucco* wrongly identified with *congestum*).

Myxostoma congestum.—Jordon, 1878c: 118, 133 (compiled: *Ptychostomus bucco* Cope erroneously assigned to synonymy of *congestum*).

Myxostoma macrolepidotum.—Cope, 1880: 36 (misidentification; Guadalupe River, Texas).

Moxostoma congestum.—Jordan, 1885a: 119-120 (compiled; wrongly includes *albidum*). 1885b: 19-20 (description based on material from the Rio Lampasas—see below under material examined—specimens from Ash Creek, Arizona [1] misidentified as *congestum*). Jordan and Gilbert, 1886 (recorded from Rio Lampasas, p. 17; Rio Colorado at Austin, p. 20; Rio San Marcos, p. 22; Rio Comal, p. 23; *albidum* wrongly included in synonymy). Evermann and Kendall, 1894: 98, pl. 16 (literature reviewed; Rio Salado, Guadalupe and Llano rivers, Rio Lampasas, Rio San Marcos records only; new material from San Antonio Springs). Woolman, 1895: 56 (Rio Grande at El Paso del Norte). Jordan and Evermann, 1896a: 242 (compiled). 1896b: 192 (*Catostomus texanus* Abbott = *Xyrauchen texanus* and *M. albidum* wrongly placed in synonymy; specimens from Ash Cr., Ariz. again misidentified as *congestum*). 1900: pl. 36 (illustration only). Regan, 1907: 146 (in part: Rio Lampasas and Rio Salado in Texas; description and other records apply to *albidum*). Fowler, 1904: 243-244 (description of specimen from Del Rio, Texas). 1913: 57 (compiled). Jordan, Evermann and Clark, 1930: 110 (compiled; *albidum* and *congestum* combined). Schrenkeisen, 1938: 93 (compiled). Bonham, 1941: 360-361 (recorded from Guadalupe River, on basis of stomach analysis of gar). Fowler, 1945: 23 (compiled: Colorado R. and Rio Grande, Texas, also the Brazos R. and the Rio San Antonio, Texas). Baughman, 1950: 129 (name only). Alvarez, 1950: 42-43 compiled; Mexican records referable to *albidum*). Jurgens and Hubbs, 1953: 13 (name only). Hubbs, 1954: 278 (range, type of *Catostomus texanus* Abbott wrongly identified with *congestum*)

Myzostoma congestum.—Meek, 1904: xxxi, 34 (El Paso record only).

Moxostoma duquesnii.—Fowler, 1945: 24 (misidentification, records from the Colorado and Guadalupe (sic) rivers, Texas.) Hubbs, 1954: 278 (record from Fowler correctly presumed to be based on material of *congestum*).

Moxostoma congestum albidum.—Baughman, 1950: 129 (name only).

Moxostoma congestum congestum.—Knapp, 1953: 45, 48, fig. 49 (range, compiled). Hubbs, Kuehne and Ball, 1953: 225, fig. 6 (distribution in upper Guadalupe R.).

Material examined.—Two cotypes, USNM 171, are present in the United States National Museum. They were taken in 1851 from the Rio Salado, Texas by John H. Clark. The largest specimen, 117 mm in standard length, was illustrated by Girard (1859: pl. 21, fig. 5) and is here designated as lectotype. It retains the catalog number USNM 171. The smaller "cotype", 91 mm in standard length, is recataloged under USNM 164525. Girard's life-size drawing (loc. cit.) is a good likeness of the lectotype except that it appears to show 11 dorsal rays (the lectotype has 12) and does not show the typical streaking of the body (see Robins and Raney, 1956, pl. 3).

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[1] The "Ash Creek" specimens have been identified with *M. aureolum* (LeSeuer) by Robins and Parey (1957) and the locality is considered erroneous.

Brazos River System.—USNM 36562 (6, 64-292), USNM 36561 (2, 145-171), USNM 36563 (3, 144-164), USNM 36510 (1, 305), SNHM 1300 (1, 153) all from the Lampasas River (Rio Lampasas) at Belton, Texas, collected in 1884 by Jordan and Gilbert. (USNM 36510 is the specimen illustrated by Evermann and Kendall, 1894, pl. 16.) USNM 166144 (7, 89-104), trib. of the Brazos R., at Salada, on U. S. Highway 81, Bell Co., Texas, April 14, 1952, E. A. Lachner, W. T. Leapley and F. J. Schwartz. UMMZ 120191 (7, 110-175), South Bosgue R., McLennan Co., Texas, June 21, 1938, C. L. Hubbs and family and L. T. Murray.

Colorado River System.—USNM 35607 (1, 190), USNM 36567 (3, 89-206), USNM 36508 (1. 206), SNHM 5871 (1, 161) all from the Rio Colorado at Austin, Texas, collected in 1884 by Jordan and Gilbert. CU 26585 (4, 161-274) Mt. Holy Lake, Johnson Fk. of Llano R. at Mt. Home, Kimble Co., Texas, March 12, 1939, A. H. Cook.

Guadalupe River System.—USNM 36538 (1, 146), Rio Comal, New Braunfels (Comal Co.), Texas, 1884, Jordan and Gilbert. USNM 58794 (1, 153), Blanco R., Texas (about 1907), Bur. Fisheries. USNM 166187 (2, 28-29) Guadalupe R., 10 mi. S. of Gonzales, Gonzales Co., May 26, 1952, Kuehne and Ball. USNM 36521 (1, 84) Rio San Marcos at San Marcos (Hays Co.), Texas, 1884, Jordan and Gilbert.

Nueces River System.—USNM 108974 (2,107-108), Sabinal R., near Sabinal, Uvalde Co., Texas, August 8, 1934, C. E. Burt expedition.

Rio Grande System.—UMMZ 120295 (4, 127-202) Pinto Cr., Kinney Co., Texas, June 25, 1938, C. L. Hubbs and family. USNM 3395 (2, 185-187), Pecos R., coll. by Capt. Pope. UMMZ 66181 (2, 89-104) New Mexico, S. of Roswell, April 3, 1916. USNM 44627 (2, 281-324), USNM 44628 (2, 150-174) Mexican Boundary, Ft. Clark (Kinney Co.), Texas, 1893, Dr. E. A. Mearns. SNHM 844 (1, 61) Rio Grande at El Paso, Texas, A. J. Woolman.

Description.—Dorsal rays usually number 12, rarely 11. The lateral line is variously developed. In most juveniles and in many adults it is absent or obsolescent. In some the pores may be seen but the canal, so conspicuous in all other species of *Moxostoma* and in *albidum*. is little developed. This lack of development is best seen in specimens from the Brazos Drainage although it is noted in specimens from the Rio San Marcos, Rio Colorado and to a lesser degree elsewhere. Specimens from the Llano River and most large adults have a well developed lateral line.

The mouth is rather small although the lips may be much expanded in large adults. The lower lip has an emarginate posterior border; the two halves usually meeting at an obtuse angle. The posterior lateral borders of the lower lip are reduced and circumscribed by fleshy folds. In extremes, (specimens from the Brazos River this infolding of the lower lip will cause the two halves to meet at an acute angle.

The body is conspicuously streaked. Again this feature is extreme in juveniles and is best marked in a series from the Brazos Drainage (USNM 166144).

Young individuals of *M. robustum* are also conspicuously streaked in contrast to the unstreaked juveniles of *mascotae* and *austrinum*.

In the reduction in lips, the streaked body and reduction in lateral line, juvenile specimens of *congestum* resemble the spotted sucker, *Minytrema melanops.* Despite its *Minytrema*-like appearance this form differs in the fundamental characters which separate the tribes Moxostomatini and Erimyzonini (see Nelson, 1948 and 1949) including the three-chambered air bladder.

Another fundamental and easily observed difference noted by us is the presence in *Minytrema* and *Erimyzon* of a wide suborbital shelf which is formed by the bones of the circumorbital series In all *Moxostoma* the circumorbitals are a narrow tube-like series of bones. Gunther (1868: 18-22) apparently also noted this broad shelf in nominal forms which we today assign to the tribe Erimyzonini. Finray counts and proportinal measurements are shown in tables 1 and 2.

Range.—Widely distributed in Texas, in tributaries of the Gulf of Mexico, from the Brazos River (as far north as Palo Pinto County) south and east in Colorado, Guadalupe and Nueces Rivers, the Rio San Antonio and the Rio Grande and its northern tributaries (Pinto Cr., the Devil's and Pecos rivers) and from the Rio Grande itself at El Paso. It occurs in New Mexico in the Pecos River (Roswell) and probably also ranges northward in the Rio Grande proper.

MOXOSTOMA CONGESTUM ALBIDUM (GIRARD)

Ptychostomus albidus.—Girard, 1856: 152 (description; type locality: Rio San Juan, Monterey, Nuevo Leon, Mexico). 1859: 36-37, pl. 19, figs. 5-8 (detailed description presented for first time).

Teretulus albidus.—Jordan and Copeland, 1876: 157 (name only).

Myxostoma albidum.—Jordan, 1878a: 315 (compiled); 1878b: 417 (compiled); 1878c: 117, 129 (compiled, scales erroneously listed as 56).

Myxostoma albidum.—Jordan and Gilbert, 1883: 141-142 (compiled).

Myxostoma albida.—Jordan, 1884: 315 (in part, compiled).

Myxostoma congestum.—Jordan, 1885a: 120 (type of *albidum* considered to be young of *congestum*); 1885b: 19 (do.). Evermann and Kendall, 1884: 98 (combined with *congestum;* record from Rio San Juan, only referable to *albidum*). Jordan and Evermann, 1896b: 192 (in part, compiled). Meek, 1902: 76 (specimens from the Rio Noavaca at Santa Rosilia in the Conchos system, Chihuahua). Regan, 1907: 146 (description and records exclusive of R. Lampasas and R. Salado in Texas). Jordan, Evermann and Clark, 1930: 110 (combined with *congestum*). De Buen, 1940: 11 (compiled). Alvarez, 1950: 42-43 (in part; Mexican range only).

Myzostoma congestum.—Meek, 1904 (xxxiv—Rio de los Conchos system in Tamaulipas; xxxi, 34—all but the El Paso record).

Moxostoma congestum albidum.—Knapp, 1953: 45 (compiled: said to intergrade with *congestum* in the Rio Grande Valley). Robins and Raney, 1956: 8 (tentatively considered a subspecies of *congestum*).

Material examined.—The type series USNM 170 consists of two specimens (74 and 84 mm standard length), the largest of which is nearly broken in two. They were taken in Rio San Juan near Monterey, Nuevo Leon, Mexico (Rio Grande Drainage) by Lt. D. N. Couch in 1853. We designate the smaller specimen as lectotype. The other one is recataloged as USNM 164524.

UMMZ 97382 (3, 142-191) subtopotypes, trib. to Rio San Juan near

Montemorelos, Nuevo Leon, Mexico by Creaser, Gordon and Ostos, April 21, 1930. UMMZ 166717 (6, 54-109) Mexico, trib. of Rio Conchos 1/4 mi. S. of Meoqui, Chihuahua, collected by Paul R. Needham and party on August 20, 1952. SNHM 47591 (1, 110) Rio San Pedro, Meoqui, Chihuahua, M. R. Brittan, August 9, 1952. USNM 55846 (2, 104-112), SNHM 9340 (2, 113-136), Rio Pilón in the Soto la Marina basin at Garza Valdez, Tamaulipas, Mexico, collected by Seth E. Meek. SNHM 47617 (1, 60) Durango, Rio Florido, near Canutillo, near Mexican hwy. 45, M. R. Brittan, August 10, 1952. SNHM 47609 (1) Durango, trib. to Rio Florido, 7 mi. N. Las Nieves, M. R. Brittain, August 10, 1952. UMMZ 161728 (1, 53) Durango, Rio Florido between El Cristo and Villa Ocampo, J. Greenbank and party, February 19, 1951.

Description.—The dorsal rays number 11 (see Table 1), a feature which appears consistent throughout the range. In the limited material available the plicae tend to break into papillae on the posterior half of the lower lip although this is not marked. The lower lip is full so that the two halves form a straight border posteriorly. The posterior-lateral border of the lips is squarish in sharp contrast to the condition found in *congestum.* No concentric folds of skin are noted around the corners of the mouth in our material. Proportional measurements are given in table 2.

Although *albidum* exists in Mexican tributaries of the Rio Grande and *congestum* is found in the Rio Grande and in some of its northern tributaries no clear pattern of intergradation is evident. Hubbs, Kuehne and Ball (1953: 22) say that their extensive series of *congestum* show no tendency toward *albidum.* Specimens collected in Pinto Creek of the Rio Grande system, UMMZ 120295 (see data above and Robins and Raney, 1956, pl. 3) and in the Rio Grande proper at El Paso, SNHM 844, closely resemble *albidum* in lip structure although they have the 12 dorsal rays of *congestum.* Conversely, two juveniles from the Pecos River near Roswell, New Mexico, UMMZ 66181, resemble *congestum* in lip structure but have 11 dorsal rays as in *albidum.* They are perhaps intergrades and certainly they come from an area where the occurrence of intergrades would be expected. Since the lower reaches of streams tributary to the Rio Grande and the Rio itself are apt to become dry in times of drought, populations in the contact area are possibly wiped out or decimated from time to time. This would serve to restrict gene flow between the two subspecies and possibly has prevented the formation of a broad zone of intergradation in the Rio Grande valley. Large series of specimens from the Rio Grande region must be available before a solution of this problem can be attempted.

Range.—In Mexican tributaries of the Rio Grande from the Rio Florido of Durango and the Rio Conchos of Chihuahua to the Rio Salado of Coahuila and the Rio San Juan of Neuvo Leon and southward in Gulf drainages to the Rio Soto la Marina in Tamaulipas. The species has not been recorded previously from Durango.

The status of Moxostoma parvidens Regan.—Regan (1907: 147,

TABLE 1.

FIN-RAY AND LATERAL-LINE SCALE COUNTS IN THREE SPECIES OF *Moxostoma*

Species	Dorsal Rays				Anal Rays			Pelvic Rays				Pectoral Rays					Lateral-line Scales								
	10	11	12	13	6	7	8	8	9	10	11	15	16	17	18	19	41	42	43	44	45	46	47	48	49
congestum congestum	—	8	53	—	—	22	—	4	65	5	—	11	61	22	1	—	—	2	16	18	12	5	—	—	—
congestum albidum	—	18	—	1	—	14	—	1	17	—	—	1	7	9	3	—	—	1	3	1	2	2	4	2	—
austrinum austrinum (Rio Grande de Santiago)	5	44	10	—	1	52	—	2	65	13	1	7	35	34	6	—	1	—	3	5	15	17	9	—	—
austrinum austrinum (Rio Armeria)	—	19	1	—	—	20	—	—	37	2	—	—	15	23	—	—	—	—	6	5	5	2	1	1	—
austrinum milleri	—	5	23*	—	—	4*	—	—	8*	—	—	—	9*	3	—	—	—	—	—	—	1	1	2	—	1*
mascotae	—	28	—	—	—	23	1	1	35	10	—	—	10	24	12	1	—	1	3	7	6	4	3	—	—

* Holotype

table 24, fig. 3) described and figured a new species of *Moxostoma* which was allegedly taken from the Rio Grande at Juarez. DeBuen (1940: 11), Fowler (1945: 23) and Alvarez (1950: 42) based their accounts on Regan (1907). Clark Hubbs (1954: 278) identifies the type of *M. parvidens* with *M. erythrurum* on the presumption that the locality was in error. Although *erythrurum* and *congestum* belong to different subgenera and differ trenchantly in numerous features they have a similar body form. The description of Regan does not treat the diagnostic features although his listing of 14 dorsal rays (= 13) would not suggest *congestum* or *albidum.* Dr. N. B. Marshall of the British Museum of Natural History has kindly re-examined the two types of *parvidens* and notes that there are 12 (5-2-5) scales around the caudal peduncle, a feature of the subgenus *Moxostoma* to which *erythrurum* belongs. While the interradial membrances of the dorsal and caudal rays are darkened (as in *erythrurum*) the conspicuous black slashes of *congestum* and its allies (*robustum, mascotae, austrinum*) were not noted. Dr. Marshall further notes that Dr. Carl L. Hubbs had earlier examined the types and considered them specimens of *erythrurum.* We concur with this identification and note that the type locality is in error since *M. erythrurum* is not known south of the Red River drainage of Oklahoma; we have seen one specimen, USNM 77942 from Cache Creek in southwestern Oklahoma. As suggested by Hubbs (1954: 278) a mix up of localities must have occurred when these specimens were sent to the British Museum along with a collection from Kentucky, where *erythrurum* is common.

MOXOSTOMA AUSTRINUM (BEAN)

Description.—A fairly large species; the largest specimen at hand is 322 mm in standard length. The body is deep forward, being deepest at or slightly forward of the origin of the dosral fin. The dorsal profile is convex in front of the dorsal-fin origin and concave behind but the shift in curvature is not so marked as that seen in *congestum.* The ventral profile is relatively flat in front of the anus although the belly is somewhat swollen. Behind the anus the ventral contour slopes upward to the caudal-fin base; the slope is steepest along the base of the anal fin. The body is compressed; its depth greatly exceeds its width.

In lateral view the head is subconical. The depth of the head at the occiput slightly exceeds its breadth. Seen from above the snout is bluntly V-shaped. The eye is situated forward of the midpoint of the head. In normal position the large mouth is included. The mouth and lips are long and the lower lip is especially broad The two halves of the lower lip form a straight posterior margin or at most meet at a very obtuse angle. The upper lip is enlarged medially; the width of the lower lip at its midpoint equals the diameter of the eye and is nearly half the greatest distance across the mouth. The gape is generally a broad arc; it is not so U-shaped as in *mascotae.*

TABLE 2.

Measurements of Adult *Moxostoma* in Thousandths of Standard Length. The Range of Variation is Listed for Each Character with the Mean Below (No Differences Were Noted Between the Sexes).

Species	*austrinum*			*mascotae*	*congestum*	
		milleri				
Subspecies	*austrinum*	Holotype	Paratypes		*albidum*	*congestum*
Locality	Rio Lerma		Durango	Rio Ameca	Rio San Juan	Rio Grande
No. of specimens	10	1	5	14	3	4
Standard length in mm	109–186	138	224–235	95–209	142–191	127–202
Head length	225–268 250	244	232–268 246	233–278 250	234–261 247	248–259 252
Snout to occiput	166–203 188	180	168–194 180	178–217 192	178–189 185	192–212 202
Snout length	91–119 105	95	94–114 104	94–117 105	99–106 102	98–108 104
Eye length	43–50 47	46	34–43 39	41–59 47	44–49 47	46–50 48
Postorbital, least	64–86 77	83	77–89 83	78–110 88	70–81 76	74–78 75
Head depth at eye	136–154 147	141	143–155 150	125–155 136	146–158 153	151–163 156
Head depth at occiput	164–190 181	165	170–186 178	150–187 165	178–184 182	178–191 184
Body depth	232–264 238	228	221–241 230	196–243 214	244–270 256	250–296 270
Body width	134–165 154	149	153–178 166	122–149 135	175–200 186	155–172 164
Gape width	57–83 69	64	59–61 59	60–81 70	50–74 64	53–62 59
Caudal peduncle, least depth	94–108 101	89	85–96 91	83–112 94	99–109 104	105–111 108
Dorsal fin, height	175–205 198	184	164–180 172	180–234 199	198–204 202	178–210 193
Anal fin, height	213–227 218	216	178–249 212	214–258 230	212–243 224	205–234 218

The subspecies *milleri* and *austrinum* differ slightly in the details of the mouth.

The mid-section of the occipital line is truncate and reaches far forward as in *mascotae.*

The origin of the dorsal fin is nearer the snout tip than the posterior edge of the hypural plate. The pectoral fin is relatively short and its depressed tip does not approach a vertical projection from the dorsal-fin origin. In this feature *austrinum* differs from *mascotae* and *congestum.* The origin of the pelvic fin is closer to the anal opening than to the insertion of the pectoral fin and lies directly under the anterior half of the dorsal fin.

The intestine is an elongate coil which is directed toward the right in the ventral part of the body cavity. As noted above, this feature differs from the large, tight, spiral-shaped coils of *mascotae.* but little is known of the variability of intestinal configuration in this and other catostomid fishes. The peritoneum is silvery. The pharyngeal arch is similar to that of *mascotae.* Its lateral shelf is much reduced (narrower than the height of the inner teeth which are longest), a feature which sets *mascotae* and *austrinum* apart from *congestum.* The teeth gradually diminish in length and thickness toward the tip of the arch. Each tooth possesses a small hook at its tip. The posterior fontanelle is rectangular and well developed as in other *Moxostoma.*

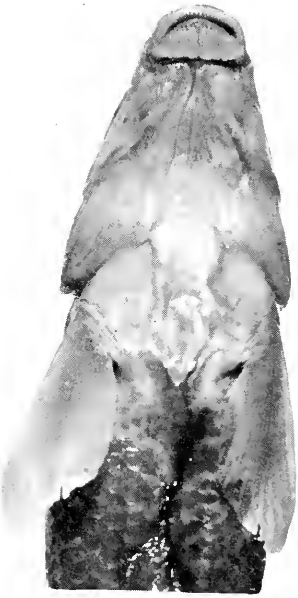
The tripus of *austrinum* has been described by Robins and Raney (1956: 35) and is similar to that of *mascotae.*

Fin-ray and lateral-line scale counts, and proportional measurements are given in tables 1 and 2.

Coloration.—The body is dark above; the dark extends ventrally almost to the paired fins. The lower surface of the body is light. Only along the lower portion of the caudal peduncle and on the lower third of the head is there a sharp division between the light ventral color and the dark dorsal color.

The scales of the dorsum and upper side are dusky throughout but the melanophores are concentrated along their edges. A dark wedge-shaped spot exists at the base of each scale. However, in contrast to *mascotae,* which also has dark scale bases, rows of spots are not a noticeable feature of the color pattern. Instead the entire side exhibits a dark diamond-shaped pattern. Generally, *M. a. austrinum* does not exhibit longitudinal streaking, since the lighter centers of the scales do not run together. *M. a. milleri* tends to be more streaked. The young and juveniles are not streaked and resemble *mascotae* in this respect. The mid-dorsal region of the young is darkest. An irregular blotch often is present before the dorsal-fin origin.

In adults the cheek and opercle are bicolored. The inner surface of the opercle is covered with melanophores. One feature of coloration which may distinguish *mascotae* and *austrinum* is the contrast in



Figures 5-8. **5**. (top left) *Moxostoma congestum albidum*, ventral view of the same specimen illustrated in figure 1; **6**. (top right) *Moxostoma austrinum milleri*, ventral view of the same specimen illustrated in figure 2; **7**. (bottom left) *Moxostoma austrinum austrinum*, ventral view of the same specimen illustrated in figure 3; **8**. (bottom right) *Moxostoma mascotae*, ventral view of the same specimen illustrated in figure 4.

color between the dorsal aspect of the head and nape. In *mascotae* the head is just as dark as the nape while in *austrinum* the head is distinctly lighter than the nape in the specimens examined.

In *mascotae* the medial portion of the dorsal-fin membrane is very dark, is less developed between the anterior rays and does not extend on the lighter distal third of the fin nor toward the basal quarter. When spread the fin shows a series of vertical dark slashes (the more posterior ones are darker. The caudal and anal fins are similar in pattern. This feature is typical of both sexes in *mascotae* but is very weakly developed in females of *austrinum*, and is far less striking in the males of *austrinum*.

Sexual dimorphism.—Dimorphism in fin shape is similar to that of *mascotae* which is described in detail below. The pattern of breeding tubercles is similar to that described below for *mascotae* but they are much less developed. Our specimens of *austrinum* were collected in March, however, and are perhaps not comparable.

Distribution.—*M. austrinum* is distributed along the Pacific coast of Mexico from the Rio Mezquital (the upper portion of the Rio San Pedro), Durango, to the upper tributaries of the Rio Armeria, Jalisco.

SUBSPECIES OF MOXOSTOMA AUSTRINUM

The population of *austrinum* in the Rio Mezquital differs in many features from those in the Rio Grande de Santiago (including the Rio Lerma) and in the Rio Armeria. Considering the constancy of meristic and other features in this genus the differences noted in the Rio Mezquital population are believed worthy of subspecific recognition. We take great pleasure in naming this subspecies after Dr. Robert R. Miller who has contributed much to our knowledge of Middle American ichthyology.

MOXOSTOMA AUSTRINUM **MILLERI** new subsp.

—*Myxostoma austrinum.*—Meek, 1904: xxxvii, 35 (in part, headwaters of the Rio Mezquital).

Moxostoma austrinum.—Regan, 1907: 146 (in part, Durango locality only), De Buen, 1940: 11 (in part, upper reaches of the Rio Mezquital), Robins and Raney, 1956: 9 (relationships).

Material examined.—All 59 specimens examined were taken in the Rio Mezquital basin in the vicinity of Victoria de Durango (Durango City), Durango, Mexico. The holotype, USNM 132446, female, 138 mm. in standard length, was taken at Rayar, about 5 mi. S. of Durango City on May 10, 1946 by Ralph G. Miller.

Taken with the holotype was a paratype, USNM 169889, 29 mm. S.L. Additional paratypes are UMMZ 173136 (2, 224-232). They are part of a collection taken May 5, 1939 from three localities near Durango City by C. L. Turner. The remainder of this series, UMMZ 173136 (53, 21-39) are very small specimens which are identified with this subspecies but are not designated paratypes. Additional material examined: UMMZ 161693 (2, 224-235), Rio Mezquital (or trib.), approximately 3 mi. S. of Durango City, Mexico, February 16, 1951, John T. Greenbank.

Diagnosis.—Dorsal rays usually 12, rarely 11. Lower lip full and plicate; the plicae are narrow, numerous (about 25) and tend to break up posteriorly. Some approach a semi-papillose condition. Pectoral and anal fins pointed (the pectoral fin has rays 3 and 4 longest rather than 4 and 5 as do other *Scartomyzon*). The distance from the midpoint of hypural to the pelvic-fin base when measured forward rarely reaches the posterior margin of the lower lip. Scales large; the dorsolateral scales from beneath the origin of the dorsal fin are as large in area as the eye.

The body features are illustrated in figures 2, 6 and 10 The fin-ray and scale counts and proportional measurements are given in tables 1 and 2.

Range.—Known only from the upper reaches of the Rio Mezquital in Durango, Mexico.

MOXOSTOMA AUSTRINUM AUSTRINUM (BEAN)

Myxostoma austrina.—Bean, 1880: 302-303 (description, type locality: Piedad in Morelia, = Michoacan).

Minytrema austrinum.—Jordan and Gilbert, 1883: 125 (compiled, based on Bean, 1880).

Moxostoma austrinum.—Woolman, 1894: 61 (Rio Lerma at Salamanca). Jordan and Evermann, 1896a: 192; 1896b: 242 (basin of the Rio Lerma - Rio de Santiago). Jordan and Snyder, 1900: 120 (Rio Verde. Aguascalientes and Rio Grande de Santiago near Atequiza; meristic data). Meek, 1902: 76 (La Palma Ocotlan and Lago de Chalco, all in the basin of the Rio Lerma). Regan, 1907: 146 (compiled; Aguacalientes and Ataquiza (sic) in Jalisco; Salamanca in Guanajuato; Lake Chapala, Morelia in Michoacan). Fowler, 1913: 57 (compiled). Jordan, Evermann and Clark, 1930: 110 (compiled. De Buen, 1940: 11 (in part, compiled; excluding Rio Mezquital).

Moxostoma austrina.—Eigenmann, 1893: 55 (Guanajuato).

Myzostoma austrinum.—Meek, 1904: xl, 35 (basin of the Rio Lerma).

Material examined.—Rio Lerma - Rio Grande de Santiago: USNM 23120 (1, 314) cotype of *M. austrina* Bean, collected at Piedad in Morelia (Michoacan) by A. Dugès. Hereby designated as lectotype. USNM 23121 (1, 322) a cotype, taken with the type. USNM 37821 (1, 209) collected later by A. Dugès apparently near the type locality. UMMZ 172231 (171, 12-184) Barranca de Barranquitos at Barranquitos, 74 mi. S.E. of Tepic, in Jalisco (el. 3200 ft.), R. R. Miller and J. T. Greenbank, March 26, 1955. SNHM 1028 (1, 64) Salamanca, A. J. Woolman. SNHM 6192 (10, 96-144) Aguascalientes, Rio Verde, J. O. Snyder.

Rio Armeria: UMMZ 172206 (1 ad, 175; 29 yg, 14-59) trib. of Rio San Pedro at bridge 9 mi. N. E. of Autlán, Jalisco (el. 3200 ft.), R. R. Miller and J. T. Greenbank.

Comparative diagnosis.—Only those features in which subspecies *milleri* and *austrinum* differ need be discussed here. The dorsal rays are usually 11, rarely 12 (see table 1). The plicae of lower lip are broader and less numerous (usually less than 20) and are entire. The pectoral and anal fins are more rounded in *austrinum* (rays 4 and 5 rather than 3 and 4 are longest) than in *milleri*. The distance from the posterior edge of the hypural to pelvic base when measured forward reaches the upper lip. The scales of *austrinum* are relatively smaller than those of *milleri* although this is not evidenced by scale counts. However scales taken from above the lateral line and below the dorsal-fin origin are decidedly smaller in area than the eye. Fin-ray counts and proportional measurements are given in tables 1 and 2. Dorsal and anal-ray counts listed by Jordan and Snyder (1900: 120) are added to our data in table 1. Their counts of lateral-line scales are somewhat higher than in specimens of *austrinum* examined by us; perhaps this reflects a difference in counting technique. These data (not added to our table) with the number of specimens in parentheses are: 45 (1), 46 (3), 47 (4), and 48 (4).

Distribution and habitat.—Widely distributed in the Rio Grande de Santiago above three thousand feet and in its upstream portion, the Rio Lerma. It has been recorded from the States of Jalisco, Aguascalientes, Guanajuato and Michoacan. Southward across the mountains it is herein recorded for the first time from the Rio Armeria which enters the Pacific Ocean in Colima. This system apparently marks the southernmost penetration of the genus.

Jordan and Snyder (1900: 115) describe the Rio Verde de Aguascalientes where specimens of *M. a. austrinum* were collected as follows: "The clear, cool water, shaded by trees and shrubs along the banks, winds here and there over a bed of fine gravel and sand. There are ripples and shallows, . . . , and many deep pools . . . "

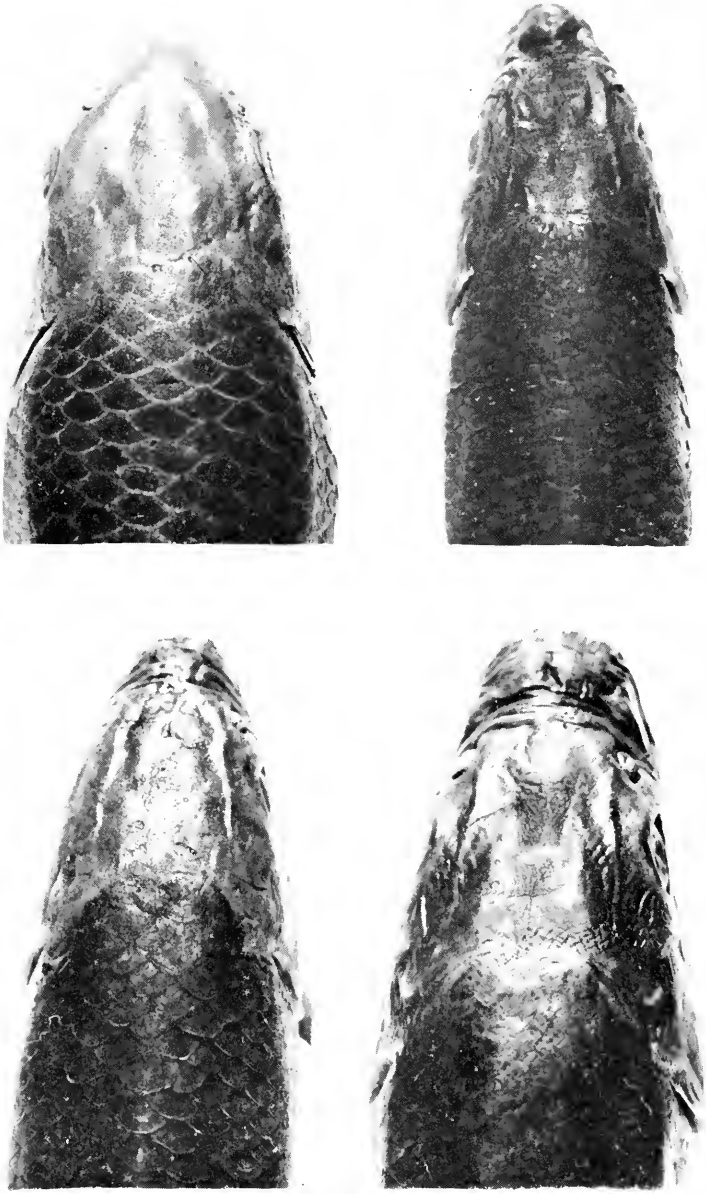
MOXOSTOMA MASCOTAE Regan

Moxostoma mascotae.—Regan, 1907: 145, 147, table 24, fig. 2 (original description, type locality: near the source of the Rio Mascota at a height of 4000 feet). Jordan and Evermann and Clark, 1930: 110 (compiled). Alvarez, 1950: 43 (translation from Regan). De Buen, 1940: 11 (compiled).

Material examined.—All collected by Robert R. Miller and John T. Greenbank. Mexico: UMMZ 172234 (19, 13-30) trib. Rio Ameca, about 1 mi. S.W. of Tetitlán, Nayarit (el. 2700 ft.), March 27, 1955; UMMZ 172125 (34, 19-210) Rio Ameca, 25 mi. by Hwy. 70 E. of Ameca Jalisco (el. 4300 ft.), February 27, 1955.

Diagnosis.—An elongate species with a flat ventral surface, subquadrate head, and large lips which are swollen and strongly plicate. Snout long and truncate. Pectoral fins elongate, apparently adapted for fast water and in this regard parallels species of *Hypentelium*. Fin membranes very dark. Dark wedge-shaped spots line the body and are especially noticeable on the first two rows of scales below the lateral line. Here the pattern is similar to that of *Minytrema melanops*. Dorsal rays number 11, a feature shared by *M. a. austrinum*, but distinct from the 12-rayed condition in *M. a. milleri*. Midline of dorsum midway between occiput and dorsal-fin origin with hard keel (formed by the anterior interneurals).

Description.—Apparently a small species, the largest seen by us is 210 mm in standard length. The body is decidedly elongate and compressed. Like related species the body is deep forward. The dor-



Figures 9-12. **9.** (top left) *Moxostoma congestum albidum*, dorsal view of the same specimen illustrated in figure 3; **12.** (bottom right) *Moxostoma mascotae*, dorsal view of the same specimen illustrated in trated in figure 2; **11.** (bottom left) *Moxostoma austrinum*, dorsal view of the same specimen illustrated in figure 1; **10.** (top right) *Moxostoma austrinum milleri*, dorsal view of the same specimen illus-
figure 4.

sal contour is strongly convex from the dorsal-fin origin to the eye. Due to the strong development of the snout large specimens tend to have the dorsal profile somewhat concave above the snout. The body narrows markedly dorso-ventrally under the dorsal fin. Between the dorsal fin base and the posterior end of the caudal peduncle the dorsal profile is straight or only slightly concave. The preanal ventral profile and the lower edge of the caudal peduncle is flat. The body deepens markedly under the anal-fin base.

The body is noticeably compressed; its depth at the origin of the dorsal fin greatly exceeds the greatest body width.

The head is subquadrate in lateral view. The head depth at occiput slightly exceeds the head width. The snout is bluntly V-shaped from above. The center of the eye is slightly in advance of the mid point of the head and is situated high on the side of the head. In lateral view the snout is truncate anteriorly.

The mouth is huge and occupies the full width of the lower surface of the head anteriorly. Both lips are strongly plicate. The plicae of the lower lip branch somewhat posteriorly. Juvenile specimens have well defined plicae whereas the largest specimens have the furrows less clear, the plicae more broken. In no sense however. does this mouth approach a papillose condition. The gape is almost semicircular; the upper lip curves far caudad laterally. The lower lip is broadly expanded but its posterior border is incised medially: the two lobes form a straight line or a very obtuse angle. In juveniles the lower lips are full. The posterior margin of the lower lip reaches a point directly under the anterior nostril. The upper lip is thickened medially.

The occipital line is located far forward and reaches to a point over the posterior edge of the cheek; its mid section is truncate. A dark occipital line continues downward on the shoulder. Ventrally it is wider and more conspicuous. It continues on the upper surface of the pectoral fin where it contrasts with the unpigmented first ray. The pigment is most intense behind the first ray and then fades slowly on the more posterior portions of the fin.

The position of the dorsal fin is subject to more variation than one generally associates with this feature. Its origin is most often slightly in front of the point midway between the snout and tip of hypural; in a few it is midway. It lies directly over the tip of the depressed pectoral and well in advance of the pelvic base. The pelvic origin is in advance of the middle of dorsal-fin base. The peritoneum is dark, becoming light posteriorly.

The dark intestine is curved on the right anteriorly. The pharyngeal arch is scythe-shaped with the lateral shelf almost lacking. Regan (1907) certainly was dealing with an incomplete or defective arch since there are easily more than 50 teeth per arch rather than 6 as he states. The inner teeth are best developed (the third tooth is largest in our example) and then the teeth gradually become shorter and thinner so that it is difficult to estimate the number near the tip of the arch. All teeth are strongly compressed and slightly hooked. The fontanelle is rectangular.

The tripus of a specimen of *mascotae* from the Rio Ameca, 25 mi. E. of Ameca was studied. This structure agrees with the description given by Robins and Raney (1956: 35) for *M. austrinum.* The inner margin of the shelf is high and convex.

Fin-ray and lateral-line scale counts, and proportional measurements are given in tables 1 and 2.

Coloration.—The dark of the dorsum extends to the first scale row below the lateral line and below gradually blends into the light belly. Each scale in the darkened portion of the body has a definite dark spot at the base. This is especially prominent in the adults. In smaller specimens the general dark color obscures the spots which are present. In half grown and young fish the scales are clear margined apically with a dark subterminal bar. This is less striking in the larger specimens. The coloration of the young (35 mm and less) is worthy of note. Robins and Raney (1956) have described the striking pattern of stripes which characterize young of the related *M. robustum.* In *mascotae* no streaks are present on the young except for a trace of dark pigment along the mid dorsum. Faint dark blotches are present at the origin of the dorsal fin, just behind the dorsal fin, and on top of the caudal peduncle; a pattern shared by many members of the genus. Juvenile specimens rarely show a faint suggestion of such blotching.

Horizontal streaks which are present even in the adults of *M. robustum* and *M. congestum* are not seen in *austrinum.* The prominent basal scale spot and subterminal vertical dark marks on the scales break up such a pattern and present a general dusky picture with the central regions of the scales being lighter.

The cheek is bicolored; dark pigment extends to below the lower margin of the orbit. The head is dark dorsally. The opercle and snout are generally dusky. The light of the lower cheek extends on to the more ventral aspect of the snout.

Sexual dimorphism.—Fins: In the male the pelvic fin is longer; its length when projected caudad from the pelvic tip, reaches the posterior end of the anal base or nearly so. In the female it falls near the anterior portion of the anal fin base. In the female the posterior edge of the pelvic fin when spread is truncate, the inner corner a rounded right angle. In its natural position the fin is rounded with the medial rays clearly the shortest. In the male the posterior edge of the fin when spread is oblique; the inner corner forms a rounded acute angle. In its natural position the fin appears pointed.

The pectoral fin is somewhat longer in the male than in the female. The male has a larger and more expanded anal fin; its tip is broadly rounded and in mature individuals reaches well beyond the end of vertebral column. In the female it falls short of this point and has an acute tip.

The dorsal fin shows marked sexual dimorphism. In development, this feature seems to be the first to exhibit sexual dimorphism clearly. The edge in the male is sigmoid, the posterior lobe broadly expanded and rounded. When fully spread the margin is almost straight. In the female the posterior lobe is straight edged and the anterior lobe more projecting so that the fin edge is clearly falcate.

Breeding tubercles: Observations were made on specimens taken in February; the tubercles are probably more pronounced at the height of the breeding season. Males of 100 mm have breeding tubercles well developed. Only the larger females have tubercles and these are small. In males the distal fourth of the anal fin is free of the tubercles in most instances, but they appear on each ray and become smaller toward the base of the rays. Some males have tubercles on tip of the anal rays but here the largest are almost one-fourth the way in from the tip. Ten or more tubercles may be present on the longer rays. In males, tubercles are present also on the caudal fin and are here best developed on the lower half of the fin. Scales on the ventral surface and lower sides of caudal peduncle bear tubercles. These may occur anywhere on the scale, and are not restricted to or even numerous on the edges. Small tubercles are scattered over the upper surface of rays of the pectoral and pelvic fins of the male. Minute scattered tubercles cover the entire upper half of head and snout. The dorsal fin, ventral surfaces of paired fins and body (except as noted) are free of tubercles in the male.

Large females have tubercles arranged on the anal fin as in males but they are much less developed. Smaller tubercles are scattered on the rays of the lower half of caudal fin and careful search may reveal a few on the upper surface of the paired fins. The body behind the anus including the entire caudal peduncle is tuberculate. These tubercles are neither pointed nor well defined but are very numerous, and cause a thickening of the entire surface of the scales on the lower half of caudal peduncle. There are far fewer tubercles on the dorsal half of the caudal peduncle and on the forward area above the anal fin. The head is not tuberculate.

Distribution.—*M. mascotae* is apparently restricted to the Rio Ameca and its tributary, the Rio Mascota, in Jalisco on the Pacific Slope of Mexico.

DISPERSAL AND RELATIONSHIPS OF THE MEXICAN SUCKERS OF THE GENUS *Moxostoma*

As we noted earlier (Robins and Raney, 1956: 37), the *robustum* species group is probably the most primitive in the subgenus *Scartomyzon.* The present distribution of this group presents a picture of geographically distant, remnant populations of a once continuous distribution.

Although one is tempted to explain this distribution by convergent evolution so many fundamental characters are shared by *robustum, congestum, austrinum* and *mascotae* that we feel confident the group is a natural one. Differentiation has been very slow as evidenced by the remarkable constancy of features from widely scattered localities.

M. mascotae and the two subspecies of *austrinum* differ as a unit from *congestum* and its subspecies in several features which we feel are indicative of a common ancestry. They seem to represent a single, old invasion of the Pacific slope by an ancestral *congestum* or *congestum-austrinum* stock. Such an opportunity may well have presented itself in some former pluvial period, although certainly not a recent one (*i.e.*, not in terms of Wisconsin glaciation). The Lerma-Santiago valley probably has served as the center for dispersal on the Pacific slope. The invasion of the Ameca basin by cross mountain capture occurred early since *mascotae* and *austrinum* are quite distinct. *M. mascotae* is apparently adapted for life in fast mountain rivers. It occurs at high elevations. Miller notes (*in litt.*) that the Ameca has a very interesting fish fauna with a high percentage of endemics on the plateau portion. In contrast, *austrinum* has apparently entered the Rio Armeria basin much more recently from the Rio Lerma by headland streams capture. The two populations have not differentiated.

The origin of *milleri* in the Mezquital basin is perplexing. Although we choose to retain it as a subspecies of *austrinum* it is well differentiated and the stock may be just as early in its origin from Rio Grande de Santiago stock as *mascotae*. The similarity to *austrinum* and *mascotae* in certain features of its anatomy we feel preclude an independent origin of *milleri* from *congestum* stock. Miller notes (*in litt.*) that although the lower portion of the Rio Mezquital (the Rio San Pedro) closely approaches that of the lower Rio Grande de Santiago, the fauna of the Lerma and the Rio Mezquital is wholly different in the Plateau and Coastal Plain portions of these drainages. For example, none of the 10 species (2 suckers, 3 minnows, 1 catfish, 1 cyprinodontid, 1 goodeid, 1 darter, and 1 atherinid) known from the Mezquital occurs on the coastal plain and similarly the fauna of the Lerma is very distinct from that of the lower part of the Rio Grande de Santiago. These faunal differences were also noted by Meek (1904, map opposite p. xlvii).

The barrier to downstream dispersal between these two systems is thus ecological as well as physical. The entrance of *austrinum* stock into the Mezquital must have been by a more upland capture and its subsequent isolation in the Mezquital has been of long duration.

The distribution of the forms of *congestum* does not pose any serious problems. The geographical relationships of these forms are treated above.

SUMMARY

The distribution, variation and relationships of *Moxostoma congestum*, *M. austrinum* and *M. mascotae* are treated. *M. albidum* is considered a subspecies of *congestum* and a new subspecies. *M. austrinum milleri* is diagnosed. With *M. robustum*, these species form a natural group within the subgenus *Scartomyzon.*

Morphological study suggests that the species of the Pacific slope of Mexico, *austrinum* (2 subspecies) and *mascotae*, are closer in their relationship than either one is to *congestum* of the drainage of the Gulf of Mexico. A common origin seems likely. The difference between the three forms found in the Pacific drainages reflect their long period of isolation since differentiation appears to progress slowly in this genus.

The southern limit of the known range of the genus *Moxostoma* is extended southward on the Pacific slope of Mexico to include the headwaters of the Armeria basin in Jalisco.

Moxostoma parvidens Regan is referred to the synonymy of *M. erythrurum.*

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ABSTRACT

Three species of *Moxostoma*, *congestum*, *austrinum* and *mascotae*, occur in Texas, New Mexico and Mexico. They are described in detail, their morphological variation noted and their distribution and relationships discussed. All belong to

the subgenus *Scartomyzon* of which *robustum* of southeastern United States is most closely related.

A new subspecies of *austrinum* is diagnosed and *M. albidum* is considered a subspecies of *congestum*.

M. austrinum and *M. mascotae* are the only members of the speciose genus, wide ranging in eastern North America, that occur on the Pacific Slope of North America. They are closely related and apparently resulted from a single transfer of fishes from Atlantic to the Pacific Slope during a past pluvial period.

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(New species and genera in boldface)

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