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A STUDY OF THE DISTRIBUTION AND TAXONOMY OF THE PERCID FISH *PERCINA NIGROFASCIATA* (AGASSIZ)

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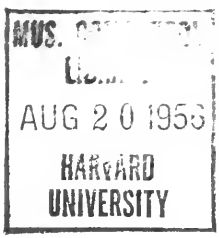

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A STUDY OF THE DISTRIBUTION AND TAXONOMY OF THE PERCID FISH *PERCINA NIGROFASCIATA* (AGASSIZ) [1]

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The writer became interested in species of *Percina* during a collecting trip throughout the southeastern United States in the spring of 1951. On this trip he was constantly impressed with the apparent adaptiveness to many different habitats of one of the species of *Percina* in particular, *Percina nigrofasciata* (Agassiz). We consistently collected this species from the black waters of the coastal plain, the rivers, streams and tributaries of the piedmont region, and the headwaters in the mountains. Not only did *P. nigrofasciata* occur in all of the aforementioned habitats, but seemed to vary in appearance from place to place.

Objectives

The objectives of this study were as follows: 1. What is the range and pattern of *P. nigrofasciata?* 2. Does this species vary throughout its range, or is it a stable form? 3. If variation is exhibited, by what characters are the differences expressed? 4. Where was the origin of this species, and by what routes did it disperse? 5. What are its relationships to other species of *Percina* throughout its range?

The study has uncovered a new subspecies here named *Percina nigrofasciata raneyi,* several intergrading populations, *P. n. nigrofasciata* X *P. n. raneyi,* and even further evidence of incipient speciation in the definition of eight well-defined races.

Ideas, based on the best evidence available at present, concerning the origin and dispersal of *P. nigrofasciata* are here expressed. Comparisons with other species of *Percina* are also included. Discussion of the above topics appears in the appropriately designated sections of the paper.

Methods

Several scale and fin counts were made. Specimens over forty millimeters in standard length were utilized in the majority of cases. However, in some drainages it was necessary to count specimens in the twenty to thirty millimeter range as larger individuals were not available.

Two counts were discarded during the course of the study. These were the number of scales on the mid-line of the belly of males and the number of anal rays. The former count is inconsistent due to the large number of adventitious scales present in many individuals. Whether belly scales were normal or adventitious was also difficult to determine. The anal ray count was eliminated after nearly five

[1] From a dissertation submitted in partial fulfillment of the requirements for the Ph. D. degree of the Graduate School of Cornell University.

hundred specimens had been counted with no appearance of consistent variation in specimens from any drainage. As a routine random samples from each additional drainage encountered were counted, and still no variation was observed. The number of anal rays (usually 9) in specimens of *P. nigrofasciata* appears to be a very stable character.

The scales and fin rays were counted according to Hubbs and Lagler (1947: 8-12).

In so far as possible, proportional measurements were taken on fishes between fifty-five and sixty-five millimeters in standard length. In some drainages, however, it was necessary to resort to larger and smaller individuals. In no instance was a specimen measured below forty-five millimeters in standard length. Representative samples from each drainage throughout the range were measured. This sample usually consisted of ten specimens from each drainage. In a few drainages from which the collections were small, less than ten specimens were measured. In the Apalachicola Bay drainage a large sample was available, and twenty specimens were measured. In the St. Johns drainage fifteen specimens were measured in order to have adequate data for comparison with *P. nigrofasciata westfalli,* which was described from this drainage on the basis of one specimen. Fifty males and fifty females were measured throughout the range of *P. nigrofasciata* to detect any apparent proportional sexual dimorphism (Table 10). No appreciable differences were present, so males and females are tabulated together in the tables of proportional measurements. For specimens of *P. n. raneyi,* ten males and ten females were compared (Table 10). Again, no appreciable differences were noted. Both sexes of this subspecies are also tabulated together.

Measurements were made with dial calipers which measured accurately to one tenth of a millimeter.

Proportions are expressed in millimeters, largely following the format of Hubbs and Raney (1939: 5-6).

Proportional measurements were for the most part, taken as described by Hubbs and Lagler (1947: 13-15).

Other proportional measurements were taken as described below:

Length of longest caudal ray; from the middle of the base of the hypural plate to the tip of the longest ray.

Distance; from the insertion of the most anterior pelvic fin ray to the union of the gill membranes.

Distance; from the tip of the mandible to the union of the gill membranes.

Distance; from the most anterior tip of the pelvic girdle to the union of the gill membranes.

Collections by drainage systems were summarized, tabulated and also presented in the form of graphs (figs. 1-8) according to Dice and Lerass (1936: 1-3) as modified by Hubbs and Perlmutter (1942: 582-92) and Hubbs and Hubbs (1953: 49-56, 92). The lone specimen from a direct tributary of the Mississippi River was not included in the plot of histograms in the graphs.

Material Examined

The following is an explanation of the symbols used in describing the material examined. The number of specimens and the range of standard length in millimeters are indicated in parentheses. In addition to standard compass directions, with the following "of" deleted, these abbreviations are used: Co. = County, R. = River, Cr. = Creek, trib. = tributary (of), Rtes. = routes, mi. = mile, Rd. = road, junct. = junction, Hwy. = highway, CU = Cornell University, UMMZ = University of Michigan, Museum of Zoology, USNM = United States National Museum, TU = Tulane University, FSU = Florida State University, FU = University of Florida, and KS = Kirk Strawn (private collection).

Mississippi River Drainage

Louisiana.—*West Feliciana Par.:* CU 16300 (1, 35), Alexander Cr., trib. Thompson Cr., 1.1 mi. E. junct. Rtes. 65 and 61.

Lake Pontchartrain Drainage

Louisiana.—*Tangipahoa Par.:* CU 21547 (1, 29) Natalbany Cr., 0.8 mi. W. Baptist; TU 2998 (1, 41), Tangipahoa R., 1 mi. E. Pontchatoula; TU 3933 (11, 32-90) Natalbany R., 0.7 mi. W. Baptist; TU 3740 (4, 51-68), Beaver Cr., 3.9 mi. S. Kentwood; B 40-89 (38, 46-80), Tchefuncte R., 10.5 mi. SW. Franklinton; B 40-88 (4, 34-40), Tangipahoa R., 1.5 mi. E. Amite. *St. Helena Par.:* TU 1076 (4, 56-65), trib. Tickfaw R., 3.3 mi. SW. Greensburg. **Mississippi.**—*Wilkinson Co.:* UMMZ 146616 (19, 43-82), trib. Amite R., 2 mi. S. Centerville; UMMZ 144713 (1, 42), trib. West Amite R.

Pearl River Drainage

Mississippi.—*Marion Co.:* CU 18862 (25, 48-64) trib. Pearl R., 8 mi. from Angie, La.; CU 16606 (8, 44-69), trib. Pearl R., 2.7 mi. N. Sandy Hook; TU 53 (4, 31-48), trib. Pearl R., 4.6 mi. N. Sandy Hook; TU 66 (3, 41-64), trib. Pearl R., 0.6 mi. N. La. State line; TU 87 (2, 46-48), trib. Pearl R., 1.2 mi. N. La. State line; TU 3967 (25, 37-64), trib. Pearl R., 4.8 mi. SE. Columbia; TU 160 (22, 22-52), trib. Pearl R., 2.5 mi. S. Hub, 8.5 mi. S. Columbia; TU 1729 (11, 35-70), Sweetwater Cr., 4.3 mi. N. Sandy Hook; TU 1864 (2, 47-51), Pearl R., 2.3 mi. E. Sandy Hook; TU 113 (13, 39-83), trib. Pearl R., 2.7 mi. N. Sandy Hook; TU 22 (1, 38), trib. Pearl R., 4.8 mi. SE. Columbia; TU 3875 (2, 57-60), trib. Pearl R., 1.7 mi. S. Sandy Hook; TU 1793 (11, 40-77), Sweetwater Cr., 4.3 mi. N. Sandy Hook. *Pearl River Co.:* CU 16606 (2, 38-41), 2.7 mi. N. Sandy Hook; TU 1635 (5, 44-49), 4.6 mi. N. junct. Rtes. 43 and 26; TU 1552 (4, 36-66), 5.7 mi. W. Angie; TU 3374 (3, 59-68), Lots Cr., 6 mi. NW. Picayune; UMMZ 163703 (1, 62), trib. Wolf R., 3 mi. NE. Poplarville; UMMZ 166132 (4, 27-48), Hobolochitto Cr., 0.9 mi. N. Picayune. *Lincoln Co.:* UMMZ 161165 (8, 33-64), Little Bahala Cr., 3.5 mi. E. Brookhaven; UMMZ 161183 (1, 48), Big Cr., 0.5 mi. N. Bogue

Chitto; UMMZ 161191 (3, 57-62), stream, 2.5 mi. N. Bogue Chitto; CU 16267 (7, 35-49), trib. Pearl R., 8.8 mi. W. Monticello. *Walthall Co.:* UMMZ 155358 (1, 66), Bogue Chitto R., 7 mi. W. Tylertown; UMMZ 144441 (1, 43), Copiah Cr., trib. Pearl R.; UMMZ 155374 (7, 41-64), trib. McGee Cr., 4.3 mi. SSW. Tylertown. *Copiah Co.:* UMMZ 144445 (3, 18-20), Beaver Dam Cr., trib. Bahala Cr. *Pike Co.:* UMMZ 113782 (1, 41), trib. Bogue Chitto R., 3 mi. N. Summitt. **Louisiana.**—*Washington Par.:* CU 16328 (2, 38-41), Bogue Lusa, 9.6 mi. E. Franklinton; TU 1552 (4, 36-66), trib. Pearl R., 5.7 mi. W. Angie; TU 1176 (2, 32-52), Pushepatapa Cr., 8.2 mi. N. Bogalusa, 0.8 mi. S. Varnado; TU 1151 (20, 32-52), trib. Pearl R., 3 mi. N. Bogalusa; TU 3602 (6, 24-48), trib. Pearl R., 8.5 mi. W. Angie; TU 2894 (4, 35-53), Bogue Chitto, 0.7 mi. W. Warnerton; TU 3828 (26, 32-80), Pushepatapa Cr., 8.2 mi. N. Bogalusa; TU 3237 (2, 21-34), trib. Pearl R., 11.8 mi. W. Angie. *St. Tammany Par.:* TU 730 (25, 43-65), trib. Pearl R., 1 mi. N. Talisheek; UMMZ 166155 (16, 32-56), cr. on Rte. 58, 0.3 mi. N. Talisheek.

Pascagoula River Drainage

Mississippi.—*Lamar Co.:* CU 15638 (12, 38-73), trib. Black Cr., 6.9 mi. W. Forrest Co. line, 7.9 mi. W. Hattiesburg city limits; TU 1620 (3, 41-57), Red Cr., 0.3 mi. N. Lumberton Hwy.; UMMZ 163725 (21, 26-63), Black Cr., below US Hwy. 11 bridge, 10 mi. SW. Hattiesburg, 4 mi. NNE. Purvis. *Clarke Co.:* CU 11763 (25, 49-85), trib. Chunky Cr., 0.6 mi. N. Enterprise; UMMZ 157797 (1), Chickasawhay R., 1 mi. N. Enterprise; UMMZ 157795 (1, 42), Wier Cr., trib. Chickasawhay R. *Forrest Co.:* CU 15668 (12, 36-57), trib. Leaf R., 3.7 mi. N. Hattiesburg; CU 12647 (3, 47-52), Pascagoula R., 6.5 mi. NW. Forrest and Perry Co. line, Rte. 24; CU 12658 (11, 39-58), Pascagoula R., 6.5 mi. NW. Forrest and Perry Co. line, Rte. 21; TU 1560 (6, 38-59), Priests Cr., 0.6 mi. S. junct. Rte. 49 and business section Hattiesburg. *Covington Co.:* CU 12583 (1, 50), trib. Bowie Cr., 10.9 mi. W. Collins. *Wayne Co.:* CU 16251 (3, 48-63), trib. Chickasawhay Cr., 11.9 mi. NW. Bucatunna; CU 16238 (1, 68), trib. Chickasawhay Cr., 7.2 mi. NW. Bucatunna. *Jackson Co.:* TU 568 (3, 31-48), trib. Pascagoula R., 3.6 mi. N. Wade. *George Co.:* TU 1136 (1, 72), Rocky Cr., 3.4 mi. SE. Lucedale; UMMZ 155792 (3, 53-71), trib. Escatawpa R., 3.3 mi. E. Lucedale. *Jasper Co.:* UMMZ 157815 (4, 19-46), trib. Big Bogue Homo R., 3.5 mi. NNW. Sandersville. **Alabama.**—*Mobile Co.:* CU 12467 (6, 47-85), Escatawpa R., Big Cr., 5.3 mi. W. Semmes on Rte. 42; TU 59 (6, 40-67), trib. Escatawpa R., 6.8 mi. E. Hurley.

Mobile Bay Drainage

Alabama.—*Mobile Co.:* CU 12637 (3, 48-58), trib. Chickasaw Cr., 5.2 mi. E. Semmes; CU 16657 (14, 44-72), Clear Cr., 4.7 mi. E. Semmes; TU 2061 (3, 25-51), Sand Hill Cr., trib. Chickasaw Cr., 6.7 mi. S. Citronelle; TU 1640 (2, 40-49), Cedar Cr., trib. Tombig-

bee R., 8.7 mi. W. Mount Vernon; UMMZ 155466 (5, 42-53) Cr., trib. Chickasaw Cr., 5.5 mi. SE. Semmes; UMMZ 86300 (3, 50-75), near Mobile Ala. *Washington Co.:* CU 16167 (3, 40-61), Gaines Cr., trib. Bassett Cr., 2.8 mi. S. Leroy; TU 1816 (3, 35-52), Bilboa Cr., trib. Tombigbee R., 12.6 mi. S. Wagarville. *Baldwin Co.:* CU 16659 (1, 47), trib., 2.5 mi. E. junct. Rtes. 90 and 31, 10 mi. E. Mobile; CU 16669 (10, 33-55), trib. Fish R., 10.2 mi. W. Roberts Dam; TU 3680 (2, 34-46), trib. 9.2 mi. WNW. Loxley; TU 3090 (6, 34-60), trib. 0.3 mi. S. junct. Rtes. 90 and 89, 3.6 mi. N. Daphne; TU 1774 (2, 43-69), trib. Fish R., 2.1 mi. SE. crossroads at Malbis Restaurant, 5.1 mi. NW. Loxley; TU 3158 (2, 34-61), trib. Fish R., 6.1 mi. E. junct. Rtes. 104 and 89. *Butler Co.:* TU 3201 (1, 43), Pine Barren Cr., 2.5 mi. S. Forest Home. *Wilcox Co.:* TU 2572 (1, 53), Big Turkey Cr., trib. Pine Barren Cr., 0.8 mi. W. Allen; TU 3436 (10, 51-67), Pursley Cr., trib. Alabama R., 3.4 mi. SW. Camden; TU 3064 (1, 50), trib. Pursley Cr., 1.8 mi. E. Camden. *Clarke Co.:* TU 2617 (2, 51-52), Bassett Cr., trib. Tombigbee R., 0.5 mi. E. Wheatley. *Montgomery Co.:* API 601 (4, 46-70), Line Cr., S. Montgomery; UMMZ 128769 (5, 43-68), Line Cr. (Oakfuskee Cr.), near Montgomery-Mason Co. line. *Lee Co.:* API 589 (1, 45), Loblockee Cr., 8 mi. N. Auburn; UMMZ 160895 (1, 43), Saugahatchee Cr., 3.0 mi. NW. Loachapoka. *Macon Co.:* API 608 (2, 59-62), Sand Springs; API 585 (3, 41-55), 3 mi. E. Tuskegee; UMMZ 111239 (1, 61), 3 mi. E. Tuskegee on Columbus Rd.; UMMZ 123986 (1, 55), Big Swamp, 5 mi. SE. Tuskegee. *Marion Co.:* UMMZ 166390 (1, 55), Luxapallila Cr., 2 mi. W. Winfield. *Lamar Co.:* UMMZ 113908 (2, 21-46), Luxapallila Cr., 7 mi. SW. Vernon. *Autauga Co.:* UMMZ 146538 (1, 53), trib. Beaver Cr., 5 mi. W. Autaugaville. *Perry Co.:* UMMZ 110500 (1, 86), trib. Cahaba R., Federal Hatchery Grounds, Marion. *Counties unknown:* UMMZ 111236 (2, 41-43), Saugahatchee Cr.; UMMZ 111234 (1, 55), Sucarnoochee Cr., trib. Tombigbee R., SE. Coatopa. **Mississippi.**—*Monroe Co.:* UMMZ 157449 (2, 27-29), Tombigbee R., 2.5 mi. N. Amory.

Black Warrior River Drainage

Alabama.—*Tuscaloosa Co.:* CU 21885 (1, 38), Carrol Cr., 8 mi. N. Northport; CU 21893 (1, 55), Blue Cr., 25 mi. N. Tuscaloosa Co. line on Crab Rd.; CU 21913 (1, 45), Pyro Cr., 4 mi. E. New Lexington, 1 mi. N. Sterling; CU 22047 (5, 33-57), 16.2 mi. N. Black Warrior R. Bridge at Tuscaloosa; CU 19621 (10, 37-59), Lower Cottondale Cr. near entrance to Hurricane Cr.; CU 13788 (10, 40-82), trib. Black Warrior R., at E. city limits Cottondale; CU 21917 (7, 40-66), trib. Black Warrior R., 29 mi. NE. Northport, 3 mi. NE. North River Bridge; TU 4161 (2, 28-31), above Lock 9, 17.5 mi. SSW. Tuscaloosa; UMMZ 166374 (3, 36-61), trib. 11.2 mi. N. Tuscaloosa, 5.5 mi. S. Samantha; UMMZ 166364 (3, 38-49), trib. 5 mi. N. Tuscaloosa. *Hale Co.:* CU 22048 (1, 55), S. Branch Big Brush Cr., 1 mi. N. Sawyersville; CU 21904 (2, 40-45), N.

Branch Hines Cr., 3 mi. S. Sawyersville; CU 21911 (2, 40-45), SE. fork Hines Cr., 3 mi. S. Sawyerville; CU 21887 (3, 30-50), in Moundville. *Jefferson Co.:* CU 21918 (2, 62-65), Mud Cr., 10 mi. E. Lock 17, 3 mi. W. Oak Grove. *Blount Co.:* USNM 162303 (6, 53-93), trib. Mulberry Fork, Blount Springs, 7.7 mi. SW. Garden City; UMMZ 158289 (8, 26-74), trib. Locust Fork, 3 mi. NNE. Oneonta. *Cullman Co.:* UMMZ 158263 (20, 32-72), Duck Cr., trib. Mulberry Fork, 12.7 mi. NE. Cullman. *Green Co.:* CU 13992 (1, 32), trib. Black Warrior R., 10.1 mi. E. Eutaw.

Coosa River Drainage

Alabama.—*Cherokee Co.:* CU 18588 (2, 20-59), Cowans Cr., trib. Coosa R., 7.4 mi. WNW. Forney, 6.5 mi. SE. Centre; CU 21157 (1, 65), trib. Terrapin Cr., at Cherokee-Calhoun Co. line; UMMZ 157945 (3, 59-93), small stream S. part Canton. *Talledega Co.:* CU 21260 (2, 49-52), Cheaha Cr., 3.3 mi. SW. Munford; UMMZ 139138 (14, 26-67), Talledega Cr., about 4 mi. S. Talledega. *Etowah Co.:* UMMZ 96775 (1, 48), Coal Cr., about 5 mi. from Gadsden (prob. Cone Cr.); USNM 16233 (3, 56-63), Coosa R., 6.4 mi. SW. Attalla. **Georgia.**—*Bartow Co.:* CU 11799 (4, 54-73), Stamp Cr., 0.3 mi. above junct. with McKaskey Cr.; CU 21279 (1, 69), trib. Etowah R., 3.9 mi. W. Kingston; CU 21234 (1, 53), trib. Etowah R., 7.7 mi. S. Adairsville; UMMZ 157933 (1), Alatoona Cr., 8.2 mi. SE. Cartersville. *Murray Co.:* CU 21192 (2, 53-9), Conasauga R., Whitfield-Murray Co. line. *Gordon Co.:* CU 18231 (1, 47), Sallacoa Cr., trib. Oostanula R., 6.5 mi. E. Sonoraville; UMMZ 239127 (3, 19-22), Oostanula R., at mouth of Spring Branch. *Cobb Co.:* CU 17644 (10, 45-91), trib. Alatoona Cr., 3.9 mi. NW. Kennesaw; CU 21178 (5, 44-59), trib. Alatoona Cr., 0.4 mi. SE. Acworth; UMMZ 88288 (2, 59-60), E. branch Alatoona Cr., 1.1 mi. S. Acworth. *Floyd Co.:* CU 17418 (1, 71), trib. Oostanula R., 11.7 mi. NE. Rome; USNM 162377 (3, 59-80), trib. Coosa R., 12 mi. SW. Rome; UMMZ 88268 (5, 15-57), Spring Cr., about 10 mi. E. Rome; UMMZ 88232 (1, 28), trib. Coosa R.; UMMZ 88242 (1, 28), Armuchee Cr. *Dawson Co.:* CU 21329 (1, 51), Amicalola Cr., 3.4 mi. W. junct. Rtes. 183 and 53; UMMZ 88222 (1, 39), trib. Conosauga R., 15 mi. W. Cleaveland. **Alabama.**—*Escambia Co.:* CU 11834 (5, 36-45), Bushy Cr., trib. Perdido R., 2.9 mi. SW. Atmore. **Florida.**—*Escambia Co.:* TU 1781 (13, 33-58), trib. Perdido R., 4.6 mi. N. Muscogee; TU 1786 (1, 52), trib. Perdido R., Meatosia Cr., 0.1 mi. N. junct. Rtes. 99 and 196; UMMZ 134606 (2, 45-63), Perdido Cr., near Pineville; UMMZ 166174 (6, 28-47), Jach Branch, 3 mi. N. Muscogee; UMMZ 166189 (6, 33-50), small Cr., 4.5 mi. N. Muscogee.

Conecuh-Escambia Rivers Drainage

Alabama.—*Escambia Co.:* CU 14005 (25, 45-62), Franklin Mill Cr., 3.9 mi. SW. Brewton; CU 13972 (2, 35-38), Escambia Cr., trib. Escambia R., 2.4 mi. W. Pollard; UMMZ 163555 (19, 20-46), Big

Escambia Cr., below Rte. 31 bridge, Flomaton; UMMZ 155517 (3, 44-48), Bear Cr., 21 mi. S. Castleberry. *Pike Co.:* CU 14037 (4, 49-53), trib. Conecuh R., 8.2 mi. W. Troy *Conecuh Co.:* CU 16148 (5, 46-65), Jay Branch, Mill Cr., 2.4 mi. E. Evergreen; CU 16202 (8, 44-76), Boggy Branch, trib. Sepula R., 4.8 mi. SW. McKensie. *Crenshaw Co.:* TU 2584 (4, 49-56), trib. Patsaliga R., 2.0 mi. W. Luverne. *Butler Co.:* UMMZ 139157 (3, 33-70), Rocky Cr., 1.0 mi. N. Georgiana, 2.8 mi. S. Chapman; UMMZ 88728 (1, 32), Persimmon Cr.

Blackwater River Drainage

Florida.—*Okaloosa Co.:* CU 12663 (1, 44), Blackwater R., 4.3 mi. NW. Baker; CU 16710 (25, 45-70), trib. Blackwater R., 100 yds. E. Santa Rosa-Okaloosa Co., line. *Santa Rosa Co.:* CU 12603 (5, 41-46), W. fork Coolwater Cr., trib. Blackwater R., 3.5 mi. E. Jay; CU 16682 (6, 43-55), trib. Coldwater Cr., 13.1 mi. N. Milton; CU 16689 (10, 35-65), trib. Blackwater R., 8.7 mi. E. junct. Rtes. 87 and 4; UMMZ 155504 (1, cr. at Milton; UMMZ 16531 (44, 23-69), Sweetwater Cr., trib. Juniper Cr., trib. Blackwater R., near Munson; UMMZ 166221 (1, 44), small cr., 3 mi. NE. Milton.

Yellow River Drainage

Florida.—*Walton Co.:* CU 12124 (10, 48-64), trib. Shoal R., 5.9 mi. NW. De Funiak Springs; CU 20749 (14, 43-59), trib. Shoal R., 6.6 mi. S. Florida; TU 1746 (13, 33-62), Pine Log Cr., 9.1 mi. E. Rte. 85; TU 1725 (1, 53), Middle Cr., 0.8 mi. SE. Liberty: UMMZ 166248 (4, 48-61), Pond Cr., 4 mi. SW. Florala, Ala.; UMMZ 166352 (18, 26-59), Big Swamp Cr., at Liberty. *Okaloosa Co.:* CU 12155 (1, 34), Yellow R., 3.2 mi. E. Crestville; TU 3150 (3, 48-57), trib. Yellow R., 2.9 mi. E. Rte. 85; TU 3715 (5, 28-42), trib. Yellow R., 2.7 mi. E. Blackman; UMMZ 110482 (2, 40-57), Bull Cr., trib. Yellow R., 11 mi. NE. Niceville.

Choctawhatchee River Drainage

Alabama.—*Dale Co.:* CU 16120 (2, 60-61), trib. Claybank Cr., 2.0 mi. W. Ozark; TU 3705 (1, 55), trib. 7.2 mi. NNW. junct. Echo Farm Rd. and Rte. 136; TU 4034 (1, 62), trib., 3.7 mi. W. junct. Rtes. 66 and 84, 1.7 mi. E. Clayhatchee; UMMZ 88689 (4, 23-48), 9 mi. S. Ozark. *Henry Co.:* CU 17146 (3, 46-52), Choctawhatchee R., 5.0 mi. W. Grabell; TU 3903 (1, 40), Blackwood Cr., 3.0 mi. NW. Echo Farm Rd. *Houston Co.:* CU 20747 (7, 49-74), trib. Choctawhatchee R., 5.7 mi. W. Dothan; TU 2504 (3, 36-46), Panther Cr., trib. Little Choctawhatchee R., 3 mi. W. Pinckard Farm Rd. *Geneva Co.:* TU 2386 (4, 38-56), trib. Choctawhatchee R., 2.8 mi. N. Hartford; TU 2422 (5, 39-64), trib. Choctawhatchee R,, 1.8 mi. N. Black; TU 1698 (1, 51), trib. Choctawhatchee R., 5.2 mi. N. Black; TU 2438 (1), Adams Cr., 6.5 mi. S. Bellwood. *Pike Co.:* TU 3209 (8, 43-59), trib. Buckhorn Cr., 7.1 mi. S. Perote. **Florida.**—*Holmes Co.:* CU 12115 (8, 36-67), Sandy Cr., trib. Choctawhatchee

R., Ponce de Leon; CU 20748 (2, 56-65), Holmes Cr., 4 mi. E. Bonifay; CU 20750 (6, 38-62), trib. Choctawhatchee R., 7.2 mi. E. De Funiak Springs; TU 1585 (25, 40-69), Holmes Cr., trib. Choctawhatchee R., S. limits Ponce de Leon; TU 187 (4, 39-62), trib. Choctawhatchee R., 4.7 mi. SSE. Geneva; TU 2457 (2, 39-42), East Pittman Cr., 1.5 mi. N. Miller Crossroads; Tu 1095 (2, 41-45), Pine Log Cr., trib. Choctawhatchee R., 12.4 mi. SSW. Geneva; TU 2275 (50, 34-72), trib. Choctawhatchee R., 3.5 mi. NW. junct. Rtes. 79 and 77; TU 3357 (3, 33-37), Blue Cr., Ponce de Leon; TU 2480 (5, 44-60), Little Cr., trib. Ten Mile Cr., 6.5 mi. NNW. junct. Rtes. 79 and 177; FSU 119 (53, 55-67), Wrights Cr., 5.9 mi. N. Bonifay; UMMZ 163504 (13, 30-67), Blue Cr., Ponce de Leon; UMMZ 166302 (2, 52-56), Wrights Cr., 2.6 mi. W. Graceville; UMMZ 166319 (46-76), Parrott Cr., 6 mi. SW. Geneva. *Walton Co.:* TU 1692 (1, 56), Turnpike Bridge, Camp Cr., trib. Black Cr., 3.6 mi. E. Freeport; TU 306 (3, 45-60), Four Mile Cr., trib. Lafayette Cr., 0.7 mi. W. Freeport; TU 1072 (5, 35-44), Black Cr., 1.5 mi. W. Bruce; FSU 127 (4, 44-59), Lafayette Cr., 0.7 mi. E. Freeport. *Okaloosa Co.:* TU 2078 (19, 38-93), Toms Cr., 1 mi. SW. Valparaiso. *Washington Co.:* TU 3644 (10, 25-58), Pine Log Cr., 2.5 mi. SE. Ebro; TU 1099 (2, 52-66), trib. Holmes Cr., 8.5 mi. W. Chipley; FSU 120 (5, 42-71), Pine Log Cr., 2.5 mi. S. Ebro.

St. Andrews Bay Drainage

Florida.—*Bay Co.:* CU 12563 (1, 37), trib. Bear Cr., 0.5 mi. W. Youngstown; CU 12670 (1, 59), Econfina R., 8.2 mi. W. Youngstown; TU 79 (3, 44-63), trib. Econfina R., Youngstown.

Apalachicola Bay Drainage

Alabama.—*Russell Co.:* CU 11838 (5, 33-64), trib. Little Uchee Cr., 0.9 mi. E. Crawford; CU 16193 (5, 34-62), Uchee Cr., trib. Chattahoochee R., 9.2 mi. S. Phoenix City; CU 15828 (11, 42-55), trib. Hatchehubee Cr., 4.0 mi. SW. Seale; CU 13978 (10, 38-56), trib. Uchee Cr., 3.1 mi. W. Marvyn; UMMZ ..... (22, 20-59), Watoolee Cr., trib. Uchee Cr., S. Marvyn. *Barbour Co.:* CU 16100 (1, 51), trib., Chattahoochee R., 5.1 mi. SW. Eufala; CU 16107 (2, 31-53), trib. Chattahoochee R., 9.8 mi. SW. Eufala; CU 16089 (1, 44), Barbour Cr., trib. Chattahoochee R., 2.3 mi. S. Eufala. *Henry Co.:* CU 17484 (3, 50-57), trib. Abbie Cr., 1.2 mi. E. Abbieville. *Houston Co.:* CU 17768 (1, 47), Chipola R., 0.9 mi. NW. Grangeburg; CU 17664 (24, 37-68), Osmussee Cr., 5.8 mi. NE. Dothan; TU 2317 (3, 21-62), Irwin Mill Cr., trib. Chattahoochee R., 1.9 mi. N. Rte. 2 on dirt rd.; TU 2339 (15, 40-74), Howards Mill Cr., 1.2 mi. SE. Gordon; TU 3320 (2, 51-64), Bryans Cr., trib. Chattahoochee R., 3.4 mi. S. junct. Rtes. 2 and 83; TU 2320 (5, 42-48), trib. Chattahoochee R., 4.2 mi. N. Gordon; TU 2339 (3, 48-62), trib. Chattahoochee R., 1.0 mi. N. Gordon; TU 2527 (4, 40-46), trib. Chattahoochee R., 4.6 mi. N. Gordon; UMMZ 128751 (10, 39-62), Brush

Cr., trib. Uchee Cr., S. Marvyn. *Lee Co.:* CU 15998 (4, 50-84), Uchee Cr., trib. Chattahoochee R., 0.7 mi. E. Marvyn; UMMZ 111235 (1, 65), 6 mi. W. Auburn. **Georgia.**—*Hall Co.:* CU 15808 (17, 42-60), trib. Upatoi Cr., 6.9 mi. S. Talbottom; CU 19821 (3, 57-65), trib. Chestatee R., 1 mi. SE. Murrayville; CU 11007 (9, 37-69), trib. Chattahoochee R., 6 mi. N. Gainesville. *Stewart Co.:* CU 17115 (1), Pataula Cr., 12.3 mi. N. Cuthbert; CU 15874 (1, 52), Hodghodkee Cr., trib. Pataula Cr., 19.4 mi. N. Cuthbert; CU 17777 (10, 32-85), Hannahatchee Cr., 8.1 mi. N. Lumpkin. *Habersham Co.:* CU 17435 (11, 56-77), trib. Chattahoochee R., 2.7 mi. E. of Chattahoochee R.; CU 22055 (16, 40-62), Tenner Branch near Cornelia; CU 17438 (8, 52-79), trib. Soque R., 1 mi. W. Soque; CU 10930 (1, 43), trib. Soque R., 3 mi. NE. Clarksville. *Lumpkin Co.:* CU 10991 (4, 48-73), Cane Cr., 1.6 mi. WSW. Dahlonega; CU 17163 (4, 60-72), trib. Chattahoochee R., 2.2 mi. W. Fort Gaines; CU 19620 (20, 38-63), Chestatee R., at mouth Yahoola Cr., 2.1 mi. SE. Dahlonega; CU 10997 (24, 54-62), Chestatee R., at Walnut, 9 mi. NNE. Dahlonega; CU 21415 (2, 52-54), Cane Cr., 1.5 mi. SW. Dahlonega; CU 21451 (33), Yahoola Cr., 1.1 mi. E. Dahlonega; CU 19629 (11, 41-66), Wards Cr., trib. Yahoola Cr., 4 mi. NE. Dahlonega; CU 19805 (30, 41-75), Yahoola Cr., 1 mi. E. Dahlonega; UMMZ 136091 (14, 19-60), Chestatee R., 9.5 mi. NW. Cleveland; UMMZ 94585 (3, 33-45), Chestatee Cr., headwater Chattahoochee R.; UMMZ 136090 (9, 35-53), trib. Chattahoochee R., below Rte. 43, E. Dahlonega; UMMZ 157962 (3, 31-42), Cane Cr., trib. Chestatee R., 1.3 mi. WSW. Dahlonega. *Early Co.:* CU 20751 (12, 37-90), trib. Chattahoochee R., 9.1 mi. W. Donaldsonville; UMMZ 88684 (8, 25-43), trib. Chattahoochee R. *Harris Co.:* CU 17517 (1), trib. Mulberry Cr., 7.7 mi. E. Hamilton; CU 17530 (25, 43-79), trib. Mulberry Cr., 0.5 mi. W. Hamilton; UMMZ 157879 (2, 28--43), Mulberry Cr., 3.5 mi. S. Hamilton; UMMZ 157886 (1, 58), Mountain Cr., 2.5 mi. SE. Chipley; UMMZ (5, 65-70), Chattahoochee R., 4 mi. above Helen. *Troup Co.:* UMMZ 157895 (2, 35-37), Flat Shoal Cr., 7.2 mi. SW. Chipley. *Fulton Co.:* CU 17533 (1, 45), Nancy Cr., on Wieuca Rd., 2 mi. N. Buckhead; CU 17126 (3), Vickery Cr., at junct. with Chattahoochee R., at city limits of Roswell; UMMZ 88299 (2, 35-38), Nancy Cr., 10 mi. N. Atlanta. *Henry Co.:* CU 17762 (1, 43), trib. Abbie Cr., 2.6 mi. S. Abbieville; CU 17484 (3, 50-57), trib. Abbie Cr., 1.2 mi. E. Abbieville. *Lee Co.:* CU 15998 (4, 50-84), Uchee Cr., trib. Chattahoochee R., 0.7 mi. E. Marvyn. **Florida.**—*Calhoun Co.:* TU 2047 (1, 59), trib. Apalachicola R., 2.9 mi. NE. Blountstown; FSU 124 (10, 41-54), Four Mile Cr., 0.6 mi. N. Clarksville; FSU 125 (6, 45-55), Ten Mile Cr., 4.7 mi. N. Clarksville. *Jackson Co.:* TU 2374 (110, 40-64), Russ Cr., trib. Waddells Mill Cr., 6.3 mi. S. Campbellton; TU 3220 (6, 39-60), trib. Chipola R., 7.2 mi. SE. Marianna; TU 2568 (6, 38-53), trib. Chipola R., 1.1 mi. S. Marianna. *Bay Co.:* CU 18150 (1, 56), cr., 8.2 mi. E. junct. Rtes. 98 and 22, toward Wewahitchka; CU

18121 (2, 37-39), Sandy Cr., W. Wewahitchka. *Gadsden Co.:* UMMZ 166267 (23, 40-78), Mosquito Cr., 1.5 mi. E. Chattahoochee.

Flint River Drainage

Georgia.—*Sumter Co.:* CU 22099 (21, 38-65), trib. Muckalee Cr., 3.4 mi. N. junct. Rtes. 19 and 280 at city limits of Americus; CU 15841 (2), trib. Flint R., 13.9 mi. NE. Americus. *Talbot Co.:* CU 21131 (2, 51-60), trib. Lazier Cr., 2.9 mi. W. Talbottom. *Baker Co.:* CU 17317 (10, 40-77), Coolawahee Cr., trib. Flint R., 1.3 mi. N. Newton; UMMZ 164071 (4, 38-58), Chickasawatchee Cr., 5 mi. S. Calhoun Co. line, 1 mi. E. Rte. 37. *Macon Co.:* CU 15881 (1, 67), trib. Hogcrawl Cr., 4.7 mi. E. junct. Rtes. 90 and 26. *Schley Co.:* CU 21101 (5), trib. Bucks Cr., 7.4 mi. N. Ellaville; CU 22100 (14, 40-82), 0.2 mi. E. Ellaville. *Terrell Co.:* CU 15794 (3, 53-65), trib. Chickasawatchee Cr., 0.2 mi. W. Dawson. *Randolph Co.:* CU 17755 (1), trib. Carter Cr., 3.3 mi. C. Cuthbert. *Taylor Co.:* CU 21146 (3, 34-45), Cedar Cr., 11 mi. N. Ellaville, 4.0 mi. S. Rupert. *Lee Co.:* UMMZ 163914 (2, 45-57), Flint R., island stretch, 100 yds. above and below ent. Abrams Cr., 11 mi. NE. power dam on N. side Albany. *Worth Co.:* UMMZ 164014 (1), Abrams Cr., N. Albany; UMMZ 163983 (1), Mill Cr., between Abrams Cr., and Piney Woods Cr., 11 mi. NE. Albany. *Dougherty Co.:* UMMZ 163958 (1, 50), Flint R., below power dam N. Albany on old Leesburg Rd.; UMMZ 164085 (1, 63), Chickasawhatchee Cr., 4 mi. SW. Docker.

Ochlockonee River Drainage

Georgia.—*Colquitt Co.:* CU 17309 (1, 77), Little Ochlockonee R., 0.7 mi. W. Hartsfield. *Grady Co.:* CU 20758 (1, 39), trib. Ochlockonee R., 5.8 mi. W. junct. Rtes. 84 and 93, N. Cairo; CU 20753 (14, 35-56), Ochlockonee R., 1.6 mi. E. Cairo; UMMZ 88671 (9), 3 mi. E. Climax. **Florida.**—*Liberty Co.:* CU 17175 (5, 40-82), Small Sandy Cr., W. Greensboro, trib. Taluga R., 0.9 mi. W. Co. line. *Leon Co.:* CU 12368 (8, 30-39), trib. Ochlockonee R., 19 mi. W. Tallahassee; FSU 123 (5, 42-61), Telogia Cr., 3.1 mi. E. Bristol. *Gadsden Co.:* CU 18182 (2, 55-56), Taluga R., 1.5 mi. W. Gretna; FSU 120 (4, 40-59), Rocky Comfort Cr., 3.2 mi. ENE. Wetumpka 0. 9. mi. S. Quincy, on dirt rd. near grist mill; FSU 121 (4, 39-56), Monroe Cr., 3.0 mi. WNW. Midway on dirt rd.; CU 18184 (1, 63), trib. Little R., 2.1 mi. W. Little R. Bridge, W. Havana.

St. Marks River Drainage

Florida.—*Jefferson Co.:* CU 12383 (1), trib. St. Marks R., 6.9 mi. W. Wakeenah; FSU 52 (25, 45-59), Lloyd Cr., 0.8 mi. E. main intersection in Lloyd, third bridge E. of town; TU 222 (25, 36-59), trib. L. Miccosukee, 0.8 mi. E. Lloyd, 17.0 mi. E. Tallahassee; TU 2666 (2, 41-54), trib. L. Miccosukee, 4.6 mi. E. junct. Rtes. 90 and 59, 1.8 mi. E. outlet. *Wakulla Co.:* FSU 50 (6, 51-75), Wakulla R., 2.3 mi. SW. Wakulla RR sta.; FSU 126 (6, 41-59), under bridge,

2.3 mi. SW. Wakulla RR sta.; USNM 92884 (1, 53), Wakulla R., near Wakulla Springs; TU 2360 (1, 51), Wakulla R., at Rte. 319 crossing.

Suwannee River Drainage

Georgia.—*Wilcox Co.:* CU 17407 (1, 56), trib. Alapaha R., 0.6 mi. W. Pitts. *Alachua Co.:* CU 10196 (1, 35), Santa Fe R., at Poe Springs. *Cook Co.:* CU 15768 (1, 49), New R., trib. Withaloochee R., 4.9 mi. W. Nashville. *Lanier Co.:* CU 15440 (7, 42-53), Five Mile Cr., trib. Alapaha R., at E. limits Lakeland. **Florida.**—*Columbia Co.:* CU 12502 (83, 20-66), trib. Suwannee R., 2 mi. S. Benton. *Union Co.:* TU 2994 (5, 49-52), trib. Santa Fe. R., 9.4 mi. E. junct. Rtes. 18, 441 and 41. *Alachua Co.:* UMMZ 87911 (1, 70), Santa Fe. R. at Poe Springs; UMMZ 101676 (3, 43-61), Santa Fe R., at Poe Springs. *Hamilton Co.:* UMMZ 163311 (34, 22-73), small trib. N. Suwannee R., SE. Genoa. *Gilcrist Co.:* KS (5, 37-46), Suwannee R., at Rock Bluff Ferry near Rock Bluff Springs.

Suwannee Springs Drainage

Florida.—*Columbia Co.:* KS (12, 50-69), Ichtuckney Springs, downriver, above second large spring; KS (13, 54-68), Ichtuckney Springs, down run above entrance second large spring; KS (6, 47-64), Ichtuckney Spring, near boil.

St. Johns River Drainage

Florida.—*Lake Co.:* CU 12026 (44, 21-51), 1.5 mi. W. Cassia, Blackwater Swamp; KS (25, 37-70), Seminole Springs Run. *Clay Co.:* 12434 (1, 57), Clark Cr., trib. St. Johns R., 7.3 mi. N. Bostwick; CU 21099 (5, 36-56), trib. S. fork Black Cr., 12 mi. S. Clay Co. line. *Seminole Co.:* CU 19825 (5, 49-69), Wekiva R., trib. St. Johns R., 9.7 mi. W. San Ford; CU 22096 (16, 30-55), Howells Cr., 2.9 mi. E. Wagner, 7.3 mi. ENE. Fern Park; CU 21130 (1, 61), trib. L. Jessup, 2.6 mi. E. junct. Rtes. 419 and 17. *Orange Co.:* USNM 13343 (1, 68), Rock and Silver Springs. *Putnam Co.:* UF 113 (8, 38-50), Little Orange Cr., 6 mi. S. Johnson. *Marion Co.:* UF (13, 32-51), Orange Cr., at Orange Spring; UMMZ 163328 (4, 38-44), Juniper Springs at head Juniper Cr., Ocala Nat. For.

Altamaha River Drainage

Georgia.—*Tatnall Co.:* CU 15766 (39, 42-67), Brazells Cr., trib. Ohoopee R., 2.3 mi. W. Reidsville; CU 20752 (3, 58), trib. Altamaha R., 13.6 mi. S. Claxton; CU 20754 (5, 36-55), trib. Altamaha R., 11.9 mi. S. Claxton. *Toomis Co.:* CU 21465 (1, 57), Cobb Cr., 15.7 mi. N. Baxley; UMMZ 158077 (2, 61-62), Rocky Cr., trib. Tendleton Cr., 6 mi. SW. Lyons. *Telfair Co.:* CU 17256 (3, 46), Little Ocmulgee R., 1.2 mi. N. Mc Rae. *Henry Co.:* CU 18461 (1, 36), trib. Cotton R., 6.6 mi. NW. Mc Donough. *Wheeler Co.:* CU 18461 (3, 35-52), trib. Oconee R., 1.5 mi. ENE. Glenwood. *Emmannuel Co.:* USNM 162456 (3, 47-63), Ohoopee R., 2.5 mi. N.

Oak Park; UMMZ 88421 (1, 25), Ohoopee R., 15 mi. S. Swainsboro. *Bibb Co.:* UMMZ 88323 (3, 26-30), Tobesofkee Cr., trib. Ocmulgee R., 5 mi. S. Macon. *Laurens Co.:* UMMZ 88382 (1, 43), Hunger and Hardship Cr., 5 mi. SW. Dublin; UMMZ 88377 (5, 17-38), Rocky Cr., 2 mi. from Beckley Co. line near Dudley. *Oconee Co.:* CU 22002 (3, 41-66), high shoals below dam Apalachee R.

Ogeechee River Drainage

Georgia.—*Bullock Co.:* CU 21757 (1, 50), trib. Ogeechee R., 2.4 mi. NE. Statesboro; CU 17470 (1, 54), Lotts Cr., trib. Ogeechee R., 7.4 mi. S. Statesboro. *Jefferson Co.:* CU 17274 (2, 87), trib. Ogeechee R., 6 mi. S. Wrens. *Candler Co.:* CU 17244 (6, 26-52), Fifteen Mile Cr., trib. Ogeechee R., 3.5 mi. W. Pulaski. *Evans Co.:* CU 20755 (21, 39-58), trib. Canoochee R., 1.1 mi. NW. Claxton.

Mid-Savannah River Drainage

Georgia.—*Jefferson Co.:* CU 18587 (7, 50-79), Ready Cr., 3.9 mi. NE. Wrens; CU 18586 (19, 41-61), Brush Cr., 0.4 mi. S. Wrens; CU 17380 (10, 44-55), Bushy Cr., trib. Briar Cr., 0.9 mi. S. Wrens. *Richmond Co.:* CU 17624 (54, 32-66), trib. Butler Cr., 1 mi. SW. Augusta city limits; CU 17213 (6, 41-52), Boggy Gut Cr., trib. Briar Cr., 22.5 mi. SW. Augusta; USNM 162472 (1, 68), Briar Cr., 6.7 mi. E. Wrens; UMMZ 158021 (8, 25-52), 6.0 mi. NNW. Augusta; UMMZ 132764 (1), Spirit Cr., 12 mi. S. Augusta, below Mc Dades pond. *Severen Co.:* CU 20756 (1, 52), trib. Savannah R., 12.9 mi. S. Savannah R. **South Carolina.**—*Allendale Co.:* CU 15142 (2, 55-56), trib. lower Three R., 3.6 mi. NW. Appleton. *Aiken Co.:* USNM 16255 (2, 42-64), upper Three R., below Rte. 28; UMMZ 145321 (1, 43), Horse Cr., Bath; HF (9, 56-87), stream below dam of pond, Henrys L.

Upper Savannah River Drainage

South Carolina.—*Abbeville Co.:* CU 19656 (4, 34-53), Little R., 5.6 mi. E. Calhoun Falls; CU 19603 (2, 40-49), Long Cave Cr., 4.4 mi. E. Abbeville; CU 19781 (3, 60-63), Savannah R., 4 mi. W. Calhoun Falls; CU 19599 (42, 45-81), Calhoun Cr., 7.6 mi. E. Calhoun Falls. *Anderson Co.:* CU 19603 (15, 60-80), Twentythree Mile Cr., 0.9 mi. NW. Sandy Springs, 11.1 mi. NW, Anderson. *Oconee Co.:* CU 10925 (2, 37-41), trib. Coneross Cr., 5.3 mi. S. Seneca; CU 19737 (6, 38-52), Keowee R., 13.2 mi. SW. Pickens. *Elbert Co.:* CU 19722 (1, 59), Morea Cr., 1.3 mi. S. Nuberg. *Franklin Co.:* CU 19623 (1, 61), trib. Nail Cr., 9.9 mi. NE. Commerce, 0.7 mi. SW. Ashland; USNM 34005 (1), Columbia. *Pickens Co.:* CU 19069 (4, 60-67), trib. Keowee R., E. crossing on Rte. 28, 10 mi. S. N.C. State Line. **Georgia.**—*Madison Co.:* CU 20762 (20, 47-67), Anthony Shoals, S. fork Broad R.

Combahee River Drainage

South Carolina.—*Allendale Co.:* CU 15320 (15, 47-79), Jack-

son Branch, trib. Combahee R., 1.8 mi. S. Sycamore. *Barnwell Co.:* CU 20761 (3, 40-50), trib. Salkehatchee R., 2.6 mi. W. Olar *Bamberg Co.:* CU 20760 (8, 53-76), trib. Salkehatchee R., 2.1 mi. S. Olar.

Edisto River Drainage

South Carolina.—*Orangeburg Co.:* CU 20759 (1, 70), Edisto R., 10.3 mi. SW. Orangeburg. *Aiken Co.:* CU 15135 (18, 40-76), trib. S. fork Edisto R., 11.9 mi. N. Aiken; CU 71949 (9, 39-50), trib. S. fork Edisto, 3.9 mi. N. Aiken.

PERCINA NIGROFASCIATA (AGASSIZ)

Range and habitat.—Mississippi River system, Louisiana, to Edisto River system, South Carolina; southward into peninsular Florida, throughout the St. Johns and Suwannee River system (Map 1).

P. nigrofasciata is found in the currents of streams and rivers throughout the coastal plain and piedmont region. It is also present in mountain tributaries of Alabama, Georgia and South Carolina. Sandy, rock or rubble bottoms are preferred, but specimens may be taken over mud or silt bottoms in the lower coastal plain drainages.

Diagnosis.—A species of *Percina* with discrete, elliptical dark lateral bars. Scales in the lateral line, 46 to 71 (usually[2] 50 to 62). The nape, cheeks, and opercles are fully scaled. The sub-triangular muscle mass between the pelvic fins is often scaled, and the breast is sometimes scaled. Dorsal fin rays number IX to XV, 10 to 13 (usually XI to XIII, 11 to 12); total pectoral rays number 23 to 32 (usually 27 to 30); anal fin II, 7 to 10 (usually 9). The preopercle is usually entire but may be serrulate. Seven dark dorsal blotches are present; three dark spots at the base of the caudal fin; sub-ocular bar present or absent.

Description.—The various body proportions appear in Tables 9-14. Other descriptive features follow. The body is moderately compressed to terete. The length of the head, including the fleshy opercular membrane is somewhat elongate. The depth of the caudal peduncle is somewhat narrow.

The dorsal fins are high and well developed. The anal fin is high. The pectoral fins are well developed and are moderate in length. The pelvic fins are moderate to slightly short in length and are well developed. The snout is short, slightly bulbous, projects upward from the anterior margin of the orbit, then slopes downward from the anterior nostril.

Teeth are present on the premaxillary, vomer and palatine bones. The teeth of the upper jaw are located along the contour of the jaw. There is present, one outer row of enlarged conical teeth and behind this single row of large teeth lies a crescent-shaped row of smaller

[2] The majority of counts fall between one standard deviation on either side of the mean.

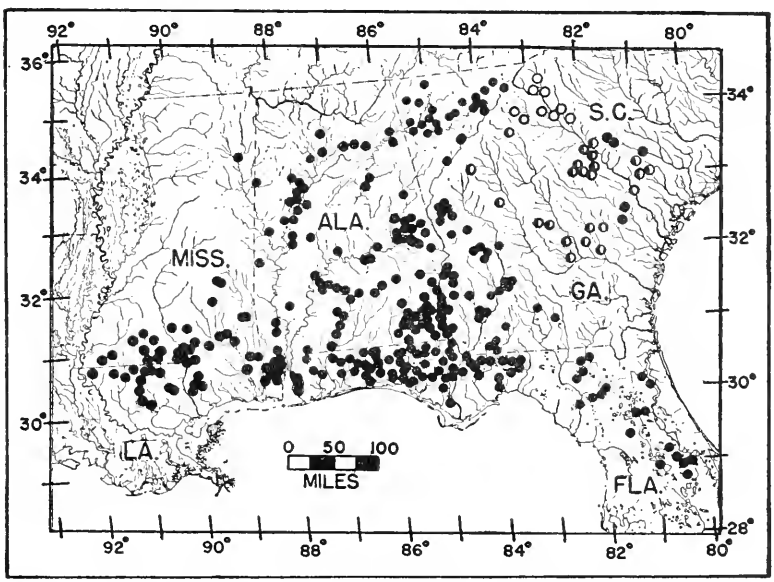
TABLE 1.

FREQUENCY DISTRIBUTIONS OF LATERAL LINE SCALES OF SEVERAL POPULATIONS OF *Percina nigrofasciata* BY DRAINAGE SYSTEMS

	71	70	69	68	67	66	65	64	63	62	61	60	59	58	57	56	55	54	53	52	51	50	49	48	47	46	N	$\bar{x}$	SD	SE
nigrofasciata																														
Mississippi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1			
L. Pontchartrain	—	—	—	—	—	—	—	—	3	4	4	6	9	10	3	6	5	4	4	1	—	—	—	—	—	—	59	57.9	2.9	0.38
Pearl & Wolf	—	—	—	—	—	—	—	—	—	6	6	12	17	19	30	29	38	19	9	9	2	2	—	—	—	—	197	56.3	2.5	0.18
Pascagoula	—	—	—	—	—	—	—	—	—	1	3	4	5	10	11	4	10	16	7	5	3	2	3	—	—	—	84	55.4	3.0	0.33
Mobile Bay	—	—	—	—	—	—	—	—	—	1	4	1	3	6	5	5	16	11	9	11	6	2	1	—	1	1	83	54.5	3.1	0.34
Black Warrior	—	—	—	—	—	—	—	1	3	6	7	9	8	8	10	4	3	4	3	2	—	—	—	—	—	—	68	58.3	2.9	0.37
Coosa	—	—	—	—	—	—	—	1	2	6	7	5	9	4	4	6	7	1	—	2	1	—	—	—	—	—	55	58.4	3.0	0.40
Perdido Bay	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	1	6	3	4	5	4	3	1	—	—	—	29	53.1	2.4	0.45
Conecuh-Escambia	—	—	—	—	—	—	—	—	—	2	2	1	2	3	7	12	3	5	8	2	—	1	—	—	—	—	48	55.9	2.7	0.39
Blackwater	—	—	—	—	—	—	—	—	—	—	—	—	1	—	3	5	6	8	11	12	13	4	6	2	1	—	72	52.5	2.4	0.29
Yellow	—	—	—	—	—	—	—	—	—	—	1	2	2	3	7	8	4	4	2	4	3	3	—	—	—	—	43	55.2	2.9	0.44
Choctawhatchee	—	—	—	—	—	—	—	—	2	2	7	2	12	8	19	14	12	15	7	8	9	6	3	2	—	—	127	55.4	3.4	0.30
St. Andrews Bay	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	—	1	—	1	—	—	5	52.0	2.9	1.30
Apalachicola	—	—	—	—	—	1	—	—	1	3	3	11	21	27	49	48	43	39	32	31	30	17	—	—	—	1	336	55.3	2.8	0.16
Flint	—	—	—	—	—	—	—	—	—	—	1	—	—	4	4	6	15	6	7	7	2	2	1	—	—	—	55	54.4	2.3	0.31
Ochlockonee	—	—	—	—	—	—	—	—	—	—	1	1	1	5	5	10	7	3	5	3	2	2	—	—	—	—	45	54.2	2.5	0.38
Apalachee Bay	—	—	—	—	—	—	—	—	—	—	1	2	7	8	10	10	11	8	3	3	2	1	—	—	—	—	66	55.9	2.3	0.29
Suwannee River	—	—	—	—	—	—	—	—	—	—	—	2	5	2	4	5	6	14	18	7	8	10	2	1	1	1	86	53.4	2.9	0.32
Suwannee Springs	—	—	—	—	—	—	—	—	—	1	2	—	3	5	8	4	3	2	1	2	—	—	—	—	—	—	31	56.8	2.4	0.43
St. Johns	—	—	—	—	—	—	4	—	2	4	6	7	14	13	13	7	8	11	8	5	—	1	—	—	—	—	103	57.3	3.2	0.32
Ogeechee	—	—	—	—	—	—	—	—	—	—	—	1	1	2	2	3	4	4	2	4	1	—	—	—	—	—	24	55.8	2.4	0.49
Edisto	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	3	4	4	2	5	3	3	1	—	—	—	27	53.2	2.4	0.46
nigrofasciata x *raneyi*																														
Altamaha	—	—	—	—	—	1	2	—	2	1	2	7	10	3	6	4	3	2	2	—	—	—	—	—	—	—	45	58.6	3.0	0.45
Mid-Savannah	—	—	—	1	—	—	1	4	6	11	6	9	13	11	3	4	4	1	—	—	—	—	—	—	—	—	74	59.9	2.7	0.31
Combahee	—	—	—	—	—	—	—	2	1	1	—	2	4	5	1	4	2	3	—	1	—	—	—	—	—	—	26	57.9	3.1	0.61
raneyi																														
Upper Savannah	3	—	3	3	4	6	16	10	12	14	9	10	2	2	3	1	1	—	—	—	—	—	—	—	—	—	99	63.2	3.2	0.32

teeth. The area of small teeth has its greatest width in the mid-portion of the jaw and tapers in width posteriorly to the end of the row of large teeth. Vomerine teeth are present and well developed. They form a triangular patch on the bone. Palatine teeth are few, but well developed, and are confined to the anterior end of the bone. The dentary teeth resemble those small teeth of the upper jaw which lie behind the first row of enlarged conical teeth. They occur in greatest numbers at approximately one quarter length of the lower jaw posteriorly from the mandibular symphysis, and decrease in number toward the symphysis and also distally from the area of greatest concentration.

Scutellation.—Imbricate ctenoid scales cover most of the body. In some specimens the lower portion of the cheek is naked. Enlarged ctenoid scales are present on the mid-line of males. The nape is nearly always scaled. Often, and especially in specimens over fifty millimeters in length which inhabit the Gulf drainages, the sub-triangular area between the pelvic bones is well scaled. Similarly, the breast of large specimens from Gulf drainages may be well scaled. The opercle is usually completely scaled. One or more enlarged ctenoid scales are present superficial to the junction of the pelvic bones near the mid-portion of the breast, as is the rule in species of



Map 1. Distribution (By Collections) of *Percina nigrofasciata* in the Southeastern United States

● *Percina n. nigrofasciata*

○ *Percina n. raneyi*

◐ *Percina n. nigrofasciata* X *Percina n. raneyi* (Intergrades)

TABLE 2.
FREQUENCY DISTRIBUTIONS OF SCALES ABOVE THE LATERAL LINE OF SEVERAL POPULATIONS OF *Percina nigrofasciata* BY DRAINAGE SYSTEMS

	9	8	7	6	5	4	N	$\bar{x}$	SD	SE
nigrofasciata										
Mississippi	—	—	—	—	1	—	1			
L. Pontchartrain	—	—	23	26	5	—	54	6.3	0.6	0.08
Pearl & Wolf	—	1	39	125	32	—	197	6.1	0.6	0.04
Pascagoula	—	4	29	34	17	—	84	6.2	0.8	0.09
Mobile Bay	—	2	10	44	25	2	83	5.8	0.8	0.08
Black Warrior	—	4	40	18	3	—	65	6.7	0.7	0.08
Coosa	—	2	27	24	2	—	55	6.5	0.6	0.09
Perdido Bay	—	—	—	11	18	—	29	5.4	0.5	0.09
Conecuh-Escambia	—	1	7	30	9	—	47	6.0	0.7	0.10
Blackwater	—	—	—	32	37	3	72	5.4	0.6	0.07
Yellow	—	—	1	25	17	—	43	5.6	0.5	0.08
Choctawhatchee	—	2	22	73	29	1	127	6.0	0.7	0.06
St. Andrews Bay	—	—	—	3	2	—	5	5.6	0.5	0.25
Apalachicola	—	3	67	191	70	—	331	6.0	0.7	0.04
Flint	—	—	5	44	6	—	55	6.0	0.4	0.06
Ochlockonee	—	1	5	30	9	—	45	6.0	0.6	0.09
Apalachee Bay	—	—	13	46	7	—	66	6.1	0.5	0.07
Suwannee River	—	—	7	58	21	—	86	5.8	0.5	0.06
Suwanee Springs	1	5	8	16	1	—	31	6.7	0.9	0.16
St. Johns	—	1	35	44	7	—	87	6.3	0.6	0.07
Ogeechee	—	—	2	11	3	—	16	5.9	0.6	0.14
Edisto	—	—	1	22	4	—	27	5.9	0.4	0.08
nigrofasciata x *raneyi*										
Altamaha	—	3	24	15	3	—	45	6.6	0.7	0.11
Mid-Savannah	—	3	20	44	6	—	73	6.3	0.7	0.08
Combahee	—	—	8	16	2	—	27	6.2	0.6	0.12
raneyi										
Upper Savannah	8	46	37	7	—	—	98	7.6	0.7	0.08

TABLE 3.

FREQUENCY DISTRIBUTIONS OF SCALES BELOW THE LATERAL LINE OF SEVERAL POPULATIONS OF *Percina nigrofasciata* BY DRAINAGE SYSTEMS

	14	13	12	11	10	9	8	7	N	$\bar{x}$	SD	SE
nigrofasciata												
Mississippi	—	—	—	—	—	1	—	—	1			
L. Pontchartrain	—	2	7	21	15	8	1	—	54	10.6	1.1	0.15
Pearl & Wolf	—	1	5	32	69	73	17	—	197	9.7	1.0	0.07
Pascagoula	—	—	1	4	44	30	5	—	84	9.6	0.7	0.08
Mobile Bay	—	—	3	10	27	29	13	1	83	9.5	1.0	0.12
Black Warrior	—	1	24	24	12	—	—	—	61	10.4	0.9	0.11
Coosa	—	—	3	14	21	15	2	—	55	10.0	0.9	0.13
Perdido Bay	—	—	—	—	1	15	10	3	29	8.5	0.7	0.14
Conecuh-Escambia	—	—	—	5	27	13	2	—	47	9.7	0.7	0.10
Blackwater	—	—	1	—	14	31	24	2	72	8.9	0.9	0.10
Yellow	—	—	1	3	12	19	7	1	43	9.3	1.0	0.15
Choctawhatchee	—	—	3	19	34	52	18	1	127	9.5	1.0	0.09
St. Andrews Bay	—	—	—	—	2	2	—	1	5	9.0	1.2	0.55
Apalachicola	—	—	10	43	133	127	17	—	330	9.7	0.9	0.05
Flint	—	—	3	5	14	23	9	—	54	9.4	1.0	0.14
Ochlockonee	—	—	—	3	10	29	3	—	45	9.3	0.7	0.10
Apalachee Bay	—	—	—	8	34	20	4	—	66	9.7	0.8	0.09
Suwannee River	—	—	1	4	30	33	16	2	86	9.2	0.9	0.10
Suwannee Springs	—	—	—	7	20	3	1	—	31	10.1	0.7	0.12
St. Johns	—	2	6	38	29	13	—	—	88	10.5	0.9	0.10
Ogeechee	—	—	—	3	7	13	—	—	23	9.6	0.7	0.15
Edisto	—	—	—	2	11	13	1	—	27	9.5	0.6	0.12
nigrofasciata x *raneyi*												
Altamaha	—	1	10	20	12	2	—	—	45	10.9	0.9	0.13
Mid-Savannah	—	2	10	35	21	6	—	—	74	10.7	0.9	0.10
Combahee	—	—	2	6	14	4	—	—	26	10.2	0.8	0.16
raneyi												
Upper Savannah	1	10	39	36	11	1	1	—	99	11.5	1.0	0.10

TABLE 4.

FREQUENCY DISTRIBUTIONS OF SCALES ABOVE PLUS BELOW THE LATERAL LINE OF SEVERAL POPULATIONS OF *Percina nigrofasciata* BY DRAINAGE SYSTEMS

	22	21	20	19	18	17	16	15	14	13	12	11	N	$\bar{x}$	SD	SE
nigrofasciata																
Mississippi	—	—	—	—	—	—	—	—	1	—	—	—	1			
L. Pontchartrain	—	—	2	4	15	12	11	7	3	—	—	—	54	16.9	1.5	0.20
Pearl & Wolf	—	—	—	4	12	41	49	57	29	5	—	—	197	15.7	1.3	0.09
Pascagoula	—	—	—	1	3	28	20	15	15	2	—	—	84	15.8	1.3	0.14
Mobile Bay	—	—	—	3	5	8	18	23	19	5	2	—	83	15.3	1.5	0.17
Black Warrior	—	—	2	3	22	20	10	6	3	—	—	—	66	17.1	1.3	0.16
Coosa	—	—	—	5	7	15	18	6	4	—	—	—	55	16.2	1.3	0.18
Perdido Bay	—	—	—	—	—	—	—	9	10	7	3	—	29	13.9	1.0	0.18
Conecuh-Escambia	—	—	—	—	2	9	16	15	5	—	—	—	47	15.7	1.0	0.15
Blackwater	—	—	—	—	1	—	13	10	33	12	1	2	72	14.3	1.2	0.14
Yellow	—	—	—	—	1	4	5	19	9	4	1	—	43	14.9	1.3	0.20
Choctawhatchee	—	—	—	2	7	20	28	39	23	6	2	—	127	15.4	1.4	0.12
St. Andrews Bay	—	—	—	—	—	—	2	1	1	—	1	—	5	14.6	1.7	0.75
Apalachicola	—	—	—	7	12	64	101	93	45	7	—	—	329	15.7	1.2	0.07
Flint	—	—	—	—	5	4	14	22	5	4	—	—	54	15.4	1.3	0.22
Ochlockonee	—	—	—	1	—	3	10	22	9	—	—	—	45	15.2	1.0	0.15
Apalachee Bay	—	—	—	—	2	12	30	16	4	2	—	—	66	15.8	1.0	0.12
Suwannee River	—	—	—	1	2	5	23	29	18	6	1	—	85	15.1	1.2	0.13
Suwannee Springs	—	—	1	—	3	11	13	2	1	—	—	—	31	16.6	1.1	0.20
St. Johns	—	—	1	4	19	32	20	7	4	—	—	—	87	16.8	1.2	0.13
Ogeechee	—	—	—	—	1	2	5	6	2	—	—	—	16	15.0	1.1	0.27
Edisto	—	—	—	—	—	3	9	12	2	1	—	—	27	15.4	0.9	0.18
nigrofasciata x *raneyi*																
Altamaha	—	—	3	9	13	6	11	3	—	—	—	—	45	17.5	1.5	0.22
Mid-Savannah	—	—	3	6	15	26	11	11	1	—	—	—	73	17.0	1.3	0.16
Combahee	—	—	—	1	4	7	9	4	1	—	—	—	26	16.6	1.2	0.23
raneyi																
Upper Savannah	4	7	25	35	13	10	2	1	1	—	—	—	98	19.0	1.4	0.14

TABLE 5.

FREQUENCY DISTRIBUTIONS OF THE LEAST NUMBER OF SCALES AROUND THE CAUDAL PEDUNCLE OF SEVERAL POPULATIONS OF *Percina nigrofasciata* BY DRAINAGE SYSTEMS

	27	26	25	24	23	22	21	20	19	18	17	16	N	$\bar{x}$	SD	SE
nigrofasciata																
Mississippi	—	—	—	—	—	—	—	—	—	1	—	—	1			
L. Pontchartrain	—	—	1	2	12	16	21	1	1	—	—	—	54	21.9	1.1	0.15
Pearl & Wolf	—	—	1	3	26	30	80	41	14	1	—	—	196	21.1	1.2	0.09
Pascagoula	—	—	—	1	5	15	40	18	5	—	—	—	84	21.0	1.0	0.11
Mobile Bay	—	—	1	3	6	4	20	31	12	5	—	1	83	20.5	1.5	0.17
Black Warrior	—	—	1	12	18	17	10	6	2	—	—	—	66	22.3	1.4	0.17
Coosa	—	—	—	6	18	17	6	5	1	1	—	—	54	22.1	1.3	0.18
Perdido	—	—	—	—	—	—	1	15	4	5	2	—	27	19.3	1.1	0.21
Conecuh-Escambia	—	—	1	—	10	11	13	7	4	1	—	—	47	21.4	1.4	0.21
Blackwater	—	—	—	—	—	3	9	24	25	7	4	—	72	19.5	1.1	0.13
Yellow	—	—	—	1	1	5	21	9	4	1	—	—	42	20.8	1.1	0.17
Choctawhatchee	—	—	—	4	13	28	35	23	22	2	—	—	127	20.9	1.4	0.13
St. Andrews Bay	—	—	—	—	—	—	—	1	3	1	—	—	5	19.0	0.7	0.32
Apalachicola	—	—	—	3	23	53	128	84	28	5	1	—	325	20.8	1.1	0.06
Flint	—	—	—	1	2	4	25	13	8	2	—	—	55	20.6	1.2	0.16
Ochlockonee	—	—	—	—	—	3	8	22	11	1	—	—	45	20.0	0.9	0.13
Apalachee Bay	—	—	—	—	—	5	25	18	17	—	1	—	66	20.2	1.0	0.12
Suwannee River	—	—	—	—	—	6	18	24	29	7	1	—	85	19.8	1.1	0.12
Suwannee Springs	—	—	—	—	3	7	17	2	2	—	—	—	31	21.2	1.0	0.17
Ogeechee	—	—	—	—	—	1	11	5	—	—	—	—	23	20.8	0.5	0.10
Edisto	—	—	—	—	—	4	12	5	5	—	—	—	26	20.6	1.0	0.19
nigrofasciata x *raneyi*																
Altamaha	—	2	3	8	15	10	5	2	—	—	—	—	45	22.9	1.4	0.21
Mid-Savannah	—	—	2	8	31	19	9	4	1	—	—	—	74	22.5	1.2	0.14
Combahee	—	—	—	—	16	3	5	—	1	—	—	—	25	22.3	1.1	0.21
raneyi																
Upper Savannah	1	—	7	24	35	13	16	3	—	—	—	—	99	22.9	1.3	0.13

percina. Means and ranges of scale counts appear in Tables 1-5.

The spinous dorsal fin is usually barely separated from the soft dorsal fin. In some specimens a wider division is found. The longest spine of the dorsal fin is usually the fourth, most of the remaining spines closely approximating each other in length. Exceptions are the first and last two spines which are shorter. The soft dorsal fin is higher than the spinous. The fourth ray is usually the longest, with the first, and the last three, the shortest. The remaining ones are nearly equal. The pelvic fins are angulate on the inner and outer margins with a pointed tendency at mid-fin. The first pelvic ray is often much thicker than the others, and the tips of the first three rays are thickened at the ends. The caudal fin is slightly emarginate and consists of seventeen rays, fifteen of which are branched. The anal fin is long. Its first spine is slightly shorter than the second, and is often thickened. The longest soft ray is usually the fourth. The remaining rays, with the exception of the first three, and the last, which are shorter, are nearly all of the same length. Means and ranges of fin counts appear in Tables 6-8.

The preopercle is usually entire, but sometimes is serrulate. The horizontal arm is longer than the vertical arm. The upper jaw extends just slightly posterior to the anterior margin of the eye. The mouth is moderate, slightly sub-terminal and somewhat oblique. Branchiostegal rays number six. Gill rakers number nine plus two. The maxillary frenum is broad and wide.

The lateral canal of the head contains five pores. The three posterior-most are equally spaced along a nearly straight line, and are located at the ends of posteriorly directed narrow tubes. The fourth most posterior is located slightly obliquely and inferiorly to the above three pores. The fifth most posterior is found approximately half way between the fourth most posterior pore and the posterior margin of the eye. The supratemporal canal is complete and consists of a median and two lateral pores. The median pore is found at the end of a narrow posteriorly projecting tube, and the two lateral pores are found at the end of tubes which project ventrad and posteriorward. The infraorbital canal contains eight pores. The first is located below and behind the anterior nostril. The second and third open from tubes which are directed downward to a point near the maxillary groove. The fourth is located dorsad and posteriorly from the latter two, and under the anterior portion of the eye. The last four open from long slender tubes. The first two of which project downwards and backward, while the last two project upward and backward. Ten preoperculomandibular pores are present. Six large ones are located on the preopercle and open from short, rather wide tubes. The remainder are located on the ventral contour of the head. The most posterior stands more or less alone, while the final three are nearly equally spaced. Two interorbital pores are present and may be out of line rather than arranged along a longitudinal plane. A single postorbital pore is present and opens

from a short posteriorly directed tube. The anterior nasal pore lies in a line with the superior portion of the tubular anterior nostril. The posterior nasal pore is oblique, anterior to the posterior nostril slit, and opens from a very short backward projecting tube. The coronal pore opens from a rather narrow long tube on the anterior portion of the occiput. The tube may appear sinuous. Terminology for head pores is after Hubbs and Cannon (1935: 10).

Coloration.—Color varies widely in specimens throughout the range. However, certain color patterns are found to be rather stable. In life, the color of the dorsum varies from light to dark olivaceous. Below, the color is lighter than the shade above. A greenish-gold sheen, which is not retained in alcohol specimens, is present on the cheek and opercle. There are as many as sixteen lateral vertical bars present. These are, as a rule, in the form of ellipses, and alternate with shorter and more ovate markings. The bars are imposed on a darkened lateral stripe which straddles the pores of the lateral line. The first elliptical vertical bar is found posterior to the insertion of the pectoral fin and the remaining ones extend to the caudal fin. Often, the bars anterior to the vent extend to a greater total vertical distance, but bars posterior to the vent may completely band the specimen in the region of the caudal peduncle. Dorsad, the bars do not cross the mid-line or conjoin with bars of the opposite side. From the anterior insertion of the second dorsal fin posteriorly, the bars often become less elliptical and become more confluent. In the Apalachicola Bay and St. Andrews Bay drainages the vertical bars scarcely extend below the lateral line, and are consistently found in the form of squarish blotches in some individuals, rather than ellipses. In females, pigmentation is often present in the form of spots and blotches below the lateral line and between the ventrad extensions of the lateral bars.

Viewed from above, seven dark blotches are present, (there may be as few as six or as many as eight) and these straddle the mid-line, terminating just superior to the furthest dorsal extension of the lateral bars. These are sometimes difficult to see in darkly colored individuals. The first blotch is located just posterior to the nape and the last is found just anterior to the caudal fin. A subocular bar may, or may not, be present. A dark band extends upward from the anterior corner of the eye, through the anterior nostril and usually conjoins the band from the opposite side of the head. This junction most often occurs on the upper lip, in the region of the maxillary symphysis. The dark band also continues backward from the posterior margin of the eye to the lateral stripe immediately posterior to the opercle. In its posterior extension, the dark band is also directly inferior to a dash of yellow pigment, which in turn, is just inferior to the lateral edge of the occiput.

The dorsal spines and rays may be clear, or pigmented with alternating dark bands. Adult males more often possess non-banded clear

TABLE 6.

FREQUENCY DISTRIBUTIONS OF THE NUMBER OF RAYS IN THE FIRST DORSAL FIN OF SEVERAL POPULATIONS OF *Percina nigrofasciata* BY DRAINAGE SYSTEMS

	15	14	13	12	11	10	9	N	$\bar{x}$	SD	SE
nigrofasciata											
Mississippi	—	—	—	—	—	1	—	1			
L. Pontchartrain	—	—	13	42	3	1	—	59	12.1	0.6	0.07
Pearl & Wolf	—	1	52	128	15	—	1	197	12.2	0.6	0.04
Pascagoula	—	1	11	63	8	1	—	84	12.0	0.6	0.06
Mobile Bay	—	—	11	52	17	2	—	82	11.9	0.7	0.07
Black Warrior	—	—	5	50	12	—	—	67	11.9	0.5	0.06
Coosa	—	—	4	31	15	—	—	50	11.8	0.6	0.08
Perdido Bay	—	—	7	17	4	1	—	29	12.0	0.7	0.14
Conecuh-Escambia	—	—	5	35	7	—	—	47	12.0	0.5	0.07
Blackwater	—	—	11	50	11	—	—	72	12.0	0.6	0.07
Yellow	—	—	5	33	4	—	—	42	12.0	0.5	0.07
Choctawhatchee	—	—	17	84	26	—	—	127	11.9	0.6	0.05
St. Andrews Bay	—	—	—	3	2	—	—	5	11.6	0.5	0.25
Apalachicola	1	5	66	224	39	2	—	337	12.1	0.6	0.03
Flint	—	—	14	36	5	—	—	55	12.2	0.6	0.08
Ochlockonee	—	—	5	32	6	2	—	45	11.9	0.6	0.10
Apalachee Bay	—	—	32	32	2	—	—	66	12.5	0.6	0.07
Suwannee River	—	—	14	61	9	—	—	84	12.1	0.5	0.06
Suwannee Springs	—	—	7	21	3	—	—	31	12.1	0.6	0.10
St. Johns	—	1	26	54	6	—	—	87	12.3	0.6	0.06
Ogeechee	—	—	2	20	1	—	—	23	12.0	0.4	0.08
Edisto	—	—	1	21	5	—	—	27	11.8	0.5	0.09
nigrofasciata x *raneyi*											
Altamaha	—	—	9	29	7	—	—	45	12.0	0.6	0.09
Mid-Savannah	—	1	27	40	7	—	—	75	12.3	0.6	0.07
Combahee	—	—	8	17	1	—	—	26	12.3	0.5	0.10
raneyi											
Upper Savannah	—	—	5	71	22	1	—	99	11.8	0.5	0.05

TABLE 7.

FREQUENCY DISTRIBUTIONS OF THE NUMBER OF RAYS IN THE SECOND DORSAL FIN OF SEVERAL POPULATIONS OF *Percina nigrofasciata* BY DRAINAGE SYSTEMS

	13	12	11	10	9	8	N	$\bar{x}$	SD	SE
nigrofasciata										
Mississippi	1	—	—	—	—	—	1			
L. Pontchartrain	—	20	37	1	—	—	58	11.3	0.5	0.07
Pearl & Wolf	4	80	107	6	—	—	197	11.4	0.6	0.04
Pascagoula	2	22	57	3	—	—	84	11.3	0.6	0.06
Mobile Bay	1	39	41	2	—	—	83	11.5	0.6	0.06
Black Warrior	—	41	25	1	—	—	67	11.6	0.5	0.06
Coosa	2	26	20	3	—	—	51	11.5	0.7	0.09
Perdido Bay	2	14	13	—	—	—	29	11.6	0.6	0.12
Conecuh-Escambia	5	35	7	—	—	—	47	12.0	0.5	0.07
Blackwater	1	34	35	2	—	—	72	11.5	0.6	0.07
Yellow	1	21	19	1	—	—	42	11.5	0.6	0.09
Choctawhatchee	8	80	38	1	—	—	127	11.8	0.6	0.05
St. Andrews Bay	—	1	4	—	—	—	5	11.2	0.4	0.20
Apalachicola	4	82	192	36	—	—	314	11.2	0.6	0.04
Flint	—	23	31	—	—	1	55	11.4	0.6	0.08
Ochlockonee	—	15	28	1	—	—	44	11.3	0.5	0.08
Apalachee Bay	—	5	37	24	—	—	66	11.7	0.6	0.07
Suwannee River	10	52	23	—	—	—	85	11.9	0.6	0.07
Suwannee Springs	1	18	11	1	—	—	31	11.6	0.6	0.11
St. Johns	2	16	60	9	—	—	87	11.1	0.6	0.06
Ogeechee	—	12	11	—	—	—	23	11.5	0.5	0.11
Edisto	1	16	10	—	—	—	27	11.7	0.6	0.11
nigrofasciata x *raneyi*										
Altamaha	—	13	27	5	—	—	45	11.2	0.6	0.09
Mid-Savannah	—	14	44	17	—	—	75	11.0	0.6	0.07
Combahee	3	22	1	—	—	—	26	12.1	0.4	0.08
raneyi										
Upper Savannah	—	17	68	14	—	—	99	11.0	0.6	0.06

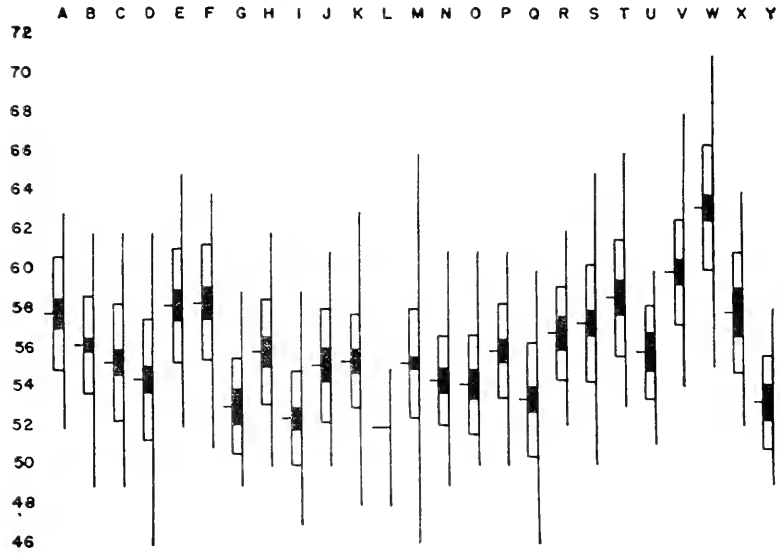


Figure 1. Comparison of the Number of Scales in the Lateral Line of *Percina nigrofasciata* by Drainage Systems. The following letters apply to the respective drainage systems. Lake Pontchartrain (A), Pearl and Wolf (B), Pascagoula (C), Mobile Bay (D), Black Warrior (E), Coosa (F), Perdido Bay (G), Conecuh-Escambia (H), Blackwater (I), Yellow (J), Choctawhatchee (K), St. Andrews Bay (L), Apalachicola Bay (M), Flint (N), Ochlockonee (O), Apalachee Bay (P), Suwannee River (Q), Suwannee Springs (R), St. Johns (S), Altamaha (T), Ogeechee (U), Mid-Savannah (V), Upper Savannah (W), Combahee (X), Edisto (Y).

rays. The soft dorsal fin often appears to have a light longitudinal stripe throughout its length. This is an expression of two large and well developed dark bands which enclose a large area of no pigmentation. The dorsal fin membranes may be clear, darkened and opaque, or peppered with dark pigment spots. The latter condition is the most common. Intense pigmentation, if present, is confined near the fin base. In a few adult males, a black border is present around the margin of the spinous dorsal fin.

The pectoral rays are usually peppered with pigment, but the connecting membranes are more often clear. The pelvic rays and membranes are both usually sprinkled with pigment. The anal fin rays and membranes follow those of the pelvics most closely in pigmentation.

The caudal fin is usually marked with two to five vertical bars but may be devoid of them. These are formed by alternating rings of dark pigment confined to the rays. In large males the fin may appear opaque. The membranes between the rays are spotted with pigment as a rule, but may be clear.

At the base of the hypural plate, two or three sometimes indiscrete dark spots are usually found. One occurs in the middle with one on each side at the dorsal and ventral margins of the plate, respectively. Often, two of the three spots conjoin and form a lunar marking.

Sexual dimorphism.—Males are larger and darker colored than females. The vertical lateral bars of males tend to be more discrete and are, as a rule, less confluent. There are present, enlarged ctenoid scales on the mid-ventral line of males. The mid-ventral line of females is either naked or covered with ctenoid scales not different in appearance from those on the body. Scutellation on the sub-triangular muscle mass between the pelvic fins is more pronounced in males. The genital papillae are short, rounded and indiscretely villiform in males, while in females they are long, conical and clearly villiform. The spaces between the ventrad extensions of the lateral vertical bars below the lateral line are nearly always without spots and blotches in males. Females, on the other hand, are often spotted and blotched in these spaces, and this pigmentation extends to the venter. Banding of the fin rays is more common in females. Males more often have fin rays which appear clear or opaque. Very little difference occurs in proportional measurements (Table 10).

Comparisons.—Of the species of *Percina, P. sciera* seems to be the closest relative. In the Pearl River and Lake Pontchartrain drainages, these two forms occur together and identification is difficult. Both may have serrulate preopercles, the condition being more common in

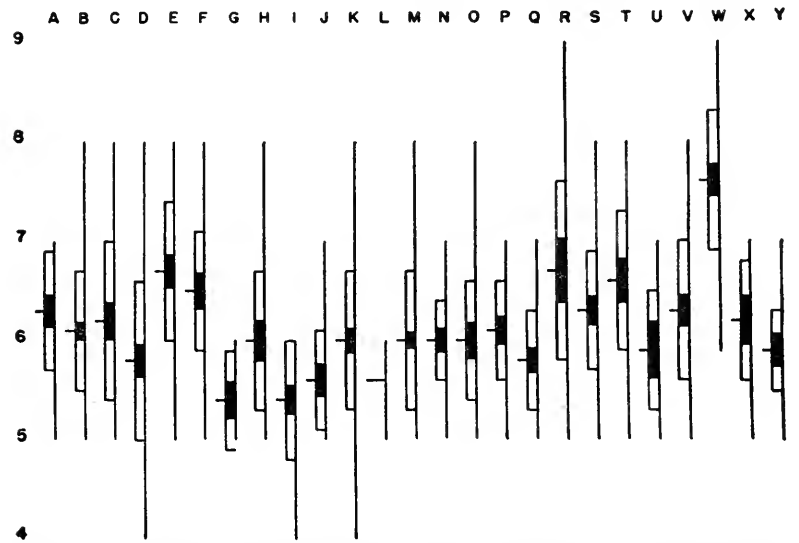


Figure 2. Comparison of the Number of Scales Above the Lateral Line of *Percina nigrofasciata* by Drainage Systems. Arrangement as in fig. 1.

TABLE 8.

FREQUENCY DISTRIBUTIONS OF THE NUMBER OF RAYS IN THE PECTORAL FINS OF SEVERAL POPULATIONS OF *Percina nigrofasciata* BY DRAINAGE SYSTEMS

	32	31	30	29	28	27	26	25	24	23	N	$\bar{x}$	SD	SE
nigrofasciata														
Mississippi	—	—	—	—	—	1	—	—	—	—	1			
L. Pontchartrain	—	—	—	2	44	4	7	—	—	—	57	27.7	0.7	0.10
Pearl & Wolf	—	—	14	10	140	19	11	—	—	—	194	28.0	0.8	0.06
Pascagoula	—	1	5	2	60	7	7	—	1	—	83	27.9	1.0	0.11
Mobile Bay	—	—	14	10	48	1	6	1	—	—	80	28.3	1.1	0.12
Black Warrior	—	—	6	4	50	4	2	—	—	—	66	28.1	0.8	0.10
Coosa	—	—	5	2	33	7	7	—	—	—	54	27.8	1.0	0.14
Perdido Bay	—	—	5	1	21	1	—	1	—	—	29	28.2	1.0	0.19
Conecuh-Escambia	—	1	12	8	22	2	2	—	—	—	47	28.6	1.1	0.16
Blackwater	—	1	29	8	33	—	1	—	—	—	72	28.9	1.0	0.12
Yellow	1	—	19	6	13	—	1	1	—	—	41	29.1	1.3	0.20
Choctawhatchee	—	2	55	15	53	2	—	—	—	—	127	29.0	1.0	0.09
St. Andrews Bay	—	—	1	—	4	—	—	—	—	—	5	28.4	0.9	0.40
Apalachicola	2	4	69	20	169	19	29	—	—	—	312	28.3	1.2	0.07
Flint	—	—	5	6	29	6	9	—	—	—	55	27.9	1.1	0.15
Ochlockonee	—	—	8	4	30	2	1	—	—	—	45	28.4	0.9	0.14
Apalachee Bay	—	—	4	5	45	9	2	—	—	—	65	28.0	0.8	0.09
Suwannee River	—	—	9	12	53	5	5	—	—	—	84	28.2	0.9	0.10
Suwannee Springs	—	—	11	1	17	1	—	—	—	—	30	28.7	1.0	0.19
St. Johns	—	—	1	2	23	18	52	3	3	1	103	26.6	1.1	0.11
Ogeechee	—	—	4	4	13	1	—	—	—	—	22	28.5	0.9	0.18
Edisto	1	—	13	4	8	1	—	—	—	—	27	29.2	1.1	0.22
nigrofasciata x *raneyi*														
Altamaha	—	—	6	—	29	—	9	—	—	—	44	27.9	1.2	0.18
Mid-Savannah	—	—	6	2	57	3	5	—	1	—	74	28.0	0.9	0.11
Combahee	—	—	2	6	13	4	1	—	—	—	26	28.2	0.9	0.18
raneyi														
Upper Savannah	—	—	4	7	66	8	14	—	—	—	99	27.8	0.9	0.09

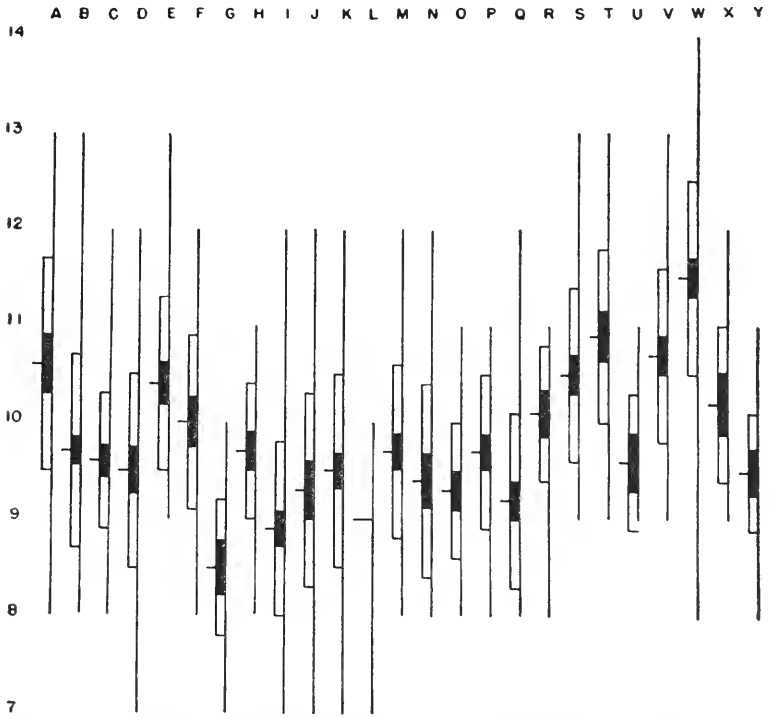


Figure 3. Comparison of the Number of Scales Below the Lateral Line of *Percina nigrofasciata* by Drainage Systems. Arrangement as in fig. 1.

P. sciera. The number of scales in the lateral line shows considerable overlap, as does the number of dorsal fin rays. However, these meristic characters may be helpful in recognizing differences between series. When these species are taken together, color pattern seems to be the one most valuable criterion in separating the two forms. In *P. nigrofasciata* the lateral vertical bars are more elliptical and extend further ventrad than those of *P. sciera* which are broadly ovate in shape and scarcely extend below the lateral stripe. A comparison between *P. nigrofasciata* and *P. sciera* in the number of scales in the lateral line and the number of spines in the first dorsal fin appears in Table 15. These specimens were taken together in two collections, from the Lake Pontchartrain drainage, by Reeve M. Bailey.

Specimens of *P. nigrofasciata* differ from specimens of *P. maculata* in the absence of scales on the nape of the latter species. Dorsal fin and lateral-line scale counts are lower in *P. nigrofasciata* than in *P. maculata.* In addition, one very prominent and distinct dark spot at the base of the caudal fin is present in *P. maculata,* differing from the three more diffuse spots of *P. nigrofasciata.*

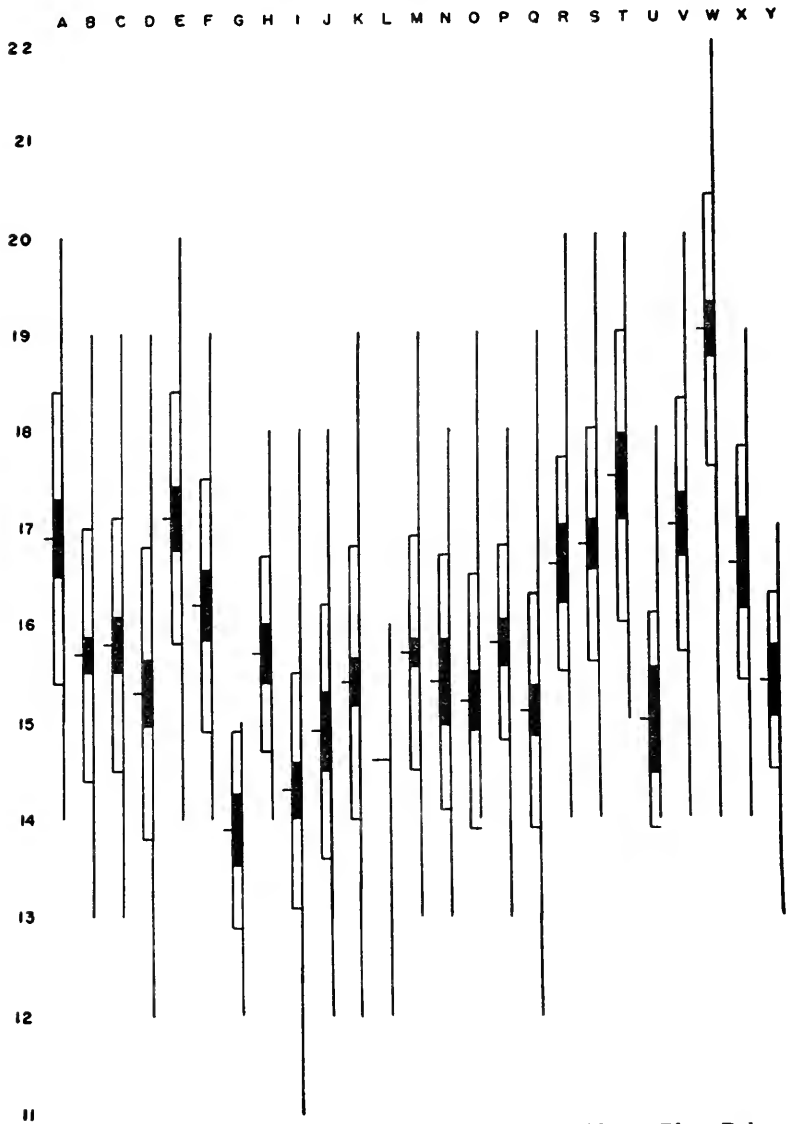


Figure 4. Comparison of the Number of Scales Above Plus Below the Lateral Line of *Percina nigrofasciata* by Drainage Systems. Arrangement as in fig. 1.

P. nigrofasciata differs markedly from *P. palmaris* in color pattern. The paired eye-like spots at the base of the caudal fin, and the white border around the spinous dorsal fin of *P. palmaris* serve to separate the two forms.

P. nigrofasciata contrasts with *P. uranidea* most obviously in the presence of seven blotches on the dorsal mid-line as opposed to four blotches for *P. uranidea.* In addition, the first dorsal fin count is higher in *P. nigrofasciata.*

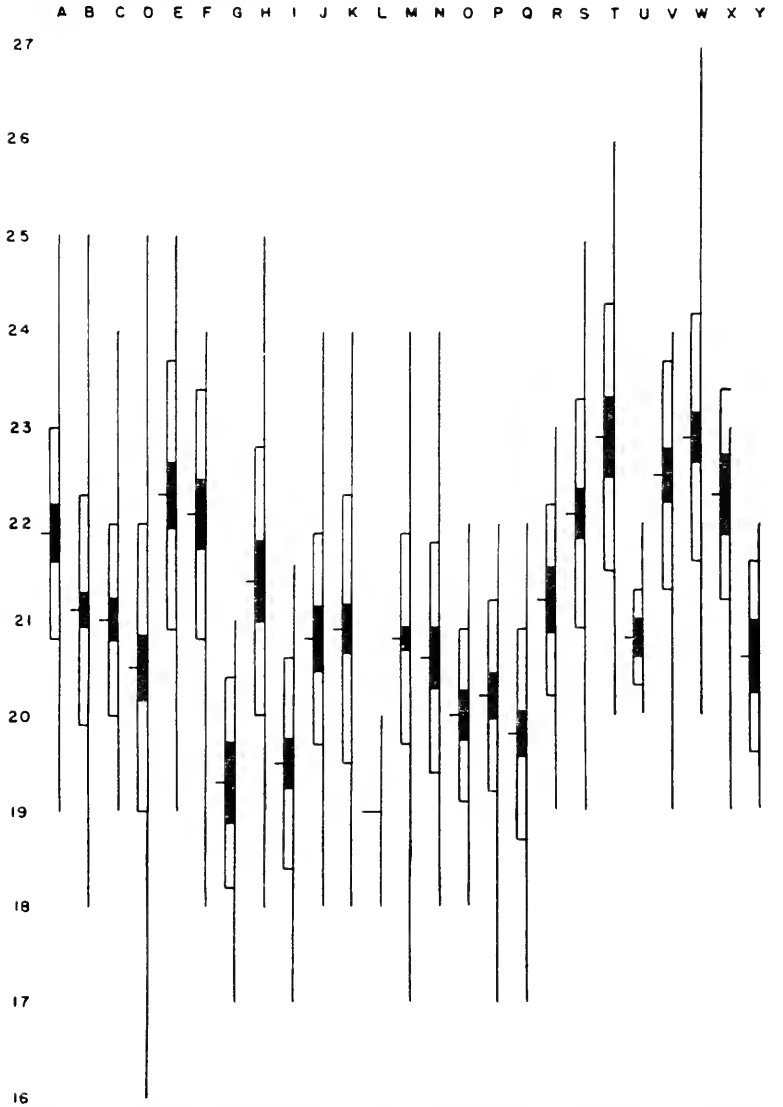


Figure 5. Comparison of the Number of Scales Around the Caudal Peduncle of *Percina nigrofasciata* by Drainage Systems. Arrangement as in fig. 1.

It differs from *P. copelandi* in many ways. Among these are the shape of the head, higher dorsal fin count and higher lateral-line scale count for *P. nigrofasciata.* The lateral markings on *P. copelandi* are reduced to short, oblong blotches rather than elliptically shaped ones for *P. nigrofasciata.*

The above comparisons apply to species of *Percina* found within the range of *P. nigrofasciata.*

Origin and dispersal.—Probably *Percina nigrofasciata* was derived from ancestral stock which closely resembled *P. sciera.* From knowledge of the range of *P. sciera* its origin was very likely at a locality west of the Mississippi River. Possibly a population segment of the *sciera* like ancestor gradually made its way down the Mississippi River drainage, and in the region southeast of the river, was cut off from the main population. This could have occurred by flooding of the river basin or by a westward drainage shift. The consequence in either case being isolation of the segment from its parent stock. Several instances of flooding by the Mississippi River are discussed by Gunter (1952: 122).

Differentiation, through mutation during isolation, of the restricted form into *P. nigrofasciata* presumably occurred. Opportunity was present for the new form to disperse eastward through the rivers and

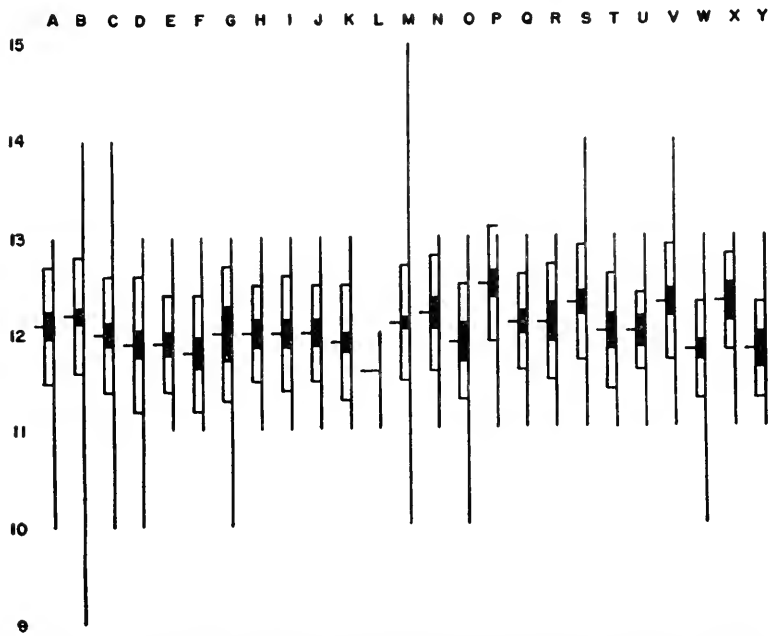


Figure 6. Comparison of the Number of Rays in the First Dorsal Fin of *Percina nigrofasciata* by Drainage Systems. Arrangement as in fig. 1.

connecting swamps of the Gulf Coastal Plain. Dispersal was perhaps further facilitated by the nearly complete absence of other species of *Percina* throughout the coastal plain. Pressure for available habitats of the new population was likely at a maximum, and the spread may have been rapid. Dispersal southward into peninsular Florida via the St. Johns and Suwannee River system was perhaps expedited again by the absence of closely related forms. Northward ascent into the piedmont region and mountains of South Carolina and Georgia may have been gradual or could have been forced during one of the submergences of the coastal plain during the Pleistocene (Carr 1940: 6; Hobbs 1942: 34, map 3). Whatever the case, the basic adaptability of this species to a variety of habitats has been shown.

It is entirely plausible to assume that even today much interchange of waters from drainage to drainage due to lowland flooding occurs along the Gulf Coastal Plain. For this reason further isolation for

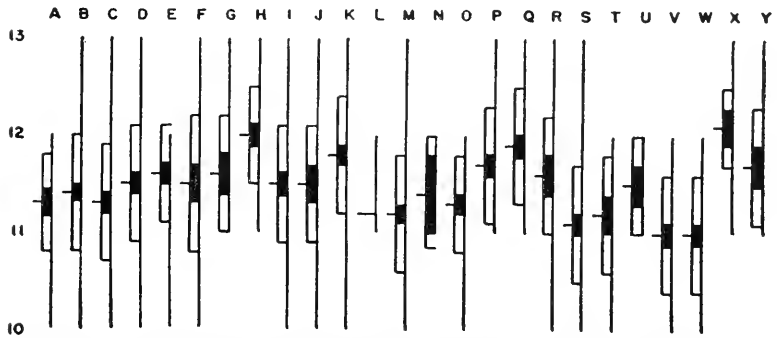


Figure 7. Comparison of the Number of Rays in the Second Dorsal Fin of *Percina nigrofasciata* by Drainage Systems. Arrangement as in fig. 1.

P. n. nigrofasciata has been limited and differentiation has been incomplete, due to gene flow between populations in adjacent rivers throughout the coastal plain. The only differentiation to be noted today is incipient, and *P. n. nigrofasciata* is relatively stable throughout the Gulf drainages. Some racial differentiation has occurred, but it is restricted to populations of *P. n. nigrofasciata* in drainages which are in themselves somewhat ecologically distinct. These are located in the extreme lowlands and mountains. One of the river systems, the Suwannee, contains springs which afford a different microhabitat.

P. nigrofasciata and *P. sciera* have been taken together in the Pearl and Lake Pontchartrain drainages of Louisiana and Mississippi. However, no evidence of intergradation has been noted, and the respective forms seem to be relatively unsuccessful in invading each others range. Perhaps this is further evidence for the closeness of relationship between the two forms.

Differentiation of *P. nigrofasciata* into *P. n. raneyi* above the fall line in the Savannah River system corresponds to a pattern well known in freshwater fishes. The lowland species making its way above the fall line with differentiation subsequently taking place has been noted previously with *Notropis cummingsae* and *Notropis altipinnis* (Hubbs and Raney 1948: 6, 1951: 4).

Two different interpretations are suggested for the dispersal and eventual differentiation of *P. nigrofasciata* above the fall line in the Savannah River system. The first favors a gradual movement up the river, with preadapted forms able to transcend the barrier. The

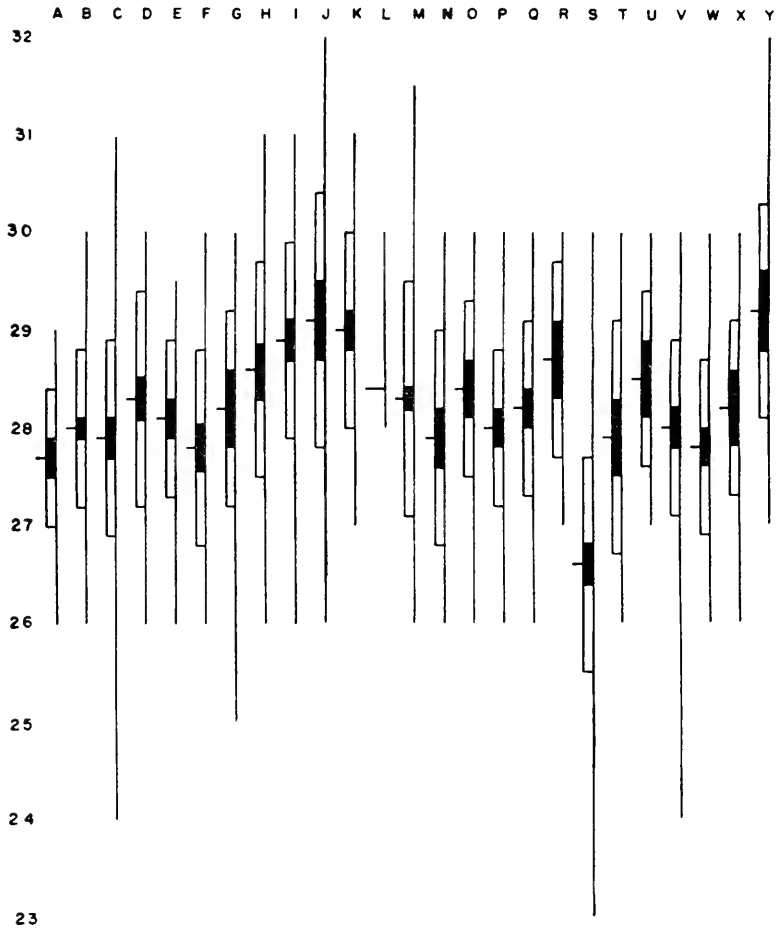


Figure 8. Comparison of the Number of Rays in the Pectoral Fins of *Percina nigrofasciata* by Drainage Systems. Arrangement as in fig. 1.

TABLE 9.
PROPORTIONAL MEASUREMENTS OF *Percina nigrofasciata* THROUGHOUT ITS RANGE

No. specimens	*nigrofasciata* 208 Mean (Range)	intergrades 30 Mean (Range)	*raneyi* Holotype Mean	*raneyi* 25 Paratypes Mean (Range)
In standard length				
body depth	5.3 (4.4-6.5)	5.3 (4.8-6.0)	4.7	5.4 (4.6-5.9)
head length	3.8 (3.5-4.1)	3.8 (3.6-4.0)	3.9	3.8 (3.6-4.1)
In head length				
head width	2.0 (1.6-2.4)	1.9 (1.7-2.1)	1.8	1.9 (1.7-2.2)
head depth	2.1 (1.9-2.5)	2.1 (1.8-2.4)	2.1	2.2 (2.1-2.3)
eye length	4.3 (3.5-5.4)	4.1 (3.6-4.8)	4.5	4.3 (3.7-4.7)
snout length	4.4 (3.7-5.0)	4.3 (3.7-5.1)	4.7	4.7 (4.3-5.1)
upper jaw length	3.8 (3.1-4.6)	3.7 (3.4-4.0)	3.9	3.9 (3.6-4.4)
depth caudal peduncle	3.3 (2.6-3.9)	3.2 (2.8-3.7)	2.7	2.9 (2.7-3.3)
longest first dorsal	2.3 (1.8-2.9)	2.1 (1.9-2.4)	2.7	2.6 (2.2-2.9)
longest second dorsal	1.9 (1.6-2.5)	1.9 (1.8-2.1)	2.1	2.0 (1.8-2.3)
longest pectoral	1.2 (1.1-1.5)	1.2 (1.2-1.3)	1.6	1.3 (1.1-1.6)
longest pelvic	1.4 (1.2-1.6)	1.4 (1.3-1.6)	1.6	1.5 (1.5-1.8)
longest caudal	1.5 (1.3-2.0)	1.5 (1.3-1.6)	1.5	1.6 (1.5-1.8)
longest anal	1.7 (1.5-2.1)	1.8 (1.5-2.0)	2.3	2.2 (1.7-2.6)
In eye length				
least fleshy interorbital width	1.3 (0.9-1.7)	1.3 (1.1-1.6)	1.3	1.4 (1.3-1.8)
least bony interorbital width	1.8 (1.1-2.7)	2.0 (1.7-2.5)	2.0	2.0 (1.5-2.8)
In distance from insertion of most anterior pelvic ray to union of gill membranes				
mandible tip to gill membranes union	1.1 (0.9-1.5)	1.1 (0.9-1.3)	1.2	1.1 (0.9-1.3)
pelvic girdle insertion to gill membranes union	2.1 (1.6-2.8)	2.2 (1.9-2.6)	2.3	2.2 (2.0-2.4)

second holds for stream capture.

If the population gradually made its way over the fall line as the first hypothesis postulates it would be hard to explain the derivation of *P. n. raneyi* in the upper Savannah River system only as *P. nigrofasciata* makes its way over the fall line in other river systems. Populations commonly occur above the fall line in the Apalachicola and Alabama River systems for example. If gradual ascent was the answer in the upper Savannah River one would expect that the only differences from *P. nigrofasciata* would be on a gradual or clinal basis much as they are in the other river systems. In these systems there is very little difference between extreme lowland populations and populations far above the fall line in meristic characters.

The second postulation, that of stream capture, seems to explain the differentiation of *P. n. raneyi* much more logically. Probably the immediate ancestors of this form made their way into the upper Savannah River through stream capture a long time before the gradual ascension of the lower Savannah population. It has been pointed out that the Tugaloo River, a tributary of the Savannah, in times past has captured a tributary of the Chattahoochee River, the Chestatee (Hayes and Campbell 1894: 63-126, 1900: 131-33; Campbell 1896: 677-78; and Johnson 1907: 211-48). This capture presumably antedated the ascension of all of the Atlantic drainage populations, but the Gulf drainages were probably populated at this time from mouth to headwaters. As a result of the capture the upper Savannah population was isolated from the basic stock in a new habitat, and differentiation presumably occurred at a rather rapid rate. Further evidence for the Chattahoochee population being the direct ancestral stock from which *P. n. raneyi* evolved is seen in several normally stable proportional measurements. Proportions of body depth into standard length, head length into standard length, and highest dorsal fin into head length show very close affinity between the two populations (Tables 9, 12).

PERCINA NIGROFASCIATA NIGROFASCIATA (Agassiz)

(Tables 1-14, figures 1-9, map. 1)

Hadropterus nigrofasciatus, Agassiz, 1854: 305 (original description, type locality, Mobile, Alabama). Jordan, 1876: 310 (description, Etowah and Oostanaula Rivers, synonymy), 1877: 14 (range in part, South Carolina to Louisiana). Jordan and Brayton, 1878: 40-45 (Chattahoochee River near Gainesville, abundant in Alabama). Jordan, 1878: 438 (range). Jordan and Gilbert, 1883: 249 (South Carolina). Jordan, 1885: 79 (range, compiled). Jordan and Evermann, 1896a: 1038 (description, range, synonymy: 1896b: 359 (range). Evermann and Kendall, 1900: 72 (Escambia, synonymy). Jordan, 1905: 312 (Georgia rivers). Radcliffe and Welsh, 1912: 31 (range, compiled). Palmer and Wright, 1920: 357 (range, after Jordan 1876, and Jordan and Brayton, 1878). Pratt, 1923: 126

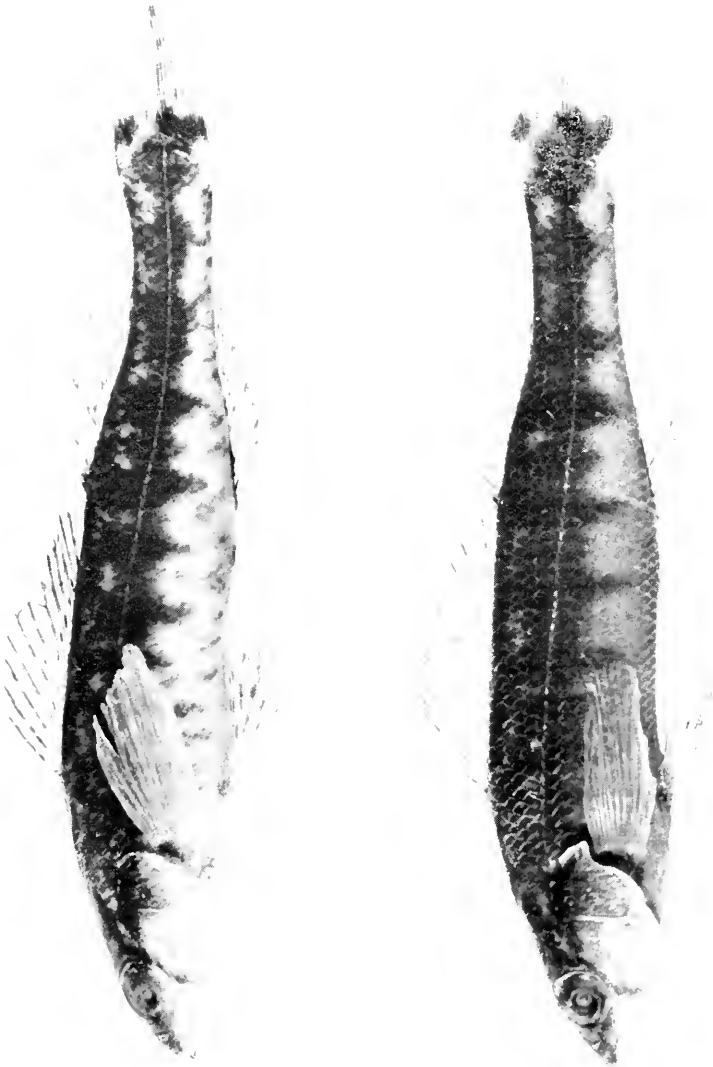


Figure 9. *Percina nigrofasciata nigrofasciata*
Above: Female, 58.0 mm., CU 16657, Semmes Co., Ala., Mobile Bay Drainage.
Below: Male, 58.0 mm., CU 16657, Semmes Co., Ala., Mobile Bay Drainage. (Photographs by Douglass M. Payne)

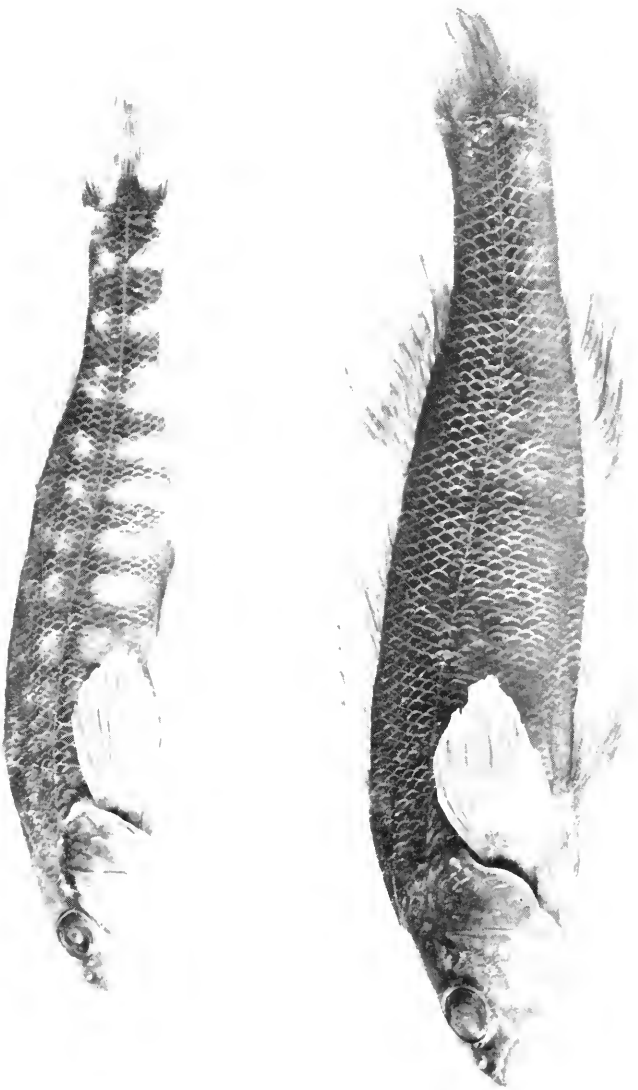


Figure 10. *Percina nigrofasciata raneyi*
Above: Female, 65.0 mm., CU 23344, Abbeville Co., So. Carolina, Upper Savannah River Drainage. (Paratype)
Below: Male, 79.3 mm., CU 23344, Abbeville Co., So. Carolina, Upper Savannah River Drainage. (Holotype) (Photographs by Douglass M. Payne)

TABLE 10.

PROPORTIONAL MEASUREMENTS BY SEXES OF *Percina nigrofasciata*

	nigrofasciata		*raneyi*	
	50 Male Mean (Range)	50 Female Mean (Range)	10 Male Mean (Range)	10 Female Mean (Range)
In standard length				
body depth	5.4 (4.6-6.1)	5.4 (4.5-6.5)	5.2 (4.7-5.8)	5.1 (4.7-5.9)
head length	3.6 (3.4-4.1)	3.8 (3.4-4.0)	3.8 (3.6-4.0)	3.8 (3.6-4.1)
In head length				
head width	2.0 (1.7-2.3)	2.0 (1.7-2.4)	1.9 (1.8-2.0)	1.9 (1.7-2.2)
head depth	2.1 (1.9-2.4)	2.2 (1.8-2.4)	2.2 (2.1-2.2)	2.2 (2.1-2.3)
eye length	4.3 (3.7-4.9)	4.2 (3.6-4.6)	4.4 (4.0-4.8)	4.2 (3.7-4.7)
snout length	4.4 (3.7-4.9)	4.4 (3.7-5.0)	4.7 (4.3-5.1)	4.8 (4.5-5.1)
upper jaw length	3.8 (3.1-4.3)	3.8 (3.3-4.6)	3.8 (3.6-4.1)	3.9 (3.7-4.3)
depth caudal peduncle	3.2 (2.8-3.9)	3.3 (2.8-3.9)	2.9 (2.7-3.0)	3.0 (2.8-3.3)
longest first dorsal	2.3 (2.0-2.7)	2.4 (2.0-2.7)	3.8 (3.6-4.0)	3.8 (3.6-4.1)
longest second dorsal	1.8 (1.6-2.1)	1.9 (1.6-2.5)	2.0 (1.8-2.1)	2.1 (1.9-2.2)
longest pectoral	1.3 (1.1-1.5)	1.2 (1.1-1.4)	1.4 (1.2-1.6)	1.3 (1.1-1.5)
longest pelvic	1.4 (1.2-1.6)	1.4 (1.2-1.6)	1.5 (1.3-1.6)	1.5 (1.3-1.7)
longest caudal	1.5 (1.3-1.7)	1.5 (1.3-2.0)	1.6 (1.5-1.8)	1.7 (1.5-1.8)
longest anal	1.7 (1.5-2.0)	1.7 (1.5-2.1)	2.1 (1.7-2.5)	2.2 (1.7-2.6)
In eye length				
least fleshy interorbital width	1.3 (1.1-1.7)	1.3 (1.1-1.6)	1.3 (1.2-1.4)	1.5 (1.3-1.8)
least bony interorbital width	1.8 (1.5-2.5)	1.9 (1.5-2.4)	2.0 (1.8-2.1)	2.1 (1.5-2.8)
In distance from insertion of most anterior pelvic ray to union of gill membranes				
mandible tip to gill membranes union	1.1 (0.9-1.3)	1.1 (0.9-1.3)	1.1 (1.0-1.3)	1.1 (1.0-1.3)
pelvic girdle insertion to gill membranes union	2.1 (1.9-2.6)	2.1 (1.8-2.8)	2.3 (2.2-2.4)	2.2 (2.0-2.4)

TABLE 11.

FREQUENCY DISTRIBUTIONS OF SEVERAL PROPORTIONAL MEASUREMENTS OF *Percina nigrofasciata* FROM ATLANTIC COAST DRAINAGE SYSTEMS

	Length of Snout into Head Length (in mm.)																	Longest First Dorsal into Head Length												
	5.1	5.0	4.9	4.8	4.7	4.6	4.5	4.4	4.3	4.2	4.1	4.0	3.9	3.8	3.7	N	Mean	2.9	2.8	2.7	2.6	2.5	2.4	2.3	2.2	2.1	2.0	1.9	N	Mean
nigrofasciata																														
St. Johns	—	—	—	1	2	2	1	2	4	2	1	—	—	—	—	15	4.4	—	—	—	1	3	1	2	1	1	—	—	9	2.4
Ogeechee	—	—	—	—	—	—	—	—	—	3	2	—	—	—	—	5	4.2	—	—	1	—	1	2	—	—	1	—	—	5	2.4
Edisto	—	—	—	—	—	—	2	2	2	2	1	1	—	—	—	10	4.4	—	—	—	1	—	—	2	1	1	—	—	5	2.3
intergrades																														
Altamaha	1	—	—	1	—	1	1	3	1	—	1	1	—	—	—	10	4.5	—	—	—	—	—	3	—	—	1	1	—	5	2.3
Mid-Savannah	—	—	—	—	—	—	1	2	1	1	—	1	2	1	1	10	4.1	—	—	—	—	—	1	—	2	1	1	—	5	2.2
Combahee	—	—	1	1	—	—	2	1	3	2	—	—	—	—	—	10	4.4	—	—	—	—	—	—	—	—	2	1	2	5	2.0
raneyi																														
Upper Savannah	1	1	4	4	6	3[1]	2	2	2	—	—	—	—	—	—	25	4.7	2	3	5	4	5[3]	2	2	2	—	—	—	25	2.6

	Depth of Caudal Peduncle into Head Length															Longest Anal into Head Length														
	3.9	3.8	3.7	3.6	3.5	3.4	3.3	3.2	3.1	3.0	2.9	2.8	2.7	N	Mean	2.6	2.5	2.4	2.3	2.2	2.1	2.0	1.9	1.8	1.7	1.6	1.5	N	Mean
nigrofasciata																														
St. Johns	—	—	—	—	1	—	3	3	—	—	4	2	2	15	3.0	—	—	—	—	—	—	1	—	6	4	4	—	15	1.7
Ogeechee	1	1	—	2	—	—	1	—	—	—	—	—	—	5	3.6	—	—	—	—	—	—	—	—	—	4	—	—	4	1.7
Edisto	—	—	—	1	1	3	4	—	—	—	1	—	—	10	3.3	—	—	—	—	—	—	1	2	3	4	—	—	10	1.8
intergrades																														
Altamaha	—	—	—	—	1	—	1	1	2	1	4	—	—	10	3.1	—	—	—	—	—	—	—	1	4	4	1	—	10	1.8
Mid-Savannah	—	—	—	—	1	—	5	1	2	—	—	1	—	10	3.2	—	—	—	—	—	—	3	3	2	2	—	—	10	1.9
Combahee	—	—	1	1	—	1	2	2	3	—	—	—	—	10	3.3	—	—	—	—	—	—	—	—	2	4	3	1	10	1.7
raneyi																														
Upper Savannah	—	—	—	—	—	—	1	3	—	3[2]	11	6	1	25	2.9	1	2	1	5	6	2[4]	2	3	1	2	—	—	25	2.2

[1] Average divergence: 82.0%. Line of separation between 4.5 and 4.6.
[2] Average divergence: 79.5%. Line of separation between 3.0 and 3.1.
[3] Average divergence: 77.7%. Line of separation between 2.4 and 2.5.
[4] Average divergence: 84.0%. Line of separation between 2.0 and 2.1.

(compiled). Jordan, Evermann and Clark, 1930: 283 (range, synonymy). Fowler, 1935: 22 (synonymy, coloration, Orangeburg, South Carolina). Pratt 1935: 119 (compiled). Carr, 1937: 84 (characters, Key, Florida). Viosca, 1937: 136 (Gulf drainages). Schrenkeisen, 1938: 214 (compiled). Bailey, 1940: 525-30 (comparison). Driver, 1942: 287 (compiled). Hubbs and Allen, 1943: 125 (Silver Springs, Florida). Driver, 1950: 297 (compiled). Crawford, 1953: 235 (characters).

Etheostoma nigrofasciatum, Vaillant, 1873: 69 (description, range, synonymy). Jordan, 1876: 223 (confused in description, range). Jordan and Copeland, 1876: 164 (range). Bollman, 1887: 464 (Escambia River). Gilbert, 1888: 229 (Ogeechee River); 1891: 155, 159 (Alabama Basin, Escambia River). Boulenger, 1895: 80 (range, description, synonymy). Palmer and Wright, 1920: 357 (range).

Plesioperca anceps, Vaillant, 1873: 37 (plate, description, synonymy).

Hadropterus spillmani, Hay, 1880: 491 (description, Chickasawha at Enterprise, synonymy); 1882: 60, 74 (Tombigbee and Chickasawha Rivers).

Hadropterus nigrofasciatus westfalli, (misidentification)—Fowler, 1942: 9 (Wekiwa River, Florida, in error, actually was Wekiva River, Florida; plate, description, synonymy); 1945: 293 (Orlando-Titusville road, coloration in part).

Hadropterus nigrofasciatus nigrofasciatus, Fowler, 1945: 354 (description, Alabama).

Percina nigrofasciata, Bailey, Winn and Smith, 1954: 141 (Escambia River, revision). Bailey and Gosline, 1955: 12, 36 (comparison, Wilkinson Co., Mississippi).

The nominal subspecies, *Percina n. westfalli,* is not considered as a subspecies herein. Henry W. Fowler described this form on the basis of one specimen and by comparison with specimens of *P. n. nigrofasciata* from Alabama only (1942: 9-11). He distinguished *P. n. westfalli* by the size of the eye: 3.25 in head; compared to 4.2 (3.5-5.4) as found by the author in specimens of *P. n. nigrofasciata* (Table 14). From critical examination of specimens from the type locality and other collections of the St. Johns River system, no appreciable or significant difference was found between eye lengths of the form called *westfalli* and specimens of *nigrofasciata.* The only character in which the St. Johns fishes showed any appreciable difference was in the number of pectoral rays. The amount of difference shown was not considered adequate to recognize this fish as a subspecies (Table 8).

Range.—Mississippi River system, Louisiana to Edisto River system, Georgia. Southward into peninsular Florida throughout the Suwannee and St. Johns River systems.

Diagnosis.—Scale counts lower than those of *P. n. raneyi:* lateral line, 46 to 66 (usually 50 to 60); above the lateral line, 4 to 9

TABLE 12.

FREQUENCY DISTRIBUTIONS OF SEVERAL PROPORTIONAL MEASUREMENTS OF FOUR RACES OF *P. n. nigrofasciata* IN THE GULF DRAINAGES

	Body Length into Standard Length (in mm.)																					Head Length into Standard Length (in mm.)									
Races	6.5	6.4	6.3	6.2	6.1	6.0	5.9	5.8	5.7	5.6	5.5	5.4	5.3	5.2	5.1	5.0	4.9	4.8	4.7	4.6	4.5	No.	Mean	4.1	4.0	3.9	3.8	3.7	3.6	3.5	3.4	No.	Mean
Western	—	—	—	—	—	—	—	—	1	—	1	—	2	2	2	—	2	—	—	—	—	10	5.20	1	1	1	1	3	3	—	—	10	3.80
Upper Alabama	—	—	—	—	1	—	—	2	3	4	1	3	2	2	1	—	1	1	—	—	—	20	5.50	2	6	8	3	1	—	—	—	20	3.95
Coastal	1	—	—	—	1	3	—	2	4	2	1	—	—	1	—	—	—	—	—	—	—	15	5.85	—	1	—	5	8	—	1	—	15	3.75
Apalachicola Bay	—	—	—	—	—	—	—	—	—	—	1	—	2	4	5	7	3	2	1	1	1	20	5.00	—	2	6	10	5	5	2	—	30	3.75
Remaining Drainages	—	—	—	—	—	1	4	1	8	5	9	13	21	16	8	8	4	2	1	1	—	103	5.30	1	13	20	34	20	8	5	2	103	3.80

	Caudal Peduncle Depth into Head Length															Head Width into Head Length											
	3.9	3.8	3.7	3.6	3.5	3.4	3.3	3.2	3.1	3.0	2.9	2.8	2.7	2.6	No.	Mean	2.4	2.3	2.2	2.1	2.0	1.9	1.8	1.7	1.6	No.	Mean
Western	—	—	—	—	—	2	2	2	2	1	1	—	—	—	10	3.20	—	—	—	3	5	1	1	—	—	10	2.00
Upper Alabama	—	—	—	—	—	1	1	3	3	5	5	1	—	1	20	3.05	—	1	1	1	8	6	3	—	—	20	1.95
Coastal	2	1	2	4	2	2	—	1	1	—	—	—	—	—	15	3.55	—	1	1	6	1	1	—	—	—	10	2.10
Apalachicola Bay	1	—	—	1	4	1	3	5	3	6	2	3	—	—	30	3.25	—	—	1	—	1	9	5	8	1	25	1.85
Remaining Drainages	3	1	2	6	8	12	19	13	15	20	3	1	—	—	98	3.30	1	1	7	23	25	20	10	1	—	87	2.00

	Longest First Dorsal into Head Length													Head Depth into Head Length									
	2.9	2.8	2.7	2.6	2.5	2.4	2.3	2.2	2.1	2.0	1.9	1.8	No.	Mean	2.5	2.4	2.3	2.2	2.1	2.0	1.9	No.	Mean
Western	—	—	—	1	2	3	1	2	—	1	—	—	10	2.40	—	1	1	4	3	1	—	10	2.20
Upper Alabama	—	1	—	1	2	3	4	7	2	—	—	—	20	2.35	—	2	3	5	7	2	1	10	2.15
Coastal	—	—	—	—	—	3	2	2	2	1	—	—	10	2.30	1	1	7	6	—	—	—	15	2.25
Apalachicola Bay	2	2	4	6	4	6	1	—	—	—	—	—	25	2.60	—	—	1	9	9	6	5	30	2.05
Remaining Drainages	—	1	—	2	12	10	25	23	12	5	2	1	95	2.30	—	5	13	29	39	14	3	103	2.10

	Least Bony Interorbital Width into Eye Length															Longest Second Dorsal into Head Length											
	2.7	2.6	2.5	2.4	2.3	2.2	2.1	2.0	1.9	1.8	1.7	1.6	1.5	1.4	1.3	No.	Mean	2.5	2.4	2.3	2.2	2.1	2.0	1.9	1.8	1.7	1.6	No.	Mean
Western	—	—	—	—	—	—	—	1	—	4	2	2	1	—	—	10	1.70	—	—	—	—	—	—	2	5	2	1	10	1.80
Upper Alabama	—	—	—	—	—	—	—	—	3	4	7	4	2	—	—	20	1.70	—	—	—	—	2	2	5	2	5	2	18	1.85
Coastal	—	—	—	—	—	—	1	1	5	4	3	—	1	—	—	15	1.80	—	—	—	—	—	—	1	5	2	2	10	1.75
Apalachicola Bay	—	—	—	—	1	—	3	2	6	2	3	1	—	—	—	30	1.95	1	—	1	3	1	8	3	6	2	—	25	2.00
Remaining Drainages	1	—	1	1	1	2	4	7	12	22	21	15	10	—	1	98	1.80	—	—	1	1	2	10	28	25	18	2	87	1.90

(usually 5 to 7); below the lateral line, 7 to 13 (usually 9 to 11); above plus below the lateral line, 11 to 20 (usually 14 to 18); around the caudal peduncle, 16 to 25 (usually 19 to 23). Depth enters the standard length 5.3 times. The following proportional measurements enter the length of head: depth of caudal peduncle, 3.3; longest dorsal spine, 2.3; longest anal ray, 1.7; length of snout, 4.4. The values for proportional measurements indicate the means (Table 9).

Racial Analysis.—Eight races of *P. n. nigrofasciata* are recognized herein. These are, according to the drainage in which they are found: Western race, Lake Pontchartrain; Upper Alabama race, Coosa and Black Warrior; Apalachicola Bay race; Chattahoochee and Flint; Coastal race, Perdido Bay and Blackwater; Suwannee River race, Suwannee; Suwannee springs race, Suwannee; St. Johns River race, St. Johns; Eastern race, Ogeechee and Edisto.

The author assumes a genetic basis for the races. Of course, this is hard to directly show in several of the cases. However, there is good evidence to surmise that the differences between the races and adjacent populations do have a genetic basis. The above named races are significantly different in meristic and proportional characters from other populations of *P. n. nigrofasciata* and are therefore pointed out. It should be noted that there is little consistency between low scale counts and low altitude and high scale counts and high altitude. Environment does not seem directly to influence meristic characters.

For purposes of analysis, the drainages which flow into the Gulf of Mexico were considered as one geographical unit, and the drainages which flow into the Atlantic Ocean were considered as another geographical unit. Comparisons of scale counts and proportional measurements were made with the given race against all other drainages of the geographical unit in which *P. n. nigrofasciata* occurs. It is felt that this procedure of comparison gives more reliable indications of divergence than a procedure in which the incipiently speciated units are compared against themselves only. Arithmetical separations which give figures for average divergences were made in accordance to Ginsburg (1938: 255-59). These divergences served as a tool to point out significant differences between populations to the author. Actual figures for average divergences are not included in the text but may be easily computed from the frequency distributions in Tables 12-14. Two exceptions to the above procedure of comparison are to be noted. When analysis of the Upper Alabama race was made, the Western race was not included with the remainder of the Gulf drainages. In the same manner, the Upper Alabama race was not included with the rest of the Gulf drainages when the Western race was analyzed. This alternative procedure was employed to prevent similarities, apparently due to convergence, from becoming masked. The second exception was in regard to comparison of the forms within the Suwannee drainage. Significant differences occur in all scale characters (Tables 1-5, 13) between specimens in the Suwannee River and its tributaries as compared to specimens which

TABLE 13.

FREQUENCY DISTRIBUTIONS OF SEVERAL PROPORTIONAL MEASUREMENTS OF TWO RACES OF *P. n. nigrofasciata* IN THE SUWANNEE RIVER AND SPRINGS

	Upper Jaw Length into Head Length (in mm.)										
	4.4	4.3	4.2	4.1	4.0	3.9	3.8	3.7	3.6	No.	Mean
River Race	—	—	—	—	2	—	3	3	3	10	3.8
Springs Race	1	1	—	3	2	1	—	2	—	10	4.0

	Caudal Peduncle Depth into Head Length						
	3.5	3.4	3.3	3.2	3.1	3.0	No.	Mean
River Race	—	—	2	3	1	4	10	3.1
Springs Race	3	1	1	1	2	2	10	3.0

	Longest First Dorsal into Head Length										
	2.8	2.7	2.6	2.5	2.4	2.3	2.2	2.1	2.0	1.9	No.	Mean
River Race	—	—	—	—	1	2	3	2	1	1	10	2.2
Springs Race	1	—	1	1	2	4	—	1	—	—	10	2.4

	Longest Second Dorsal into Head Length						
	2.2	2.1	2.0	1.9	1.8	1.7	No.	Mean
River Race	—	—	—	3	4	3	10	1.8
Springs Race	1	—	1	6	1	1	10	1.9

	Longest Pelvic into Head Length													
	1.6		1.5		1.4		1.3		1.2				No.	Mean
River Race	—		—		4		5		1				10	1.3
Springs Race	1		4		3		2		—				10	1.4

	Longest Caudal into Head Length													
	1.6		1.5		1.4								No.	Mean
River Race	—		2		8								10	1.4
Springs Race	8		2		—								10	1.6

	Least Bony Interorbital Width into Eye Length													
	2.7	2.6	2.5	2.4	2.3	2.2	2.1	2.0	1.9	1.8	1.7	1.6	No.	Mean
River Race	—	—	—	—	—	—	1	3	1	2	2	1	10	1.9
Springs Race	1	—	1	1	1	2	1	—	2	1	—	—	10	2.2

TABLE 14.

FREQUENCY DISTRIBUTIONS OF SEVERAL PROPORTIONAL MEASUREMENTS OF TWO RACES OF *P. n. nigrofasciata* IN THE ATLANTIC DRAINAGES

Races	Body Depth into Standard Length (in mm.)													No.	Mean
	6.0	5.9	5.8	5.7	5.6	5.5	5.4	5.3	5.2	5.1	5.0	4.9	4.8		
St. Johns	—	—	1	1	—	—	1	4	2	—	5	—	1	15	5.2
Eastern	—	1	—	1	3	—	2	3	1	1	—	1	1	14	5.4

	Head Length into Standard Length							
	4.0		3.9		3.8		3.7		3.6		3.5			
St. Johns	4		4		6		1		—		—		15	3.9
Eastern	—		—		2		1		8		4		15	3.6

	Eye Width into Head Length														
	5.0	4.9	4.8	4.7	4.6	4.5	4.4	4.3	4.2	4.1	4.0	3.9	3.8	No.	Mean
St. Johns	—	—	—	—	—	1	3	1	4	2	1	—	3	15	4.2
Eastern	1	—	1	1	3	1	3	1	3	1	—	—	—	15	4.4

	Caudal Peduncle Depth into Head Length														
	3.9	3.8	3.7	3.6	3.5	3.4	3.3	3.2	3.1	3.0	2.9	2.8	2.7	No.	Mean
St. Johns	—	—	—	—	1	—	3	3	—	—	4	2	2	15	3.0
Eastern	1	1	—	3	1	3	5	—	—	—	1	—	—	15	3.4

	Least Bony Interorbital Width into Eye Length												
	2.1	2.0	1.9	1.8	1.7	1.6	1.5	1.4	1.3	1.2	1.1	No.	Mean
St. Johns	1	—	2	5	4	1	2	—	—	—	—	15	1.8
Eastern	—	3	3	1	—	5	—	2	—	—	1	15	1.7

inhabit springs in the Suwannee drainage. Consequently, the fishes of the Suwannee drainage could not be logically regarded as a single unit. As a result, spring specimens were compared against river specimens as two discrete populations. For analysis of the two races, comparisons were made only with specimens from the Suwannee drainage, as two definite ecological niches are present. It could be that this is an example of dual invasion into the Suwannee of two populations of closely related stock. If this is the case, the most recent population to enter had to resort to the microhabitat the older population was not inhabiting. Isolation, and swift differentiation may have ensued. It seems probable that it is the spring populations that are differentiating in relation to the much higher scale counts found. Certainly a very concrete isolating mechanism is available here in the presence of the two microhabitats. The very interesting situation here seems to afford an excellent opportunity for regional study in the future.

The Western race diverges in all scale characters (Tables 1-5). The number of body scales is high and is quite similar to those of specimens of the Upper Alabama race. This is a prime example of no correlation between high scale counts and high elevation, as the Lake Pontchartrain drainage is restricted to the lowlands. Even so, scale counts for this race are the highest of any of the populations in the Gulf drainage with the exception of the Black Warrior system (Tables 1-5).

The Upper Alabama race differentiates from the Gulf Coast forms by the presence of a greater number of body scales (Tables 1-5). The head is longer and the caudal peduncle is deeper in specimens of this race (Table 12). The race occurs in rivers which extend above the fall line, and while no definite isolating mechanism is known for the race, it is a well known fact that many species after making their way above the fall line have subsequently differentiated.

The Apalachicola Bay race contrasts in body depth and has a wider head (Table 12). Specimens of this race are robust. In addition, they differ in color pattern. Many male specimens are marked with block-shaped bars which extend ventrad only to the lateral stripe. Females are often profusely spotted. Members of this race are one more example of fishes which occur from the coastal plain to the mountains, far above the fall line, with no correlation between high number of scales and a low number of scales in relation to altitudinal gradient (Tables 1-5).

The number of body scales is consistently lower in specimens of the Coastal Race (Tables 1-5) than in other adjacent lowland coastal plain rivers. In body proportions the Coastal Race diverges from the remaining Gulf Coast forms in: depth of caudal peduncle, head depth, head width, and body depth (Table 12). Forms of this race, as a whole, appear elongate and less robust than do most populations of *P. n. nigrofasciata*. This could, of course, be a nutritional factor. Scale counts are uniformly lower for specimens of this race than

TABLE 15.

FREQUENCY DISTRIBUTIONS OF THE NUMBER OF SCALES IN THE LATERAL LINE AND THE NUMBER OF SPINES IN THE FIRST DORSAL FIN OF SPECIMENS OF *Percina nigrofasciata* AND *Percina sciera*

	Total Scales in the Lateral Line																
Species	67	66	65	64	63	62	61	60	59	58	57	56	55	54	53	No.	Mean
P. nigrofasciata	—	—	—	—	1	—	1	1	2	6	3	1	3	2	1	21	57.3
P. sciera	1	1	2	3	1	2	2	4	3	1	1	—	1	—	—	22	61.4

	Total Spines in the First Dorsal Fin				
Species	13	12	11	No.	Mean
P. nigrofasciata	3	15	4	22	12.0
P. sciera	7	8	—	15	12.5

they are for specimens from adjacent lowland drainages.

The Eastern and St. Johns River races of the Atlantic drainages separate from one another in all scale and fin counts (Tables 1-5). In body proportions they contrast in: body depth, head length, eye length, depth of caudal peduncle, and least bony interorbital width (Table 14). The St. Johns River specimens also differ in coloration. Males often have a black border around the dorsal margin of the spinous dorsal fin. The St. Johns River extends deep into peninsular Florida and the fishes of this system are in a recognized center of endemism. The Eastern race occurs in drainages nearly exclusively confined to the piedmont region. In comparing the two races, it should be noted that the St. Johns River race which is found at a much lower altitude has consistently higher scale counts than the Eastern race which occurs at much higher elevations.

PERCINA NIGROFASCIATA **RANEYI,** subsp. nov.

(Tables 1-11, 15, figures 1-8, 10, map 1)

Hadropterus nigrofasciatus, Jordan and Brayton, 1878: 30 (Toccoa Creek near Toccoa Falls, Georgia).

Holotype: An adult male (CU 23344), collected in a tributary to the Savannah River, 7.6 miles east of Calhoun Falls, Abbeville County, South Carolina, on Route 72, March 27, 1951 by Edward C. Raney, Ronald W. Crawford, Richard H. Backus, C. Richard Robins, James N. Layne and Roland L. Wigley.

Scale and fin counts for the holotype are: lateral line, 61; above lateral line, 8; below the lateral line, 12; above plus below lateral line 20; caudal peduncle, 22; first dorsal, 11; second dorsal, 11; total of pectorals, 29. Proportional measurements appear in Table 9.

Paratypes: 41 specimens which were taken with the holotype (CU 19599). Other specimens studied are listed under material examined.

The new form is named for Dr. Edward C. Raney of Cornell University whose investigations on darters and other freshwater fishes of the southeastern United States are well known.

Range.—Savannah River system, Georgia and South Carolina, above the fall line.

Diagnosis.—Scale counts higher than in subspecies *nigrofasciata:* lateral line, 55 to 71 (usually 60 to 66); above the lateral line, 6 to 9 (usually 7 to 8); below the lateral line, 8 to 14 (usually 9 to 13); above plus below the lateral line, 14 to 22 (usually 17 to 20); around the caudal peduncle, 20 to 27 (usually 21 to 24) (Tables 1-5). Depth enters the standard length 5.1 times. The following proportional measurements enter the length of head: depth of caudal peduncle, 2.9; longest dorsal spine, 2.6; longest anal ray, 2.2; length of snout, 4.7 (Table 9). The values given for proportional measurements indicate the means.

Comparison of P. n. nigrofasciata and P. n. raneyi.—The subspecies *raneyi* differs from *nigrofasciata* in: the number of scales in the

lateral line; above the lateral line; below the lateral line; above plus below the lateral line; and around the caudal peduncle. Average divergences for all scale characters, exclusive of the scales around the caudal peduncle, with the best lines of separation are summarized below, and may be applied to (Tables 1-4).

Scale Character	Average Divergence	Line of Separation
Lateral line	92.0%	59-60
Above lateral line	85.0%	6-7
Below lateral line	75.2%	11-12
Above plus below	86.2%	17-18

By the use of proportional measurements additional average differences may be shown by comparison of the following measurements. Length of head divided by: longest dorsal spine; longest anal spine; length of snout; and depth of caudal peduncle (Table 9).

Since intermediacy was not expressed by comparison of proportional measurements in the intergrades between the two subspecies, they are included with populations of *P. n. nigrofasciata* in comparison with *P. n. raneyi* (Table 9).

P. N. NIGROFASCIATA X P. N. RANEYI (Intergrades)

(Tables 1-9, 11, figures 1-8, map 1)

Hadropterus nigrofasciatus, Jordan and Brayton, 1878: 34 (flat shoals in the south fork of the Ocmulgee River). Freeman, 1953: 269 (Aiken and Barnwell counties, South Carolina).

Intermediate between subspecies *nigrofasciata* and *raneyi* in four scale counts: lateral line, 53 to 68 (usually 56 to 62); above the lateral line, 5 to 8 (usually 6 to 7); below the lateral line, 9 to 13 (usually 10 to 12); above the lateral line plus below the lateral line, 14 to 20 (usually 16 to 20) (Tables 1-5).

As proportional measurements do not consistently show intermediate tendencies, the intergrades were summed together with populations of *P. n. nigrofasciata* in the Atlantic drainages, when average divergences were computed in comparison with *P. n. raneyi* (Table 11).

Range.—Altamaha River system, Georgia; Savannah River system, Georgia and South Carolina, below the fall line; Combahee River system, South Carolina.

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Summary

Percina nigrofasciata is distributed widely in the southeastern United States. Its range is bounded to the west by the Mississippi River and to the east by the Edisto River, South Carolina. *P. nigrofasciata* extends southward into peninsular Florida by way of the Suwannee and St. Johns River systems. It extends northward as far as the headwaters of the Chattahoochee and Savannah River systems in Georgia and South Carolina.

Two subspecies of *P. nigrofasciata* are recognized herein. *P. n. nigrofasciata,* which has, in the past, usually been referred to as *Hadropterus nigrofasciatus,* and a new subspecies, *P. nigrofasciata raneyi. P. n. raneyi* has more body scales than does *P. n. nigrofasciata* and also differs in several body proportions.

The nominal subspecies *H. nigrofasciatus westfalli* is placed in synonymy. Populations of intergrades between the two subspecies are present in the Altamaha, Combahee and Savannah (below the fall line) River systems. Their intermediate tendencies are expressed mainly in the number of body scales.

Eight races of *P. n. nigrofasciata* are designated in this paper. Assignment of races was based on divergence of meristic characters and average body proportions from adjacent populations in immediate areas.

P. n. nigrofasciata apparently orignated on the coastal plain near the mouth of the Mississippi River from stock closely allied to *P. sciera,* which is the closest relative of *nigrofasciata* today. Dispersal of the new form proceeded eastward through connecting swampy areas during periods of high water. Dispersal northward may have been forced and rapid due to one of the submergences of the coastal plain during the Pleistocene, or it may have been gradual through the ascent of the populations up the streams.

P. n. raneyi originated above the fall line in the Savannah River system. Its immediate ancestors probably made their way over this barrier in one of two ways; by gradually ascending the barrier into waters above the falls, or through stream capture of the Chattahoochee River by the Savannah River, allowing fishes from the former system to enter the new habitat of the upper Savannah River. The author favors the latter explanation, as it explains the isolating mechanism necessary for differentiation to occur.

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ABSTRACT

Percina nigrofasciata is distributed widely in the southeastern United States. Its range is bounded to the west by the Mississippi River and to the east by the Edisto River. *P. nigrofasciata* extends southward into peninsular Florida by way of the Suwannee and St. Johns River systems. It extends northward as far as the headwaters of the Chattahoochee and Savannah River systems in Georgia and South Carolina.

Two subspecies of *P. nigrofasciata* are recognized: *P. n. nigrofasciata*, which has usually been referred to as *Hadropterus nigrofasciatus*, and *P. n.* **raneyi**, a new subspecies. The latter has more body scales than the former and also differs in several body proportions. Populations of intergrades between the two subspecies are present in three river systems. Eight races of *P. n. nigrofasciata* are designated.

P. n. nigrofasciata apparently originated on the coastal plain near the mouth of the Mississippi River. Dispersal proceeded eastward through connecting swampy areas during periods of high water. Dispersal northward may have been forced and rapid due to one of the submergences of the coastal plain during the Pleistocene, or it may have been gradual.

P. n. raneyi originated above the fall line in the Savannah River system. Its immediate ancestors probably made their way over this barrier in one of two ways: by gradually ascending the barrier into water above the falls, or through stream capture of the Chattahoochee River by the Savannah River, allowing fishes from the former system to enter the new habitat of the upper Savannah River. The writer favors the latter explanation, as it explains the isolating mechanism necessary for differentiation to occur.

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EXPERIMENTAL F_1 HYBRIDS BETWEEN *BUFO VALLICEPS* AND *BUFO FOWLERI*

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EXPERIMENTAL F_1 HYBRIDS BETWEEN *BUFO VALLICEPS* AND *BUFO FOWLERI*[1]

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Investigators familiar with the bufonid fauna of Louisiana have long suspected the occurrence of hybridization between *Bufo valliceps* Wiegmann and *Bufo fowleri* Hinckley. The distributional ranges of the two species overlap in southern Louisiana, and both species may be found breeding in the same body of water. Orton (1951) and Liner (1954) have observed interspecific matings at different localities in Louisiana. Sixteen mis-mated pairs have been noted by the author during the spring and summer months of 1954 and 1955 at a local breeding site (Audubon Park, New Orleans) occupied by both species. Seven of the cross-mated pairs involved females of *B. valliceps* clasped by males of *B. fowleri;* the other nine comprised reciprocal mis-mated pairs.

Laboratory crosses between the two species have revealed the extent to which interspecific gene exchange is possible. F_1 hybrids from the experimental cross *B. valliceps* ♀ X *B. fowleri* ♂ died in an early stage of development. In contradistinction, the majority of F_1 hybrids from the reciprocal cross *B. fowleri* ♀ X *B. valliceps* ♂ were viable. The metamorphosed F_1 hybrids more closely resembled the *B. valliceps* than the *B. fowleri* parent. The effects of the *B. fowleri* parent were more pronounced in the larval period of the F_1 hybrid than in the transformed stage.

The purpose of this paper is to describe and illustrate the appearance of laboratory-raised F_1 hybrid tadpoles and metamorphosed young. This information is an essential prerequisite to analysing the constituent individuals of a natural hybrid population.

Materials and Methods

Breeding adults of *B. valliceps* and *B. fowleri* were collected on several occasions during the spring and summer months of 1954 and 1955 from a pond at Audubon Park, New Orleans. In the laboratory hybridizations performed in 1954 the method of artificial fertilization was employed. Fertilized eggs were obtained by the routine procedure (Rugh, 1934) of inducing ovulation by pituitary injection and stripping the eggs into a sperm suspension. The latter was prepared by crushing a pair of testes in 20 cc of 0.10 Ringer's solution. In order to eliminate any possible variability caused by individual genetic dif-

[1] Research supported by a grant from the National Science Foundation (NSF-G1319). This study is part of a long-term project aimed at reconstructing experimentally the sequence of events that has led to the establishment and maintenance of hybrid individuals between *Bufo valliceps* and *Bufo fowleri* at Audubon Park, New Orleans. The illustrations were prepared by Mrs. Carolyn Thorne Volpe.

ferences, the eggs of a single female were fertilized in two batches; the first with sperm of the same species ("normal" cross), and the second with sperm of the other species ("hybrid" cross). Eggs of *B. valliceps* were fertilized with sperm of *B. fowleri* on six different occasions (each accompanied by a normal cross); the reciprocal cross *B. fowleri* ♀ X *B. valliceps* ♂ was performed nine times (each accompanied by a normal cross).

In the experiments carried out in 1955, the eggs were fertilized by the natural process. The eggs were inseminated by the male (during amplexus) as they emerged from the cloaca of the female. No difficulty was encountered in inducing males of one species to clasp females of the other species. Six interspecific crosses were made, three of which involved females of *B. valliceps* mated with males of *B. fowleri.* The other three were reciprocal crosses.

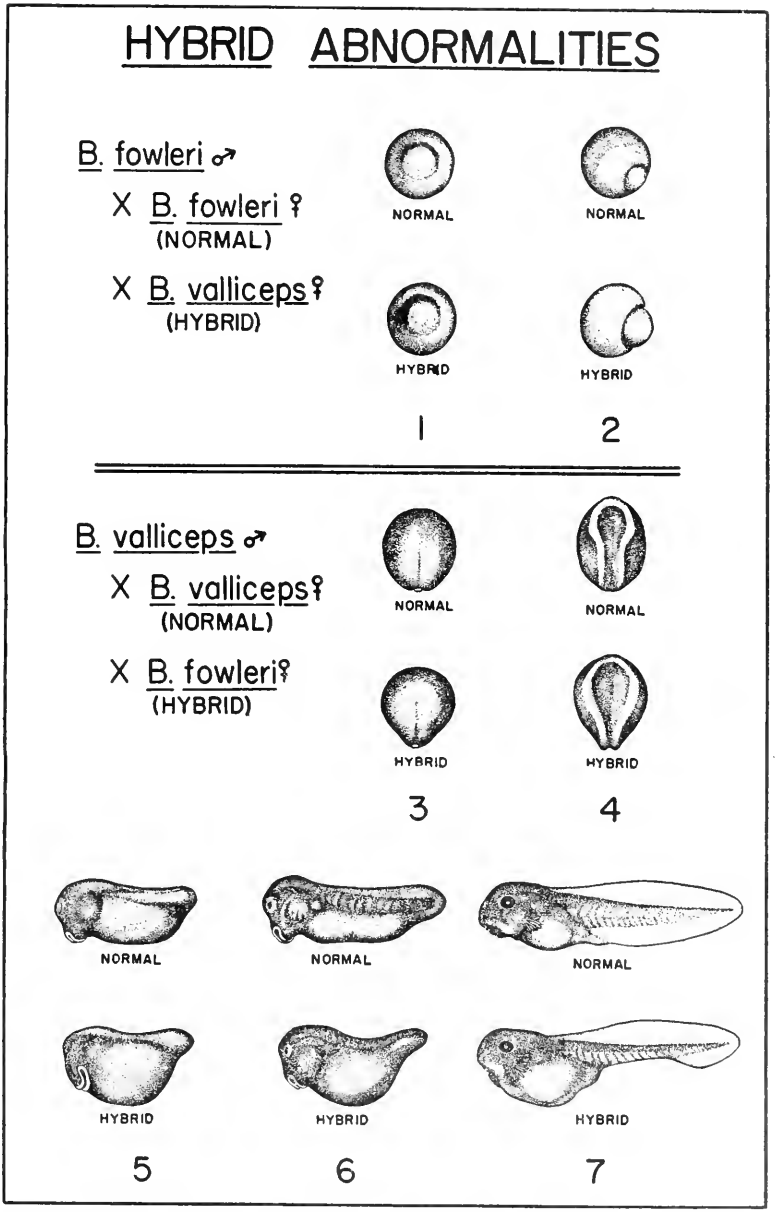
The procedures used in rearing the embryos were essentially similar to those employed in other work of this type (Volpe, 1952, 1954, 1955a, b). The egg strings from each fertilization were cut into small groups. Approximately seventy-five eggs were placed in a finger bowl containing 200 cc of pond water. Four finger bowls were used for each cross. The embryos in the pre-feeding stages (embryonic stages 1-25; defined in Shumway, 1940) were maintained in a 25° C. "Precision Scientific" constant temperature unit. At the onset of feeding activity (larval stage 1; defined in Taylor and Kollros, 1946), at least one hundred embryos from each of the successful crosses were transferred to enamel pans (12″ X 8″ X 2″) containing pond water at a depth of one inch. Each enamel pan, containing approximately twenty embryos, was kept at room temperature. Tadpoles were fed slightly boiled spinach. As the tadpoles approached metamorphosis, the water level in the pans was reduced and pebbles were added to enable the young toads to emerge from the water. Juvenile toads were fed vestigial-winged fruit flies, meal-worm larvae, and pieces of liver dipped in bone meal.

The embryos were examined at regular intervals during their development. At each observation, records were made of the external features of the embryos, types and proportions of abnormalities, and mortality. Embryos derived from the artificial crosses (1954 experiments) developed in an identical manner as those obtained from the natural crosses (1955 experiments). The data from the artificial and natural crosses are treated collectively in the discussion of the results.

Results

A. The Crosses: *B. valliceps* ♀ X *B. fowleri* ♂ (Hybrid)
B. valliceps ♀ X *B. valliceps* ♂ (Normal)

Embryos from the hybrid crosses (nine experiments) died in the late gastrula stages. The cleavage furrows in the early stages of development (stages 3-9; Shumway, *op. cit.*) were normal. The first indication of hybrid abnormality occurred during early gastrulation.



Figures 1-7. Abnormalities in the embryonic stages of F_1 hybrids from reciprocal crosses between *Bufo valliceps* and *Bufo fowleri*.

The dorsal blastopore lip was more heavily pigmented and undercut the embryo more deeply than in the normal gastrula (fig. 1). As the lateral and ventral blastopore lips formed in the hybrid embryo, a large mass of yolk was extruded through the open blastopore. Figure 2 illustrates the exogastrular condition of the hybrid embryo. Shortly thereafter all hybrid embryos cytolysed. No defects were noted in embryos from the normal crosses. The external appearance of a tadpole of *B. valliceps* derived from a normal cross is shown in Figure 8. Its features will be discussed later.

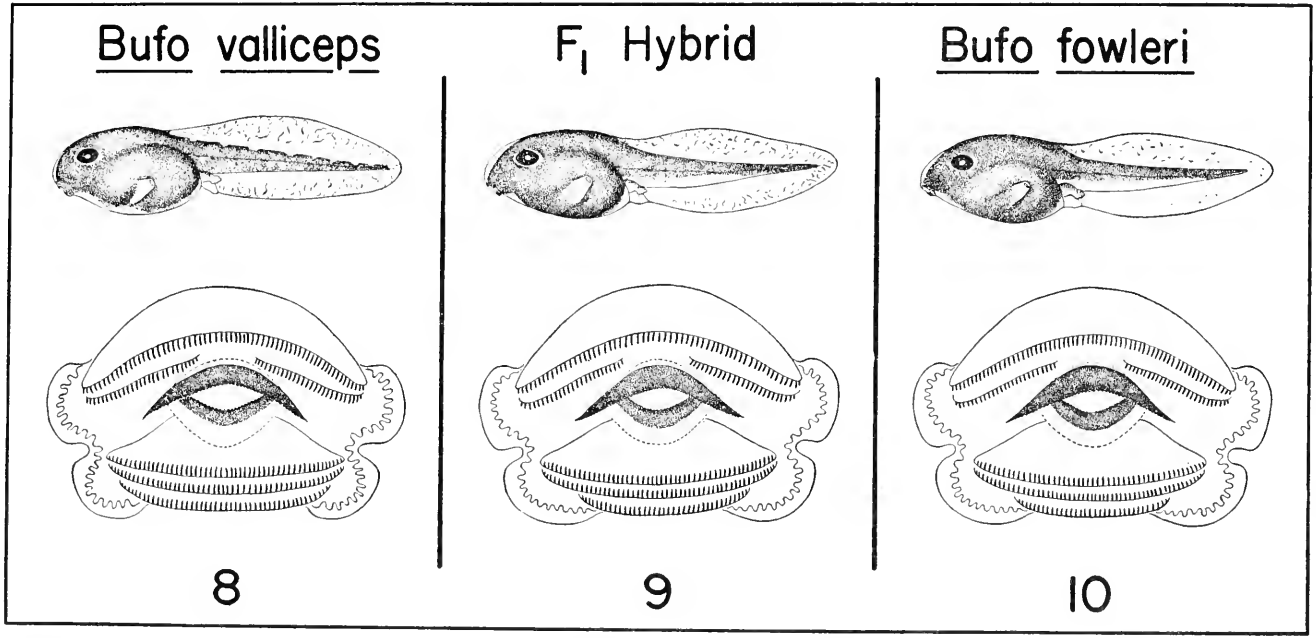
B. The Crosses: *B. fowleri* ♀ X *B. valliceps* ♂ (Hybrid)
B. fowleri ♀ X *B. fowleri* ♂ (Normal)

Early embryonic development (pre-feeding stages).—The cleavage and gastrulation processes (stages 3-12) in all hybrid embryos were normal. In later development, twenty-six to thirty-eight percent (minimum and maximum percents in twelve experiments) of the hybrid embryos died at various stages of development.

The defects observed in the hybrid embryos are illustrated in Figures 3-7. When the neural plate formed dorsally (stage 13), the abnormal hybrid embryos were tapered in the region of the blastopore (fig. 3). During the formation of the neural folds (stage 14), the lateral posterior folds in the defective hybrid embryos were more convergent than in the normal embryos (fig. 4). This condition foreshadowed the narrow tail that appeared in later development. At the tail bud stage (stage 17), the abnormal hybrid embryos exhibited a slight dorsal bending, an upturned tail, an enlarged abdomen, and divergent suckers (fig. 5). The gill plate was compressed against the sensory structures of the head region. The ectodermal surface of the abdominal region was thin and an excessive amount of fluid filled the abdominal cavity. Most of the defective hybrid embryos died at this stage. A few survived to stage 18 (fig. 6). The head structures appeared more normal, apparently due to regulative processes, but the dorsal bending was more pronounced, the tail bud was more irregularly curved, and the abdominal region remained enlarged. Some of these embryos continued to develop as far as stage 23 (fig. 7). Development was arrested at this stage, and the embryos invariably cytolysed. The most conspicuous defects were the dorsal flexure, the edematous abdomen, and the absence of a large portion of the ventral tail fin.

Sixty-two to seventy-four percent of the hybrid embryos were normal, or exhibited the above-mentioned defects to such a small degree as not to have affected their later development.

Late embryonic development (feeding stages).—In terms of survival, the most critical period in hybrid development was the embryonic pre-feeding phase. No abnormalities were observed in the hybrid embryos (tadpoles) during the feeding stages. Samples of hybrid tadpoles were preserved at various stages of development and compared with a similarly preserved series of tadpoles of each parental



Figures 8-10. External features and mouthparts of tadpoles of *Bufo valliceps* (fig. 8), *Bufo fowleri* (fig. 10), and the F_1 hybrid derived from the cross *Bufo valliceps* ♂ X *Bufo fowleri* ♀. The distribution of black chromatophores (melanophores) is shown in the tadpoles; the yellow and white chromatophores are omitted.

species.[2]

During the differentiation of the hind limb buds (stages I-XVII; Taylor and Kollros, *op. cit.*), the tadpoles acquired a characteristic pattern of body pigmentation and a specific arrangement of mouthparts. The most reliable method of distinguishing the tadpoles of the F_1 hybrids from those of each parental species was that based on utilizing both the distributional pattern of pigment and the structural arrangement of mouthparts. In Figures 8-10, the tadpole of an F_1 hybrid is compared with that of *Bufo valliceps* and *Bufo fowleri.*

The dorsal and ventral tail fins of tadpoles of *B. valliceps* (fig. 8) are heavily mottled with reticulate melanopores. The dorsal edge of the tail musculature is characterized by an alternating series of light and dark areas, an effect created by a group of yellow pigment cells interposed among the melanophores at regular intervals along the dorsal edge. The remainder of the tail musculature is black except for a few light areas or blotches (of yellow pigment cells) in the ventral half. Wright (1929) characterized the pigmentation of the tail of tadpoles of *B. valliceps* as follows: ". . . upper edge of tail musculature with 8-10 black bars with intervening pale olive-buff areas; irregular black or brown band on tail with cartridge buff or tilleul buff below it; . . .". I surmise that the 8-10 black bars refer to the dark areas interrupted by light areas on the dorsal edge of the musculature. I am unable to interpret the latter part of Wright's description.

The tail musculature of tadpoles of *B. fowleri* (fig. 10) is covered uniformly with melanophores in the dorsal half; most of the ventral half is devoid of melanophores. The tail fins contain stellate melanophores, more abundant in the dorsal half than in the ventral half. This description compares favorably with that found in Orton (1952).

The pigmentation in the tail fins of F_1 hybrid tadpoles (fig. 9) resembles the pattern in tadpoles of *B. valliceps.* However, the reticulate melanophores are less numerous, and a few stellate melanophores, characteristic of tadpoles of *B. fowleri,* are present. Compared with those in tadpoles of *B. fowleri,* the melanophores covering the tail musculature extend farther, and more irregularly, into the ventral half of the tail musculature. The alternating series of light and dark areas on the dorsal edge of the tail musculature, characteristic of tadpoles of *B. valliceps,* is not present in the F_1 hybrid tadpoles. Although the pigmentation pattern varies at different stages of development, the F_1 hybrid tadpoles always possess a *fowleri*-like pigmentation of the tail musculature and a *valliceps*-like pigmentation of the tail fins.

The mouthparts of tadpoles of *B. valliceps* (fig. 8) and *B. fowleri* (fig. 10) are almost identical. The length of the third lower tooth row constitutes the only difference between the two species. In *B.*

[2] Approximately 200 tadpoles of each group (F_1 hybrid, *B. valliceps*, and *B. fowleri*) have been deposited in the amphibian collections of Tulane University.

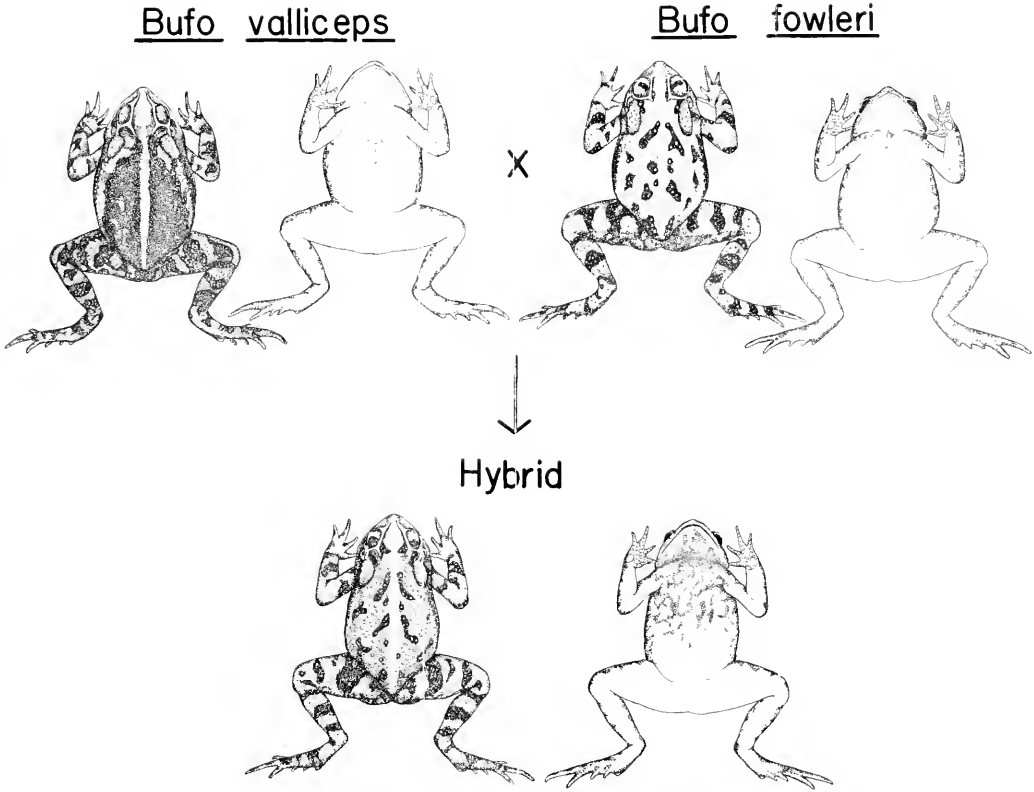


Figure 11. External features of the parents used in one of the interspecific crosses performed in 1954 and of the F_1 hybrid derived from this cross.

fowleri, the third lower tooth row is considerably shorter than the first and second lower tooth rows, as has also been noted by Nichols (1937) and Orton (1952). In *B. valliceps,* the lower tooth rows are essentially equal in length. In other respects, the mouthparts are identical in the two species. The labial tooth formula is 2/3. In the upper labium, the first upper tooth row is continuous and the second is divided medially. Each lateral segment of the second tooth row is approximately twice the length of the median space. The labial papillae are confined to the sides and extend to slightly below the edge of the third lower row. Each lateral fringe bearing the papillae is folded inward between the upper and lower tooth rows.

The mouthparts of tadpoles of the F_1 hybrid (fig. 9) resemble those of *B. fowleri.* Compared with that of *B. fowleri,* the third lower tooth row is as short, or slightly longer. The third lower tooth row is never as long as the corresponding row in *B. valliceps.*

Thus, the F_1 hybrid tadpoles can be readily identified by the *fowleri*-like pigment pattern on the tail musculature, the *valliceps*-like pigment distribution on the tail fins, and the *fowleri*-like arrangement of the mouthparts.

Metamorphosis.—Two hundred and sixty-three F_1 hybrid tadpoles transformed from the twelve experiments.[3] At metamorphosis, the young toad exhibits the dorsal pattern of warts and the median dorsal stripe, but lacks the cranial crests, the tympana, and the parotoid glands. The metamorphosed toads were raised in an air-conditioned laboratory, in which the temperature was approximately 20° C. Rearing the toads at this low temperature has the disadvantage of retarding differentiation, but has the advantage of permitting a closer examination of the structural changes occurring during growth. The parotoid glands were not fully developed until four months after metamorphosis. The cranial crests and tympana made their appearance at five months after metamorphosis. Thus, under laboratory conditions, the young toad approached the adult in external features after five months or more of growth after metamorphosis.

Mortality is considerable in young toads maintained under laboratory conditions. Thirty-two toads have been reared for a period of five months or more.

The young hybrid toads were consistent in their external features. Figure 11 illustrates the appearance of each parental species and an F_1 hybrid. Their characteristics are listed in Table 1. The strong influence of *B. valliceps* is evident in the nature of the cranial crests, the character of the dorsal median stripe, the nature of the metatarsal tubercles, the type of lateral stripe, and the shape of the snout. The F_1 hybrids are modified in the direction of *B. fowleri* mainly with respect to the pattern of spots on the dorsal surface. The dorsal spots

[3] One hundred and eighty-six experimental F_1 hybrids, exhibiting varied degrees of structural differentiation, have been deposited in the amphibian collections of Tulane University.

TABLE 1

SEGREGATION OF CHARACTERS IN AN F_1 HYBRID BETWEEN A MALE *Bufo valliceps* AND A FEMALE *Bufo fowleri*

Character	*B. valliceps*	*B. fowleri*	F_1 Hybrid	Remarks
I. Cranial Crests				
a. Interorbitals (between orbits)	Divergent from nostrils; high and trenchant; widely separated.	Parallel to each other; low; not widely separated.	Divergent from nostrils; high and trenchant; widely separated.	Like *valliceps*.
b. Postorbitals (below orbits)	Meet interorbitals at an angle greater than 90° (approximately 120°).	Meet interorbitals at approximately right angles.	Meet interorbitals at an angle greater than 90° (approximately120°).	Like *valliceps*.
c. Preorbitals (above orbits)	Distinct.	Weakly developed.	Distinct.	Like *valliceps*.
d. Preparotoids (between parotoid gland and postorbital crest)	Conspicuous connecting ridge.	Absent (parotoid gland generally in direct contact with postorbital).	Conspicuous connecting ridge.	Like *valliceps*.
e. Parietals (junction of interorbitals and postorbitals)	Prominent; curve inward toward mid-line.	Short, spur-like.	Prominent; curve inward toward mid-line.	Like *valliceps*.
f. Supratympanics (between tympanum and orbit)	Well-defined.	Weakly developed.	Well-defined.	Like *valliceps*.
g. Canthals (extension of interorbitals cephalad)	Prominent; extend to nostrils.	Absent.	Prominent; extend to nostrils.	Like *valliceps*.

h. Infraorbitals (ventral to orbit)	Well-defined.	Absent.	Well-defined.	Like *valliceps*.
II. Parotoid gland	Small; triangular; dark brown tubercles on pitted surface.	Long and narrow; pitted surface not conspicuously warted.	Subtriangular (apex of triangle more rounded); dark brown tubercles on pitted surface.	Shape approaching *fowleri;* size and warts like *valliceps*.
III. Dorsal spots and warts	Body covered with closely-set, spiny-tipped warts; no spots on dorsum; irregular pattern of bands on legs.	Spots with rounded warts; skin between spots finely warted; regular pattern of bands on legs.	Two prominent pairs of spots along mid-dorsal line; several smaller spots on dorsum; skin between spots contain spiny-tipped warts; regular pattern of bands on legs.	More like *fowleri*.
IV. Ventral spotting	Yellow-green throat; skin over subgular vocal sacs colored dark green; venter sprinkled with light brown spots.	Immaculate to moderately spotted venter (black throat and gular vocal sacs in male).	Yellow-green throat mottled with black; subgular vocal sacs; heavily reticulated venter.	Throat pigmentation combination of both species; subgular vocal sacs like *valliceps;* heavy, unique mottling of venter.
V. Dorsal median stripe	Light, broad streak.	Light, narrow streak.	Light, broad streak.	Like *valliceps*.
VI. Lateral stripe	Broad, light lateral area extending diagonally backward to the groin.	Irregular, light lateral area.	Narrow, light lateral area.	More like *valliceps*.
VII. Metacarpal tubercles	Prominent inner palmar; prominent outer thenar.	Prominent palmar; weakly developed thenar.	Prominent palmar; prominent thenar.	Like *valliceps*.
VIII. Snout shape (lateral profile)	Longer and more pointed.	Shorter and blunter.	Longer and more pointed.	Like *valliceps*.

in individuals of *B. fowleri* tend to be arranged in pairs along the mid-dorsal line. At least two pairs of spots are present in all hybrids, each spot containing several warts. The pigmentation of the ventral surface of the hybrids is unique. The clear, yellow-green throat (characteristic of males of *B. valliceps*) is mottled with black pigment (males of *B. fowleri* possess a black throat). The abdominal surface is heavily reticulated. Individuals of each species may be found with pigment markings in the abdominal region, but the pigmentation is not as strongly expressed as in the F_1 hybrids. The extent of ventral spotting in *B. fowleri* and *B. valliceps* varies from unspotted (omitting the pigmentation on the throat of males) to moderately mottled.[4] The hybrid condition is apparently independent of the extent of ventral markings of either parental species. Relatively unspotted parents (as illustrated in fig. 11) give rise to hybrids which possess the same reticulated ventral condition as offspring resulting from two mottled parents.

The sex of the experimental hybrids presents a challenging problem. The throat region of the hybrids is pigmented as in males, but the gonads are composed of half ovarian and half testicular tissue. This condition apparently does not represent a bipotential gonad in the process of differentiation, since all natural hybrids (discussed below) exhibit the same structural arrangement of ovarian and testicular tissue.

Discussion

As mentioned in the introduction, seven mis-mated pairs involving a female *B. valliceps* and a male *B. fowleri* have been observed in nature. Reproductive energy has been wasted, since no viable hybrids could result from these mis-matings. With respect to the nine reciprocal cross-mated pairs (*B. fowleri* ♀ X *B. valliceps* ♂) that have been noted in the field, approximately seventy percent of the embryos could develop normally. The survival of the hybrid embryos in nature would depend upon many factors, one of which would be their ability to compete successfully with embryos of each parental species. It is of interest that an F_1 hybrid embryo can be identified on a morphological basis. A study of samples of tadpoles taken at regular intervals from a hybrid population would provide information as to the relative survival of hybrid and non-hybrid tadpoles.

At least some of the F_1 hybrids in a natural population have reached

[4] Confirming Blair's (1943) observations, *B. fowleri* individuals from the lower Mississippi valley region are characterized by more extensive ventral markings than representatives of this species from the eastern seaboard. Bragg (1955; also Bragg and Sanders, 1951) does not deny the possibility that the ventral spotting in Louisiana *B. fowleri* (=*B. woodhousei fowleri*) may have been derived from past hybridization with *B. terrestris* or a *terrestris*-like stock, but favors the interpretation that Fowler's toad of southeastern Louisiana is either the new subspecies *B. woodhousei velatus* Bragg and Sanders or an intergrade between this subspecies and *B. woodhousei fowleri*.

maturity, as evidenced by fifteen adult F_1 hybrids that have been collected to date from Audubon Park, New Orleans. The natural hybrids are identical to the experimental hybrids described in the preceding section. All natural hybrids exhibit male secondary sexual characters, *i.e.,* a darkened thumb and a pigmented throat. Their calls consist of feeble, discontinuous trills. Only two of the fifteen hybrids have been found in amplexus; in each case with a female of *B. fowleri.* As in the experimental hybrids, the gonads are atypical. The testis portion of each gonad is much reduced. The anterior portion is composed of a large mass of ovarian tissue, which may represent an overdeveloped Bidder's organ. The ovary-like Bidder's organ is small in relation to the size of the testes in both *B. fowleri* and *B. valliceps.* A histological study of the gonads of F_1 hybrids is in progress. The fertility of the F_1 hybrids is also being tested.

The data presented here compare favorably with Thornton's (1955) results of experimental hybridization between *B. valliceps* and *B. woodhousei.* The latter species is closely related to *B. fowleri.* Embryos derived from the cross-mating of a *B. valliceps* female with a *B. woodhousei* male died during the early stages of development. Persistent yolk plugs were noted in the hybrid embryos. The same abnormality (fig. 2) was observed in hybrid embryos from the cross *B. valliceps* ♀ X *B. fowleri* ♂. Viable hybrids resulted from the reciprocal cross *B. woodhousei* ♀ X *B. valliceps* ♂. In one experiment, Thornton estimated that seventy to eighty percent of the fertilized eggs developed to the tadpole stage. I suspect that the other twenty to thirty percent died of the same defects as illustrated in Figures 3-7. The metamorphosed F_1 hybrids more closely resembled the *B. valliceps* parent than the *B. woodhousei* parent. Thornton also described two unique features of the hybrids; the first, the heavy spotting on the ventral surface, and the second, the peculiar appearance of the testes.

Apparently the sperm of *B. valliceps* interacts with the eggs of *B. fowleri* and *B. woodhousei* in a similar manner. This finding is striking confirmation of the prevalent view that *B. fowleri* and *B. woodhousei* are closely related (in fact, the two are often referred to as subspecies). The limited amount of gene exchange possible between *B. valliceps* and *B. fowleri* or *B. woodhousei* provides additional support for the thesis that *B. valliceps* belongs to an entirely different phylogenetic series. Hybridization studies not only yield information as to the degree to which interspecific gene exchange is possible, but serve also to substantiate or clarify assumed systematic relationships.

Summary

1. Experimental F_1 hybrids from the cross *Bufo valliceps* ♀ X *Bufo fowleri* ♂ are inviable. The embryos die in the late gastrula stage.

2. Sixty-two to seventy-four percent (minimum and maximum percents in twelve experiments) of the hybrid embryos from the reciprocal cross *Bufo fowleri* ♀ X *Bufo valliceps* ♂ develop normally. The

external defects observed in the remaining percent of the embryos have been described and illustrated.

3. The F_1 hybrid tadpoles are distinguishable from those of the parental species. They are characterized by a *fowleri*-like pigment pattern on the tail musculature, a *valliceps*-like pigment pattern on the tail fins, and a *fowleri*-like arrangement of the mouthparts.

4. The F_1 hybrid young toads possess more features of *B. valliceps* than of *B. fowleri*. Their characteristics have been described in detail.

5. The F_1 hybrid tadpoles and metamorphosed young have been illustrated so as to facilitate the identification of the tadpoles and adults in nature. A natural population in which hybridization is suspected can not be properly analyzed without precise knowledge of the embryonic and adult features of its constituent individuals.

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ABSTRACT

The distributional ranges of *Bufo valliceps* and *Bufo fowleri* overlap in southern Louisiana. Both species of toads may be found breeding simultaneously in the same pond, and males of each species will readily clasp females of either species both in nature and in the laboratory.

Laboratory crosses have revealed the extent to which interspecific gene exchange is possible. Experimental F_1 hybrids from the cross *B. valliceps* ♀ X *B. fowleri* ♂ are inviable. All embryos die in the late gastrula stage. Approximately seventy percent of the F_1 hybrid embryos from the reciprocal cross *B. fowleri* ♀ X *B. valliceps* ♂ develop beyond metamorphosis. The F_1 hybrid tadpoles can be distinguished from those of the parental species. They are characterized by a *fowleri*-like pigment pattern on the tail musculature, a *valliceps*-like pigment distribution on the tail fins, and a *fowleri*-like arrangement of the mouthparts. The transformed F_1 hybrid toads possess cranial crests characteristic of the *valliceps* parent, a modified form of dorsal spotting inherited from the *fowleri* parent, and a unique reticulated pattern of pigment on the ventral surface which is not found in either parental species. Consequently, adult F_1 hybrids may be identified easily in the field.

All experimental and natural F_1 hybrids are apparently males. They exhibit male secondary sexual characteristics, but their testes are atypical. The anterior portion is composed of an unusually large mass of ovarian tissue, which may represent an overdeveloped Bidder's organ. The testicular portion is much reduced. A histological study of the gonads of experimental and natural F_1 hybrids is in progress.

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AN OUTLINE FOR THE STUDY OF AN AMPHIBIAN LIFE HISTORY

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AN OUTLINE FOR THE STUDY OF AN AMPHIBIAN LIFE HISTORY

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The life histories of many amphibians remain unknown and much of the information in the current literature cannot be used in synthesis because it is vaguely presented or lacks supporting data (Cole, 1954a). The renewed interest in natural history and the extensive use of amphibians in experimental biology demand an attempt to formulate an outline suggestive of needs, problems and procedures in life history investigations.

Often the experimental biologist's knowledge of the animal as it exists in nature has been inadequate as a basis for evaluation of his experimental results. The laboratory worker is sometimes not cognizant of the need of ecologic information and his interpretations are thus limited. The present pattern of training biologists often fails to provide the essential background relating to the entire organism or population. Rarely does the physiologist, the embryologist, the taxonomist or the geneticist utilize the potentialities of the study of the organism under natural conditions.

The ecologist or the systematist does not often utilize the techniques of the laboratory. He is sometimes unaware of knowledge reported by his laboratory-centered colleague, or of information on the anatomy, physiology, genetics or embryology of the animals involved. Yet his investigations often lead to the laboratory where, under conditions of control and experiment, he may hope to resolve the problems developed in the field. Often he must face an attitude of his experiment-minded colleague suggesting that the field observations explain nothing. The general physiologist insists on the need for a second step, the endocrinologist a third, and biochemist a fourth—each believing an answer resides in his realm although the totality of the knowledge is essential.

The wide breach between the laboratory researcher and the field researcher has been infrequently closed. The herpetologist can contribute much to the narrowing of the gap by broadening the scope of his investigations and his bibliographic research. More than 2800 serials contain information potentially pertinent to herpetology. The herpetologist cannot depend on any one or a series of abstract journals.

The biologist is confronted by a great mass of statistical theory and extensive debate about the application of statistics to ecological problems. Statistics has corrupted as well as benefited biology. Often the use of statistical procedures has contributed little and the development of statistical theory has overshadowed the addition of new biological knowledge. The "research" in natural history may be grouped into three categories: (1) general observations that present no new

ideas or conclusions; (2) documented observations brought into sharp focus and used to develop generalizations; (3) investigations placing primary emphasis on the elaboration of observations through the application of statistical techniques (Packer and Pearson, 1952).

The herpetologist studying the life history of an amphibian should be cognizant of the relation of his research to broad ecological concepts. The natural history stage is thus essential to studies of population processes and interspecies reactions which are, in turn, essential to the analysis of the whole eco-system and the physico-chemical interpretation of the biodemographic picture (Elton and Miller, 1954).

The need for a reexamination of the standards and customary procedures in natural history investigations on reptiles has been previously stressed (Cagle, 1953). This annotated outline is an attempt to ascertain the ideal requirements in an investigation of the life history of an amphibian. The references cited were selected because of their value as guides to the literature on a particular topic or because they present new knowledge, approaches, or techniques.

I. *What are the morphologic characteristics of the population to be studied? Were the data reported obtained only from individuals of the genus, species or subspecies intended to be studied?*

A. What is the taxonomic status of the population? What are the diagnostic features? How are these related to the formal description of the species or subspecies? Are these sharply or only obscurely characterized?

Information must often be discarded by subsequent workers because the author failed to indicate clearly the characteristics of the individual or population studied. Description must thus be such that any investigator can recognize the population or source of a sample regardless of changes in nomenclature.

B. What morphological features discerned by the investigator are pertinent to the generic and familial level of classification? to the group phylogeny?

Features of the internal anatomy have been generally utilized at these and higher levels of classification. The autecologist often is led to explore the anatomy of the organism he is concerned with and should be aware of the possible biologic and phylogenetic significance of the structure he observes. Studies of anatomy should not be foreign to his interests (Theron, 1952). He must be particularly cognizant of those researches useful in evaluating taxonomic characters (Serafínski, 1955; Balinsky, 1955).

C. What other names have been attached to the population?

D. What samples of the population were collected and pre-

served and where are they deposited? Museum numbers?

A representative series supporting the description given should be deposited in a suitable public museum collection. Failure to do this is almost characteristic of ecological, physiological and anatomical investigations; yet the conclusions submitted are often not acceptable because of questionable identification of the material on which they were based. Much of the experimental research utilizing amphibian larvae is deceiving as investigators have depended on biological supply houses to provide material. Often such shipments have been composite collections of several species. Deposited specimens provide a basis for permanent verification of identification.

E. What variation is observed in the individuals composing the population? Of what is this variation a reflection?

Precise analysis and explanation of individual variation is an obligation. Dice (1952b) points out that few museums have adequate storage or curatorial facilities to retain the large number of specimens necessary for the analysis of variation in local populations. Simpson (1944) has stressed the concept of the hypodigm and the difficulties involved in the use of a preserved sample to represent the attributes of a population. The investigator must often utilize materials that cannot be available to future workers; his responsibility is thus multiplied. Through such studies associated with field investigations we may hope to accumulate the data basic to systematic studies at the intraspecies level. The presence of natural hybridization in populations and its influence on variations in ecology and morphology must be recognized (Moore, 1944, Blair, 1951, Volpe, 1953; Ruibal, 1955).

1. What changes in color intensity, in pattern or morphology occur from hatchling (birth) to old age? Are there any correlated sex differences? How are these changes related to taxonomic investigations?

The analysis of color and color patterns is of particular importance in the study of amphibians. The consideration of the cause of variations in color patterns prior to their use in systematics is necessary but often ignored. The utilization of such characters should rest on an understanding of the chemical and physical bases of color (Kreig and Forster, 1937; Juszczyk, 1952) as well as an appreciation of their functional value (deRuiter, 1956). Meristic characters, widely used in zoogeographic studies, may have phenotypical relation to environmental factors

(Ernst, 1952). Phenocopies of widely distributed forms of fishes may be produced in the laboratory (Tåning, 1952).

2. What variation in physiological characters is associated with the morphological variation?

   Exploration of intraspecific, physiological variation has provided clarification of problems in evolution. The need for physiological study of variation is stressed by Prosser (1955).

3. Is the variation correlated with differences in the external environment? With a gradient in the external environment? Is the variation due to differences in genotypes or does it reflect the responses of a specific genotype to different environments?

   Investigators often query the status of the variation described but do not perform the simplest of experiments aimed at evaluating the genotypic flexibility of the organism studied. Some investigators suggest that some of the characters considered to be of taxonomic importance are merely phenotypic modifications (Rostand, 1951).

4. What are the ontogenetic changes in mass as expressed by measurements or weight? What is the maximum size attained? Sex differences?

   Although absolute size may not be a satisfactory taxonomic character for amphibians, genetic differences in potential natural longevity or growth potentials may be reflected in differences in maximum sizes between populations (Moriya, 1954).

5. What procedures were used in mensuration? Weighing?

   Care must be used to insure adequate mensuration practices and to insure that the investigator clearly reports his procedures (Simpson and Roe, 1939). Much confusion has been caused by misunderstandings resulting from failure to specify the methods followed. The significance of the limits of error in such data should be borne in mind.

6. What are the principal differential growth changes in each sex? How are these changes related to the major phases of the life history? Do they vary geographically or seasonally?

   Failure to recognize differential growth has led to erroneous use of proportions. If detailed, quantitative studies cannot be made, the investigator should, as a minimum, designate the gross changes in proportion. This is a particularly acute problem in poikilothermic

vertebrates. The investigator must be aware of the statistical hazards of expressing differences in terms of ratios. The review of Marr (1955) on the use of morphometric data should be consulted.

Terentjev (1943) found a temporary acceleration of growth in the hind limbs of male frogs (*Rana ridibunda*) wtih the attainment of maturity. Variation of proportions in correlation with distribution is often evident (Schmidt, 1938; Blair, 1941; Hairston, 1949; Schuster, 1950; Dely, 1952; Mecham, 1954; Snyder, 1956).

II. *What is the geographic range?*

The range should be expressed first in terms of museum specimens or records of authorities. All questionable records should be deleted. These data may then, in connection with other information, form the basis for the statement of a supposed "true range." The range definition should indicate the distribution of existing populations (Grobman, 1950). Analysis of distribution should be sufficiently detailed to provide a basis for detection of the actual pattern. Whenever feasible, the pattern of occurrences of mature adults during the breeding season should be contrasted with occurrences at other times. The problems of determining allopatry and sympatry should be considered (Cain, 1953).

The herpetologist has not made sufficient use of the occurrence of amphibian larvae in determining distribution patterns. This, a reflection of the difficulty of identification of larvae, emphasizes the need for further researches on larval forms. Much pertinent information has been published by experimental embryologists and morphologists. The work of Lieberkind (1937) is useful in evaluation of mouth parts and adhesive organs.

A. What are the factors limiting the range?

These must be considered in terms of the ecological data assembled during the progress of the investigation with particular reference to the total knowledge of the ecological valence of the animal and possible barriers to dispersal (Darlington, 1948; Hairston, 1949; Dice, 1952b; Smith, 1952). It is especially important to note that the limiting factors may be entirely different on the various borders of the range of a species (Schmidt, 1950). Bannikov (1943) found that the northern limits of distribution of *Rana ridibunda* were determined by the lengths of the periods of hibernation and development; the southern limits by the temperature range in which the animal could be active. Cei (1947) found a cor-

relation between the reproductive habits of *Rana temporaria* and its ability to live at high altitudes. Strűbing (1954) reports data on temperature responses. Bullock (1955) supports the thesis that many poikilotherms are, within limits, relatively independent of temperature in nature. Explanation of the range should be related to the paleontological history, but this is rarely possible.

B. What physiographic and climatic factors are characteristic of the range?
   1. What is the significance of temperature and humidity?
      a. What are the annual temperature and rainfall cycles?
      b. What are the mean annual, minimum and maximum temperatures in the warmest and coldest parts of the range?

         Whenever feasible, temperature and rainfall data collected by the investigator in the areas of study should be utilized. Of necessity, the investigator must often use meterological and climatological temperatures, but their interpretation should be based on the data of the researcher (Baum, 1950).
      c. Does temperature summation (heat summation) affect the distribution of the species investigated?
   2. Do physiographic features determine the range?

C. What is the principal habitat? Marginal habitat?
   Any habitat is difficult to describe. Rarely it is possible to utilize published descriptions to obtain comparative information. The difficulties and some suggestions are ably described by Elton and Miller (1954).
   1. Are microclimates of significance? throughout the range? at the periphery? (Geiger, 1950; Diem, 1951).

      The tendency for many amphibians to occur in small populations in a restricted area suggests the significance of specific knowledge of microclimates. Often the usual, general descriptive data are an unsatisfactory basis for explaining occurrence (Marshall and Buell, 1955).

      Knowledge of cyclic changes in metabolic rates are of importance in evaluating the influence of the microclimate (Vernberg, 1951).
   2. What vegetational types characterize the habitat? Is any particular plant or groups of plants always associated with the habitat? How does our knowledge of the biology of the plant aid in understanding the occurrence of the amphibian?
   3. Do size, age or sex groups tend to occupy different

habitats? Do they characterize specific parts of the range?

Juvenile amphibians often select a habitat different from that occupied by adult forms (Anderson, 1954). This has caused some confusion in the studies based on sampling procedures not recognizing this situation. Hairston (1949) demonstrated a correlation between altitude and size in *Desmognathus*. Margalef (1955) reviews relationships between temperature and size.

4. Does the animal have an innate habitat recognition mechanism? Is the mechanism of significance in restricting distribution or in controlling migration?
5. What behavioral traits are associated with the preferred microenvironment or change in the microenvironment?

   Variation in factors of the microenvironment may bring about substantial responses in behavior characteristic of the species (Thorson and Svihla, 1943; Sealander, 1953; Bogert, 1952). Cohen (1952) has described the varying reactions of 3 species of salamanders to dehydration. Test (1946) studied the reaction of a salamander to light and contact.
6. What are the principal adaptations advantageous to the animal in its optimum habitat?

D. What are the principal barriers to movement between populations?

   Amphibians tend to occur in local colonies. Some forms are narrowly adapted and are found only under a specific complex of conditions. Barriers insignificant to other vertebrates may restrict population expansion (Stebbins, 1954).

E. What are the principal means of dispersal?
   1. What extrinsic factors are involved in dispersal?
   2. What intrinsic factors are involved in dispersal?
      a. What is the extent of individual mobility? Age or sex differences in mobility?
      b. What is the extent of larval adaptability? Significance in dispersal?

         Those forms having aquatic larval stages tend to be more generally dispersed than those with terrestrial stages. Larvae or adults may be dispersed by flood waters; such dispersal may be the primary mechanism.

      c. Do group movements occur? extent? seasonal?

F. What isolating mechanisms prevent gene interchange between the populations of the form studied and related forms?

Hybrid inviability, hybrid sterility, gametic isolation, sexual isolation, seasonal isolation, ecological isolation and geographic isolation have been reported as occurring in amphibia (Pariser, 1932; Hamburger, 1936; Lantz, 1939; Chen-Chao-Hsi, 1940; Moore, 1944; Volpe, 1952; Kawamura, 1953; Moriya, 1954; Blair, 1955). The field observer, if cognizant of knowledge gained from hybridization experiments, can supplement our knowledge of isolating mechanisms. Field investigations are essential to determine the operation of laboratory-observed mechanisms in natural populations (Twitty, 1955).

III. *What is the age and sex composition of a local population?*

A knowledge of the structure and dynamics of the local population is essential to systematic studies. Studies usually will include an undisturbed population for observation, another for the tracing of marked individuals, and a third as a source of samples.

The mark-release-recovery technique provides information on many problems. Tattooing, tagging, and scarring have been useful in marking; the best method appears to be toe-clipping (Raney and Lachner, 1947; Hendrickson, 1954; Stebbins, 1954).

A. What annual changes occur in the composition of a local population?

1. What is the sex ratio in mature individuals during the breeding season? How does this change during a single year?

   Sex ratios are often reported without reference to maturity or to the breeding season although radical changes do occur in some populations. Estimates of the relation of sex ratios to natality should be based on the relative frequency of sexually active individuals. Sex identification is frequently reported without reference to the criteria used. What are these criteria? Secondary sex characters? Gonad conditions? If dissected, on what basis was sex determined?

2. What is the sex ratio in juveniles? in larvae? in age groups?
3. What annual changes occur in the ratio of juveniles to adults? What is the potential contribution from "young of the year" to the adult segment of the population?
4. Can an ecological life table be constructed?

   The difficulty of determining mortality rates in most amphibians forbids the successful completion of such tables. An attempt to collect data basic to the esti-

mation of survivorship curves should be made (Chitty, 1952).

5. What are the major predators? Is predation pressure a significant factor in annual and long-term cyclic changes? In determining selection pressure? What is the relation of loss from predation to population density?

B. What long-term cyclic changes occur in the composition of the local populations? Do random oscillations occur? What is the cause of such cycles or random oscillations? Is exhaustion of the adrenopituitary system a factor as has been demonstrated for some mammal populations?

No specific information on population cycles or random oscillations is available for amphibians, yet these animals are potentially useful in the study of such changes and their basic causes. Sufficient general information is available to suggest rapid extreme changes susceptible to more precise measurement than most bird or mammal populations (Lynn and Wachowski, 1951; Cole, 1954b; Errington, 1954; Frank, 1954).

C. Do local populations differ in composition? If so, what is the basis of such differences?

Adequate local sampling may provide a basis for obtaining answers to such questions. It has been demonstrated that substantial differences may be present in the composition of local populations. Comparison of population samples must be tempered with an awareness of the difficulties of obtaining such a sample. Series of specimens preserved in museum collections are rarely unbiased samples of natural populations. The student should note particularly those few long-term or intensive studies in local areas (Pacaud, 1951).

IV. *What is the density of the population?*

There should be more than a vague estimate of density expressed as rare, common or abundant. The objective should be to gain a measure of the number of individuals in a given area expressed in terms clearly defined by the investigator. The use of the concepts of abundance and relative apparent abundance as suggested by Marr (1951) is recommended. The method selected for this determination of abundance must rest on the knowledge of the ecological requirements of the individual. Kendeigh (1944) provides a suggestive review of the procedures for measurement of bird populations. Information of particular value in estimating populations from recovery of marked specimens is given by Ricker (1948) and Leslie (1952).

A. What is the relation of density to the questions posed in

sections I, E and III A to C (Blair, 1951)?

B. What is the relation of density of the form studied to that of other amphibians inhabiting the area?

C. Does the individual animal or the mated pair occupy a home range, activity range, or center of activity (Hayne, 1949)? Territory?

Territorial behavior in amphibians has been reported by Martof (1953) and Test (1954). Lutz (1954) suggested that *Elosia* has "an incipient notion of territory."

1. What is the size of the home range and of the territory?

The statistical concept of home range that includes the definition of "activity loci," a "center of activity," "recapture loci," a "recapture center" and "recapture radii" may be applied to studies of amphibians movements (Dice and Clark, 1953). Knowledge of the comparatively restricted home ranges of most amphibians is of importance to the systematist and ecologist (Kalela, 1954).

a. What features of the habitat may influence the extent of the territory or home range?

b. What is the relation of the size of the territory or home range to density? What is the spacing between individuals?

A measurement of the tendency to form pairs or small groups is essential to population studies directed toward evaluation of gene flow. Clark and Evans (1955) discuss the problem of spacing between neighbors.

c. Does the individual have homing ability? If so, what are the mechanisms involved in orientation?

The recovery of marked individuals in short-term and long-term studies will provide information on these questions (Stebbins, 1954). Griffin (1952) discusses radioactive tagging, a technique potentially useful in establishing the contribution of a group of larvae to an adult population.

2. Is the territory selected by the male, female or both? Do both sexes participate in its defense?

a. What are the characteristic behavior patterns used in defense of territory?

b. What is the chief stimulus to maintenance of territory?

c. Is the territory maintained throughout the year or only during short periods?

V. *What is the potential reproductive capacity? What is the relation to realized reproductive performance? What are the best measures of natality?*

A. At what age and/or size does the animal become sexually mature?

The age at which an animal begins to reproduce is one of the most significant characteristics of a species, but is frequently not recorded (Cole, 1954). Investigators often fail to indicate what they mean by sexual maturity. Care must be exercised that the criteria for maturity are defined. In amphibians these may concern the presence of oviducal eggs in females, or of ovarian follicles of a specified size, or ovaries of a specified weight or volume. In males a specific stage of spermatogenesis, a specified testicle weight or volume in relation to an indication of total body mass, or the presence of motile sperm may be useful.

The development of neoteny among some groups of salamanders (perennibranchs, newts, ambystomids, and plethodontids) furnishes a possible evolutionary advantage in reproduction. The question of the processes leading to the evolution of neotenic forms is unanswered (Kezer, 1952; Toivonen, 1952).

No adequate techniques are available for determining the age of an individual amphibian. The procedures used by Bryuzgin (1939) should be further explored. Bryuzgin concluded that rings discernible in cleared skull bones of snakes could be used to determine age. Similar procedures have been applied to amphibians with varying success. Senning (1940) found that rings in some skull elements were useful in estimating age of *Necturus*. The study of marked and released specimens has yielded the best growth data (Raney and Lachner, 1947; Highton, 1956). The analysis of size groups (frequency-modes) has been useful in estimating age (Force, 1933; Blanchard and Blanchard, 1931).

1. When are the secondary sex characters developed? What is the relation of time of their appearance to the potentiality of sexual functioning?
2. What cyclic changes occur in secondary sex characteristics?
3. What is the relation of age of attainment of maturity to the annual reproductive cycle?

B. What is the total period of reproductive activity in the life of an animal?

1. Does the annual reproductive potential remain the same, decrease or increase with age?
2. When does senility occur?
3. What is the ecological longevity?

C. What is the annual realized reproductive performance?

1. What is the annual period of reproductive activity in females? in males? What is the significance of this period in the total annual activity cycle?

The annual sexual cycles of many species have been studied and this phase is the best known aspect of amphibian biology (Cheng, 1932; Galgano, 1947; Cei, 1949; Miller and Robbins, 1954). Bullough (1951) discusses breeding. Marshall and Coombs (1952) in discussing the lipoid changes in the gonads of birds suggest avenues of research. The breeding period is usually considered as that in which the females are "carrying" young or are laying eggs. Much confusion has resulted from failure to delimit this period. Thus it may be stated that a female having eggs "ready for deposition" or "enlarged ova" was collected on a given date. Yet this is not clearly indicative of the time when eggs may be deposited or the young borne. Each investigator should insure preciseness of definition. Jameson (1955) states "Only the observance of deposition or of freshly laid eggs can accurately delimit the times of actual breeding." Forms of the same general region may exhibit quite different sexual cycles. Caruso (1949) points out that *Hyla raddiana* of Northern Argentina has continuous reproductive activity, but *Phyllomedusa sauvagi* of the same region breeds only during rains and the secondary sexual characters develop only at that time.

The specific factors stimulating breeding are unknown. The hormone reflex generally involved is known but the conditions releasing the reflex are but vaguely indicated for amphibians.

a. What is the relation of the "calling" of anurans to breeding activities? What factors initiate the calling response?

Confusion of periods in which individuals were calling with the breeding period has been frequent. There may be no correlation between these periods other than that the calling period includes the breeding season.

The function of the anuran voice is not clear. The

use of the voice may result in aggregations essential to reproduction. Jameson (1955) believes the call is used to establish home sites, attract and stimulate the female and win sex recognition. The specific functions of the call differ in various anurans. Thus in some species aggregations occur prior to the initiation of calling. Differences in call characteristics may be of great importance in speciation of some groups. Blair (1955) has demonstrated the value of the "Sona-Graph" in the analysis of calls.

b. What is the relation of the development of secondary sex characters to the breeding season? Does the presence of the secondary sex characters indicate that individuals are prepared for reproduction?

Miller and Robins (1954) point out that the development of the secondary sex characters of the male *Triturus torosus* begins 4-6 weeks before expulsion of sperm from the testis, and that males remaining in the water after the breeding season retain the secondary sex characters.

c. What is the relation of the breeding migration to egg deposition? What factors initiate the breeding migration?

A complex of interrelated factors, usually relative humidity, temperature, precipitation or flooding variously stimulates the breeding migration when the physiological condition of the amphibian is appropriate (Blanchard, 1930; Baldauf, 1953). Storm and Pimentil (1954) outline a procedure for making a census of amphibians moving to ponds.

2. What correlation is there between courtship, copulation or amplexus, and ovulation? What is the significance of the sex ratio and population density in relation to annual, realized, reproductive performance?

These are little explored areas in herpetology yet important ones if we are to arrive at an understanding of those factors controlling changes in populations. The fact that many amphibians have external fertilization, may produce several broods after a single fertilization, or may be parthenogenetic suggests that unbalanced sex ratios may be of but scant consequence (Angel and Lamotte, 1944). Hermaphroditism in anurans is reviewed by Ponse (1951). Population density may markedly affect breeding success.

a. What is the method of sex recognition?

Differing reactions of the female and male anurans to amplexus (Aronson, 1944), differences in structure (Hinsche, 1926), differences in call (Blair, 1955) are some of the established bases for identification. Olfaction appears to function in sex recognition in plethodontid salamanders.

b. What is the pattern of courtship?

Exploration of the courtship patterns with emphasis on interspecies differences promises to yield much of value in explaining the development of physiological isolation. Too, behavior patterns associated with reproduction are of value in tracing phylogenies (von Wahlert, 1952).

(1) How does it differ from that of related forms?

(2) What advantages in reproduction are provided by the courtship pattern?

(3) What selective factors function in courtship?

(4) What secondary sex characters are of most significance in courtship?

(5) What senses are involved in courtship?

(6) Is a spermatophore formed? If so, what is its structure and relation to the courtship pattern?

c. What is the pattern of amplexus?

d. When does ovulation occur? What is the stimulus required to initiate ovulation?

(1) Is courtship and/or amplexus essential to ovulation? to egg deposition?

Amplexus or courtship may be essential in some species (Bragg, 1941; Anderson, 1954) but not in others (Noble and Aronson, 1942).

(2) Can a female continue to produce offspring for a prolonged period after a successful courtship?

Baylis (1940) kept a spotted salamander isolated in captivity and observed that a brood of larvae was produced in May, 1937 and another in April, 1939, an interval of nearly two years. Is this an example of delayed fertilization or parthenogenesis? Angel and Lamotte (1947) suggest the occurrence of parthenogenesis in *Nectophrynoides occidentalis*. Stebbins (1954) reported that *Ensatina* retained spermatozoa for at least one month.

3. How many eggs or young are produced in each group?

Some investigators have depended solely upon counts of ovarian eggs or of eggs found in clutches. Both procedures are subject to substantial error as the worker can but rarely be confident that no eggs have been previously deposited, that ovulation is completed or that two or more females have not utilized the same nest (Wood, 1953). Certainly the typical extreme variation in number of eggs and young produced emphasizes that little significance may be attached to many of the literature reports of the number of young in single females or nests. Counts of young present in the uteri of viviparous forms possibly provide the most reliable criteria of clutch size. (The terms, viviparous and ovoviviparous, have been used in varied ways in herpetological literature. It is suggested that the term, ovoviviparous, be restricted to describe a situation in which the developing young gains no sustenance from the female).

a. Is there a correlation between reproductive capacity and size or age? How is this related to estimates of natality in local population?

The large difference in reproductive capacity between small and large females makes it exceedingly difficult to utilize much of the published data on reproductive capacity as bases for estimates of natality. Although it is often assumed that larger females deposit a larger number of eggs, this generalization is not adequately supported. Too, there may be a correlation between the number of ovarian follicles and size yet no correlation between the number of eggs deposited and/or hatched and female size. Wood (1953) indicated this situation in *Hemidactylium scutatum.*

b. Is there a correlation between reproductive capacity and the condition (stress) in previous generations?

The possibility of the condition of one generation affecting breeding success in subsequent generations has been suggested (Chitty, 1952). No information is available for amphibians.

VI. *What are the major factors controlling the relation of the number of surviving young to the number of eggs or young produced by females?*

A. What are the characteristics of the egg, egg mass or larva at deposition?

1. How do the egg or egg clusters vary in size and volume?
2. Is there any correlation in size, number and/or volume and size or age of females?

   Racial studies involving egg size must recognize the possible correlation between body size of females and egg size. As body size variation often is clinal, egg size may be expected to be so. Moriya (1954) reports such correlation and racial variation.
3. Is there a correlation between yolk quantity and the pattern of development? Between yolk quantity and number of eggs?

   The trend in the anurans from the microlecithal to the macrolecithal egg is associated with a reduction in the number of eggs. *Sminthillus* lays a single, large egg; *Eleutherodactylus,* 20-25 large eggs; North American ranids may lay several thousand small eggs.
4. What changes occur in size and weight of eggs and capsules during development?

   The weight and volume of eggs and capsules may change, often irregularly, with age and environment. The reporting of egg size without reference to the age or conditions under which the eggs were retained is of scant significance. Geographic variation in egg size (Moore, 1944) suggests the necessity for review of data in relation to geographic sources of material.
5. In what stage of development is the egg at deposition?
   a. Does the stage of development vary with the time eggs are retained by the female? If so, does this influence the development period?
   b. How is the stage of development related to the egg size and volume?

B. Where and in what manner are eggs deposited?
   1. What is the behavior pattern of the female? Significance?
   2. Does the female remain with the eggs? return to them? What is the influence of female behavior to survival of young?
      a. Does the female or male "defend" the eggs?

         Behavior of amphibians is sufficiently variable that repeated observations are essential to description of behavior patterns. In most situations the investigator can gain but restricted field data on these questions and is compelled to study captive specimens as a basis for evaluation of field-collected data. Female *Desmognathus* will oppose

intrusion to the nest; adult *Cyclorhamphus* reportedly guard their spawn.

b. Do the adults contribute to the maintenance of the eggs through physical action or the contribution of substance? Does either sex "brood" the eggs?

Stebbins (1954) speculated that the female *Ensatina* may release excess water from the urinary bladder into the egg cluster. Noble (1931), Gordon (1952) and others have reported the growth of mold on the eggs in the absence of the female salamander. Many anurans retain the eggs until hatching: *Rhinoderma* in gular sac; *Nectophrynoides* is ovoviviparous; *Cryptobatrachus* on back; *Amphignathodon* in folds of skin on back.

3. Is a nest or container provided for the eggs?

The nesting habits are poorly correlated with phylogeny. Related members of the same family (especially Hylidae and Ranidae) may thus exhibit widely different habits. Too, there have been no adequate studies reporting the variation of nesting habits of any species in relation to varying environments. Foam nests occur in the Bufonidae and the Polypedatidae; eggs in basins near water occur in the Brevicipitidae and the Hylidae. The salamander, *Batrachuperus,* deposits 7-12 eggs in a well-formed egg case attached to stone.

a. What factors determine the site?

b. How is the nest or container constructed?

c. What is the relation of choice of nest site to potential survival of eggs?

Bragg and Bresler (1951) note that contamination of pools may prevent hatching of eggs (*Bufo cognatus*) and report a 34 percent hatch of one egg group.

d. Does the female use the same site for subsequent clutches? In subsequent years?

C. What factors determine development rates?

1. What is the period of development? in the field? in the laboratory?

The factors modifying rate of development are not clearly known. The toads of the genus *Atelopus* are known for rapid development (19 hours).

a. What is the relation of temperature and humidity levels

or changes to development time? of degree-humidity-hours to development time?

The failure to report development time in terms of degree-hours makes extremely difficult the synthesis of published data. Too, temperature and humidity may be paired factors with neither playing a master role (Shelford and Yeatter, 1955).

b. Is there a correlation between rate of development and the nature of the egg site?

2. How sensitive are eggs to low or high temperatures during the period of development? What extremes are the eggs subjected to in the typical field site? Potential mortality?

3. What factors initiate hatching? birth?

The functioning of hatching enzymes has been described (Noble and Brady, 1933; Kawahara, 1952) but the precise mechanism is unknown. The herpetologist should report observations on fluctuation in hatching behavior and rates.

4. What is the stage of development at hatching? birth?

a. How is the time of development related to the stage of development at hatching or birth?

b. Is the time required for development related to the quantity of yolk retained? Significance of quantity of yolk retained?

The apparent general trend in the anurans toward withdrawal from the water is correlated with an increase of yolk and acceleration of development. This is reflected by the novel reproductive habits in many different evolutionary lines.

c. What are the behavior patterns and their sequence of development in larvae?

VII. *What are the characteristics of the larvae? Diagnostic features?*

1. What is the adaptive significance of the morphological features?

Cheng (1932) traces the development of reproductive organs and germ cells in tadpoles. Orton (1955) stresses the possible significance of larval adaptability in distribution.

2. What is the adaptive significance of the behavior traits?

3. What are the primary factors determining growth rate? influence of density, food, temperature, light?

Crowding is sometimes a factor (Adolph, 1931; Noble, 1931; Savage, 1935). Both temperature and food are

of great importance in regulating growth (Wilder, 1924; Krohn, 1930; Gosner and Black, 1955; Snyder, 1956). Reports of growth rates should attempt to present data on such factors.

4. What are the factors apparently related to metamorphosis?
   a. Do the larvae have the potentiality of being neotenic or must they metamorphose in order to reproduce?
   b. If neotenic, is this a result of insensitivity of tissues to thyroid hormone (perennibranchid amphibian), the absence of the stimulating agent or a deficient relationship between the anterior lobe of the pituitary and the thyroid gland?

      Kezer (1952) succeeded in inducing metamorphosis in the neotenic salamanders, *Eurycea neotenes* and *E. tynerensis,* although these forms are not reported to metamorphose under natural conditions.

5. What is the size at metamorphosis? the time of metamorphosis?

   There is typically much variation in size at metamorphosis. This is related to the temperatures experienced during development, the availability of food to the larvae and other environmental factors. (Adolph, 1931; McCarrison, 1921; Tobler, 1947; Lynn and Wackowski, 1951; Snyder, 1956.) Ryan (1953) reports that *R. clamitans* vary 26-38 mm in body length at metamorphosis. The technique of Richards and Riley (1937) for study of growth of salamander larvae is useful in comparing samples.

VIII. *What are the characteristics of the young adults? Are there any typical behavior traits? What is the relation of the behavior pattern to survival? to growth?*

A. What advantageous resources in morphology, physiology, behavior patterns do the young adults possess? (Freisling, 1948).

B. What are the behavior hazards to which the young adults are exposed immediately after metamorphosis?

IX. *What are the characteristics of the growth curve of individuals of the local population?*

A. What is the length of the growing season?

1. What are the factors serving to delimit the growing season? Availability of food? Changes in environmental temperature? Cyclic changes independent of temperature?

Various procedures have been attempted for determining the limits of the growing season. The actual observation of initiation and cessation of growth through study of seasonal samples is best but such observations are difficult to obtain. Too, once the minimum and maximum effective temperatures of a form are known they may be utilized to approximate the time of initiation or slowing of activity (Ryan, 1953). This does not, however, necessarily define the growing season as it has been demonstrated that amphibians may become quiescent during the winter although retained at constant temperature.

2. What variations in length of growing season occur within the area of investigation?

   Some researchers indicate that the time of initiation or cessation of growth may vary significantly from one local situation to another.

B. What is the annual increment (in that measure selected as the best indicator of total change in mass) during each season of the animal's life? What sex differences occur?

1. What are the factors influencing the rate of growth? (size and/or egg; senility, length of growing season, social dominance).

   Growth rates in larvae and adults are exceedingly variable. Wilder (1924) demonstrated correlation of growth rate and food finding success. Noble (1931) thought crowding restricted growth of tadpoles. Bragg (1943) thought that aggregations stimulate feeding. Climatic factors influence growth. The diet influences growth rate and body proportions. Powers (1907) found that cannibalistic *Ambystoma tigrinum* differed from non-cannibalistic salamanders in flatness of head, length of teeth and body proportions.

2. What are the limits of variation in growth rates? How does growth rate affect the attainment of maturity, natality, mortality?
3. What age or size groups may be discerned?
4. Is growth potentially continuous throughout the life of the individual?

C. What is the natural (ecological) longevity?

1. What longevity records are available from captive specimens?

   Few records of known ages are available. Angel (1947) summarizes these. *Megalobatrachus* may live 55 to 60 years. Other salamanders have been in

captivity for 30 years. Anurans have survived for 36 years.

2. What estimates of age may be made from the population samples?

   The value of size groups must be estimated for each population. Age may be determined from anatomical attributes (Senning, 1940).

3. What are the characteristics of youth, maturity, old age?

D. What is the relation of ecdysis to growth? What are the factors inducing ecdysis? How does it occur? Habits associated with ecdysis?

X. *What is the annual cycle of activity and what factors exert primary influence on the cycle?*

A. What is the relation of the growing season to the period (periods) of courtship, development of eggs and larvae?

   Related species may respond differently to similar conditions (Powers, 1933). The annual sexual cycle is often closely associated with the recent evolutionary history.

   Caruso (1949) found no difference in the cyclic gametogenetic activity of *Hyla raddiana* from the plains and mountains of northern Argentina. The ovaries were mature during all months of the year and secondary sex characters were developed throughout the year. In contrast, *Phyllomedusa sauvagi* of northern Argentina breeds only during rains and the secondary sex characters are developed only during the breeding season.

B. What are the optimum, minimum and maximum effective body temperatures? Incipient lethal temperature?

   Freisling (1948) describes behavior of *Bufo viridis* in relation to temperature. Vernberg (1952) reports that *Plethodon cinereus* and *Eurycea bislineata* have highest metabolic rates at 10° C during May and June, lowest in October and November. At 1° C *Plethodon cinereus* had higher rates in October and November than in May and June. The cessation of activity at designated temperature levels has been frequently reported (Mullally, 1952; Bannikov, 1943; Bohnsack, 1952; Freisling, 1948; Marx, Metz and Kayser, 1946). Bullock (1955) discusses compensation for temperature. Incipient lethal temperatures and their relation to acclimation are known for few amphibians (Gibson, 1954).

C. What is the seasonal cycle in diel behavior?

D. Are the animals quiescent during any period of the year?

   Many amphibians have periods of relative quiescence during the year. The use of the terms "hibernation" and

"estivation" in designating these periods should be avoided as these words have specific physiological connotations developed through their use in the ecology of mammals.

1. What preparations are made for the period of quiescence?

   Cyclic, physiological modifications may bring about quiescence (Holzapfel, 1937). Morphological evidence derived from study of fat bodies and total weights is of concern here. Fromm and Johnson (1955) found oxygen consumption of frogs retained at constant temperature was maximum during the spring and decreased 40% in the winter.

2. Where do the animals spend the winter?

   Amphibians usually live in an environment buffered from thermal extremes. Information on the winter quarters of amphibians suggests that aquatic forms tend to aggregate while terrestrial forms remain isolated (Cagle and Smith, 1939; Bohnsack, 1952). Terrestrial forms may burrow into the ground to escape thermal extremes or drying. Cagle (1942) reported toads buried 6-20 inches in hard baked clay in October; Stebbins (1954) reported the intermittent movement of salamanders to underground retreats.

   Many amphibians have the ability to resist near-freezing temperatures during winter quiescence. Bohnsack (1952) reports that the temperature of the soil surrounding a bullfrog dropped to 23° F.

3. What environmental factors cause the initiation of quiescence? renewed activity?

   The role of paired factors as well as master factors must be considered. Biased attempts to recognize a master factor has often led to inconclusive answers for these questions.

   The significance of light cycles, especially ultra-violet, in amphibian activity has not been thoroughly explored. Researches on other vertebrates suggest the probable importance of light (Sabrosky, Larson and Nabours, 1933; Bailey, 1950).

4. What is the composition (age groups, size groups, sex ratios) of a winter aggregation?

5. What is the role of winter quiescence in limiting the geographic distribution?

XI. *What is the diel cycle of activity?*

A. Is feeding restricted to any particular part of the day? How

is the feeding behavior or length of feeding period influenced by food availability?

B. Are breeding activities (courtship, egg-deposition) restricted to any part of the day?

C. When does the peak of activity occur in the daily cycle?

The relation of temperature to activity was studied by Marx, Metz and Kayser (1946) who outlined techniques for recording activity and temperature simultaneously. Bannikov and Denissova (1943) demonstrated a correlation between digestion and movement from land to water in *Rana ridibunda* and found 2 peaks of activity, a nocturnal and a diurnal one.

D. How is the diel cycle modified by weather changes, population density?

Interspecies differences in the diel cycle of activity may affect the entire life history (Bannikov and Denissova, 1943; Chernomordikov, 1943). The activity threshold in relation to temperature may be characteristic of the species. Mullally (1952) points out that *Bufo boreas haplophilus* are active only when their body temperatures are greater than 3° C. Bogert (1951-2) expresses the opinion that salamanders cannot exercise control over their body temperature but that unpublished data indicate that some of the *Salientia* may do so. Exploration of the cycle may yield the key to many of the problems presented here.

XII. *What are the feeding and drinking habits of larvae, adults? Their relation to growth and survival?*

A. How does the animal obtain its food and water?

1. Can the animal pursue and catch actively moving prey? What senses are used?
2. What food preferences are exhibited in the field and laboratory?

B. What are the principal foods? Relation to availability?

1. What is the relative importance of the food items?
2. How do feeding habits vary during the life of the animal?
3. Is there any seasonal variation in feeding habits?

Most studies of food habits have reported a high percentage of empty stomachs. It is essential that the investigator utilize intestinal as well as stomach contents.

C. Does the animal act as a controlling or limiting predator?

D. What is the significance of the food habits in determining the distribution of related forms?

Competition for food has been stressed as a limiting factor in the distribution of related species. The unlimited acceptance of Gause's hypothesis should be carefully considered (Gilbert, Reynoldson and Hobart, 1952). Although larvae of related species may live together, their food habits may be different. Inger (1956) suggests that the larvae of three species of *Rhacophorus,* living in the same pool, have different feeding habits.

XIII. *Does this form exhibit any characteristic and genetically limited patterns of group behavior?*

The study of behavior under natural conditions often yields information of basic importance to the explanation of population problems and phylogeny (Freisling, 1948; Kortlandt, 1955). Few zoologists have developed the ability to profit from the observation of field behavior patterns. Herpetologists particularly have not utilized this procedure. Behavior of amphibian larvae is in many forms of great value in identification and may be used in the field and laboratory in the absence of morphological characters (Oyen, 1953).

A. Do aggregations occur? If so, what are the stimuli and binding forces in aggregation? the function of the aggregation? (Allee, 1951).

B. Do group movements occur? Migration?

C. Are social hierarchies present?

1. If dominance hierarchy is present, what is the relation to territoriality, natality?
2. How does the social hierarchy affect the migrating individual? the juvenile seeking a territory? (Freisling, 1948).
3. Does the social hierarchy influence growth and reproductive potential?

D. Are there typical defensive or offensive behavior patterns? (Hediger, 1953.)

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ABSTRACT

An annotated outline designed to suggest the ideal requirements in an investigation of the life history of an amphibian.

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NOTES ON HABITATS, SYSTEMATIC CHARACTERS AND LIFE HISTORIES OF TEXAS SALT WATER CYPRINODONTES

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NOTES ON HABITATS, SYSTEMATIC CHARACTERS AND LIFE HISTORIES OF TEXAS SALT WATER CYPRINODONTES

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In September 1950 the first author, following the suggestion of the second, began a study of the Cyprinodontes living in the salt waters of Texas. Sixty stations were set up from the Rio Grande to the Sabine River, a distance of about 400 miles. It was planned to visit these localities once every three months for at least one year. The whole area was covered about one and a half times, when the first author was called into the United States Air Force. The data were then turned over to the second author who is responsible for the writing.

The Cyprinodontes in Texas salt waters are an abundant, vigorous group of fishes living in the shallows next to the shores of the bays, and in the adjacent sloughs, bayous and ponds, which are often isolated from the open waters. Here they are exposed to great diurnal and seasonal extremes of temperature and abnormally high salinities. They also withstand sudden freshets and can tolerate wide and rapid salinity changes. They seem to be the most resistant of all fishes in these waters to variations of the physical environment. Evidence for these statements has been given before by Gunter (1945, 1950). When cold waves strike and millions of pounds of fishes are killed on the Texas coast (Gunter, 1952) dead cyprinodonts are not seen on the bay shores. Instead they are found at this time, and at this time only, out from the shores in water three feet deep or more. Since they are found in waters of abnormally high salinities but are extremely rare on the Gulf beach, only being found occasionally near the mouths of the passes (Gunter, 1945; Kramer and Gunter, *in press*), it seems that they are restricted to the bay areas by the presence of cover, which may be shells, plant debris or merely a rugose or muddy bottom. When disturbed these fishes do not rush headlong into flight; instead they go to the bottom leaving a cloud trail of stirred mud for a few feet, which stops abruptly as they hide in a depression, under a shell or in the mud itself. Kilby (1955) found that *Cyprinodon variegatus* will bury itself in mud or plant debris when the tide falls.

The cyprinodonts are ecological dominants in their environment and they have some commercial value as bait, for which their general

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TABLE 1.
NUMBERS OF SPECIMENS CAUGHT AT THE VARIOUS LOCATIONS, WITH TEMPERATURE AND SALINITY.

Date 1950	Location	Temperature (°C)	Salinity (per mille)	*Cyprinodon variegatus*	*Fundulus similis*	*Fundulus grandis*	*Fundulus pulvereus*	*Fundulus jenkinsi*	*Adinia multifasciata*	*Lucania parva*	*Gambusia affinis*	*Mollienesia latipinna*
IX:21	Redfish Point; #1; Copano Bay	35.0	33.2									
" "	Redfish Point; #2; tidal ponds	35.0	38.1	20	33	3						
IX:22	Port Bay; #1; N of road, W of bait house, Copano	35.0	36.0	4	5	3						
" "	Port Bay; #2; NE of bait house on shore, Copano	35.0	35.3		1					35		
" "	Port Bay; tidal ponds on ranch SE of causeway, Copano	34.5	47.6	376		1	1		1			1
IX:26	South Bay near Boda Chica, Laguna Madre	27.0	32.0									
" "	Creek by Yacht Club, road to Boca Chica, Laguna Madre	27.5	10.0			3						13
IX:27	Port Isabel; Laguna Madre; 3 mi. from Lighthouse	33.0	35.6	56								
" "	Port Isabel; Laguna Madre; 4 mi. from lighthouse	33.0	37.5	12		1						1
" "	Port Mansfield; Redfish Bay	27.5	54.4	132	32	4						
IX:28	Riviera Beach; Baffin Bay	34.0	64.9	354								
IX:29	Nueces Bay; midway White Point and causeway	30.0	39.8									
X:2	Hynes Bay at Austwell	29.0	22.1	2								
" "	Cavasso Creek at Hwy. #35.	30.0	35.2									
" "	Aransas Bay, mainland of Goose Island, near cafe	31.5	32.3	223	14	1	2		1			
X:5	Oso Creek, Yorktown Road near Rodd Field	27.5	60.9	703	4							
" "	Laguna Madre, across from Pita Island	30.0	42.4	361	39	37						
X:6	St. Charles Bay; 1 mi. NE of Goose Island bridge	31.5	31.5	69		17			3	1		
X:9	Small pond N of Fulton near Oakshore Apts.	27.0	34.1	347		5				1		41

" "	Crescent Beach; Aransas Bay	26.0	15.7									
" "	Little Bay, Rockport	26.0	34.2	203	82	2						1
X:10	Mission Bay shore approached from Lucas ranch	27.0	37.0									
" "	Sloughs around Mission Bay on Lucas ranch	27.5	42.3	79	2	1			1			
" "	Sloughs along road to Bayside of causeway	30.5	43.5	76		120						
" "	Bill's Point, Copano Bay	31.5	36.4	9	6	1				1		
X:18	Big Devil Bayou (connects with St. Charles Bay)	21.0	37.7	26	10	7						
" "	St. Charles Bay S of dam, Aransas Refuge	22.0	62.5	82		12						
" "	E side of spillway, upper St. Charles Bay, Aransas Refuge		Fresh									
" "	Mustang Slough, Aransas Refuge, ¼ mi. S of Flowing Well	26.5	32.4	420		13	2		13	10		145
" "	Mustang Slough, Aransas Refuge; at Flowing Well	25.5	31.8	472	1	2	1		1	2		67
" "	San Antonio Bay; Dagger Point, in tidal flats	25.5	27.4	39	7	2						
X:23	Gulf, Galveston beach at Stewart Rd.	25.5	28.5									
" "	Creek across Stewart Rd.; Galveston Island; West Bay	26.0	30.1	102	20	124	16		31	1		260
" "	Dickinson Bayou at Dickinson	25.5	3.4	41				2		1	13	
X:24	West Bay; Andy's Place; Galveston Island	21.0	20.9	1	75	10						
" "	West Bay off first causeway to Galveston	22.0	22.0			3						
" "	Port Bolivar at pass from Galveston Bay; #1	27.0	20.4									
" "	Port Bolivar; tidal pond; #2	26.5	19.8	15	21	1						
" "	Gulf Beach between High Island & Sabine	26.5	27.6									
" "	Sloughs E side of Hwy. between High Island and Sabine	27.0	20.7	213								
" "	Neches River E of Bridge on Orange-Port Arthur Hwy.	25.5	11.6	26		199	2				1	
X-25	Cedar Bayou at Hwy. #146 into Baytown	26.5	3.5								18	
" "	San Jacinto Bay W of Hog Island	26.5	16.6	5	3	29			1			5

TABLE 1.—Continued

NUMBERS OF SPECIMENS CAUGHT AT THE VARIOUS LOCATIONS, WITH TEMPERATURE AND SALINITY.

Date 1950	Location	Temperature (°C)	Salinity (per mille)	*Cyprinodon variegatus*	*Fundulus similis*	*Fundulus grandis*	*Fundulus pulvereus*	*Fundulus jenkinsi*	*Adinia multifasciata*	*Lucania parva*	*Gambusia affinis*	*Mollienesia latipinna*
" "	Scott Bay Near Baytown	26.5	11.6	7		161	1					12
" "	Trinity Bay at mouth of Double Bayou	24.5	7.0	37						7		
X-26	West Bay at N end of causeway on Galveston Hwy. *75	29.5	21.0		1							2
" "	Slough on N side of Dickinson Bay	27.0	15.4	1	1	8	3	6	1		2	
" "	Galveston Bay at Seabrook	24.0	13.1	57	56	15		2	6			
X:27	Snip Channel near Dow Chemical Plant at Freeport	25.0	27.7	28		3						
" "	Ship Channel at Velasco	24.0	27.9									
XI:3	Two mi. S of Magnolia Beach, tidal pond	18.0	18.4	23	1	14	2			14		
" "	Slough N of Powderhorn Lake at Indianola	18.5	26.6	17	4	25			4			141
" "	Carancahua Bay along NE shore	19.0	23.9	15	6	115	5		6			
" "	Mud puddle in dry creek, NW side of Lavaca Bay	17.0	44.8	11		29	10		8	4		9
XI:8	Ingleside Cove; SE shore	25.5	41.4	17	12	4						
" "	Tidal pond (2 mi. inland from Redfish Bay); 3 mi. S of Aransas Pass	28.0	88.8	795								
" "	Bill's Point; Port Bay (Copano)	28.0	38.2	21						7		
" "	Slough on farm Hwy. to Bill's Point near Port Bay Club	28.0	142.4	2009								
" "	Tidal pond E of Aransas Pass shipyard on causeway	27.0	48.5	171	2	1						
XI:27	Rattlesnake Point (Port Bay) Copano	18.0	35.2	14	1	2	1		3	1		
" "	Bill's Point (Copano)	20.0	37.4	20					1	9		
XII:22	Bill's Point (" ")	17.0	38.3	98	1	1				7		

" "	Slough across Farm Hwy. *288 near Port Bay Club											
1951 I:9	Ingleside Cove	16.5	36.8		10							
I:19	Aransas Bay, mainland of Goose Island	26.0	31.6	2		1			48			
" "	Bill's Point (Copano)	24.5	31.5	104						2		
" "	Slough across Hwy. *288 near Port Bay Club		130.8									
" "	Port Bay; tidal ponds on ranch SE of causeway	25.0	53.9	127			8		13			8
I:28	Dickinson Bayou at Dickinson	18.0	11.3	1		1		2			7	2
" "	2nd Creek across Stewart Rd., Galveston Island	22.0	20.9	9		12	1		111			
" "	Flooded pits N of Stewart Rd., Galveston Island	20.0	1.8	12		6				1	15	1
" "	Dickinson Bay; E of bridge, Hwy. *146 near San Leon	18.0	20.1	7		6		1	1			
" "	Slough N side Dickinson Bay at San Leon (Lum Terrace Rd.)	18.5	20.6	38		13	1	11	10	1	1	
" "	Galveston Bay at Seabrook	17.0	19.9	30	2	4						
II:22	NE shore of Carancahua Bay	18.0	29.6	28		41						
" "	Tidal pond ½ mi. NW of Indianola	22.0	25.4	162	33	14						
" "	Slough N of Powderhorn Lake at Indianola	21.0	31.3	201	4	9	2		46			
III:2	Loyola Beach; Baffin Bay; *1; slough	28.0	147.2									
" "	Loyola Beach; Baffin Bay; *2; Bay proper	25.0	76.1	259	16	1						
" "	Nueces Bay near airport at Portland	24.0	39.9	2								
III:3	Port Mansfield; Laguna Madre	22.0	48.2	28						1		
" "	S end of resaca SW of Olmito, Texas	25.0	<1.0							1	95	7
" "	Resaca del Rancho Viejo near Olmito, Texas	25.0	5.4	26		13				48		55
" "	Irrigation ditch 2⅔ mi. NE Olmito, Texas	25.0	7.2	14						5		9
	TOTALS			8859	505	1099	60	24	310	130	152	780

hardiness fits them well. However, the monetary measure of this use is unknown for no statistics are kept.

A few life history notes have been given in the papers cited above. Kilby (1955) gave considerable information including length frequency curves for four species, but the life cycles are still known incompletely.

Method

Stations were visited in a jeep with four-wheel drive, which permitted approach to almost any selected point on the bay shore. A fifty-foot minnow seine, with mesh of one-quarter of an inch stretched, was the collecting gear. One haul was made at each station, but length of haul was not standardized. All cyprinodonts taken were counted and the presence of commercial shrimp of the family Penaeidae was noted. A general physical description of each station was recorded. The stations were always in the same general area, but some changed with stages of the tide and drying of the ponds. Water temperatures were taken with a thermometer reading to tenths of a degree centigrade. A water sample was taken and the salinity was determined later in the laboratory by sea water hydrometers. Samples in which salinity was extremely high or low were checked by titration. Many samples of the fishes were preserved and are now in the Institute of Marine Science collections.

The authors made a few hauls together, but most of the time the first author had the assistance of Mr. C. A. Schultz. Others who occasionally helped haul the seine were H. H. Hildebrand and W. D. Simpson. The slope of the bottom, its type, depth and other factors varied not only from place to place but from time to time. Therefore, it was impossible to set up a standard drag and this matter was perforce ignored, except that at each station attempts were made to haul the seine in such a way that samples of what was present were obtained.

The Data

General Habitat Relationships

Table 1 gives the localities, temperatures, salinities, and shows the numbers of the various species caught at each station. Eighty-four stations were made from September 1950 to March 1951.

Examination of this table shows that the cyprinodonts are predominantly fishes of tidal ponds, sloughs, salt water creeks and bayous, rather than bays or open waters. *Gambusia affinis* (Baird and Girard) were not taken at all in open waters; *Fundulus jenkinsi* (Evermann) was taken once out of six times on a bay shore; *F. pulvereus* (Evermann) was taken four out of 16 times on a bay shore; and *Mollienesia latipinna* (Lesuer) was taken once in 19 times. Gunter (1945) and Kilby (1955) found the same distribution of the last species. *Lucania parva* (Baird and Girard) is slightly more of an open water fish than the above species and was taken one-third of the time on the open shores. *Fundulus grandis* (Baird and Girard), *F. similis* (Baird and

Girard) and *Cyprinodon variegatus* (Lacépède) are quite common along the bay shores, but even these species were found more often in protected waters. *Adinia multifasciata* (Girard) belongs in the same group, but its distribution is more spotty and it is less abundant.

Table 2 lists the species in order of numbers caught and gives the number of times they were caught. The numbers caught in three other studies, two in Texas and one in Florida, are also given.

TABLE 2.
NUMBERS OF CYPRINODONTS CAUGHT IN THE COURSE OF THIS WORK WITH SIMILAR FIGURES FROM THREE OTHER STUDIES.

	Times taken*	No.	Gunter (1945)	Gunter (1950)	Kilby (1955)
Cyprinodon variegatus	63	8,859	6,673	924	6,191
Fundulus grandis	49	1,099	454	74	1,979
Mollienesia latipinna	19	780	1	67	10,846
Fundulus similis	32	505	1,362	252	1,954
Adinia multifasciata	21	323	44	37	5,303
Gambusia affinis	8	173	—	421	2,026
Lucania parva	21	160	476	1,522	4,205
Fundulus pulvereus	16	60	—	8	—
Fundulus jenkinsi	6	24	—	—	—
TOTALS		11,845	9,010	3,297	32,504

*number of stations out of 84 total.

The figures given in the first column probably show a truer picture of the relative abundance of the Cyprinodontes in Texas coastal waters than the other two reports by the second author, because hauls were made in every type of environment in which these fishes live from one end of the Texas coast to the other. The hauls made by Gunter (1945) were all on the open shores of Copano and Aransas bays in south Texas, and are typical of the bay shores only. Thus, he did not take *Gambusia affinis* and *Mollienesia* was taken only once, although salinities were often quite low. The cyprinodonts reported by Gunter (1950) were taken in the sloughs and ponds (some of them fresh water) of Blackjack Peninsula on the Aransas Refuge in south Texas. This accounts for the larger numbers of *Gambusia.* The case of *Lucania parva* is less easily explained and will be discussed under salinity relations. The figures given by Kilby (1955) relate to two brackish marsh areas in Florida, where, in both species (several of which are not present in Texas waters and are therefore not listed) and numbers, the predominance of the Cyprinodontes is certainly overwhelming. Of 54,687 fishes he caught, over 40,000 were cyprinodonts.

The chief conclusion to be drawn from this table is that *Cyprinodon variegatus* is very abundant in most places where killifishes live. Two species of *Fundulus, grandis* and *similis,* are also widely distributed and abundant, the first more on open shores and the second more in protected waters. It may be significant that *grandis,* the more open

water species, grows to a larger size. *Mollienesia latipinna,* especially, and also *Adinia multifasciata* and *Lucania parva* are more abundant in protected waters.

Salinity Relationships

The catches of the various species as related to salinity of the water are set forth in Tables 3 and 4. The ranges and averages are given in Table 3; the numbers caught at certain arbitrary salinity groupings are given in Table 4. Over 30 per cent of the salinities encountered were well above that of normal sea water, and no such salinities were found during the previous work. It should be noted that all of these high salinities were found in south Texas, with several records from the Laguna Madre which is a notoriously hypersaline body of water. The south Texas region is semi-arid and it was subjected to a severe drouth before and during the time of this study. The previous work by the second author was carried out during wetter years.

Gambusia affinis is, of course, a fresh water fish which ventures into waters of moderate salinity. Eleven fish, or 7.2 per cent of the catch, were taken in water ranging from 11.3 to 20.6 parts per thousand saline. The remainder were caught at salinities of 3.5 or below.

Fundulus jenkinsi is reported only from a restricted area of the Texas coast. Our records indicate that it is found in waters of rather low salinity. Two specimens, 8.3 per cent of the catch, were taken at a salinity of 3.4, the remainder being caught at salinities ranging from 11.3 to 20.6.

Gunter (1945) found *Lucania parva* most abundant at salinities between 10.0 to 15.0 *per mille.* On the other hand Gunter (1950) found that 99.9 per cent of the catch on the Aransas Refuge was at salinities between 0.9 and 2.5. In the Florida west coast marshes Kilby (1955) found that 81 per cent of this species was taken at salinities of 10.0 or less. In this work, however, only 39.4 per cent of the catch was taken at salinities below 10.0 and the larger part was taken at salinities from 18.4 to 48.2, over 17 per cent being found in waters saltier than normal sea water. Certainly the fish tolerates a very wide salinity range and possibly its distribution is determined by factors other than salinity, which cause it to be found at low salinities in normal years.

It has been shown previously by both Gunter (1945) and Kilby *(op. cit.)* that *Adinia multifasciata* is found most often at medium salinities. The same thing was found in the present work, except that the salinities were toward the higher ranges, and over nine per cent of the fish were taken at hypersalinities. This fish is truly a brackish water species and is not found ordinarily at either the lowest or the highest salinities of coastal waters.

Fundulus similis was abundant only at medium and high salinities. *F. grandis* occurred over a wider range.

Mollienesia latipinna was found widely scattered over a broad sa-

TABLE 3.

SALINITY RANGES AND AVERAGE SALINITY AT ALL LOCALITIES WHERE EACH SPECIES WAS CAUGHT. RANGES AT WHICH THE SPECIES WERE TAKEN IN THREE OTHER STUDIES ARE GIVEN FOR COMPARISON.

	Salinity ‰ Range	Salinity ‰ Avg.	Salinity Range Gunter (1945)	Salinity Range Gunter (1950)	Salinity Range Kilby (1955)
Gambusia affinis	1-20.6	8.5	not taken	0.4-3.1	1.2-25.2
Fundulus jenkinsi	3.4-20.6	14.0	not taken	not taken	not taken
Lucania parva	1-48.2	24.9	2.1-24.2	0.7-16.3	0.1-28.2
Fundulus pulvereus	11.6-47.6	28.9	not taken	0.4-16.0	not taken
Mollienesia latipinna	1-53.9	24.1	10.0	0.4-16.3	1.2-37.6
Adinia multifasciata	13.1-53.9	30.4	8.4-35.7	3.1-16.3	0.8-37.6
Fundulus grandis	1.8-76.1	30.1	2.0-37.1	0.4-18.6	0.8-35.6
Fundulus similis	13.1-76.1	33.5	2.0-37.1	1.4-18.6	0.8-37.6
Cyprinodon variegatus	1.8-142.4	34.5	2.0-35.7	0.4-18.6	0.0-35.6

TABLE 4.

NUMBERS OF FISHES CAUGHT AT CERTAIN ARBITRARY SALINITY CLASSES.

	1	1-9.9	10.0-19.9	20-29.9	30-36.9	37-49.9	50-79.9	above 80.0
Gambusia affinis	95	46	10	1	—	—	—	—
Fundulus jenkinsi	—	2	10	12	—	—	—	—
Lucania parva	1	62	14	1	54	27	—	—
Fundulus pulvereus	—	—	8	7	24	19	—	—
Mollienesia latipinna	7	65	31	143	514	1	19	—
Adinia multifasciata	—	—	8	126	100	3	9	—
Fundulus grandis	—	19	439	249	181	200	17	4
Fundulus similis	—	—	28	130	140	99	48	56
Cyprinodon variegatus	—	130	165	569	2,226	1,318	922	2,804

linity range, but was taken only once at a hypersalinity.

Cyprinodon variegatus tolerates a very wide range of salinity, especially towards the higher ranges.

It is clear that except for *Gambusia affinis* all species had their greatest abundance between 20 and 36.9 parts per thousand salt. With regard to *Cyprinodon variegatus* the tendency was for the abundance to be greatest at an even higher salinity. However, the great abundance at salinities above 80 parts per thousand should not be taken as the normal distribution or preference of this species, because in such cases both the fishes and the salts were concentrated in drying ponds. They were withstanding the salinity but they probably had not selected it. This was certainly the case where the salinity was 142.4 parts per thousand, calculated as if it were sea water. It should be understood, however, that water at such salinities is not sea water, for some salts are precipitated before sea water attains such concentrations and the complex is changed. This determination was made with hydrometers. Titration gave a salinity of 130.0 *per mille,* but it was not certain that all the chloride was precipitated and at this concentration. So far as we know this is the highest salinity at which living fish have been reported. This salinity must be very close to the toleration limit, for one haul in the Laguna Madre where the salinity was 147.0 showed only dead *C. variegatus.*

Tables 3 and 4 show that *Fundulus grandis, F. similis* and *Cyprinodon variegatus* have very high salinity preferences and tolerances, and these three species should in our opinion be classed as fully marine.

Species Characteristics

The Cyprinodontes in this area are not easy to separate on the basis of external meristic characters and for some species it is virtually impossible. However, the field worker quickly learns to distinguish them all by color and subtle differences of shape, some of which are difficult to describe.

Table 5 gives a series of body measurements and scale counts for both sexes of the various species over a fairly wide length range. The species with lower scale counts are *Cyprinodon variegatus, Adinia multifasciata, Lucania parva* and *Mollienesia latipinna;* the species with higher counts are *Fundulus grandis, F. similis* and *F. pulvereus.*

It is also clear from Table 5 that the deeper-bodied species are *Cyprinodon variegatus, Adinia multifasciata* and *Mollienesia latipinna.* The slimmer species are *Fundulus jenkinsi, F. similis* and *F. pulvereus.*

The fishes with the smallest eyes, proportionally, are *Fundulus grandis* and *F. similis.* Those with the largest eyes are *Gambusia affinis* and *Lucania parva.* The latter two are also the smallest species.

The so-called longnose killifish, *Fundulus similis,* was found to have a slightly longer snout than the other fishes at lengths of 25 to 100 mm, but the difference was not great.

Table 6 gives the dorsal and anal ray counts of the various species,

TABLE 5.

PROPORTIONAL MEASUREMENTS AND SCALE COUNTS OF BOTH SEXES OF A NUMBER OF SPECIES.
(Length Readings in Millimeters)

		Number	Total Length		Standard Length		Depth in S. L.		Head in S .L.		Snout in Head		Eye in head		Scales	
			Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.
Gambusia affinis	♂	4	23–31	26.0	19–23	20.8	4.0-4.5	4.25	3.7-4.0	3.93	3.1-3.5	3.35	2.5-3.1	2.90	32-34	32.5
	♀	22	20–32	26.9	16-26	21.6	3.8-4.5	4.16	3.3-4.0	3.60	3.0:4.0	3.47	2.8-3.5	3.06	30-33	31.7
Mollienesia latipinna	♂	30	24–52	35.4	18-40	27.9	2.7-3.3	2.98	3.0-3.7	3.40	2.9-4.0	3.32	2.8-3.5	3.17	27-31	28.8
	♀	44	17–57	38.3	13-46	30.1	2.8-3.5	3.13	2.9-3.7	3.36	3.0-4.0	3.42	2.7-4.0	3.29	26-31	28.8
Fundulus jenkinsi	♂	9	26–45	37.8	21-37	30.6	4.4-5.3	4.79	3.2-3.5	3.29	3.0-4.0	3.38	2.9-3.8	3.23	34-37	34.8
	♀	15	26–60	37.5	20-49	28.9	4.6-5.8	4.69	3.2-3.5	3.39	3.0-4.0	3.49	2.8-3.8	3.14	33-37	34.9
Fundulus pulvereus	♂	17	30–51	38.4	24-47	31.9	3.5-5.0	4.32	2.8-3.5	3.25	3.4-4.0	3.75	3.0-4.0	3.47	36-40	38.1
	♀	41	16–50	31.4	12-47	25.1	4.0-5.5	4.51	3.0-3.5	3.20	3.3-4.5	3.79	3.0-4.0	3.33	35-42	38.2
Fundulus similis	♂	11	21–80	48.7	17-64	38.5	4.0-5.2	4.52	2.9-3.3	3.05	2.8-3.5	3.12	3.0-4.5	4.03	35-40	37.5
	♀	5	25–100	75.6	20-80	60.2	3.9-5.5	4.50	3.0-3.2	3.08	2.7-3.3	2.84	3.3-5.9	4.96	37-38	37.6
Fundulus grandis	♂	17	37–112	67.5	30-92	57.7	3.2-4.5	3.83	3.0-3.6	3.32	3.0-3.7	3.39	3.4-5.0	4.08	36-42	38.8
	♀	21	29–115	64.5	23-96	52.9	3.5-5.0	3.94	3.0-3.6	3.36	3.0-3.8	3.45	3.0-4.8	3.91	35-41	38.5
Lucania parva	♂	19	23–38	29.2	19-31	24.2	3.5-4.3	3.81	3.0-3.7	3.34	3.6-4.5	3.96	2.5-3.3	2.99	26-30	28.3
	♀	34	19–36	28.3	16-32	23.4	3.5-4.5	3.94	3.0-4.0	3.37	3.5-5.0	3.78	2.5-3.5	2.99	26-31	28.8
Adinia multifasciata	♂	39	16–36	27.5	13-28	22.1	2.5-3.5	2.96	2.8-3.3	2.98	3.0-4.0	3.53	2.5-3.5	3.03	25-28	26.8
	♀	48	16–37	27.6	12-28	21.9	2.6-3.6	3.13	2.7-3.4	3.04	2.8-4.0	3.45	2.5-3.5	3.07	24-28	26.9
Cyprinodon variegatus	♂	5	35–52	43.8	27-42	34.0	2.2-2.7	2.38	2.8-3.2	3.06	3.5-4.0	3.62	3.5-4.0	3.62	27-29	28.2
	♀	15	20–51	34.8	16-40	27.1	2.3-3.0	2.58	2.8-3.3	3.01	3.4-4.1	3.69	2.9-3.6	3.36	25-29	27.3

TABLE 6.

DORSAL AND ANAL RAY COUNTS FOR BOTH SEXES OF THE VARIOUS SPECIES. NUMBERS ARE THE NUMBER OF SPECIMENS WITH THE RAY COUNT LISTED AT THE TOP OF THE COLUMN.

		Number of Rays																Dorsal insertion relative to anal
		Dorsal											Anal					
		6	7	8	9	10	11	12	13	14	15	9	10	11	12	13	
Gambusia affinis	♂		4									4					
	♀	1	21									20	2				Behind
*Mollienesia latipinna**	♂								7	27	4	1	34	2			Distinctly
	♀						3	3	19	52	6	4	50	2			Before
Fundulus jenkinsi	♂			1	8									4	3	2	Distinctly
	♀			2	13									2	11	2	Behind
Fundulus pulvereus	♂				1	4	12						17				Slightly in front
	♀			1	2	24	12	1				11	27	2			to slightly behind
Fundulus grandis	♂						10	3	4				4	12	1		Over to
	♀					1	7	12	1				5	12	4		Slightly before
Fundulus similis	♂						2	2	4	3			3	6	2		
	♀						1		1	2			1	3			Slightly before
Lucania parva	♂					1	3	10	4				4	8	6		
	♀				1	2	6	21	4			1	10	18	5		Before
Adinia multifasciata	♂				31	8							2	32	5		
	♀				41	5							2	36	8		Before
Cyprinodon vareigatus	♂						4	1					1	3	1		
	♀					1	4	10					4	10	1		Before

* Fewer anals than dorsals counted, hence numbers do not correspond.

with remarks on the insertion of the dorsal relative to the anal.

Examinations of color markings were made on live specimens and these are given under the individual species accounts in the next section.

It should be noted at this point that the "Amazon molly" females, *Mollienesia formosa* Girard, which have their northern limit on the Texas side of the Rio Grande, were not found during this investigation. However, specimens were collected later by other workers in resacas near the Rio Grande. They are not included in this account because we saw no specimens and we are not certain that they belong with the salt water fauna.

Life History Notes

Gambusia affinis

Forty-four fish taken along the eastern part of the coast between October 23 and 25, 1950 ranged from 20 to 32 mm in total length. Twenty-three specimens caught on January 28, 1951 in the Galveston Bay ranged from 22 to 48 mm in length. Ninety-five caught in a resaca near the Rio Grande on March 3, 1951 ranged from 23 to 40 mm in length. Only two females had attained a length of 40 mm.

In this account we have not used subspecific names, since the measurements, locality records and presumably the specimens themselves will serve the purposes of taxonomists who wish to relate these fishes to other populations. However, all indications are that this fish corresponds to *G. a. affinis* of most authors (*cf.* Knapp, 1953).

Specimens from the Galveston region had a rather prominent, but fine cross-hatching of gray and black on the back and sides. The fins were colorless, except that the dorsal was black-edged with two vertical rows of black dots. In some males there were three rows of these dots on the dorsal. A row of these dots formed an indistinct vertical stripe on the mid-caudal. The gonopodia on four males, 23 to 31 mm long, ranged from 6 to 8 mm in length.

The stomachs of two specimens contained only animal food, consisting of small fish, small crustaceans and annelids.

Mollienesia latipinna

Seventeen specimens taken in September, 1950 were 12 to 43 mm long; 533 fish caught in October were 13 to 56 mm long; 141 fish caught in November were 31 to 53 mm in length; 12 taken in January 1951 were 12 to 41 mm, and 71 taken in March 1951 were 24 to 71 mm long. Among these, thirty were males. A group of 260 fish caught in the Galveston area in September 1950 showed a ratio of 64 males to 196 females; another group of 141 taken in November, 1950 near Indianola had a ratio of 30 males to 111 females. The largest male caught was 53 mm long, the largest female 71 mm.

Both males and females had seven or eight horizontal bluish stripes along the body. There were also three to six vertical stripes under what could be called the shoulder region. There were small yellow

spots on the sides of some females. In some females the dorsal, anal and caudal were black-edged. In others the anal was pale and the caudal was dusky; in still others the caudal was pale or faintly black-edged. There were three or four rows of horizontal spots on the dorsal. The males differed from the females chiefly in more vivid coloration and the fact that the caudal was yellow and more heavily black-edged.

All specimens examined had a purely black peritoneum.

Two females taken on August 26, 1950 had bright yellow eggs, 1.5 to 2 mm in diameter. A fish with young presumably nearing birth was taken on September 23, 1950.

One male, 31 mm long, had a gonopodium 6.5 mm in length.

Fundulus jenkinsi

Of the 24 specimens caught, nine were males from 26 to 45 mm long. The 15 females were 25 to 60 mm long.

Both males and females are cross-hatched on the back and sides and spotted on the sides. The spots may be round or sometimes elongated into little vertical bars. The cross-hatching may be very faint or a prominent gray-green. In some the spots are above the midline and in a few the spots form an almost continuous midline along the side. In some females there is a faint midline with no spots. Every fish collected had an almost horizontal bar on the opercle at about the eye level.

A female with eggs less than 0.25 mm in diameter was taken on September 26, 1950. On January 28 1951 a female was taken with clear eggs, 0.25 mm in diameter; another taken at the same time had clear eggs 0.5 mm in diameter.

This fish has not been mentioned often in the literature since it was described by Evermann from Dickinson Bayou, where it was found again during this investigation and at that location only. However, it is known to extend over most of the northern Gulf coast, although its distribution is scattered and spotty and is doubtless determined by some special ecological requirement which is unknown. Garman (as cited by Hubbs, 1926) recorded it from Alabama in 1895 and Hubbs (1926) reported a specimen from Prevost Island, St. Tammany Parish, Louisiana, Fowler (1945) listed five specimens from Moss Lake, Louisiana and, in a table (p. 34), listed it from the Rio Grande drainage of Texas. Bailey, Winn and Smith (1954) recorded 80 specimens from the Escambia River, Florida, where the salinity ranged from 4.5 to 24.4 *per mille.* Miller (1955) gave the known range as from the Escambia River to Houston. Galveston would have been a little more specific. He also states that Fowler *(op. cit.)* listed the species from the Rio Grande. However, Fowler's table refers only to river basins or drainages, and the record is very indefinite and doubtful, especially since he did not mention the fish in his account of Texas species. Since our own rather extensive col-

lections did not reveal *F. jenkinsi* west of Dickinson Bayou, it seems best to consider the range limits set by Miller *(op. cit.)* as correct until more information is available.

Fundulus pulvereus

Of the fifty specimens sexed 15 were males from 30 to 46 mm long. The females were 16 to 45 mm long. No fish under 20 mm long was caught except at one haul in Lavaca Bay on November 3, 1950, where eight of ten specimens were from 15 to 17 mm long.

The base color of the females ranged from olive to dark gray-blue above, shading to gold on the sides and to silvery or cream on the belly; large discrete dark dots are scattered over the body, but are chiefly confined to the area above the midline or slightly below. However, this dotting is quite variable. Five females had the dots only above the midline; in one fish they formed a row. Six females had dots only along the midline and ten of them had the dots both above and below, although they were most numerous above. A few females had faint, broken horizontal stripes. The fins were pale to dusky and pectorals were yellowish at the base. The suborbital was sometimes rather golden.

The males had 12 to 17 bluish vertical stripes, with silvery interspaces of the same width. There were some fainter horizontal stripes. They were olive on the back and silvery on the belly. There were black and white horizontal stripes on the posterior part of the dorsal. The anals and dorsals were dusky or the anal was yellowish dusky. The caudal was also dusky yellowish. A dorsal ocellus was clear, faint or absent.

A fish with a developing ovary was seen on October 3, 1950. Ovaries with very small eggs were seen on October 23. Ovaries with egg 0.2 mm in diameter were also seen on that date, on October 25, and October 2. Clear eggs 0.33 mm in diameter were seen on November 3. A fish, apparently ripe, with yellowish eggs 1.0 mm across, was taken on October 2. Fish with clear eggs, 0.5 mm in diameter were taken on January 19 and 28, 1951. It appears that this species spawns in the fall and winter, if not other seasons as well.

Aquatic insects were found in one stomach and two isopods, about 1.0 mm long, were found in another.

Miller (1955) gives the range as Bay Minette, Alabama to Corpus Christi, Texas.

Fundulus similis

It has been previously stated that ripe males and females are present in the Aransas Bay area from April to August (Gunter, 1945). The second author has observed this fish spawning in July on the shores of Copano Bay. They get as close to shore as possible and seek small depressions and cups of water similar to those of a horse track, connected to the bay by the merest fingerlet of water through which the fish skitter adeptly. In the little potholes they wriggle excitedly and

convulsively with the usual motions of spawning fish, sometimes standing almost upright on their tails. Eggs were not recovered.

In the present work the smallest specimens caught for each month from September to March respectively were 20, 23, 25, 31, 32, 38 and 43 mm long. The larger fish ranged from 83 to 114 mm long, but not in sequential order by months. The largest was taken in February. Five large males ranged from 77 to 92 mm in length and averaged 81.6 mm; eight large females were 86 to 114 mm long and averaged 99.7 mm. These were not taken in the breeding season and the sizes are somewhat larger than those given by Gunter *(op. cit.)*.

This species has from 8 to 17 vertical black stripes on the sides. The posterior one or two may end dorsally in a round spot. There is sometimes a more faded spot ventral to these posterior stripes. The dorsal, anal and caudal fins are pale or dusky and black-edged.

Fundulus grandis

The numbers of fish caught by months and the size ranges are shown in Table 7.

TABLE 7.

NUMBER OF *Fundulus grandis* CAUGHT EACH MONTH AND THE LENGTH RANGES.

Month	Number caught	Length ranges (in mm)
September	15	22-93
October	832	22-111
November	186	18-88
December	1	42
January	37	29-91
February	23	30-86
March	14	28-131

Gunter (1945) found the smallest fish from June to August and the greatest catches in midsummer and midwinter. These data are somewhat different, possibly because the total area where the fish lives was sampled. The winter of 1950-51 was rather severe, which probably accounts for the low winter catch, the fish having moved out of the shallows. In shallow ponds, which froze over at the time of the severe freeze and fish kill of January 28 - February 1, (*cf.* Gunter, 1952) the fish may have been wiped out, as was particularly noted for *Cyprinodon variegatus*. Kilby (op. cit.) found small fishes at all periods of the year and small abundance increases in certain months in winter, spring and fall.

Nine males ranged from 62 to 131 mm long and averaged 93.5. Seven females were 82 to 114 mm long with an average of 105.4.

The fish is predaceous and three specimens were found with partially swallowed mollies sticking out of their mouths. Two stomachs contained aquatic insects and vegetable matter.

The base color is a dull greenish above shading to lemon yellow

below. There are 12 to 19 faint stripes on the sides. The anal and lower half of the caudal may be yellow or the anal, dorsal and caudal may be dark with white splotches at the base. The first two may be edged with yellow, and the caudal may be edged with white. The ventrals are yellow and the pectorals are pale. In some males the dorsal and caudal are flecked with silver and the anal is pale. In the males coloration is much more vivid with the silver flecking and striping noticeable, while the larger females may appear olive to dull olive yellow below.

Yellow eggs, 2.0 mm in diameter, were stripped from females on October 10, 24 and 25, 1950.

Lucania parva

The length range of this species was 17 to 48 mm. Only three specimens below 20 mm were caught, in October and November.

The upper part of the body is pale green or olivaceous shading to pearly on the belly. The scales are black-edged, making a dark cross-hatching on the back and sides. The anal is black-edged, and there is a dark blotch on the leading edge of the dorsal in the male. The males also have some yellow or yellowish orange on the base of the dorsal, anal and caudal and the subopercle is faintly washed with gold; in the female this area is more silvery. The caudal may or may not be black-edged in the male. There is a faint midline stripe.

None of the above color differences hold invariably for the males and females and it may be that the colors are enhanced during the breeding season. Only one thing seemed to hold and that was concentrations of the melanophores at about one-third the height of the dorsal of the males, between the first and second and second and third rays, which appear with the naked eye to be two darkly drawn lines. In the females these melanophores are not so closely associated as to look like a black streak.

Eggs 0.33 to 0.5 mm across were taken in the latter part of November. They were clear. A fish with yellow eggs, 1.0 mm in diameter was taken on January 28, 1951.

Larval crustaceans and small annelids were taken from one stomach; another contained small white mollusc shells and crustaceans.

Adinia multifasciata

The size range of 360 fish was 16 to 38 mm. Eleven fish under 20 mm long were taken in October, November and January, seven being taken in one haul on the Lavaca Bay shore in November.

All fins except the pectorals may be yellow or more rarely they are all pale; or there may be combinations of yellow and pale fins, in which case the anal is always yellow, or the anal and ventrals are yellow.

The body base color is greenish on the back, with a yellowish tinge on the side shading into white on the belly. There are many narrow vertical stripes of dark blue gray separated by silvery areas. The

stripes are not straight but are somewhat irregular, giving a variegated appearance.

Four ripe females with yellow eggs, 0.75 to 1.0 mm in diameter, were taken on October 18, 1951.

One stomach contained algal detritus and one contained pieces of a dragonfly.

Cyprinodon variegatus

Gunter *(op. cit.)* found that small fish were added to the population from June to December. The present data are not greatly at variance with that statement, although some quite small fish were taken in January. Gunter also found the greatest abundance in winter, but in the present study it was found in the fall. Kilby (1955) found fish 15 mm in length or less in every month except January, February and March. He took the greatest numbers of fish in August and October.

Forty-two males taken during this investigation ranged from 35 to 58 mm long and averaged 45.0 mm. Thirty-six females were from 31 to 55 mm long and averaged 46.5 mm. The distributions are shown in Table 8.

TABLE 8.

NUMBER OF SPECIMENS OF *Cyprinodon variegatus* CAUGHT EACH MONTH AND THE LENGTH RANGES.

	Number	Length Range (in mm)
1950		
September	875	9-43
October	3,215	13-64
November	3,093	13-47
December	98	17-42
1951		
January	329	16-45
February	419	21-58
March	299	21-50

Although this fish is resistant to cold, and no dead cyprinodontid has ever been found on the open shores following the fish-killing freezes which strike the Texas coast, many in the shallow isolated ponds were wiped out by the hard cold wave which struck on January 28, 1951.

This is a pugnacious little fish and it puts all other cyprinodonts to flight. In aquaria it finally kills the larger species by chasing them incessantly and nipping off their fins.

The color of this common little fish is too well known to deserve comment.

The stomachs of five females contained vegetable matter.

Raney, *et al.* (1953) described the breeding habits of this fish in Florida, in which the males set up certain territories and hold them against all comers except for the females, with which they breed or

attempt to breed. The second author observed the same behavior of the species in a roadside ditch connecting with Redfish Bay at Aransas Pass, Texas.

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Abstract

Sixty stations were set up between the Rio Grande and the Sabine River, covering the habitats of the salt water Cyprinodontes along the bay shores, sloughs and tidal ponds. These were visited eighty-four times, about one and a half rounds of all stations, between September 1950 and March 1951. Drags were made at each station with a fifty foot minnow seine with mesh one quarter of an inch stretched. Water temperatures were taken and salinities were determined later by hydrometer. Some samples were checked by titration. All cyprinodonts captured were counted and measured. Sexual condition and coloration were noted and some stomach contents were noted. External meristic counts were made.

In order of abundance the nine species taken were: *Cypri-*

nodon variegatus, Fundulus grandis, Mollienesia latipinna, Fundulus similis, Adinia multifasciata, Gambusia affinis, Lucania parva, Fundulus pulvereus and *F. jenkinsi.* There were 8,859 of the first taken and only 24 of the last. *C. variegatus* was almost three times as abundant as all other species together. *C. variegatus, F. grandis and F. similis* are fairly abundant on open shores, while the others are found mostly in protected waters. As a whole, the cyprinodonts are more inhabitants of sloughs and ponds than bay shores and they are extremely rare on the Gulf beach. Due to a severe drouth the salinities at many stations were quite high and in drying ponds they were about 80 $^{0}/_{00}$. Only *Gambusia affinis* and *F. jenkinsi* were not taken at salinities higher than 30 $^{0}/_{00}$; *F. grandis, F. similis* and *C. variegatus* were sometimes caught, the latter quite abundantly, at salinities above 80 $^{0}/_{00}$ and on one occasion this fish was taken where the density measurement was equivalent to 142.4 $^{0}/_{00}$ saline, calculated as sea water. It is assumed that the fishes taken at extremely high salinities did not select them, but were merely withstanding them after having been caught in drying ponds and sloughs.

Species with lower scale counts were: *C. variegatus, Adinia multifasciata, Lucania parva* and *Mollienesia latipinna;* species with higher counts were *F. grandis, F. similis* and *F. pulvereus.* The deeper bodied species were *C. variegatus, A. multifasciata* and *M. latipinna;* the slimmer species were *F. jenkinsi, F. similis* and *F. pulvereus.* The fishes with smallest eyes proportionally were *F. grandis* and *F. similis;* the two smallest species, *G. affinis* and *Lucania parva,* had the largest eyes. Detailed color markings were given for all species except for the well known *C. variegatus.* The smallest *Mollienesia* were taken in September and January and a fish with young nearing full term was taken in late September. Female *F. jenkinsi* averaged several mm longer than males. They were found with developing eggs in September and January. The species was taken only at the type locality, Dickinson Bayou. Male and female *F. pulvereus* were found to be about the same size. The smallest fish were taken in early November. Ripe fish were taken in November, but females with developing eggs were also found in January. *F. similis* were observed spawning in minute potholes or depressions on the bay shores in July. The smallest fish taken increased from 20 mm in total length in September to 43 mm in March. Females were slightly larger than males. Ripe female *F. grandis* were taken in October and the smallest fish were taken in November. Ripe *Adinia* were taken in October. The smallest *C. variegatus* were found in September, October and November. The territorial defense of males during the breeding season, as previously described by other workers, was observed. Stomachs of two *Gambusia* contained fish, crustaceans and annelids. Aquatic insects were found in one F. *pulvereus* stomach and two isopods were found in another. Two *F. grandis* contained aquatic insects and vegetable matter, and three had incompletely swallowed small *Mollienesia.* One stomach of *Adinia multifasciata* contained algal detritus and another contained pieces of a dragonfly. The stomachs of five female *C. variegatus* contained vegetable matter.

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DOMINANCE-SUBORDINANCE RELATIONSHIPS IN THE CRAWFISH *CAMBARELLUS SHUFELDTII*

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DOMINANCE-SUBORDINANCE RELATIONSHIPS IN THE CRAWFISH *CAMBARELLUS SHUFELDTII*[1]

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Hierarchies based on dominance and accompanying subordination have been known among vertebrates for a number of years. Modern studies of this subject are generally dated from the 1922 paper by Schjelderup-Ebbe (from Schjelderup-Ebbe 1955). He found that individuals in small flocks of domestic chickens usually were arranged in a definite linear order of dominance based upon pecking. This was termed peck-right. Within a flock, Bird A could peck B, C, D, E; B could peck C, D, E; and so on down to E which lacked a subordinate individual on which to peck. This hierarchy was established during the first few meetings between two individuals and remained constant until a subordinate bird pecked back. If the resisting bird was successful, a new dominance order was established. Masure and Allee (1934) found a less strict type of dominance order among pigeons. In this order the dominant animal may receive some pecks from subordinates and still remain dominant. This was called peck-dominance.

Further advances have been summarized by Allee (1942, 1945, 1952), Allee et al. (1950) and Collias (1944). Hierarchies based on dominance have been reported for all vertebrate classes except Agnatha and Amphibia.

Recently Allee and Dickinson (1954) reported a dominance order based on size in the smooth dogfish, *Mustelus canis.* When two animals were swimming along paths that would meet, the smaller swerved enough to avoid contact with the larger. Only two instances were recorded in which one individual either chased or "pecked" another.

Dominance hierarchies have been found in fish; the subject has been summarized by Noble (1939). Both the peck-right and the peck-dominance types of hierarchy have been found. In some species, as in the green sunfish (Greenberg, 1947), dominance relationships were complicated further by the defending of territory by the males during breeding season. Tinbergen (1953) has published on territoriality of the three-spined stickleback in great detail. Newman (1956) found that two species of trout set up interspecific dominance orders under natural and artificial conditions.

While no hierarchies of dominance have been reported for amphibians, aggressive behavior has been shown. If two or more male wood frogs, *Rana sylvatica,* held the same female, they tried to dislodge each other by kicking with the hind legs (Banta 1914 from

[1] This work was done in partial fulfilment of the requirements for the Master of Science degree at Tulane University.

Collias 1944). Martof (1953) has recently shown territoriality in the green frog, *Rana clamitans* . Small groups of frogs tended to maintain the same spatial relation to each other for several nights even while moving from one pond to another.

The social behavior of the American chameleon, *Anolis carolinensis,* has been studied more than any other reptile (Greenberg and Noble, 1944). Usually one male dominated the individuals in a large cage with the other males equally subordinate to him. Females formed their own dominance order within the territory held by the dominant male.

More is known about social organization in domestic fowl than in any other group of vertebrates. Studies are being continued on chickens and other birds and the concept of dominance hierarchies has been extended to birds in semiferal and feral conditions (Odum, 1942; Sabine, 1949).

Uhrich (1938) was the first to study dominance relations in mice. He found one animal dominant and the others equally subordinate; in effect, a two-ranked dominance order. Carpenter (1952) reviewed the behavior of infra-human primates in natural conditions. Here dominance implied leadership and also several animals as a group might be dominant over another group. Hierarchies based on dominance have been reported for mice, rats, squirrels, cats, lions, dogs, horses, cows, monkeys, apes and men (Allee, 1945).

Pardi (1948, summarizing Italian articles of 1942 and 1946) demonstrated the existence of a dominance order among the females of the wasp *Polistes gallicus.* When two individuals met in the nest, one behaved as dominant, the other as dominated. Typically the dominant struck the head of the dominated quickly and repeatedly while the latter remained motionless. In a series of contacts between two individuals, the same individual always dominated. Occasionally two individuals appeared equivalent. They fought violently and struck one another with the prothoracic legs, the antennae and the stings.

A rigorous linear hierarchy resulted from contacts between inhabitants of the same nest, with only the reproductive females and the workers participating in the organization. All males behaved as dominated and did not establish hierarchies among themselves. The hierarchy was established initially in accordance with small ovarian differences, the female having the largest ovaries taking the dominant position. The ovaries of the other reproductives began to atrophy. Older workers dominated younger. If the queen died or was removed the oldest worker (in subdominant position) took her place and soon was able to lay fertile eggs. Deleurance (1952) confirmed Pardi's findings.

Jacobs (1955) reported the occurrence of aggressive behavior in the dragonflies *Perithemis tenera* and *Plathemis lydia.* He found that

during the mating season males defended an area around oviposition sites and drove other males from this territory.

The beginning of a hierarchy based on size and strength was found in the hermit crab *Pagurus longicarpus* (Allee and Douglis, 1945). The crab lived with its soft abdomen tucked into an otherwise empty snail shell. If the shell was taken away and no vacant shell was available, the crab forcibly removed a smaller animal from its shell and immediately occupied the shell. An animal with an imperfect shell might take over a more perfect shell from its smaller companion. Hermit crabs without shells attacked others that were housed regardless of size differences. The attacker was never successful when the two were of equal size or when the housed individual was the larger.

Two-, three-, and four-ranked hierarchies have been reported by Douglis (1946a) in the lobster *Homarus americanus.* When two animals were placed together, the subordinate was kept at one end of an aquarium and attacked whenever it attempted to leave the area. In groups of three and four lobsters, signs of dominance were seldom seen when the dominant was present. The lower ranking animals became more aggressive when the animals dominating them were removed. Larger animals were dominant over smaller and males generally were dominant over females.

In another experiment Douglis (1946b) found lobsters dominant over the blue crab, *Callinectes sapidus,* the spider crab, *Libinia emarginata,* and the large hermit crab, *Pagurus polycarus.* Blue crabs dominated the spider and hermit crabs.

Bovbjerg (1953) studied dominance relations in the crawfish *Orconectes virilis.* Experimenting with groups of four equal-sized animals of the same sex, he found they established four-ranked dominance orders. An animal did not necessarily win every encounter with a subordinate crawfish. Even the lowest ranking animal won a few fights, but a definite dominance pattern could be distinguished readily by comparing the total number of encounters between individuals. Within five days a dominance order was established in each of the ten groups that Bovbjerg studied. This order remained stable for the duration of his experiment, for fifteen more days. Later Bovbjerg (1956) extended his studies to include the crawfish *Procambarus alleni* and found essentially the same relationships as in *Orconectes.* This indicated that a dominance order based upon learned recognition of individuals may occur in an invertebrate group.

Aggressive behavior has been noted in cuttlefish *Sepia officinalis* by Tinbergen (1939). While studying chromatophore changes he found that one male would fight another when certain color patterns were displayed during the mating season. Aggressive actions have been reported in common squids, *Loligo* spp. by Bovbjerg (1953) and Allee and Dickinson (1954). Allee and Dickinson (1954) stated that many invertebrates have been observed without detecting

any sign of dominance behavior; fiddler crabs, termites, and ants serving as examples.

The present paper extends observations of dominance-subordinance relationships to another invertebrate species, *Cambarellus shufeldtii,* a small crawfish seldom larger than 25 mm in total length. This study again verifies the occurrence of a dominance order in invertebrate animals and, in particular, confirms Bovbjerg's finding that crawfish establish dominance hierarchies.

Materials and Methods

The experimental animals were obtained by dip-netting from a lowland pond at Crown Point, Louisiana. The pond was mud-bottomed and the water clear and exposed to direct sunlight a large part of each day. The crawfish were collected in the shallow water around the edge of the pond where the principal aquatic plant was alligator weed, *Alternanthera philoxeroides.* This habitat is typical for the species (Penn, 1950). Four collections were made.

Stock animals, maintained in two and one-half gallon aquaria, were fed on lettuce every evening and on dog food every third day. Water was changed after each meat meal. Seventy-five to 100 animals were placed in each aquarium. Except for initial mortality, probably due to injury during collection, the crawfish were maintained with very low mortality for a three-month period.

Experimental animals were maintained in shallow round plastic dishes nine centimeters in diameter. No attempt was made to simulate natural conditions but only to confine the crawfish in an environment that would induce the greatest number of encounters between individuals.

Only adult animals, 17 to 22 mm total length, were used unless otherwise indicated. Individual animals were identified by marking the carapace with various colors of fingernail polish. The four colors used were purple (P), green (G), yellow (Y), and red (R). When more than four experimental animals were placed together, a combination of colors was used to identify the additional individuals; yellow and purple (YP), yellow and green (YG), etc.

Dominance relations were manifested through tension contacts; *i.e.,* any encounter between two crawfish in which one clearly retreated following a head-on meeting. As adopted from Bovbjerg (1953) four types of tension contacts were observed; fight (F), strike (S), threat (T), avoidance (A).

The *fight* is bilateral: two crawfish meet, each striking out at the other, often locking chelae, occasionally catching the other's rostrum or a walking leg. Infrequently one animal attempts to jerk away while being held by the other, thereby losing a part of its body. The fight generally lasts less than a minute but the longest observed was eight minutes. It is terminated by the quick backward retreat of one of the animals. After this backward movement the two crawfish are

no longer in contact, and the animal which retreated turns and moves to another part of the dish. The victor frequently follows the loser and hits at its tail as it departs.

The *strike* is a unilateral aggression in which one animal approaches with spread chelae which are suddenly thrust out to hit the other crawfish. The second animal retreats without defending itself.

The *threat* is merely an approach with chelae held in strike position. This is sometimes sufficient to cause retreat of the other animal before the aggressor actually strikes the other.

In *avoidance* no sign of threatening behavior is discernible yet the subservient crawfish retreats from a moving animal or gives another a wide berth in its own movements.

Only head-on encounters between individuals were included. Random crawling over one another, retreat from a rear contact, or a general movement of the whole group were not considered tension contacts.

Each group was observed for fifteen minutes every day for the duration of each experiment, five to 20 days. Observations were made between six and eight o'clock in the morning because the crawfish were most active during this period. The animals were active also in the evening. This daily rhythm of activity reflects metabolic activity as shown by Fingerman (1955). He found that respiratory rate was maximal about 6 a.m. with a secondary peak at 3-6 p.m.

A Dominance Order

A preliminary investigation was carried out to determine whether *Cambarellus shufeldtii* would establish four-ranked dominance orders. Six groups of four animals were used. Later ten additional groups were set up. Each dish contained animals of similar size ($\pm$ 0.5 mm) and sex. Only form I males and adult females were used.

The data recorded from daily observation periods were compiled into a table as adapted from Bovbjerg (1953). The data on one group are shown in Table 1. The letters heading the vertical and horizontal columns designate individuals by the first letter of the identifying color to enable comparison between any two individuals in the group. Dominance is read horizontally and subordinance vertically. In recording avoidance a dominant contact was credited to the animal avoided. This shows as subordinance for the animal doing the avoiding. Each group was observed for twenty days.

Data from 16 groups of four animals are summarized in Table 2. Each animal is listed by rank. Also given for each animal are the total "dominance contacts" indicating the number of contacts in which it was dominant. The percentage of contacts in which each was dominant, listed as "percent dominant", was obtained from the original tabulations of data (as in Table 1) by dividing the "total dominance contacts" of a particular crawfish by its total number of contacts (*i.e.*,

TABLE 1.
DOMINANCE-SUBORDINANCE RELATIONSHIPS AMONG FOUR INDIVIDUALS (GROUP A-1)

Code Letter	Type of Tension Contact	Code Letter of Individuals P	G	Y	R	Total Dominance Contacts	Rank
P	Fight		2	1		3	4
	Strike		1			1	
	Threat						
	Avoidance					4	
G	Fight	8		2	1	11	3
	Strike	1		1		2	
	Threat						
	Avoidance					13	
Y	Fight	12	18		9	39	2
	Strike	14	6		1	21	
	Threat	3	5			8	
	Avoidance		1			1	
						69	
R	Fight	10	30	21		61	1
	Strike	16	8	15		39	
	Threat	13	3	5		21	
	Avoidance	4		2		6	
						127	
Total Subordinance Contacts		81	74	47	11	213	

"total dominance contacts" plus "total subordinance contacts"). For example, the "percent dominance" of crawfish R (Table 1) would be calculated:

$$\frac{127}{127 + 11} = \frac{127}{138} = 0.92 = 92\%$$

Groups C-9 and C-10 are not included in analyzing Table 2 as the dominant animal in each of these two groups was carrying eggs. These results are thus not comparable with the other fourteen groups as an ovigerous female reacts differently than other females in its group.

The tabulated data for the remaining fourteen groups included a total of 3326 observed tension contacts, varying from 192 to 297 contacts per group, with a mean of 237. Females were slightly more active than males with a mean of 245 and extremes of 207 and 297. The number of tension contacts among males ranged from 192 to 279 with a mean of 231.

TABLE 2.

DOMINANCE ORDER OF SIXTEEN GROUPS OF FOUR CRAWFISH ESTABLISHED OVER A PERIOD OF 20 DAYS

Social Group	Dominance Order	Dominance Contacts	Group Total	Percent Dominant	Social Group	Dominance Order	Dominance Contacts	Group Total	Percent Dominant
A-1 male	R	127		92	C-3 male	G	123		95
	Y	69		59		Y	60		57
	G	13		15		P	37		31
	P	4		5		R	4		4
			213					224	
A-2 male	R	151		94	C-4 male	P	121		79
	Y	72		55		G	66		55
	G	31		27		R	14		19
	P	7		6		Y	15		18
			261					216	
A-3 male	G	150		93	C-5 female	P	122		92
	P	45		48		R	64		58
	R	17		18		Y	15		15
	Y	4		5		G	6		6
			216					207	
A-4 male	G	119		90	C-6 female	Y	152		96
	P	41		55		R	73		57
	Y	26		27		P	48		36
	R	6		7		G	5		4
			192					278	
A-5 female	R	163		94	C-7 female	P	143		88
	Y	63		57		G	71		50
	P	22		20		Y	55		39
	G	5		4		R	28		19
			253					297	
A-6 female	G	162		82	C-8 female	P	130		95
	P	113		63		Y	73		57
	R	37		27		R	20		23
	Y	5		4		G	3		3
			217					226	
C-1 male	Y	144		87	C-9 female	R	167		77
	R	76		59		G	92		60
	G	39		32		Y	48		36
	P	20		15		P	13		10
			279					320	
C-2 male	G	140		90	C-10 female	G	151		79
	R	67		54		Y	108		48
	P	31		26		P	76		52
	Y	9		10		R	11		9
			247					346	

Forty-six percent of the tension contacts were fights (Table 3). The strike accounted for 31% of the total contacts; the threat, 15%; and avoidance, 8%. The percentages were not appreciably different for male and female groups. Totals for groups C-9 and C-10 were not included.

Comparison of tension contacts of any two crawfish furnished the criterion for ranking the individuals of a group. This was less reliable in determining the third- and fourth-ranking individuals where contacts between these low-ranking animals were few. Ranking by total number of dominant contacts corroborated pair-contact data with one exception (C-4). Percent dominance calculations also agreed. Rank-

TABLE 3.
TYPES OF TENSION CONTACTS TOTALS FOR TABLE 2

Type Contact	Number of Contacts	Percent of Total
F	1530	46
S	1031	31
T	499	15
A	266	8
Total	3326	

ing by total subordinate contacts always pointed out the dominant and often revealed the other three ranks, but occasionally was unreliable for the lower ranks.

Pair-contact data refers to the comparison between two animals of the same group; *i.e.,* Table 1, "G" had nine positive tension contacts over "P" (eight fights, one strike) while "P" had only three positive contacts over "G". The term positive tension contacts refers to the contacts in which an animal was dominant over another animal in the same dish.

No pattern of selective behavior toward lower-ranking animals was noted. The dominant animals had positive contacts with the second-ranking animals 621 times, with the third-ranking 640 times, and with the fourth-ranking 667. The subdominant crawfish had 156 positive contacts with the dominants and 377 and 359 positive contacts with the third- and fourth-ranking animals, respectively. The third-ranking individual had 363 contacts over the fourth, but only 42 and 87 such contacts with the dominant and subdominant. The fourth-ranking animal had 12, 36, and 73 positive contacts respectively with the three individuals above it in dominance. Higher ranking individuals often fought when attacked while lower ranking crawfish retreated at the strike or threat of a more dominant animal.

Table 4 shows the results of experiment C-1 tabulated by five-day periods. At first there were many fights in the group but as dominance patterns became established fighting gave way to strike, threat and avoidance. During the first few days an animal seldom completely avoided another or responded to a threat. The lower ranking animals were the first to retreat at signs of milder forms of aggression and then the subdominant reacted. Aggressive behavior and thus the number of tension contacts between individuals became less the longer the animals remained together.

Within the first five days a dominance order, which remained constant throughout the period of observation, was usually established. The dominant individual generally asserted its dominance during the initial period of observation; the subdominant became apparent soon afterward. The third- and fourth-ranking animals often took a little longer to establish their final positions.

This formation of dominance order corroborates the results obtained

TABLE 4.
DOMINANCE RELATIONSHIPS OF GROUP C-1 BY FIVE-DAY PERIODS

Code Letter	Type of Tension Contact	June 18-22				June 23-27				July 28-July 2				July 3-7				Total				Total	Rank
		P	G	R	Y	P	G	R	Y	P	G	R	Y	P	G	R	Y	P	G	R	Y		
P	F		4	2	1		3	1	1		2	1							9	4	2	15	4
	S		1				1	1			2								4	1		5	
	T																						
	A																						
	Total		5	2	1		4	2	1		4	1							13	5	2	20	
G	F	4		2	4	4		1	1	4		1		1				13		4	5	22	3
	S	1			2	1		1	1	2		1		4				8		2	3	13	
	T									2				1				3				3	
	A									1								1				1	
	Total	5		2	6	5		2	2	9		2		6				25		6	8	39	
R	F	5	8		6	4	4		1	8	4			2	2		1	21	18		8	47	2
	S		1			3	3		2	2	2		1	5				10	6		3	19	
	T									3				3	1			6	1			7	
	A									1				2				3				3	
	Total	5	9		6	7	7		3	14	6		1	12	3		1	40	25		11	76	
Y	F	6	5	9		4	10	6		4	3	4		1	2	2		15	20	21		56	1
	S	3	4	2		6	6	8		1	3	5		2	1	2		12	14	17		43	
	T	2	2	1		5	3	4		4	1			5	3	3		16	9	8		33	
	A					2				2				4	3	1		8	3	1		12	
	Total	11	11	12		17	19	18		11	7	9		12	7	8		51	46	47		144	

by Bovbjerg (1953) with *Orconectes virilis*. In Bovbjerg's experiment, however, the subordinate animals were less aggressive, especially the subdominant. As a consequence there was less fighting and a corresponding increase in the response to strike and threat.

As a check on the interpretation of these observations the crawfish were shifted to new dishes in a manner which Bovbjerg termed social inversion. From each of the above groups, the dominant individual was removed and isolated. Observations were continued on the behavior of the three remaining in the original dish. After a five-day period the emergent dominant was removed and placed with the isolated dominant animal. Observations were then made on the behavior of this inverted group as well as on the remaining two in the original grouping. The next emergent dominant from the original group was placed with the inverted group after five days. Finally, after another five-day period, the remaining fourth-ranking crawfish was transferred, completing the inversion.

Table 5 illustrates this procedure. These are the same animals used in group C-4, Table 2. The figures above the double lines show tension contacts before inversion. Contacts after inversion are shown below the lines. Dominance and subordinance are read in the same manner as in Table 1.

Fourteen of the 16 groups (Table 2) were inverted as described above. With one exception all of the individuals were re-established in their original positions. In two dishes the third and fourth ranks

TABLE 5.
SOCIAL INVERSION
(GROUP D-4)

Individual's Code Letter	Type of Tension Contact	1-5 days Y R G P	6-10 days Y R G P	11-15 days Y R G P	16-20 days Y R G P	Rank
Y	F	2 1	4		1	4
	S					
	T					
	A					
R	F	2	3	1 1	6 1	3
	S	3	6		3	
	T					
	A					
G	F	1 5	5	5 1	1 2 1	2
	S	6 4		3 2	6 3	
	T	3 1		3 1	4 2	
	A	1				
P	F		7	2 4	4 1 1	1
	S		5	4 7	2 7 6	
	T		1	1 6	1 6 3	
	A			1	3 2	

were not confirmed due to the death of these animals. In one group the top-ranking animal dropped to second place after loss of a claw. This animal lost its claw five days before conclusion of experiment A-2 but retained its rank until inversion.

In each case, after the top-ranking crawfish was removed, the next ranking individual became more active and asserted its dominance over its remaining companions.

When the subdominant, with its five-day period of dominance, was reintroduced to the original dominant a series of fights soon established the old relationship. Frequently the subdominant repeatedly attacked the dominant, although the dominant won the fights. This behavior gradually ceased and strike and threat by the dominant often were enough to intimidate the subservient animal. To a lesser extent the same behavior was observed when the third-ranking individual was placed with the inverted group.

On the last day of this experiment a few of the animals molted. Within the next two days all except one of the animals under observation had molted and this one molted the following day. This occurred from July 27-29. Only one animal did not complete the molt successfully and none was victimized by its companions. These same animals had molted also between June 12-15. Thus in this experiment molting had little influence on the dominance order.

Four Ranked Dominance Order Among Unlike Individuals

In the previous experiments only animals of similar size and sex were used. To study the effect of size and sex on the dominance order unlike individuals were brought together. Three experiments were performed.

Two Males and Two Females of Similar Size

From eight groups of previously established dominance hierarchies the dominant individuals were removed to create two new groups of four animals, all of the same rank. Two females and two males were placed in each dish. The same procedure was followed for ranks two, three and four. Eight new groups were thus set up, each group containing two males and two females which previously held the same rank. These animals were observed for nineteen days. The results are summarized in Table 6.

In five of the eight groups a female was the dominant animal, while a male was subdominant in a majority of the groups (6 out of 8). Male and female appeared with equal frequency for the third rank, while five females and three males held lowest rank.

Additional data from five similar groups of two males, two females were included with the above in compiling Table 7. These animals were not previously ranked but animals of similar size were placed together. Table 7 shows how the sexes were distributed in each

group of four as well as the total number of males and females holding each rank.

In the 13 groups, eight (61.5%) of the dominant animals were female, and five (38.5%) were male. Second-ranking position was the reverse of this; eight males to five females, as was the third rank. The lowest rank was again eight females to five males. This shows that neither sex is greatly dominant over the other. As these groups consisted of similar sized individuals, either male or female may dominate a group depending upon inherent aggressiveness.

TABLE 6.

DOMINANCE ORDER OF EIGHT GROUPS OF FOUR CRAWFISH ESTABLISHED OVER A PERIOD OF 20 DAYS. EACH GROUP CONSISTED OF TWO MALES AND TWO FEMALES OF PREVIOUSLY EQUAL RANK

Group Number	Rank	Dominance Contacts	Percent Dominant	Sex
E-1	R	99	77	♀
	G	86	53	♂
	Y	51	52	♂
	P	9	9	♀
E-2	Y	98	85	♀
	R	60	66	♂
	P	16	22	♂
	G	4	5	♀
E-3	G	93	100	♀
	P	34	44	♂
	Y	18	33	♀
	R	1	2	♂
E-4	R	121	82	♂
	P	77	56	♀
	G	35	28	♀
	Y	3	6	♂
E-5	P	105	77	♀
	R	67	56	♂
	G	52	43	♂
	Y	21	19	♀
E-6	Y	126	91	♂
	P	69	52	♂
	G	22	24	♀
	R	10	11	♀
E-7	P	83	90	♂
	G	64	71	♀
	Y	14	16	♀
	R	4	7	♂
E-8	G	72	82	♀
	P	61	71	♂
	R	30	42	♂
	Y	6	7	♀

TABLE 7.
SEX DISTRIBUTION BY RANK IN GROUPS OF FOUR INDIVIDUALS

Group Number	1	2	3	4
E-1	♀	♂	♂	♀
E-2	♀	♂	♂	♀
E-3	♀	♂	♀	♂
E-4	♂	♀	♀	♂
E-5	♀	♂	♂	♀
E-6	♂	♂	♀	♀
E-7	♂	♀	♀	♂
E-8	♀	♂	♂	♀
E-9	♀	♂	♂	♀
E-10	♂	♀	♂	♀
E-11	♀	♀	♂	♂
E-12	♀	♂	♂	♀
E-13	♂	♀	♀	♂
Totals	5♂ 8♀	8♂ 5♀	8♂ 5♀	5♂ 8♀

A curious fact is brought out by further analysis of the data in Table 7. When a female dominated the group, the other female most often was ranked last with the two males holding ranks two and three. This same phenomenon occurred under male domination. As this appeared in nine of 13 groups, the occurrence seemed rather high to be by chance alone. Only twice were first- and second-ranking animals of the same sex; once two females held these positions and once two males. Why the dominance order should be arranged in this fashion is a question that deserves further study.

Four Animals of Random Size and Sex

Animals were taken at random from the stock aquaria and placed four to a dish. No notes were taken on size or sex until the experiment was concluded. These groups were perhaps slightly closer to natural conditions in including different-sized animals of both sexes, although the groups were still abnormally small and confined to small dishes with no hiding places.

The animals were measured under a binocular microscope with dividers and a millimeter rule. The cephalothorax length was taken to the nearest 0.5 mm. In taking measurements, length of cephalothorax was more convenient to determine than total body length. Total length was twice that of the cephalothorax.

Each group was observed for twenty days except group F-8 (Table 8). As two animals died in this group, it was observed for only eleven days. The data from this group were included in the table as the dominance order had remained constant for seven days before the deaths. In general, larger animals were dominant over smaller regardless of sex (Table 8).

Table 9 shows the size difference between an animal and its next

TABLE 8.
DOMINANCE RELATIONSHIPS AMONG GROUPS OF FOUR CRAWFISH INCLUDING DIFFERENT SIZED INDIVIDUALS OF BOTH SEXES

Group Number	Rank	Dominance Contacts	Percent Dominant	Size (mm) [c] & Sex
F-1	P	150	95	10.5 ♀ [a]
	G	55	51	9.0 ♂
	Y	27	26	8.0 ♂
	R	9	8	9.0 ♂
F-2	R	125	92	10.0 ♂
	Y	50	55	7.5 ♀
	P	31	28	8.5 ♂
	G	17	16	8.5 ♂
F-3	Y	120	84	9.5 ♀
	G	100	68	10.0 ♀
	R	14	15	8.5 ♂
	P	3	3	7.0 ♀
F-4	Y	122	94	9.5 ♀
	G	58	54	6.5 ♀
	P	26	25	7.5 ♂
	R	2	5	5.5 ♂
F-5	G	154	97	10.5 ♀ [a]
	R	32	39	7.0 ♀
	Y	27	24	7.5 ♂
	P	17	16	7.5 ♂
F-6	R	177	95	9.5 ♀ [a]
	Y	42	41	9.0 ♂
	G	26	30	8.0 ♂
	P	7	5	6.5 ♀
F-7	Y	128	86	9.0 ♂
	G	52	47	9.0 ♂
	R	34	30	6.5 ♀
	P	15	17	7.0 ♂
F-8 [b]	G	53	79	9.5 ♀
	Y	33	52	9.5 ♂♀
	P	18	45	7.5 ♀
	R	9	16	7.5 ♀
F-9	G	101	89	10.0 ♂
	R	51	45	7.0 ♂
	Y	47	42	7.5 ♀
	P	2	3	5.0 ♂
F-10	Y	106	93	9.5 ♀
	R	39	44	7.0 ♀
	P	21	24	7.5 ♂
	G	12	18	6.0 ♀
F-11	P	77	90	10.5 ♂
	G	36	63	8.0 ♀
	Y	9	16	6.5 ♀
	R	1	2	5.5 ♀
F-12	P	95	80	9.5 ♀
	G	63	68	10.0 ♂
	R	12	16	7.5 ♀
	Y	4	16	7.0 ♂

[a] Females carrying eggs at beginning of experiment
[b] This group observed for 11 days only due to death of G and R.
[c] Cephalothorax length.

immediate subordinate. An asterisk indicates that the dominant animal was smaller than its immediate subordinate. This table includes all four ranks. 1.5 mm cephalothorax length, the equivalent of 3 mm total length, appeared to be the critical figure. No animal was dominated by another 3 mm smaller than itself. Of the 48 animals 11 were dominated by individuals one to two millimeters (0.5-1.0 mm cephalothorax length) smaller than themselves. In only two cases was the top-ranking animal smaller than its subordinate and then by only 0.5 mm cephalothorax length. There was no difference in size between animals of adjacent rank in five cases. These size relationships held true throughout all of the experiments.

For the June 11, 1955, collection the 50 largest females and the 50 largest males were measured (Table 10). Both sexes included two animals with a cephalothorax length of 11 mm, but the females as a group were considerably larger than the males. Thus females would dominate males in more encounters than the reverse on the basis of size alone. The observation that either male or female may dominate a group of similar sized individuals (Table 7), leads to the conclusion that females of *C. shufeldtii* may be the more dominant sex because of their larger size.

TABLE 9.
DIFFERENCE IN CEPHALOTHORAX LENGTH BETWEEN ANIMALS OF ADJACENT RANK

Cephalothorax Length (mm)	Number Of Individuals
3.5	1
3.0	2
2.5	4
2.0	2
1.5	9
1.0	3
0.5	2
0.0	5
0.5*	7
1.0*	4

From his observations on *Orconectes virilis,* Bovbjerg (1953) reported that the male appeared more dominant and that low-ranking males were seen fighting and then copulating with high-ranking females. In the present experiments only one pair was seen in copulation and these were two top-ranking animals.

Ovigerous Females with Males and Non-ovigerous Females

As noted from Table 2 (C-9 and C-10) and shown again in experiment F, females with eggs appeared more aggressive than those without eggs (note F-1, F-5, F-6, Table 8). Each of these groups included one female with eggs. This animal was dominant and very aggressive. However, these females were also the largest of their

groups. In C-9, C-10, (Table 2) is seen the comparison of crawfish of similar size and sex. In both instances a female carrying eggs was dominant over females without eggs. The average number of tension contacts for the group was 333 as compared to 245 in groups of non-ovigerous females.

TABLE 10.
THE FIFTY LARGEST MALES AND THE FIFTY LARGEST FEMALES OF THE JUNE 11, 1955, COLLECTION

Cephalothorax Length in mm	Number of Males	Number of Females
11.0	2	2
10.5	7	21
10.0	11	17
9.5	15	10
9.0	10	
8.5	5	

In crawfish the eggs are attached to the female's pleopods where they hatch and where the young remain attached through the second instar (Andrews, 1904). In *C. shufeldtii* the time from hatching to the time the young leave the pleopods is about a week to ten days. As no experimental females were seen to lay eggs, the time between egg extrusion and hatching is not known.

Four groups of four animals were established in which every individual carried eggs at the beginning of the experiment. These animals were more active than non-ovigerous females. There was more active fighting among the animals and a stable dominance order was not established as quickly (Table 11). Often the number of positive tension contacts between two individuals was very nearly equal; *e.g.,* in Table 11 (observations from June 18-22) "Y" had 9 victories over "G" to eight defeats; "Y" over "R", 6 to 5; "G" over "R", 15 to 11. As the young were dropped the dominance order changed. In three of the four groups the female whose eggs hatched first was the initial dominant. Very shortly after losing the young she dropped to low rank and another ovigerous female became dominant. When this animal dropped the young it, in turn, was succeeded in the dominant position by an animal which was still carrying young. The experiment was not continued long enough to determine whether the last animal to drop its young remained in the top position or whether one of the other females again gained dominance over the group.

The total number of tension contacts varied from 334 to 417 with an average of 362 (Table 12) as compared with the non-ovigerous females' group average of 245. Fights and strikes accounted for 87% of the total tension contacts as compared to 77% for males and for females not carrying eggs (Table 3). Avoidance was elicited in only 3% of meetings between individuals (compared to 8%).

TABLE 11.
Dominance Relationships Among Group G-1
Four Females Carrying Eggs

Code Letter	Type of Tension Contact	June 18-22 P	Y	G	R	June 23-27 P	Y	G	R	July 28-July 2 P	Y	G	R	July 3-7 P	Y	G	R	Total P	Y	G	R	Total	Rank
P	F		5	3	3		4	2	1		6		2		1	1	3		16	6	9	31	4
	S		3				2				4				2				11			11	Eggs did
	T		1				4								1				6			6	not develop
	A																						
	Total		9	3	3		10	2	1		10		2		4	1	3		33	6	9	48	
Y	F	9		7	5	7		6	2	5		2	1	3				24		15	8	47	3
	S	6		2	1	12		7	7	5		2		2		7		25		18	8	51	Dropped
	T									2				3				5				5	young 6-27
	A									2				4				6					
	Total	15		9	6	19		13	9	14		4	1	12		7		50		33	16	109	
G	F	4	7		11	7	5		9	3	11		2		1			14	24		21	59	2
	S	3	1		4	13	5		3	4	9			9	2			29	17		7	53	Dropped
	T										3				5				8			8	young 6-30
	A																						
	Total	7	8		15	20	10		12	7	23		2	9	8			43	49		28	120	
R	F	7	4	8		5	9	5		1	8	6		3	2	6		16	23	25		64	1
	S	8	1	3		7	3	3		3	2	5		6	1	1		24	7	12		43	Dropped
	T	1					6			4	7			4	3	3		9	16	3		28	young 7-4
	A	1								1				3				5				5	
	Total	17	5	11		12	18	8		9	17	11		16	6	10		54	46	40		140	

Six groups of four similar sized (± 0.5 mm) animals were set up, each group containing one female carrying eggs. C-9 and C-10 (Table 2) were included in the data, making a total of eight groups. Three groups were all female, three consisted of two males, two females, and two groups contained one female and three males.

In all eight groups the ovigerous female asserted its dominance as soon as the groups were formed. Due mainly to this animal's greater activity the average number of tension contacts increased to 307 as compared to 237 in experiment A, C (Table 2). As they dropped the young, these females became less aggressive and soon descended in the dominance order. Three dropped from dominant to third-ranking animal and three dropped to fourth. One became subdominant and only one female retained dominance after the young left the pleopods.

TABLE 12.
TENSION CONTACTS OF OVIGEROUS FEMALES

Group Number	Total Number Number of Tension Contacts
G-1	417
G-2	345
G-3	344
G-4	334
Average	362

Type Contact	Types Number of Contacts	Percent of Total
F	775	53
S	496	34
T	145	10
A	44	3
Total	1460	

When another animal struck at its eggs or abdomen, the ovigerous female turned and fought. Males and non-ovigerous females often did not turn to defend themselves from a rear contact. If an animal turned to meet a rear contact, this was then considered a head-on encounter and credited to the victor. In all eight groups a female with eggs or young was seen to retreat only twice and no instance was recorded in which such a female avoided encounter with another animal.

One female carried eggs that did not develop (Table 11). Therefore she was carrying eggs on her pleopods during the entire time of observation, yet the animal remained in fourth rank. This is the only female observed whose eggs did not develop but this fact may indicate that it is not alone the presence of objects attached to the

pleopods which stimulates aggressiveness but also that some other control mechanism may be present.

A Dominance Order of Eight Ranks

As experiments A, C (Table 2) established that *C. shufeldtii* formed stable four-ranked dominance orders, an experiment was performed to discover if larger groups also assumed a hierarchy pattern. Consequently, six groups of eight animals each were set up. Two of these groups were formed by combining groups of four in which the animals were already ranked in a dominance order (H-1, H-2, Table 13). Other crawfish were grouped from the stock aquaria. These experimental animals were maintained in shallow white enameled pans twelve centimeters in diameter. In groups H-1, H-2, and H-5 there was only 0.5 mm difference in cephalothorax length from largest to smallest animal. In the other three groups the difference was 1.5 mm.

The more dominant animals were active and often, after winning a fight, chased the loser around the dish, striking at its tail. These extra strikes were not considered additional tension contacts but only further manifestation of the original fight. Some of the lower ranking animals hardly moved but remained in the same spot until attacked by a more dominant individual.

The first three ranks were well defined in all six groups. In two hierarchies, however, there was a question as to which animal should be ranked fourth and which fifth. In group H-5 the fourth- and fifth-ranking individuals showed the same number of positive tension contacts and pair contacts but percentage of contacts which were dominant established YG in fourth place. In H-6 YP ranked over YR in pair contacts and in total number of dominance contacts but showed the same percentage dominance. In H-3 this same question arose between fifth- and sixth-ranking animals. In H-6 the sixth- and seventh-ranking crawfish had the same total number of positive tension contacts and the same percentage of dominance, but YY had one more positive pair contact over YG. In each of two groups one animal died. In the remaining four dishes the eighth-ranking individuals were subordinate to the seventh, both in number of positive tension contacts and percent of contacts which were dominant.

The relationships between individuals were not so clearly defined as in the smaller groups of four animals, especially in the lower ranks. How large a group could be assembled and still establish a definite order of dominance is not known. These groups of eight still represented communities much smaller than are found in nature and the animals were confined in a much smaller space than is available in the field. Yet this showed experimentally that *C. shufeldtii* in groups as large as eight individuals established dominance hierarchies based on tension contacts

TABLE 13.

DOMINANCE ORDER OF SIX GROUPS OF EIGHT CRAWFISH ESTABLISHED OVER A PERIOD OF SIXTEEN DAYS

	Rank	Dominance Contacts	Percent Dominant	Social Group
H-1	Y	152	80	♀
	YP	80	60	♀
	YG	69	56	♀
	R	61	50	♀
	P	47	48	♀
	G	36	40	♀
	YY	8	10	♀
	YR	3	4	♀
H-2	P	145	80	♀
	YP	70	68	♀
	YY	40	45	♀
	YR	29	31	♀
	G	11	22	♀
	R	9	18	♀
	Y	4	9	♀
	YG	died 7-8-55[a]		♀
H-3	G	125	98	♀, eggs
	P	68	71	♀
	YP	47	48	♂
	YR	32	37	♂
	YY	12	18	♀
	R	9	18	♂
	YG	7	15	♀
	Y	5	13	♂
H-4	YY	130	88	♀
	P	80	73	♂
	G	58	59	♂
	Y	31	38	♀
	YP	15	22	♂
	R	13	18	♀
	YR	11	20	♀
	YG	1	2	♂
H-5	Y	92	88	♂
	YR	57	66	♀
	R	34	52	♂
	YG	10	26	♀
	YR	10	22	♂
	YY	6	15	♀
	G	3	12	♀
	P	1	4	♂
H-6	P	124	95	♀, eggs
	G	48	72	♂
	Y	24	36	♂
	YP	10	21	♀
	YR	8	21	♂
	YY	4	9	♂
	YG	44	9	♂
	R	died 7-19-55		♂

[a] Experiment was started July 8, 1955, concluded July 23.

Changing the Dominance Order

In a previous experiment (Table 2, A-2) a crawfish which had lost a claw retained its top rank in the dominance order until the group was inverted. To study this further, twelve groups of four animals each were established and tension contacts recorded. After five days one cheliped was removed from the dominant animal in four of the dishes. In a second set of four groups a claw was removed from the dominant individual after ten days. From the remaining four groups one of the dominant's claws was removed at the end of 15 days. Each group was observed for a period of 20 days.

When a claw was removed from the dominant individual after only five days the animal did not retain its dominance but dropped to third or fourth rank. One female carrying young did maintain her position after cheliped removal but fell to fourth rank after the young were dropped.

Among animals in which claw removal took place after ten days' dominance, two retained the top-ranking position while two became subordinate to the original second-ranking animal.

Claw removal after 15 days affected the dominance order in only one group. In this group the subdominant replaced the former dominant, while the one-clawed animal retained its place over the third- and fourth-ranking individuals.

This experiment furthers the idea that crawfish can recognize each other as individuals. In groups which had been together only five days, subordinates immediately usurped the handicapped dominant's position. In groups which had been together ten days, two reversals of dominance occurred, both involving only the dominant and subdominant individuals. After the crawfish had been together 15 days only one reversal occurred and this animal was evidently weakened, for it soon died. In these latter groups very little active fighting occurred during the few days before removal of a dominant's claw. The strike and threat were sufficient to intimidate a low-ranking individual. After the claw was removed this same behavior continued, subordinates reacting to the strike and threat of the one-clawed dominant by retreating without attempting to defend themselves. When the dominant's claw was removed after only the first five days, active fighting still occurred and the handicapped dominant could no longer win over its unhindered subordinates.

From each of the above dishes the one-clawed crawfish were removed and placed with groups of three strange individuals for five days. All of these animals were strangers to each other. In this new setting the handicapped individuals ranked low; four of the twelve ranked third and the remaining eight were fourth-ranked.

After this five-day period the one-clawed individuals were placed back with their original groups. In the groups where claw removal had taken place after ten days, both individuals which had dropped

to second rank before the five-day absence regained their subdominant position. The two individuals which had retained their dominance after claw removal could gain only second and third ranks in their hierarchies. In groups where claw removal had taken place after 15 days one animal died, one regained its former dominance, and the other two attained subdominance in the original groups. To this can be added group A-2 (Table 2) in which the dominant lost its claw after fifteen days and retained its dominance but dropped to second rank after inversion (after five days' isolation).

While these experiments are preliminary they indicate that crawfish may retain some recognition of individuals after a five-day absence. That these particular animals were not just superior fighters and more aggressive by nature is shown by their more subordinate position with a strange group and by the animals whose claws were removed after only five-days' dominance. These animals dropped immediately to low rank.

Dominance and Hiding Places

As there would be many hiding places available to subordinate crawfish in a natural setting, there was the question of how hiding places would modify behavior of subordinate versus dominant.

Groups of four crawfish with an already established dominance order were used and three hiding places were provided in a dish with four animals. There was some difficulty in obtaining acceptable hiding places. U-shaped pieces of thin opaque plastic were cemented to the bottom of several dishes. The crawfish ignored them. Next, the plastic was painted brown. The animals stopped momentarily under these and moved on. The plastic was then cemented tent-like to the dishes. The animals occasionally frequented the hiding places but often two crawfish were found under the same tent. Finally shells of the clam *Rangia cuneata,* 20 to 25 mm long with ventral border broken at one point, solved the problem. The crawfish readily frequented these shells and although the area under them was greater than under the tents, two animals never were observed to occupy a particular shell at the same time.

The animals faced out of the shells, body diagonally across the opening with abdomen and part of the thorax hidden. As the identifying markings on the animals were placed well forward, individuals could be distinguished without disturbing the shells or animals. Three shells were placed in a triangular pattern away from the sides of the dish. Each dish contained four animals.

Eight dishes containing shells were observed for five days. Every half hour from 7:00 A.M. to 7:00 P.M. the crawfish under shells were noted by recording which shell each was under. Also, each group was observed for 15 minutes every day during the five-day period and their behavior recorded in narrative style. Four groups were observed in the morning, two at midday, and two in the early evening. These

times were for convenience only, but, as previously mentioned, the crawfish were more active in early morning and early evening. There was less movement during the midday observation period.

A five-day placement record of one group and the number of times each individual was found under each shell is shown in Table 14. Table 15 is the account of the movements of this group during the daily 15-minute observation periods.

The total amount of movement in the groups was considerably less than in dishes without hiding places. Often only two crawfish were found under shells although three shells were available (Table 14). The dominant animal often remained outside the shells. The fourth-

TABLE 14.
ANIMALS OCCUPYING HIDING PLACES
RECORDED AT HALF-HOUR INTERVALS

Time	1st Day			2nd Day			3rd Day			4th Day			5th Day		
	Shell No.			Shell No			Shell No.			Shell No.			Shell No.		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
7:00		Y		R	Y		G		R					Y	
7:30	Y													Y	
8:00	G	Y			G					Y					
8:30				Y	G					Y	R		G	Y	
9:00	Y						Y	R							P
9:30							Y		G	G					P
10:00	R			G						G			Y		R
10:30	Y		R	G			G			R				Y	
11:00	R			G			G							R	
11:30						G	G			R	G	Y	G	R	Y
12:00				P	R	G	G	Y			G		Y		G
12:30		Y		G	Y		G		P				G	Y	P
1:00	R	Y			R	Y	G			G	Y		G	Y	P
1:30		G		Y			G			G	P		Y		R
2:00					R	P	G				G	P			
2:30	R			G	R		G				G	P	G	Y	
3:00	R	G			G			R	G			R	Y	R	
3:30	G	R	Y	G	R	P	R			G	R	Y	G		
4:00				G		P	R		Y	G					
4:30	Y			G		R		Y	G	Y				Y	
5:00	Y	R		G	R			G	Y	Y					P
5:30	Y			G			R	G	Y				G		
6:00	Y			G					Y				G		
6:30	Y			G					G	Y					
7:00	Y		G	G			G	R	Y						

TOTALS

Dominance Order	Shell No. 1	2	3
R	11	16	6
Y	22	17	10
G	40	11	8
P	1	1	11

ranking animal also remained in the open much of the time. Its actions, however, were quite different from those of the dominant. The low-ranking animal remained in one place and moved only when another animal approached. It remained much more stationary than the fourth-ranking animals in groups not provided with hiding places, probably because some of the animals with which it would have come in contact were under shells, and it did not have to react to their movements. The dominant animal moved around quite freely. Animals occasionally entered or left different shells without apparent reason.

TABLE 15.

RECORD OF BEHAVIOR OF ONE GROUP OF FOUR CRAWFISH PROVIDED WITH THREE HIDING PLACES FIVE DAYS' OBSERVATION

August 10. 7:00 A.M. Y under shell #2, P stationary. R wins fight over G. G enters shell #1. R strikes out at Y in #2, Y retreats further into shell, R goes into shell #3 and out again. R wins fight over Y, R enters #2 shell. P enters #3. R comes out of #2. Y approaches #1, G comes out and fights, Y enters #1. R fights P, P defends weakly and leaves shell #3. 7:15—Y #1, R #3.
August 11. 7:00 A.M. R under #1 shell, Y under #2. R comes out, strikes P. G enters #1. R threatens P. R fights G in #1, G comes out, R does not enter. G threatens Y in #2, Y retreats into shell, G moves on. 7:15—Y #2, G #1.
August 12. 7:00 A.M. G under #1, R #3. P moves into #2. Y fights G, Y gains #1 shell. R comes out, R fights Y in #1, Y comes out, R does not enter. G enters #2. Y returns to #1. 7:15—Y #1, G #2.
August 13. 7:00 A.M. None under shells. Y under #3. R enters #1 and out again. G fights Y, G gains shell #3. Y strikes at P. R strikes Y. 7:15—G #3.
August 14. 7:00 A.M. Y under shell #2. R strikes Y, Y retreats into shell, R goes to #3. P not moving. 7:15—Y #2, G #1.

Crawfish under shells seldom gave up the hiding place to another animal without a fight. They sometimes retreated completely into the shell without fighting when another appeared and the challenger would not pursue. If a crawfish attempted to enter a shell occupied by another, the defender immediately reappeared at the entrance and engaged in the fight it had previously backed away from. As the fight continued the defender frequently was drawn completely out of the shell. As soon as the telson was no longer in contact with the shell, this animal terminated the fight by retreating; sometimes into the shell again and sometimes away from it. When this animal remained outside the shell, the challenger generally took possession, at least for a short time. If the defender retreated into the shell after a fight, sometimes another fight took place immediately, and sometimes the attacker turned away. Occasionally encounters terminated when

the attacker retreated without drawing the other completely out of the shell.

Each crawfish established possession of a shell only temporarily. For nine consecutive half-hour intervals, or four hours, one crawfish was under the same shell (Table 14, third day, G). Several others were recorded under a particular shell for three and one-half hours. Whether the animals remained under these shells for the total time or whether they were out and under several times is not known.

The second- and third-ranking crawfish found shells and often remained under them until forced out by another animal. The dominant moved around freely, sometimes entered a vacant shell or evicted the occupant of another shell, but seldom remained long under any shell. Only very seldom was the dominant animal unsuccessful in obtaining a shell occupied by another animal. Movement of the fourth-ranking animal was greatly inhibited and it often remained in the open and moved only when a higher-ranking individual approached. When it had possession of a shell it remained until another crawfish attacked and then left with only feeble resistance. Except for the fourth-ranking individuals, an animal in possession of a shell never gave up the hiding place without a fight. Second- and third-ranking individuals could obtain a shell possessed by the other about as often as the defender retained possession. Occasionally a subordinate could defend its hiding place from animals higher in the dominance order. If, however, the higher-ranking animal repeatedly attacked one of these crawfish, the subordinate eventually relinquished its shell.

There appeared a tendency by all of the animals to occupy the same shell (Table 14, shell #1). This occurred in five of the eight groups and was especially evident in the second- and third-ranking individuals. This apparent choice by all the crawfish for the same shell may be explained by Bell's experiments (1906). While investigating vision of crawfish, he found that there was no response to stationary objects but there was an immediate response to moving objects. Thus the crawfish may not have been reacting to any greater advantages offered by the shell but directly to the animal occupying the shell.

When food was placed in the water the animals in hiding places often did not leave the shells. The dominant immediately came to the food. The dominant animals seemed to have no great need for places of concealment while lower ranking individuals sought them out and often remained hidden until driven out by another animal.

Discussion

Cambarellus shufeldtii established four-ranked dominance orders that remained stable for more than forty days. Usually the dominant individuals were apparent during the first observation period. After the first five days 13 of 14 groups maintained the rankings at all four levels for the entire initial series of observations.

As the crawfish remained together over a period of days the fighting diminished and the less violent forms of tension contacts became relatively more numerous. The total number of contacts also decreased with time. Lower ranking animals responded to strike and threat of the dominant and practically ceased to attack animals higher in the dominance scale.

Conditioning may occur in the relationships of *C. shufeldtii.* Dominant animals with one claw removed after active fighting had diminished generally retained their high position. Upon removal of these top-ranking animals, the second-ranking crawfish became dominant and somewhat more aggressive. Ranks three and four became further conditioned to subordinance, while the former subdominant became conditioned to dominance. When the one-clawed individuals were returned, the second-ranking crawfish fought and became dominant while the third- and fourth-ranking crawfish were bluffed by one-clawed strike and threat.

The findings in the foregoing experiments indicate the recognition of individuals by crawfish and the occurrence of true learning. Yerkes and Huggins (1903) demonstrated the ability of crawfish to learn a simple maze and to retain this learning from day to day. How long crawfish will retain a learned response is not known. They apparently continue to show some recognition of individuals over a five-day period of absence. This retention may depend on the amount of time given to learn the response before retention is tested. The upper limit of items that may be retained is still to be determined.

The problem of specific cues involved in the recognition of individuals remains to be investigated. The color markings used to identify animals were placed in the mid-dorsal line directly over the heart. While these markings may have facilitated learning, it is doubtful that one crawfish could see the marking of another in a head-on encounter.

An animal will attack another or will retreat from a threat before antennae touch. Eyestalkless animals, as observed in a different study, often blundered into each other before raising chelae to strike position. There was little fighting among these animals. When they met, chelae often were interlocked and held so without fighting. These crawfish were not seen to threaten or to avoid another individual before antennae touched.

Bovbjerg (1956) found that *P. alleni* which had had the eyes painted over with nail lacquer but with intact antennae still established dominance orders. Contact with any part of another individual or with a pencil elicited avoidance in the most subservient ranks while the dominant animals responded to any contact with immediate orientated aggressive posture and strike. Dominance order was also established in groups of four from which antennae were clipped but vision was unimpaired. The animals were able to orient, strike and fight in quite normal fashion without antennae. In absence of both

vision and antennae the behavior pattern tended to disintegrate. Often no order was formed but when a dominant did emerge, this animal frequently charged around the bowl, striking indiscriminately at the others in the group and striking at the sides of the bowl.

Pearse (1909) found no evidence that crawfish possessed any power of sex discrimination. Copulation appeared to be only a matter of chance and depended largely upon the reactions of the individual with which copulation was attempted. This was also found true in the crawfishes *Cambarus bartonius bartoni* (Childester, 1908) and *Cambarus affinis* (Andrews, 1910). This apparent inability to discriminate sex would result in inability to react differentially to animals of the opposite sex in head-on encounters and may be associated with the fact that animals of either sex may be dominant over a mixed group. With *Procambarus alleni* Bovbjerg (1956) found that in adults the male was generally dominant over the female but in the juvenile stages males were dominant in only two of nine groups consisting of two males and two females. Bovbjerg (1953) remarked that males appeared to dominate females in *O. virilis.* In *Polistes* wasps, females dominated males (Pardi, 1948).

In some vertebrate species male and female do not fight but the smaller and less showy sex shows passive submission to the other and each sex establishes separate dominance hierarchies (Greenberg and Noble, 1944; Greenberg, 1947). In animals where sexual dimorphism is slight male and female tend to be more equal in aggressiveness (Allee, 1952).

By injecting the hormone testosterone proprionate Allee, Collias and Lutherman (1939) succeeded in increasing aggressiveness in low ranking hens which soon rose to higher rank in the peck-order. Such implantation into California valley quail that were allowed to remain free-ranging in their native habitat did not alter the position of either males or females in the peck-order (Allee, 1952).

The problem of hormonal control of aggressiveness in invertebrates has not been investigated. As mentioned above, eyestalkless *C. shufeldtii* seldom fought. Whether this was due solely to loss of sight or also partially to the effect caused by the accompanying sinus gland ablation is not known. Scudamore (1948) postulated the existence of sex hormones controlling the sexual activities and bodily changes connected with these activities in crawfish but as yet there is no conclusive histological or experimental evidence of secretory cells within the gonads.

Size has a definite influence on an individual's rank in a hierarchy. In these experiments 3 mm or approximately 15 percent of the total body length proved the critical measurement. No animal dominated another this much longer than itself. However, 28 percent of the crawfish tested were dominated by animals 1 to 2 mm longer than themselves. A larger animal would generally be stronger than a smaller one but because of injury, disease, lack of food, or heredity,

the large animal may be weak in which case the smaller animal could dominate it.

The stage in the breeding cycle also had an important effect on the dominance order, at least among females. A female carrying eggs dominated her associates, whether male or non-ovigerous females. She usually lost this dominant status as soon as the young left the pleopods. One instance was observed in which a female carried eggs that did not develop. This female never dominated her group. This indicates that the presence of objects attached to the pleopods does not in itself stimulate aggressiveness but that some other control mechanism may be present. An idea that has not been investigated is that the developing eggs give off a substance which is absorbed by the female and which stimulates aggressiveness. Since the undeveloped eggs do not extrude this substance the female was not stimulated to fight.

Under natural conditions molting may be a factor influencing dominance order. Animals in the actual process of molting are helpless and for a short time afterwards the new exoskeleton is very soft. Bovbjerg (1953) reported that a newly molted crawfish, regardless of rank, became completely subordinate and if not removed for a few days was cannibalized. After recovery from this period the individual moved back into its previous dominance rank. In the present investigation all animals under observation molted within the same two-day period and thus all of the animals in a group were incapacitated at the same time.

Taking into consideration all of the above factors, there still seems to be some sort of innate aggressiveness, for dominance orders were established among similar-sized unisexual groups. That this aggressiveness may be controlled partially by heredity is suggested by some work done on vertebrates. Scott (from Ginsburg and Allee, 1942) and Ginsburg and Allee (1942) found differences in aggressiveness in three different laboratory strains of mice. Hall and Klien (1942) succeeded in establishing two strains of mice by selectively breeding for timidity and fearlessness from original common stock. Noble (1939) reported that a white strain of *Betta splendens* reared in the same tanks as colored varieties proved inferior to the colored in dominance, even when they greatly exceeded the colored in weight.

Extrinsic factors such as population density, population size and availability of hiding places may also influence the dominance order. *C. shufeldtii* established eight-ranked dominance orders but the time required for their establishment was longer than when only four animals were placed together. In some groups a few of the lower ranking positions remained in question throughout the experiment. Organization of larger groups appears to depend upon the number of animals a crawfish can learn to recognize and react to differentially.

When shells were provided as hiding places for a group, the movement of the animals was greatly reduced. Lower ranking animals often

remained hidden until drived out by another animal. The dominant animal moved about freely and seldom remained long under any shell. If this type relationship occurs in nature the dominant freely-moving crawfish would obtain a larger share of food and would mate more frequently than the more subordinate animals. However, as *C. shufeldtii* occurs in large numbers and the contacts between any two specific individuals would be few, low ranking animals probably would not be as inhibited in their movements.

Only the most transient type of territoriality was seen. An animal defended a hiding place from attack by another but did not consistently remain in the same hiding place over long periods of time. In dishes where no hiding places were provided the animals spaced themselves about the bowl and did not aggregate but there was no consistent selection by an animal for a particular part of the dish.

To what extent the laboratory demonstration of dominance order is applicable under natural conditions is questionable. *Cambarellus shufeldtii* occurs in large numbers within small areas. Although fifteen or twenty animals may be captured in several sweeps of a dip net, this density would still be less than that used in the laboratory. Given natural conditions with hiding places and plenty of vegetation, communities of *C. shufeldtii* probably would not be organized in a hierarchy of dominance, but rather each pair contact would be essentially an initial one. The outcome of each contact would depend on the intrinsic factors of size, stage of breeding cycle in the female, and some degree of innate aggressiveness, and perhaps also upon a type of temporary possession of a desirable hiding place.

Summary

1. *Cambarellus shufeldtii* established four-ranked dominance orders under laboratory conditions. Larger groups of eight animals also established hierarchies but often the lower ranks were not diagrammatically clear as in the smaller groups.

2. These dominance orders were based on tension contacts, of which there are four types: fight, strike, threat, avoidance. As animals remained together over a period of time, fighting decreased and the subordinate animals retreated at the milder forms of tension contacts.

3. Larger animals were dominant over smaller.

4. Either male or female dominated a mixed group. As adult females were larger than males, the female might dominate males more often than not on the basis of size alone.

5. Females carrying eggs were more aggressive and dominated their groups, whether composed of males or of females without eggs. When these animals lost the young they became less active and often dropped to lower rank.

6. When a claw was removed from a dominant animal after only five days with a group the animal dropped to low rank. If a claw

was removed from the dominant after the order was well established and fighting occurred infrequently, the animal often retained its high rank.

7. When a one-clawed individual which had retained dominance was placed with a strange group, it ranked third or fourth. When replaced with its original group it often regained dominance over third- and fourth-ranking animals but only occasionally attained dominance over the former subdominant.

8. When hiding places in the form of shells were provided, the dominant often moved about actively in the open and usually obtained a hiding place any time it tried. Second- and third-ranking crawfish generally remained under a shell until forced out by another animal. Each could defend a shell from attack by the other but not from attack by the dominant. The movements of the fourth-ranking individual were greatly inhibited. It remained in one place, either in the open or under a shell, until attacked by a more dominant animal, then it defended its position only feebly or not at all.

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ABSTRACT

The crawfish *Cambarellus shufeldtii* established four-ranked and eight-ranked dominance orders under laboratory conditions. These hierarchies were based on tension contacts. As animals remained together over a period of time, active fighting decreased and the subordinate animals retreated from an attack without defending themselves.

In general, larger animals were dominant over smaller. Either males or females dominated mixed groups. Females carrying eggs were aggressive and dominated their groups, whether composed of males or of females without eggs. When these females lost the young, they became less active and often dropped to lower rank.

When a claw was removed from the dominant animal of a group which had been organized only five days this animal dropped to low rank. If a claw was removed from the dominant after the order was well established and fighting occurred infrequently, this animal often retained its high rank.

When hiding places in the form of shells were provided the dominant animal moved about actively and usually obtained a hiding place any time it tried. Lower-ranking crawfish often remained under shells until forced out by another animal. Second- and third-ranking individuals each could defend a hiding place from attack by the other but not from attack by the dominant. The movements of the lowest-ranking animal were greatly inhibited. It remained in one place until attacked, and often gave up its position without defending itself.

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PROPAGATION OF THE WHITE SHRIMP, *PENAEUS SETIFERUS* (LINN.), IN CAPTIVITY

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In July, 1952 a research project was initiated at the Marineland Research Laboratory, Marineland, Florida to explore the possibilities of cultivating marine animals in ponds. The project was privately sponsored with the immediate objective of obtaining preliminary data on species suited to pond cultivation and appropriate management techniques to that end. Ultimately these data were to be used as the basis for a commercial enterprise on an expanded scale.

Initial experiments were conducted on the production of the striped mullet, *Mugil cephalus* (Linn.), in fertilized and unfertilized brackish water (Johnson, 1954a). The results of this work indicated that an intensive type of culture of a sea-food with an inherently higher market value than mullet would be necessary to support a commercial venture.

A rearing experiment in 1953 indicated that the production of the white shrimp, *Penaeus setiferus* (Linn.), in ponds had definite possibilities.

From the biological standpoint the continuance of such a program would depend primarily on a dependable source of small shrimp, or "seed-stock" for stocking the ponds. In certain estuaries of the Gulf Coast of the southern United States small shrimp are present seasonally in countless numbers. In those areas they could be collected from the nursery grounds in quantities sufficient to supply a commercial scale pond system.

This system of securing seed-stock is almost universally used in those world areas where brackish water pond culture is presently practiced. The pond culturist who uses this method is improving a natural resource immeasurably by promoting growth, reducing mortality due to predation, and simplifying harvest. However, he is still dependent on wild stocks and his aquiculture program is closely related to the natural fishery.

By contrast, if the pond-culturist were able to produce his own seed-stock from his own pond-reared adults he would, in effect, have created an entirely new resource. For, though the species were the same in both natural and pond waters, the fish farmer would control a self-perpetuating population in an entirely independent community. For this reason experiments on propagating the white shrimp in addition to those on rearing it were initiated as a major part of the overall experimental program.

The subsequent successful attempts at propagation were considered not only to have important implications for a well rounded pond-culture program, but purely scientific ones as well. A great deal is known of the life history of the white shrimp. However, much of this knowledge was gained through necessarily indirect methods due to the vast water areas involved. Although Pearson (1939) had described what he believed to be the metamorphic forms of *P. setiferus* from an extensive series of material obtained in plankton tows, they had never been observed *in toto* from known parentage.

It was not within the scope of this work to study the life-history of the white shrimp, or to describe its larvae and define their exact requirements except as a means to an end — the production of seed-stock for cultivation in ponds.

The authors do not wish to appear apologetic. However, they do wish to acknowledge the fact that from the standpoint of specifically furthering the understanding of the life history of the shrimp, their work could stand many refinements.

Special acknowledgement is due Mr. Nicholas S. Ludington of Philadelphia, Pennsylvania, whose private grant made this and allied research possible. Thanks are also due the management and staff of Marine Studios, whose facilities and cooperation contributed so greatly to their work. The authors also wish to thank Dr. Gordon Gunter for his critical analysis of the manuscript.

The senior author wishes to give full credit to Mr. Stanley (Bubs) Colee of St. Augustine, Florida, for his participation as project aid in 1954. Mr. Colee's interest, insight, and efforts were greatly appreciated and played no small part in the initial success of the propagation experiment.

Materials and Equipment

The general problems that were considered in designing the experimental propagation plant were divided into two major categories. The establishment of a controlled area in which the adults would find suitable conditions in which to spawn, and a rearing technique by which the hatchlings could be carried through the metamorphic stages.

Throughout the summer of 1953 a number of groups of sexually mature white shrimp were caught on the offshore fishing grounds and placed in ten-gallon aquariums and a wooden tank 12 x 4 x 2 feet at the laboratory. Within twenty-four hours all of the female shrimp in each case had shed their eggs. Heegaard (1953) had the same experience at Port Aransas in 1948. Heegaard referred to this as "spawning." We preferred to call it "aborting" as in all cases the eggs were infertile, and probably had been merely jettisoned by the shrimp due to unfavorable conditions. It was not known if the Marineland shrimp carried spermataphores, or, if so, by what means they were able to release infertile eggs. These experiments obviated the use of small tanks in securing viable eggs.

Penaeids are thought to be restricted to relatively deep offshore waters for their natural spawning grounds (Hudinaga 1935, 1942; Pearson *op. cit.;* Heegaard *op. cit.*). However, to the authors it seemed improbable that the trigger mechanism that precipitates successful spawning could be so intricate as to prevent spawning in smaller areas of lesser depths.

It was thought, rather, that each shrimp at any one time lives in its own little circle of gloom and is unaware of the vast expanses which surround it. The fact that Hudinaga *(op. cit.)* had observed copulation and obtained viable eggs from *P. japonicus* in a concrete tank 18 x 18 x 1 meters substantiated this theory.

It did seem advisable, however, to have as large an enclosure as possible for a spawning tank. Size was compromised with available funds and a tank 70 x 30 x 4 feet was built at ground level. The bottom of the tank was a poured six-inch concrete slab. The sides were of concrete block filled with cement and adequately interlaced with reinforcing steel. The tank was equipped with a floor-drain and the bottom was covered with about four inches of fine coquina gravel to serve as a substrate.

To rear the larvae of *P. japonicus* Hudinaga *(op. cit.)* removed the eggs from the spawning tank and hatched them in glass jars. He used similar containers as nurseries.

Although this method was considered adequate for purely scientific studies it was thought to be too involved and costly to furnish seed-stock on a large scale. This assumption was correct, for Hudinaga later told the senior author in personal conversation that even the Japanese economy would not support it. The logical alternative then was to spawn the adults and rear the larvae in the same facility.

Methods

Other than furnishing water of the apparent quality of sea water to a supply of healthy, sexually mature shrimp, nothing was done to induce spawning.

In January, 1954, 175 large white shrimp were caught off-shore and held in a dirt pond ⅛-acre in size.

It was anticipated that in the event larval shrimp were obtained from these adults when they were transferred to the spawning tank the following spring, the facility would then become a nursery and would be managed as such.

Pearson *(op. cit.)* was unsuccessful in rearing nauplii of *P. setiferus* hatched from eggs in aquariums past the first zoea stage. He attributed this failure mainly to his inability to furnish microscopic food in quantities large enough to feed the larvae, yet small enough to prevent its entanglement in their plumose appendages. Entangled larvae precipitated to the bottom where they soon died. Hudinaga *(op. cit.)* and Herrick (1909) also considered this as one of the major problems in rearing decapod larvae.

Hudinaga further stated that the non-feeding nauplii, and the mysis and post-mysis stages were hardy and easily reared, the critical metamorphic stages being the zoea which are weak, have restricted habitat tolerances and must have an adequate, but not too heavy supply of microscopic food. It was planned to manage the nursery with these facts in mind.

During all of the experiments at Marineland, male shrimp were said to be "ripe" when the spermataphores were easily discernible as opaque whitish bodies. The females were considered to be ripe when the distended ovaries could be readily traced for the entire abdominal length by the "butterscotch" color of the mature eggs.

Breeding Experiment, 1954

Beginning March 1, 1954, periodic inspections were made of the brood-stock being held in the dirt ponds. Most of the males were obviously ripe by March 26, but only one female examined was in breeding condition on this date. However, ripe females were found more and more frequently from then on.

Size above a certain minimum seemed to have no bearing on time of maturity; individuals of uniform size were found to mature at random over the entire period to May 15, when the ponds were drained.

On March 8 the tank was filled with water pumped from a dirt pond that did not contain shrimp. On March 10 it was fertilized with five pounds of fish meal and 25 pounds of 7-9-0 inorganic fertilizer. This very heavy application of fertilizer was made erroneously by an assistant because of a displaced decimal point. It resulted in a heavy bloom of phytoplankton (mostly *Chlorella*) within a few days. Within a week the phytoplankton was supporting a tremendous population of copepods. Large numbers of barnacle, chaetognath, and crab larvae had also been pumped into the tank from the pond.

On March 15, twenty-two pairs of the adult ocean-caught shrimp were removed from the holding pond and placed in the brood tank. These animals were selected strictly on the basis of large size as none of the females were considered fully ripe at this time.

Plankton tows were made several times daily and the material examined microscopically. One month later on April 15, one (1) fourth nauplius of *P. setiferus* was found. Repeated plankton tows failed to produce more larvae. The specimen in hand was held in a syracuse dish in which it molted twice, reaching the first zoea stage within twenty-four hours. No attempt was made to rear the larva in the laboratory; it was killed and preserved on April 16.

By April 26 no evidence of eggs could be seen in any of the female shrimp in the tank. The phytoplankton and micro-crustacean population was so dense at this time as to render the tank a murky brown. For this reason it was thought that if further spawnings had occurred, the resulting larvae had become entangled with suspended matter and

died, or that they had been consumed by larger and more robust organisms. The tank was drained and allowed to sun-dry.

On May 13 the tank was refilled with clear salt-water pumped from the Intracoastal Waterway. The tank was immediately stocked with six pairs of the ocean-caught shrimp from the holding pond. The following day eleven pairs of freshly caught ocean shrimp were added. All of the individuals of both sexes were ripe.

A total of five pounds of 7-9-0 inorganic fertilizer was tied up in small parcels in cloth bags and suspended near the surface at intervals around the tank. It was hoped that the fertilizer would dissolve slowly but continuously and would be sustaining a light but continuing phytoplankton population by the time any shrimp larvae would be produced. This later proved to be the case.

No quantitative plankton studies were made in either experiment. However, visibility in the tank during the first experiment was less than six inches while in the one now under discussion, the floor of the tank could easily be seen in four feet of water.

No plankton tows were made until 8:00 a.m., May 17. At this time many fifth nauplius and first zoea stages of *P. setiferus* were found. In the afternoon of the same day two first nauplii were taken in the net, and the following day one embryonated egg was found. Hudinaga *(op. cit.)* and Pearson *(op. cit.)* reported rapid incubation of penaeid eggs and rapid ecdysis in the nauplius stages. In an experiment in 1955 the present writers found that *P. setiferus* larvae whose hatching time was known passed into the first zoea stage in less than forty-eight hours. Therefore, there are believed to have been at least three distinct spawns.

The fifth nauplius and first zoea stages found concurrently are considered as coming from one spawn. It does not necessarily follow that their parentage was the same. The first nauplii found the same day and the embryonated egg found the next are definitely from two later spawns.

The two more advanced broods survived the metamorphic stages. The last brood, identified by the embryonated egg, did not progress past the very early stages, if it hatched at all, as it was never identified in later samples.

The exact hatching time of the first brood is unknown. However, on the basis of the available knowledge of the length of time it takes penaeid larvae to pass through the nauplius stages, (Hudinaga; Pearson, *op. cit.*) May 15 was assumed to be the hatching date. The validity of this assumption was supported by observations in 1955 of the metamorphosis of *P. setiferus* larvae whose time of hatching was known.

The metamorphic pattern of the first brood as indicated by daily plankton tows was as follows:

Elapsed Time (Days)	Date	Time	Stage
0	May 15, 1954	—	Estimate eggs hatched
2	May 17, 1954	8:00 a.m.	1st zoea
3	May 18, 1954	8:00 a.m.	1st zoea
4	May 19, 1954	8:00 a.m.	2nd zoea
5	May 20, 1954	8:00 a.m.	2nd zoea
6	May 21, 1954	8:00 a.m.	3rd zoea
7	May 22, 1954	8:00 a.m.	1st mysis
8	May 23, 1954	8:00 a.m.	1st mysis
9	May 24, 1954	8:00 a.m.	1st mysis
10	May 25, 1954	8:00 a.m.	2nd mysis
11	May 26, 1954	8:00 a.m.	2nd mysis
12	May 27, 1954	8:00 a.m.	1st postlarva

The second surviving brood followed the same pattern, but remained exactly one day behind.

Feeding was begun on May 28 when all of the young shrimp had reached the first postlarval stage. Ground fresh fish and fish meal were added to the tank at the rate of 0.25 pound and 0.05 pound per day respectively. The bloom resulting from the suspended fertilizer was still apparent at this time. Feeding was continued at the same rate until the tank was drained.

The growth rate of the postlarval shrimp was phenomenal. The average sizes of the young shrimp sampled at weekly intervals prior to draining the tank and transferring them to a rearing pond were as follows:

May 28, 1954 (1st postlarvae)	4.5 mm
June 7, 1954	14.0 mm
June 14, 1954	39.0 mm
June 21, 1954	55.0 mm

The average increment for the twenty-four day period was 50.5 mm. The greatest increases recorded by Pearson *(op. cit.)* were 21 mm and 29 mm in a forty-three day period for two postlarvae held in a one-gallon aquarium. With any increase in population density, his growth increment suffered accordingly.

Periodic analyses of the tank water are tabulated in Table 1. The temperature of the surface six inches ranged from 78° F to 90° F. The minimum salinity recorded was 30.5 $^{0}/_{00}$. Salinity increased to 37.1 $^{0}/_{00}$ while the larvae were in the zoea stages, but was immediately reduced by diluting with fresh water and maintained between 32.7 $^{0}/_{00}$ and 34.7 $^{0}/_{00}$ for the duration of the metamorphic period.

When the tank was drained (June 21) 1,024 small shrimp averaging 55.0 mm total length were recovered. Thirty of the original thirty-four brood animals were found to be alive.

The dirt pond that was used to hold the brood-stock had been used in fertilization experiments in 1953 (Johnson, 1954 a and b). The increased fertility carried over into 1954 and resulted in a dense

plankton bloom. The pond was also contaminated with several species of fish including breeding populations of cyprinodonts.

Throughout the breeding experiments, daily plankton tows were made in the pond as well as the tank. No eggs or larvae were found in any of the material taken from the pond. Due to the consistency with which ripe shrimp spawned in the tank, it was unlikely that spawning did not also occur in the pond. Probably such eggs or larvae as were produced were eliminated through predation or "smothered" by the suspended micro-organisms. The latter was considered the more likely event in view of the poor results obtained with turbid tank water but with no contamination by fish.

Breeding Experiments, 1955

In 1954, four ⅛-acre dirt ponds were used in an experiment to approximate the pounds of shrimp that could be produced per acre per year in ponds, and the size to which individual shrimp could be grown at different rates of stocking.

Small shrimp with which to stock the ponds were taken from the tidal flats in the vicinity of Marineland. On June 21, 1954, the shrimp that were produced in the 1954 propagation experiment were stocked in one of the ponds with several thousand of these wild-caught shrimp. All of the shrimp were approximately the same size (400 per pound) at this time.

The brood-stock used in the 1955 breeding experiments were taken from this pond; if any of the tank-bred individuals were selected it was merely by chance for, of course, there was no way of identifying them. However, the brood-stock was certainly well conditioned to pond life. They had been grown from an approximate weight of 400 per pound to an average weight of 15.5 per pound in ponds. Detailed results of the rearing experiments are to be reported elsewhere.

The tank was flooded with water pumped from one of the ponds that did not contain adult shrimp, and immediately stocked with 59 female and 69 male white shrimp on April 22, 1955. All of these shrimp were ripe.

Well embryonated eggs were found in large numbers at 9:30 a.m., April 24. By 10:30 a.m. eggs held in syracuse dishes and observed with a stereoscopic microscope were hatching. Another plankton tow revealed that they were hatching in the tank as well.

At 11:00 a.m. fourth nauplii as well as first nauplii were taken in the net indicating a separate, earlier hatch.

At 3:30 p.m. the first and fourth nauplius stages plus newly spawned eggs were found. Subsequently the first two spawns could be distinguished by a difference in stages, but evidently none of the third spawn (3:30 eggs) hatched, as their nauplii were never found.

The metamorphic pattern of the brood observed hatching as indicated by daily plankton tows was as follows:

Elapsed Time (Days)	Date	Time	Stage
0	April 24, 1955	10:30 a.m.	Eggs hatching into 1st nauplius
0		9:00 p.m.	1st & 2nd nauplius
1	April 25, 1955	8:00 a.m.	2nd & 3rd nauplius
		12:30 p.m.	5th nauplius
2	April 26, 1955	8:00 a.m.	1st zoea
3	April 27, 1955	8:00 a.m.	1st zoea
4	April 28, 1955	8:00 a.m.	1st zoea

On April 28, live larvae could be found only with difficulty and in small numbers. They appeared to be very weak and were not feeding for no ingested material could be seen in their very transparent gut. The tank was heavily contaminated with copepods and chaetognath larvae. Therefore, the tank was drained and an attempt made to improve conditions for another brood.

A filter box three feet by eight feet was built by walling off an area in one corner of the tank with concrete blocks. The sides of the filter were made level with the sides of the tank, and one-half-inch end spaces were left between the blocks in the two lower courses. Successive six-inch layers of river gravel, coquina gravel, and mason's sand in that order from the bottom were used as filter material. A thinner layer of river gravel covered the sand to break the force of the inflowing water.

When the tank was refilled from the same pond as before the filter was found to be effective in eliminating micro-crustaceans and minute larvae.

The tank was immediately stocked with eighteen pairs of ripe adult white shrimp on May 5, 1955.

On May 6 plankton tows produced no eggs or larvae. On May 7 many fourth nauplius larvae were found.

The metamorphic pattern of this brood as indicated by daily plankton tows was as follows:

Elapsed Time (Days)	Date	Time	Stage
0	May 6, 1955	—	Estimate eggs hatched
1	May 7, 1955	8:30 a.m.	4th nauplius
2	May 8, 1955	8:30 a.m.	5th nauplius; 1st zoea
3	May 9, 1955	8:30 a.m.	1st zoea
4	May 10, 1955	8:30 a.m.	1st and 2nd zoea
5	May 11, 1955	8:30 a.m.	1st, 2nd, & 3rd zoea
6	May 12, 1955	8:30 a.m.	1st mysis
7	May 13, 1955	8:30 a.m.	1st & 2nd mysis
8	May 14, 1955	8:30 a.m.	2nd mysis
9	May 15, 1955	8:30 a.m.	2nd mysis
10	May 16, 1955	8:30 a.m.	2nd mysis; 1st postlarva

The water had not been fertilized and remained clear until the larvae entered the first feeding stage. To make food immediately available at this time, water was pumped in from a dirt pond that

had a heavy bloom of rotifers and minute planktonic algae. The water was not filtered, which proved to be a serious error as several hundred killifish were introduced at the same time.

During the entire metamorphic period, larvae in each stage were much more abundant than in any prior experiment. Larvae from this brood were obviously the most active and hardy yet produced, especially in the zoea stages. They also became postlarvae two days quicker than those reared in 1954. This alone was considered substantial evidence that conditions were much more favorable for their welfare than in the preceding experiments.

TABLE 1.

WATER ANALYSIS OF THE SHRIMP BROOD TANK, 1954

Date	Salinity, ‰	pH	O_2 ppm	CO_2, ppm
March 8	31.5	—	—	—
March 10	31.5	8.1	—	—
March 11	31.5	8.1	—	—
March 15	31.8	8.4	12.5	0.0
March 22	31.5	8.6	8.5	0.0
March 23	—	8.6	9.9	0.0
March 26	31.2	8.9	13.8	0.0
April 1	32.3	9.1	9.0	0.0
April 5	33.7	9.0	6.3	0.0
April 12	33.6	8.5	8.6	0.0
May 17	37.1	—	—	—
May 18	35.5	—	—	—
May 19 a.m.	35.7	—	—	—
May 19 p.m.	34.7	—	—	—
May 20	32.7	—	—	—
May 21 a.m.	33.2	—	—	—
May 21 p.m.	33.4	8.4	—	—
May 22	33.5	8.3	—	—
May 24	34.0	8.3	—	—
May 25	34.0	8.5	7.6	0.0
May 26	34.0	8.8	—	—
May 27	34.1	8.7	—	—
May 28	34.1	8.7	—	0.0
May 31	30.5	8.6	—	—
June 1	33.2	8.5	10.3	0.0
June 4	32.3	8.1	9.7	0.0
June 7	32.8	—	—	0.0
June 14	32.3	8.6	10.2	0.0

The small differences in water chemistry (Tables 1 & 2) in this experiment and the successful 1954 experiment were not considered significant. As the accumulated data included no other exact habitat criteria, the specific factor causing the improvement was not definitely known. However, suspended material in relatively small quantities during the nauplius stages, and a light, but adequate and continuous supply of microscopic food during the feeding stages, would seem to be closely related to the successful rearing of white shrimp larvae in confinement. Any other theories such as pond-conditioned parentage, etc., would be highly speculative.

TABLE 2.
WATER ANALYSIS OF THE SHRIMP BROOD TANK, 1955

Date	Salinity, $^0/_{00}$	pH	O_2 ppm	CO_2, ppm
May 5	37.0	8.1	6.5	0.0
May 6	33.3	8.1	6.2	0.0
May 7	33.1	8.1	7.2	0.0
May 9	33.5	8.3	7.6	0.0
May 12	34.3	—	—	0.0
May 13	34.9	8.4	—	0.0
May 16	34.7	8.6	—	0.0
May 19	34.5	8.7	6.5	0.0
May 23	34.0	8.3	—	0.0
May 24	34.8	8.6	7.2	0.0
May 26	35.7	—	—	—
May 27	35.4	8.3	7.5	0.0
May 30	36.1	—	—	—
May 31	36.7	8.3	7.2	0.0
June 1	34.6	—	—	—
June 2	34.6	8.3	6.6	0.0

On May 23, feeding was begun at the rate of 1.0 pounds of ground fish per day and continued until the tank was drained.

The tank water had a total salt content of 37.0 $^0/_{00}$ when the brood-stock was introduced. This was immediately lowered by dilution and maintained between 33.1 $^0/_{00}$ and 34.9 $^0/_{00}$ throughout the metamorphic period. Temperature records during this period were inadvertently destroyed. However, the range is known to have been much the same as that for the May, 1954, experiment. Periodic analyses of the tank water are tabulated in Table 2.

The tank was drained June 13, 1955, and only 103 small shrimp were recovered. Evidently the killifish had consumed the rest of the brood, which had seemed much heavier at least to the postlarval stage than any previous brood. All of the brood-stock (36) were found alive and in good condition.

The young shrimp averaged 53.4 mm total length; the average growth increment for the twenty-eight day period beginning May 16 was 48.9 mm.

The pond in which the brood-stock was held was contaminated by fish and sustained a heavy plankton bloom throughout the period. Daily plankton tows were made in the pond, but no eggs or larvae of *P. setiferus* were taken.

THE EGGS AND LARVAE

Both newly spawned eggs, and eggs containing fully developed nauplius larvae were observed under a compound microscope. The purplish-blue color of the egg membrane described by Pearson *(op. cit.)* was easily seen when the margins were illuminated with a relatively soft light transmitted through a substage condenser.

The color of the yolk was considered to be a yellow-brown in newly spawned eggs, but could possibly be said to have a greenish

tinge if viewed with strong transmitted light. The egg just prior to hatching was completely filled with the dark brown embryo. The embryo seemed to break out of the shell by expanding its appendages, and several minutes elapsed before it became active.

To date no minute examinations of the larvae have been made. The nomenclature for the various larval stages used in this paper is that of Pearson *(op. cit.)*. It can not be stated definitely that Pearson was correct as to species in his description of the larvae of penaeid shrimp. However, each of the stages, and only those stages described by him as being *P. setiferus* were easily recognized with a stereoscopic microscope under 36X magnification. The distinctive differences in each of the larval forms with the exception of the second and third nauplii would in all probability not appear without actual ecdysis. These facts should lend added significance to Pearson's work.

Salinity and the Rate of Growth of *Penaeus setiferus*

Although much remains unknown concerning the life history of the white shrimp, the ecological pattern for each life stage (larval, juvenile, and adult) is recognized but not fully understood.

Generally, it is this: (1) the adults spawn at sea in water of normal sea-water salinity; (2) while passing through a number of larval stages many of the young shrimp are carried toward the inlets to bays by shoreward currents; those that are not, apparently perish; (3) by the time they enter the inland waters the young shrimp are postlarvae or pre-adults and tend to migrate toward shallow, marginal waters; these waters are generally waters of low salinity due to river discharge and local land drainage; (4) as the small shrimp increase in size they tend to migrate back to the deeper open waters of higher salinity, and finally to the sea, where they in turn spawn when about one year old.

These movements may be explained theoretically in terms of stimulus to migration. The three more obvious theories are:

(a) The postlarval and small adult shrimp seek low salinities; the larger adults seek high salinities *per se*.

(b) The postlarval and juvenile shrimp seek the marginal waters because of high concentrations of plankton and organic detritus on which they feed. Low salinities are merely coincident in these areas.

(c) The migratory pattern is atavistic in origin, and is not controlled directly in individual shrimp by any one stimulus. It has, however, inadvertently enabled the shrimp to evolve into a highly successful species.

Gunter and Hildebrand (Hildebrand and Gunter, 1953; Gunter and Hildebrand, 1954) found a strong statistical correlation between the white shrimp catch for a given year and total rainfall for that and the two preceding years in Texas. Although they recognized that

rainfall could affect the production of white shrimp by enriching the estuarine waters with nutrients washed from the land or by some more complicated ecological relationship, they were inclined to accept salinity as the "probable effective factor."

In briefly outlining the life history of the white shrimp, these writers (Gunter and Hildebrand, 1954) made the concluding statement: "This type of life history is necessary for the white shrimp and those postlarvae that fail to enter inside waters perish." This is probably true as most workers are agreed upon it. However, since it appeared in the introduction to a paper purporting to show an inverse relationship between shrimp production and estuarine salinities, it could imply that postlarvae that fail to enter inside waters succumb to high salinity. For this reason it is emphasized here that at Marineland the postlarvae were reared in water with a total salt content roughly equal to that of the open sea.

Nevertheless, the correlation between rainfall and shrimp catch in Texas was well defined. If low salinity as a function of rainfall was the effective factor in high catch years, it could have been effective in either of two ways: by increasing the growth rate of the smaller individuals or by having some sort of survival value for the same group. That is, pounds catch would be up because either larger or more shrimp were available than in drier years. Actually, the former probably would not occur without the latter because a fast growing juvenile population would leave the nursery grounds more quickly than a slower growing one and thus make more rapid recruitment possible.

If the salinity *per se* theory were true it would have important implications for the pond culture of shrimp as arrangements could be made to regulate salinity for maximum growth. Therefore, preliminary to relocating and expanding the pond culture project it was considered desirable to know if a large supply of fresh, as well as salt water should be a major consideration in selecting a site.

Ten, ten-gallon aquariums were stocked with five small white shrimp each. The shrimp were carefully weighed before being placed in the tanks and again weekly for two weeks. The small shrimp in each tank were fed fresh fish at the rate of 10% of their initial body weight per day. Invariably all of the food was eaten.

Five of the tanks contained water with a salinity of 34.0 $^{0}/_{00}$; the other five contained water with a salinity of 18.5 $^{0}/_{00}$. This salinity differential (almost 50% based on the higher concentration) certainly should have shown any growth differential due to the amount of dissolved salts. The results are tabulated in Table 3.

The shrimp at the higher salinity grew faster and converted their food more efficiently than those at the lower salinity. It should also be mentioned that the phenomenal growth tabulated in the sections "Shrimp Propagation, 1954; 1955" occurred in water with a salinity equal to or exceeding that of sea-water.

TABLE 3.
A COMPARISON OF THE GROWTH RATE OF WHITE SHRIMP AT DIFFERENT SALINITIES
AUGUST 16 TO AUGUST 30, 1954
Salinity = 18.5 $^0/_{00}$

Tank No.	Initial Weight, Gms.	Terminal Weight, Gms.	Total Gain, Gms.	Percent Gain	Total Food Consumed, Gms.	Conversion Ratio
1 1st week	—	—	—	—	—	—
2nd week	8.8	8.4	0.4	0.0	5.4	0.00
2 1st week	6.6	7.4	0.8	12.1	4.2	5.25 : 1
2nd week	11.3	11.6	0.3	2.6	6.6	20.00 : 1
3 1st week	10.5	11.5	1.0	9.5	6.0	6.00 : 1
2nd week	—	—	—	—	—	—
4 1st week	7.9	8.8	0.9	11.4	4.8	5.33 : 1
2nd week	—	—	—	—	—	—
5 1st week	4.4	5.0	0.6	13.7	2.4	4.00 : 1
2nd week	5.0	5.2	0.2	4.0	3.0	15.00 : 1
Salinity = 34.0 $^0/_{00}$						
6 1st week	10.3	12.0	1.7	16.5	6.0	3.53 : 1
2nd week	12.0	12.1	0.1	0.8	7.2	72.00 : 1
7 1st week	10.8	11.9	1.1	10.2	6.2	6.00 : 1
2nd week	11.9	12.0	0.1	0.8	7.2	72.00 : 1
8 1st week	—	—	—	—	—	—
2nd week	7.4	7.5	0.1	1.3	4.2	42.00 : 1
9 1st week	8.2	9.2	1.0	12.2	4.8	4.80 : 1
2nd week	9.2	10.3	0.5	5.4	5.4	10.80 : 1
10 1st week	3.4	4.2	0.9	26.5	1.8	2.00 : 1
2nd week	4.2	4.5	0.3	0.7	2.4	8.00 : 1

For reasons unknown the rate of growth of the shrimp in all tanks was insignificant during the second week. Therefore the totals for only the first week's growth for the two treatments are compared below.

Salinity	Int. Wt. Gms.	Terminal Wt. Gms.	Gain Gms.	Percent Gain	Food Consumed	Conversion Ratio
34.0 $^0/_{00}$	32.7	37.3	4.6	14.1	19.2	4.09 : 1
18.5 $^0/_{00}$	29.4	32.7	3.3	11.2	17.4	5.27 : 1

Although this work was not sufficient to reflect the detailed effect of salinity on rate of growth, it did give the project personnel some confidence in selecting a site for a commercial pond system by indicating that, except beyond wide limits, salinity is not a critical factor in the rearing of shrimp. It must be remembered, however, that small white shrimp generally grow up in salinities below 18.0 $^0/_{00}$. These experiments did not encompass this lower range and further tests will be necessary before more definite conclusions can be drawn.

General Discussion

Sexually mature white shrimp spawned readily in the concrete tank at Marineland. In the experiments in which the brood-stock was obviously mature when it was placed in the tank, spawning took place within forty-eight hours. It would be interesting to know if normal spawning would have occurred in the holding ponds within the same period, or if the removal of the brood-stock to "new" water precipitated spawning. Although both male and female shrimp were stocked in the tank, it is probable that copulation had taken place in the holding ponds and viable eggs would have been produced without the inclusion of the males. Neither an optimum number of brood-stock to use nor a minimum size tank in which they would spawn is known.

It was clearly pointed out in the introductory portion of this paper that the work outlined herein was directed primarily towards developing a practical shrimp-hatchery operation; an attempt was made throughout to present the material from that standpoint. It therefore appears needless to recapitulate this material in summary. However, there are certain moot questions concerning the life history of the white shrimp that may be clarified to some extent by information gained from the captive adults and larvae. Only those data concerned with questions subject to speculation are summarized and in some instances briefly expounded.

The larvae of *P. setiferus* go through probably five, but certainly four nauplius, three zoea, and two mysis stages before becoming postlarvae. By gross examination these larvae and the eggs of the white shrimp seem to have been accurately described by Pearson *(op. cit.)*.

The duration of the metamorphic period is not fixed, but depends to some extent on local conditions of food and habitat. The brood reared in 1954 required twelve days to become postlarvae; the one in 1955 only ten.

The postlarvae of *P. setiferus* did not perish, but thrived at salinities approximately equal to that of offshore waters.

Captive postlarvae grew at the rate of 2.1 mm a day for twenty-four days in 1954, and 1.7 mm a day for twenty-eight days in 1955. Very rapid growth was first observed in juvenile white shrimp by Viosca (1920) and later estimated for wild populations at 1.0 mm a day by Gunter (1950) and 1.2 mm a day by Williams (1955). The theoretical maximum growth rate of any species is usually modified by available food; the tank reared postlarvae are believed to have been full-fed and to have approached this maximum rate. Hudinaga *(op. cit.)* obtained daily growth increments below 1.0 mm in a four month period in 1940 with tank-reared *P. japonicus*.

White shrimp stocked in ponds at an approximate weight of 1.1 gm in July, 1954, spawned in April, 1955, at an average weight of 29.3 gm. There is little doubt that wild shrimp hatched one summer spawn the following summer at an age of one year or less.

The adult shrimp used in the experiments remained in excellent condition for over thirty days after spawning; they were killed when the tank was drained at the termination of each experiment. It is not known if adult shrimp survive from one spawning season to the next; however, it can be said that they do not die immediately as a result of spawning.

Gunter and Burkenroad in editing the work of Heegaard *(op. cit.)* remarked that all females that had been examined to date whose ovaries showed evidences of prior spawnings also showed some degree of reripening. It was therefore not certain if *P. setiferus* had ever been seen within the first few days after spawning. The ovaries were removed from two female white shrimp exactly five days after they had spawned in the brood tank. Sections of these ovaries examined by Mr. Albert Stenger, histologist at New York University, were found to contain large numbers of both degenerating and developing ova. It is likely that wild females whose ovaries contain egg remnants and ova in the early stages of development have spawned within the last few days.

Embryonated eggs and a number of each of the larval forms of *P. setiferus* recovered from the brood tank in 1954 and 1955 were preserved. These specimens and mounts of the ovarian sections of the recently spawned females are on file at the Fisheries Building, Alabama Polytechnic Institute, Auburn, Alabama, where they are undergoing more critical examination by Dr. John S. Dendy.

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ABSTRACT

In 1954 and 1955, sexually mature white shrimp, *Penaeus setiferus* (Linn.), that had been reared or held in dirt ponds, spawned viable eggs when placed in a concrete tank filled with salt water. The resulting larvae were reared through the metamorphic stages and to a pre-adult length of approximately 50.0 mm in the same facility.

The metamorphic forms could be identified by the descriptions of Pearson (1939); no additional stages were observed. The metamorphic period lasted twelve and ten days in the two years respectively. Upon becoming postlarvae the young shrimp grew at a daily rate of 2.1 mm in 1954 and 1.7 mm in 1955.

Observations on the captive larvae, juvenile, and adult shrimp are discussed where appropriate to a better understanding of the life history of *P. setiferus*.

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