TULANE STUDIES IN ZOOLOGY

VOLUME 9
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TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the waters and adjacent land areas of the Gulf of Mexico and the Caribbean Sea. Each number is issued separately and contains an individual monographic study, or several minor studies. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

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VOLUME 9
INDEX TO AUTHORS AND SCIENTIFIC NAMES
(New genera, species, and subspecies in boldface)

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Volume 9, Number 1 October 20, 1961

LARVAL TREMATODES FROM THE APALACHEE BAY AREA, FLORIDA, WITH A CHECKLIST OF KNOWN MARINE CERCARIAE ARRANGED IN A KEY TO THEIR SUPERFAMILIES

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TULANE STUDIES IN ZOOLOGY

Volume 9, Number 1 October 20, 1961

CONTENTS

I. Dedication

This study is dedicated to Dr. George R. LaRue, Professor Emeritus of the University of Michigan, in recognition of his contributions to the field of helminthology.

LARVAL TREMATODES FROM THE APALACHEE BAY AREA, FLORIDA, WITH A CHECKLIST OF KNOWN MARINE CERCARIAE ARRANGED IN A KEY TO THEIR SUPERFAMILIES [1]

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II. Introduction and Historical Review

The major objective of this study was to investigate the cercarial fauna in marine mollusks from the littoral zone and shallow waters of Apalachee Bay, Gulf of Mexico. The following general outline of the trematode life cycle indicates the role of cercariae:

Adult digenetic trematodes are common parasites of vertebrates. Most species live in the digestive tract or its appended organs but others are found in various systems of the host. The adult worm produces eggs which escape from the host. A larva, the miracidium, develops within the egg and ultimately gains access to an intermediate host which is usually a mollusk or very rarely an annelid. Within this host larval multiplication occurs by polyembryony and is almost always enhanced by the intermediate generations of germinal sacs known as sporocysts and rediae. These sacs produce cercariae, each of which develops into an adult trematode upon reaching the vertebrate host by one of several ways, either directly or indirectly. Usually, cercariae emerge from the intermediate host to live free for a short time and can be obtained by isolating the host as was done to study most of the species reported here. Some cercariae, however, remain in the mollusk to be eaten with it by the definitive host and, in order to study these forms, it is necessary to dissect the mollusk to recover them.

The study of marine cercariae has lagged behind that of their adults. Furthermore, descriptions of many marine cercariae are inadequate for purposes of comparison. It is recommended that the features of cercarial morphology, behavior, reactions to vital dyes and germinal sac morphology be recorded in all future descriptions of cercariae to facilitate comparisons. Prior to the present study, cercariae have been separated primarily by comparative morphology, and many closely related forms are difficult to separate on this basis alone. The present study has shown that features of behavior, reaction to dyes and germinal sac morphology are relatively constant for a given species, and differ sufficiently between species to be of systematic value.

Because research on marine cercariae has been done mostly near marine laboratories, great areas of continental coastlines remain unexplored. The present study is the most extensive investigation of its kind from the Gulf of Mexico. A similar study is that of Cable (1956a) for Puerto Rico.

Life history studies have shown that morphologically dissimilar cercariae may be closely related within a single family. Therefore, the obvious solution to a natural system of classification of cercariae lies not only in the study of comparative morphology but in the elucidation of the life cycles of larvae, particularly in families whose taxonomic position is uncertain.

A secondary objective of this study was to provide information on local marine cercariae that would be of value in future life history investigations. That the basis of classification of digenetic trematodes should be founded on life history studies and embryonic development has been supported by the work of LaRue (1938, 1957), Stunkard (1940, 1953b), Hussey (1941, 1943), Kuntz (1950, 1951, 1952), Cable (1956a) and others.

While surveying the literature of marine cercariae of the world, the need for a key to these larvae became increasingly apparent. The latter part of this volume is an attempt to fulfill this need, using LaRue's (1957) scheme of classification as a basis for a key to Superfamilies. An attempt has been made to accumulate a complete bibli-

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[1] This study was submitted to the Graduate School of The Florida State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

ography on marine cercariae of the world through December, 1959.

The first description of a cercaria was published by Swammerdam in 1773 from the fresh water snail, *Paludina vivipara.* In 1773, Otto F. Müller first used the term *Cercaria* as a generic name for tailed microscopic animals. He placed them in the Infusoria and described the first marine species, *Cercaria inquieta,* a biocellate form found in a plankton sample. The second, *Cercaria setifera,* was described by Johannes Müller (1850). This trichocercous larva has probably been the most completely investigated marine cercaria; over 15 other names have been considered as synonyms by various authors.

Diesing (1855) published a revision of cercariae known at that time, and described 5 new marine species. He recognized 9 genera and 20 species, and regarded these forms as zoologically distinct and free living but corrected that mistake in 1858 when he recognized cercariae as trematode larvae.

An extensive but artificial system of classification of cercariae was proposed by Lühe (1909). He used external morphological characteristics, such as stylets, collars, spines and caudal form as his basis of taxonomy. He introduced many new descriptive terms for "groups" or "types" of cercariae (e.g., trichocercous, microcercous, cystocercous, leptocercous). Lühe pointed out that the cercariae of closely related forms show a very striking similarity of structure. Consequently, he believed that his classification of cercariae would be correlated with the taxonomy of adults. The morphological terms introduced by Lühe, although of less taxonomic importance than he assumed, are still useful as descriptive terms.

Lebour (1911) advocated a "natural" scheme of classification of cercariae separating them into two groups based on the type of germinal sacs (rediae or sporocysts) in which they develop. Within each group she proposed smaller groups of apparently related forms based on morphological characteristics. Her system is no longer accepted because allocreadioids, opisthorchioids and other groups are known to develop in both sporocysts and rediae.

The major contributions to morphology and taxonomy of marine cercariae in the twentieth century have been the studies of Lebour (1904-1923) and Rothschild (1935-1941) in England and Scotland; Palombi (1924-1942), primarily in the Gulf of Naples; H. M. Miller (1925-1930) at Puget Sound, Washington, and Dry Tortugas, Florida; Martin (1938-1956) at Wood's Hole, Massachusetts, and the California coast; Cable (1934-1956) at Wood's Hole, Massachusetts, and Puerto Rico; and the investigations of Stunkard (1929-1959) at Wood's Hole, Massachusetts, and at Roscoff, France.

The cercariae in the present work are arranged in categories corresponding to families or superfamilies. Allocation has been based on a comparison with cercariae whose life cycles are known. Family and superfamily names are used to designate cercarial types. For example, the larvae known to belong to the Microphallidae will be referred to as microphallids, and those in the Opisthorchioidea as opisthorchioids. The morphological terms introduced by Lühe (1909), Sewell (1922), and others will be used occasionally in a descriptive sense (*e.g.,* cystophorous hemiuroid, pleurolophocercous heterophyid).

Although the term *Cercaria* was introduced as a generic name, it obviously encompasses a much larger category than that of a genus. The term is, however, a convenient group name for larvae whose relationships to adult trematodes are unknown, and it is used in this manner herein.

The author wishes to express gratitude to Dr. Robert B. Short of Florida State University under whose direction this study was done, and to Drs. George R. LaRue, Raymond M. Cable, and Franklin Sogandares-Bernal for reading the manuscript and for many helpful suggestions.

III. Materials and Methods

The mollusks examined were collected along the coast of Apalachee Bay, Gulf of Mexico, from St. Marks lighthouse to St. Teresa, Florida, with the exception of three lots obtained at the jetties at Panama City, Florida. A total of 69 collections were made from the Apalachee Bay area from September 1956 to September 1959.

Mollusks were taken by hand from salt marshes and the littoral zone, and from deeper waters with a beam dredge operated from a small boat. Identification was based on Abbott's (1954) *American Seashells.*

In the laboratory, mollusks were isolated individually in a small quantity of filtered sea water for 24 hours at room temperature 23°-24° C.). At the end of that period, the water was examined with a stereomicroscope. If no cercariae were observed, the water was replaced and if no cercariae emerged during a second 24 hour period, the mollusk was generally considered negative for cercarial infections and was discarded. If, however, a large number of mollusks from a single collection appeared negative after two examinations, some of these individuals were crushed and examined.

It was found that cercariae would emerge from *Cerithidea scalariformis* Say, an operculate, prosobranch snail of salt marshes adapted to fairly warm water, if that host was first dried on blotting paper for a few hours and then isolated in sea water at 30° to 35° C.

Cercariae which had emerged from a mollusk were transferred to an embryological watch glass with a micro-pipette to study swimming habits, tropisms and longevity. In a few instances where cercariae did not emerge spontaneously, they were found by dissection of the host. Unless otherwise stated descriptions are based on cercariae that emerged naturally.

For microscopic study, cercariae were transferred in a drop of sea water to a slide and a No. 1 coverslip was added. Coverslip pressure was controlled by addition of sea water to the edge of the coverslip or by absorption of water with blotting paper. Numerous preparations of material of each species were examined during the course of making the preliminary drawings. Particular effort was made to discern the excretory tubules and flame cell formulae.

Neutral red and Nile blue sulfate were used as vital dyes at a concentration of 0.5% in sea water. Cercariae in a drop of sea water were added to a drop of the dye in a watch glass and their reactions were recorded.

After each cercaria was studied, its host was crushed and the sporocysts or rediae were examined and drawn. The average number of cercarial embryos per germinal sac was determined by counting the embryos from 20 sporocysts or rediae ruptured by coverslip pressure.

Measurements were made on preserved material which had been fixed according to the method of Talbot (1936): Living cercariae, in 200 ml. of sea water, were dashed into 200 ml. of steaming 10% formalin. Rediae and sporocysts were fixed in the same manner. Cercariae thus fixed were killed in a relaxed and extended position and were rather uniform in shape and size.

Measurements were made on 20 cercariae and 20 germinal sacs of each species and a maximum, minimum and average for each feature is recorded in the descriptions, the average being in parentheses. All measurements are in millimeters.

All preliminary drawings were made free hand from living material under an oil immersion objective. Final drawings, except for habit sketches, were made to scale using preliminary sketches and average measurements.

IV. Results

Over 200 species of mollusks are known from both littoral and deep waters of Apalachee Bay. A total of 16,577 mollusks were examined, representing 29 species. Seven of 19 species of gastropods and 4 of 10 species of pelecypods were infected with larval trematodes. Cercariae belonging to 31 species were found, 21 in gastropods, and 10 in pelecypods. Twenty-eight of these cercariae were studied in detail. Of these cercariae, 24 are described as new and four previously known forms are redescribed. Trematode larvae were found in 2622 individual mollusks, an incidence of infection of 15.2%.

Each of the following descriptions contains a general diagnosis of the group where known, a telegraphic description of the species, a description of larval behavior, and a discussion of affinities including a comparison of the larva with its most closely related form.

A. *Cyathocotylid Cercaria*

One cercaria in the family Cyathocotylidae is reported here as a new species. The general characteristics of cercariae from this family, as given by Cable (1956a), are:

Furcocercous cercariae developing in elongate sporocysts in fresh water and marine gastropods. Oral sucker, pharynx and ceca well developed, ventral sucker a primordium or lacking. Tail longifurcate with long, slender stem. Tail stem with long setae, furcal fins present or absent. Tail attached dorsally near posterior end of body. Larva rests suspended in water with the tail stem flexed near its middle. Body ventrally concave, covered with spines. Papillae and bristles present. Eyespots absent. Excretory system diagnostic for the family. The thin walled excretory vesicle gives rise to 4 tubules, a median pair and a lateral pair. The median pair converge to form a single tubule which connects, in the anterior region of the body, with the lateral tubules by means of a cross commissure. Posterior to its junction with the lateral tubules, a recurrent collecting tubule joins each lateral tubule and extends posteriorly a short distance to receive an anterior and posterior collecting tubule, each with typically 3 groups of flame cells, although other flame cell patterns have been described. Posterior flame cell group on each side almost always in the tail stem. Encyst in fishes or, rarely, in the molluscan host.

Cercaria leighi, sp. nov.

(Figures 1-6)

Description: body 0.204-0.219 (0.213) long, 0.092-0.099 (0.094) wide at maximum width posterior to midbody. Tail stem 0.296-0.311 (0.305) long, 0.036-0.041 (0.037) wide at base. Furcae 0.209-0.230 (0.221) long, 0.026-0.031 (0.027) wide at base. Dorso-ventral finfolds on furcae, with maximum width of 0.012, extending dorsally and ventrally entire length of furcae and projecting about 0.010 beyond tip. Furcal fins with fine striae and marginal papillae with minute bristles, 6 papillae dorsally and 6 ventrally. Tail stem with diagonal and transverse muscle fibers and scattered nuclei. Surface of tail stem with numerous bristles. Furcae filled with conspicuous vacuolated parenchyma. Body covered with very fine spines and scattered bristles, shorter than those on tail stem. Cephalic region surrounding mouth with short and long bristles, and anterior half of oral sucker with concentric rows of spines slightly heavier than those elsewhere. Oral sucker resembling protrusible cephalic organ with weak sucking capacity, 0.045-0.051 (0.049) long, 0.029-0.030 (0.029) wide in maximum width; mouth terminal. Fourteen penetration glands found in oral sucker whose ducts open around circumference near midlevel of sucker. An additional set of 4 penetration glands imbedded deeply within sucker, their ducts opening symmetrically around mouth. Prepharynx short; pharynx 0.018 in diameter. Esophagus short, ceca wide, sinuous and empty. Numerous cystogenous glands opening on body surface in anterior third of body. Granular cystogenous glands, irregular in shape, scattered throughout body. Two primordia evident, anterior to excretory bladder in posterior half of body; smaller anterior mass probably representing developing acetabulum, larger posterior mass representing the developing tribocytic organ or reproductive system. Medial excretory tubules encompassing both primordia and converging just anterior to smaller one. Minute excretory concretions found in single medial tubule, cross commissure, in anterior ends of lateral tubules and in bifurcated projections of lateral tubules anterior to junction with cross commissure. Excretory bladder with island of Cort. Caudal excretory tubule supported in tail stem by transverse fibers, bifurcating and discharging through pores at tips of furcae. Excretory formula $2[(3+3+3)+(3+3+3)]=36$; the last group of 3 flame cells on each side widely separated in anterior 2/3 of tail stem. Development in elongate, motile, cream-colored sporocysts with prominent circular muscle bands giving sporocyst a segmented annelid-like appearance. Ninety-two sporocysts counted from branchial region of one host. Sporocyst 1.995-2.610 (2.361) long, 0.210-0.270 (0.249) wide. Anterior end more pointed, surrounded by minute bristles, birth pore subterminal. Thirty-five to 24 embryos per sporocyst: in all stages of development. Flame cells very numerous, grouped in each circular muscular band of body.

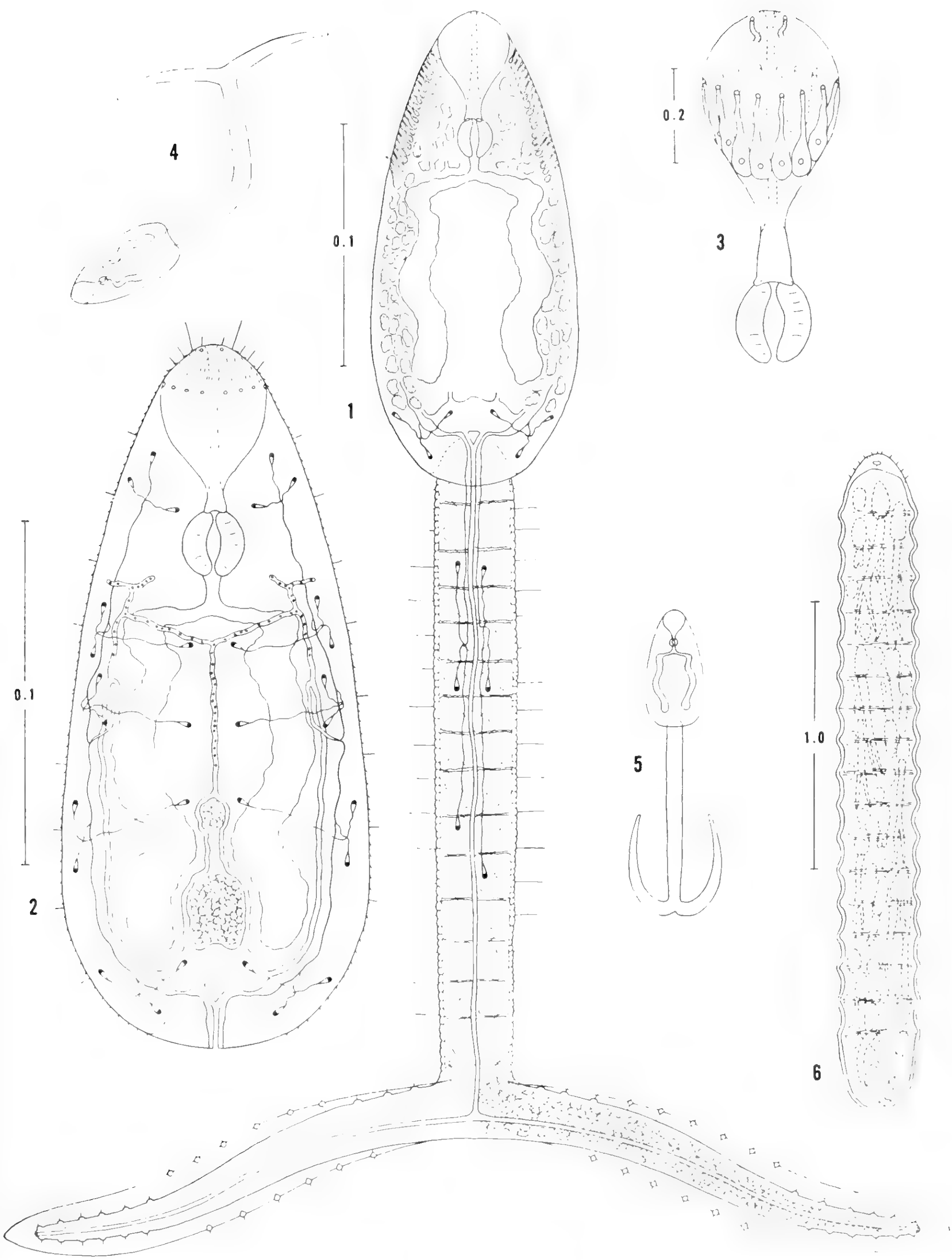
Host: Cerithidea scalariformis Say.

Incidence of infection: One of 5,508 snails.

Locality: Salt marsh, St. Marks Light, Wakulla County, Florida.

This cercaria is named in honor of Dr. W. Henry Leigh, who introduced the author to the discipline of helminthology.

Cercariae of this species emerged at any time provided the infected snail had been



Figures 1-6. **1.** *Cercaria leighi*, sp. nov., ventral view showing details of body and tail. **2.** Same, cercarial body, ventral view, showing details of excretory system, digestive system and primordia. **3.** Same, ventral view of cephalic organ showing penetration glands and ducts. **4.** Same, swimming posture. **5.** Same, creeping posture. **6.** Same, sporocyst.

dried prior to isolation. No phototropisms were observed. Cercariae are strong, energetic swimmers starting with a dash over an erratic path followed by a rest period. They swim in response to a light tap on the wall of the vessel. At rest, they are suspended, body downward at various levels in the water, with the tail stem flexed laterally at an angle of about 120° with the body and the furcae widely spread. After about 10 hours of swimming and rest periods, this larva settles to the bottom where creeping movement was observed for a period of about 14 hours. The life span of this cercaria is about 24 hours following emergence.

Neutral red is highly toxic, stimulating the release of penetration gland secretions and cystogenous fluids. The ceca are filled with a concentration of this stain and are readily visible. Nile blue sulfate, not as toxic as neutral red, stains the contents of the penetration glands and cystogenous glands readily.

This cercaria is most closely related to *C. caribbea* LI Cable, 1956, but differs from it in the shape of the oral sucker, presence of concretions in the excretory tubules, relative positions of flame cells in the tail stem, extent of the furcal finfold, point of convergence of the medial excretory tubules, extent of the cystogenous glands, host, and other less apparent features.

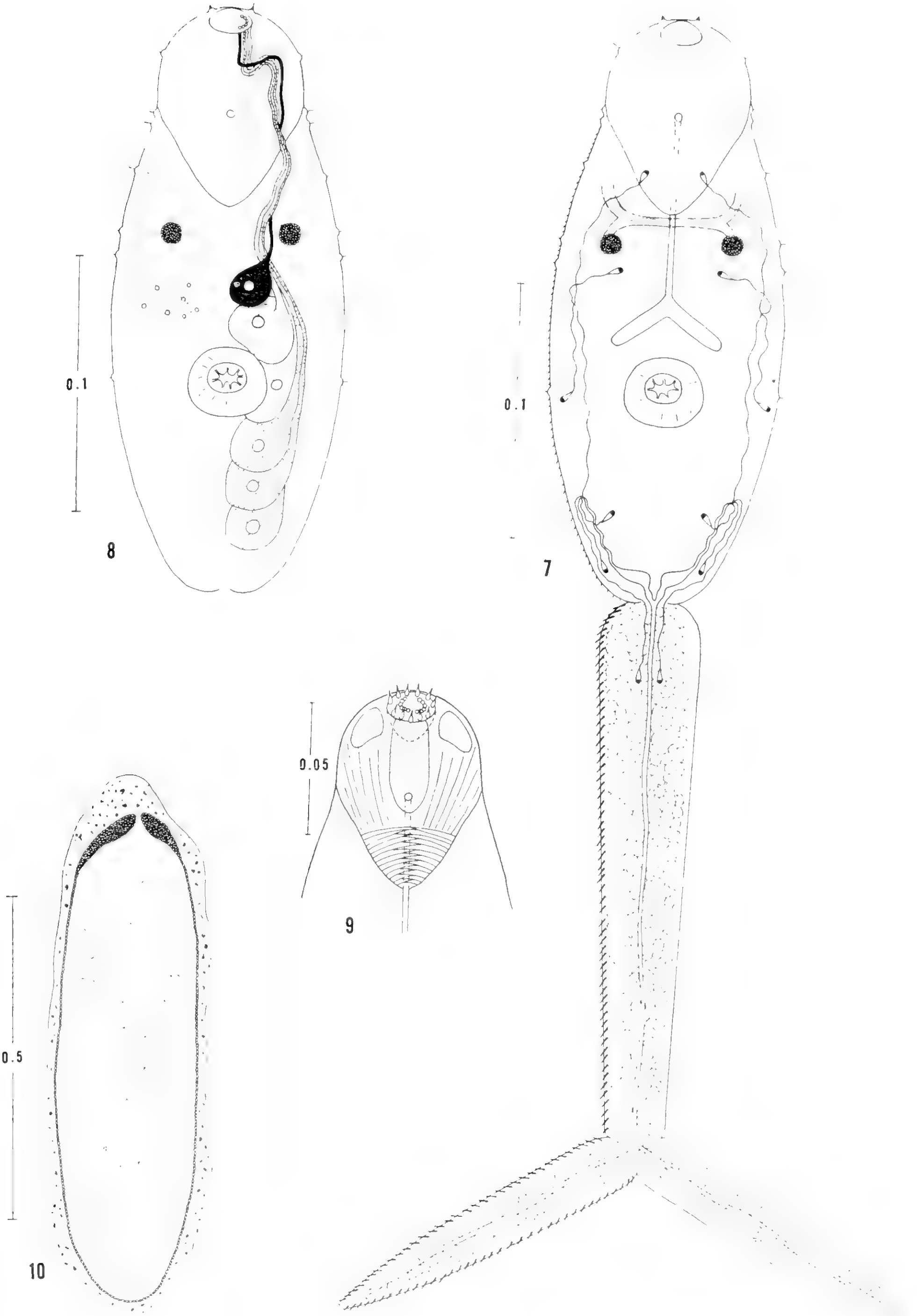
B. *Schistosome Cercaria*

A single new cercaria of the family Schistosomatidae was found. Its larval type is characterized by the fololwing general diagnosis:

Apharyngeate, distome cercariae with oral sucker replaced by a protrusible cephalic organ. Six pairs of penetration glands, one pair being exhausted in the escape from the sporocyst. Pigmented eyespots present or absent. Development in simple sporocysts in gastropods. Cercariae penetrating into final host and living as adults in the blood vascular system. Parasites of birds and mammals.

Cercaria of *Austrobilharzia penneri* Short and Holliman, 1961 (Figures 7-10)

Description: body 0.209-0.250 (0.232) long, 0.071-0.102 (0.087) wide at midbody. Tail stem, measured from body-tail junction to base of furcae on lateral surface of stem, 0.179-0.240 (0.215) long, 0.031-0.051 (0.041) wide at base. Stem and furcae filled with small vacuolated parenchyma and minute, scattered refractile granules. Body and entire tail covered with spines, those on tail coarser. Papillae and bristles on body and penetration organ; papillae on anterior tip of organ with bristles mounted on minute nipples. Penetration organ pyriform, 0.078-0.098 (0.086) long, 0.046-0.063 (0.052) wide at widest point, with distinct longitudinal and circular muscles and three indistinct granular glands (?), one elongate and medial, other two reniform to oval, and lateral. Mouth minute, ventral, subterminal; esophagus narrow; ceca short, terminating anterior to acetabulum. Cecal contents staining well with neutral red. Acetabulum 0.023-0.029 (0.024) long, 0.027-0.033 (0.030) wide, located just posterior to midbody. Six large, overlapping, granular penetration glands on each side extending from level just posterior to eyespots almost to excretory bladder. First gland (escape gland) anterior and ventral, visible only in cercariae dissected from sporocysts; next two glands finely granular; posterior 3 more coarsely granular. Single bundle of gland ducts on each side extending medially to eyespots; then anteriorly to terminal eversible depression, here ducts discharging through individual pores arranged in crescent. Margin of anterior depression ringed with approximately 11 indistinct spines directed anteriorly. Additional penetration (?) glands consisting of an undetermined number of poorly defined cells on each side, with ducts extending forward lateral to eyespots and appearing to open dorsally on cephalic organ. Right and left halves of excretory bladder separate, each half giving rise to posterior excretory duct; these converging at junction of body and tail stem, forming single duct extending through tail stem. Island of Cort absent. Caudal excretory duct bifurcating at furcal junction and discharging at tips of furcae. Main excretory tubule, on each side of body, short, receiving long anterior collecting tubule and extremely short posterior one. Flame cell formula $2[(1+1+1) + (1+1+1)] = 12$, with one pair of flame cells in base of tail. Flame cell activity increased by addition of neutral red. Eyespots circular, 0.008 in di-



Figures 7-10. **7.** Cercaria of *Austrobilharzia penneri* Short and Holliman, 1961, ventral view, showing details of body and tail. **8.** Same, ventral view of cercarial body showing small penetration glands and ducts on left side only, and large glands and ducts on right only. **9.** Same, ventral view of cephalic end showing details of penetration organ. **10.** Same, sporocyst.

ameter, each composed of small, spherical, brown granules. Cephalic ganglia readily stained with Nile blue sulfate and neutral red. Cross commissure dorsal to gut and penetration gland ducts and anterior to eyespots. Development in cream-colored, oval to cigar-shaped sporocysts in liver of snail. Sporocyst 0.357-1.29 (0.832) long, 0.180-0.300 (0.230) wide. Sporocyst wall composed of small spherical cells surrounded by granular paletot; birth pore terminal. Eight to 50 embryos per sporocyst in various stages of development.

Host: Cerithidea scalariformis Say

Incidence of infection: 24 of 10,510 snails.

Locality: Salt marsh, Shell Point, Wakulla County, Florida.

This cercaria is the larval form of *Austrobilharzia penneri* Short and Holliman, 1961, adults of which were recovered from experimentally infected chicks, parakeets and pigeons (Short and Holliman, 1961).

The cercaria swims tail first with a rapid vibration of the tail, and comes to rest on the surface of the water, dorsal side up, with tail stem held relatively straight. It has a life span at room temperature of about 36 hours. Cercariae emerged at any time after the snail had been dried for a few hours on blotting paper. No phototropisms were observed. Nile blue sulfate is toxic and neutral red slightly toxic.

This cercaria can cause a severe dermatitis in man, as the author demonstrated. Cercariae, transferred to the skin of the forearm and abdomen in a water film by a wire loop, penetrated within 5 minutes, as the water evaporated. Cercariae likewise penetrated from a vessel of seawater taped to the medial surface of the upper arm. Here again, penetration was apparently accomplished in about 5 minutes accompanied by another 5 minutes of severe itching. Formation of papules at sites of penetration was noticeable about 3 hours after exposure. About 48 hours was required for maximum dermatitis to develop. Papules remained, accompanied by itching, for a week, and were still visible at the end of 2 weeks.

The cercariae of 4 species of *Austrobilharzia* are known: *Austrobilharzia variglandis* (Miller and Northup, 1926) Penner, 1953; *Austrobilharzia terrigalensis* Johnston, 1917, as described by Bearup (1956); *C. littorinalinae* Penner, 1950; and probably *C. caribbea* XLIX Cable, 1956. *Cercaria penneri* is most closely related to C. *variglandis,* but differs from it in the relative size of cuticular spines, presence of cephalic spines, position of the tail when at rest on the surface film, and possibly in the form of the main excretory bladder ducts and bladder. *C. variglandis,* as illustrated by Stunkard and Hinchliffe (1950), has spines of uniform size covering the body and tail, with no cephalic spines around the openings of the ducts of the penetration glands. That species also rests on the surface film but the tail curves anteriad beside the body; furthermore, the main excretory ducts in the caudal end of the body are in contact; they separate in the base of the tail and then fuse to form a single caudal excretory tubule. Small, diffuse penetration glands were not reported in this cercaria.

C. *Aporocotylid Cercariae*

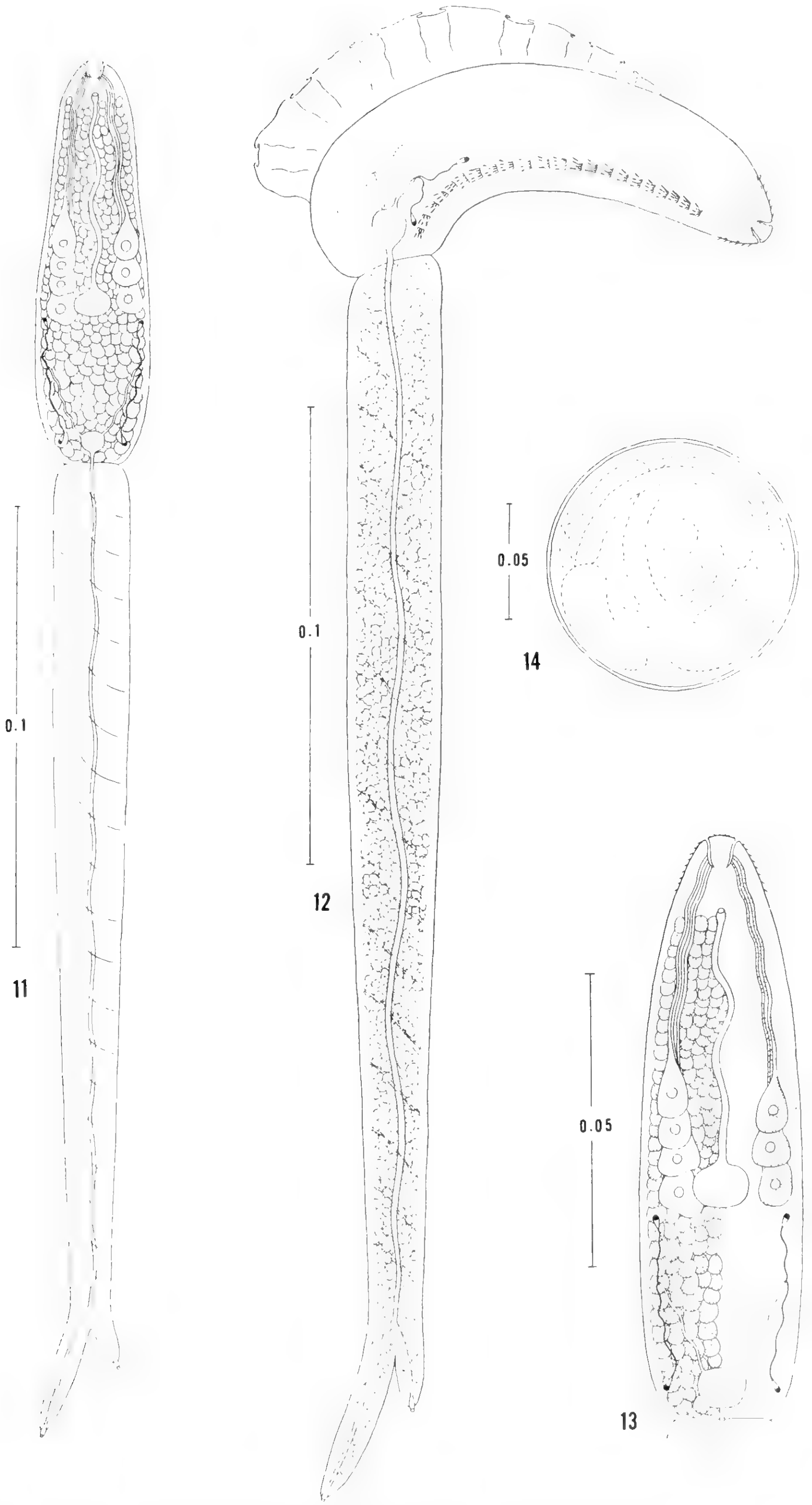
Cercariae of the family Aporocotylidae were found. Marine larvae of that group have the following general diagnosis:

Apharyngeate, non-ocellate, brevifurcate cercariae developing in marine lamellibranchs and annelids. The tail is variously modified with symmetrical or asymmetrical furcae, no furcae, or reduced to a small pointed structure. Finfold present or absent on the dorsal body surface and on the furcae. Cephalic organ reduced or lacking; penetration gland ducts discharge through pores on spinous anterior end of body. Acetabulum absent except in *C. hartmanae* Martin, 1952. Cercariae penetrate the definitive host and develop to adult worms in the blood vascular system or rarely in the coelom of fishes.

Cercaria asymmetrica sp. nov.

(Figures 11-14)

Description: body 0.092-0.121 (0.112) long, 0.025-0.032 (0.027) in maximum width posterior to midbody. Tail stem 0.219-0.265 (0.247) long, 0.020-0.028 (0.023) in maximum width. Right furca 0.033 long; left furca 0.010 long. Body with plicated, dorsal finfold, 0.090 long and 0.008 wide. Anterior tip of body encircled with parallel rows of minute spines; cuticle of body and tail smooth with exception of a row of 22-24 groups of retrorse



Figures 11-14. **11.** *Cercaria asymmetrica*, sp. nov., ventral view showing details of body and tail. **12.** Same, lateral view showing arrangement of ventrolateral row of body spines. **13.** Same, ventral view of cercarial body. **14.** Same, sporocyst.

spines, 3 or 4 spines per group, extending most of length of each ventrolateral surface of body; spines in each group diverging from bases set close together. Body filled with granular cells making observation of internal structure difficult. Apparently four overlapping, granular penetration glands on right side and three on left side of midbody, with ducts opening at base of protrusible cephalic papilla terminal in position. Mouth subterminal, ventral; esophagus narrow, slightly sinuous, joining small, sac-shaped cecum located just posterior to midbody. Excretory bladder small, spherical. Main excretory tubules short, each receiving short anterior and posterior collecting tubule. Flame cell formula $2(1+1)=4$. Caudal excretory duct extending through tail stem, bifurcating into furcae and discharging through minute vesicle at tip of each furca. Tail stem and furcae filled with vacuolated parenchyma and scattered nuclei, stem with oblique muscles giving stem spiral appearance. Development in minute, whitish, granular sporocysts in gonad of host. Sporocysts spherical to slightly oval, 0.087-0.128 (0.113) in diameter, each containing 4 to 8 embryos in various stages of development; birth pore not observed.

Host: Donax variabilis Say

Incidence of infection: 8 of 1,763 clams.

Locality: Gulf Beach, Alligator Point, Franklin County, Florida.

The specific name of this cercaria refers to its asymmetrical tail.

Spontaneous emergence of this cercaria from only 2 of the 8 clams was observed; the other 6 were diagnosed by microscopic examination of smears from the gonads, without which it was difficult to detect the presence of the parasite. *Donax variabilis* is a dioecious species in which the testes are cream colored and the ovaries pink. Because sporocysts of this cercaria are cream colored and minute, their presence may be overlooked in the normal male gonad or in the ovary of the heavily infected female. Studies of varying degrees of parasitism in both male and female *Donax* suggest that the clam may be castrated by the infection.

Exposure of infected clams to alternating periods of dark and light, and others to constant light, failed to stimulate emergence of cercariae. Such a stimulus may be concerned with tidal fluctuations, water temperature, currents, or other phenomena which are difficult to duplicate in the laboratory.

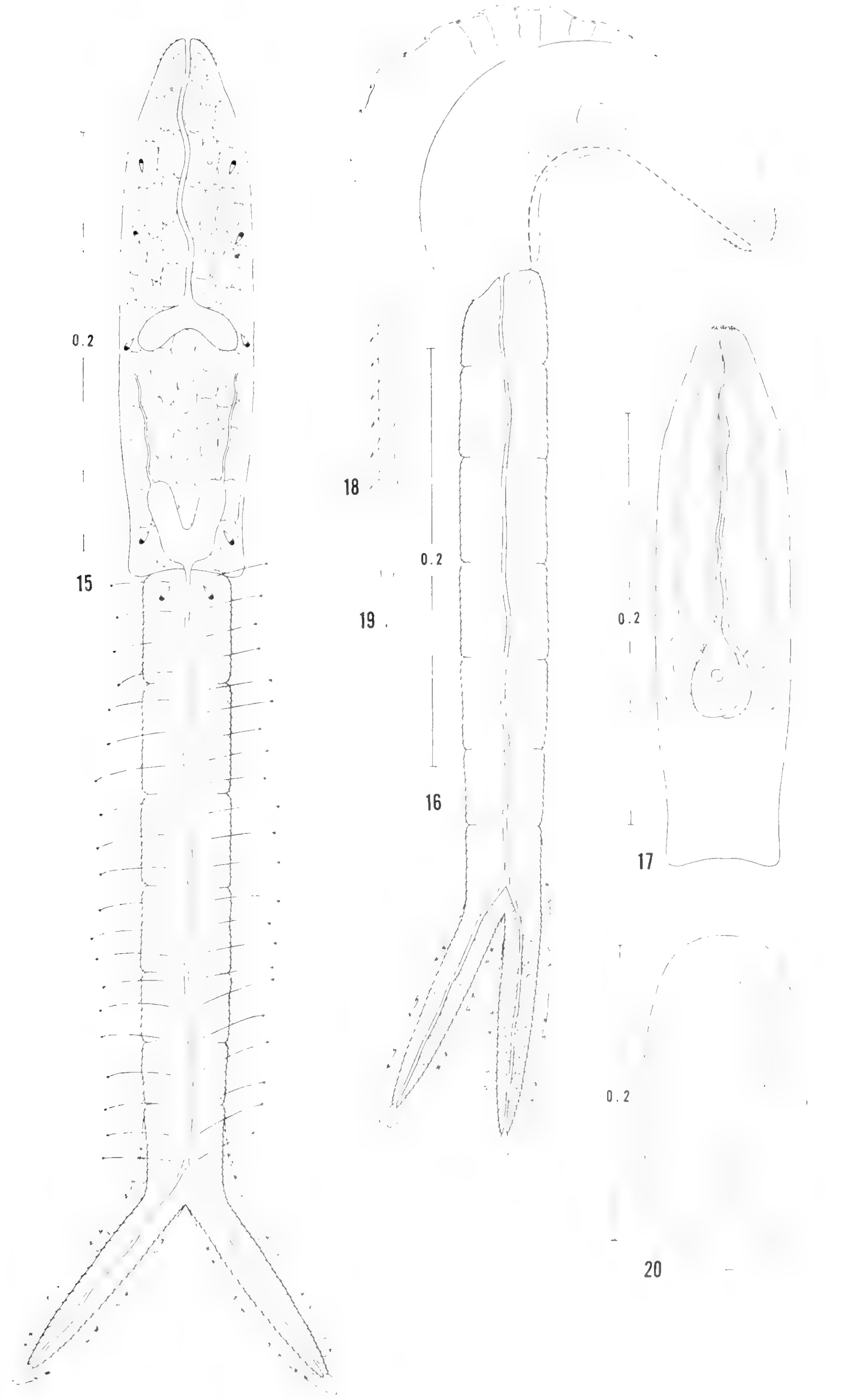
This cercaria swims with a rapid vibratory motion followed by a rest period during which it slowly sinks, with the body flexed ventrally, the tail stem straight and at a right angle to the body axis, and the furcae together. The body is capable of extension and contraction, during which time the cephalic papilla is protruded and retracted. The life span is about 12 hours. No phototropisms were observed. Neutral red stains the penetration glands and nuclei in the tail and is relatively non-toxic. Nile blue sulfate also stains the penetration glands and is toxic.

Cercaria asymmetrica does not closely resemble any of the other 4 reported species of marine aporocotylid larvae. The furcae are considerably more asymmetrical than in *C. loossi* as reported by Stunkard (1929). Ventro-lateral rows of spines on the body were reported by Martin (1944a) for *C. solemyae,* but that species has 5 pairs of penetration glands and its tail is reduced to a small, pointed structure.

Cercaria cristulata sp. nov.

(Figures 15-20)

Description: body 0.240-0.275 (0.260) long, 0.028-0.036 (0.033) wide at midbody. Tail stem 0.265-0.316 (0.297) long, 0.029-0.035 (0.032) in maximum width. Furcae 0.063-0.075 (0.068) long, 0.012-0.015 (0.014) wide at base. Plicated furcal finfold extending along entire medial and lateral surfaces of furcae and appreciably onto tail stem; lateral portion of finfold 0.085-0.098 (0.093) long, 0.007 in maximum width at about middle of furca. Dorsal finfold of body plicated, 0.107-0.133 (0.120) long, 0.025-0.029 (0.026) wide at widest point. Anterior tip of body protrusible, encircled with parallel rows of minute spines. Longitudinal row of about 94 spines on each ventro-lateral surface of body. Remainder of body smooth. Tail stem and furcae with minute spines. Body filled with large granular cells, making observation of excretory system and penetration glands difficult. Mouth terminal; esophagus narrow, slightly sinuous, bifurcating into short, wide ceca at midbody. Penetration glands located just posterior to midbody in 4 pairs, 2 lat-



Figures 15-20. **15.** *Cercaria cristulata*, sp. nov., dorsal view showing details of body and tail. **16.** Same, lateral view with ventrolateral row of spines represented by dotted line. **17.** Same, dorsal view of cercarial body showing arrangement of penetration glands. **18.** Same, longitudinal section through cuticle showing arrangement of spines in ventrolateral rows. **19.** Same, surficial view of single spine from row. **20.** Same, sporocyst.

eral, one dorsal and one ventral; their ducts extending anteriorly in four pairs to open symmetrically around mouth. Small genital primordium situated ventrally in posterior half of body. Excretory bladder small, U-shaped. Main excretory tubules discharging into anterior tip of each arm of bladder. Anterior and posterior collecting tubules not discernible. Four pairs of flame cells in body, one pair in anterior end of tail stem. Caudal excretory duct bifurcating into furcae and terminating in small vesicles opening through finfolds at tips of furcae. Dorsal surface of tail stem with right and left submedial longitudinal rows of long bristles appearing to terminate in minute knobs. Tail stem with oblique muscle fibers and scattered nuclei. Furcae filled with vacuolated parenchyma. Development in minute, oval, whitish, granular sporocysts in gonad of host. Sporocysts 0.204-0.286 (0.227) long, 0.071-0.128 (0.102) wide; each with 4 to 8 tightly packed embryos in various stages of development. Birth pore not observed.

Host: Chione cancellata Linné

Incidence of infection: One of 120 clams.

Locality: Bay mouth sand bar, Alligator Harbor, Franklin County, Florida.

The specific name of this cercaria is taken from the Latin *cristulatus,* meaning "with a small crest" and refers to the body finfold.

Naturally emerging cercariae swim with an extreme vibratory motion for a short interval followed by a rest period with gradual settling to the bottom where the tail stem is held straight and the body flexed ventrally. Creeping movement occurs only occasionally. Emergence occurs during either the day or night; life span of cercaria about 12 hours.

This larva is killed quickly with Nile blue sulfate. Neutral red is only slightly toxic and readily stains the penetration glands, their ducts, and the cecal contents. No phototropisms were observed.

This cercaria resembles *C. solemyae* Martin, 1944, and the preceding species in having longitudinal rows of body spines. It differs, however, from *C. solemyae* in almost all other morphological features (*e.g.,* size and shape of tail, number and arrangement of penetration glands, flame cell pattern, and shape of ceca). It differs from all other known marine aporocotylids by having: furcae of equal length with finfolds, 4 pairs of pentration glands and a discernible genital primordium.

D. *Fellodistomatid Cercariae*

The larvae of the family Fellodistomatidae are probably the most widely studied, yet poorly described, of all marine cercariae. The next 5 species described below are larvae in the subfamily Gymnophallinae. Cable (1953) elucidated the life cycle of *Parvatrema borinqueñae,* a marine gymnophalline having a minute, fork-tailed cercaria. He emended the Fellodistomatidae to receive the Gymnophallinae, basing his conclusions on similarities of the excretory systems, host relationships of larval forms, and morphological affinities of the adults. The Gymnophallinae, whose larvae develop in bivalves and become metacercariae in gastropods and bivalves, had formerly been included in the Microphallidae. Members of this family, however, have xiphidiocercariae developing in gastropods and encysting in various other intertebrates; whereas metacercariae of the Gymnophallinae do not encyst, but live between the mantle and shell, commonly in bivalves and rarely in gastropods. Lebour (1908, 1911), Palombi (1924), and others have described these unencysted metacercariae as cercariae, and have thus confused the literature. Giard (1907), Jameson (1902), Jameson and Nicoll (1913), and others have reported pearl formation around gymnophalline larvae in *Mytilus edulis,* due to irritation of the mantle by the metacercariae.

Stunkard and Uzmann (1958) published an excellent review of *Gymnophallus* and *Parvatrema.* They pointed out that many adult gymnophallines are not clearly distinguished by their descriptions, that little correlation has been made between known cercariae, metacercariae and adults, and that many unencysted metacercariae have been mistaken for cercariae. Concerning these two genera, they stated in conclusion that "the situation is chaotic and one of utter confusion."

Four closely related species of minute furcocercous cercariae were found in the present survey; these all probably have adults of the genus *Parvatrema.* A single species of tailless larva was found which is typical of the "cercariaeum" group proposed by

Lühe (1909) and elaborated upon by Sewell (1922) and Dubois (1929). This larva is probably a member of the genus *Gymnophallus.*

Fellodistomatid cercariae are characterized by the following general diagnosis abstracted from Cable (1956a):

Distome cercariae lacking eyespots and stylet. Tail well developed, reduced or lacking; if well developed, either trichocercous, trichofurcocercous, or furcocercous. Suckers well developed, prepharynx short or lacking, ceca varying from short and wide to slender and elongate. Excretory bladder U- or V-shaped, thin walled, with short stem and long arms extending anterior to ventral sucker; bladder more or less filled with refractile concretions. Main excretory tubules ciliated. Flame cells absent from tail stem of furcocercous forms. Caudal excretory tubule conspicuous, extending through tail stem, dividing at furcal junction and opening through pores on furcae. Development in sporocysts in marine lamellibranchs. Metacercariae in invertebrates so far as known; adults in intestines and gall bladders of aquatic birds and fishes.

Cercaria imbecilla sp. nov.
(Figures 21-22)

Description: furcocercous gymnophalline larva. Body 0.122-0.133 (0.128) long, 0.036-0.046 (0.040) wide at level of acetabulum. Tail stem 0.037-0.038 (0.037) long from point of attachment to posterior notch between furcae, 0.016-0.017 (0.016) wide at base. Furcae 0.035-0.037 (0.035) long, 0.009-0.010 (0.009) wide at base. Oral sucker 0.028-0.030 (0.029) long, 0.023-0.025 (0.024) wide; mouth subterminal; prepharynx absent; pharynx 0.012-0.013 (0.012) long, 0.010-0.012 (0.011) wide; esophagus long; ceca short, thick walled, extending only slightly posterior to anterior edge of acetabulum. Acetabulum 0.022 long, 0.022-0.024 (0.023) wide, located in posterior half of body, with double row of minute spines in cavity. Entire body and tail spinose; anterior half of body with scattered bristles. Two pairs of submedial penetration glands dorsal to ceca. Anterior gland of each pair just anterior to cecum, overlapping anteromedial border of excretory bladder arm; posterior gland overlapping cecum and medial border of excretory bladder arm, conforming to anterior curvature of acetabulum, and only slightly overlapping its anterior border. Two pairs of penetration gland ducts adhering closely to esophagus and pharynx, passing dorsally to oral sucker, and discharging through individual pores on dorsal lip. Excretory bladder U-shaped with arms extending just beyond bifurcation of gut, with spherical to oval concretions. Ciliated main excretory tubules joining anterolateral margins of arms, extending anteriorly a short distance and receiving anterior and posterior collecting tubule. Excretory tubules and flame cells visible only after staining with Nile blue sulfate. Flame cell formula $2[(1)+(1)] = 4$. Caudal excretory pores on posteromedial surface of each furca near tip. Body filled with indistinct, large, lightly granular cells. Tail with many minute nuclei. Development in cream colored, saccular sporocysts infiltrating gonad of host; wall composed of minute spherical cells. Sporocysts 0.347-0.719 (0.479) long, 0.133-0.250 (0.190) wide. About 50-300 densely packed embryos in all stages of development per sporocyst; birth pore terminal.

Host: Mulinia lateralis Say

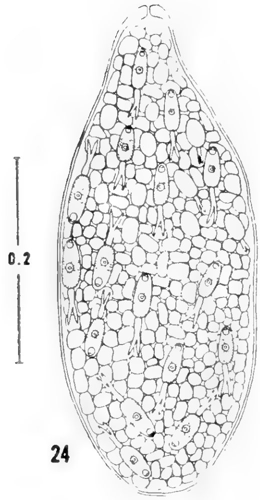
Incidence of infection: 30 of 446 clams.

Locality: Salt marsh, St. Marks Light, Wakulla County, Florida.

The specific name of this cercaria is taken from the Latin *imbecillus,* meaning "feeble" and refers to the swimming ability of the species.

This minute species emerges at all hours and displays no phototropisms. The life span is about 18 hours. Neutral red is slightly toxic and stains the granular cells of the cecal walls and the penetration glands. Nile blue sulfate, which is more toxic and kills cercariae in about 10 minutes, stains the penetration glands, stimulates flame cell activity, and causes the enlargement of the excretory tubules. Swimming is typical of small furcocercous gymnophalline larvae; the tail lashes feebly from side to side with the body flexed ventrally and hanging downward. Periods of swimming alternate with creeping on the bottom with the furcae held together.

This cercaria differs from any previously described larvae of its type in having the combined features of 2 pairs of penetration glands, 2 pairs of flame cells, excretory pores



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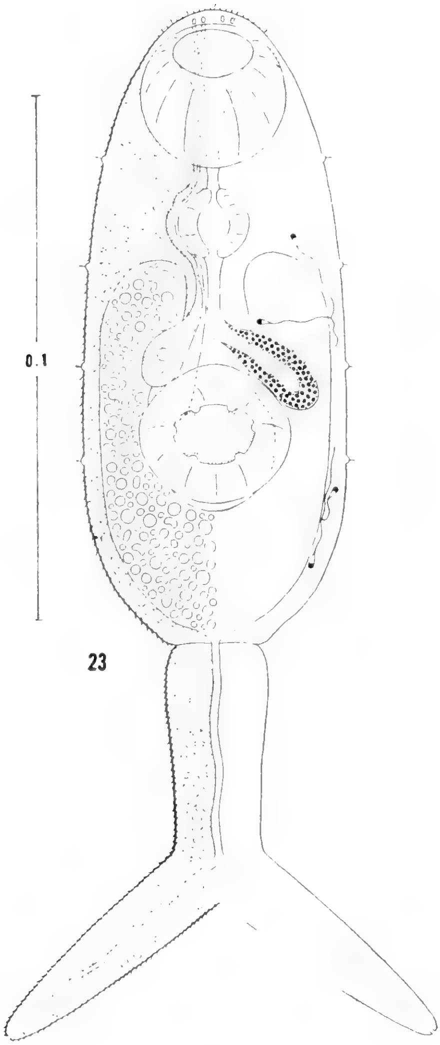

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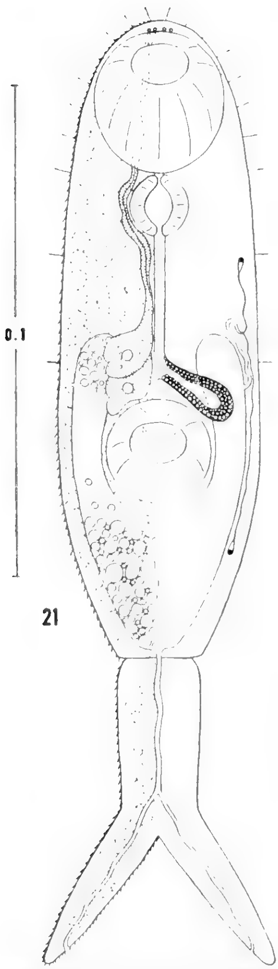

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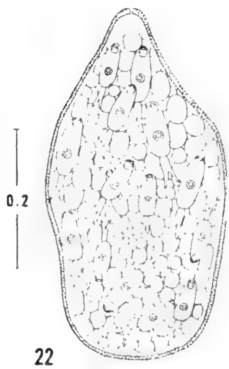

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Figures 21-24. **21.** *Cercaria imbecilla*, sp. nov., ventral view showing details of body and tail. **22.** Same, sporocyst. **23.** *Cercaria fragosa*, sp. nov., ventral view showing details of body and tail. **24.** Same, sporocyst.

on posteromedial surfaces of furcae and uneven distribution of concretions in the excretory bladder. It resembles *C. pusilla* (described below); both have the same excretory formula, same number of penetration glands, similar digestive system and similar location of excretory pores but differ in respects that will be given in discussing *C. pusilla.*

Cercaria fragosa, sp. nov.
(Figures 23-24)

Description: furcocercous gymnophalline larva. Body 0.110-0.125 (0.118), long, 0.041-0.053 (0.048) wide at level of ventral sucker. Tail stem 0.044-0.048 (0.047) long from point of attachment to posterior notch between furcae, 0.018-0.016 (0.017) wide at base. Furcae 0.044-0.047 (0.046) long, 0.009-0.010 (0.010) wide at base. Oral sucker 0.025-0.030 (0.028) in diameter; mouth subterminal; prepharynx very short. Pharynx 0.012-0.014 (0.012) long, 0.014-0.016 (0.014) wide; esophagus 0.012 long; ceca short, thick walled, conforming to and only slightly overlapping anterior margin of acetabulum. Acetabulum 0.025-0.031 (0.028) long, 0.027-0.032 (0.030) wide, in posterior half of body. Several rows of minute spines lining cavity, with six papillae around opening of sucker. Entire body and tail spinose. Cephalic region with fine bristles. Body surface between posterior margins of oral and ventral suckers with scattered short bristles set in papillae. Two pairs of penetration glands, submedial and dorsal to ceca. Anterior glands overlapping medial border of excretory bladder arm and cecum; posterior glands overlapping medial border of bladder arm and anterior border of acetabulum; their ducts as in preceding species. Excretory bladder U-shaped, each arm with short median bulge at anterior margin of ventral sucker, with anterior extension of arm barely or not quite reaching level of pharynx. Spherical, oval and reniform concretions filling excretory bladder. Excretory tubules not visible; four pairs of flame cells. Flame cell formula probably $2[(2)+(2)]=8$. Caudal excretory pores at furcal tips. Body filled with indistinct, lightly granular cells. Tail with many minute nuclei. Development in whitish, saccular sporocysts with thin, smooth walls in liver and gonad of host. Sporocyst 0.315-0.735 (0.500) long, 0.120-0.270 (0.194) wide. About 50-150 densely packed embryos in all stages of development per sporocyst; birth pore terminal.

Host: Donax variabilis Say

Incidence of Infection: 18 of 1763 clams.

Locality: Gulf beach, Alligator Point, Franklin County, Florida.

The specific name of this cercaria is taken from the Latin *fragosa,* meaning "fragile."

This species was not observed to emerge spontaneously. It may do so and reenter the molluscan host, which would account for the large number of metacercariae found in the mantle chambers of *Donax variabilis* that did not harbor sporocysts. To recover mature cercariae for this study, sporocysts were teased from the gonad of the host, and only those cercariae which freely emerged from the sporocysts were used. No phototropisms were observed. Neutral red, only mildly toxic, stains the granular ceca and their contents, and the penetration glands. Nile blue sulfate, also only mildly toxic, stimulates flame cell activity and stains the ceca, their contents and the penetration glands. The swimming movements of this form are typical for the group.

This cercaria appears to be most closely related to the cercaria of *Parvatrema donacis* Hopkins, 1958, from *Donax variabilis* collected at Mustang Island, Texas. The following table is a comparison of certain features of these two forms. The differences indicated are considered to be of specific value.

	Cercaria of *Parvatrema donacis*	*Cercaria fragosa,* sp. nov.
Penetration glands	"too inconspicuous to count"	2 pairs
Flame cells	3 pairs on each side	$2[(2)+(2)]=8$
Papillae and bristles	none noted	on body
Embryos per sporocyst	6	50-150

Cercaria pusilla, sp. nov.
(Figures 25-26)

Description: furcocercous gymnophalline larva. Body 0.122-0.153 (0.139) long, 0.046-0.056 (0.052) wide at level of acetabulum. Tail stem 0.036-0.040 (0.037) from point of attachment to notch between furcae, 0.015-0.017 (0.016) wide at base. Furcae 0.046-0.053 (0.051) long, 0.009-0.010 (0.010) wide at base. Oral sucker 0.023-0.026 (0.025) in diameter; mouth subterminal; prepharynx extremely short; pharynx 0.015

0.017 (0.015) long, 0.012-0.014 (0.013) wide; esophagus long; ceca short, with thick, granular walls only slightly overlapping anterior margin of ventral sucker. Ventral sucker 0.023-0.025 (0.024) in diameter, in posterior half of body and with several rows of minute spines inside its cavity. Body and tail entirely spinose except narrow perimeter around mouth. Body, anterior to ventral sucker, with short bristles, densest and slightly shorter in cephalic region. Two pairs of small penetration glands in close proximity to esophagus. Anterior glands just overlapping anterior arms of excretory vesicle; posterior glands overlapping anteromedial borders of excretory arms, and reaching level of gut bifurcation; their ducts extend anteriorly, passing around pharynx and dorsal of oral sucker to open individually on dorsal lip. Genital primordium medial, just anterior to acetabulum. Excretory bladder U-shaped with arms extending slightly anterior to gut bifurcation; filled with spherical concretions. A short ciliated main excretory tubule joining the anterolateral region of each arm, and extending anteriorly to receive anterior and posterior collecting tubule, each draining one flame cell. Flame cell formula $2[(1) + (1)] = 4$. Caudal excretory pores on the posteromedial surfaces of furcae. Body filled with indistinct, large, lightly granular cells. Development in cream colored, saccular sporocysts in gonad of host; their walls thin and smooth. Sporocysts 0.420-0.735 (0.570) long, 0.120-0.180 (0.146) wide. About 40-200 densely packed embryos in all stages of development per sporocyst; birth pore terminal.

Host: Chione cancellata Linné

Incidence of infection: 3 of 120 clams.

Locality: Bay mouth sand bar, Alligator Harbor, Franklin County, Florida.

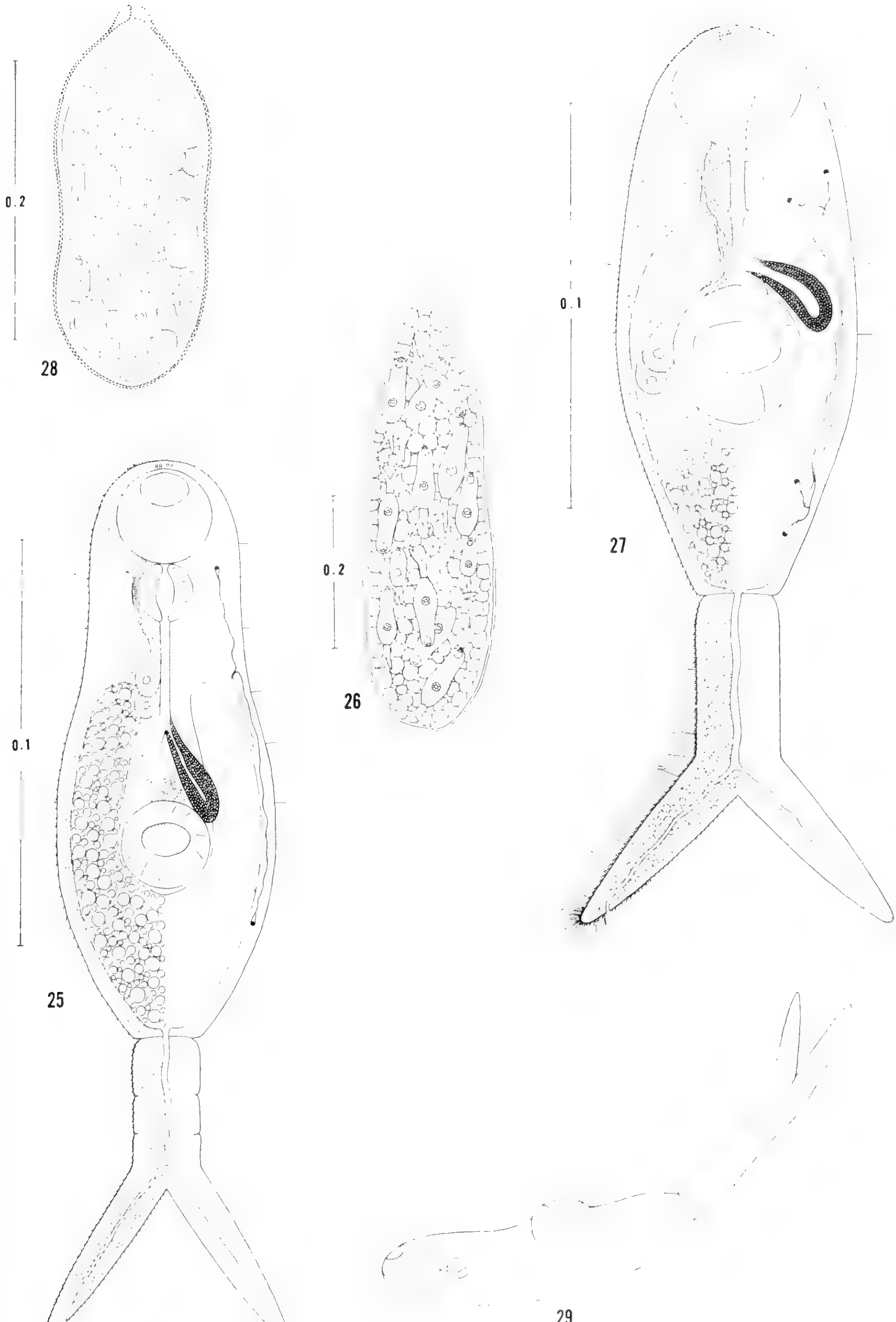
The specific name of this larva is taken from the Latin *pusillus,* meaning "weak" or "very small."

This cercaria emerges at any hour in small numbers, and displays no phototropisms. Neutral red is moderately toxic and stains the walls of the ceca. Nile blue sulfate is very toxic and also stains the ceca. The penetration glands do not react to either stain. The swimming movements are typical for this group.

This cercaria resembles *Cerceria imbecilla* but differs from it in the size, position and staining reaction of the penetration glands, host, presence of the genital primordium, distribution of concretions in the excretory vesicle, and the position of flame cells. *C. imbecilla* and *C. pusilla* are both closely related to the larva of *Parvatrema borinqueñae* Cable, 1953, but differ from it in having 2 pairs of pentration glands instead of one pair, and by lacking medial bulges of the excretory bladder arms.

Cercaria fimbriata, sp. nov.
(Figures 27-29)

Description: furcocercous gymnophalline larva. Body 0.128-0.153 (0.140) long, 0.053-0.063 (0.059) wide at level of acetabulum. Tail stem 0.047-0.052 (0.049) long from point of attachment to posterior notch between furcae, 0.018-0.021 (0.019) wide at base. Furcae 0.047-0.051 (0.049) long, 0.012-0.014 (0.013) wide at base. Oral sucker 0.026-0.032 (0.029) long, 0.028-0.035 (0.031) wide; mouth subterminal; prepharynx very short; pharynx 0.013-0.016 (0.014) in diameter; esophagus long; ceca short, thick walled, conforming to anterior curvature of acetabulum but not quite touching it. Acetabulum 0.031-0.037 (0.034) long, 0.030-0.033 (0.031) wide, located just posterior to midbody. Entire body and tail spinose. Anterior half of body with scattered bristles, those at cephalic end of two lengths. Lateral surfaces of tail stem and furcae covered with dense brush-like bristles diminishing in length and disappearing about half way up medial surfaces of furcae. Two pairs of small penetration glands, lateral to acetabulum and overlapping arm of excretory vesicle; their ducts passing anteriorly dorsal to ceca and oral sucker to open separately at pores on dorsal lip. Excretory bladder U-shaped with arms extending to mid-esophageal level; with spherical concretions less numerous in arms than in body of bladder; a ciliated, main excretory tubule joins each arm middorsally, some distance from its anterior end, extends laterally a short distance to receive short anterior and long posterior collecting tubule, both ciliated. Flame cell formula $2[(2) + (2)] = 8$. Excretory system of tail as in preceding species. Body filled with indistinct, lightly granular cells. Development in saccular, white sporocysts in gonad of host, their walls with minute, spherical nuclei imparting a granular appear-



Figures 25-29. **25.** *Cercaria pusilla*, sp. nov., ventral view showing details of body and tail. **26.** Same, sporocyst. **27.** *Cercaria fimbriata*, sp. nov., ventral view showing details of body and tail. **28.** Same, sporocyst. **29.** *Cercaria imbecilla*, sp. nov., *C. fragosa*, sp. nov., *C. pusilla*, sp. nov., and *C. fimbriata*, sp. nov., lateral view showing swimming posture.

ance. Sporocyst 0.219-0.444 (0.278) long, 0.087-0.128 (0.108) wide. About 10-30 embryos per sporocyst in all stages of development; birth pore terminal. Light stimulates movement of immature cercariae within sporocyst.

Host: Semele proficua Pulteney

Incidence of infection: 7 of 9 clams.

Locality: Salt marsh, north of St. Marks Light, Wakulla County, Florida.

The specific name of this larva is taken from the Latin *fimbriatus*, meaning "fringed," as applied to the tail.

This cercaria emerges in response to light, is phototropic, and has a life span of about 12 hours. Neutral red is not toxic and stains the ceca and their contents, whereas Nile blue sulfate is very toxic, stains the cecal contents, stimulates flame cell activity and causes the enlargement of the excretory tubules; neither stains the penetration glands.

The swimming movements are typical of the group. If the container is tapped gently, the cercariae contract suddenly. After a few seconds they slowly begin to relax and return to swimming. At rest, they sink to the bottom and lie motionless or show creeping movements.

This cercaria resembles *Cercaria fragosa* but differs from it in body and tail bristles, position and size of penetration glands, and distinctness of main collecting tubules.

The insertion of the main excretory tubules on the dorsal surface of the excretory bladder arms has been reported also for the metacercaria of *Parvatrema borinqueñae* Cable, 1956, and for the cercaria of *Parvatrema donacis* Hopkins, 1958.

Cercaria granosa, sp. nov.
(Figures 30-32)

Description: tailless gymnophalline larva. Body 0.230-0.255 (0.243) long, 0.102-0.143 (0.126) in maximum width slightly anterior to level of ventral sucker. Oral sucker 0.059-0.070 (0.064) long, 0.066-0.076 (0.072) wide including pair of large lateral papillae; mouth subterminal with 8 surrounding papillae; prepharynx absent; pharynx 0.018-0.023 (0.022) long, 0.021-0.026 (0.023) wide; esophagus very short; ceca short, voluminous, filling body to posterior margin of acetabulum, and containing spherical and rod-shaped granules and large hyaline globules. Acetabulum 0.028-0.035 (0.031) in diameter, with 5 papillae bordering its cavity. Dorsal body surface with parallel rows of small spines; those on ventral surface even smaller; bristles scattered over body surface, those in cephalic region set in papillae. Additional papillae on anterior rim of oral sucker. Nine small penetration glands on each side of pharynx and along posterior edge of oral sucker, some separate and some in groups with their arrangement laterally from pharynx apparently being 3, 1, 2, 1, 1, 1, with ducts opening at anterior end of body. Excretory bladder Y-shaped with short stem and canal with pore at posterior end of body, and long arms extending to sides of oral sucker. Bladder filled with spherical concretions of various sizes. A short anterior and long posterior collecting tubule joining to form short, ciliated main tubule discharging into lateral margin of bladder arm. Flame cell formula $2[(2+2)+(2)]=12$. Primordium of ovary between anterior margin of acetabulum and bifurcation of ceca; testicular primordium on each side of excretory vesicle occupying indentations in the margins of vesicle. Primordia best observed when stained with neutral red. Indistinct, lightly granular cells in body obscured by contents of ceca and excretory vesicle. Development in light-orange, thin walled sporocysts in gonad of host. Sporocyst 0.306-0.403 (0.355) long, 0.112-0.194 (0.148) wide. Not more than 4 embryos per sporocyst in various stages of development. Birth pore not observed.

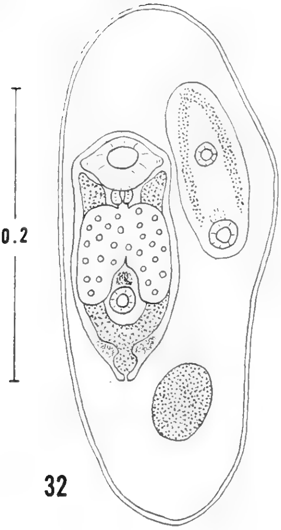
Host: Mulinia lateralis Say

Incidence of infection: 56 of 446 clams.

Locality: Salt marsh, St. Marks Light (type locality), and Live Oak Point, Wakulla County, Florida.

The specific name of this cercaria is taken from the Latin *granosus*, meaning "full of grains" and refers to the contents of the ceca and excretory vesicle.

Spontaneous emergence of this larva from the host was not observed. The above description is based on cercariae that freely emerged from sporocysts teased from the gonad of the host. Although lacking a tail and unable to swim, this species creeps on the bottom, using the suckers for holdfasts. No phototropisms were observed. Neutral red, only slightly toxic, stains the cecal contents and the genital primordia. Nile blue sulfate, which is more toxic,



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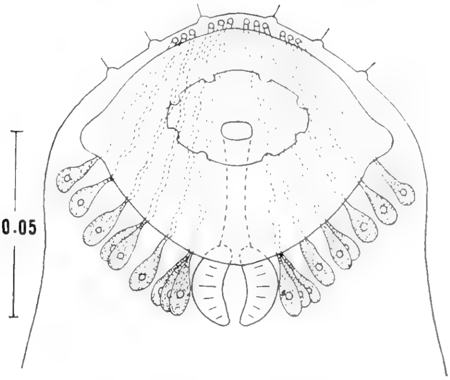

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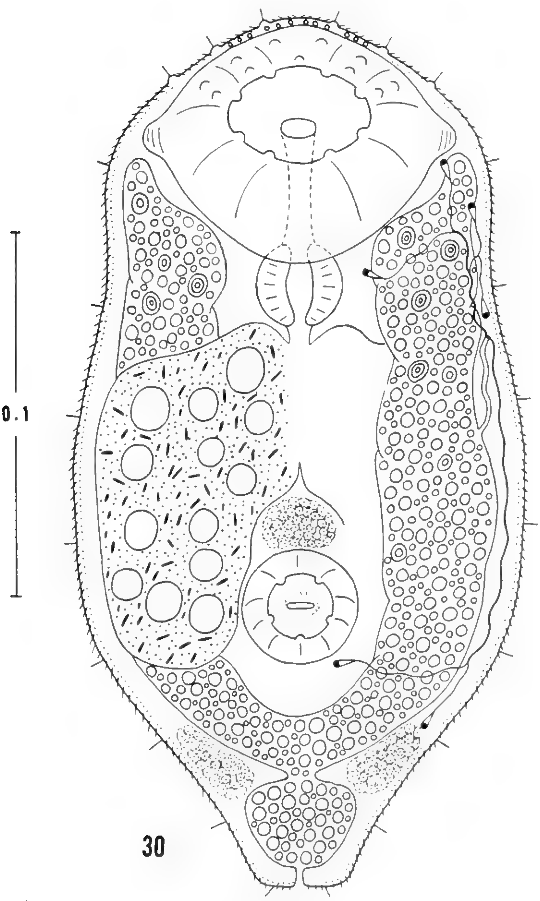

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Figures 30-32. **30.** *Cercaria granosa*, sp. nov., ventral view showing details of body. **31.** Same, ventral view of cephalic end showing cephalic glands and ducts. **32.** Same, sporocyst.

stains the pentration glands and their ducts.

This larva probably becomes the metacercaria found unencysted on the mantles of *Cerithidea scalariformis* in the same localities. Almost all these snails are infected with this metacercaria that appears slightly larger than *Cercaria granosa,* and has a greater development of the genital primordia..

Cercaria granosa resembles *C. cambrensis* Cole, 1938, from *Cardium edule,* but differs from that species in respects summarized as follows:

Cercaria cambrensis Cole, 1938	*Cercaria granosa* sp. nov.
Testicular primordia present, ovarian absent	Testicular and ovarian primordia present
Oral sucker small, lateral papillae absent	Oral sucker large, with lateral papilla
Two anterior flame cells 4 posterior	Four anterior flame cells, 2 posterior
Ceca thick walled, anterior to acetabulum	Ceca thin walled, extending behind acetabulum

The relationship of cercariae of this type to the adults of the genus *Gymnophallus* has been established by Jameson (1902), Lebour (1908, 1911), Dollfus (1912), and Jameson and Nicoll (1913).

E. *Bucephalid Cercaria*

A single representative of this group is reported here.

Cercariae of the family Bucephalidae are characterized by the following general diagnosis:

Modified furcocercous cercariae with short, wide tail stem and furcae of complex structure that are long and extensile. Mouth ventral, near midbody, opening through pharynx into rhabdocoele intestine. Cephalic organ glandular, not associated with digestive tract. Development in branched sporocysts in marine and fresh water lamellibranchs.

Cercaria apalachiensis, sp. nov.
(Figures 33-36)

Description: body 0.153-0.209 (0.193) long, 0.051-0.061 (0.057) wide at midbody. Basal portion of tail stem 0.056-0.066 (0.061) long, 0.112-0.143 (0.130) wide. Furcae about 1.53 long, 0.015-0.020 (0.017) wide at base. Cephalic organ 0.044-0.058 (0.052) long, 0.030-0.037 (0.033) wide, with subterminal, mouth-like depression into which open ducts of undetermined number of penetration glands contained in organ. Cephalic organ slightly protrusible through depression, latter surrounded by 5 lips. Pharynx spherical, located just posterior to midbody, 0.012-0.016 (0.014) in diameter; cecum short, thick walled, with its free end pointing anteriorly. Cuticle of body spinose. Excretory bladder saccular, extending about half way from posterior end of body to pharynx; excretory pore at junction of body and basal portion of tail. Excretory tubules obscured by dense cystogenous cells. Six flame cells on each side, 2 pairs just behind cephalic organ, 4 pairs posterior to pharynx. Genital primordium medial, just posterior to pharynx. Oval, granular cystogenous cells in body so arranged to cause clear longitudinal area, devoid of cells on each side. Tail stem crenate and anteriorly granular, with numerous muscle fibers and scattered nuclei; posterior area of stem with many minute nuclei. Furcae granular, with rough cuticle. Development in whitish, granular, greatly branched sporocysts infiltrating gonad and liver of host. Sporocysts not measured.

Host: Mulinia lateralis Say

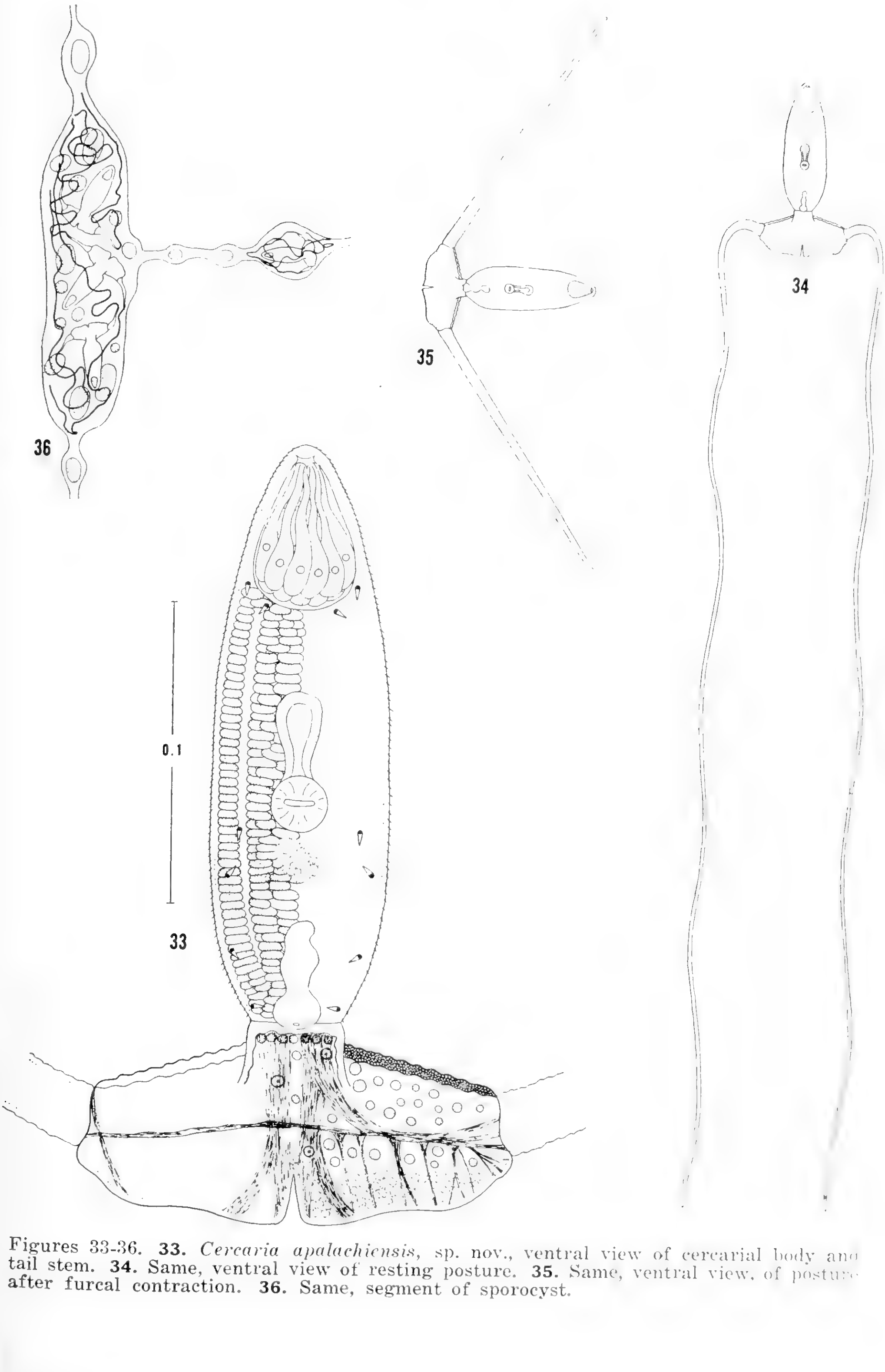
Incidence of infection: 1 of 446 clams.

Locality: Salt marsh, Live Oak Point, Wakulla County, Florida.

The specific name of this cercaria is based on the Indian word *Apalachee,* referring to the type locality.

This species emerges at any hour, day or night, in small numbers, and displays no phototropisms. It has a life span of about 18 hours. Neutral red, which does not seem to impair vitality, readily stains the genital primordium and the penetration glands. Nile blue sulfate is highly toxic and kills the cercaria quickly before stain reactions can be noted. No true swimming movements were observed, although the furcae elongate and contract. When water containing these cercariae is stirred, the furcae are violently contracted to about twice the body length and are temporarily oriented at an angle of about 60 degrees with the body in a rod-like manner (Figure 35). As the turbulence in the water subsides, the furcae slowly extend and form tangled masses. Cable (1956a) described a marine bucephalid cercaria from Puerto Rico that responded to agitation in water as does *Cercaria apalachiensis.*

Most of the published descriptions of marine bucephalid larvae are inadequate for comparison. Cable's (1956a) description of



Figures 33-36. **33.** *Cercaria apalachiensis*, sp. nov., ventral view of cercarial body and tail stem. **34.** Same, ventral view of resting posture. **35.** Same, ventral view, of posture after furcal contraction. **36.** Same, segment of sporocyst.

C. caribbea XLII is an exception. *C. apalachiensis* differs from it in having the combined features of a saccular excretory bladder, location of the genital primordium, and a distinctive tail stem.

F. *Echinostomatoid Cercariae*

The largest group of closely related cercariae recorded in the present study belong to the superfamily Echinostomatoidea. Three species, *C. favulosa, C. fuscata,* and *C. pustulosa* are new. Three species, cercaria of *Parorchis acanthus* (Nicoll, 1906), *Cercaria caribbea* III Cable, 1956, and cercaria of *Himasthla quissetensis* (Miller and Northup, 1926) are redescribed, with new information on their morphology and behavior.

Marine echinostomatoid cercariae are characterized by the following general diagnosis:

Distome cercariae bearing a cephalic collar, well-developed suckers and a non-bifurcated tail. Collar may be armed with a row of spines interrupted by an unarmed ventral space, or unarmed "Echinostomoid" group, Cable (1956a). Prepharynx and pharynx present, esophagus long, bifurcating anterior to ventral sucker. Excretory system with anterior and posterior secondary tubules which join ascending primary tubule at midbody, extend to anterior end of body, turn posteriorly, and empty into ante-chamber or directly into bladder. Rarely, a single secondary tubule may form ascending primary tubule in posterior end of body. Excretory bladder thin walled, spherical or sacculate; refractile concretions sometimes present in bladder and descending primary tubules. Body filled with dense cystogenous glands. Produced by rediae in gastropods. Encystment in snails, lamellibranchs, fishes or on substrate.

The first three cercariae in the following descriptions are placed in the Echinostomatidae and the remaining three in the Philophthalmidae. Philophthalmid cercariae, as have been described for *Parorchis, Philophthalmus* and *Cloacitrema,* have invaginated, glandular tail tips.

a. *Echinostomatid Cercariae*

Cercaria fuscata, sp. nov.

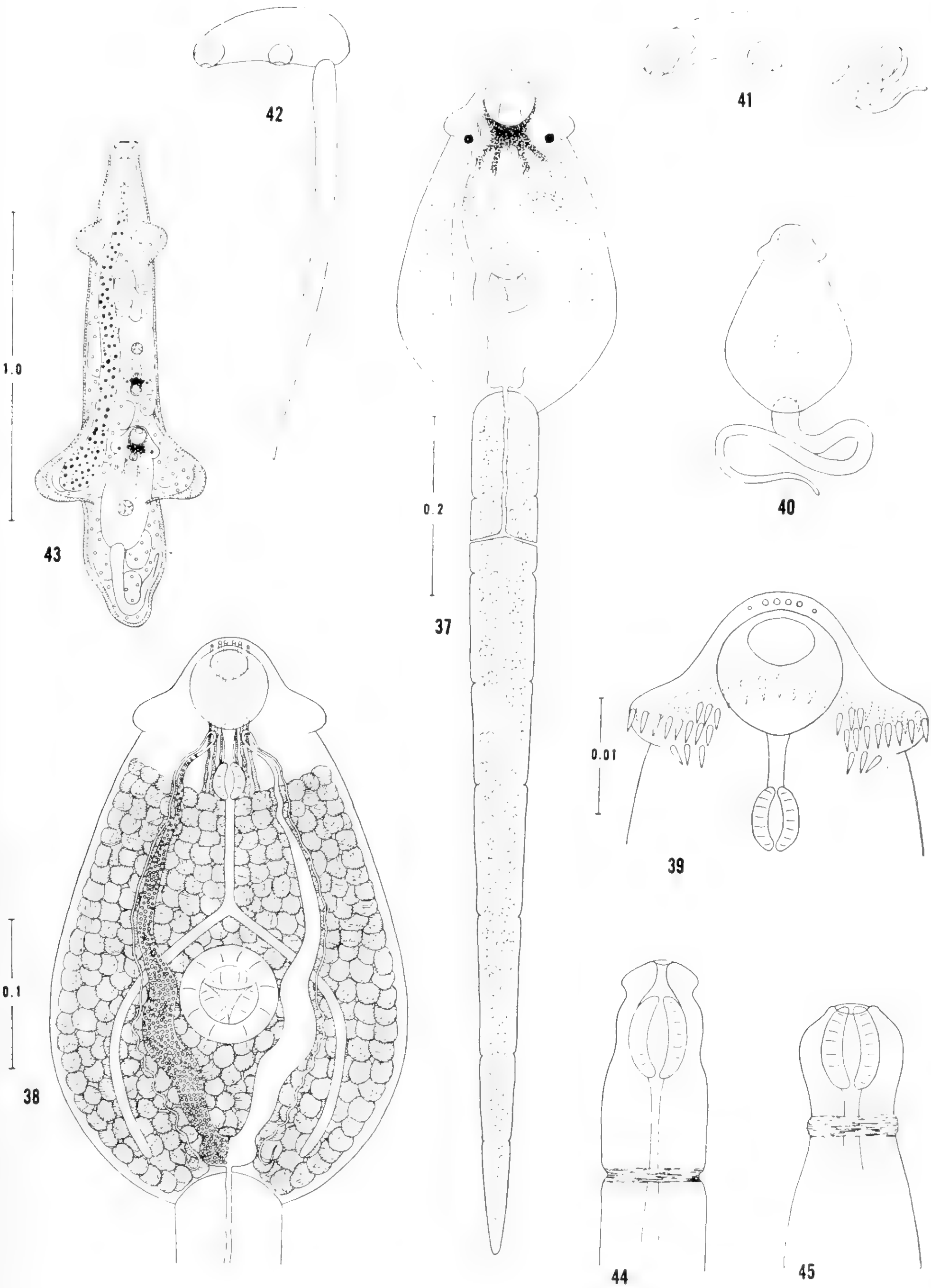
(Figures 37-45)

Description: body 0.306-0.408 (0.376) long, 0.219-0.255 (0.237) wide at posterior margin of acetabulum. Tail 0.870-1.035 (0.942) long, 0.066-0.077 (0.072) wide at base. Oral sucker 0.052-0.062 (0.056) long, 0.051-0.054 (0.052) wide; mouth subterminal; prepharynx 0.012-0.025 (0.022) long; pharynx 0.023-0.028 (0.025) long, 0.015-0.022 (0.018) wide; esophagus long, bifurcating at about 3/4 distance from pharynx to acetabulum; ceca narrow, extending to level of excretory bladder. Acetabulum posterior to midbody, 0.064-0.072 (0.068) long, 0.067-0.071 (0.069) wide. Body and tail smooth; papillae and bristles absent. Collar 0.112-0.128 (0.120) wide with 49 spines 0.015 long, arranged in a single row of 37 interrupted ventrally with 3 anterior and 3 posterior angle spines on each side. Body with dorsal layer of dense, rod-filled cystogenous cells obscuring many internal structures including cephalic ganglia, cephalic glands, and fine details of the excretory system. Cephalic glands poorly defined with ducts close to each side of pharynx and prepharynx, passing dorsally to oral sucker to open at small lateral, and 2 larger and more medial pores. Excretory bladder small, oval, receiving wide, descending limbs originating from narrow, ciliated ascending tubules at posterior margin of the oral sucker; secondary tubules, obscured by cystogenous glands, forming ascending limbs at level of excretory bladder. Bladder and descending limbs filled with small, spherical concretions. Caudal excretory tubule extending 1/6 length of tail to bifurcate and open on sides of tail. Two small eyespots of granular pigment lateral to prepharynx. Anterior 2/3 of body with similar pigment being generally denser anteriorly and concentrated around posterior margin of oral sucker to form dark zone with 4 streaks extending posteriorly to blend with granular pigmentation of forebody. Development in orange-brown rediae parasitizing liver and gonad of host and measuring 1.125-1.815 (1.586) long, 0.225-0.330 (0.282) wide; with appendages well developed; cuticle thick; cecum yellow-orange, granular, reaching level of posterior appendages; average of 10 embryos per redia, in all stages of development. Birth pore dorsal, just posterior to anterior appendages. Flame cells not apparent.

Host: *Cerithidea scalariformis* Say

Incidence of infection: 19 of 5,508 snails.

Locality: Salt marsh, St. Marks Light



Figures 37-45. **37.** *Cercaria fuscata*, sp. nov., ventral view showing body pigmentation and tail structure. **38.** Same, ventral view of cercarial body. **39.** Same, ventral view of cephalic end showing collar spines. **40.** Same, dorsal view showing swimming posture. **41.** Same, lateral view showing swimming posture. **42.** Same, lateral view showing posture when cercaria is killed in formalin. **43.** Same, redia. **44.** Same, cephalic end of redia extended. **45.** Same, cephalic end of redia retracted.

(type locality), and Shell Point, Wakulla County, Florida.

The name of this cercaria is from the Latin *fuscatus,* meaning "dusky" and refers to the pigmentation of the body.

This larva emerges in small numbers after the host has been dried and then immersed. It is positively phototropic, and has a life span of about 24 hours if encystment does not occur. Encystment can be stimulated by evaporation, cover slip pressure and vital dyes. The cyst is very similar to that of *Cercaria favulosa,* except for the brown tint imparted by pigment in *C. fuscata.* Nile blue sulfate is more toxic than neutral red and neither is specific for particular structures.

This cercaria is a strong, active swimmer, lashing the tail from side to side in a figure 8 motion while driving the vibrating body forward through the water either dorsally or ventrally oriented. The body is contracted and slightly flexed ventrally while swimming (Figures 40, 41). At rest, the larva lies on the bottom with body contracted and tail extended, prior to encystment. Cercariae preserved in formalin have the tail extended and at a right angle to the body axis (Figure 42).

This cercaria differs from all other marine echinostomes by having 49 collar spines and pigment scattered throughout the body.

Cercaria of *Himasthla quissetensis* (Miller and Northup, 1926) (Figures 46-50)

Description: body 0.418-0.530 (0.468) long, 0.112-0.143 (0.127) wide at level of acetabulum. Tail 0.316-0.352 (0.332) long, 0.031-0.036 (0.033) wide at base. Oral sucker 0.040-0.044 (0.042) in diameter; mouth subterminal; prepharynx 0.020-0.031 (0.024) long; pharynx 0.022-0.025 (0.025) long, 0.017 -0.022 (0.019) wide; esophagus long, bifurcating at about 3/4 distance from pharynx to acetabulum; ceca narrow, extending to level of excretory bladder. Acetabulum 0.063-0.070 (0.067) long, 0.066-0.075 (0.069) wide, just posterior to midbody. Cuticle of body and trail aspinose; anterior half of body with scattered bristles set in papillae. Collar 0.092-0.107 (0.098) wide with 31 spines in single row interrupted ventrally and 2 additional angle spines posterior to each end of row; those in row, 0.010 long; angle spines, 0.007 long. A group of small cephalic glands on each side between levels of pharynx and cecal bifurcation, with 2 ducts passing laterally to oral sucker and opening through individual pores on dorsal lip. One small gland, with no apparent duct, on each side of prepharynx just posterior to oral sucker. Excretory bladder small, oval, with short anterior stem receiving wide, descending limbs originating from narrow, ciliated ascending tubules at level of oral sucker; secondary tubules forming ascending limbs at level of excretory bladder; smaller tubules obscured by cystogenous glands. About 24 flame cells on each side. Descending limbs from junction with bladder stem to level of acetabulum almost filled with oval concretions and with scattered concretions anterior to that level. Caudal excretory tubule short, bifurcating to open at lateral pores on tail. Cephalic ganglia and cross commissure at level of prepharynx. Two genital primordia evident, one just anterior to junction of excretory bladder arms, other just anterior to acetabulum. Body with dorsal layer of dense, rod-filled cystogenous cells. Tail attached subterminally, filled with vacuolated parenchyma; cuticle indented at intervals over tail surface. Development in non-motile, whitish rediae in gonad and liver of host. Redia 1.110-1.455 (1.300) long, 0.225-0.330 (0.278) wide. Birth pore anterior and lateral; cuticle thin; appendages absent, cecum short, narrow, with granular contents. About 45 tightly packed embryos per redia, in all stages of development. Flame cells not apparent. Rediae, fixed in formalin, with posterior third of body bent at obtuse angle to remainder of body (Figure 50).

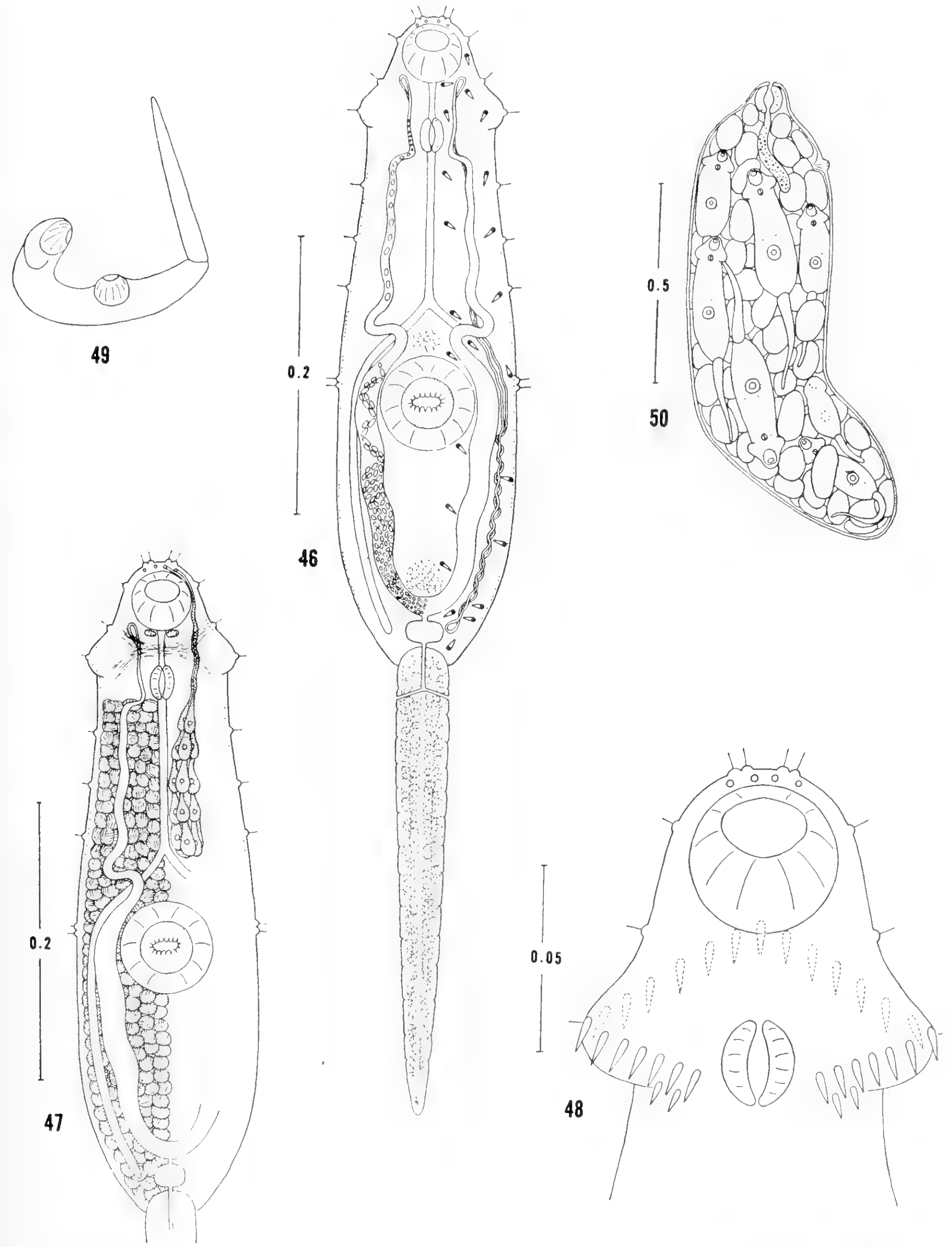
Host: Nassarius vibex Say

Incidence of infection: 40 of 1,083 snails.

Locality: Bay mouth sand bar, Alligator Harbor, Franklin County; sand bar, 3 miles SSW, St. Marks Light, Wakulla County, Florida.

This larva emerges in greatest numbers after dark. It shows no phototropisms and has a life span of about 48 hours; encystment was not observed. Neutral red is not toxic and stains penetration glands and ducts, genital primordia and cecal contents; Nile blue sulfate is very toxic.

This cercaria swims slowly with the body inverted, flexed ventrally between the suck-



Figures 46-50. **46.** Cercaria of *Himasthla quissetensis* (Miller and Northup, 1926), ventral view showing details of excretory system and tail. **47.** Same, ventral view of cercarial body showing cystogenous cells and cephalic glands. **48.** Same, ventral view of cephalic end showing collar spines. **49.** Same, lateral view showing swimming posture. **50.** Same, showing posture when redia is killed in formalin.

ers and with the tail held at a right angle to the body and lashing from side to side causing the body to vibrate vigorously. Cercariae are normally found near the bottom of the vessel, swimming around the periphery, but may creep by use of the suckers.

This larva is identified as the cercaria of *Himasthla quissetensis* (Miller and Northup, 1926), a trematode from the herring gull. The present study extends previous descriptions with respect to number of flame cells and cephalic gland ducts, and records a new host and locality.

Cercaria caribbea III Cable, 1956
(Figures 51-55)

Description: body 0.418-0.536 (0.486) long, 0.179-0.209 (0.192) wide at midbody. Tail 0.413-0.510 (0.472) long, 0.056-0.061 (0.060) wide at base, with dorsal and ventral plicated finfold, 0.372-0.485 (0.442) long, 0.023 wide. Oral sucker 0.052-0.060 (0.056) long, 0.051-0.056 (0.054) wide; mouth subterminal; prepharynx 0.008-0.025 (0.019) long; pharynx 0.025-0.033 (0.030) long, 0.014-0.020 (0.017) wide; esophagus long, bifurcating just anterior to acetabulum; ceca narrow, extending to level of excretory bladder. Acetabulum 0.076-0.085 (0.081) long, 0.076-0.085 (0.080) wide, located at midbody. Body surface finely granular, no distinct spines; tail smooth; short bristles scattered over anterior 4/5 of body surface, those on cephalic end set in papillae. Collar 0.092-0.107 (0.102) wide; with 31 spines, 0.0127 long, in a row interrupted ventrally and 2 additional angle spines on each side. Cephalic glands poorly defined, obscured by cystogenous glands; 4-6 ducts on each side passing laterally to oral sucker and opening at indistinct pores on dorsal lip. Six poorly defined glands within oral sucker opening at 6 pores on dorsal perimeter of oral sucker. Excretory bladder small, oval, with short anterior stem receiving wide, descending limbs originating from narrow, ciliated ascending tubules at sides of oral sucker; secondary tubules, obscured by cystogenous glands, forming ascending limbs at level of excretory bladder. Descending limbs filled to level of esophagus with irregular concretions. Caudal excretory tubule bifurcating, with lateral pores on tail. Cephalic ganglia and cross commissure at level of prepharynx. Body filled with granular cystogenous cells, obscuring flame cells. Tail with vacuolated parenchyma and few nuclei. Development in granular, yellow to whitish rediae parasitizing liver of host and measuring 0.870-1.590 (1.265) long, 0.225-0.405 (0.320) wide; birth pore lateral, just behind anterior appendage; area around mouth with minute bristles. Young redia whitish with well developed appendages, containing 12-15 embryos; cecum reaching posterior appendages. Old redia yellow, with less evident appendages and containing 20-25 cercariae in all stages of development. Flame cells not apparent.

Host: Cerithidea scalariformis Say

Incidence of infection: 1 of 5,508 snails.

Locality: Salt marsh, Shell Point, Wakulla County, Florida.

This larva emerges after the host has been dried prior to isolation. Cable (1956a) stated that this cercaria develops in and reenters the same species of snail to encyst, a finding not confirmed in the present study. The life span is about 24 hours and no phototropisms were observed. Neutral red, only slightly toxic, does not stain any feature well. Nile blue sulfate is very toxic and stains only the cephalic ganglia.

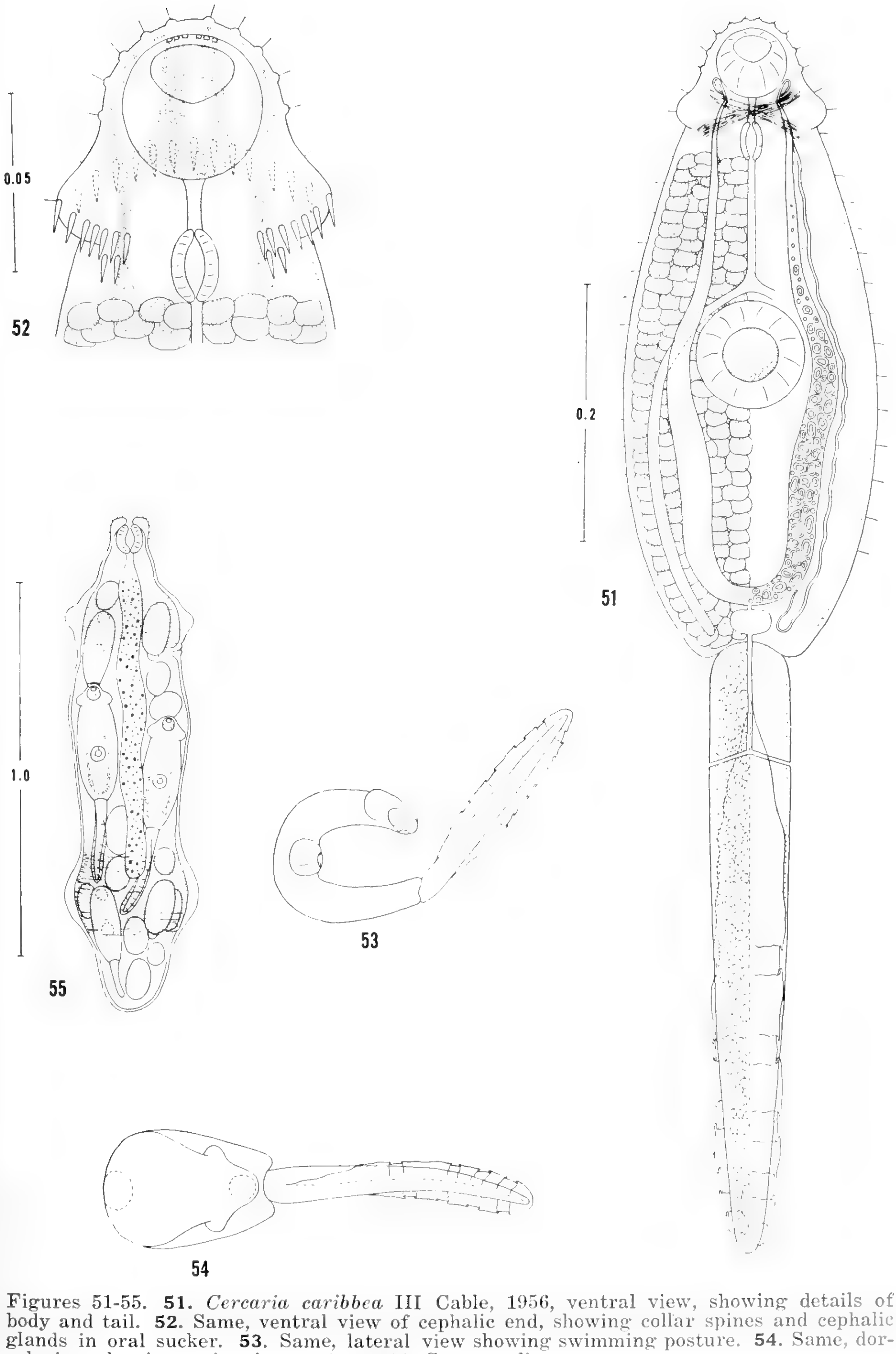
This cercaria swims rapidly near the surface by lashing the tail from side to side in a figure 8 motion with the body inverted and sharply flexed ventrally. Swimming direction can be abruptly changed from forward to backward. When at rest, the larva settles to the bottom in the attitude shown in Figures 53 and 54.

This cercaria is identified as *C. caribbea* III Cable, 1956, from *Cerithidea costata* in Puerto Rico. The minutely granular or scaly rather than spinose cuticle of the Florida species is not considered of specific importance and may be due to development in different hosts. A new host and locality record for this cercaria is here established.

b. *Philophthalmid Cercariae*

Cercaria of *Parorchis acanthus*
(Nicoll, 1906)
Syn. *Cercaria purpurae* Lebour, 1911
Syn. *Cercaria sensifera* Stunkard and Shaw, 1931
(Figures 56-58)

Description: body 0.570-0.921 (0.653) long, 0.163-0.214 (0.191) wide at level of acetabulum. Tail 0.450-0.675 (0.542) long,



Figures 51-55. **51.** *Cercaria caribbea* III Cable, 1956, ventral view, showing details of body and tail. **52.** Same, ventral view of cephalic end, showing collar spines and cephalic glands in oral sucker. **53.** Same, lateral view showing swimming posture. **54.** Same, dorsal view showing swimming posture. **55.** Same, redia.

0.051-0.082 (0.061) wide at base. Oral sucker 0.062-0.075 (0.069) long, 0.070-0.084 (0.078) wide; mouth subterminal; prepharynx 0.018-0.024 (0.022) long; pharynx 0.028-0.033 (0.030) long, 0.020-0.025 (0.022) wide; esophagus long, bifurcating about 3/4 the distance from pharynx to acetabulum; ceca narrow, extending to level of excretory bladder. Acetabulum 0.076-0.086 (0.081) long, 0.070-0.084 (0.078) wide, located just posterior to midbody. Body covered with minute spines, tail smooth; short bristles scattered over body, with those at cephalic end and around mouth set in papillae. Collar 0.102-0.122 (0.107) wide with about 70 spines in one row, interrupted ventrally. Undetermined number of indistinct cephalic glands on each side between level of acetabulum and pharynx. Several gland ducts on each side passing anteriorly dorsal to oral sucker and discharging through indistinct pores on dorsal lip. Excretory bladder small, spherical; descending limbs bending medially anterior to acetabulum and originating from ascending tubules at posterolateral margins of oral sucker; anterior and posterior secondary tubules forming ascending limb at level of acetabulum; smaller tubules obscured by cystogenous glands. Descending limbs with minute, spherical concretions from posterior level of acetabulum to level of pharynx. Embryonic caudal excretory tubule disappearing in parenchyma of tail short distance from body. Eighteen flame cells observed on each side of body. Cephalic ganglia and cross commissure at level of prepharynx. Body with dorsal layer of rod-filled cystogenous cells. Tail with vacuolated parenchyma and terminating with invaginated, glandular tip. Development in yellow, granular rediae in liver and gonad of host. Redia 0.900-1.335 (1.026) long, 0.210-0.390 (0.285) wide. Birth pore lateral and anterior; cuticle thin, with minute bristles around mouth. Young redia with short anterior and long posterior appendages becoming barely visible in old redia. Cecum, yellow, slightly overreaching posterior appendages. Usually ten to 12 embryos per redia, in various stages of development. Flame cells not apparent.

Host: Cerithidea scalariformis Say

Incidence of infection: 189 of 5,508 snails.

Locality: Salt marsh, St. Marks Light and Shell Point, Wakulla County, Florida.

In behavior and staining reaction, this larva is similar to *Cercaria favulosa,* and the two species can be distinguished only by detailed study of structures under oil immersion.

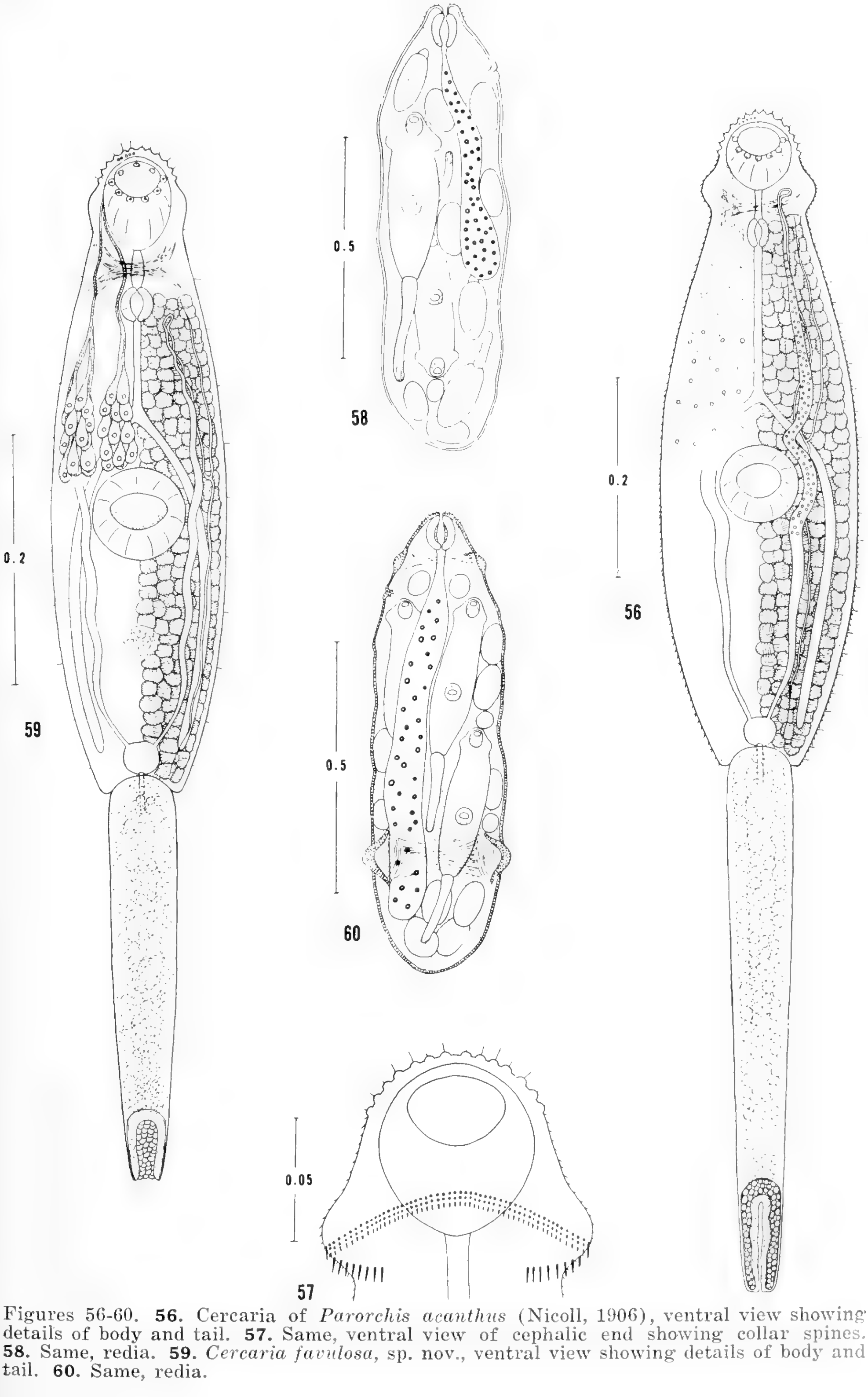
The present one is identified as the cercaria of *Parorchis acanthus* (Nicoll, 1906), adults of which were reared by feeding metacercariae to chicks. A new host and locality record thus is established for the larva. However, the cercaria as observed by the writer differed from the description given by Rees (1937) in respects that are summarized in the following table:

Cercaria purpurae Lebour (from Rees 1937)	*Cercaria purpurae* Lebour (from present study)
Caudal excretory tubule bifurcating and opening through individual pores on lateral margins of tail.	Caudal excretory tubule disappearing in parenchyma of tail a short distance from body. Excretory pore not observed.
64 collar spines	About 70 collar spines
Six cephalic glands with 6 ducts and 6 pores on each side.	Cephalic glands, ducts and pores too indistinct to count.
Concretions filling descending primary tubules.	Concretions in descending primary tubules only between postacetabular level and post-pharyngeal level.

Confronted with the problem of identifying *Parorchis* from gulls in Australia, Angel (1954) proposed *Parorchis acanthus* var. *australis,* based on minute differences between her cercaria and that described by Rees (1937). This degree of subdivision seems unnecessary, because some degree of variation in cercariae might be expected when produced in different gastropod species.

Cercaria favulosa, sp. nov.
(Figures 59-60)

Description: body 0.495-0.540 (0.515) long, 0.107-0.168 (0.137) wide at level of acetabulum. Tail 0.225-0.465 (0.323) long, 0.041-0.056 (0.052) wide at base. Oral sucker 0.054-0.063 (0.060) long, 0.051-0.058 (0.053) wide; mouth subterminal; prepharynx 0.026-0.044 (0.031) long; pharynx 0.030-0.035 (0.032) long, 0.021-0.024 (0.023) wide; esophagus long, bifurcating at about 2/3 distance from pharynx to acetabulum; ceca narrow, extending to level of excretory bladder. Acetabulum 0.068-0.076 (0.073) long, 0.070-0.076 (0.073) wide, located just posterior to midbody. Body and tail surface aspinose, with scattered short



Figures 56-60. **56.** Cercaria of *Parorchis acanthus* (Nicoll, 1906), ventral view showing details of body and tail. **57.** Same, ventral view of cephalic end showing collar spines. **58.** Same, redia. **59.** *Cercaria favulosa*, sp. nov., ventral view showing details of body and tail. **60.** Same, redia.

bristles, those of cephalic region set in papillae; papillae also around mouth and on inner dorsal surface of oral cavity. Collar 0.071-0.102 (0.078) wide, unarmed. Two groups of granular cephalic glands on each side between level of acetabulum and pharynx; number of glands per group not determined. Their ducts extend anteriorly in two bundles, median one close to esophagus and pharynx and lateral bundle, which converge at side of oral sucker, then separate to pass dorsal to sucker and open at 5 pores on its dorsal lip. Excretory bladder small, spherical; descending limbs originating from ascending tubules at level of pharynx; anterior and posterior secondary tubules forming ascending limb at anterior level of acetabulum; smaller tubules obscured by cystogenous glands. Excretory concretions absent. Embryonic caudal excretory tubule disappearing in parenchyma of tail short distance from body; definitive excretory pore not observed. Eighteen flame cells observed on each side of body. Genital primordium about half way between excretory bladder and acetabulum. Cephalic ganglia and cross commissure at level of prepharynx. Body with dorsal and ventral layers of dense rod-filled cystogenous cells. Tail filled with vacuolated parenchyma, terminating with invaginated, glandular tip. Development in yellow, granular rediae in liver and gonad of host. Redia 0.765-1.080 (0.920) long, 0.180-0.345 (0.257) wide. Birth pore lateral and anterior; cuticle thick; area around mouth with minute bristles. Young redia with short anterior and long posterior appendages, much reduced in old redia; cecum yellow, reaching level of posterior appendages. Average of 12 embryos per redia, in various stages of development. Eight flame cells in each redia, one pair in each quarter of body.

Host: Cerithidea scalariformis Say

Incidence of infection: 149 of 5,508 snails.

Locality: Salt marsh, St. Marks Light (type locality), and Shell Point, Wakulla, County, Florida.

The specific name of this cercaria is taken from the Latin *favulosus,* meaning "full of small cells" and refers to the cercarial body filled with cystogenous cells.

This larva emerges when the host has been dried prior to isolation. Encystment occurs on the wall of the container and the life span of the cercaria is about 36 hours if encystment does not occur. No phototropisms were observed. Encystment can be induced by evaporation of water, chilling, addition of Nile blue sulfate or neutral red, and coverslip pressure. Transfer of this cercaria from one vessel to another is difficult because of the tendency to encyst on the inside of the pipette. The cyst wall is a thin, elastic membrane, surrounded by a thick, brittle adhesive layer which attaches the cyst to the wall of the vessel. Neutral red stains all cercarial features evenly except the suckers. Nile blue sulfate is more toxic than neutral red and stains the same features.

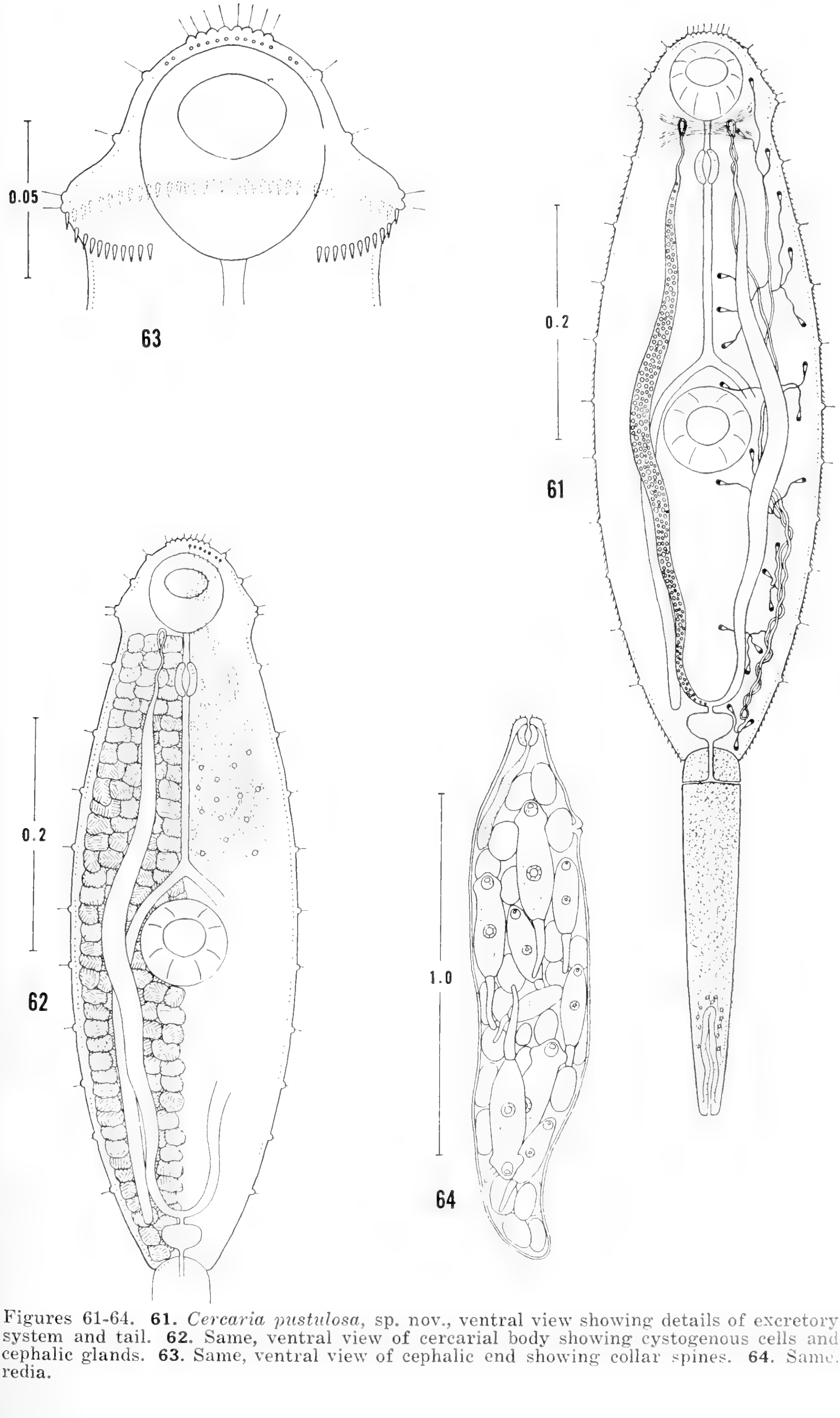
Swimming is by a dorso-ventral sigmoid undulation of the extended tail and body and is not effective in propelling the larva. The tip of the tail is adhesive, attaching the cercaria to the substrate while the body and tail are held erect and lash as when the larva is swimming. It may lie on the bottom, ventral side down, with the tip of the tail attached to the vessel and be very difficult to dislodge with pipette suction. This larva can contract to about 1/4 its extended length.

This species belongs to the "Echinostomoid" group of cercariae proposed by Cable (1956a), the larvae of which have all the characteristics of echinostomatoids except collar spines. Collar spines probably are of little family significance, however, since *Philophthalmus* does not have them as an adult and some species of *Parorchis* have them well developed but others do not. In behavior, this larva resembles the cercaria of *Parorchis acanthus* (Nicoll, 1906). Morphologically, *C. favulosa* resembles *C. caribbea* V Cable, 1956, but differs from it in the length of the descending execretory limbs, number of pores of the cephalic gland ducts, absence of cuticular spination and gross measurements.

This cercaria is placed in the Philophthalmidae pending the determination of the life history.

Cercaria pustulosa, sp. nov.
(Figures 61-64)

Description: body 0.540-0.720 (0.647) long, 0.153-0.214 (0.196) wide at midbody. Tail 0.270-0.398 (0.324) long, 0.041-0.051 (0.045) wide at base. Oral sucker 0.066-0.077 (0.071) long, 0.051-0.067 (0.061)



Figures 61-64. **61.** *Cercaria pustulosa*, sp. nov., ventral view showing details of excretory system and tail. **62.** Same, ventral view of cercarial body showing cystogenous cells and cephalic glands. **63.** Same, ventral view of cephalic end showing collar spines. **64.** Same, redia.

wide; mouth subterminal; prepharynx 0.017-0.032 (0.025) long; pharynx 0.030-0.038 (0.34) long, 0.018-0.028 (0.023) wide; esophagus long, bifurcating just anterior to acetabulum; ceca narrow, extending to anterior level of excretory bladder. Acetabulum 0.074-0.087 (0.080) in diameter, just posterior to midbody. Body surface spinose with scattered short bristles set in papillae which are more abundant on cephalic end; tail smooth. Collar 0.102-0.117 (0.110) wide with about 58 spines in single row, interrupted ventrally. Indistinct cephalic glands in forebody, with 14 minute ducts passing dorsally over oral sucker to open at individual pores in row on dorsal lip; two lateral pores on each side distinctly separated from others. Excretory bladder small, oval, with short anterior stem receiving descending limbs originating from narrow, ciliated ascending tubules just posterior to oral sucker; secondary tubules, originating in forebody, becoming sinuous in hindbody, forming ascending limbs at level of excretory bladder. Descending limbs filled with small, spherical concretions. Flame cell formula $2 (3 + 3 + 3 + 3 + 3 + 3 + 3 + 3) = 48$. Caudal excretory tubule short, bifurcating to open at pores on sides of tail near its base. Cephalic ganglia and cross commissure at level of prepharynx. Body with dorsal layer of rod-filled cystogenous cells. Tail filled with vacuolated parenchyma, terminating with invaginated, glandular tip. Development in cream colored rediae in liver of host. Redia 0.870-2.055 (1.457) long, 0.165-0.450 (0.311) wide, containing about 36 embryos in all stages of development. Birth pore anterior and lateral; area around mouth with minute bristles. Appendages absent; cuticle thin; cecum with granular contents, about 1/4 length of redia. Flame cells not apparent.

Host: *Melongena corona* Gmelin
Incidence of infection: 6 of 69 conchs
Locality: Live Oak Point, Wakulla County, Florida.

The name of this larva is taken from the Latin *pustulosus,* meaning "full of pimples" and refers to the papillae on the body.

This cercaria emerges at any hour and has a life span of about 36 hours if encystment does not occur. Neutral red, only mildly toxic, stains the penetration glands and ducts. Nile blue sulfate, which is more toxic, stains the cephalic ganglia and commissure and stimulates flame cell activity. All other behavioral characteristics, reactions, and cyst features are similar to those of *Cercaria favulosa.*

This cercaria does not closely resemble any other known marine echinostomatoid. It is distinctive in having the combined features of 58 collar spines, an invaginated tail tip, and a single secondary collecting tubule draining flame cells instead of an anterior and posterior tubule. This pattern of excretory tubules, however, has been reported by this writer for *C. fuscata, C. caribbea* III Cable, 1956, and cercaria of *Himasthla quissetensis* (Miller and Northup, 1926) and by Mathias (1925) for the cercaria of *Hypoderaeum conoideum* Dietz, 1909, from fresh water snails (*Linnaea* spp.).

This larva differs from known philophthalmid cercariae in the arrangement of excretory tubules but resembles members of that group in swimming characteristics, invaginated tail tip, cystogenous glands and encystment. It is tentatively placed in that group pending the determination of the life history.

G. *Plagiorchioid Cercariae*

A single plagiorchioid cercaria of the family Microphallidae was found. Cercariae of this family are characterized by the following general diagnosis:

Small cercariae with acetabulum and pharynx nearly always undeveloped; oral sucker with prominent stylet. Penetration glands usually 4 pairs, consisting of 2 pairs each of 2 types distinguished by position, size, character of granulation and configuration of ducts. Usually 2 anterior pairs of one type and better defined than 2 posterior pairs; exceptions are recorded by Palombi (1940), Schell and Thomas (1955), Lebour (1911), Cable (1956a) and for the species described below. Excretory vesicle U- or V-shaped with tubules entering its arms anterolaterally. Development in sporocysts in prosobranch gastropods. Encystment in arthropods, usually crustaceans; adults generally in intestines of birds, occasionally in other vertebrates, especially fishes.

Cercaria lanceolata, sp. nov.
(Figures 65-68)

Description: body 0.168-0.194 (0.181) long, 0.056-0.071 (0.062) wide at level of acetabular primordium. Tail 0.184-0.209 (0.195) long, 0.017-0.020 (0.018) wide at base. Oral sucker 0.041-0.046 (0.044) long, 0.029-0.035 (0.032) wide; mouth subterminal; other features of digestive system not evident. Stylet 0.029 long, 0.003 wide, laterally compressed, slightly enlarged at base of point; with slight ventral curvature. Genital or acetabular primordium located in posterior third of body. Cuticle of body and tail surfaces aspinose, that of tail thick and minutely wrinkled; a pair of long bristles at cephalic end of body. Three large, overlapping penetration glands on each side, nuclei just posterior to midbody; ventral gland lightly granular, staining darkly with Nile blue sulfate; middle gland with coarse granules staining darkly with neutral red as does the moderately granular dorsal gland. Dorsal and ventral gland ducts sinuous, passing over dorsolateral surface of oral sucker to open at individual pores within oral cavity near tip of stylet. Duct of middle gland bending toward midline at level of cerebral ganglia and then curving laterally around oral sucker and opening through pore within oral sucker anterior to other pores. Excretory bladder small, U-shaped, with short arms; excretory tubules sinuous, originating at level of penetration glands and receiving anterior and posterior collecting tubules. Flame cell formula $2[(2+2)+(2+2)]=16$. Excretory pore at body-tail junction. Cephalic ganglia and cross commissure at about 1/6 distance from oral sucker to genital (or acetabular) primordium. Body filled with granular cystogenous cells. Tail filled with small nuclei and with central, longitudinal strand of muscle fibers. Development in minute, oval, whitish, sporocysts in liver of host. Sporocyst 0.189-0.281 (0.231) long, 0.102-0.179 (0.139) wide, each with 5 to 6 embryos in various stages of development; birth pore not observed.

Host: Cerithidea scalariformis Say

Incidence of infection: 130 of 5,508 snails.

Locality: Salt marsh, St. Marks Light (type locality) and Shell Point, Wakulla County, Florida.

The specific name of this cercaria is taken from the Latin *lanceolatus,* meaning "lance-like," and refers to the stylet.

From previously dried snails, cercariae emerge at all hours in large numbers. They have a life span of about 18 hours and are positively phototropic. Netural red is not toxic whereas Nile blue sulfate is toxic. Swimming movement is typical of xiphidiocercariae with the body slightly flexed ventrally and hanging downward, and with the tail lashing in a figure-eight motion (Figure 67). They swim continuously for the first 12 hours after emergence, then settle to the bottom and, for about 6 hours, creep by extension of the body and attachment of the oral sucker to the substrate.

This is the first report of a marine microphallid cercaria with three pairs of penetration glands and a flame cell formula of $2[(2+2)+(2+2)]=16$. Other such larvae usually have 4 pairs of penetration glands but 2 pairs have been described for *C. minima* Schell and Thomas, 1955, and *C. misenensis* Palombi, 1940; and 6 pairs for *C. ubiquita* Lebour, 1911, and *C. ubiquitensis* Palombi, 1940.

Cercaria lanceolata may encyst in a fiddler crab (*Uca* sp.) abundant in the type locality. The adult probably occurs in a crab-eating bird to judge from known microphallid life cycles.

One distome plagiorchioid xiphidiocercaria was found in the present study. The family relationship of cercariae of this type is unknown; only 4 species have been described adequately: *C. caribbea* XXXII Cable, 1956, *C. caribbea* XXXIII Cable, 1956, *C. roscovita* Stunkard, 1932, and *C. parvicaudata* Stunkard and Shaw, 1931. They have the following general diagnosis:

Marine distome xiphidiocercariae with small, poorly developed stylet. Body cuticle spinose, tail smooth. Dense, granular cystogenous glands filling body, obscuring details of penetration glands and excretory network. Excretory bladder Y-shaped with excretory tubules joining stem at base of arms. Pharynx present. Development in sporocysts in prosobranch snails. Adults probably in birds or mammals.

Cercariae opaca, sp. nov.
(Figures 69-73)

Description: body 0.209-0.240 (0.228) long, 0.097-0.107 (0.103) wide at midlevel. Tail 0.209-0.235 (0.222) long, 0.023-0.025 (0.024) wide at base. Oral sucker 0.036-0.039 (0.037) in diameter; mouth subterminal, with surrounding row of small triangular spines, interrupted ventrally; prepharynx absent; pharynx 0.013 in diameter; esophagus obscured by cystogenous glands. Stylet 0.009 long, 0.005 wide, rod-like with conical point. Acetabulum 0.037-0.038 (0.037) in diameter, just posterior to midbody. Body cuticle thin, covered with minute spines, tail smooth. Numerous granular penetration glands in large group on each side, between levels of pharynx and acetabulum; each group with 4 gland ducts passing through lateral wall of oral sucker to open close together near base of stylet. Arms of excretory bladder embracing posterior margin of acetabulum. Four groups of 3 flame cells observed on each side; their formula probably $2[(3+3)+(3+3)]=24$. Excretory pore at junction of body and tail. Body with scattered refractile spherules in addition to cystogenous cells. Tail filled with small cells and central strand of longitudinal muscle fibers; its cuticle indented at intervals. Development in orange sporocysts with granular cuticle. Sporocysts 0.352-0.556 (0.462) long, 0.163-0.291 (0.222) wide, containing 7 to 20 embryos in various stages of development; birth pore terminal. Fully developed cercariae in sporocyst very active.

Host: Littorina irrorata Linné

Incidence of infection: 2 of 1,538 snails.

Locality: Salt marsh, St. Marks Light, Wakulla County, Florida.

The specific name of this cercaria is taken from the Latin *opacus,* meaning "opaque" or "shaded" and refers to the dense appearance of the body.

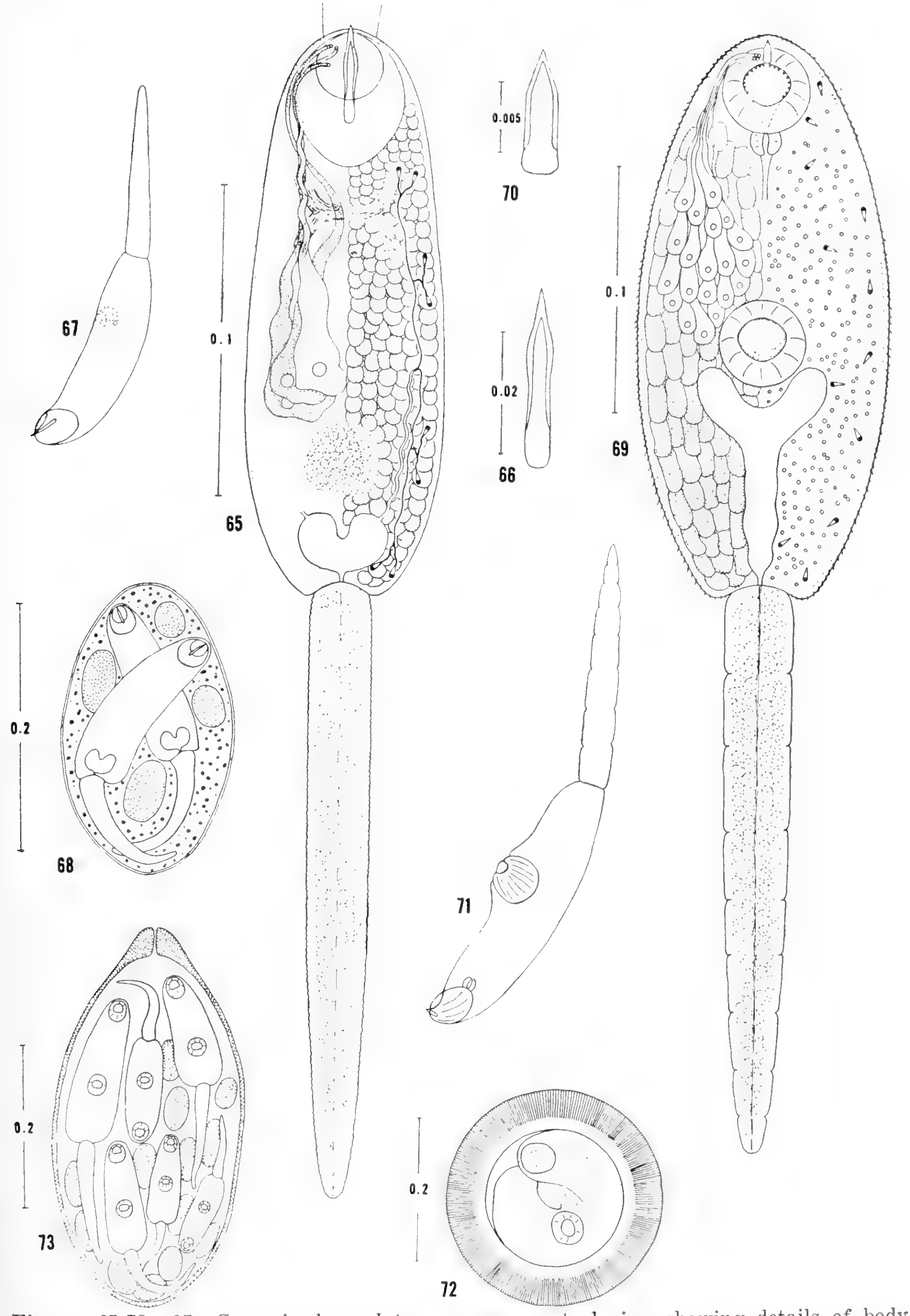
Cercariae emerge from the snail at all hours, but are never seen in large numbers because they immediately return to that host and encyst in its gonad. No phototropisms were noted. The cyst is spherical, 0.281-0.316 (0.296) in diameter, with a thick, brittle outer layer and a thin, elastic inner membrane. The outer layer appears to be radially striated and dissolves in artificial digestive juice (0.5% HCl and 1% pepsin) which does not affect the thin, inner membrane. The metacercaria appears similar to the cercarial body without the stylet. The cyst has the appearance of a tiny translucent pearl, and is very similar to the cysts described by Stunkard (1932) as those of *Spelotrema* spp. provis. from crabs, and by Pelseneer (1906) from *Littorina rudis.*

Neutral red is mildly toxic; it stains the penetration glands lightly and the cystogenous glands darkly. Nile blue sulfate is very toxic and kills the cercaria before staining reactions become evident. Swimming movements are as described for *Cercaria lanceolata* and terminate with the larva sinking to the bottom where it may lie motionless or creep about, using the suckers for attachment to the substrate.

This species resembles *C. caribbea* XXXII Cable, 1956, but differs from it by having spines in the oral sucker, a visible pharynx, a distinctive stylet, and 4 instead of 3 penetration gland ducts. The adult probably is in a snail-eating shore bird.

The systematic position and affinities of the next two species pose a problem. They resemble *C. opaca* in the important features of Y-shaped excretory bladder, dense cystogenous glands, and development in sporocysts in mudflat snails of the order Mesogastropoda. It is known that the stylet may be absent in larvae of certain natural adult groups in which xiphidiocercariae may predominate. It is likewise known that tail form has little taxonomic value; in the psilostomes, echinostomes, and opisthorchioids some cercariae have narrow tails, with or without fins, and others have magnacercous, even zygocercous.

Pending further study on the life cycles, the following two species are tentatively placed in the Plagiorchioidea based on the features mentioned above.



Figures 65-73. 65. *Cercaria lanceolata*, sp. nov., ventral view showing details of body and tail. **66.** Same, ventral view of stylet. **67.** Same, lateral view showing swimming posture. **68.** Same, sporocyst. **69.** *Cercaria opaca*, sp. nov., ventral view showing details of body and tail. **70.** Same, ventral view of stylet. **71.** Same, lateral view showing swimming posture. **72.** Same, living metacercarial cyst. **73.** Same, sporocyst.

To date, no adequate descriptions have been published on marine leptocercous cercariae which lack stylets. Eight poorly described species are known, probably representing larvae of several different families. For this reason, a general diagnosis of the group is omitted.

Cercaria nubeculata, sp. nov.
(Figures 74-76)

Description: body 0.112-0.122 (0.120) long, 0.056-0.071 (0.067) wide at midbody. Tail 0.082-0.102 (0.092) long, 0.020 wide at base. Oral sucker 0.017-0.026 (0.021) long, 0.020-0.023 (0.022) wide; mouth subterminal; prepharynx very short, pharynx 0.006 in diameter; remainder of digestive tract obscured. Acetabulum 0.021-0.023 (0.022) in diameter, just posterior to midbody. Body covered with rows of spines in quincunx pattern except for small bare area on oral sucker just anterior, and another on ventral surface posterior to oral cavity. Tail smooth, with vacuolated parenchyma around central core of longitudinal muscle fibers resembling duct through tail. Bristles and papillae absent. Penetration glands in forebody obscured by dense, granular cystogenous glands and scattered large pigment granules. Six gland ducts on each side extending anteriorly to open at separate pores on dorsal lip. Ducts grouped into a median pair passing close to pharynx and dorsal to oral sucker, and laterally into 1, 2 and 1 ducts converging at side of oral sucker and curving around it to their individual pores. Excretory bladder Y-shaped, anepithelial, with arms embracing posterior margin of acetabulum. Excretory tubules and flame cells obscured by cystogenous glands. Excretory pore at junction of body and tail. Development in large, orange-colored sporocysts in pericardium and surrounding tissues of host. Sporocysts 0.750-1.29 (1.07) long, 0.165-0.270 (0.215) wide, containing 200 to 400 densely packed embryos in all stages of development; cuticle thin, smooth; birth pore terminal.

Host: Cerithidea scalariformis Say

Incidence of infection: 17 of 5,508 snails.

Locality: Salt marsh, St. Marks Light (type locality) and Shell Point, Wakulla County, Florida.

The specific name of this cercaria is taken from the Latin *nubeculatus,* meaning "cloudy" and "with dark spots," and describes the body.

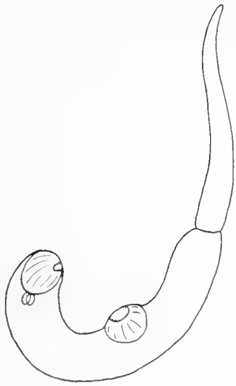
This minute larva emerges from the host in large numbers at all hours, has a life span of about 24 hours and displays no phototropisms. Neutral red and Nile blue sulfate are only slightly toxic and stain the cystogenous glands equally well but show no affinity for other structures.

It swims very much like the xiphidiocercariae with body inverted, ventrally flexed and the tail lashing from side to side in a figure 8 manner. Swimming is interrupted by rest periods and after several hours, the larvae settle to the bottom and lie motionless between periods of creeping over the substrate with the aid of the suckers.

One new species of non-ocellate, pharyngeate, magnacercous cercaria was found in the present investigation.

Cercaria ingentis, sp. nov.
(Figures 77-82)

Description: body 0.250-0.281 (0.265) long, 0.071-0.087 (0.081) in maximum width. Tail magnacercous, 0.810-0.960 (0.884) long, gradually enlarging from base for about 2/5 its length to a maximum width of 0.204-0.235 (0.221), then becoming abruptly narrower and tapering gradually to tip. Oral sucker 0.031-0.040 (0.035) long, 0.023-0.029 (0.025) wide; mouth subterminal; prepharynx very short; pharynx spherical, 0.012 in diameter; remainder of digestive system not apparent. Acetabulum 0.026-0.031 (0.029) in diameter, just anterior to midbody. Body covered with widely spaced spines in quincunx arrangement (Figure 80); cuticle of tail smooth; papillae and bristles absent. Two groups of penetration glands on each side between ganglia and acetabulum; three large distinct, overlapping glands in lateral group anterolateral to acetabulum with a bundle of 3 ducts passing anteriorly in lateral region of forebody and discharging through inividual pores on the dorsal lip; second group of 2 small, indistinct glands medial to the first group, just anterior to genital primordium, with poorly defined ducts passing anteriorly close to midline and dorsally to oral sucker to open at minute pores on



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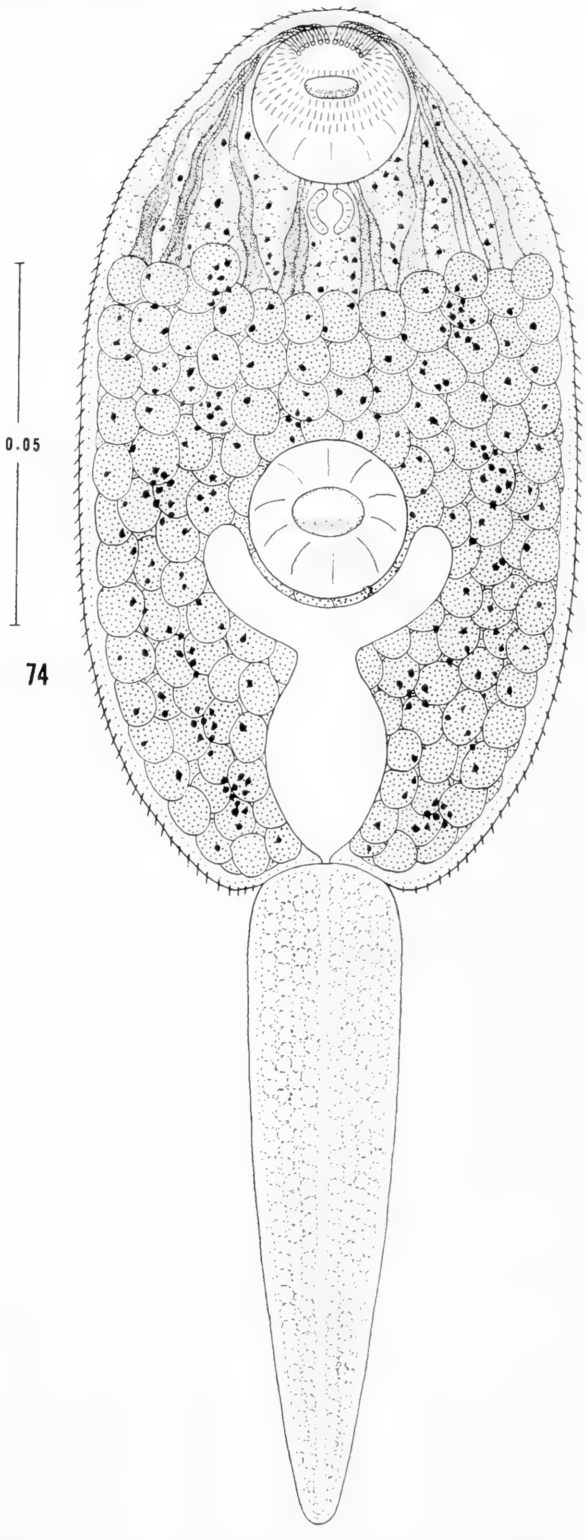

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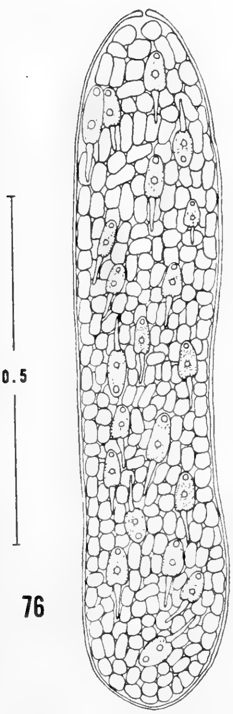

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Figures 74-76. **74.** *Cercaria nubeculata*, sp. nov., ventral view. **75.** Same, lateral view showing swimming posture. **76.** Same, sporocyst.

dorsal lip, medial to the pores of larger glands. Excretory bladder Y-shaped, its wall with a single layer of flattened cells; arms short, embracing acetabulum posteriorly and laterally. Excretory pore at junction of body and tail. Anterior and posterior collecting tubules forming short main collecting tubule which joins bladder laterally at base of each arm. Genital primordium a small sphere of nuclei at anterior margin of acetabulum. Eyespots absent; cerebral ganglia and commissure just posterior to pharynx. Body filled with dense, granular cystogenous cells posterior to cerebral ganglia. Proximal half of tail filled with small cells and dense, brown, pigment granules, distal half with clear, vacuolated parenchyma. Entire tail with small superficial gland cells apparently opening to surface through minute individual ducts (Figure 81). Muscle fibers distinct in tail near body junction. Development in large, orange-brown sporocysts in the branchial region of host. Sporocysts 0.750-1.575 (1.188) long, 0.255-0.375 (0.324) wide, each containing 30 to 35 embryos, in all stages of development; birth pore terminal.

Host: Cerithidea scalariformis Say

Incidence of infection: 3 of 5,508 snails.

Locality: Salt marsh, St. Marks Light (type locality) and Shell Point, Wakulla County, Florida.

The specific name of this cercaria is taken from the Latin *ingentis,* meaning "remarkable" or "great".

This cercaria emerges in small numbers when the host has been dried prior to isolation. The life span is about 18 hours; no phototropisms were observed. Neutral red is only slightly toxic and readily stains the cystogenous glands. Nile blue sulfate is mildly toxic and stains the cystogenous glands, penetration glands and ducts, and cephalic ganglia.

During swimming, the larva is nearly horizontal with the body slightly lower than the tail and flexed ventrally. The tail is held straight with the distal half lashing slowly in all directions. At rest, the larva is suspended in the water (Figure 79) with the body downward and rhythmically elongating and contracting. Under coverslip pressure, the tail detaches and the body creeps about with the aid of the suckers.

Cercaria ingentis is very closely related to *C. buchanani* Martin and Gregory, 1951, but differs from that species in the number of penetration glands, length of the prepharynx, absence of papillae on acetabulum and non-aggregating behavior.

This new species does not fit the general diagnosis of magnacercous opisthorchioids in lacking eyespots, and having a well-developed pharynx and a Y-shaped excretory bladder.

H. *Monorchiid Cercariae*

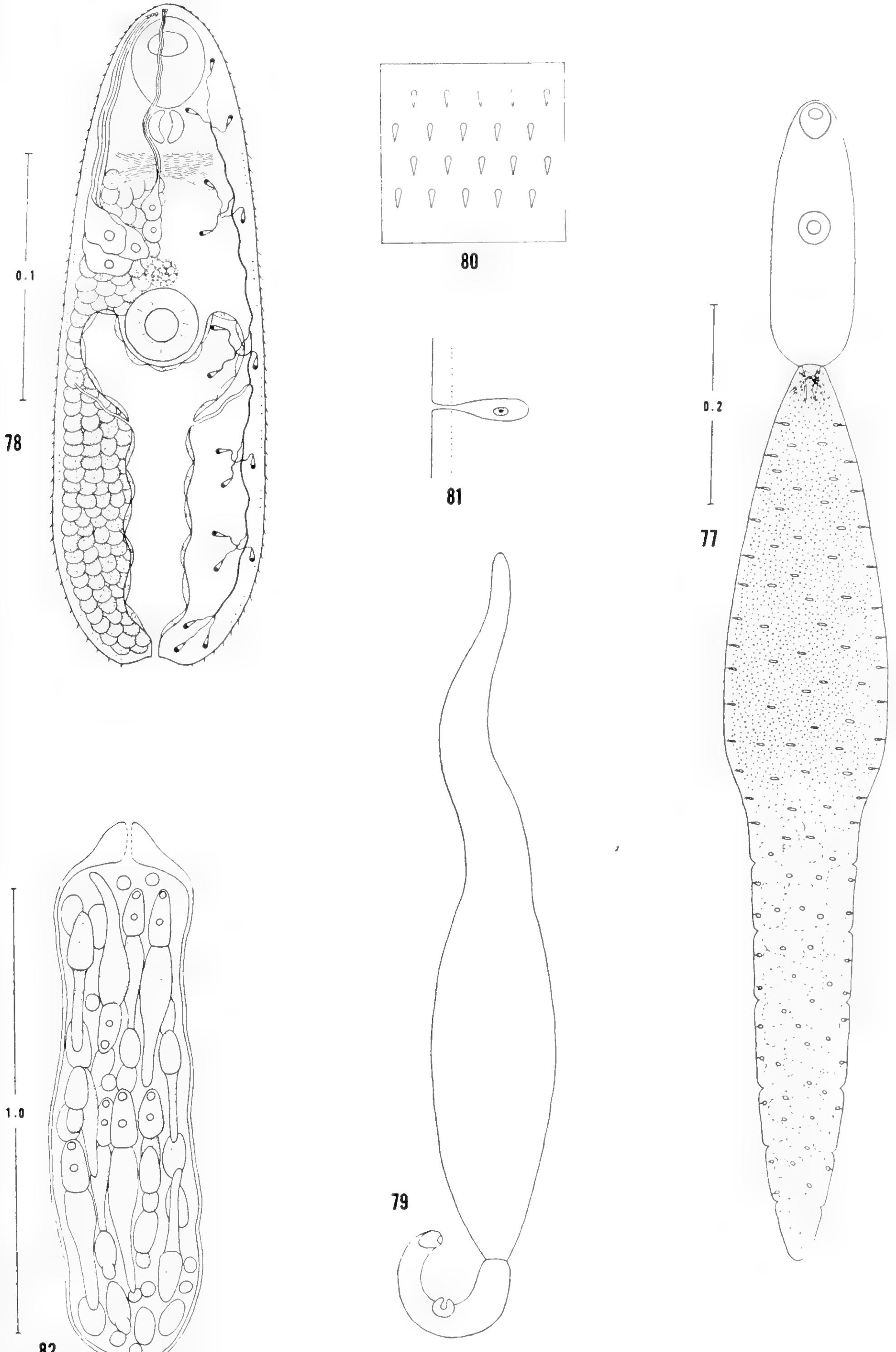
Cercariae of the family Monorchiidae are a relatively obscure group concerning which little work has been done. The investigations of Martin (1940), Young (1953) and Cable (1956a) are the principal contributions. Two species are reported in the present study, *C. caribbea* XXXVI Cable, 1956, and *C. pocillator,* sp. nov.

A general diagnosis of monorchiid cercariae, abstracted from Cable (1956a), follows:

Distomate, pharyngeate cercariae with spinose cuticle, developing in sporocysts in marine lamellibranchs. Tail variable: long and slender with cuticular extensions, reduced or possibly lacking. Eyespots present in larvae with well developed tails, absent in others; stylet absent, penetration glands present. Excretory bladder saccate or tubular, thick walled. Flame cell formula, where known, $2 [(2+2) + (2+2)] = 16$. Encystment, where known, in invertebrates, particularly mollusks. Adults in intestines of marine fishes.

Cercaria caribbea XXXVI Cable, 1956
(Figures 83-85)

Description: body 0.249-0.301 (0.276) long, 0.066-0.092 (0.078) wide at midbody. Tail a tiny knob, 0.009-0.010 in diameter. Oral sucker 0.041-0.046 (0.044) long, 0.046-0.051 (0.048) wide; mouth subterminal; prepharynx 0.008-0.026 (0.020) long, sinuous, with longitudinal muscles; pharynx 0.023-0.028 (0.025) long, 0.025-0.029 (0.027) wide; esophagus thick walled, short, bifurcating about half way between pharynx and acetabulum; ceca relatively thick walled, sinuous, extending almost to posterior end of body. Acetabulum 0.041-0.049 (0.046) in diameter, located at midbody. Cuticle of body spinose with bristles set in papillae scattered over cephalic end; tail smooth.



Figures 77-82. **77.** *Cercaria ingentis*, sp. nov., ventral view showing pigmentation and glandular nature of tail. **78.** Same, ventral view of cercarial body. **79.** Same, lateral view showing resting posture. **80.** Same, surface of body showing arrangement of spines. **81.** Same, surface of tail showing unicellular gland and duct through cuticle. **82.** Same, sporocyst.

Undetermined number of small, granular penetration glands on each side at level of prepharynx, with indistinct ducts passing laterally and dorsally to oral sucker to open at indistinct pores on dorsal lip. Large irregular cystogenous cells with granular cystoplasm scattered through body parenchyma. Excretory bladder I-shaped with thick wall of small, sperical cells, reaching almost to acetabulum and displaced to one side by genital primordium. Main excretory tubules ciliated, joining bladder laterally, anterior to its midlevel and extending almost to midlevel of acetabulum where each receives anterior and posterior collecting tubule. Flame cell formula 2 [(2+2) + (2+2)] = 16. Duct of bladder with small sphincter, and pore at junction of body and tail. Genital primordium large, immediately posterior to acetabulum. Development in cream colored sporocysts in gonad of host. Sporocysts 0.255-0.638 (0.418) long, 0.087-0.097 (0.094) wide, containing 4 to 5 loosely packed embryos in various stages of development; cuticle rough; birth pore not observed.

Host: Chione cancellata Linné

Incidence of infection: 16 of 120 clams.

Locality: Bay mouth sand bar, Alligator Harbor, Franklin County, Florida.

These cercariae emerge from the gonad of the host, and from cysts which are ejected from the clam through the excurrent siphon. They measure 0.087-0.097 (0.094) in diameter, and appear as minute whitish spheres stuck together in bunches by the gelatinous outer covering which is thick and granular; inner cyst layer thin, membranous (Figure 84). Ciliated ducts and flame cells of larvae visible in cysts.

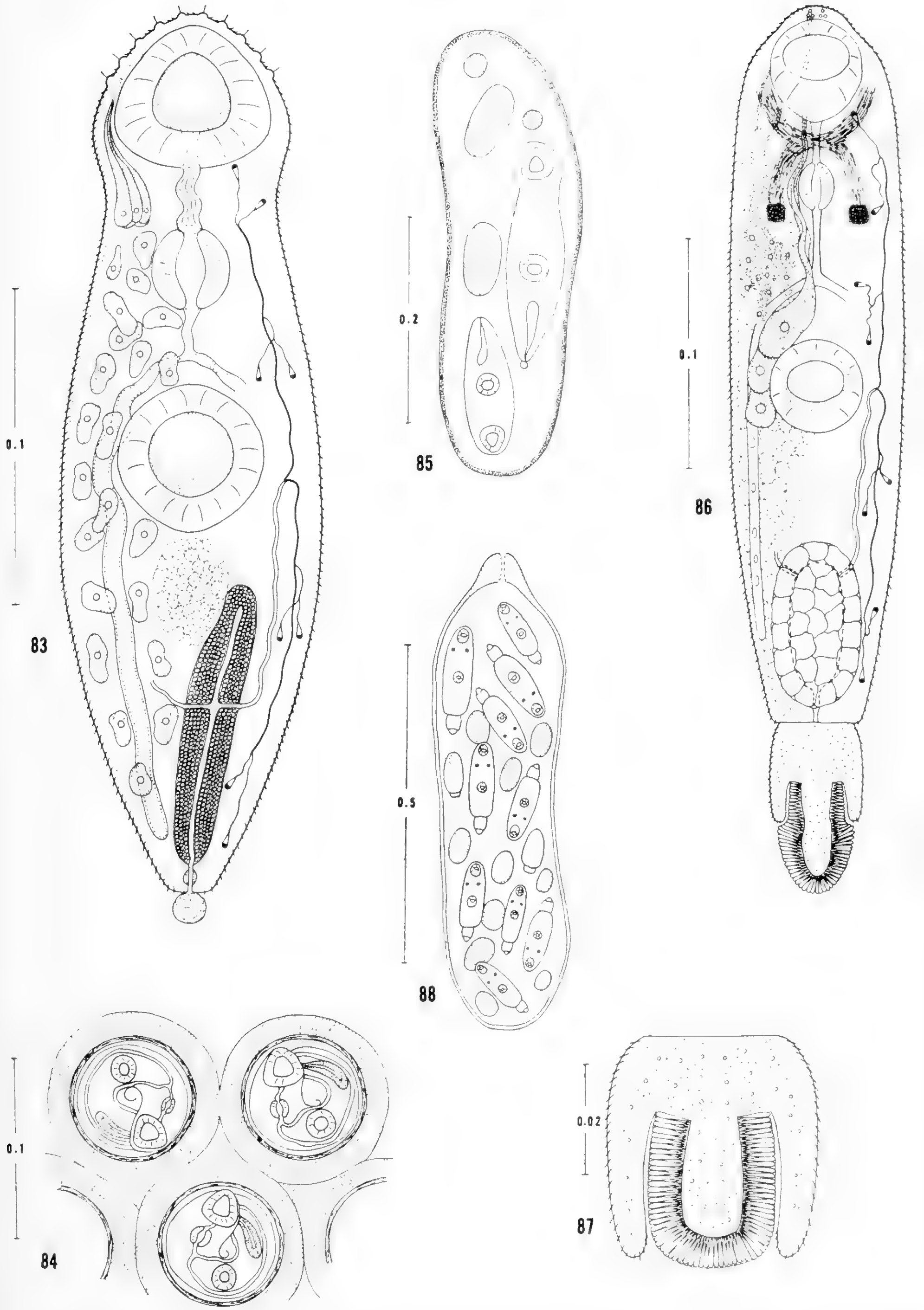
The description of this cercaria is based on larvae teased from sporocysts and only the largest and presumably fully developed ones were used. Such carcariae are active and creep about on the bottom of the dish.

Neutral red, only slightly toxic, stains the cystogenous glands. Nile blue sulfate stains the penetration glands and stimulates encystment, but apparently is not toxic.

The present study records a new host and locality record for *Cercaria caribbea* XXXVI which Cable (1956a) described from *Gemma purpurea* in Puerto Rico. He observed that the species did not emerge but he failed to note its encystment in the mollusk, or the genital primordium.

Cercaria pocillator, sp. nov.
(Figures 86-88)

Description: body 0.286-0.316 (0.308) long, 0.061-0.077 (0.068) wide at level of acetabulum. Tail composed of cup-like basal segment containing glandular, protrusible portion, and measuring 0.034-0.046 (0.040) long by 0.034-0.046 (0.038) wide when contained portion is retracted (Figure 87); with glandular portion extended, tail measures 0.071-0.079 (0.074) long (Figure 86). Oral sucker 0.041-0.048 (0.045) long, 0.037-0.043 (0.040) wide; mouth subterminal; prepharynx 0.013-0.017 (0.016) long; pharynx 0.020-0.021 (0.020) long, 0.015-0.016 (0.015) wide; esophagus 0.035-0.044 (0.040) long, bifurcating about midway between pharynx and acetabulum; ceca narrow, containing few small oval concretions and extending to midlevel of excretory vesicle. Acetabulum at midbody, 0.038-0.044 (0.041) long, 0.037-0.043 (0.039) wide, with several rows of minute spines bordering cavity. Body with parallel rows of spines; those of tail restricted to cup-like portion; bristles and papillae absent. Penetration glands of 2 types: one group of 3 large, granular, overlapping glands on each side along lateral and anterolateral margins of acetabulum, with ducts extending anteriorly close to esophagus and pharynx, passing dorsal to oral sucker and opening at 3 submedian pores forming triangle on the dorsal lip; glands of second type poorly defined, finely granular, grouped on each side between levels of eyespots and cecal bifurcation with 2 groups of poorly defined ducts passing laterally and dorsally over oral sucker to indistinct pores on dorsal lip. Excretory bladder elongate, oval, thick walled, extending about half way to acetabulum with wall of large, irregularly shaped cells; excretory pore at junction of body and tail. Main excretory ducts ciliated, joining bladder anterolaterally and extending to midlevel of acetabulum where each receives anterior and posterior collecting tubule. Flame cell formula 2[(2+2) + (2+2)] = 16. Cephalic ganglia and cross commissure at level of prepharynx. Eyespots on each side of pharynx, rectangular, 0.009 long and 0.010 wide, composed of spherical brown



Figures 83-88. **83.** *Cercaria caribbea* XXXVI Cable, 1956, ventral view showing details of body. **84.** Same, living metacercarial cysts. **85.** Same, sporocyst. **86.** *Cercaria pocillator*, sp. nov., ventral view showing details of body and tail. **87.** Same, ventral view showing tail stem with glandular core retracted. **88.** Same, sporocyst.

granules. Body filled with indistinct cystogenous cells. Distal segment of tail stem with many small, fusiform glandular cells perpendicular to its surface. Development in cream colored, elongate sporocysts in gonad and liver of host. Sporocyst 0.525-0.960 (0.749) long, 0.150-0.270 (0.216) wide; cuticle smooth, birth pore terminal; containing 14 to 22 embryos, in all stages of development.

Host: Donax variabilis Say

Incidence of infection: 5 of 1,763 clams.

Locality: Gulf beach, Alligator Point, Franklin County, Florida.

The specific name of this cercaria is taken from the Latin *pocillator,* meaning "bearer of a cup" and refers to the shape of the tail.

Because this cercaria was not observed to emerge spontaneously, it is described from specimens dissected from the clam and selected for their apparent complete development. No swimming movements were observed but the larva lies on the bottom writhing, twisting and creeping with momentary rest periods during which the body is flexed ventrally. The life span of larvae removed from the sporocyst is about 24 hours.

Neutral red is toxic; it stains the large penetration glands, their ducts, the contents of the ceca, and cells of the excretory bladder. Neutral red also stimulates the glands of the tail stem to secrete an adhesive substance whereby the larva adheres to the vessel and is difficult to dislodge. Nile blue sulfate is not toxic; it stains the cephalic ganglia, large penetration glands, their ducts, cells of the excretory bladder; and it stimulates flame cell activity.

Cercaria pocillator resembles most *C. choanura* Hopkins, 1958, in *Donax variabilis* from Mustang Island, Texas. It differs from that species in having diffuse as well as distinct penetration glands, long ceca, and by lacking a genital primordium. Hopkins did not describe features of the excretory system other than the bladder. *C. pocillator* may encyst in the first intermediate host, as reported by Hopkins for *C. choanura,* but this writer observed no cysts in the infected clams. The adult of *C. pocillator* probably occurs in mollusk-eating fishes.

I. *Allocreadioid Cercariae*

Life history studies have shown that trematodes assigned to the family Allocreadiidae by some workers have at least three types of cercariae (leptocercous, cotylocercous, xiphidiocercariae). For that reason, others have recognized separate families for the adults of each type of cercaria and combined them in the superfamily Allocreadioidea. One such family is the Opecoelidae in which the cercariae are of the type characterized in the following general diagnosis which applies to two species found in the present study:

Non-ocellate distome cercariae with aspinose cuticle and a stylet set vertically in the anterior wall of the oral sucker. Cuticle thick, with bristles set in papillae. Tail an adhesive organ; usually short and either cup-like with glandular walls or with a glandular core that may be protrusible; less often, tail longer, rarely exceeding body in length and then with a non-protrusible core of glands at distal end only. Number of penetration glands variable; their ducts in one or two bundles on each side, opening near tip of stylet. Excretory bladder with thick wall composed of large, granular cells. Excretory pores lateral at junction of body and tail. Flame cell formula of marine species, where known $2[(2+2)+(2+2)]=16$. Development in sporocysts in prosobranch gastropods and encystment commonly in crustaceans. Adults in the Opecoelidae, a family of trematodes occurring in both marine and fresh water fishes.

Cercaria contorta, sp. nov.
(Figures 89-91)

Description: body 0.179-0209 (0.191) long, 0.036-0.046 (0.040) wide at midlevel. Tail 0.066-0.076 (0.069) long, 0.018-0.021 (0.019) wide at base. Oral sucker 0.029-0.033 (0.031) long, 0.024-0.029 (0.026) wide; mouth subterminal, surrounded by band of minute scales or spines; prepharynx indistinct; pharynx difficult to see at posterior level of ganglionic commissure about half way between oral sucker and acetabulum; remainder of digestive tract not evident. Stylet in anterior wall of oral sucker, 0.006 long and 0.003 wide; not curved dorsoventrally; with two short points. Acetabulum 0.024-0.029 (0.026) long, 0.023-0.024 (0.023) wide, posterior to midbody;

a band of minute scales or spines around acetabular cavity. Body and tail aspinose; bristles set in papillae scattered over anterior 2/3 of body, denser on cephalic end. Three overlapping, granular penetration glands on each side between levels of pharynx and acetabulum; their ducts extending anteriorly and dorsal to oral sucker to open at pores near tip of stylet; ducts and pores of middle and ventral glands medial to those of dorsal gland. Excretory bladder voluminous, extending about 3/4 distance from posterior end to acetabulum; with thick wall of large, irregular, granular cells; with short duct to lateral pores in body-tail furrow. Main excretory tubules joining anterolateral margins of bladder, extending to level of acetabulum where each receives anterior and posterior collecting tubule. Proximal end of anterior collecting tubule ciliated. Flame cell formula $2[(2+2)+(2+2)] = 16$. Cephalic ganglia and large commissure very distinct, overlapping anterior margin of pharynx. Two genital primordia present, the larger along anterior margin of acetabulum and smaller one posterior to pharynx. Body filled with indistinct cystogenous cells. Tail filled with vacuolated parenchyma; expanded cup-like tip enclosing protrusible core of longitudinal fusiform gland cells. Development in orange, granular sporocysts in liver of host. Sporocysts 0.306-0.490 (0.389) long, 0.102-0.173 (0.135) wide, containing 15 to 20 embryos in all stages of development; cuticle thin, smooth; 4 flame cells observed in equatorial region; birth pore not apparent.

Host: Anachis obesa C. B. Adams (type host), and *Mitrella lunata* Say

Incidence of infection: 21 of 268 *Anachis obesa;* one of one *Mitrella lunata.*

Locality: Mud Cove, Alligator Point, Franklin County, Florida.

The specific name of this cercaria is taken from the Latin *contortus,* meaning "twisted", and refers to the characteristic movements of this species.

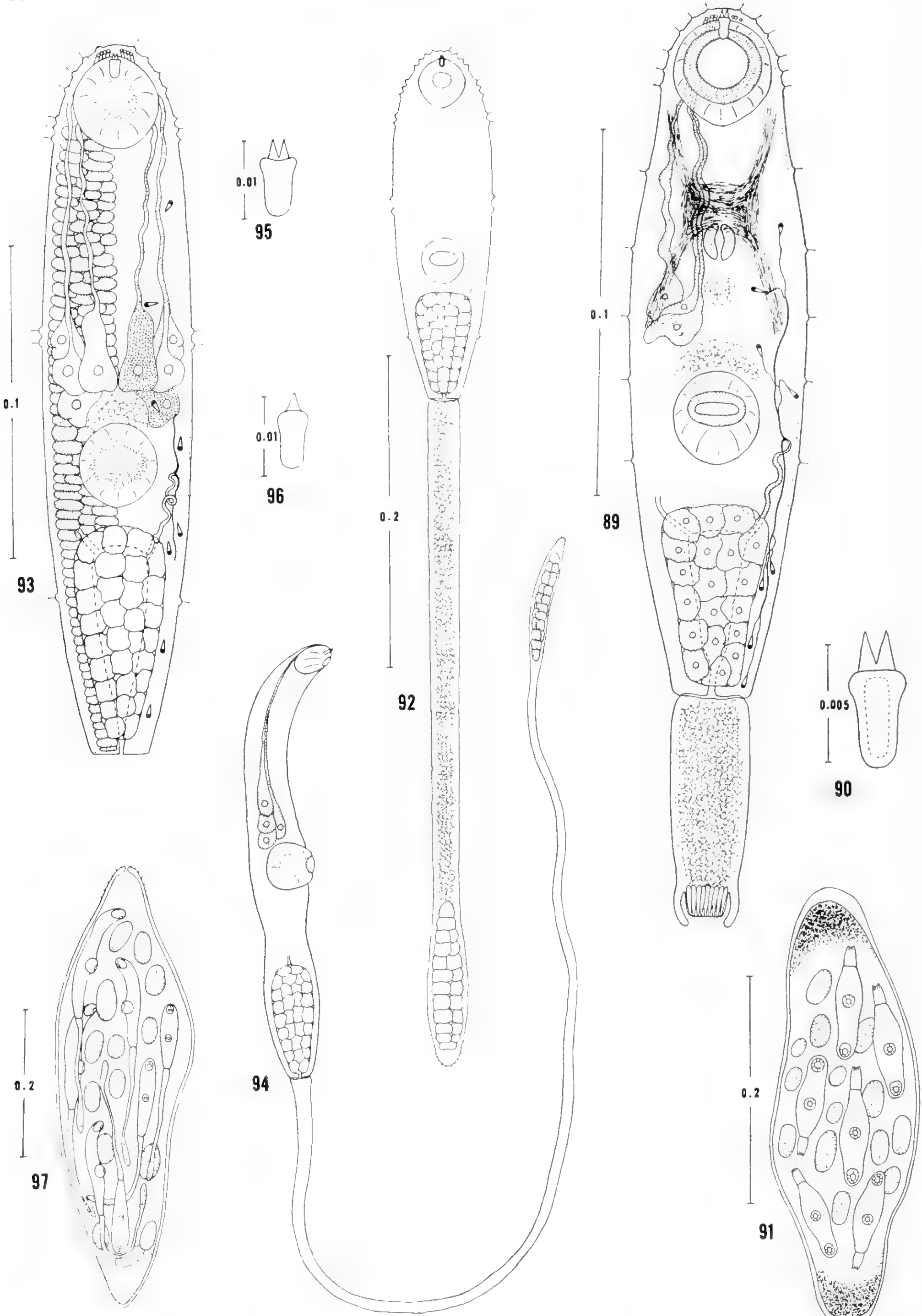
The larva emerges at all hours in large numbers, has a life span of about 36 hours, and shows no phototropisms. Neutral red is non-toxic and readily stains the penetration glands and the adhesive glands in the tail. Nile blue sulfate is relatively non-toxic and stains cephalic ganglia, and the same features as neutral red.

It does not swim, but attaches to the substrate by means of the adhesive glands in the tail tip and either stands erect or lies on its side and contracts ventrally, rolling into a spring-like coil. It has also been observed to contract and contort violently as if trying to tie itself in a knot. The tail can contract to about 1/2 its extended length, the body to about 1/3. When creeping by means of the suckers, the tail length does not change appreciably.

This species resembles most the larval form of *Opecoeloides manteri* described by Hunninen and Cable (1941), but is smaller and has body papillae, and a ciliated anterior collecting tubule. Hunninen and Cable (1943a) observed such cilia in the larva of *Podocotyle atomon,* another closely related form.

Cercaria paradoxa, sp. nov.
(Figures 92-97)

Description: body 0.214-0.240 (0.227) long, 0.038-0.047 (0.042) wide at midlevel. Tail 0.347-0.530 (0.424) long, 0.014-0.016 (0.015) wide at base. Oral sucker 0.029-0.031 (0.030) long, 0.022-0.025 (0.024) wide; mouth subterminal, surrounded by several rows of minute scales or spines; remainder of digestive tract not apparent. Stylet in anterior wall of oral sucker, 0.010 long, 0.006 wide, with two short points; not curved dorso-ventrally; its body circular in cross-section. Acetabulum 0.025-0.029 (0.027) long, 0.023-0.025 (0.023) wide, slightly posterior to midbody; about 6 rows of minute scales or spines around cavity of acetabulum. Body and tail surfaces aspinose; short bristles set in papillae just anterior to midlevel of excretory bladder, at anterior level of penetration glands, and on cephalic end. Tip of tail with few minute bristles. Four overlapping penetration glands on each side, in posterior 1/3 of forebody, with ducts extending anteriorly to open at individual pores on dorsal lip near tip of stylet. Dorsal and ventral glands coarsely granular, staining darkly with neutral red, their ducts and pores medial to those of the middle two glands which are finely granular and stain darkly with Nile blue sulfate. Excretory bladder voluminous, with thick wall composed of large irregularly-shaped cells occupying most of body posterior to acetabulum; with short duct to lateral pores in



Figures 89-97. **89.** *Cercaria contorta*, sp. nov., ventral view showing details of body and tail. **90.** Same, ventral view of stylet. **91.** Same, sporocyst. **92.** *Cercaria paradoxa*, sp. nov., ventral view showing details of tail. **93.** Same, ventral view of cercarial body. **94.** Same, lateral view showing extended resting posture. **95.** Same, ventral view of stylet. **96.** Same, lateral view of stylet. **97.** Same, sporocyst.

body-tail furrow. Main excretory tubules ciliated, joining anterolateral margins of bladder, extending to midlevel of acetabulum where each receives anterior and posterior collecting tubule; their distal portions obscured. Four pairs of flame cells on each side; formula probably $2[(2+2) + (2+2)] = 16$. Genital primordium at anterior margin of acetabulum, stained by neutral red. Body filled with oval, granular cystogenous cells. Tail filled with vacuolated parencyhma, distal portion slightly swollen, containing group of granular gland cells, secreting adhesive substance at tip of tail. Development in motile, whitish sporocysts in gonad and liver of host. Sporocysts 0.510-0.705 (0.588) long, 0.150-0.225 (0.180) wide, cuticle smooth; birth pore terminal, surrounded by minute bristles. About 20 embryos, in all stages of development, per sporocyst.

Host: Anachis translirata Ravenel

Incidence of infection: 1 of 5 snails.

Locality: Apalachee Bay, off St. Marks Light, Wakulla County, Florida.

The specific name of this cercaria is taken from the Latin *paradoxus,* meaning "strange" or "contrary to expectation", and refers to the unusual tail structure for a larva of this type.

This species emerges at any hour, has a life span of about 24 hours and displays no phototropisms. Neutral red is non-toxic and stains the genital primordium and dorsal and ventral penetration glands. Nile blue sulfate is non-toxic and stains middle sets of penetration glands.

Being unable to swim, the larva nevertheless displays unusual behavior. At rest, it lies on its side on the bottom with the tail greatly extended (Figure 94). If the vessel is tapped, the larva contracts quickly and coils ventrally. It responds to stirring of the water also by immediate contraction but then slowly relaxes and becomes elongated as it is carried around by the water current. Rapid contraction and relaxation with coiling and uncoiling also occur spontaneously as does creeping with the aid of the suckers. The tip of the tail attaches to the substrate with a weak adhesive secreted by the caudal glands.

Cercaria paradoxa does not closely resemble any other known marine opecoelid larva in having the combined features of 4 pairs of penetration glands, a two-pointed stylet, and the unusually long tail.

J. *Opisthorchioid Cercariae*

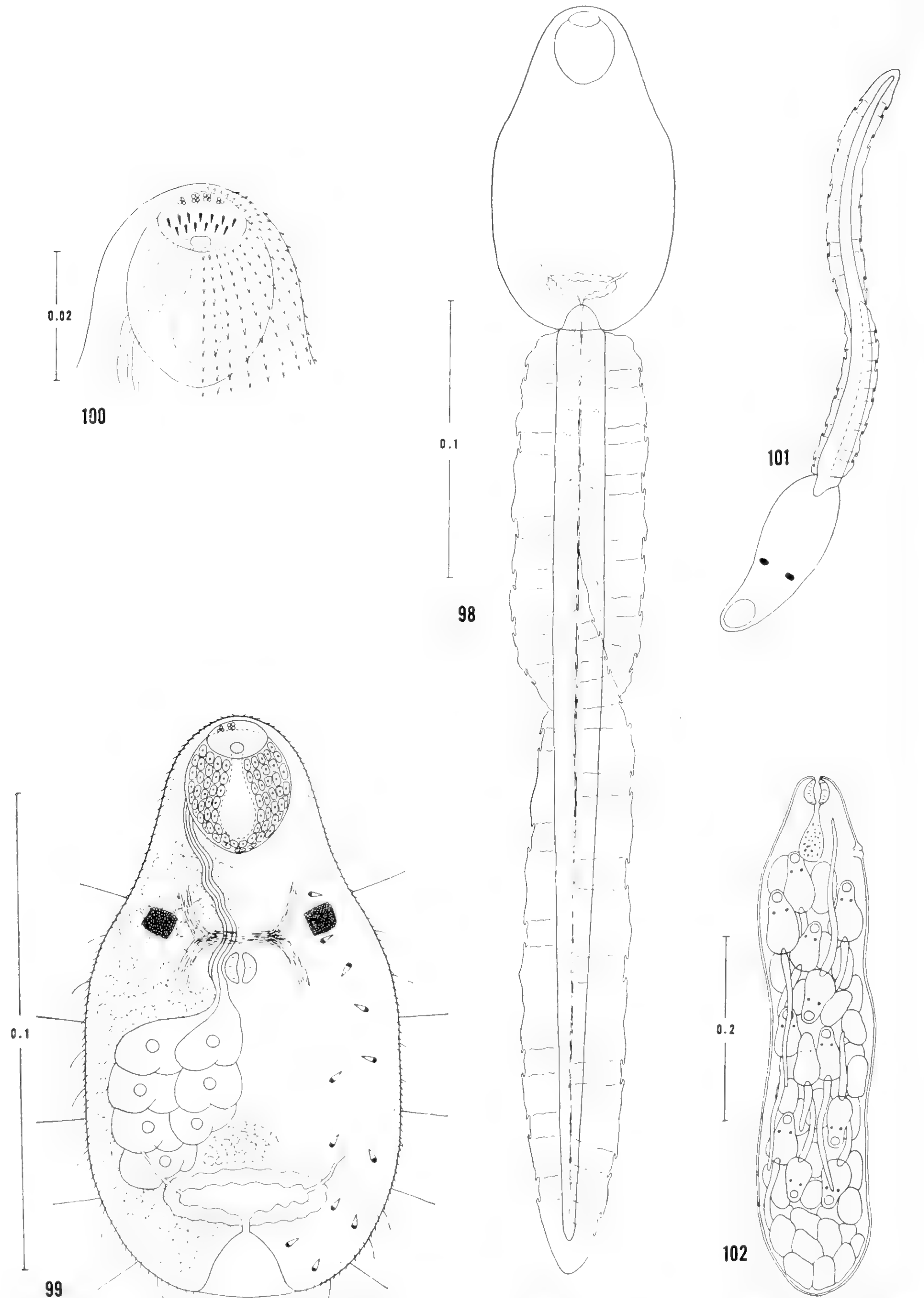
Three new species of pleurolophocercous cercariae were found in the present investigation. All resemble closely larvae in the families Opisthorchiidae and Heterophyidae. The term "pleurolophocercous" was introduced by Sewell (1922) for biocellate, monostome cercariae having well developed caudal finfolds.

Pleurolophocercous cercariae have been studied extensively and many life histories have been elucidated, including several in which man may harbor the adult stage. The following general diagnosis of the cercarial type is abstracted from Cable (1956a):

Biocellate cercariae, with acetabulum embryonic or absent. Oral sucker a protrusible penetration organ generally having spines on the dorsal lip. Tail long, with dorsal, ventral, and sometimes lateral finfolds. Penetration glands usually 7 pairs, with ducts usually opening at 4 groups of pores in crypt dorsal to mouth. Pharynx present or rudimentary, remainder of digestive system undeveloped. Excretory bladder thick walled and granular; empirical flame cell formula, where known, usually $2[(n+n) + (n+n)]$ or $2[(n+n+n) + (n+n+n)]$. Development in simple rediae in prosobranch gastropods; encystment generally in fishes; adults in piscivorous vertebrates.

Cercaria cursitans, sp. nov.
(Figures 98-102)

Description: body 0.107-0.138 (0.123) long, 0.056-0.077 (0.065) wide at midlevel. Tail attached subterminally; excluding finfolds, measuring 0.326-0.372 (0.351) long, 0.015-0.020 (0.016) wide at base; proximal end of tail with plicated lateral finfolds 0.138-0.153 (0.144) long, 0.015 wide. Distal portion of tail with plicated dorsal finfold, 0.250-0.286 (0.270) long, 0.021 wide, continuous around tip of tail with similar ventral finfold, 0.230-0.245 (0.235) long, 0.018 wide. Oral sucker 0.025-0.030 (0.028) long, 0.020-0.023 (0.021) wide, its dorsal lip with anterior row of 7 spines and posterior row of 6. Mouth transversely oval, small, subterminal; oral cavity flask-shaped; prepharynx not observed; pharynx small, well developed, somewhat over 1/3 body



Figures 98-102. **98.** *Cercaria cursitans*, sp. nov., dorsal view showing details of tail stem and finolds. **99.** Same, ventral view of cercarial body. **100.** Same, ventral view of cephalic end showing arrangement of spines in oral crypt. **101.** *Cercaria cursitans*, sp. nov., *Cercaria vivata*, sp. nov., and *Cercaria coruscantis*, typical resting postures. **102.** *Cercaria cursitans*, sp. nov., redia.

length from anterior end; remainder of digestive system not observed. Acetabulum undeveloped. Entire body with minute spines forming parallel transverse rows; tail stem smooth. Posterior 3/4 body with scattered, long, stiff bristles and short, curved ones; papillae absent. Seven large penetration glands on each side, 4 lateral, 3 medial, between pharyngeal level and excretory bladder. Gland ducts in single bundle on each side, passing close to pharynx, then in sinuous path to side of oral sucker and dorsally over it to open in crypt above mouth through pores in groups of 3, 4, 4, 3. Excretory bladder transversely oval, with thick granular wall; main excretory tubules joining bladder at its anterolateral margins, extending anteriorly a short distance beyond which they and collecting tubules are obscured by cystogenous glands; 12 flame cells on each side, their formula probably being $2[(2+2+2)+(2+2+2)]=24$. Excretory pore at body-tail junction. Genital primordium a crescent of cells just anterior to excretory bladder. Eyespots well separated, about midway between oral sucker and penetration glands, cuboid, 0.007 × 0.007, composed of spherical brown granules. Cerebral ganglia and commissure between eyespots. Body filled with cystogenous glands, less distinct in anterior half. Development in smooth, whitish rediae in liver of host and measuring 0.418-0.724 (0.560) long, 0.092-0.133 (0.111) wide; pharynx small; cecum short, extending to level of birth pore; cuticle thin, birth pore near anterior end. Twelve to 25 embryos per redia, in all stages of development.

Host: Cerithidea scalariformis Say

Incidence of infection: 1,017 of 5,508 snails.

Locality: Salt marsh, St. Marks Light (type locality), and Shell Point, Wakulla County, Florida.

The specific name of this cercaria is taken from the Latin *cursitans,* meaning "running about", and refers to the swimming movements of the larva.

This species emerges in large numbers at any hour, lives about 24 hours, and is positively phototropic. Neutral red, which is non-toxic, stains the cystogenous glands and genital primordium. Nile blue sulfate is toxic, and both dyes stain the penetration glands equally well.

This cercaria is a strong but intermittent swimmer, moving in an erratic, zig-zag pathway as the tail lashes rapidly. Swimming periods of 2-3 seconds alternate with rest periods of 2-10 seconds, with the body downward and slightly flexed ventrally, and the sigmoid tail above (Figure 101). At rest, the body-tail length ratio is about 1:3; with the body extended, about 1:2. Resting cercariae swim when disturbed.

This species resembles most the cercaria of *Parastictodora hancocki* Martin, 1950, but differs from it in respects given in the following summary:

Cercaria of *Parastictodora hancocki* Martin, 1950	*Cercaria cursitans,* sp. nov.
Oral crypt with 3 rows of spines; 5 in first row, 5-6 in second row, 6-8 in third row.	Oral crypt with 2 rows of spines; 6 in first row, 7 in second row.
Eyespot shape not described; figures show eyespots irregular.	Eyespots cuboidal.

Other larvae less similar to *C. cursitans* but much like it are cercaria of *Euhaplorchis californiensis* Martin, 1950, and *Cercaria caribbea* X Cable, 1956.

Cercaria vivata, sp. nov.
(Figures 103-105)

Description: body 0.148-0.158 (0.151) long, 0.077-0.081 (0.079) wide at midlevel. Tail attached subterminally; excluding finfolds, measuring 0.367-0.413 (0.398) long, 0.021-0.022 (0.022) wide at base; proximal end of tail with plicated lateral finfolds, 0.117-0.128 (0.122) long, 0.014-0.016 (0.015) wide. Distal portion of tail with plicated dorsal finfold, 0.291-0.316 (0.303) long, 0.015-0.016 (0.016) wide, continuous around tip of tail with similar ventral finfold, 0.179-0.199 (0.187) long, 0.013-0.014 (0.013) wide. Oral sucker 0.026-0.029 (0.028) long, 0.023-0.024 (0.024) wide; its structure as in preceding species except spines on dorsal lip apparently lacking and mouth circular. Prepharynx not observed; pharynx small, well developed, about 2/5 body length from anterior end, 0.008 in diameter; remainder of digestive system not observed. Acetabulum undeveloped. Body covered with minute spines and encircled by about 5 irregular rows of long bristles, 2 rows on anterior half of body and 3 on posterior half; papillae absent; cuticle of tail smooth. Seven large, overlapping penetration glands on each side, 5 lateral and 2 medial, between level of pharynx and midlevel of excretory bladder; their ducts in single bundle on each side, close to midline, passing dorsally over oral sucker to open through pores grouped 3, 4, 4, 3 in crypt above mouth. Excretory bladder transversely oval to V-shaped, with thick, granular wall; excretory pore at body-tail junction. Main excretory tubules joining anterolateral tips of bladder, but after extending anteriorly a short distance, becoming obscured by cystogenous glands as are other excretory tubules. Twelve flame cells on each side, their formula probably $2 [(2+2+2) + (2+2+2)] = 24$. Genital primordium a globular mass of nuclei just anterior to excretory bladder. Eyespots midway between oral sucker and pharynx, cuboid, measuring 0.007×0.007, composed of brown granules. Similar pigment granules throughout body posterior to eyespots, giving larva brown appearance under low magnification (10X). Cerebral ganglia and commissure just posterior to level of eyespots. Body filled with finely granular cystogenous cells. Development in yellow-brown rediae in liver of host. Rediae 0.357-0.561 (0.476) long, 0.077-0.122 (0.095) wide; containing 10 to 20 embryos in all stages of development; cuticle thin, with minute bristles at cephalic end; pharynx small; cecum indistinct, short, extending to level of birth pore. Body wall with scattered fat-like globules and lateral birth pore near anterior end. Excretory network confined to anterior half of body; flame cell formula $2 [(3) + (3)] = 12$.

Host: Cerithidea scalariformis Say

Incidence of infection: 24 of 5,508 snails.

Locality: Salt Marsh, St. Marks Light (type locality) and Shell Point, Wakulla County, Florida.

The specific name of this cercaria is taken from the Latin *vivatus,* meaning "vigorous" or "animated" and refers to the swimming activity of this species.

Emergence, life span and behavior of this larva are very similar to those of the preceding species. The penetration glands stain darkly with neutral red which is non-toxic. Nile blue sulfate is very toxic; it stains the penetration glands and the cephalic ganglia quickly.

This species resembles *Cercaria caribbea* X Cable, 1956, but differs from it in respects summarized as follows:

Cercaria caribbea X Cable, 1956	*Cercaria vivata,* sp. nov.
Six spines in oral crypt.	Oral crypt unarmed.
Dorsal and ventral caudal fins equal, about 0.114 long.	Dorsal caudal fin 0.291-0.316 long; ventral fin 0.179-0.199 long.
Body pigment absent.	Body pigment present.
Eyespots cuboid, 0.009 X 0.009	Eyespots cuboid, 0.007 X 0.007

Other similar species include the cercariae of *Parastictodora hancocki* Martin, 1950, and *Euhaplorchis californiensis* Martin. 1950.

Cercaria coruscantis, sp. nov.

(Figures 106-108)

Description: body 0.106-0.129 (0.117) long, 0.049-0.056 (0.053) wide at midlevel. Tail attached subterminally; excluding finfolds, measuring 0.270-0.316 (0.297) long, 0.017-0.018 (0.018) wide at base; proximal end of tail with plicated lateral finfolds, 0.112-0.132 (0.121) long, 0.009-0.010 (0.009) wide. Distal portion of tail with plicated dorsal finfold, 0.158-0.173 (0.165) long, 0.007 wide, continuous around tip of tail with similar ventral finfold, 0.138-0.158 (0.149) long, 0.007 wide. Oral sucker 0.023-0.025 (0.024) long, 0.017-0.018 (0.018) wide; its dorsal lip without evident spines; mouth circular, subterminal; oral cavity flask-shaped; prepharynx not observed; pharynx embryonic, about midway between oral sucker and excretory bladder; remainder of digestive system not observed. Acetabulum undeveloped. Minute cuticular spines on anterior third of body; entire surface posterior to oral sucker with scattered long, stiff bristles and short ones; papillae absent; cuticle of tail smooth. Seven large, granular penetration glands on each side between level of pharyngeal primordium and posterior end of body, arranged as shown in Figure 107; their ducts wide, in single bundle on each side close to midline and passing dorsolaterally over oral sucker to open dorsally in oral crypt at pores in groups of 3, 4, 4, 3. Excretory bladder inverted U-shaped, with thick wall; its pore at body-tail junction. Main excretory tubules joining anterolateral margins of bladder, extending from bladder to level of genital primordium where each receives long anterior and short posterior collecting tubule.

Flame cell formula $2[(2+2)+(2+2)] = 16$. Genital primordium an oval mass of nuclei just anterior to excretory bladder. Irregularly oval eyespots of brown granules at level of pharyngeal primordium, measuring about 0.007×0.007. Similar pigment granules in body posterior to eyespots, concentrated in lateral regions. Cerebral ganglia and commissure at level just anterior to eyespots. Body filled with indistinct cystogenous cells, those posterior to eyespots staining most intensely with neutral red or Nile blue sulfate. Development in whitish, granular rediae in liver and gonad of host. Rediae 0.408 - 0.673 (0.559) long, 0.061-0.107 (0.088) wide, containing 10 to 15 embryos in various stages of development; cuticle thin, with minute bristles near mouth. Pharynx small; cecum short, extending only slightly beyond level of birth pore.

Host: Cerithidea scalariformis Say

Incidence of infection: 389 of 5,508 snails.

Locality: Salt marsh, St. Marks Light (type locality) and Shell Point, Wakulla County, Florida.

The specific name of this cercaria is taken from the Latin *coruscantis,* meaning "vibrating" and refers to the swimming movements.

Emergence, life span, and behavior of this larva are very similar to those of *C. cursitans* and *C. vivata.* Neutral red is not toxic and stains the genital primordium. Nile blue sulfate is very toxic and stains the cephalic ganglia. The penetration glands are stained equally well with both dyes. The resting cercaria has a body-tail ratio of about 1:2.5 and the body can be extended until the ratio is about 1:1.5.

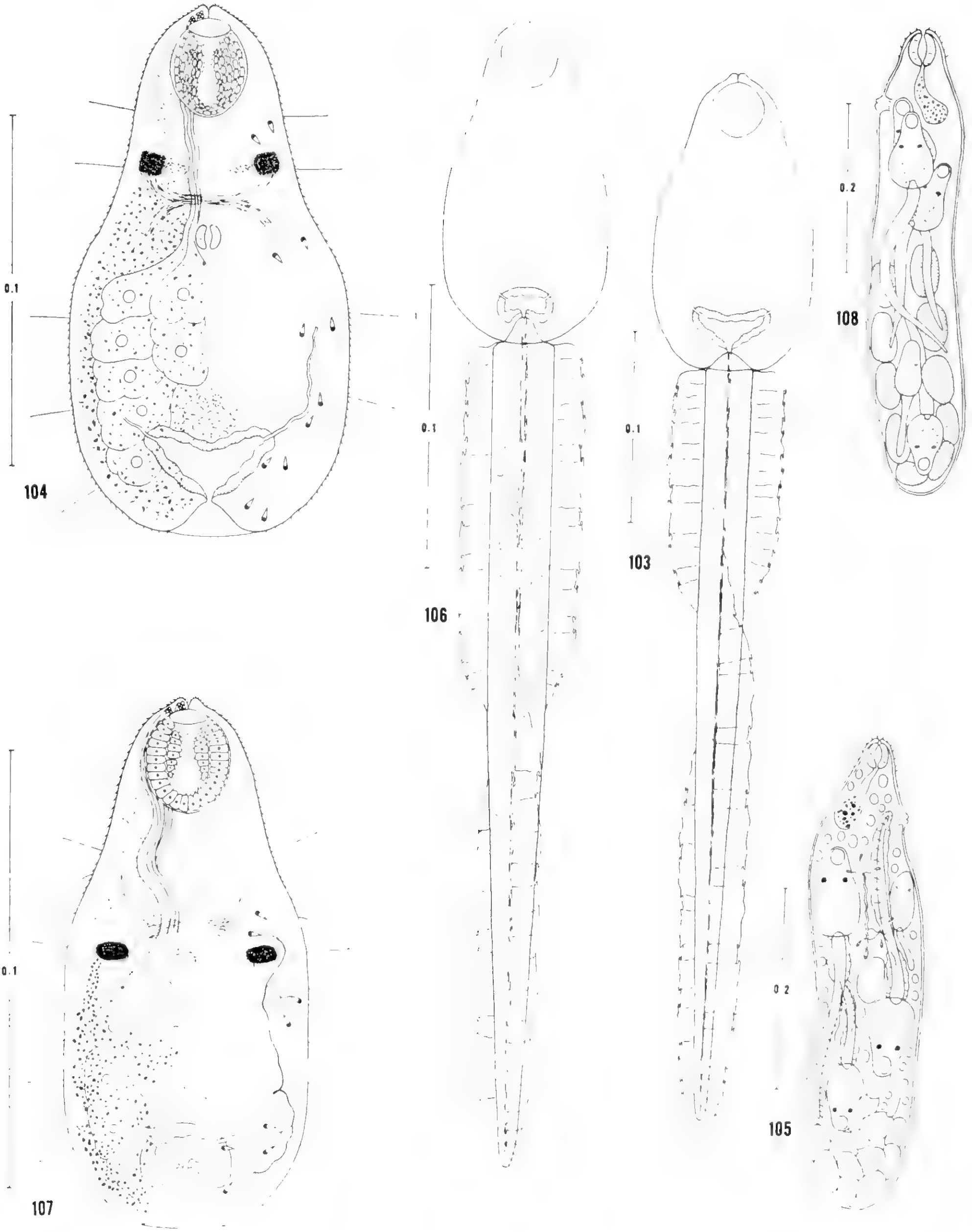
This larva is most closely related to *Cercaria caribbea* X Cable, 1956, and the cercaria of *Euhaplorchis californiensis* Martin, 1950, but differs from them in respects summarized as follows:

Cercaria caribbea X Cable, 1956	Cercaria of *Euhaplorchis californiensis* Martin, 1950	*Cercaria coruscantis* sp. nov.
Six spines in oral crypt.	Five spines in oral crypt.	Oral crypt unarmed.
Entire body spinose.	Entire body spinose.	Anterior 1/3 of body spinose.
Excretory bladder slightly U-shaped.	Excretory bladder transversely oval.	Excretory bladder inverted U-shaped.
Pharynx developed.	Pharynx developed.	Pharynx embryonic.

K. *"Hemiuroid" Cercaria*

One remarkable new cercaria of uncertain family position was found in the present study. It is of the type of *Cercaria caribbea* XXXIV which Cable (1956a) described from Puerto Rico and assigned to the superfamily Hemiuroidea because the larva resembled cystophorous cercariae of that group in certain respects and seemed to illustrate how such cercariae may have been derived from a more generalized type. In a recent personal communication, Cable has stated that his analysis of adults collected in Puerto Rico and further studies in the Caribbean region, including the discovery of an additional species, have raised doubts that such cercariae become adults of the superfamily Hemiuroidea. In his opinion, determination of their status must await solution of the life history. Because such information could justify the recognition of a distinct family for trematodes having such cercariae, a general diagnosis of their type is given:

Biocellate, distome cercariae with a distinctive tail consisting of an enlarged vesicular basal portion with a long, narrow appendage which is an effective swimming organ and, in its embryonic development, bears the primary excretory pores. Forebody narrow, with cuticular spines and conspicuous cephalic glands with ducts opening at anterior end. Hindbody expanded, with numerous peculiar masses, perhaps cystogenous glands. Prepharynx long, pharynx small, esophagus short, intestinal bifurcation near anterior margin of acetabulum; form and extent of ceca uncertain but possibly filling most of the hindbody not occupied by dorsal and ventral parenchymal (muscle?) strands and excretory structures. Excretory bladder not reaching posterior margin of acetabulum, tubular to saccate, with thick wall of columnar cells. Main excretory tubules join anterolateral margins of bladder and extend well into forebody where each receives anterior and posterior collecting tubules; excretory tubules and flame cells coursing in, and supported by dorsal parenchymal strands; flame cells restricted to body. Development in simple rediae in marine prosobranch gastropods. Further hosts unknown.



Figures 103-108. **103.** *Cercaria vivata*, sp. nov., dorsal view showing details of tail stem and finfolds. **99.** Same, ventral view of cercarcarial body. **105.** Same, redia. **106.** *Cercaria coruscantis*, sp. nov., dorsal view showing details of tail stem and finfolds. **107.** Same, ventral view of cercarial body. **108.** Same, redia.

Cercaria portosacculus, sp. nov.
(Figures 109-113)

Description: body pyriform, 0.209-0.306 (0.255) long, 0.112-0.148 (0.131) in maximum width. Tail stem 0.362-0.388 (0.376) long, 0.046-0.051 (0.047) wide at base to which is attached dorsally a large, sac-like structure, 0.138-0.158 (0.147) long, 0.204-0.224 (0.218) wide, and with a wall thickness of 0.150. Oral sucker 0.038-0.047 (0.044) long, 0.037-0.045 (0.041) wide; mouth subterminal; prepharynx not apparent; pharynx spherical, 0.007-0.012 (0.010) in diameter, about 3/4 distance from oral sucker to acetabulum; esophagus very short, bifurcating just anterior to acetabulum; ceca not apparent. Acetabulum at midbody, 0.043-0.045 (0.044) long, 0.046-0.053 (0.050) wide, with single row of minute spines around opening. Anterior 2/3 of body surface spinose; tail surfaces smooth. Papillae and setae absent. Body with dorsal and ventral tracts of longitudinal parenchymal (muscle?) fibers from which many others diverge to internal structures and to body wall (Figure 109). Two groups of cephalic glands on each side; lateral group of 4 large, conspicuous granular glands extending from level of eyespots to midlevel of acetabulum; an undetermined number of small, indistinct glands in a medial group just overlapping pharynx. From each lateral group, a bundle of 4 ducts extends anteriorly near side of body to open at group of pores on dorsal lip; medial glands with minute ducts passing dorsal to oral sucker and opening through indistinct pores near those of large glands. Excretory bladder I-shaped, with wall a single layer of columnar cells, its posterior duct disappearing into parenchyma of tail, probably opening through lateral pores on stem, as in other "hemiuroids". Main collecting tubules extending in sinuous path to level of medial penetration glands where each receives short anterior and long posterior collecting tubule; other tubules obscured; 18 flame cells on each side. Eyespots spherical, 0.012 in diameter. Bilobed, hyaline structure (cephalic ganglia?) at level of eyespots between oral sucker and pharynx. Posterior half of body, near excretory bladder, with small, oval cystogenous cells, densely packed in linear order. Tail stem filled with vacuolated parenchyma and rod-like, granular bodies. Caudal vesicle apparently filled with vacuolated parenchyma and internal network of muscles forming a fibrous mat. Development in whitish, smooth rediae in liver of host. Rediae 0.332-0.490 (0.395) long, 0.143-0.189 (0.165) wide, containing about 35 embryos in various stages of development; birth pore not apparent; pharynx small; cecum short. Caudal vesicle and tail stem develop simultaneously on each embryo. Cercarial body never retracted into vesicle or tail stem.

Host: Anachis obesa C. B. Adams

Incidence of infection: 2 of 268 snails.

Locality: Mud Cove, Alligator Point, Franklin County, Florida.

The specific name of this cercaria is derived from the Latin *porto* + *sacculus* meaning "to carry a small sac", and refers to the vesicular structure attached to the base of the tail stem.

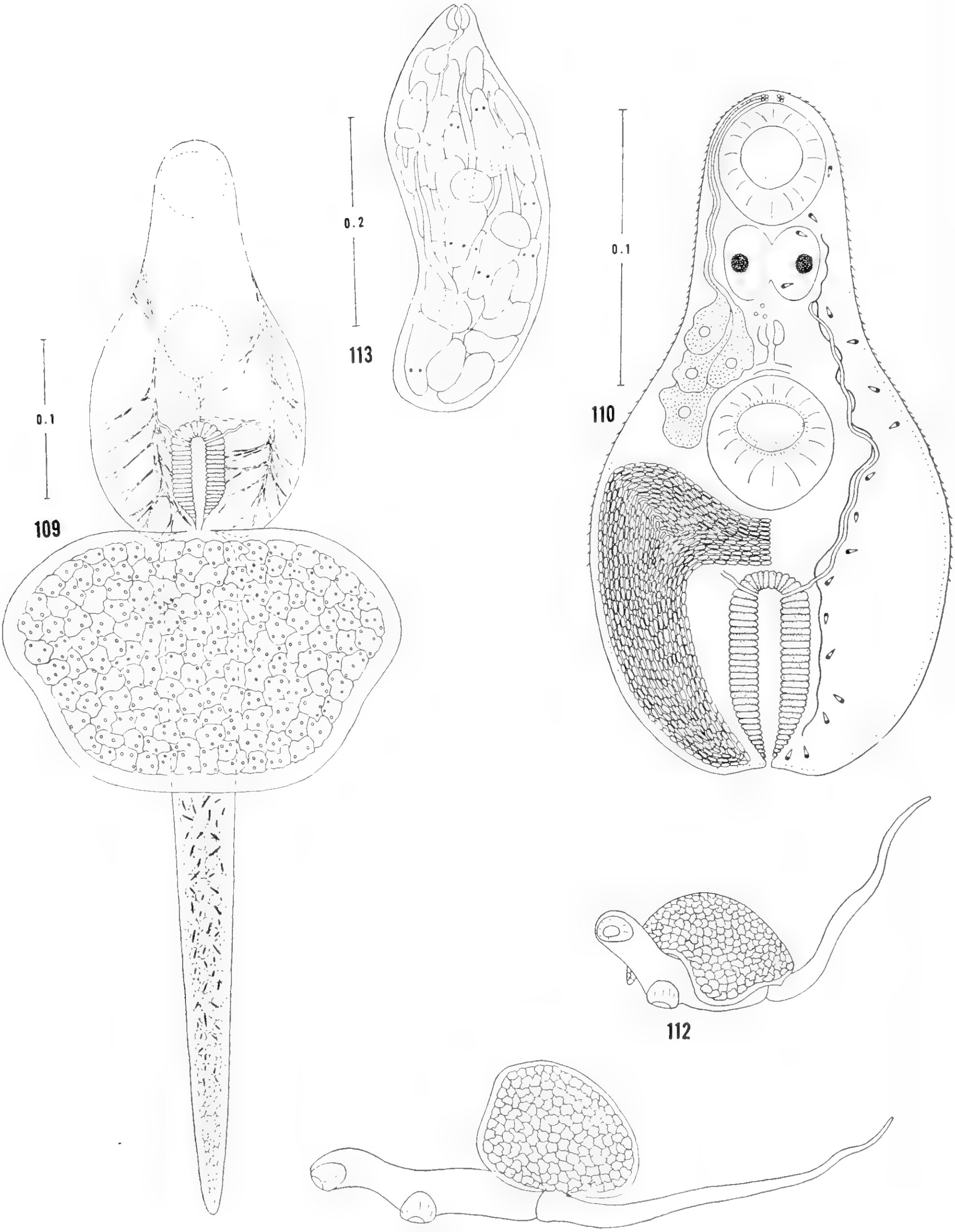
This larva emerges at night in small numbers, has a life span of about 36 hours and is photopositive. Neutral red is slightly toxic; it stains the large penetration glands lightly, the small glands darkly, and it stimulates flame cell activity. Nile blue sulfate is very toxic and stains the cystogenous glands and cephalic ganglia.

This species swims vigorously, lashing the tail from side to side with the forebody slightly arched (Figure 111). When resting, the larva sinks to the bottom, ventral side down, with the body contracted into a depression in the anteroventral side of the caudal vesicle and the tail stem pointing upward at an angle of about 45° (Figure 112). At times, the larva will lie on its side with its parts in the same relative positions.

Cercaria portosacculus resembles *C. caribbea* XXXIV Cable, 1956, but differs from it in the number of cephalic glands, shape of the caudal vesicle, shape and size of the body, and other less apparent features.

V. Introduction to Key and Bibliography

A survey of marine cercariae necessarily entails a comprehensive study of the literature. Since no keys to marine cercariae exist, except Cable's (1956a) which deals with 51 species from Puerto Rico, a study of the world's literature has been undertaken with the purpose of abstracting pertinent data concerning each described cer-



Figures 109-113. **109.** *Cercaria portosacculus*, sp. nov., dorsal view showing dorsal parenchymal (muscle?) fibers on left side and ventral fibers on right side of body, and details of vesicle and tail. **110.** Same, ventral view of cercarial body. **111.** Same, lateral view showing swimming posture. **112.** Same, laterofrontal view showing resting posture. **113.** Same, redia.

caria. These cercariae have been categorized as far as possible according to LaRue's (1957) scheme of classification in a Key to Superfamilies with the species listed according to families, where possible.

The names of all described marine cercariae encountered, regardless of the accuracy and quality of their descriptions, have been included in the key. Almost all of the cercarial descriptions published prior to 1900 are inadequate by modern standards and one would have difficulty recognizing and comparing these larval stages with living material.

In using the key, the readers must realize that external morphology is no longer the sole basis for classifying cercariae. For example, trichocercous forms are found in the Allocreadioidea and Fellodistomatoidea; tailless forms are found in the Plagiorchioidea, Allocreadioidea and Fellodistomatoidea; and xiphidiocercariae are found in the Plagiorchioidea and Allocreadioidea. An effort has been made to categorize forms of uncertain affinities properly by comparing them with cercariae whose life cycles are known. There is little or no question concerning the taxonomic position of many cercariae. Where no suggestion of affinity was made by another author, or a suggestion seemed incorrect, the writer used his own judgment in placing the cercaria. These examples are marked by an asterisk.

At the conclusion of the key, a category of cercariae of unknown status has been included. These larvae were either inadequately described or their descriptions do not fit any category in the key.

The assemblage of "type" and "group" names introduced by Sewell (1922), Lühe (1909), Cort (1915), and others are used only to a limited extent. These terms, which were originally devised to show morphological relationships between cercariae, are now obsolete. We now know through life history studies, as indicated above, that morphologically dissimilar cercariae can be members of the same family.

The key contains 334 different species of marine cercariae. Thirty-six additional names have been reduced to synonymy. Eighteen per cent, or 60 species, have had their life cycles partially or completely elucidated.

The bibliography includes not only cited references but all references to authors of specific names that appear in the key and elsewhere.

Key To Superfamilies Of Cercariae With a Checklist of Known Marine Species

I. Primitive excretory bladder retained, i.e. not replaced by cells from mesoderm, hence definitive excretory bladder not epithelial. Cercariae with forked or single tails, sometimes absent in Fellodistomatidae, caudal excretory vessels present in developing cercariae (except perhaps in certain species of Renicolidae); stylet always absent .... Superorder Anepitheliocystidia LaRue, 1957

A. Cercariae usually fork-tailed........Order Strigeatoidea LaRue, 1926

1. Cercariae fork-tailed; usually distomate; excretory bladder V-shaped; protonephridia mesostomate or stenostomate; penetration glands present; active penetration into next host .... Suborder Strigeata LaRue, 1926

a. Cercariae usually longifurcate, tail-stem usually slender; oral sucker well developed; acetabulum usually present; two to four pairs of large penetration glands located in acetabular zone (Strigeidae, Diplostomidae), or many glands near cecal bifurcation (Cyathocotylidae); protonephridia mesostomate; development in filiform sporocysts; three-host life cycle ....Superfamily Strigeoidea Railliet, 1919

Family Strigeidae Ralliet, 1919

**Cercaria* sp. (abnormal) Mathias, 1930

Cercaria nassa Martin, 1945

**Cercaria* "K" Hutton, 1952

Family Cyathocotylidae Poche, 1926

Cercaria utriculata Lutz, 1933

Cercaria "R" McCoy, 1928

Cercaria sp. Maxon and Pequegnat, 1949

Cercaria caribbea L Cable, 1956

Cercaria caribbea LI Cable, 1956

Cercaria ogatai Ito, 1956

No marine cercariae described for the following families:

Family Diplostomidae Poirier, 1886

Family Brauninidae Bosma, 1931

Family Bolbocephalodidae Strand, 1935

Family Proterodiplostomidae Dubois, 1937

b. Cercariae brevifurcate; apharyngeate; oral sucker replaced by extensible penetration organ as in Schistosomatidae; acetabulum rudimentary; penetration glands as in Strigeidae and Diplostomidae; eyespots pigmented; develop in rediae; three-host life cycle .... Superfamily Clinostomoidea Dollfus, 1931

Family Clinostomidae Luhe, 1901. No marine cercariae described for this family.

c. Cercaria brevifurcate; apharyngeate; oral sucker replaced by extensible penetration organ; six or seven pairs of penetration glands; with or without pigmented eyespots; development in simple sporocysts; cercariae penetrating into final host. . Superfamily Schistosomatoidea Stiles and Hassal, 1926

Family Schistosomatidae Looss, 1899

Cercaria of *Austrobilharzia variglandis,* Penner, 1953; *syns: Cercaria variglandis,* Miller and Northup, 1926; *Microbilharzia variglandis,* Stunkard and Hinchliffe, 1952

Cercaria littorinalinae Penner, 1950

Cercaria "H" Hutton, 1952

Cercaria of *Gigantobilharzia huttoni* (Leigh, 1953) Leigh, 1955; *syns: Cercaria huttoni* Leigh, 1953; *Cercaria* "J" Hutton, 1952

Cercaria of *Ornithobilharzia canaliculata* (Odhner, 1912) Penner, 1953

Cercaria Caribbea XLIX Cable, 1956

Cercaria tympanotoni Ito, 1956

Cercaria of *Austrobilharzia terrigalensis* (Johnston, 1917) Bearup, 1956

Family Aporocotylidae Odhner, 1912

Cercaria loossi Linton, 1915

Cercaria sp. Linton, 1915

Cercaria solemyae Martin, 1944

Cercaria hartmanae Martin, 1952

Cercaria sp. Holliman, 1958; *syn: C. asymmetrica,* sp. nov.

Family Spirorchiidae Stunkard, 1921. No marine cercariae described for this family.

2. Cercariae fork-tailed or variously modified from that condition; distomate or gasterostomate. Cercariae usually furcocystocercous; distomate or monostomate; protonephridia stenostomate, with flame cell groups in the tail; development in rediae ....Suborder Azygiata LaRue, 1957

a. Cercariae furcocystocercous ... Superfamily Azygioidea Skrjabin and Guschanskaja, 1956

Family Azygiidae Odhner, 1911. No marine cercariae described for this family.

Family Bivesiculidae Yamaguti, 1939

Cercaria sp. Katsuta, 1932

Cercaria caribbea XLVIII LeZotte, 1954; syn: *Cercaria* "A" Hutton, 1952

Cercaria caribbea XLVI LeZotte, 1954; syn: *Cercaria* "B" Hutton, 1952

Cercaria caribbea XLIV LeZotte, 1954; syn: *Cercaria* "C" Hutton, 1952

Cercaria caribbea, XLIII LeZotte, 1954

Cercaria caribbea XLV LeZotte, 1954

Cercaria caribbea XLVII LeZotte, 1954

b. Cercariae brevifurcate; tail stem bearing a pair of anteriorly placed appendages; body leaflike: distomate; apharyngeate; eyespots pigmented; branches of gut fused posteriorly ...Superfamily Transversotrematoidea LaRue, 1957

Family Transversotrematidae Yamaguti, 1953. No marine cercariae described for this family.

3. Cercariae distomate; tail very short and bilobed (*Pseudhyptiasmus*) or lacking; excretory bladder V-shaped; developing in rediae; encysting in or near rediae ...Suborder Cyclocoelata LaRue, 1957

Characterisitcs the same as for Suborder .... Superfamily Cyclocoelidea Nicoll, 1934

No marine cercariae described for the following families:

Family Cyclocoelidae Kossack, 1911

Family Typhlocoelidae Bittner and Sprehn, 1928

Family Bothrigastridae Dollfus, 1948

4. Cercariae distomate; tail forked, of moderate size, greatly reduced, or lacking; protonephridia stenostomate; development in sporocysts.. Suborder Brachylaimata LaRue, 1957

a. Tail functional, rudimentary, or lacking; excretory vesicle V-shaped with short arms; development in branching sporocysts in aquatic or terrestrial snails; life cycle with 2 or 3 hosts; those with 3 hosts provided with penetration glands near acetabulum and in oral sucker ....Superfamily Brachylaimoidea Allison, 1943 (emend. LaRue, 1957)

Family Brachylaimidae Joyeux and Foley, 1930. No marine cercariae described for this family.

b. Cercariae with tail forked, modified to single tail, or lacking; tail stem with or without paired multiple setae; excretory vesicle U- or lyre-shaped, with short stem and long broad arms; protonephridia stenostomate; penetration glands numerous and far anterior; development in simple sporocysts in marine lamellibranchs; 3 host life cycle ..... Superfamily Fellodistomatoidea LaRue, 1957

Family Fellodistomatidae Nicoll, 1913 Fork-tailed cercariae:

Cercaria dichotoma Muller, 1850

**Cercaria fissicauda* LaValette, 1855

**Cercaria* sp. Huet, 1888

Cercaria sp. Haswell, 1903; *syn: Cercaria tergestia haswelli,* Dollfus, 1927

Cercaria syndosmyae Pelseneer, 1906

Cercaria of *Fellodistomum fellis* Nicoll, 1909

Cercaria margaritae Lebour, 1911

**Cercaria* sp. Odhner, 1911

**Cercaria discursata* Sinitzin, 1911

Cercaria sp. Stafford, 1912

Cercaria kenti Dollfus, 1927

Cercaria baltica Markowski, 1936

Cercaria of *Haplocladus* sp. Rees, 1947

Cercaria mathiasi Dubois, Baer and Euzet, 1952

Cercaria myae Uzmann, 1952; syn: *Cercaria* sp. I Stunkard and Uzmann, 1958
Cercaria caribbea XLI Cable, 1953; *syn*: Cercaria of *Parvatrema borinquenae* Cable, 1953
Cercaria reesi Hutton, 1953; syn: *Cercaria* sp. II Stunkard and Uzmann, 1958
Cercaria sp. Loesch, 1957
Cercaria of *Parvatrema donacis* Hopkins, 1958
Cercaria sp. III Stunkard and Uzmann, 1958

Trichocercous cercariae:
Cercaria of *Bacciger bacciger* (Rud., 1819) Palombi, 1932; syns:
Cercaria lata Lespes, 1857; Huet, 1891; *Cercaria lutea* Giard, 1897; *Cercaria* sp. Fujita, 1906; *Cercaria* sp. Pelseneer, 1906.
Cercaria pectinata Chilton, 1905
Cercaria pennata Sinitzin, 1911
Cercaria plumosa Sinitzin, 1911
Cercaria chiltoni Dollfus, 1925
Cercaria laevicardium Martin, 1945; syn: *Cercaria laevicardii*, Cable, 1954
Cercaria caribbea XXXIX Cable, 1956

Tailless cercariae:
Cercaria of *Gymnophallus somateriae* Jameson, 1902; *syns*: *Cercaria glandosa* Lebour, 1911; *Cercaria strigata* Lebour, 1911; Cercaria of *Gymnophallus oedemiae* Jameson and Nicoll, 1913
**Cercaria crispata* Pelseneer, 1906
Cercaria sp. Dubois, 1907
Cercaria cambrensis Cole, 1938
Cercaria of *Rhodotrema quadrilobata* Bazikalova, 1932
Cercaria fulbrighti Hutton, 1952
Cercaria branchidontis Hopkins, 1954

Microcercous cercariae:
Cercaria milfordensis Uzmann, 1953; syn: Cercaria of *Proctoeces maculatus* (Looss, 1901), Stunkard and Uzmann, 1959
Cercaria adranocerca Stunkard and Uzmann 1959

Furcotrichocercous cercaria:
Cercaria caribbea XL Cable, 1956

c. Cercariae gasterostomate: tail stem short and bulbous; furcae very long and active; excretory vesicle cylindrical; protonephridia mesostomate; development in branched sporocysts in lamellibranchs of fresh and brackish waters; life cycle with 3 hosts Superfamily Bucephaloidea LaRue, 1926

Family Bucephalidae Poche, 1907
Cercaria of *Bucephalus* (*Bucephalopsis*) *haimeanus* Lacaze-Duthiers, 1854
Cercaria of *Bucephalus cuculus* McCrady, 1874
Cercaria of *Bucephalus crux* Levinsen, 1881
Cercaria sp Haswell, 1903
Cercaria of *Bucephalus syndosmyae* Lebour, 1911
Cercaria hydriformis Sinitzin, 1911; syn: Cercaria of *Bucephalus haimeanus tapes rugatus* Sinitzin, 1909
Cercaria "X" Miller, 1925
Cercaria of *Bucephalus margaritae* Ozaki and Ishibashi, 1934
Cercaria of *Bucephalus mytili* Cole, 1935
Cercaria of *Prosorhynchus squamatus* (Odhner, 1905) Chubrik, 1952
Cercaria caribbea XLII Cable, 1956
Cercaria of *Bucephalus loeschi* Hopkins, 1958

B. Cercariae with large bodies and strong tails; cystogenous glands numerous; protonephridia stenostomate; miracidia with one pair of flame cells; development in rediae .... Order Echinostomida LaRue, 1957

1. Cercariae echinostomate or exhibiting modifications therefrom in time of appearance of collar and collar-spines and in degree of development of these structures; development in collared rediae with stumpy appendages; life cycle usually involving 3 hosts .... Suborder Echinostomata Szidat, 1939

Characteristics the same as for Suborder .... Superfamily Echinostomoidea Faust, 1929

Family Echinostomidae Looss, 1902
Cercaria with collar spines:
Cercaria proxima Lespes, 1857
Cercaria of *Echinostomum leptosomum* Lebour, 1911
Cercaria of *Echinostomum secundum* Lebour, 1911
Cercaria littorinae obtusatae Lebour, 1911
Cercaria of *Himasthla quissetensis* (Miller and Northup, 1926); *syn*: *Cercaria quissetensis* Miller and Northup, 1926
Cercaria of *Acanthoparyphium* sp. Yamaguti, 1934
Cercaria granifera Ogata, 1943
Cercaria I Maxon and Pequegnat, 1949
Cercaria III Maxon and Pequegnat, 1949
Cercaria "G" Hutton, 1952
Cercaria "L" Hutton, 1952
Cercaria caribbea II Cable, 1956
Cercaria caribbea III Cable, 1956
Cercaria ophthalmoechinata Ito, 1957
Cercaria yamaguti Ito, 1957

Cercariae without collar spines:
Cercaria "F" Hutton, 1952
Cercaria caribbea IV Cable, 1956
Cercaria caribbea VI Cable, 1956

Family Philophthalmidae Travassos, 1918
**Cercaria* sp. Lebour, 1907
Cercaria of *Parorchis acanthus* (Nicoll, 1906); *syns*: *Cercaria purpurae* Lebour 1911; Cercaria of *Parorchis avitus* Linton, 1914; *Cercaria sensifera* Stunkard and Shaw, 1931; *Cercaria* II Maxon and Pequegnat, 1949; *Cercaria purpurae* var. *australis* Angel, 1954

**Cercaria patellae* Lebour, 1911
**Cercaria* "O" Miller, 1925
Cercaria of *Cloacitrema michiganensis* McIntosh, 1938, Robinson, 1952
**Cercaria caribbea* V Cable, 1956
**Cercaria pseudogranifera* Ito, 1957

Family Haplosplanchnidae Poche, 1926
Cercaria of *Haplosplanchnus acutus*, Cable, 1954; *syn*: *Cercaria caribbea* XXXVIII Cable, 1954
**Cercaria digitalis* Schell and Thomas, 1955

No marine cercariae described for the following families:
Family Fasciolidae Railliet, 1895
Family Rhopaliidae Looss, 1898
Family Psilostomidae Odhner, 1911
Family Campulidae Odhner, 1926
Family Rhytidodidae Odhner, 1926
Family Cathaemasiidae Fuhrmann, 1928

3 Cercariae amphistomate or monostomate; penetration apparatus lacking; bodies heavily pigmented; two or three pigmented eyespots; development in rediae lacking collar and usually lacking stumpy appendages; cercariae emerging from rediae before completing growth; 2 host life cycle; encystment on substrate .... Suborder Paramphistomata Szidat, 1936

a Cercariae typically amphistomate; pharynx present and often replacing oral sucker ...... Superfamily Paramphistomatoidea Stiles and Goldberger, 1910

Family Mesometridae Poche, 1926
Cercaria of *Mesometra orbicularis* (Rud., 1819), Palombi, 1937

No marine cercariae described for the following families:
Family Paramphistomatidae Fischoeder, 1901
Family Gastrodiscidae Stiles and Goldberger, 1910
Family Gastrothylacidae Stiles and Goldberger, 1910
Family Heronimidae Ward, 1918
Family Microscaphidiidae Travassos, 1922
Family Cladorchiidae Southwell and Kirschner, 1937
Family Brumptidae Skrjabin, 1949
Family Diplodiscidae Skrjabin, 1949
Family Stephanopharyngidae Skrjabin, 1949

b. Cercaria monostomate; pharynx lacking; main collecting vessels fused anteriorly; protrusible cup-shaped attaching structures situated posterolaterally .... Superfamily Notocotyloidea LaRue, 1957

Family Notocotylidae Luhe, 1909
Cercaria ephemera Lebour, 1907
Cercaria inkermanni Sinitzin, 1911
Cercaria zostera Sinitzin, 1911
Cercaria "Q" Miller, 1926
Cercaria lebouri Stunkard, 1932
Cercaria sp. Maxon and Pequegnat, 1949
Cercaria caribbea I Cable, 1956
Cercaria of *Catatropis johnstoni* Martin, 1956

No marine cercariae described for the following families:
Family Pronocephalidae Looss, 1902
Family Rhabdopoeidae Poche, 1926

C. Cercariae of rhodometopa type (distomate; pharyngeate; body large, two or four groups of small penetration glands anterior to ventral sucker; tail large, frequently provided with dorsal, ventral, and lateral fins; excretory bladder large, Y-shaped, with lateral diverticula arising from stem and arms, post-acetabular commissure present or lacking; protonephridia mesostomate; caudal vessels usually present in developing cercariae; development in simple sporocysts in marine gastropods; 3-host life cycle) Order Renicolida LaRue, 1957

Characteristics the same as for Order .... Suborder Renicolata LaRue, 1957

Characteristics the same as for Order ..... Superfamily Renicoloidea LaRue, 1957

Family Renicolidae Dollfus, 1939
Cercaria rhodometopa Perez, 1924, 1926
Cercaria "D" Miller, 1925
Cercaria "E" Miller, 1925
Cercaria "H" Miller, 1925
Cercaria ampelis Rothschild, 1935
Cercaria doricha Rothschild, 1935; *syn*: *Cercaria doricha-pigmentata* Wright, 1956
Cercaria herpsyllis Rothschild, 1935
Cercaria nicarete Rothschild, 1935
Cercaria pythionike Rothschild, 1935
Cercaria ranzii Rothschild, 1935
**Cercaria prehensa* Schell and Thomas, 1955
Cercaria caribbea VII Cable, 1956
Cercaria caribbea VIII Cable, 1956
Cercaria caribbea IX Cable, 1956
Cercaria cooki Wright, 1956

II. Primitive execretory bladder surrounded by, and then replaced by, layer or cells derived from mesoderm, hence definitive bladder thick-walled and epithelial, cercarial tail single, reduced in size, or lacking; caudal excretory vessels present or lacking .... Superorder Epitheliocystidia LaRue, 1957

A. Cercariae completely lacking caudal excretory vessels at any stage of development; stylet present or lacking .... Order Plagiorchiida LaRue, 1957

1. Cercaria typically distomate and pharyngeate; of various xiphidiocercarial types (armatae, ornatae, virgulae, microcotylae, or tailless); stylet horizontal; protonephridia mesostomate; encystment in invertebrates (chiefly arthropods, rarely in vertebrates .... Suborder Plagiorchiata LaRue, 1957

a. Characteristics the same as for Suborder ...... Superfamily Plagiorchioidea Dollfus, 1930

Family Microphallidae Travassos, 1921
Tailless cercariae:
**Cercaria dentalii* Pelseneer, 1906
**Cercaria giardi* Pelseneer, 1906
Cercaria oocysta Lebour, 1907
Cercaria littorinae-rudis Lebour, 1911

Cercaria sinuosa Sinitzin, 1911; *syn*: *Cercaria plicata var. rissoa* Sinitzin, 1910
**Cercaria suctoria* Sinitzen, 1911
**Cercaria* sp. Linton, 1915
Cercaria tenuans Cole, 1935
**Cercariaeum hydrobiae ventrosae* Markowski, 1936
Cercaria franci Arvy, 1952

Distome xiphidiocercaria:
Cercaria of *Microphallus pirum* (Afanassjew, 1941) Schiller, 1959

Monostome xiphidiocercariae:
Cercaria of *Microphallus similis* (Jagersk, 1900), Stunkard, 1957; *syns*: *Cercaria ubiquita* Lebour, 1911; Cercaria of *Spelotrema simile* Lebour, 1911; *Cercaria ubiquitoides* Stunkard, 1932; *Cerceria* sp. Rees, W. J., 1936
Cercaria grisea Markowski, 1936
Cercaria of *Levinseniella cruzi* (Travassos, 1920) Young, 1938
Cercaria of *Gynaecotyla adunca* (Linton, 1905) Hunter and Vernberg, 1953; *syns*: *Cercaria nassicola* Cable and Hunninen, 1940; *Cornucopula nassicola* (Cable and Hunninen, 1938); *Gynaecotyla nassicola* (Cable and Hunninen, 1938) Rankin, 1940
Cercaria of *Spelotrema nicolli* Cable and Hunninen, 1940
Cercaria misenensis Palombi, 1940
Cercaria ubiquitensis Palombi, 1940
Cercaria sp. Maxon and Pequegnat, 1949
Cercaria minima Schell and Thomas, 1955
Cercaria caribbea XXV Cable, 1956
Cercaria caribbea XXVI Cable, 1956
Cercaria caribbea XXVII Cable, 1956
Cercaria caribbea XXVIII Cable, 1956
Cercaria caribbea XXIX Cable, 1956
Cercaria caribbea XXX Cable, 1956
Cercaria caribbea XXXI Cable, 1956

Plagiorchioid cercariae of unknown affinity:
Distome xiphidiocercariae:
**Cercaria brevicauda* Pelseneer, 1906
**Cercaria emasculans* Pelseneer, 1906
**Cercaria cribrata* Sinitzin, 1911
**Cercaria plicata* var. *cerithiolus* Sinitzin, 1910; syn: *Cercaria dimorpha* Sinitzin, 1911
**Cercaria* "G" Miller, 1925
**Cercaria parvicaudata* Stunkard and Shaw, 1931
**Cercaria roscovita* Stunkard, 1932
Cercaria caribbea XXXII Cable, 1956
Cercaria caribbea XXXIII Cable, 1956

*Family Brachycoeliidae Johnston, 1912
**Cercaria cerithidia* Porter, 1938

No marine cercariae described for the following families:
Family Plagiorchiidae Luhe, 1901
Family Dicrocoeliidae Odhner, 1910
Family Lecithodendriidae Odhner, 1910
Family Cephalogonimidae Nicoll, 1915
Family Collyriclidae Ward, 1918
Family Eucotylidae Skrjabin, 1924
Family Lissorchiidae Poche, 1926
Family Mesotretidae Poche, 1926
Family Stomylotrematidae Poche, 1926
Family Urotrematidae Poche, 1926
Family Haplometridae McMullen, 1937
Family Macroderoididae McMullen, 1937
Family Ochetosomatidae Leao, 1944

b. Cercariae of various types (ophthalmoxiphidiocercariae, microcercous, cotylomicrocercous, macrocercous, rhopalocercous, ophthalmotrichocercous, tailless, or of megaperid type with muscular tail having lateral and ventral fins); stylet usually not horizontal, if present; protonephridia usually mesostomate; excretory bladder saccate or Y-shaped; development in rediae or sporocysts, in snails or lamellibranchs; encystment in invertebrates (chiefly arthropods), rarely in vertebrates; usually 3 host life cycle ...... Superfamily Allocreadioidea Nicoll, 1934

Family Acanthocolpidae Luhe, 1909
Ophthalmoxiphidiocercariae:
**Cercaria microsoma* Sinitzin, 1911
Cercaria of *Stephanostomum tenue* (Linton, 1898) Martin, 1939
Cercaria of *Stephanostomum baccatum* (Nicoll, 1907) Wolfgang, 1955

Family Allocreadiidae Stossich, 1903
Leptocercous cercariae:
**Cercaria parvirenalis* Pelseneer, 1906
Cercaria of *Acanthopsolus lageniformis* Lebour, 1911
Cercaria of Lepodora rachion (Cobbold, 1858) Lebour, 1911
**Cercaria mesentera* Sinitzin, 1911
**Cercaria metentera* Sinitzin, 1911
**Cercaria trivesicata* Sinitzin, 1911
**Cercaria zernowi* Sinitzin, 1911
**Cercaria* sp. Rothschild, 1939
**Cercaria dicearchiae* Palombi, 1940

Family Lepocreadiidae Nicoll, 1934
Oculate trichocercous cercariae:
**Histrionella echinocerca* Diesing, 1855; *syn*: *Cercaria echinocerca* Diesing, 1858
**Cercaria echinocerca* Filippi, 1855
**Cercaria elegans* LaValette, 1855; *syn*: *Distomum carinariae* Carus, 1885
**Cercaria coni mediterranei* Filippi, 1857
*Cercaria of *Macrurochaeta acalepharum* Costa, 1864

**Cercaria fascicularis* Villot, 1875
**Cercaria* sp. Fewkes, 1882
**Histrionella setosicauda* Daday, 1888
Cercaria of *Opechona bacillaris* (Molin, 1859) Lebour, 1916
**Cercaria quintareti* Dollfus, 1925
**Cercaria* sp. Dollfus, 1925
Cercaria of *Lepocreadium setiferoides* (Miller and Northup, 1926); *syn*: *Cercaria setiferoides* Miller and Northup, 1926
Cercaria of *Lepocreadium* sp. Dollfus, 1927
Cercaria of *Lepocreadium album* (Stossich, 1890) Palombi, 1937
Cercaria of *Deropristis inflata* (Molin, 1859) Cable and Hunninen, 1942; *syn*: *Cercaria inflata* Cable and Hunninen, 1942

Non-oculate trichocercous cercariae:
Cercaria setifera Muller, 1850
**Distomum hippopodii* Vogt, 1853
**Cercaria thaumantiatis* Graeffe, 1858
**Cercaria villoti* Monticelli, 1888
**Cercaria pelseneeri* Monticelli, 1914
**Cercaria claparedei* Dollfus, 1925

Trichocercous cercariae (presence or absence of eyespots unknown):
**Distoma carinariae* Chiaie, 1841
**Distomum physophorae* Philippi, 1843

Family Megaperidae Manter, 1934
Cercaria of *Megapera gyrina* (Linton, 1907), Cable, 1954; *syns*: *Cercaria "K"* Miller, 1925; *Cercaria caribbea* XXXVII, Cable 1954

Family Monorchiidae Odhner, 1911
**Cercaria myocerca* Villot, 1878
**Cercaria myocercoides* Pelseneer, 1906
**Cercaria nigrotincta* Pelseneer, 1906
**Cercaria neptuneae* Lebour, 1911
**Cercaria ophiocerca* Palombi, 1934
Cercaria of *Monorcheides cumingiae* Martin, 1940; *syn*: *Cercaria cumingiae* Martin, 1938
Cercaria of *Postmonorchis donacis* Young, 1953; *syns*: *Cercaria donacis* Young, 1953; (?) *Cercaria myocerca* Villot, 1878
Cercaria caribbea XXXV Cable, 1956
Cercaria caribbea XXXVI Cable, 1956
Cercaria choanura Hopkins, 1958

Family Opecoelidae Ozaki, 1925
Cotylocercous cercariae:
**Cercaria pachycerca* Lespes, 1857; *syns*: *Cercaria pachycerca* Diesing, 1858; *Cercaria brachyura* Lebour, 1911
**Cercaria collumbellae* Pagenstecher, 1863
**Cercaria cotylura* Pagenstecher, 1863
**Cercaria buccini* Lebour, 1911
**Cercaria linearis* Lespes, 1857; syn: *Cercaria linearis* Lebour, 1911
Cercaria of *Hamacreadium mutabile* Linton, 1901, McCoy, 1929; *syn*: *Cercaria "A"* Miller, 1925
Cercaria of *Hamacreadium gulella* Linton, 1910, McCoy, 1930; *syn*: *Cercaria "B"* Miller, 1925
Cercaria of *Helicometrina nimia* Linton, 1910, Manter, 1933; syn: *Cercaria "J"* Miller, 1925
**Cercaria inconstans* Sinitzin, 1911
**Cercaria "I"* Miller, 1925
**Cercaria "M"* Miller, 1925
**Cercaria searlesiae* Miller, 1925
**Cercaria "V"* McCoy, 1929
**Cercaria pisaniae* Palombi, 1938
**Cercaria ruvida* Palombi, 1938
**Cercaria stunkardi* Palombi, 1938
**Cercaria tridentata* Palombi, 1938
Cercaria of *Opecoeloides manteri* Hunninen and Cable, 1941
Cercaria of *Podocotyle atomon* (Rud., 1802) Huninen and Cable, 1943
Cercaria caribbea XX Cable, 1956
Cercaria caribbea XXI Cable, 1956
Cercaria caribbea XXII Cable, 1956
Cercaria caribbea XXIII Cable, 1956
Cercaria caribbea XXIV Cable, 1956
Cercaria cotylicerca A Dollfus, 1959
Cercaria cotylicerca B Dollfus, 1959
Cercaria cotylicerca C Dollfus, 1959
Cercaria cotylicerca D Dollfus, 1959
Cercaria cotylicerca E Dollfus, 1959
Cercaria cotylicerca F Dollfus, 1959
Cercaria cotylicerca G Dollfus, 1959
Cercaria cotylicerca H Dollfus, 1959
Cercaria cotylicerca I Dollfus, 1959
Cercaria sp. Gaillard, 1959

Family Zoogonidae Odhner, 1911
Cercaria of *Zoogonus viviparus* (Olsson, 1868) Lebour, 1916
Cercaria of *Zoogonus rubellus* (Olsson, 1868), Stunkard, 1938; *syns*: (?): *Distomum lasium* Leidy, 1891; *Cercariaeum lintoni* Miller and Northup, 1926
Cercaria of *Diphterostomum brusinae* (Stossich, 1899) Palombi, 1930; *syns*: (?): *Distoma buccini mutabilis* Filippi, 1857; *Cercaria crispata* Pelseneer, 1906; *Cercaria inconstans* Sinitzin, 1911
Cercaria reticulatum Stunkard, 1932
Cercaria of *Zoogonoides laevis* (Linton, 1940) Stunkard, 1943
Cercaria of *Diphtherostomum luteum* Yamaguti, 1958; *syns*: *Cercaria lutea* Giard,

1897; Cercaria of *Brachycoelium luteum* Giard, 1897
No marine cercariae described for the following families:
Family Gorgoderidae Looss, 1901
Family Gyliauchenidae (Goto and Matsudaira) in Ozaki, 1933
Family Opistholebetidae Fukui, 1929
Family Troglotrematidae Odhner, 1914

B. Cercariae with caudal excretory vessels during development; stylet always lacking .... Order Opisthorchiida LaRue, 1957

1. Primary excretory pores on margins of tail near body-tail furrow; bodies of opisthorchioid type; oral sucker protrusible, with large spines and openings of penetration glands in crypt anterior to subterminal mouth; ventral sucker usually rudimentary; tails pleuro- or parapleurolophocercous, magna- or even zygocercous; protonephridia mesostomate or stenostomate; bladder V-shaped or globular; development in sporocysts or rediae; encystment in lower vertebrates .... Suborder Opisthorchiata LaRue, 1957

Characteristics the same as for Suborder .... Superfamily Opisthorchioidea Faust, 1929

Family Heterophyidae Odhner, 1914
Magnacercous cercariae:
**Cercaria sp Fujita,* 1906
**Cercaria equitator* Sinitzin, 1911
**Cercaria "F"* Miller, 1925
**Cercaria purpuracauda* Miller, 1925
**Cercaria "T"* Miller, 1929
**Cercaria "U"* Miller, 1929
**Cercaria "W"* Miller, 1929
Cercaria caribbea XVI Cable, 1956
Cercaria caribbea XVII Cable, 1956
Cercaria caribbea XVIII Cable, 1956
Cercaria caribbea XIX Cable, 1956
Cercaria komiya Ito, 1956
Cercaria nigrocaudata Ito, 1956

Pleurolophocercous cercariae:
Cercaria quadripterygia Sinitzin, 1911
Cercaria floridensis McCoy, 1929; *syn*: *Cercaria "P"* Miller, 1926
Cercaria of *Cryptocotyle lingua* (Crepl., 1825), Stunkard, 1930; *syns*: *Cercaria lophocerca* Filippi, 1859; *Cercaria lophocerca,* Lebour, 1911
Cercaria of *Cryptocotyle jejuna* (Nicoll, 1907) Rothschild, 1938
Cercaria of *Pygidiopsis summa* (Onji and Nishio, 1916) Ochi, 1931
Cercaria coronanda Rothschild, 1938
**Cercaria* sp. Rothschild, 1938
Cercaria sp. Rothschild, 1941
Cercaria of *Euhaplorchis californiensis* Martin, 1950
Cercaria of *Parastictodora hancocki* Martin, 1950; *syn*: *Cercaria pleurolophocercous* I Maxon and Pequegnat, 1949
Cercaria of *Heterophyes* sp. Martin and Kuntz, 1955
Cercaria of *Stictodora tridactyla* Martin and Kuntz, 1955
**Cercaria bermudensis* Schell and Thomas, 1955
Cercaria caribbea X Cable, 1956
Cercaria caribbea XI Cable, 1956
Cercaria caribbea XII Cable, 1956
Cercaria of *Heterophyes aequalis* Looss, 1902, Kuntz and Chandler, 1956

Magnacercous opisthorchioid cercariae of unknown affinity:
Cercaria clausii Monticelli, 1888
Cercaria buchanani Martin and Gregory, 1951
Cercaria dipterocerca Miller and Northup, 1926

Family Opisthorchiidae Braun, 1901
Cercaria of *Phocitremoides ovale* Martin, 1950; *syn*: *Cercaria pleurolophocercous* II Maxon and Pequegnat, 1949

Family Cryptogonimidae Ciurea, 1933
Cercaria of *Siphodera vinaledwardsii* (Linton, 1901) Cable and Hunninen, 1942; *syn*: *Cercaria vinaledwardsii*, Cable and Hunninen, 1942
Cercaria caribbea XIII Cable, 1956
Cercaria caribbea XIV Cable, 1956
Cercaria caribbea XV Cable, 1956

Gymnocephalous cercariae whose family relationship is unknown:
Cercaria neptuneae Lebour, 1911
Cercaria foliatae Miller, 1925
No marine cercariae described for the following families:
Family Acanthostomidae Poche 1926
Family Pachytrematidae Baer, 1944
Family Ratziidae Baer, 1944

2. Primary excretory pores on tail distant from body-tail furrow; cercariae of cystophorous type or modified therefrom; bladder saccate or cylindrical; protonephridia stenostomate; main collecting vessels fused anteriorly, development in rediae; second intermediate host a copepod .... Suborder Hemiurata Skrjabin and Guschanskaja, 1954

Characteristics the same as for Suborder .... Superfamily Hemiuroidea Faust, 1929

Family Hemiuridae Luhe, 1901
Cercaria sp. Vaullegeard, 1896
Cercaria appendiculata Pelseneer, 1906
Cercaria vaullegeardi Pelseneer, 1906
Cercaria laqueator Sinitzin, 1911
Cercaria sagittarius Sinitzin, 1911
Cercaria calliostomae Dollfus, 1923
Cercaria "L" Miller, 1925
Cercaria "A" Miller, 1925
Cercaria "B" Miller, 1925
Cercaria "K" Rothschild, 1936
Cercaria sinitzini Rothschild, 1938
Cercaria rothschildi Palombi, 1940
Cercaria prenanti Arvy, 1949
Cercaria dollfusi Arvy, 1951

Cercaria tregouboffi Arvy, 1952
Cercaria appendiculata Chubrik, 1952
Cercaria naticae Chubrik, 1952
**Cercaria* "X" Hutton, 1952
Cercaria sp. Chabaud and Biguet, 1955
Cercaria melanocystea Arvy and Gaillard, 1956

"Hemiuroid" cercaria:
Cercaria caribbea XXXIV Cable, 1956
Family Ptychogonimidae Dollfus, 1937
Cercaria of *Ptychogonimus megastoma* (Rud., 1819), Palombi, 1942; *syn*: *Cercaria dentali* Pelseneer, 1906
Family Lecithasteridae Skrjabin and Guschanskaja, 1954
Cercaria of *Lecithaster confusus* (Odhner, 1905), Hunninen and Cable, 1943
No marine cercariae described for the following families:
Family Didymozoidae Poche, 1907
Family Halipegidae Poche, 1926
Family Isoparorchiidae Poche, 1926
Family Bathycotylidae Dollfus, 1932
Family Dinuridae Skrjabin and Guschanskaja, 1954
Family Lecithochiridae Skrjabin and Guschanskaja, 1954

Cercariae of unknown taxonomic position:
Cercaria sagittata Lespes, 1857
Cercariacum tellinae baltica Diesing, 1858
Cercaria hymenocerca Villot, 1875
Cercaria sp. (fork-tail) Morgan, 1891
Cercaria obtusicaudata Pelseneer, 1906
Cercaria naricularia Sinitzin, 1911
Cercaria sp. Jones and Rothschild, 1932
Cercaria caulleryi Markowski, 1936
Cercaria "D" (fork-tail) Hutton 1952
Cercaria "E" (leptocercous) Hutton, 1952
Cercaria "I" (leptocercous) Hutton, 1952
Cercaria "M" (leptocercous) Hutton, 1952
Cercaria turritellae (magnacercous monostome) Hutton, 1955

VI. Summary

This work constitutes the first major effort to study the cercarial fauna of the Gulf of Mexico and each species establishes a new host and locality record. The present work supports the contention that detailed specific diagnoses are necessary to separate closely related forms, and that the study of the redial or sporocyst stage, the behavior, and cercarial reaction to vital dyes are helpful in diagnosis.

Twenty-eight marine cercariae are reported herein; 24 are new species; 4 previously reported larvae are redescribed: cercaria of *Parorchis acanthus* (Nicoll, 1906), *Cercaria caribbea* III Cable, 1956, cercaria of *Himasthla quissetensis* (Miller and Northup, 1926), and *Cercaria caribbea* XXXVI Cable, 1956.

The following numbers and types of cercariae are described: 1 cyathocotylid, 1 schistosome, 2 aporocotylids, 4 furcocercous fellodistomatids, 1 tailless fellodistomatid, 1 bucephalid, 6 echinostomoids, 4 plagiorchioids, 2 monorchiids, 2 opecoelids, 3 opisthorchioids, and 1 "hemiuroid".

Sixty-nine collections of mollusks were made from Apalachee Bay between September, 1956, and September, 1959. Nineteen species of gastropods were examined involving 13,961 individuals. Of this total 17.7%, or 2,477 individuals, were infected with larval trematodes. Twenty-one trematode cercariae were obtained from gastropods. Ten species of pelecypods were examined involving 2,616 individuals. Of this total 145 individuals, or 5.5%, were infected. Ten species of cercariae were obtained from pelecypods.

A review of the literature on marine cercariae of the world has been made up to January, 1960, and a bibliography has been compiled. All of the known marine cercariae encountered, 334 species, have been taxonomically separated, where possible, according to the classification of LaRue (1957) and have been placed in checklists within the key based on his system.

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VIII. ABSTRACT

A morphological and taxonomic study of the trematode cercariae from 39 species of marine mollusks from Apalachee Bay, Gulf of Mexico, was conducted during the period September, 1956 to September, 1959. It is the first comprehensive report of these parasitic forms from the Gulf of Mexico, and all host and locality records therein are new.

A historical review of the literature on marine cercaria is given, and techniques and methods for cercarial study are discussed.

Twenty four new species of cercariae are described: 1 cyathocotylid, 1 schistosome, 2 aporocotylids, 4 furcocercous fellodistomatids, 1 tailless fellodistomatid, 1 bucephalid, 6 echinostomoids, 4 plagiorchioids, 2 monorchiids, 2 opecoelids, 3 opisthorchioids, and 1 "hemiuroid".

Four previously reported larvae are redescribed: cercaria of *Parorchis acanthus* (Nicholl, 1906), *Cercaria caribbea* III Cable, 1956, cercaria of *Himasthla quissetensis* (Miller and Northup, 1926), and *Cercaria caribbea* XXXVI Cable, 1956.

Each of the cercarial descriptions in the study contains a general diagnosis of the group where known, a telegraphic description of the species, a description of larval behavior, and a discussion of affinities including a comparison of the larva with its most closely related form.

Nineteen species of gastropods were examined involving 13,961 individuals. Of this total, 2477 or 17.7% were infected with larval trematodes (18 species). Ten species of pelecypods were examined involving 2616 individuals. Of this total, 145 or 5.5% were infected with larval trematodes (10 species).

A survey of the literature on marine cercariae of the world revealed 334 descriptions up to January, 1960. All of these larvae were taxonomically separated into family groups and placed in the key to cercariae proposed by LaRue (1957). References to all known marine cercariae are included in the bibliography.

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TULANE STUDIES IN ZOOLOGY

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SPAWNING SEASONS AND GROWTH OF THE CODE GOBY, *GOBIOSOMA ROBUSTUM* (PISCES: GOBIIDAE), IN THE TAMPA BAY AREA

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SEVEN TREMATODES FROM SMALL MAMMALS IN LOUISIANA

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and

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INTRODUCTION

Ginsburg (1933A) described the code goby from Corpus Christi, Texas, and (1933B) recorded its distribution from Corpus Christi across the northern Gulf of Mexico and around southern Florida to the Indian River area on the middle Florida east coast. He also reported a single specimen from Bahia, Brazil. This range has been increased only by a record from Yucatan, Mexico (Hubbs, 1936), and an unpublished record from Brownsville, Texas (USNM 176203). Ginsburg (1933B) gave meristic data and discussed relationships (closest to *G. bosci*). He concluded on the basis of museum specimens that in the genus *Gobiosoma* males average larger and are more numerous than females, and that males and females may be differentiated externally by the nature of their genital papillae (triangular, compressed, pointed flap in males; short thick, truncated cone with lateral terminal fimbriae in females). Hildebrand and Cable (1938) were, however, unable to sex *G. bosci* and *G. ginsburgi* by external characters. One of us (V. G. S.) has found the genital papilla a reliable index of sex in both species.

Fowler (1940) illustrated color pattern variations of the code goby from Lee County, Florida.

At Cedar Key, Florida (ca. Lat. 29°10′ N., Reid, 1954) *G. robustum* was commonest on flats covered with vegetation and occurred at temperatures and salinities ranging from 10.5-30.5°C. and 17.5-31.5 ‰ respectively. The breeding season in this area as inferred from young fish 11-20 mm S.L. extended from spring to fall (June, September, December). Ripe females occurred in June; males with developing gonads were observed in April and August. Winter-caught individuals were pale while summer-caught ones were darker.

In Tampa Bay (ca. Lat. 27°45′ N., Springer and Woodburn, 1960), *G. robustum* was common all year on grass flats, but absent from sandy bottoms. Maturing females were found during November and December, 1957, and February through May, 1958. Maximum average size, 26.9 mm S.L., was attained in May followed by a gradual decrease in average size. The species was most abundant at moderately high salinities, usually between 22 and 32 ‰. Water temperatures during collections ranged from 10.0-32.5°C.

At Palmetto Key (Florida west coast, ca. Lat. 26°50′ N.) Breder (1942) found *G. robustum* abundant among mangrove roots and on sandy beaches (two habitats from which we have procured no specimens in collections from both coasts of Florida and the Florida Keys). He obtained specimens from depths as great as 20 feet, which was as deep as he collected, and from over a variety of bottoms: grass, sponge beds, scallop beds, sand bars and soft spots of flocculent mud. Males guarded eggs in nests of shells and sponges at least from March to June. The largest male was 24 mm S.L. and the smallest ripe one 16.5 mm. Males were generally larger than females. Ripe females were 16.5-21.5 mm S.L. Breder described incubation of naturally spawned eggs (of unknown age at collection) through 117.25 hours at temperatures ranging from 15.5-18.5°C. All eggs died before hatching. He reported that fertilized eggs varied from 1.30-1.79 mm along their longest axes and from .50-.70 along their shortest axes, and mentioned that March eggs were larger than June eggs. Considerably more data than the ten measurements he made will be necessary to establish a seasonal difference in egg size.

Shropshire (1932) described four Florida specimens as *G. molestum* (= *G. bosci*);

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however, the fin-ray counts (second dorsal-10, anal- 11) and general appearance of his figures leave little doubt that the species was *G. robustum*, undescribed at the time of his writing. The four specimens included two larvae, 2.54 and 6.37 mm (total length?) and a postlarva and juvenile, both 8.78 mm. The specimens were collected in plankton hauls during May and June, 1931.

Station Description

Material for the present study, unless otherwise indicated, was collected from the "B" portion of the Tampa Bay station, St. Petersburg (see Springer and Woodburn, 1960, p. 5). Considerable environmental data for this station are available (Springer and Woodburn, 1960; Phillips, 1960A, 1960B). Salinities and temperatures for the present study are included in Table 1. These are similar to the ranges over the past few years (excluding the exceedingly cold winter of 1957-58). During most of the study, vegetation extended from 25 yards below the highest high tide level to a distance of 300 yards out from this point. From November, 1959, through June, 1960, grasses (*Diplanthera, Thalassia*) were dense over the area. In June much of the station was heavily blanketed by *Ulva*. By July the *Ulva* had died and decayed leaving a large area in which any disturbance of the bottom caused decomposition gases to be released. In July and August, gobies were taken only along the periphery of this area. From September through the close of the study the bottom was clear of decaying debris, and the grasses that remained were sparse. *Gobiosoma robustum* was collected only from the grassy areas.

Depths over the grassy portions ranged from a few inches to about four and one-half feet. During the October collection the greatest depth in the sampling area was about one foot. This was shallower than for any other collection.

Methods

Specimens were collected in a pushnet (Strawn, 1954) with a mesh diameter of under one mm, or less than that of a fertilized egg of *G. robustum* (Breder, 1942). All specimens collected were preserved in 10 percent formalin. To insure that all fishes were removed from the pushnet, a plastic scraper with holes less than a millimeter in diameter was used to scape the net. After preservation in formalin for a few days specimens were leached in fresh water and preserved in 40 percent isopropyl alcohol.

Surface temperatures of the water at the collection locality were taken at least 100 feet from the shore line and at a point where the depth was at least one foot; tenths of a degree centigrade were estimated. Densities of water samples taken at the same site as the temperatures were measured using a densimeter. Readings were corrected for temperatures and converted to salinities using a table supplied with the density kit.

To determine comparative monthly relative abundances of *G. robustum*, collections were made in as uniform a manner as possible. A collection of the same single transect of the station area was made each month, but it was soon realized that the varying depths of water and amounts of algae present each month affected collections and made comparisons of abundance impossible. However, each collection almost certainly reflects the relative frequencies of occurrence of the sexes and size groups for its particular month.

Standard lengths (S.L.) were taken with a pair of needlepoint dividers and stepped off on a millimeter ruler. Measurements were recorded to the nearest millimeter; where fractions of a millimeter are given they were estimated.

Specimens were sorted in the laboratory and measured within a few days after collection. They were sexed externally using the genital papilla and supporting color features.

In males the genital papilla is compressed and has the shape of a slender triangle. It is longer in the breeding season and usually there are melanophores covering it. In almost all males examined the prepelvic region is sprinkled with melanophores, increasingly so with size. This area rarely shows more than a faint yellow color in freshly preserved specimens. The pelvic fins and body are generally more heavily pigmented than in females and the number of melanophores reaches its maximum during the breeding season (accounting for Reid's observation that summer-caught individuals were darker than winter-caught ones).

TABLE 1.
Egg diameter frequencies for Gobiosoma robustum *

	1959			1960									
Month	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.
Day	23	21	22	17	21	25	19	24	25	22	23	26	22
Salinity ‰	23.0	24.7	25.6	25.6	23.0	19.2	23.8	27.1	27.7	19.0	15.5	21.6	23.8
Temperature °C.	25.5	18.0	15.5	18.5	19.5	28.2	26.4	28.2	30.8	31.0	28.5	29.4	25.0
Micrometer Divisions													
1	III	XI											
2	XI	IV	VII	V	I							XIII	IV
3			VI	VIII 10	II			1	6			II	XIII
4			IV	35	VI 16			I 20	32	I 33	7	I 3	III
5	1			5	9	6		31	34	34	16	20	
6	1			1	7	32	2	24	23	47	25	2	
7				9	17	54	14	7	5	54	9		
8				12	25	34	11	18	5	29	19		
9				4	15	16	7	22	26	20	34		
10				4	21	32	36	52	35	35	47		
11				15	27	24	48	38	42	33	76		
12	2			26	27	26	68	36	68	45	68	11	
13	6			16	36	34	47	38	91	39	56	9	
14	7			9	23	45	72	48	66	52	62	19	
15	7			3	19	52	65	60	44	35	35	11	
16	1			1	8	66	52	35	13	13	19	7	
17	2				11	34	39	19	8	6	8	6	
18					8	14	20	11			10	2	
19					3	5	9	6			6	3	
20					1		7	7			1	4	
21					2	1	1	1			1		
22							2	1			1	1	
23												2	
No. Females	16	15	17	20	20	20	20	20	20	20	20	20	20

* Roman numerals in a particular micrometer division class represent the total number of females in which diameter of largest egg fitted into a particular class (see also Methods section).

In females the genital papilla is a broad, thick, flap-like organ with a shallowly indented tip. The organ is best developed in large females and reaches its greatest elaboration during the breeding season. On each side of the indented tip of well developed papillae there is frequently found a single melanophore; the remainder of the organ is unpigmented. The prepelvic region is usually without melanophores to a point beneath the posterior level of the head. On rare occasions there is a sprinkling of melanophores in this area, but never so much as in comparably sized males. In freshly preserved females the prepelvic area is bright yellow.

Frequent gonadal checks were made to test ability to distinguish the sexes externally. Although specimens as small as 12 mm S.L. can be sexed externally, error-free sexing was possible only in specimens 16 mm (= 15.5-16.5 mm) or greater. Graph 1 records all specimens less than 16 mm S.L. as sex indeterminate and allocates their length measurements to the two sexes on a 50-50 basis. A chi-square test for a 1:1 sex ratio (one degree of freedom) was made for each month using the sex ratios of specimens 16 mm and larger (Table 2). The 1:1 ratio was found to be statistically feasible for all but one month, September, considering a *P* value of .05 as the critical level of significance. We have no explanation for the variation in sex ratios encountered during that month. (Richard Rosenblatt, personal communication, has suggested that on the basis of chance alone one of the 13 samples would be expected to have a significant *P* value.)

Our smallest gobies were postlarvae (Hubbs, 1943), 5.6-8.5 mm S.L. At this size the fins have developed their full complements of elements. Of the six species of gobies, other than *G. robustum*, found inshore in the Tampa Bay area, *Gobisoma bosci, G. longipala, Gobionellus boleosoma, G. hastatus, Microgobius gulosus* and *M. thalassinus*, only *G. longipala* could be confused with small individuals of *G. robustum*. The rest have consistently higher counts for either the second dorsal or anal fins, or for both. Adults of *G. longipala* are easily distinguished from those of *G. robustum* by the presence of a pair of ctenoid scales on each side of the base of the caudal fin, but the very young of *G. longipala* are unknown. We have collected only one *G. longipala* (14.9 mm) in the Tampa Bay area, but many thousands of *G. robustum*, and thus feel confident that our material is *G. robustum*.

TABLE 2.

Chi-square and P values (one degree of freedom) for the assumption that the monthly sex ratios of specimens of Gobiosoma robustum 16 mm. and larger are 1:1

Month	Observed sex ratio	Chi-square value	*P* value (Between)
1959			
Nov.	12 males 16 females	.572	.30 & .50
Dec.	14 males 15 females	.034	.80 & .90
1960			
Jan.	18 males 17 females	.028	.80 & .90
Feb.	119 males 130 females	.484	.30 & .50
Mar.	44 males 64 females	3.70	.05 & .10
Apr.	215 males 224 females	.184	.50 & .70
May	81 males 85 females	.096	.70 & .80
Jun.	64 males 71 females	.362	.50 & .70
Jul.	39 males 50 females	1.36	.20 & .30
Aug.	23 males 33 females	1.79	.10 & .20
Sep.	39 males 66 females	6.94	.01 & .005
Oct.	121 males 122 females	.004	.95 & 1.0
Nov.	104 males 104 females	.000	1.0

Egg diameters were measured at a magnification of 27X using an ocular micrometer (one micrometer division equal .034 mm). Ovaries were removed from specimens after they had been in alcohol for one to several months. Eggs were teased from the ovaries and all adherent tissue removed. Random egg diameter measurements (for justification see Clark, 1925) were made on 25 eggs of the largest egg class (see below) in each right ovary. Measurements on groups of eggs from various sections of ovaries disclosed no obvious local segregation of large eggs; nevertheless eggs were measured routinely from both ends and the middle of each ovary. Because of the small gradation in egg diameters in ovaries with no egg diameter greater than about four micrometer divisions, only the diameter of the obviously largest egg in such an ovary was measured. Roman numerals in Table 1 indicate the numbers of such measurements. In one ovary there were only two obviously large eggs (November, 1959) separated by two micrometer divisions from the next largest eggs. In this particular instance only the diameters of the two large eggs were listed.

The oöcyte stages (Harrington, 1959) correlating with the egg diameters were not determined, but it is a generally established fact that in maturing ovaries the egg diameter varies directly with the maturity of the egg, and, therefore, ovaries with the highest average egg diameters are the ripest.

Description of Eggs and Ovaries

In preserved ovaries the developing eggs are transparent until a maximum diameter of (.102-.136 mm) is attained, at which time the eggs become increasingly opaque. They remain opaque, and with no obvious perivitelline space, until the chorion (?) is separated from the vitelline membrane. After this separation there is an opaque area (germinal) comprising about one-third of the vitellus and a translucent area (yolk) comprising the remaining two-thirds. A widely variable number of oil droplets is present in the egg. Random diameters of these eggs, which we consider ripe, range from .476-.782 mm with differences of as much as .238 mm between the longest and shortest axes of a single egg. A comparison with Breder's (1942) diagrams of spawned eggs indicates that the chorion elongates considerably after spawning. This, as well as shrinkage from preservation, would account for differences between our measurements and his.

Table 3.
Total counts of the largest egg class in single ovaries of individual females of Gobiosoma robustum

Month	Standard Length mm.	Number of Large Eggs
Sep.	15 (14.6)	56
Aug.	16	105
Apr.	21	193
Feb.	24	200
Feb.	26	269 (Lee Co., Fla.)
Apr.	26	402
Feb.	27	266
May	27	349
Apr.	28	397

As also noted by Breder for spawned eggs, a large group of filaments is found attached to the chorion of ripe eggs. The presence of these filaments in goby eggs has frequently been noted in the literature; they serve to attach the eggs. Our observations indicated that the filaments were always present at the germinal end of the egg.

In ripe females the ovaries extend the entire length of the coelom and occupy over half its volume. Both ovaries ripen equally and contain approximately equal numbers of eggs of the largest egg class (see below). A 27 mm female taken in May had 349 eggs of the largest egg class in its right ovary and 346 in its left. A few total counts of eggs of the largest egg class of individual females were made (Table 3). These indicate that the number of eggs increases with size, but may vary as much as 50 percent in females of the same size. None of these females had spawned recently as the ovaries in each instance were tightly packed and filled the coelom; and the February females would not have spawned (see below).

The plotting of random diameters of all eggs three micrometer divisions and greater in an ovary sample (Table 4) indicates at least two well-developed groups (classes) of eggs in ovaries in which the smallest diameter of any of the obviously larger eggs is about 9 or 10 micrometer divisions. Part of the spread of measurements is the result of the eggs having both long and short axes, and random, instead of longest or shortest, diameters were measured. The second egg class occurs primarily at from four through six micrometer divisions. Below three divisions our frequencies are neither absolute nor roughly relative to the others.

Since they mature synchronously, the eggs of the largest egg class are apparently spawned in toto during one short time interval. Further evidence for this is supplied by our finding only what appear to be total complements of the largest eggs in either ripe or ripening ovaries. Only once did we find a partial complement of ripe eggs (June, 26 mm, 59 eggs). Pos-

TABLE 4.

Frequency distributions of random egg diameter measurements of all eggs over 2 micrometer divisions in ovary samples of Gobiosoma robustum

Micrometer Divisions	Month Size mm.	Feb. 24*	Feb. 27	Feb. 26†	Apr. 28	Apr. 26	Apr. 21
1			1	3	2	2	4
2		3	2	8	6	3	4
3		7	7	4	2	3	11
4		13	21	12	6	4	32
5		10	16	38	7		15
6		13	2	24		1	
7		2	3	9			
8		1	3				
9			5	1		1	
10		5	17	1		9	
11		30	46			21	
12		63	53			11	
13		63	22	1		4	1
14		29	8	5	2	1	8
15		9		26	7		13
16				33	15		17
17		1		36	10		9
18				31	6		6
19				14	5		
20				7	1		
21				2	1		
22					1		

* Total ovarian egg complement with diameters over 2 divisions measured.
† Lee County, Florida, approximately 100 miles south of Tampa Bay.

sibly, the female was in the act of spawning when collected, or was the only one from which we had squeezed eggs while checking ripeness in the field.

After the largest egg class has reached maturity and been spawned it is possible that sufficient time will remain during the breeding season for the second largest egg class to mature and be spawned. We have no evidence for a third spawning by any female.

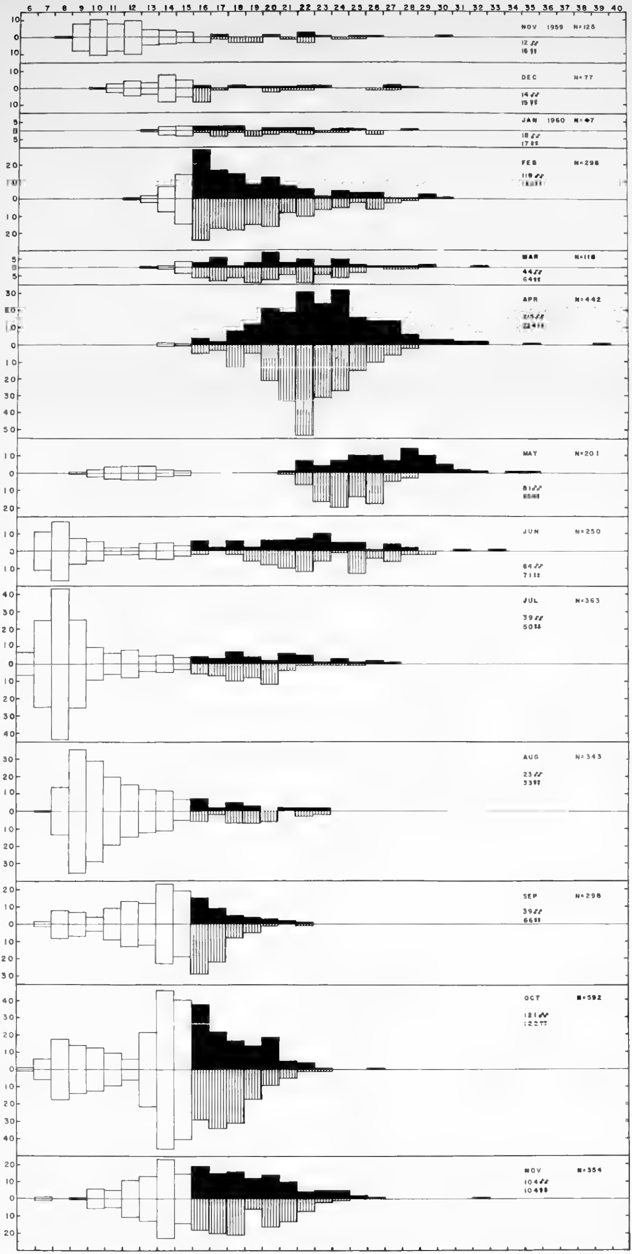
Spawning Season and Length Classes

Table 1 gives the egg diameter distributions for each month from November, 1959, through November, 1960. In November, 1959, a few females (one in 16) were approaching ripeness; it is questionable that they spawned after the collection date as the standard length-frequency distributions (Graph 1) give no indication of the entrance of a group of young into the population until the following spring. During December the ovaries reached their maximum regression, and there was only a slight advance from this state during January. In February there was a rapid advance in maturity of about one-third of the females. During March about one-half of the females were advanced and there was spawning by some of these (females from Lee County, Florida, approximately 100 miles south of Tampa Bay, were possibly spawning in February, Table 4). By April, the entire population had advanced to functional maturity and spawning continued through April, May and June. During July and August, the warmest months of the year, spawning appears to have been suppressed, or at least repressed. In September there was a resurgence of maturation followed by

TABLE 5.

Monthly average standard length of males and females of Gobiosoma robustum 16 mm and larger

Month	Males	Females
1959	mm.	mm.
Nov.	21.8	19.5
Dec.	21.4	18.7
1960		
Jan.	19.8	20.4
Feb.	19.1	19.5
Mar.	21.4	20.3
Apr.	23.2	22.2
May	26.6	24.5
Jun.	22.0	22.6
Jul.	20.3	19.0
Aug.	18.5	18.8
Sep.	17.5	17.0
Oct.	18.0	17.7
Nov.	19.2	18.7



Graph 1. Monthly standard length frequency histograms for specimens of *Gobiosoma robustum*. The solid areas above each base line represent males, the vertically lined areas represent females and the open areas represent sex-indeterminate specimens. The ordinate denotes frequency of occurrence and the abscissa standard lengths in millimeters.

a marked decline in October, with only 20 percent of the females with maturing eggs. This probably represents the last spawning of the year. In November, 1960, all the females had either regressed or unregenerate ovaries.

The overlap of temperatures (Table 1) during spawning and non-spawning periods suggests that some factor other than temperature may be involved in the regulation of the breeding season.

Monthly length - frequency histograms (Graph 1) provide further evidence of the spawning cycle as inferred from egg diameter measurements. The first young of the year, taken in May, were moderately advanced. The absence of young in the March and April collections when, according to egg diameters, breeding probably occurred may have resulted from incubation periods protracted by low temperature. Water temperature at the time of the May collection was lower than during the April collection. However, the air temperatures in St. Petersburg, to which the shallow bay waters are highly responsive, averaged 62.8°F. in March, 81.8° F. in April and 84.5° F. in May (U. S. Weather Bureau Climatological Data, 1960), indicating that the low water temperature at the time of the May collection was a temporary depression.

Batches of young including post-larvae were taken in June, July, September, October and November, 1960. The absence of a new batch of young in August is evident from the progression of the modal class and the absence of strong peaks to the left of it. On the basis of the length-frequency histograms spawning would have been suspended from sometime after the July collection to some point before the date of the September collection.

Gunter (1945) surmised that *Harengula pensacolae* (reported as *H. macrophthalma*) and *Menidia beryllina* on the Texas coast spawned twice, or had two spawning peaks, a year (spring and late summer, or early fall). Springer and Woodburn (1960) found supporting evidence for Gunter's beliefs for both these species in the Tampa Bay area. In Texas ripe females of *Etheostoma lepidum* (Hubbs and Strawn, 1957) were fewest in July and young fish were absent only in August in populations living near springs and subject to temperatures ranging from 14-24°C. Ripe fish were absent from May through October in downstream populations where temperatures ranged from 7-35°C. Harrington (1959), on the basis of experimental evidence, postulated a slackening of spawning for *Fundulus confluentus* on the middle Florida east coast during the warmer, long-day middle portion of its spawning period.

Growth, Size at Maturity and Maximum Size

The growth pattern of *G. robustum* is apparent from Graph 1. Maximum average size of the population, exclusive of the new year class, was reached during May, 1960. This was also noted by Springer and Woodburn (1960) for May, 1958. Thereafter the average size undergoes a decrease for several months. The cause of this appears to be a mortality of the older and larger individuals. After July growth of the various batches of young of the year and average decrease in size of the old population due to mortality fuse and obscure the average growth picture. Not until the fall spawning had ceased do the frequency histograms indicate consistent average increase in size (assuming spawning ceases by November).

The graph indicates that *G. robustum* is an annual fish with few individuals, if any, ever attaining an age of much over one year. On the basis of size, some males may live two years. The largest females obtained in several years collecting did not exceed 29 mm S.L., and specimens of this size are uncommon. The progression of the frequency histograms indicate a maximum growth of 29 mm is quite feasible during the first year of life. The largest males we have obtained are 42 mm (April 28, 1958) and the largest found after examining many museum collections are 44 mm (Pensacola and Corpus Christi).

From the regression in size of both males and females indicated on the graph it would appear that after July the adults, representing the previous year's spawning, comprised only a small part, or no part at all, of the population. The smallest specimens (exclusive of the new year class) obtained in May were 21 mm. By August the largest specimens present were only 23 mm. This probably means that almost the entire population, spawners included, from August on, was comprised of specimens spawned no earlier than the previous March.

On the basis of museum specimens Ginsburg (1933B) concluded that males of the genus *Gobiosoma* not only attained a larger size than females, but averaged larger. Breder (1942) believed this of *G. robustum.* In Table 5 we have listed the monthly average sizes of males and females 16 mm and larger. We find that during some months females were, on the average, larger than males. The females never averaged more than .6 mm larger than males, whereas males may average as much as 2.7 mm larger than females.

Only females were examined for sexual maturity. From the beginning of breeding through June, no females of less than 17 mm S.L. were seen with maturing eggs. Advanced eggs were almost entirely restricted to females of about 19 mm or greater. After June, females as small as 16 mm were commonly found with maturing eggs and by September specimens as small as 14.6 mm (15 mm class) had advanced eggs. Obviously these small females were only a few months old, and on the basis of the size of the May young of the year could have been only two months old. Orton (1920) referring to his invertebrate studies made the following germane statement: "There are indications, however, that in all animals born into suitable breeding conditions gonad development occurs very early during the period of growth and at the expense of increased size." Females born early in the spawning season spawn before the season is over while those born later must await the following spring.

Summary

The spawning cycle and growth of *Gobiosoma robustum* was studied in the Tampa Bay area (ca. Lat. 27°45′ N.). Monthly collections were made from November, 1959, through November, 1960. Diameters of 25 eggs of the largest egg class of from 15 to 20 females were measured each month. These showed that the species has two spawning periods a year: early spring to early summer and late summer to fall. Spawning was not evident during the middle of the summer when water temperatures were highest. Monthly length frequencies give additional support for conclusions derived from egg diameters.

The sex ratios are usually about 1:1. Males achieve a considerably larger maximum size (44 mm S.L.) than do females (29 mm) and usually average larger. Females of the new year class may be ripe when only a few months old and at a size as small as 14.6 mm S.L. After July almost the entire, if not the entire, population, including spawners, is comprised of the new year class. Few, if any, individuals achieve an age of more than one year.

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ABSTRACT

Egg diameter measurements indicate that *Gobiosoma robustum* spawned from early spring to early summer and from late summer to fall during 1960 in the Tampa Bay area. The middle nonspawning period occurred during highest temperatures. Standard length frequency progressions support egg diameter data and also indicate that *G. robustum* is an annual species.

Sex ratios are usually about 1:1. Males achieve a larger size than females. Females may mature at 14.6 mm. standard length when only a few months old.

SEVEN TREMATODES FROM SMALL MAMMALS IN LOUISIANA[1]

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Several mammals from Louisiana localities have been examined for trematodes in connection with studies of trematodes encysted in crayfishes. During these studies, a collection of small mammals was trapped in the vicinity of the Goodhope oilfield near Norco, Louisiana. The locality is a cypress-tupelo swamp, approximately 20 miles west of New Orleans, Louisiana, bounded on the south by U. S. Highway 61 and on the north by Lake Pontchartrain.

The following were examined for helminth parasites: one river otter, *Lutra canadensis* (Schreber); one raccoon, *Procyon lotor* (Linn.); one short-tailed shrew, *Blarina brevicauda* (Say); two muskrats, *Ondatra zibethicus* (Linn.); two swamp rabbits, *Sylvilagus aquaticus* (Bachman); four minks, *Mustela vison* Schreber; four opossums, *Didelphus virginiana* Kerr; and sixteen rice rats, *Oryzomys palustris* (Harlan). The otter, shrew, and two muskrats were found uninfected with trematodes.

Trematodes were fixed in boiling water or between a coverslip and slide in aceto-formol-alcohol (AFA), stained with Van Cleave's combination-hematoxylin or Delafield's hematoxylin, and mounted in piccolyte. Unless otherwise cited, all measurements were taken from mounted specimens, and are given in millimeters.

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Family DIPLOSTOMATIDAE Poirier, 1886

Fibricola cratera (Barker and Noll, 1915) Dubois 1932
(Figures 1 to 2)

Synonymy.—Hemistomum craterum Barker and Noll, 1915; *Fibricola laruei* Miller, 1940; *Fibricola nana* Chandler and Rausch, 1946.

Hosts.—Mustela vison Schreber and *Procyon lotor* (Linn.).

Location.—Small intestine.

Locality.—Goodhope oil field, Louisiana [new locality record].

Diagnosis (based on 10 mature specimens, 5 each from *Mustela vison* and *Procyon lotor*).—*Fibricola.* Body superficially bisegmented, 0.602 to 1.435 long. Forebody longer and wider than hindbody, widest near junction with hindbody, 0.390 to 0.875 long by 0.319 to 0.630 wide. Lateral portions of forebody folded ventrally, meeting in midline of body at point of junction with hindbody. Junction of fore- and hindbody marked by a slight constriction (or by reduction in transverse diameter of forebody in small specimens). Hindbody 0.212 to 0.560 long by 0.177 to 0.525 wide, tapering slightly to rounded tip. Cuticular spines present on anterior forebody, diminishing in size and number posteriorly; hindbody smooth. Oral sucker 0.047 to 0.087 long by 0.050 to 0.067 wide. Acteabulum oval, in middle of forebody, usually wider than long, 0.041 to 0.064 long by 0.041 to 0.078 wide, often in contact with or overlapping posterior tribocytic organ, or separated from tribocytic organ by less than longitudinal diameter of acetabulum. Sucker ratio 1:0.872 to 1.12. Prepharynx short, sometimes appearing absent. Pharynx often in contact with oral sucker, 0.040 to 0.116 long by 0.030 to 0.084 wide. Esophagus usually shorter than pharynx, 0.011 to 0.056 long. Ceca two, extending to posterior end of body, terminating at level of genital atrium. Tribocytic organ oval, slightly longer than broad, 0.160 to 0.371 long by 0.160 to 0.243 wide, with a median, longitudinal cleft. Genital atrium posterior, subterminal, opening on dorsal surface of body.

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Testes two, irregular in shape and size; anterior testis sinistral to midline, just posterior to junction of fore- and hindbody, 0.076 to 0.230 long by 0.073 to 0.358 wide; posterior testis in middle of hindbody, wider than long, with a median constriction, 0.053 to 0.282 long by 0.138 to 0.448 wide. Seminal vesicle posterior to hind testis, mesial, extending anteriorly to middle of posterior testis then looping posteriorly to enter genital atrium *via* narrow ejaculatory duct. Ovary median or sinistral to midline, anterior to and dorsally overlapping fore testis, 0.034 to 0.102 long by 0.056 to 0.230 wide. Mehlis' gland dextral to ovary. Laurer's canal opening dorsally on midline between levels of ovary and vitelline reservoir. Uterus J-shaped, ascending from Mehlis' complex to a point midway between anterior border of ovary and tribocytic organ, then turning posteriorly, proceeding mesially to genital atrium. Eggs 0.090 to 0.115 long by 0.060 to 0.090 wide. Vitellaria follicular, generally confined to forebody, densest in region of tribocytic organ. Anterior extent of vitelline follicles to or slightly beyond level of fore margin of acetabulum; a few follicles extending posteriorly on ventral surface into hindbody to or just beyond posterior margin of vitelline reservoir. Vitelline reservoir median, intertesticular. Excretory system not observed.

Discussion.—A discussion of this species follows the diagnosis of *Fibricola lucida.*

Fibricola lucida (LaRue and Bosma, 1927)

Dubois and Rausch, 1950

(Figure 3)

Synonymy.—*Neodiplostomum lucidum* LaRue and Bosma, 1927; *Theriodiplostomum lucidum* (LaRue and Bosma, 1927) Dubois, 1944.

Hosts.—*Didelphis virginiana* Kerr and *Mustela vison* Schreber.

Location.—Small intestine.

Locality.—Goodhope oil field, Louisiana.

Diagnosis (based on 10 mature specimens, 5 each from *Didelphis virginiana* and *Mustela vison*).—*Fibricola.* Body superficially bisegmented, 1.097 to 1.750 long. Forebody longer and wider than hindbody, separated from latter by a well-defined constriction. Forebody 0.708 to 1.120 long by 0.525 to 0.814 wide, widest at level of tribocytic organ. Sides and posterior margin of forebody folded ventrally. Hindbody usually longer than wide, 0.390 to 0.525 long by 0.238 to 0.460 wide, tapering to a rounded end, Cuticular spines present on anterior forebody, diminishing in size and number posteriorly; hindbody smooth. Oral sucker 0.062 to 0.098 long by 0.067 to 0.075 wide, usually in contact with pharynx. Acetabulum oval, in middle of forebody, 0.062 to 0.078 long by 0.059 to 0.090 wide, usually separated from posterior tribocytic organ by a distance equal to longitudinal diameter of acetabulum. Sucker ratio 1:1.000 to 1.600. Prepharynx short, appearing absent in some specimens, 0.000 to 0.014 long. Pharynx 0.046 to 0.070 long by 0.041 to 0.065 wide. Esophagus 0.040 to 0.112 long. Ceca two, extending to posterior end of body, terminating at level of genital atrium. Tribocytic organ longer than broad, with a median, longitudinal cleft, 0.217 to 0.448 long by 0.127 to 0.269 wide. Genital atrium posterior, subterminal, opening on dorsal surface of body. Testes two, variable in size and shape; anterior testis sinistral to midline, just posterior to junction of fore- and hindbody, 0.138 to 0.243 long by 0.095 to 0.307 wide; posterior testis in middle of hindbody, wider than long, with a median constriction, 0.138 to 0.218 long by 0.265 to 0.358 wide. Seminal vesicle extending from middle of posterior testis to enter genital atrium *via* narrow ejaculatory duct. Ovary sinistral to midline, anterior to fore testis, 0.064 to 0.128 long by 0.106 to 0.148 wide. Mehlis' gland dextral to ovary. Laurer's canal extending dorsally from oviduct, opening on median dorsal surface of body between levels of ovary and vitelline reservoir. Uterus ascending from Mehlis' complex to fore margin of ovary then descending in midline of body to genital atrium. Eggs 0.093 to 0.116 long by 0.060 to 0.070 wide. Vitelline follicles most numerous in forebody at level of tribocytic organ, extending as two lateral bands from midway between acetabulum and cecal bifurcation to level of genital atrium. Vitelline reservoir median, intertesticular. Excretory system not observed.

Discussion.—There are five species in the genus *Fibricola:* (1) *F. cratera* (Barker and Noll, 1915) Dubois, 1932; (2) *F. lucida*

(LaRue and Bosma, 1927) Dubois and Rausch, 1950; and (3) *F. texensis* Chandler, 1942, all in North America; (4) *F. caballeroi* Zerecero, 1943; from Mexico, and (5) *F. minor* Dubois, 1936; from Australia.

F. lucida has been previously reported from Louisiana opossums (Dikmans, 1932) as *Neodiplostomum lucidum.* The present record constitutes the first report of *F. cratera* from Louisiana.

Each of four opossums was lightly infected with *F. lucida.* A single raccoon was infected with several hundred *F. cratera.* Four minks harbored heavy, mixed infections of *F. cratera* and *F. lucida.*

Mature specimens of *F. lucida* from the opossums were somewhat larger (1.133 to 1.750 long) than those recovered from the minks (1.097 to 1.330 long). Specimens of *F. cratera* from the minks were generally larger (0.814 to 1.435 long) than those from the raccoon (0.602 to 0.800 long). Dubois (1938) reported a size range of 1.50 to 1.74 for *F. lucida;* LaRue and Bosma's (1927) specimens reportedly attained a maximum length of 1.94. Dubois' (1938) measurements for *F. cratera* were 1.0 to 1.5; Barker's (1915) measurements for this species were given as 0.75 to 1.89. Chandler (1942) noted that size and shape of *F. texensis* were affected by the host species and the density of the infection. Perhaps the smaller size of some of our specimens can be explained by the numbers of worms present in each host. The raccoon was more heavily infected with *F. cratera* than any of the minks examined. The opossums harbored the lightest strigeid infection, but were heavily infected with another trematode, *Rhopalias macracanthus.*

F. cratera, F. lucida, and *F. texensis* are separated primarily by the vitelline distribution. The vitelline follicles of *F. lucida* are present in the hindbody as two lateral bands which extend posteriorly to the level of the genital atrium. In *F. cratera* a thin sheet of vitellaria on the ventral surface of the hindbody may extend to the level of the vitelline reservoir or slightly beyond. Ulmer (1955) observed that an intermediate condition may exist between the posterior extent of the vitellaria as originally described for *F. cratera* and *F. texensis.* Read (1948) differentiated *F. cratera* from *F. texensis* on the basis of a thin sheet of vitellaria limited to the ventral side of the hindbody in the latter. Ulmer found that, in some specimens recovered from white mice fed metacercariae of *F. cratera* from the pelvic musculature of *Rana pipiens,* the vitellaria extended to the anterior margin of the posterior testis. In other specimens recovered from the same host the vitellaria on one side of the body extended to the posterior margin of the hind testis, whereas the vitelline follicles on the other side of the body extended only to the anterior margin of the hind testis. Chandler (1942) reported that the vitellaria of *F. texensis* extended anteriorly to the level of the pharynx. Dubois (1938) showed the anterior exent of vitellaria in *F. cratera* to be approximately midway between the acetabulum and the cecal bifurcation, and Ulmer's (1955) figures picture a similar condition. The vitellaria in our specimens of *F. cratera* extended slightly anterior to the fore margin of the acteabulum, never to the cecal bifurcation. Dubois and Rausch (1950) suggested that *F. cratera* and *F. texensis* are physiological species.

Family RHOPALIASIDAE Yamaguti, 1958

Rhopalias macracanthus Chandler, 1932

(Figures 4 to 5)

Hosts.—Didelphis virginiana Kerr, and *Mustela vison* Schreber [new host record].

Location.—Small intestine.

Locality.—Goodhope oil field, Louisiana [new locality record].

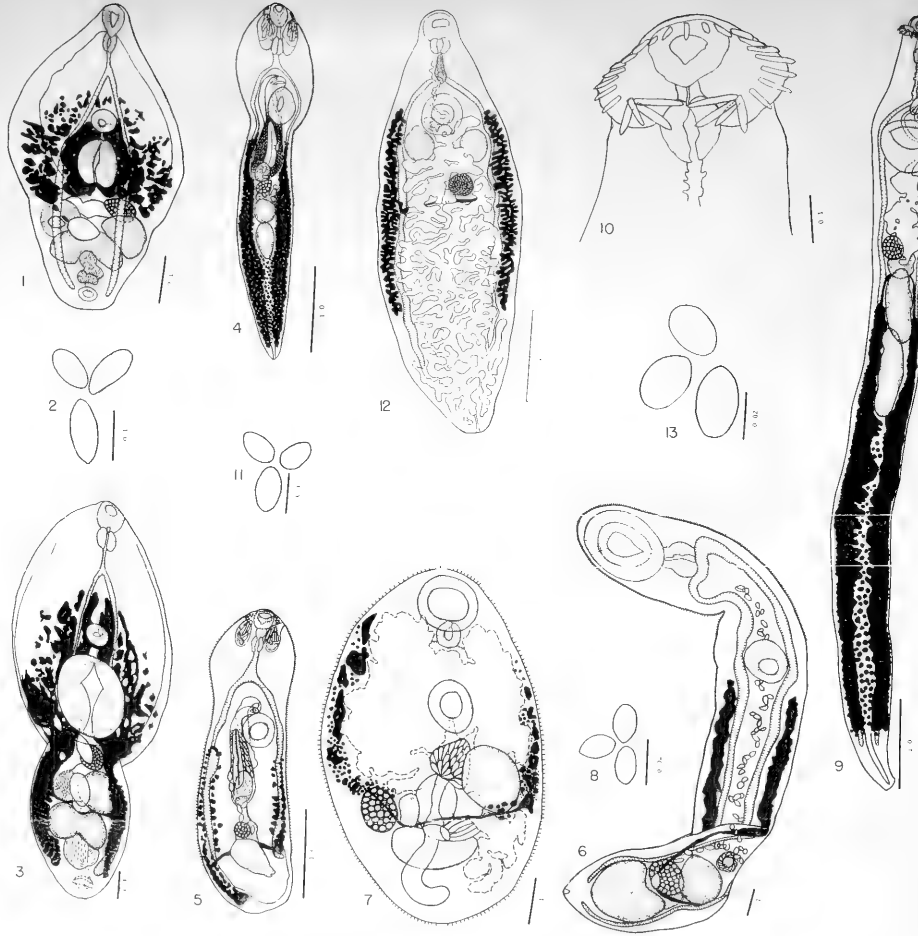
Diagnosis (based on 10 mature specimens from *Didelphis virginiana*).—*Rhopalias.* Body elongate, 2.45 to 5.0 long, superficially bisegmented by post acetabular constriction. Anterior body segment expanded laterally, concave ventrally. Posterior body segment narrower, two and one-half times length of anterior body segment, gradually tapering posteriorly to a point. Body with dorsal flexure at level of junction of fore- and hindbody. Forebody 0.700 to 1.500 long, hindbody 1.750 to 3.50 long. Cuticle spinous to level of posterior testis; spines largest and most numerous on forebody, diminishing in size and number posteriorly. Oral sucker subterminal, 0.145 to 0.230 long by 0.128 to 0.230 wide. Acetabulum well developed, its ventral protrusion visible when viewed laterally, 0.256 to 0.422

long by 0.102 to 0.384 wide. Sucker ratio 1:1.76 to 1.83. Prepharynx 0.44 to 0.145 long. Pharynx 0.142 to 0.256 long by 0.099 to 0.154 wide. Esophagus short, sometimes appearing absent, 0.000 to 0.087 long. Ceca two, extending along sides of body to terminate blindly, 0.260 to 0.333 from posterior extremity. Two proboscis sacs, one on each side of oral sucker, 0.256 to 0.333 long by 0.115 to 0.180 wide. Each eversible proboscide with 10 well developed spines measuring 0.078 to 0.128 long by 0.015 to 0.026 wide at their bases; posterior proboscis spines longest and widest. A single row of alternately arranged spines, six to eight in number and 0.023 to 0.035 long, present on each side of forebody on anterior margin between openings of proboscis sacs and oral sucker. Genital pore median, preacetabular, connecting with genital atrium containing openings of metraterm and male duct. Testes intercecal, tandem, in middle third of hindbody. Anterior testis 0.256 to 0.490 long by 0.230 to 0.350 wide; posterior testis often in contact with anterior testis, 0.346 to 0.875 long by 0.205 to 0.280 wide. Cirrus sac prominent, dextral to acetabulum, extending 0.700 to 1.085 posteriorly from genital pore, 0.180 wide at its base. Cirrus sac containing S-shaped seminal vesicle, large *pars prostatica,* prostate gland cells, and stout, unspined cirrus. Ovary pretesticular, sinistral to base of cirrus sac, separated from anterior testis by irregularly shaped Mehlis' gland, 0.128 to 0.154 long by 0.090 to 0.230 wide. Uterine coils pretesticular, ascending from Mehlis' gland to genital atrium; distal portion of uterus forming a large metraterm dextral to cirrus sac. Eggs 0.102 to 0.115 long by 0.051 to 0.064 wide. Vitellaria follicular, filling entire posttesticular region of hindbody, extending anteriorly as two lateral rows on ventral surface of hindbody to posterior margin of acetabulum. Vitelline reservoir posterior and dorsal to Mehlis' gland. Excretory system not observed.

Discussion: Rhopalias macracanthus Chandler, 1932, is a common parasite of *Didelphis virginiana* and has a wide distribution. Chandler (1932) described the species from opossums in the vicinity of Houston, Texas. Byrd *et al.* (1942b) found *R. macracanthus* in two of every three opossums examined at Reelfoot Lake, Tennessee. The species has also been reported from Illinois (Babero, 1957) and Georgia (Babero, 1960 a). Yamaguti (1958) cited *Didelphus mesamexicana tabascensis* as a host for *R. macracanthus* in Mexico. Other species of the genus are *R. baculifer* Braun, 1901, *R. coronatus* (Rudolphi, 1819), and *R. horridus* (Diesing, 1850); these three species were described from South American opossums. Loftin (1960) reported *R. baculifer* and *R. coronatus* from opossums in Florida. Loftin's identification of these species is difficult to evaluate, as no figures or descriptions were presented in his paper.

The four opossums autopsied were heavily infected with *R. macracanthus* as well as with the strigeid, *Fibricola lucida.* Although *R. macracanthus* is predominantly found in opossums, this parasite is apparently capable of infecting a variety of hosts. McKeever (1961) reported a single mature specimen from the intestine of a wild turkey, *Meleagris gallopavo,* in Georgia, and we have recovered a single *R. macracanthus* from the intestine of a mink, *Mustela vison,* in Louisiana. Our specimen was evidently an immature worm, as judged by its small size (2.1 long), the absence of eggs in the uterus, poorly developed vitellaria, and relatively small ovary, Mehlis' gland and testes.

The location of the parasites in the host and the density of the infection appear to have a considerable effect on the size of the worms. Specimens from one heavily infected opossum showed a definite gradation in size with respect to the section of the intestine in which they were found. The majority of worms were found in the anterior third of the small intestine; these were large (3.8 to 4.62 long) and well developed. Several medium-sized worms (3.5 to 4.0 long) were found in the middle third of the small intestine, and a few, much-stunted (1.96 to 3.15 long) specimens in the posterior third of the small intestine. Most of the smaller worms, as well as the larger ones, were sexually mature, as judged by the presence of eggs in the uterus. One worm from the posterior section of the small intestine showed striking abnormalities (fig.-5). This specimen measured 3.15 long; there was only slight differentiation into anterior and posterior segments, and the posterior end of the body was bluntly rounded rather than tapered to a point. A single testis was pres-



Figures 1-13. **1.** *Fibricola cratera*, ventral view of whole mount from *Procyon lotor*. **2.** Same, uterine eggs. **3.** *Fibricola lucida*, ventral view of whole mount from *Didelphis virginiana*. **4.** *Rhopalias macracanthus*, ventral view of normal specimen from *Didelphis virginiana*. **5.** Same, from posterior third of small intestine. **6.** *Brachylaemus virginianus*, ventral view of whole mount. **7.** *Hasstilesia texensis*, ventral view of whole mount. **8.** Same, uterine eggs. **9.** *Euparyphium beaveri*, ventral view of whole mount. **10.** Same, ventral view of anterior end showing shape and arrangement of crown spines. **11.** Same, uterine eggs. **12.** *Zonorchis komareki*, ventral view of whole mount. **13.** Same, uterine eggs. Figs. 1-8, 10, 11 and 13 drawn with the aid of a Leitz camera lucida. Figs. 9 and 12 drawn with the aid of a microprojector. Projected scales have the approximate value in millimeters.

ent, the vitellaria were sparse and confined to the sides of the body, and the Mehlis' gland and ovary were somewhat reduced in size. There were, however, ten eggs in the uterus. The cirrus sac, with its contained structures, as well as the structures of the forebody, appeared normal. This unusual morphology appears to be degenerate or teratological rather than definitive in nature. Only a single specimen with the forementioned morphology was found, though evidence of some reduction of the hindbody was seen in other specimens recovered from the posterior regions of the opossum intestine.

It appears that in hyperinfections some individuals are forced posteriorly in the intestine, apparently with deleterious effects. The posterior regions of the digestive tract of the opossum may be unsuitable for normal development and/or proper maintenance of *R. macracanthus.*

Family BRACHYLAEMIDAE Joyeux and Foley, 1930

Brachylaemus virginianus Dickerson, 1930 (Figure 6)

Synonymy.—*Brachylaemus migrans* of Sinitzin, 1931.

Host.—*Mustela vison* Schreber [new host record].

Location.—Small intestine.

Locality.—Goodhope oil field, Louisiana.

Diagnosis (based on one mature specimen).—*Brachylaemus.* Body elongate with bluntly rounded extremities, 2.195 long by 0.319 wide at level of acetabulum. Cuticle spinose to level of midbody, remainder smooth. Oral sucker large, subterminal, 0.180 in diameter. Acetabulum smaller than oral sucker, 0.127 long by 0.138 wide, located 0.498 from anterior end of the body. Sucker ratio 1:0.705. Prepharynx very short. Pharynx in contact with oral sucker, 0.084 long by 0.106 wide. Esophagus very short. Ceca bifurcating almost immediately posterior to pharynx, extending laterally, then posteriorly, terminating midway between posterior testis and posterior end of body. Genital pore median on ventral surface of body just anterior to fore testis. Testes two, tandem, near posterior end of body; anterior testis 0.127 long by 0.148 wide; posterior testis 0.170 long by wide. Tubular seminal vesicle and prostate gland cells between anterior testis and genital pore. Ovary sinistral to midline, intertesticular, 0.098 long by 0.112 wide. Mehlis' gland dextral to ovary. Uterus ascending on midline to a point midway between acetabulum and cecal bifurcation then descending to genital pore. Eggs 0.025 to 0.036 long by 0.014 to 0.020 wide. Vitelline follicles lateral, extending from posterior margin of acetabulum to fore margin of anterior testis. Vitelline ducts extending posteriorly from vitelline follicles to posterior margin of ovary, joining to form vitelline reservoir. Excretory system not observed.

Discussion.—This is the first report of *Brachylaemus virginianus* from the mink, *Mustela vison. B. virginianus* is commonly found in opossums, though Babero (1960b) reported Louisiana skunks, *Mephitis mephitis* (Schreber), infected with this trematode. Krull (1934) experimentally exposed white rats, dogs, cats and chickens to metacercariae from *Polygyra thyroides* and recovered mature specimens of *B. virginianus* from each of these hosts. We have also recovered specimens of a *Brachylaemus* sp., probably *B. virginianus,* from *Mesodon thyroideus* in Audubon Park, New Orleans. Other species of *Brachylaemus* in the United States are *B. dolichodira* Mason, 1953 in *Blarina brevicauda* (Say), *B. fuscata* (Rudolphi, 1819) in *Bonasa umbellus* (Linn.), *B. mcintoshi* Harkema, 1939, in *Strix varia* Barton, *B. opisthotrias* (Lutz, 1895), in *Didelphis virginiana, B. pellucida* Sinitzin, 1931, in *Planesticus migratorius* and *Procyon lotor, and B. peromysci* Reynolds, 1938, in *Peromyscus leucopus* (Rafinesque).

B. virginianus resembles *B. opisthotrias,* differing primarily in the anterior extent of the uterus. The uterus in our specimens of *B. virginianus* ascended to a point at least midway between the acetabulum and the cecal bifurcation. Byrd *et al.* (1942b.) reported that in most of their specimens of *B. virginianus* recovered from opossums in Georgia and Tennessee the uterus reached the cecal bifurcation. The uterus in a single specimen of *B. opisthotrias,* recovered by Byrd *et al. (loc. cit.)* from an opossum in Tennessee, ascended only to the posterior margin of the acetabulum. Other differences noted by Byrd *et al.* between the two species included the larger size (4.06 long by 0.548 wide), smaller eggs (0.021 to 0.027 long by 0.012 to 0.015 wide) and a smooth cuticle in *B. opisthotrias.* In contrast, specimens of *B. virginianus* averaged 2.18 long and 0.348 wide, had eggs 0.029 to 0.033 long by 0.016 to 0.021 wide, and had cuticular spines present to the midlevel of the body.

Hasstilesia texensis Chandler, 1929
(Figures 7 to 8)

Host.—*Sylvilagus aquaticus* (Bachman).

Location.—Small intestine.

Locality.—Goodhope oil field, Louisiana [new locality record].

Diagnosis (based on 50 mature specimens.—*Hasstilesia.* Body oval to round in outline, 0.496 to 0.850 long by 0.420 to 0.665 wide. Cuticle entirely spinose, spines denser in anterior regions of body. Oral sucker well developed, 0.098 to 0.139 in diameter. Acetabulum usually smaller than than oral sucker, 0.095 to 0.132 in diameter, 0.192 to 0.384 from anterior extremity as measured from center of acetabulum. Sucker ratio 1:0.875 to 1.165. Prepharynx very short, appearing absent. Pharynx oval, in contact with or overlapping oral sucker, 0.034 to 0.050 long by 0.041 to 0.064 wide. Esophagus not visible. Ceca two, bifurcating immediately behind pharynx, extending on each side of body to terminate near posterior extremity with the blind ends almost in contact with one another. Genital pore median on ventral surface of body anterior to posterior testis, 0.138 to 0.180 from posterior extremity. Genital atrium shallow, containing openings of metraterm and male duct. Anterior testis sinistral to midline, 0.085 to 0.192 long by wide; posterior testis median, 0.074 to 0.141 long by 0.106 to 0.179 wide. Cirrus sac long, extending from posterior margin of acetabulum to genital atrium, containing numerous prostate gland cells at its base; cirrus long, stout, 0.230 to 0.256 long by 0.0233 to 0.058 wide. Ovary dextral to midline, between testes, 0.053 to 0.077 long by wide. Mehlis' gland slightly smaller than ovary, between ovary and posterior testis. Laurer's canal present. Uterus much convoluted, almost filling space between testes and engorging body to level of pharynx. Distal loop of uterus forming metraterm which enters genital atrium sinistral to male duct. Eggs 0.015 to 0.023 long by 0.009 to 0.015 wide. Vitellaria in lateral regions of body from level of pharynx to level of ovary. Vitelline reservoir mesial to Mehlis' gland, receiving ducts from vitelline follicles on each side of body. Excretory system not observed.

Discussion.—Each of the two swamp rabbits collected was infected with thousands of *Hasstilesia texensis* Chandler, 1929. The infections were so dense that the wall of the intestine had a brown color imparted by the uterine eggs of the closely packed parasites.

There is one other species of *Hasstilesia, H. tricolor* (Stiles and Hassall, 1894) Hall, 1916. Chandler (1929) believed his specimens of *Hasstilesia* from *Sylvilagus floridanus* (Allen) in Texas to be specifically distinct from *H. tricolor* in; (1) the larger size of the suckers; (2) the more posterior location of the acetabulum; (3) absence of an esophagus; (4) the looser arrangement of the uterine coils; (5) the longer cirrus; (6) the less profuse and more scattered vitellaria; and (7) a distinct Laurer's canal. Marker and Cheng (1960) have proposed that *H. texensis* and *H. tricolor* are the same species. They based this conclusion on observations of specimens of *Hasstilesia* taken from cotton tail rabbits, *Lepus sylvaticus* (=*Sylvilagus floridanus* (Allen)), in Pennsylvania, and on life history studies of *H. tricolor* by Rowan (1955). Rowan observed that in young specimens of *H. tricolor* the uteri may be loosely coiled, a Laurer's canal is present, and the esophagus may sometimes appear absent. Robinson (1959) recognized *H. texensis* as a distinct species from *H. tricolor,* citing the larger sucker sizes in the former as a distinguishing character. Marker and Cheng *(loc. cit.)* discounted the validity of sucker sizes in separating the two forms. They noted that overlap exists in the lower size range of the acetabulum in *H. texensis* as reported by Chandler (1929) and in the upper size range of the acetabulum cited for *H. tricolor.* These investigators further stated that three microns existed between the smallest dimensions of the oral sucker reported for *H. texensis* (Chandler, 1929) and the largest dimensions of the oral sucker reported for *H. tricolor.* Marker and Cheng added that in their specimens of *Hasstilesia* there was variation in the position of the acetabulum, the vitellaria were sometimes diffuse and scattered, and the cirrus was within the size range given by Chandler (1929) for *H. texensis*.

We have studied fifty specimens of *H. texensis* removed from the intestine of one of the two swamp rabbits collected. In order to minimize distortion of the muscular organs these worms were killed in boiling water prior to introduction into AFA. Measurements of body length and sucker diameter were analyzed statistically and compared with data reported for *H. tricolor* by Rowan (1955) and Marker and Cheng (1960) (fig. 14). There was a difference between the means of the diameters of the oral sucker and acetabulum for our sample and Rowan's sample in excess of twice the sum of the standard errors. Marker and Cheng reported only the range and mean for their measurements. It should be noted, however, that the mean diameter of the oral sucker and mean diameter of the acetabulum reported by Marker and Cheng are even less than the means of the diameters of these structures in Rowan's material. Mean body length of our specimens was somewhat less than that of Rowan's specimens, and slightly

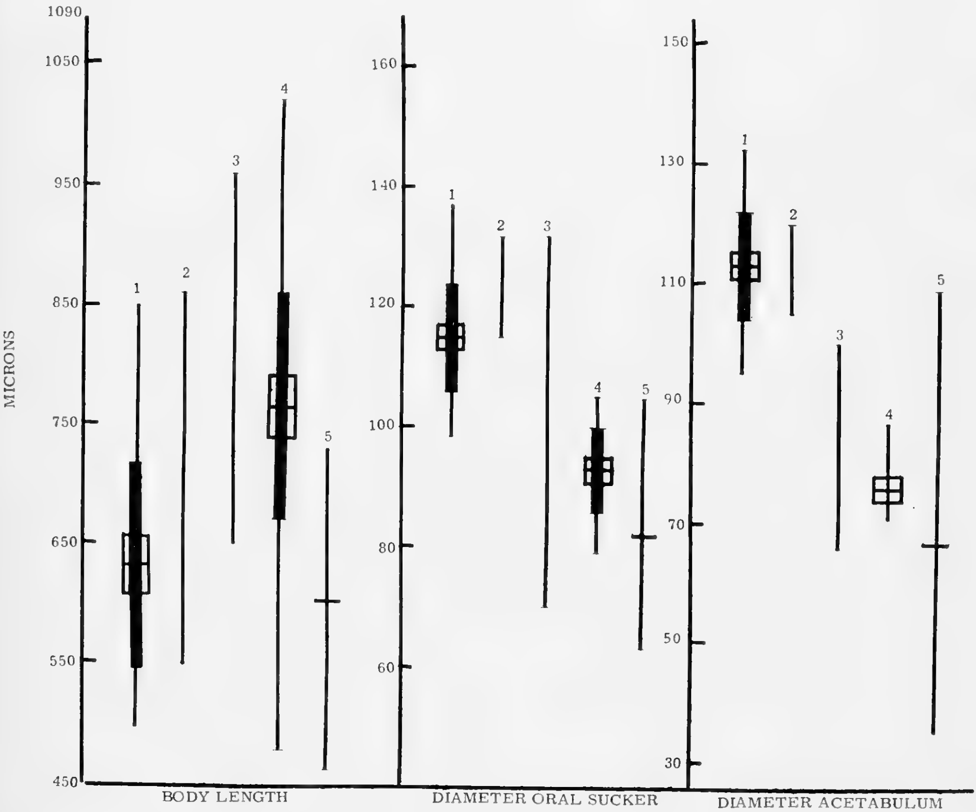


Figure 14. Comparison of measurements for *Hasstilesia texensis* and *H. tricolor*. In each sample the vertical line indicates the range of measurements; the crossbar, the mean; the solid rectangle, one standard deviation on each side of the mean; the hollow rectangle, two standard errors on each side of the mean. Numbers above each vertical line identify the sample. Sample 1. Lumsden and Zischke (1961). 50 specimens of *H. texensis* from *Sylvilagus aquaticus* in Louisiana. Sample 2. Chandler (1929). Unknown number of specimens of *H. texensis* from *Sylvilagus floridanus* in Texas. Sample 3. Byrd and Reiber (1942a.). Unknown number of specimens of *H. texensis* from *Sylvilagus aquaticus* and *S. floridanus* in Tennessee and Mississippi. Sample 4. Rowan (1955). 50 specimens of *H. tricolor* from domestic rabbits. Sample 5. Marker and Cheng (1960). 50 specimens of *H. tricolor* from *Lepus sylvaticus* in Pennsylvania.

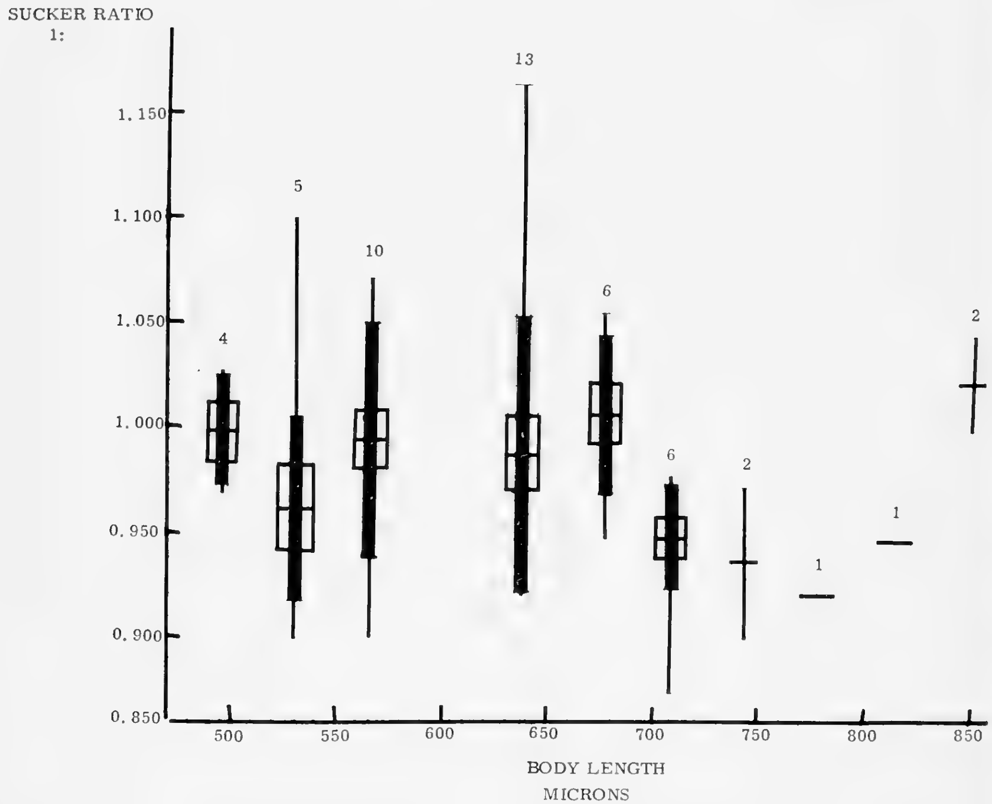


Figure 15. Relationship between sucker ratio and body length for 50 specimens of *Hasstilesia texensis* from *Sylvilagus aquaticus* in Louisiana. Numbers above each vertical line denote the number of specimens comprising each group. The hollow rectangle indicates one standard error on each side of the mean.

larger than that of Marker and Cheng's. We conclude from these results that the difference with regard to sucker size between our sample and the samples of Rowan and Marker and Cheng is statistically significant, and hence the samples were not drawn from the same population.

Marker and Cheng ascribed all of their specimens of *Hasstilesia* to a single species, *H. tricolor,* contending it was improbable that two or more closely related species would be parasitic within a single host specimen. They therefore considered morphological variation within their sample of trematodes as intraspecific. There are, however, reports in the literature indicating certain closely related species are often found together within an individual host. Sogandares (1959) has reported mixed infections of *Dinurus* spp. in single hosts of *Coryphaena* spp. The poeciliid, *Mollienisia latipinna* LeSueur, serves as a second intermediate host for *Ascocotyle* spp. in Louisiana. One of us (RDL) has frequently recovered metacercariae of *A. leighi* Burton, 1956, and *A. tenuicollis* Price, 1935, from the same *conus arteriosus.* Mixed infections of adult *A. leighi* and *A. tenuicollis* have also been found in Louisiana raccoons. This paper reports mixed infections of *Fibricola cratera* and *F. lucida* in *Mustela vison.*

H. texensis has been reported from New York, Ohio, and Georgia by Robinson (1959) from Tennessee and Mississippi by Byrd and Reiber (1942), from Texas by Chandler (1929), and this paper reports the species from Louisiana. *H. tricolor* has been reported from New York by Hall (1916), from Virginia by Stiles and Hassall (1894), and from Pennsylvania by Marker and Cheng (1960). The geographic range of *H. texensis* thus overlaps the geographic range of *H. tricolor.* The possibility of mixed infections of *H. texensis* and *H. tricolor* occurring in lagomorphs in the eastern U. S. exists. Measurements which denote the upper ranges of the sucker diameters for *H. tricolor* conceivably could have been taken from specimens of *H. texensis* in in mixed infections with the former species.

Adult morphology of the two forms is very similar, apparently differing only in the relative sizes of the muscular organs. Sucker sizes in proportion to body size in *H. texensis* and *H. tricolor* are significantly different, although there may be slight overlap or proximity in the range of actual measurements of the suckers for the two species. These data do not support the proposal of Marker and Cheng to synonymize *H. texensis* with *H. tricolor.* We believe that the status of *H. texensis* will be resolved only when the complete life histories of both *H. texensis* and *H. tricolor* are known. For this reason, the retention of *H. texensis* as a distinct species from *H. tricolor* is advocated at this time.

Family ECHINOSTOMATIDAE Poche 1926

Euparyphium beaveri Yamaguti, 1958 (Figures 9 to 11)

Synonymy.—*Euparyphium melis* (Schrank, 1788) of Beaver, 1941 *nec. Isthmiophora melis* (Schrank, 1788) Luehe, 1909.

Host.—*Mustela vison* Schreber.

Location.—Duodenum.

Locality.—Sarpy, Louisiana [new locality record].

Diagnosis (based on four mature specimens).—*Euparyphium.* Body elongate, 6.0 to 9.49. Maximum width at level of acetabulum, 0.64 to 0.85. Posttesticular region of body 2.83 to 5.31 long by 0.637 wide. Cuticular spines present nearly to posterior extremity, shorter and more numerous between oral sucker and acetabulum, becoming longer and less numerous posteriorly. Well defined circumoral collar 0.354 to 0.460 wide, bearing 27 long, abruptly tapered spines. Seven of these crown spines alternately arranged on dorsal surface, 0.085 to 0.106 long by 0.011 wide; 6 crown spines arranged in a single row on each lateral surface, 0.062 to 0.070 long by 0.011 to 0.014 wide; 4 crown spines present on each ventral angle, directed medially, in anterior and posterior pairs, 0.103 to 0.109 long by 0.020 wide. Oral sucker 0.160 to 0.205 long by 0.166 to 0.218 wide. Acetabulum large, 0.403 to 0.595 long by 0.445 to 0.603 wide, in anterior third of body, 0.70 to 1.05 from anterior extremity. Sucker ratio 1:2.89 to 3.32. Prepharynx 0.023 to 0.115 long. Pharynx 0.166 to 0.192 long by 0.128 to 0.141 wide. Esophagus 0.333 to 0.397 long. Ceca two, one on each side of body, terminating blindly 0.256 to 0.448 from posterior extremity. Genital pore immediately preacetabular, just posterior to cecal bifurcation. Testes intercecal, tandem, elongate with a slight twist; anterior testis 0.512 to 0.840 long by 0.256 to 0.280 wide, 1.925 to 2.66 from anterior end of body; posterior testis 0.640 to 0.910 long by 0.218 to 0.245 wide. Cirrus sac elongate, extending dorsally and posteriorly to midlevel of acetabulum, enclosing seminal vesicle, prostatic gland cells, and cirrus. Cirrus long, covered with short stout spines. Ovary 0.230 to 0.294 long by 0.180 to 0.230 wide, dextral to midline, 0.460 to 0.673 behind acetabulum, separated from anterior testis by oval Mehlis' gland; Mehlis' gland 0.166 to 0.230 long by 0.218 to 0.307 wide. Laurer's canal opening dorsally on midline. Uterus in transverse loops between ovary and posterior margin of acetabulum, forming distally metraterm which lies sinistral to cirrus sac. Eggs 0.116 to 0.123 long by 0.061 wide. Vitelline follicles extending from level of ovary to termination of ceca, confluent in dorsal posttesticular region of body, present in lateral fields on ventral surface of hindbody. Vitelline reservoir posterior and dorsal to Mehlis' gland, receiving vitelline ducts from each side of body. Excretory pore subterminal, dorsal.

Discussion.—Law and Kennedy (1932) recovered echinostomes from Ontario mink which they reported as *Euparyphium melis* (Schrank), previously known only from European Mustelidae. Beaver (1941) elucidated the life history and redescribed this North American form. He noted that his specimens differed from *E. melis* as described by Dietz (1910) in the shape and position of the crown spines, but were identical in all other respects to the European species. The crown spines of Beaver's specimens were abruptly pointed at the outer ends, and only four were oral in position. The spines of the European form were described by Dietz (1910) as being rounded at both ends, and ten were oral in position. Yamaguti (1958) proposed that the North American form, as described by Beaver (1941) warranted specific designation, differing from European species not only in the nature of the crown spines, but also in egg size (narrower in the American form) and in the type of cirrus (thickly spined in North American form, unspined in the European form). He named the North American form *Euparyphium beaveri.*

One of the four mink collected from the Sarpy locality was found to be infected with five echinostomes which are unquestionably the same species described by Beaver (1941) from *Mustela vison* and *Lutra canadensis* in Michigan and Minnesota.

Family DICROCOELIIDAE Odhner, 1911

Zonorchis komareki (McIntosh, 1939) Travassos, 1944
(Figures 12 to 13.)

Host.—Oryzomys palustris (Harlan) [new host record].

Location.—Bile duct.

Locality.—Bonnet Carre Spillway at Norco, St. Charles Parish, Louisiana [new locality record].

Diagnosis (based on six mature specimens).—*Zonorchis.* Body lanceolate, 3.675 to 5.250 long by 1.487 to 1.735 wide. Cuticle aspinose. Forebody 0.743 to 1.062 long. Body posterior to anterior edge of acetabulum 2.932 to 4.188 long. Oral sucker subterminal, 0.319 to 0.390 long by 0.354 to 0.390 wide. Acetabulum in anterior third of body, 0.425 to 0.496 long by 0.460 to 0.531 wide. Sucker ratio from 1:1.27 to 1.36. Prepharynx short, appearing absent. Pharynx 0.177 to 0.390 long by 0.212 to 0.390 wide. Esophagus extending from pharynx to half the distance from posterior border of oral sucker to anterior border of acetabulum. Ceca two, narrow extending along sides of body lateral to acetabulum ending blindly in about posterior sixth of body. Genital pore at level of posterior margin of pharynx opening into very shallow genital atrium. Testes two, roundish, juxtaposed at posterior border of acetabulum, 0.248 to 0.425 long by 0.212 to 0.354 wide. Cirrus sac ventral to esophagus, extending from genital atrium to cecal bifurcation; anterior two thirds containing unspined cirrus; posterior third containing convoluted internal seminal vesical and surrounding prostate gland cells. Ovary roundish, posttesticular, sinistral to mid-line of body, 0.212 to 0.283 long by 0.212 to 0.319 wide. Seminal receptacle dorsal to dextral margin of ovary. Ootype and Mehlis' gland median. Laurer's canal not observed. Vitellaria lateral to ceca, extending from level of anterior border or midlevel of acetabulum to posterior third of body. Vitelline reservoir dextral to ovary. Uterus intercecal, occupying most of hindbody, intruding between ovary and testes, perforating genital atrium dextral to cirrus sac. Eggs 0.025 to 0.031 long by 0.011 to 0.022 wide. Posterior portion of excretory vesicle tubular, anterior extension not observed.

Discussion.—The bile duct of a single rice rat, *Oryzomys palustris,* from the Bonnet Carre Spillway at Norco, Louisiana, was found infected with *Zonorchis komareki.* In subsequent collections of rice rats at the Goodhope oil field at Norco, one was found infected with *Z. komareki.* This rat died in the trap and partial cytolysis and contraction left the worms in a much distorted condition. Measurements of these five trematodes are not included. However, the diagnosis for these specimens is comparable to that of the six specimens given above, and both groups are unquestionably members of the same species.

Since no life cycle has been elucidated for any member of the genus *Zonorchis,* the host specificity and morphological variation of the adult specimens of several species remain an enigma. It is doubtful if studies of the adults from natural infections will yield much definitive information concerning the status of several species of *Zonorchis.* Present information indicates a great degree of overlap and convergence of adult characteristics in this genus. Our specimens from the rice rat closely resemble *Zonorchis komareki,* though they differ in; (1) size (3.68 to 5.25 long by 1.49 to 1.74 wide vs. 2.8 long by 0.8 wide in *Z. komareki*); (2) sucker ratio (1: 1.27 to 1.36 vs. 1: 1.72 in specimens for record collection); (3) ceca extending only to posterior sixth of body (as compared to posterior end of body in

Z. komareki); and (4) in a sinistral as compared with a dextral ovarian position. These small differences do not seem to warrant the naming of a new species at this time.

Summary

The following trematodes are reported from Louisiana for the first time: *Fibricola cratera* (Barker and Noll) Dubois, 1932, *Hasstilesia texensis* Chandler, 1929, *Euparyphium beaveri* Yamaguti, 1958, *Zonorchis komareki* (McIntosh, 1939) Travassos, 1944, and *Rhopalias macracanthus* Chandler, 1932.

New host records are: *Rhopalias macracanthus* Chandler, 1932, and *Brachylaemus virginianus* in *Mustela vison* Schreber, and *Zonorchis komareki* in *Oryzomys palustris* (Harlan).

Mixed infections of *Fibricola cratera* and *F. lucida* were found in four minks examined. The former was also recovered from a single raccoon, and the latter from four opossums. Our specimens of *Fibricola* from the raccoon and the minks which we have identified as *F. cratera* correspond to the description of Dubois (1938) for that species, primarily in the anterior extent of the vitellaria. Vitelline follicles apparently extend into the hindbody at least to the fore-margin of the posterior testis in both *F. cratera and F. texensis* Chandler, 1942.

The development and/or maintenance of *Rhopalias macracanthus* appears to be influenced by the location of these worms in the opossum's intestine. The normal site for these parasites is apparently the anterior third of the digestive tract. The more posterior regions of the opossum's gut may be suboptimal, as worms found in these areas were of small size or abnormal morphology.

Comparison of sucker sizes reported for *Hasstilesia tricolor* and our measurements of sucker diameters from specimens of *H. texensis* in Louisiana swamp rabbits indicates a significant difference in this character between the two species. The retention of *H. texensis* as a separate species from *H. tricolor* is advocated.

Specimens ascribed to *Zonorchis komareki* are reported from Louisiana rice rats, but differences are noted from the original descriptions of this species in body size, sucker ratio, posterior extent of the ceca, and position of the ovary. A dearth of information regarding host specificity and morphological variation of adult specimens of several species in *Zonorchis* preclude the naming of a new species at this time.

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ABSTRACT

The following trematodes were found in mammals collected at Norco, Louisiana and vicinity: *Fibricola cratera* (Barker and Noll, 1915) Dubois, 1932, in the mink, *Mustela vison* Schreber; *F. lucida* (LaRue and Bosma, 1927) Dubois and Rausch, 1950, in *Mustela vison* and the opossum, *Didelphis virginiana* Kerr; *Brachylaemus virginianus* Dickerson, 1930, in *Mustela vison; Hasstilesia texensis* Chandler, 1929, in the swamp rabbit, *Sylvilagus aquaticus* (Bachman); *Euparyphium beaveri* Yamaguti, 1958, in *Mustela vison; Zonorchis komareki* (McIntosh, 1939) Travassos, 1944, in *Oryzomys palustris* (Harlan); and *Rhopalias macracanthus* Chandler, 1932, in *Didelphis virginiana* and *Mustela vison. Fibricola lucida* and *Brachylaemus virginianus* have been previously reported from Louisiana; all other species represent new locality records. New host records include *Rhopalias macracanthus* and *Brachylaemus virginianus* in *Mustela vison,* and *Zonorchis komareki* in *Oryzomys palustris.*

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TWO NEW DICYEMID MESOZOANS FROM THE GULF OF MEXICO

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TULANE STUDIES IN ZOOLOGY

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CONTENTS

TWO NEW DICYEMID MESOZOANS FROM THE GULF OF MEXICO[1]

ROBERT B. SHORT,

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The dicyemid mesozoan fauna of the Atlantic and Gulf coasts of the United States has received little attention. Only three species have been reported heretofore, all from the coast of Florida: *Dicyema typus* van Beneden, from near St. Augustine (McConnaughey and Kritzler, 1952); *D. aegira* McConnaughey and Kritzler, from near St. Augustine (McConnaughey and Kritzler, 1952) and the northern Gulf (Short, 1957); and *D. briarei* Short from off Long Key (Short, 1961). Herein are described two additional species from the northern Gulf of Mexico.

The descriptions are based on coverslip smear preparations of octopus kidneys fixed in Bouin's and Sanfelice's fixatives, stained with Ehrlich's acid haematoxylin and iron haematoxylin, and mounted in Damar. All drawings were made with the aid of a camera lucida. Cilia, which are always present on peripheral cells of vermiform stages, have been omitted from most drawings.

I wish to thank Dr. Meredith L. Jones for collecting octopuses, Dr. Gilbert L. Voss for help in identification of them, and Mr. Raymond T. Damian for aid in preparation of mesozoan material for study and for reading the manuscript.

Dicyema **hypercephalum** sp. nov.

(Figures 1 to 27, 45 to 48)

Description.—Dicyema: Mature vermiform stages relatively small; lengths of two longest nematogens, 0.259 and 0.264 mm; rhombogens seldom longer than 0.550 mm; lengths of ten longest rhombogens, 0.483 to 0.657 mm. Somatic cell number almost invariably 14: 4 propolars, 4 metapolars, 2 parapolars, 2 diapolars, 2 uropolars.

Calotte markedly elongate, about 1/3 or more of body length in fully developed vermiform larvae (Figures 3-5), in young free vermiform individuals (Figures 6-15, 47), often 1/3 to 1/2 and in largest adults (Figure 21), 1/7 to 1/5 total length; orthotropal, especially in young vermiform stages, slightly plagiotropal in some older individuals. Calotte usually narrower than widest body region, more or less pointed in vermiform larvae, less pointed in older stages, often bluntly rounded anteriorly and constricted where propolars and metapolars meet (Figures 20-22). Propolars and metapolars about equal in size.

Body usually with no conspicuous cephalic swelling, commonly widest at diapolars, sometimes at the parapolars (Figures 46-48). Parapolar cells usually shorter than calotte, sometimes equal to calotte in length in largest rhombogens (Figure 21). Parapolars usually rounded or bluntly pointed posteriorly. Trunk cells in opposed pairs. Cytoplasm of parapolar and trunk cells usually with irregular particles which are characteristically darkest and most plentiful in parapolars (Figures 19, 45-48). No verruciform cells.

Nuclei of calotte cells about equal in size. Nuclei of all somatic cells with relatively small nucleoli. Accessory nuclei in parapolar and trunk cells of rhombogens few, usually one or two per cell.

Cilia on calotte shorter, more closely set, more conspicuous and apparently stiffer than those on trunk.

Axial cell usually extending anteriorly to propolars, occasionally ending bluntly near bases of metapolars (Figures 8, 11, 13, 18).

Vermiform larvae at eclosion about 40 to 50 microns long, containing two axoblasts with one axial cell nucleus between them (6 larvae) or anterior to both (7 larvae).

Rhombogens containing a single infusorigen which is usually postequatorial.

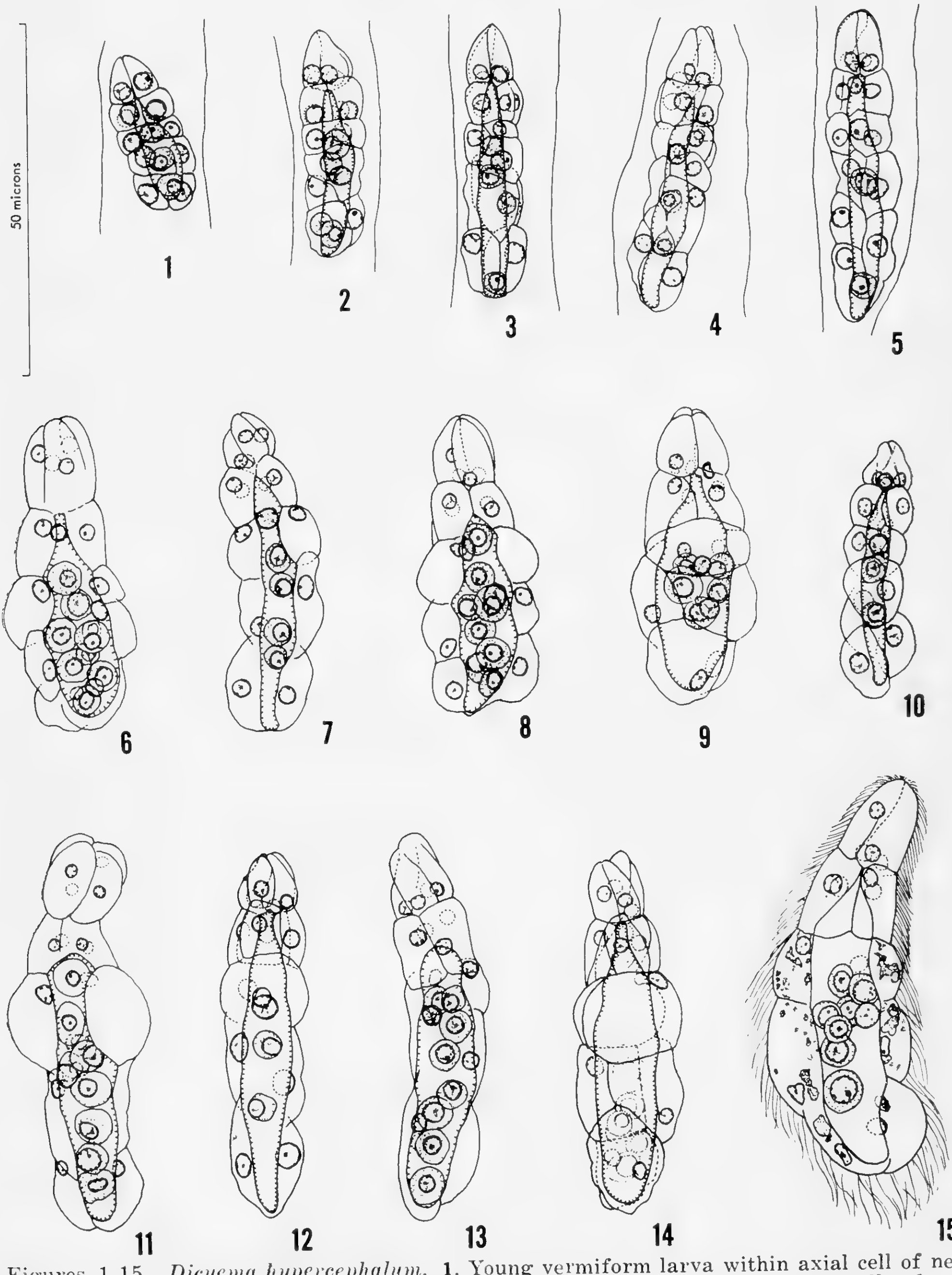
Infusorigens small with few female cells; for 50 infusorigens: range of three to seven female cells per individual; mode, four.

Infusoriforms rounded posteriorly. Average length of five apparently mature individuals in axial cells: 28.6 microns, range 24.8 to 32.5. Two relatively large refringent

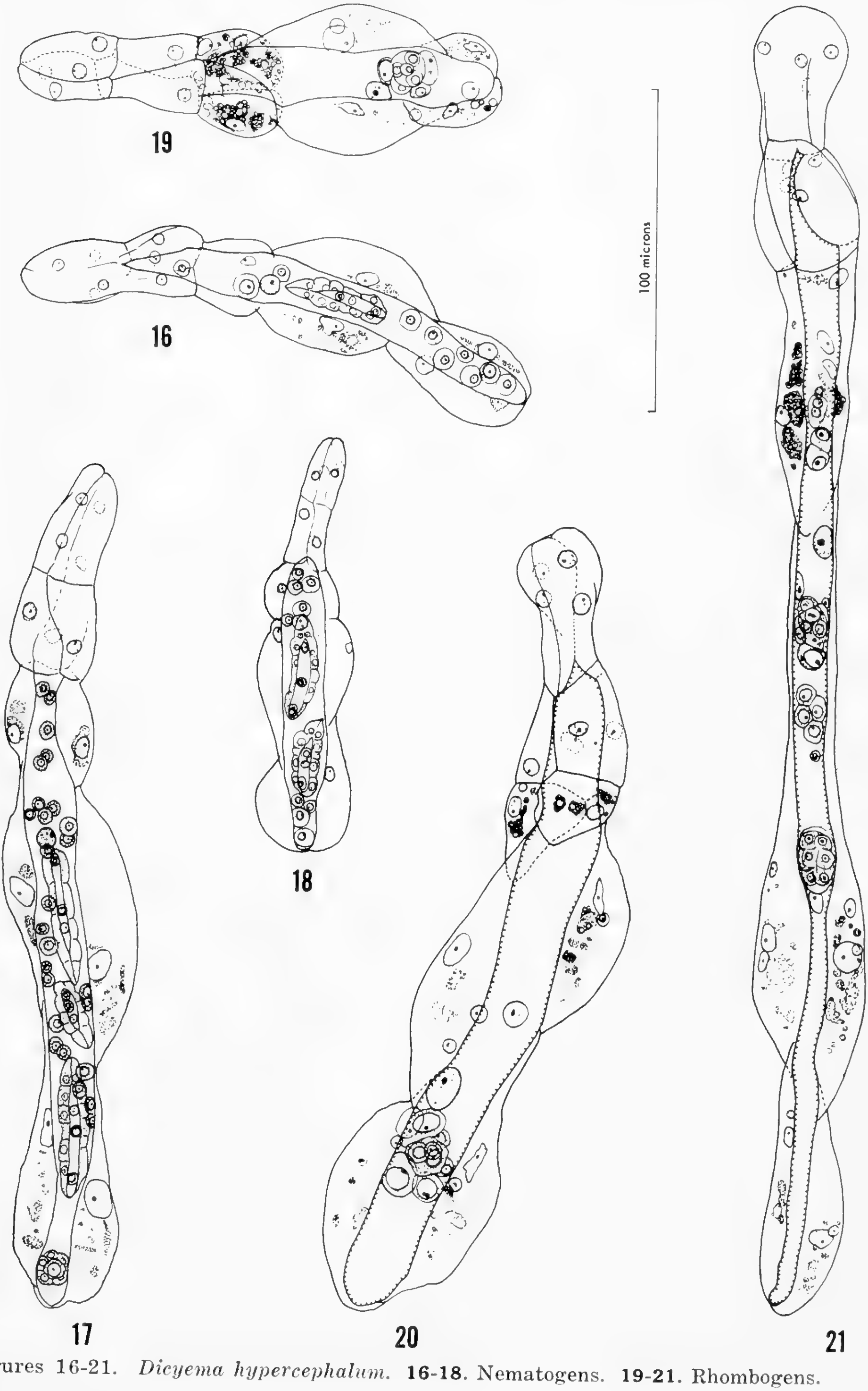
[1] This study was supported by Research Grants G-4449 and G-7466 from the National Science Foundation.

bodies extending about to midbody, appearing in lateral view larger than urn contents. Capsule cells without conspicuous granules, apparently unusual in their ventral position, with nuclei ventrolateral to urn contents. Each urn cell containing a single germinal cell and two somatic nuclei.

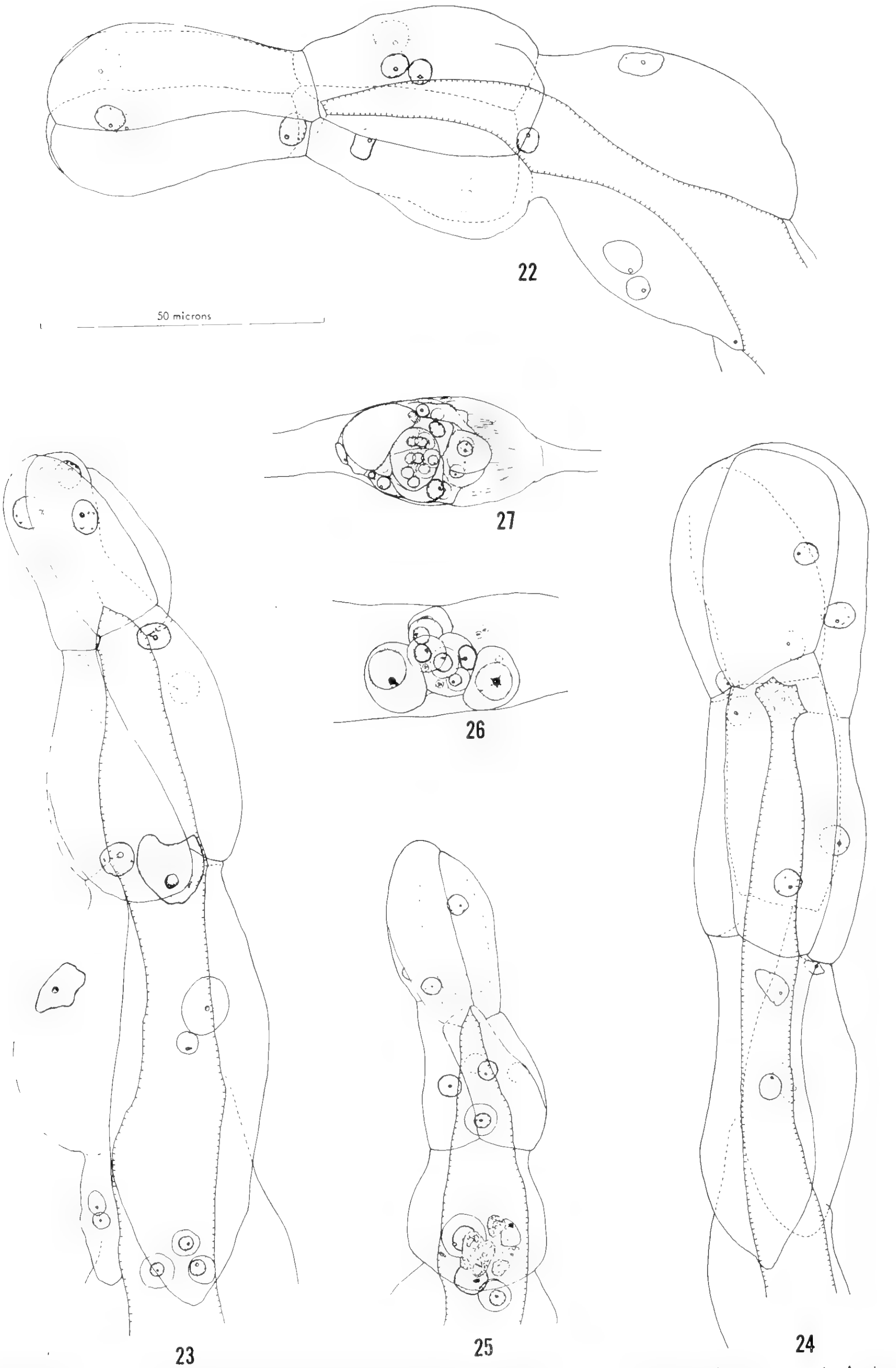
Host.—Octopus joubini. One small speci-



Figures 1-15. *Dicyema hypercephalum*. **1**. Young vermiform larva within axial cell of nematogen. **2-5**. Older vermiform larvae, apparently fully developed, within axial cells of nematogens. **6-15**. Young, free vermiform stages, probably all rhombogens.



Figures 16-21. *Dicyema hypercephalum.* **16-18.** Nematogens. **19-21.** Rhombogens.



Figures 22-27. *Dicyema hypercephalum*. **22-24**. Anterior ends of rhombogens. **25**. Anterior end of nematogen. **26**. Infusorigen. **27**. Infusoriform larva, parasagittal optical section, within axial cell of parent rhombogen.

men with a mantle length of 15 mm. This dicyemid was the only species in this host individual.

Locality.—Apalachee Bay, Gulf of Mexico, about six miles south of Light House Point, Franklin Co., Florida.

Type specimens.—Syntypes on slide 542-8 (U. S. N. M. Helm. Coll. 59615) and other slides from host 542 (author's collection).

Discussion.—For the above description, young vermiform stages (presumably immature rhombogens) and older rhombogens were plentiful, but very few of the latter contained mature infusoriforms or even large embryos. The account of the infusoriform is based on six apparently mature specimens in axial cells. Nematogens and vermiform larvae were also scarce, only 13 nematogens and 16 vermiform larvae within axial cells being seen. Thus, descriptions of nematogens and infusoriforms are not as complete as desirable. Also an accurate account of cilia was hampered by their poor visibility in the fixed material. On the calotte of free vermiform stages cilia were conspicuous and brush like, but on other body regions they were seen only with difficulty on a few specimens, and then with phase contrast microscopy.

Although the somatic cell number is almost always 14, other numbers were encountered. Cell counts were made on 114 individuals (45 rhombogens, 5 nematogens, 16 vermiform larvae, 46 young free vermiforms, and 2 transitional individuals). Except for six specimens, the somatic cell number was 14. Of these six, three each possessed 15 somatic cells and one each possessed 12, 13 and 16.

One hundred rhombogens were examined for number and position of infusorigens; single infusorigen occurred in every one. However, during subsequent study two immature infusorigens were seen in one rhombogen.

D. hypercephalum differs from all other described species of *Dicyema* in the shape and proportions of its calotte. It is also unusual in possessing typically 14 somatic cells; only two other known species have this low a number. *D. oligomerum* Bogolepova, 1960, usually has 14 to 16 peripheral cells (Bogolepova, 1960), and *D. apalachiensis* (described below) has typically 14. Besides having a relatively much longer calotte, *D. hypercephalum* differs from *D. oligomerum* in being considerably smaller. Differences between *D. hypercephalum* and *D. apalachiensis* will be indicated after description of the latter.

In somatic cell number *D. hypercephalum* is close to *D. monodi* Nouvel, 1934, *D. megalocephalum* Nouvel, 1934, and *D. caudatum* Bogolepova, 1960, all with 16. In *D. megalocephalum* fewer than 16 cells may occur; exact counts were rendered difficult by flattening and possible fusion of peripheral cells (Nouvel, 1934). *D. monodi* and *D. megalocephalum* are also similar to D. *hypercephalum* in having unusually long calottes. In *D. monodi,* however, the metapolar cells become much longer than the propolars and the axial cell does not penetrate to the propolars. The metapolar cells of *D. megalocephalum* are likewise longer than propolars and the entire calotte is considerably wider than the trunk.

Dicyema **apalachiensis** sp. nov.

(Figures 28 to 44, 49 to 66)

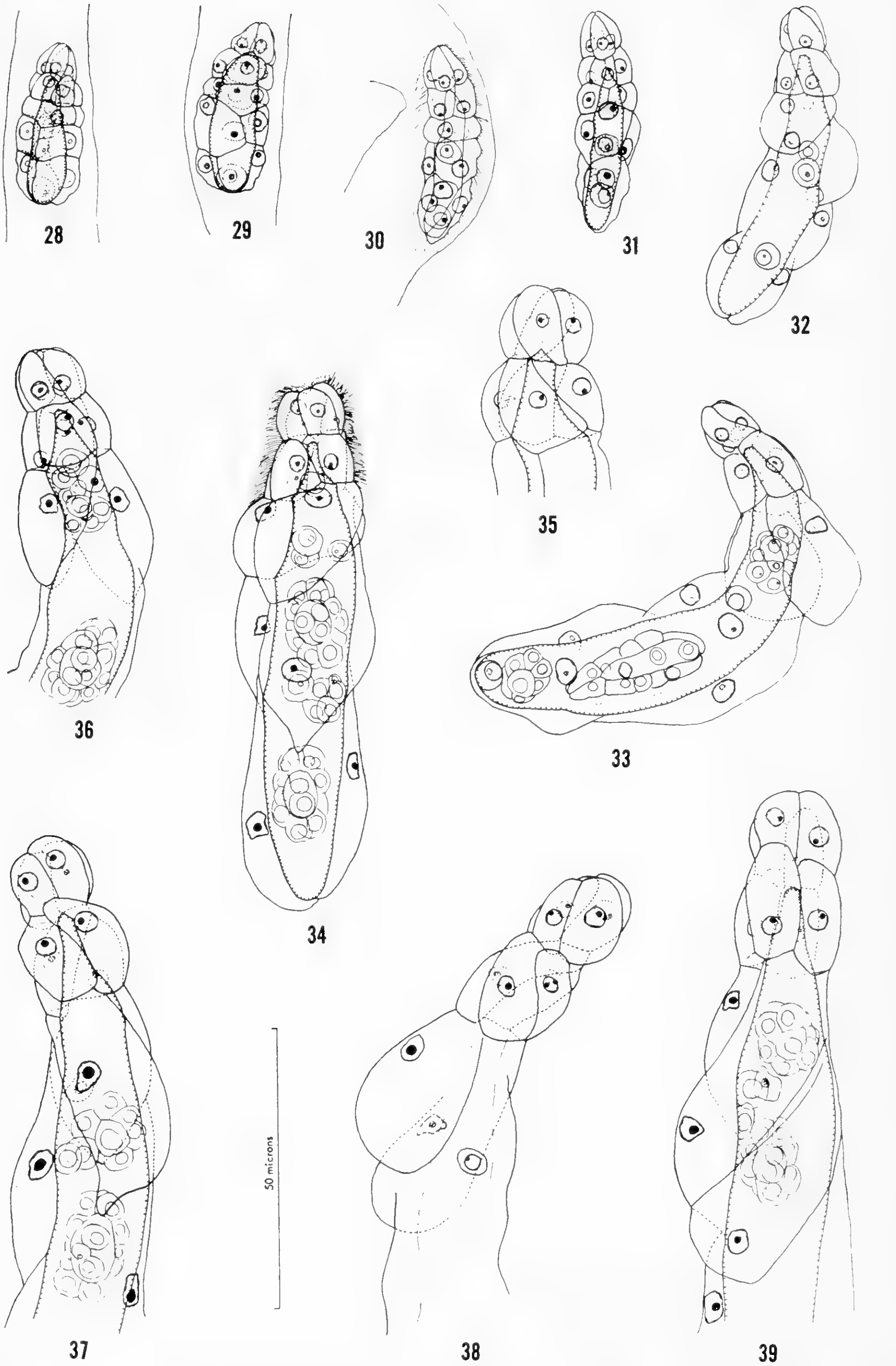
Description.—Dicyema: Mature nematogens seldom longer than 0.350 mm; range of ten longest specimens 0.299 to 0.645 mm. Somatic cell number usually 14, sometimes 15, occasionally 16 or 17. Results of cell counts on 123 individuals summarized in Table 1.

Calotte orthotropal, sometimes apparently plagiotropal; typically narrower than parapolar and widest trunk regions; longer than wide; in vermiform larvae more or less pointed, in adults bluntly pointed to rounded. Propolar and metapolar cells of younger

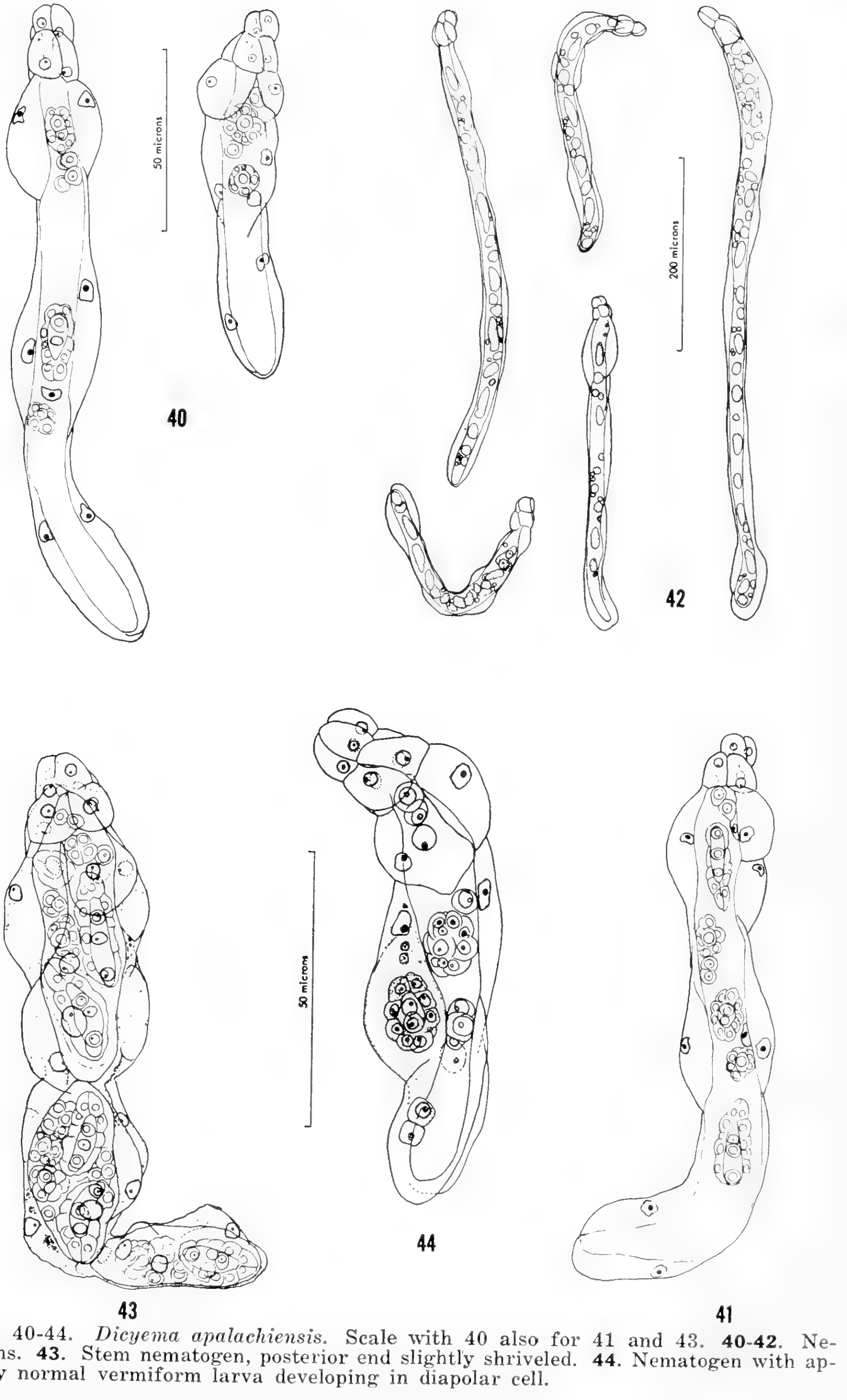
TABLE 1.
Somatic cell numbers of Dicyema apalachiensis

Cell No.	Phase		Totals
	Veriform larva	Nematogen	
12	2*	0	2
13	0	0	0
14	88	10	98
15	13	3	16
16	1	6**	7
Totals	104	19	123

* Anomalies?
** Four of these were among the longest nematogens.



Figures 28-39. *Dicyema apalachiensis*. **28-29**. Young vermiform larvae within axial cells of nematogens. **30**. Older vermiform larva, within axial cell, apparently fully developed. **31-32**. Young, free vermiform individuals. **33-34**. Small nematogens. **35-39**. Anterior ends of nematogens.



Figures 40-44. *Dicyema apalachiensis.* Scale with 40 also for 41 and 43. **40-42.** Nematogens. **43.** Stem nematogen, posterior end slightly shriveled. **44.** Nematogen with apparently normal vermiform larva developing in diapolar cell.

individuals about equal in size, metapolars of old nematogens usually longer than propolars. Calotte often twisted clockwise (Figure 38).

Body of young nematogens often widest at parapolars (Figure 40), in longest specimens usually slight if any cephalic swelling (Figure 42). Parapolar cells of vermiform larvae shorter than calotte, becoming longer than calotte in larger nematogens; parapolars in young vermiform stages bluntly rounded (Figure 32); in older individuals often more pointed posteriorly (Figure 37). Parapolars sometimes asymmetrically disposed (Figures 38, 39) with one diapolar cell extending between them to base of metapolars. Trunk cells usually in opposed pairs. Usual granular material in somatic cells (Figures 62-65); no verruciform cells.

Nuclei of calotte about equal in size. Nucleoli, especially of parapolar and trunk cells, typically prominent, sometimes very large.

Axial cell usually ending anteriorly in a blunt point at bases of propolars (Figures 33-37); in vermiform larvae rarely ending near middle of metapolars (Figure 31). Axial cell of largest nematogens often with many vermiform larvae and embryos.

Vermiform larvae at eclosion about 25-40 microns long, containing two axoblasts with one axial cell nucleus between them or anterior to both.

Rhombogens, infusorigens and infusoriforms unknown.

Host.—This species was found in 11 very small specimens of *Octopus joubini*, all from the same locality. Seven hosts also harbored another unidentified larger species of dicyemid with more than 14 peripheral cells.

Locality.—Apalachee Bay, Gulf of Mexico, about six miles south of Light House Point, Franklin Co., Fla.

Type specimens.—Syntypes on slide 516-13 (U. S. N. M. Helm. Coll. 59616) and other slides from hosts 516, 520, 523, and 525 (author's collection).

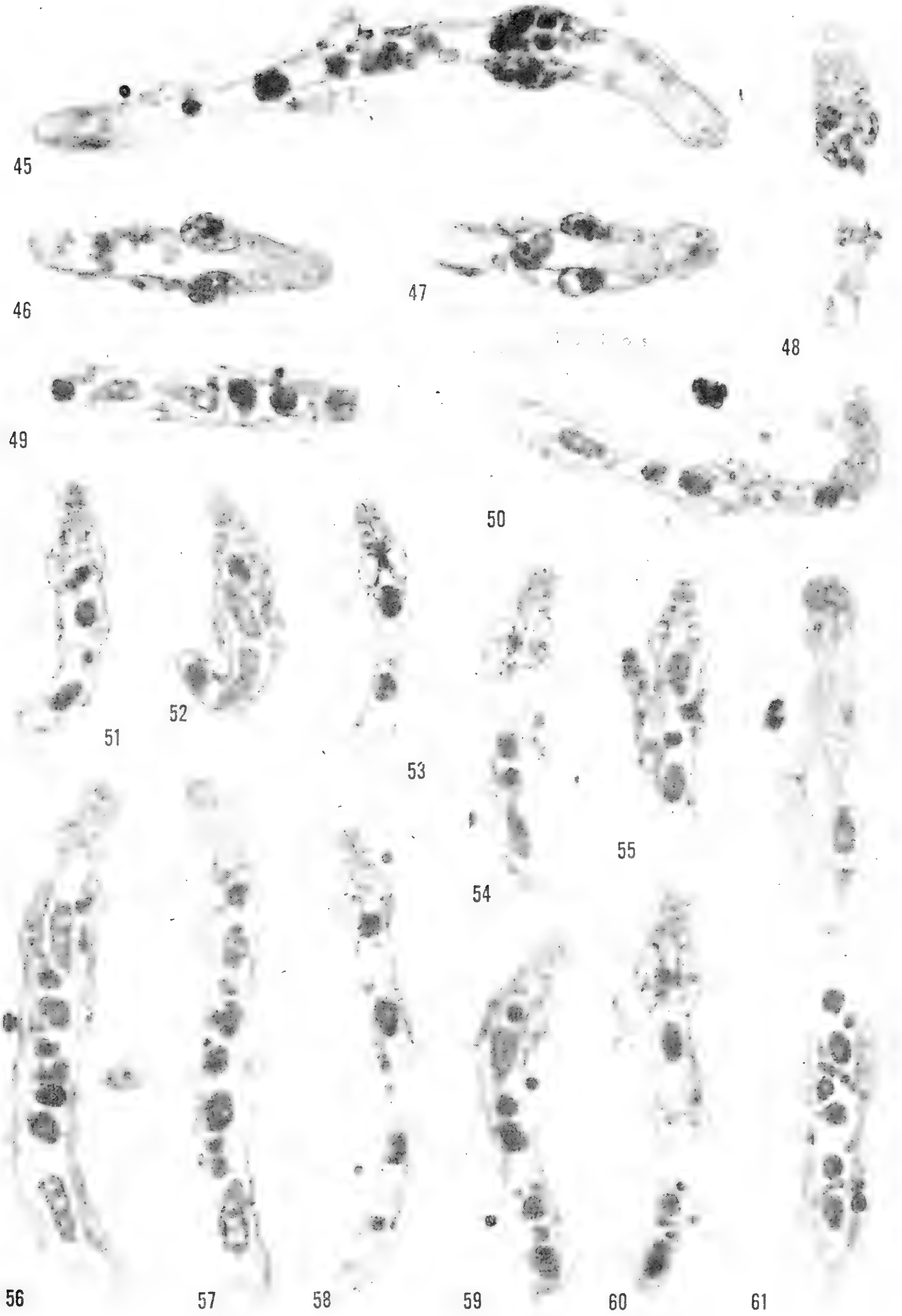
Discussion.—The above description is based mainly on material from host 516. All cell counts of Table 1 were made on specimens from this octopus as well as all figures except 32 (host 520), 33 (host 523), 43 (host 525), 63 and 65 (host 520).

Some variation from the usual appearance was noted in populations from hosts 520 and 521. Parasites from these octopuses contained more conspicuous granular material in the somatic cells, especially in the parapolars (Figures 63, 65), and the calottes of some appeared more elongate than usual (Figure 33). Nucleoli were usually not as prominent in these specimens, but this may have resulted from poor staining.

Part of a large stem nematogen, apparently of this species, and an entire, smaller specimen were found in two different hosts. The fragment is 505 microns long and consists of the two anterior axial cells, the calotte and four or five diapolar cells. Each axial cell contains vermiform larvae, embryos and axoblasts; the anterior cell is longer and possesses more reproductive elements than the other. Somatic cell counts on four vermiform larvae gave: 14, 14 and 15 or 16.

The smaller, entire stem nematogen (Figure 43) is 192 microns long and appears to be in good condition except for a slightly shriveled posterior end. There are three axial cells, each with apparently a single nucleus. The anterior cell is the longest and the most productive; it contains two mature vermiform larvae, five embryonic vermiform larvae and five axoblasts. The middle cell contains two slightly smaller vermiform larvae, four embryonic vermiforms and three axoblasts; the posterior cell holds one vermiform larva (smaller than the other four), three embryonic vermiforms and two (?) axoblasts. The calotte consists of eight cells, four propolars and four metapolars. In this specimen and the fragment the propolars appear to alternate with the metapolars, a condition described in other stem nematogens (Nouvel, 1947). The number and disposition of parapolars could not be determined. There appears to be a single uropolar cell. Besides the calotte, there seem to be 14 somatic cells, giving a total of 22. The five largest vermiform larvae each have 14 somatic cells, the number typical for the species. More detailed information on the stem nematogen of this species must await examination of more favorable material.

Several anomalies were observed besides the two vermiform larvae each with 12 somatic cells (Table 1). In one young nema-



Figures 45-61. Photomicrographs. **45-48.** *Dicyema hypercephalum*, rhombogens. **49-61.** *D. apalachiensis*, nematogens.

Figures 62-66. Photomicrographs. *Dicyema apalachiensis*, nematogens. **62.** Small specimen and posterior end of larger one, showing granular material in peripheral cells. **63.** Small specimens; note heavier concentration of granules in parapolar cells of one. **64.** Anterior end of large nematogen. **65-66.** Small nematogens; note granules in parapolar cells of 65.

togen, 92 microns long, there are two axial cells side by side, the one about twice the length of the other. Each axial cell has a nucleus, axoblasts and embryonic vermiform larvae. One larva in the longer cell appears almost mature. The somatic cell number is doubled (28) with 16 calotte cells, four parapolars and eight trunk. This anomalous individual resembles that of *Dicyema typus* reported by Nouvel (1948, Figure 90) except for a normal somatic cell number in Nouvel's specimen.

A more unusual finding is the presence of 19 apparently normal vermiform larvae of various sizes in *somatic cells* of 14 otherwise normal nematogens, ten from one octopus, three from another (Figures 44, 61). These nematogens range in length from 60 to 360 microns. Eleven each contain one vermiform in a somatic cell, two each contain two, and one has four. Twelve of the larvae are in diapolar cells, five in uropolars, and two in parapolars. All such larvae occur singly within vacuoles; all appear normal. Two axoblasts are in axial cells of at least ten and the two largest individuals are 24.8 and 27.9 microns long respectively, the latter being well within the range of full sized vermiform larvae. Two apparently normal single axoblasts were also noted in somatic cells of these nematogens, one in a diapolar, the other in a uropolar cell.

Single axoblasts have been reported in somatic cells of dicyemids, especially in transitional individuals (Nouvel, 1948; McConnaughey, 1951). Such axoblasts have been stated to be digested completely (McConnaughey, 1951) or to lose their cytoplasm and contribute their nuclei as accessory nuclei in the peripheral cells (Nouvel, 1948). Two rarer findings similar to the present ones have been reported by Nouvel (1948). One was a rather large nematogen of *Dicyema typus* with germinal cells and vermiform embryos in a uropolar cell; the other was a rhombogen of *Dicyemennea lameeri* which contained in a peripheral cell near the middle of the body an infusorigen and embryonic infusoriforms.

The presence of apparently normal axoblasts, vermiform larvae of various sizes and infusorigens in somatic cells indicates that such cells are capable of assuming at least part of the reproductive function of the axial cell. There seems to be a definite tendency for this phenomonen in *D. apalachiensis.*

As indicated above, *D. apalachiensis* shares the low somatic cell number of 14 with only two other species of *Dicyema: D. hypercephalum* and *D. oligomerum.* Fifteen and 16 peripheral cells occurred more often in *D. apalachiensis* than in *D. hypercephalum* and exceptionally 17 were observed in the former; however, this difference may not be significant because most individuals of *D. hypercephalum* were rhombogens, whereas only nematogens of *D. apalachiensis* were available. *D. apalachiensis* differs markedly from *D. hypercephalum* in having a relatively much shorter calotte and usually larger nucleoli.

D. apalachiensis is unlike *D. oligomerum* in having a smaller body size, a relatively longer and narrower calotte and, especially in young individuals, relatively smaller diapolar and uropolar cells.

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Abstract

Dicyema **hypercephalum** and *D.* **apalachiensis** are described from *Octopus joubini* from Apalachee Bay, off the Florida coast. Both new spp. have typically 14 peripheral cells. The calotte of *D.* **hypercephalum** is unusually long.

Nineteen vermiform larvae of *D.* **apalachiensis** were found developing in peripheral cells of 14 nematogens.

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THE SWAMP DARTERS OF THE SUBGENUS *HOLOLEPIS* (PISCES, PERCIDAE)

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THE AMERICAN PERCID FISHES OF THE SUBGENUS *VILLORA*

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I. Introduction

The object of this paper is to clarify the relationships within and among the darters of the subgenus *Hololepis,* genus *Etheostoma.*

Hubbs and Cannon (1935) thoroughly reviewed the darters of the nominal genera *Hololepis* and *Villora* on the basis of the specimens then available. Extensive collecting in recent years has greatly increased available material and necessitates a modification of some of their conclusions.

Bailey (1951), in Bailey, Winn, and Smith, 1954; and in Bailey and Gosline, 1955 reduced the many nominal genera of darters to three. These are *Percina, Ammocrypta,* and *Etheostoma.* He based this decision on "evidence that the characters employed to define and delimit the groups . . . are highly variable both intraspecifically and interspecifically, are subject to complete overlap from group to group, and are commonly the product of convergent evolution" (Bailey, Winn, and Smith, 1954, page 141). Bailey utilized some of the former genera as subgenera (Bailey and Gosline, 1955: Fig. 1). Although it would be better to have data published before nomenclatorial changes are made, I will follow his use of the name *Hololepis* as a subgenus of *Etheostoma.* However, I can not agree with his implication that the subgenus *Villora* Hubbs and Cannon be made a synonym of *Hololepis* (See Collette and Yerger, 1962). Upon replacing *Etheostoma edwini* in the subgenus *Villora,* the subgenus *Hololepis* constitutes a group of eight forms of small specialized swamp darters. Four of these forms are found in the swamps, lakes, and backwaters of the Coastal Plain, one in the lowlands of the Mississippi Basin, and the other three are limited to the backwaters of Piedmont streams along the Atlantic Coast.

II. Acknowledgments

This study was begun at the suggestion of Edward C. Raney and completed under his guidance in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Cornell University. In addition to his constant interest, Dr. Raney provided support through National Science Foundation Grants 2893 and 9038.

The section on pored lateral-line scales in *Etheostoma fusiforme* was submitted as a minor problem in limnology to Clifford O. Berg to whom I express my appreciation for his comments and interest. The New York State Museum and Science Service provided support for field work on the Long Island populations of *E. fusiforme* through a Graduate Student Honorarium.

This study could not have been satisfactorily completed without the use of specimens from a number of museums and universities. Appreciation is expressed to the following persons and their institutions for having loaned specimens under their care and for making facilities at their institutions available: Joseph R. Bailey, Duke University (DU); Reeve M. Bailey, University of Michigan Museum of Zoology (UMMZ); James E. Böhlke, Academy of Natural Sciences of Philadelphia (ANSP); Frank B. Cross, Museum of Natural History, University of Kansas (KU); Harry W. Freeman, University of South Carolina (specimens transferred to Cornell University); Shelby D. Gerking, University of Indiana (UI); Robert H. Gibbs, Jr., Boston University (BU); A. Frederick Hemphill, Spring Hill College, Alabama (UAIC); Clark Hubbs, University of Texas (TNHC); Robert H. Kanazawa, Ernest A. Lachner, Leonard P. Schultz and W. Ralph Taylor, Fish Division, United States National Museum (USNM); Y. J. McGaha, University of Mississippi (UM); Romeo Mansueti, Maryland Department of Research and Education (M); George A. Moore, Oklahoma State University (OAM); E. E. Prather, Alabama Polytechnic Institute (API); Edward C. Raney, Cornell University (CU); C. Richard Robins, University of Miami Marine Laboratory (UMML); Donald C. Scott, University of Georgia (UG); Philip W. Smith, Illinois Natural History Survey

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Darrell E. Louder, North Carolina Wildlife Resources Commission, has aided immeasurably by collecting specimens of *E. fusiforme fusiforme* from the North Carolina Bay Lakes for me. Daniel M. Cohen, Robert H. Gibbs, Jr., Ernest A. Lachner, William A. Lund, and Royal D. Suttkus have made many valuable suggestions. Rudolph J. Miller kindly drew the figures of the genital papillae and the distribution of the breeding tubercles (Fig. 1). Douglass M. Payne made the photographs. Sara E. Collette typed several early drafts of the paper and Alice B. Holland typed the final draft.

III. Characters Studied and Their Significance

Counts were made in accordance with the methods outlined by Hubbs and Lagler (1947, 1958) and Hubbs and Cannon (1935) except as modified below. Each group of characters will be discussed to give my interpretation of their relative value in this study.

Lateral-line scales: The total number of lateral-line scales was valuable in distinguishing some species and also in separating races of *E. serriferum.* The number of pored lateral-line scales was especially valuable in the recognition of subspecies of *E. fusiforme.* However, it is subject to developmental variation which made its use somewhat complicated as discussed under development and geographic variation in *E. fusiforme.* The number of unpored lateral-line scales was not studied separately because it is merely an expression of the same factors represented by the total and pored lateral-line scales. Hubbs and Cannon (1935), Bailey (1950), and Bailey and Frey (1951) used the ratio of pored to unpored lateral-line scales. The value of this ratio is negated by the extreme variation of the pored lateral-line scales in *E. fusiforme.* In the other species it merely reflected the number of pored scales and therefore seemed unnecessary.

Scale rows above and below the lateral line: This character was of value in studying the neotenic populations of *E. fusiforme* and is further discussed under geographic variation in *E. fusiforme.* The two species of the subgenus *Villora* have fewer scales below the lateral line than the species of the subgenus *Hololepis,* since the scales are generally larger in *Villora. E. serriferum* has more scales both above and below the lateral line than the other species of the subgenus *Hololepis.*

Fin Rays: The number of first dorsal spines and second dorsal rays was of little taxonomic value. The high number of spines and rays in *E. serriferum* is an indication of its relatively primitive position in the subgenus *Hololepis.* Several populations of *E. fusiforme,* including the Nantucket population named as *fusiforme insulae* by Hubbs and Cannon (1935), had abnormally low dorsal spine counts. The low number of anal rays in *E. zoniferum* helped show its position as a specialized offshoot of *E. gracile* but proved of little value otherwise. The number of anal spines proved significant in the *E. collis* group although Hubbs and Cannon stated that it was consistently two. All *E. collis* and one third of the related *E. saludae,* had only one anal spine. The vast majority of specimens of the other species of *Hololepis* had two anal spines although a few unusual specimens had one or three. There were modal differences between species in the numbers of pectoral rays but the character holds no promise of value in future work. Pelvic elements were I, 5 in all species of *Hololepis,* with only a few specimens having I, 4 or I, 6. For ease of physical handling, the pectoral and pelvic fins were counted on the right side. Segmented caudal rays were also counted but proved of no systematic value.

Branchiostegal Rays: These were counted on the right side. Virtually all the specimens examined had six branchiostegals, with a few deviations to five or seven.

Cephalic Pores: As pointed out by Hubbs and Cannon (1935), the arrangement and number of pores in the various canals on the head of the species of *Hololepis* are of great systematic importance. The preoperculomandibular pores (operculomandibular pores of Hubbs and Cannon) show strong modes at ten pores for the *E. gracile* group and at nine for the other species of *Hololepis. E. serriferum* and *E. saludae* usually have both interorbital pores present while most specimens of the other species of *Hololepis* usually lack these pores. There was no appreciable intra-specific variation in these two canals. The coronal pore is usually present in *Hololepis* but several populations of *Etheostoma fusiforme fusiforme* from the North Carolina Bay Lakes either lack the pore entirely or have it poorly developed. Studies of the relative development of the coronal pore may be of systematic value as mentioned under variation in *E. f. fusiforme.* Development also complicated the use of the supratemporal canal as a systematic character. Most *E. fusiforme, serriferum,* and *gracile* had this canal complete with the left and right branches uniting in a median pore at the occiput. Individuals of the *E. collis* group were about equally divided between complete and incomplete supratemporal canals, a feature which I consider specialized. The general picture of the growth of this canal is discussed under development in section IV. The infraorbital pores showed a number of different patterns which were modally species specific. *E. serriferum* (six pores) and *E. gracile* (eight pores) have complete infraorbital canals. The other species of *Hololepis* have incomplete canals with the anterior portion of the canal separated from the posterior portion. The northern subspecies of *E. fusiforme* has 2 + 3 (posterior plus anterior portion) pores while the southern subspecies has 1 + 3 pores with many interesting variations which are discussed fully under geographic variation in *E. fusiforme.* For ease of handling, pore counts of the infraorbital and preoperculomandibular canals were made on the right side of the specimens.

Condition of the Preopercle: The right side of the preopercle was examined for serrae. The condition was recorded as S (serrate), PS (partially serrate, or E (entire or non-serrate). Hubbs and Cannon (1935) stated that *E. serriferum* could be distinguished from the other species of *Hololepis* by the presence of serrations on its preopercle. The presence of a few preopercular serrations in some specimens of *Etheostoma fusiforme barratti* led some workers to believe that these specimens might represent hybrids between *E. serriferum* and *E. f. barratti.* Bailey (1950) used the presence of many preopercular serrations in specimens of *barratti* from the French Broad River as a diagnostic character of his *Hololepis barratti appalachia.* As discussed under geographic variation in *E. fusiforme,* the presence of these serrations varies in a roughly clinal manner, the percentage of individuals with them increasing from north to south.

Squamation: The parietal, interorbital, breast, opercle, preopercle, and nape were examined for the development of squamation. The number of scales was counted in the interorbital region while the area covered and the type of scales were recorded in the other areas. The interorbital region is defined as the area between the orbits anterior to the nares and posterior to a line between the eyes at the level of the coronal pore, where the parietal area begins. In *E. serriferum* and *E. fusiforme,* the skin with contained scales was dissected off and the scales were removed and counted under magnification. The scales were frequently small, imbedded, and sometimes in a number of vertical layers, making counting difficult. This scale count allowed the separation of races in *E. serriferum* and subspecies in *E. fusiforme.* As with the other squamation examinations, only adult specimens were used since these regions are less scaled or naked in juveniles.

The area covered by scales in the other regions was estimated to the nearest 10% (similar to the method used by Lagler and Bailey, 1947). The amount of imbedding was recorded: X (posterior edges of the scales completely exposed), PX (scales with their posterior margins partly exposed), or I (scales completely imbedded in the epidermis). The type of ctenoid or cycloid scales was recorded: T (ctenoid scales with at least one spine on the posterior margin), or C (cycloid scales, completely lacking ctenii). When two conditions were present in a given region, both symbols were recorded, separated by a diagonal. Thus the formula for a region might be: 50% I/PX-C/T meaning half the region was covered by scales of which some were imbedded and others partly exposed and some were cycloid and others ctenoid. These symbols are used in the squamation tables to save space.

The parietal region is the area from the interorbital region posterior to the supratemporal canal bounded laterally by the light line that runs just above the lateral canal. This definition excludes the single row of scales usually present beween the lateral canal and the light line. The nape region is a roughly triangular area with its base at the supratemporal canal and its apex at the origin of the first dorsal fin. The breast region is the triangular area starting on a line just anterior to the origin of the pelvic fins and extending forward to immediately behind the union of the gill covers. The opercular and preopercular regions include the surfaces of those bones and were examined on the right side.

Breeding Tubercles: Specimens were examined for breeding tubercles while counts were being made. The specimens showing maximum development of tubercles were selected for study. Breeding males of all species of the subgenus *Hololepis* have tubercles on the rays of the anal and pelvic fins, although the number and exact distribution of the tubercles varies between and within species. In the descriptions of breeding tubercles of each species, the rays of the anal and pelvic fins are numbered, starting behind the spines. Tubercle distributions of several species are pictured (Fig. 1).

The use of breeding tubercles as a systematic character in darters has been totally neglected. There are literature reports of breeding tubercles in nine species of darters while I have found them in more than 40 species in a study that has not been completed. As in the Cyprinidae and Catostomidae, tubercle patterns characterize some taxonomic groups. Two instances of tubercle pattern pertinent to this study are: (1) the subgenus *Villora* differs from the subgenus *Hololepis* in lacking breeding tubercles; and (2) the close relationship of *E. gracile* and *E. zoniferum* is demonstrated by their being the only species of *Hololepis* to have accessory breeding tubercles on their lower jaws.

Genital Papillae: As pointed out by Hubbs and Cannon (1935), breeding female *E. serriferum* possess flattened and bilobed genital papillae as contrary to the conical pointed genital papillae present in the other species of the subgenus *Hololepis.* As noted under the subgeneric diagnosis, *Hololepis* can be distinguished from *Villora* by its elongate genital papilla. Drawings of the different types of genital papillae are presented (Fig. 1) to supplement text descriptions.

Sex: Dissections were made on a relatively few specimens to verify external sex determinations. Thereafter sex was determined externally by the enlargement of the female genital papilla and by the more pigmented venter and dorsal, anal, and pelvic fins of the males. These characters allowed the determination of sex in specimens as small as 20 mm. Smaller specimens were listed as juveniles.

Measurements: Due to the great abundance of other characters, and to the statement by Hubbs and Cannon (1935) about the slight value of morphometrics in *Hololepis,* only the standard length was taken. Standard length is particularly important in *Hololepis* because variation in several characters is correlated with specimen size (Section IV, development).

Range: Figures 3, 5, and 8 show the distribution of each form (based upon specimens personally examined) in relation to the Fall Line which is important in limiting the distribution of all the species of the subgenus *Hololepis,* except *E. gracile.* When several collections were available from a small area, all were not plotted. Collections of all specimens examined are given by museum number, county, and state for the various drainages. More complete locality data are given for rare forms, range extensions, or other reasons. Complete data for most collections examined may be found in my thesis (Collette, 1960).

Ecology and Habits: To become more familiar with *Hololepis* I have made several hundred collections in 21 of the 27 states where they are found. I have maintained *E. serriferum, gracile, fusiforme fusiforme,* and *f. barratti* in aquaria for varying lengths of time to obtain some understanding of their feeding, courtship, and other behavior.

Synonymies: I have attempted to examine all references that mention any of the *Hololepis* in any manner. The synonymies under each form include all references since the publication of Hubbs and Cannon's (1935) revision and all significant ones prior to that time.

Sampling: I made complete counts on

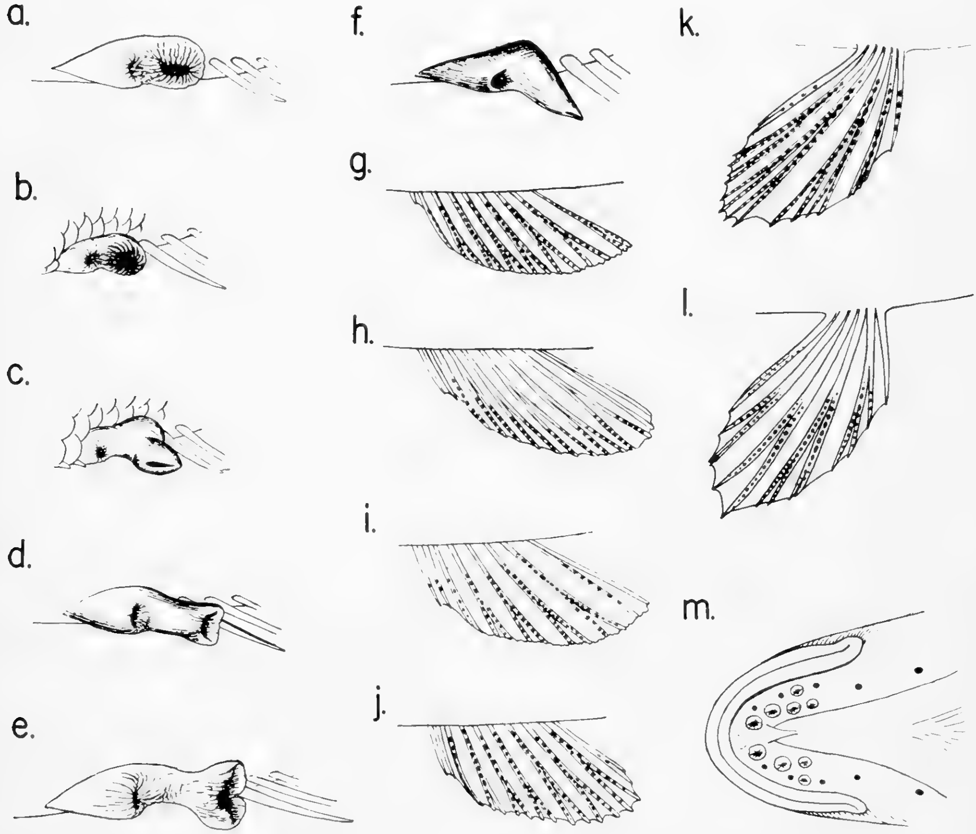

Figure. 1. Genital papillae and breeding tubercles in some of the species of the subgenera *Hololepis* and *Villora*. **a**. *Etheostoma edwini.* Genital papilla of 38.1 mm female taken on March 26. (CU 29754, Ga., Apalachicola dr.) **b**. *Etheostoma edwini.* Genital papilla of 38.5 mm female taken on March 26. (CU 29754, Ga., Apalachicola dr.) **c**. *Etheostoma gracile.* Genital papilla of 40.4 mm female taken on March 7. (TNHC 2750, Tex. San Jacinto dr.) **d**. *Etheostoma serriferum.* Genital papilla of 42.3 mm female taken on March 24. (CU 29976, Va., Chowan dr.) **e**. *Etheostoma serriferum.* Genital papilla of 56.6 mm female taken on March 31. (CU 15614, N. C., Cape Fear dr. f. *Etheostoma f. fusiforme.* Genital papilla of 37.0 mm female taken on April 19. (CU 31847, N. Y., L. Yaphank). **g**. *Etheostoma c. collis.* Breeding tubercles on the anal fin of 34.4 mm male taken on March 22. (CU 11988, N. C., Yadkin-Pee Dee dr.) **h**. *Etheostoma gracile.* Breeding tubercles on the anal fin of 36.4 mm male taken on March 8. (TNHC 2575, Tex., Neches or Trinity dr.) **i**. *Etheostoma serriferum.* Breeding tubercles on the anal fin of 36.0 mm male taken on March 23. (CU 30122, S. C., Pee Dee dr.) **j**. *Etheostoma f. fusiforme.* Breeding tubercles on the anal fin of 36.0 mm male taken on April 19. (CU 31847, N. Y., Lake Yaphank) **k**. *Etheostoma gracile.* Breeding tubercles on the right pelvic fin of 37.2 mm male taken on April 15. (OAM 4192, Okla., Red dr.) **l**. *Etheostoma serriferum.* Breeding tubercles on the right pelvic fin of 43.9 mm male taken on March 23. (CU 30122, S. C., Pee Dee dr.) **m**. *Etheostoma gracile.* Breeding tubercles on the chin of 37.2 mm male taken on April 15. (OAM 4192, Okla., Red dr.) (Drawings by Rudolph J. Miller)

virtually all the specimens at the beginning of this study. In a few cases, where a large series was available from a single locality, some specimens were omitted. As the study progressed and certain characters were shown to be either constant or to vary within a narrow range with no significant geographical variation, counts were made only on part of the available specimens. Thus, fewer counts were made on pectoral and pelvic fin rays, branchiostegals, segmented caudal rays, and coronal pore development. The number of specimens examined for squamation is less than for meristic counts because only adult specimens could be used (Section IV, development).

Presentation of Results: Only characters that are virtually constant for the subgenus are given in the subgeneric diagnosis. Counts that show significant interspecific, but relatively little intraspecific variation are presented in the species comparisons tables (Tables 38-49). The two species of the subgenus *Villora* are also included in these tables for comparison. Characters showing geographic variation are presented in tables by species or species groups. In these tables populations are listed down the page in geographic order from north to south along the Atlantic Coast and from east to west along the Gulf Coast. The Mississippi River was divided into sections and subsections for the analysis of variation in *Etheostoma gracile.* A relatively large number of tables is presented so that the reader may see clearly why certain taxonomic decisions were made and, more importantly, so that the entire picture of variation in a particular species can be seen.

IV. Causes of Variation

In any variational study, it is necessary to examine the types of variation present and to consider the factors that may be involved in causing them. While all types of variation are interesting from an evolutionary point of view, it is desirable to eliminate non-genetic sources of variation for taxonomic purposes. The following sections consider variation due to asymmetry, sexual dimorphism, year classes and development.

Left and Right Sides: As has frequently been done by ichthyologists, Hubbs and Cannon (1935) in their revision of *Hololepis* sometimes made counts on the left side, sometimes on the right side, and sometimes on both sides. Nowhere do they mention why they feel this is justified or even the fact that they are doing it. However, by comparing the number of specimens they examined with the number of counts of median and bilateral structures, I found that for median counts, they gave counts for up to the number of specimens examined while for bilateral counts, they gave up to twice as many counts as specimens examined. I do not feel that this is proper for two reasons. Firstly, as stated clearly by Hubbs and Hubbs (1945, page 300): "Since many superficial as well as internal characters are often more or less different on the two sides, it is obviously a wise policy in systematic studies to count or measure given characters consistently on one side, or to study both sides." Secondly, even if there are no differences between sides, use of both sides can lead to misinterpretations unless the two sides are independent, which seems quite unlikely.

In order to interpret some of Hubbs and Cannon's conclusions, the possibility of left-right correlation was examined using collections of *Etheostoma f. fusiforme* made in two Long Island, N. Y. ponds. Pored and total lateral-line scales were counted on both sides of these fish and the left side was plotted against the right (Collette, 1960: Figs. 1-2). With regard to the pored lateral-line scales, the percent of individuals having the same count on each side was 23%, a difference of plus or minus one or two scales 30 and 34%, and a difference of greater than two scales 8 and 4 %. For the total lateral-line scales, the percentages were 19 % no difference, 24 and 25 % with a difference of plus or minus one or two scales, and 11 and 11 % with a difference greater than two scales between sides. This means that if both sides were counted and put into a single frequency distribution, the sample size would appear to be doubled with the probability that the range would not be increased nearly as much as if the sample size had really been doubled. In the case of three of Hubbs and Cannon's subspecies of *E. fusiforme* (*f. insulae* from Nantucket Island, *f. metaegadi* from Cape Cod, and *f. atraquae* from the Potomac River), each of which is based upon a single sample, the supposed subspecies appears more homogeneous and therefore more different from other populations of the species than is really the case. (The validity of these forms are discussed at length under geographic variation in *E. fusiforme.*)

Sexual Dimorphism and Year Class Variation: The variation due to sexual dimorphism and year class differences is frequently not considered in taxonomic studies. Inspection of the data showed that such variation could be significant only in the number of lateral-line scales. Table 1 shows comparisons between males and females in the number of pored and total lateral-line scales. Samples for single localities were used for all but one species. A sufficiently large sample of *E. saludae* was not available, so it was necessary to lump all the samples. This should not introduce error due to geographic variation because this species has a restricted range. No significant differences are apparent between the sexes in these characters (Table 1).

Little material of different year classes from single localities is available. Three year classes of *E. collis collis* from the Yadkin River and year classes of *E. fusiforme fusiforme* from two of the North Carolina Bay Lakes and a Long Island pond were employed in comparisons. The relative contributions of sexual dimorphism and year class variation were analyzed by the use of an R X 2 table with disproportionate subclass numbers (Snedecor, 1956). The preliminary analyses of variance show that there is no significant variation due to sexual dimorphism or year class variation for *E. c. collis* ($F = 1.782$ for pored lateral-line scales and 1.636 for total) or for *E. f. fusiforme* from Lake Yaphank ($F = 0.938$ and 1.027) and Jones Lake ($F = 0.931$ and 1.834). There are also no significant differences in pored lateral-line scales between different year classes in White Lake ($F = 2.219$). There is a significant difference at the 99% level ($F = 4.116$) in total lateral-line scales (Table 2). To determine whether this was due to sexual dimorphism or year class variation the analysis was completed. Table 2 presents the means for year classes and sexes, the preliminary analysis, and the completed analysis. The difference between sexes is significant at the 95% level. This is not deemed important taxonomically because the total number of lateral-line scales in *E. fusiforme* is not a significant character in analyzing geographic variation.

Development: The development of squa-

TABLE 1.
Variation between sexes in pored and total lateral-line scales in Etheostoma (Hololepis) species

Species	*serriferum*		*gracile*		*f. barratti*	
Locality	Pee Dee		Red		Savannah	
Pored Lateral-line Scales						
Sex	M	F	M	F	M	F
N	23	22	21	26	33	44
Range	29-38	28-39	17-25	15-23	20-37	18-34
x̄	32.8	34.9	20.0	18.3	26.3	25.0
Total Lateral-line Scales						
N	24	23	21	26	33	47
Range	50-60	48-62	45-53	42-50	51-62	50-63
x̄	54.1	54.4	48.1	46.9	56.2	54.8

Species	*fusiforme fusiforme*				*saludae*		*c. collis*	
Locality	Chowan		Chesapeake		All specimens		Yadkin	
Pored Lateral-line Scales								
Sex	M	F	M	F	M	F	M	F
N	31	54	39	21	26	56	17	14
Range	11-17	11-19	13-23	14-24	11-23	5-29	9-23	11-24
x̄	14.2	14.6	17.9	18.0	17.2	16.7	15.5	15.5
Total Lateral-line Scales								
N	31	56	39	23	29	54	17	13
Range	41-54	42-54	46-58	48-58	36-47	37-50	42-49	40-47
x̄	48.3	48.4	51.6	51.2	41.2	42.1	44.8	44.1

TABLE 2.
Variation of total lateral-line scales between year classes and sexes in Etheostoma f. fusiforme from White Lake, N. C.

Year	n_1	F_1	n_2	F_2	W	D	WD
	Male		Female				
1947	37	49.51	34	50.06	17.7183	0.55	9.7451
1958	11	48.64	37	49.38	8.4792	0.74	6.2746
1959	13	48.54	31	51.32	9.1591	2.78	25.4623
	61		102				41.4820

Preliminary Analysis of Variance of Original Data

Source of Variation	d.f.	Sum of Squares	Mean Square	F
Treatments	5	119.341	23.868	4.116**
Years	2	38.408	19.204	
Sexes	1	41.975	41.975	
Error	157	872.377	5.556	
Total	162	991.718		

Completed Analysis

Source of Variation	d.f.	Sum of Squares	Mean Square	F
Sexes	1	48.669	24.334	4.380*
Years	2	18.039	9.020	1.623 N.S.
Interaction	2	32.112	16.056	2.890 N.S.
Error	157	872.377	5.556	
Total	162	991.718		

(Analysis of variance with an R x 2 table and disproportionate subclass numbers, is significant at the 95% level, ** at the 99% level)*

mation, pored lateral-line scales, supratemporal canal, infraorbital canal, and coronal pore proved to be important in studying variation in *Hololepis*. This was especially true in understanding the extreme variation in number of pored lateral-line scales in *Etheostoma fusiforme fusiforme* from the North Carolina Bay Lakes and in *E. f. barratti* from Crystal Lake, Georgia. While specific information on development will be found under each species, I think it will be of value to briefly state the over-all pattern of development as I understand it.

Scales first appear on the caudal peduncle at the base of the caudal fin when the fish are about 15 mm SL. They then extend forward along the lateral line and spread dorsally and ventrally from the lateral line. The breast, belly, nape and head are the last regions to develop scales. Areas that have ctenoid scales in the adult develop scales faster than areas that have imbedded cycloid scales in the adult. The pattern of scale development is thus very similar to that given for *Micropterus dolomieui* (Everhart, 1949), *Pomoxis nigromaculatus* (Ward and Leonard, 1954), *Perca flavescens* (Pycha and Smith, 1955), etc.

Pored lateral-line scales do not develop until after the body squamation is virtually complete. Two lateral ridges form on each of the most anterior scales in the lateral line. These ridges grow higher and then meet over the middle of the scale to form the pore. The number of pored scales increases rapidly through 5-10 mm until the definitive number is reached by about 25 mm SL (Figs. 11, 12). Populations of some species (*e.g., E. fusiforme*) are neotenic in retaining a reduced number of pored scales.

The supratemporal canal is incomplete in juveniles of all species of *Hololepis,* and becomes complete in adults of most species by the two branches growing together leaving a median pore as a vestige of their former separation. An incomplete supratemporal canal may be characteristic of populations of a species, an entire species, or larger categories. The infraorbital canal grows posteriorly from its origin behind the nostril and anteriorly from its junction with the lateral canal. In some species the canal is interrupted while in others the two portions grow together to form a complete canal. The coronal pore grows posteriorly from the connection between the supraorbital canals. Specimens sufficiently small were not available for a study of the development of the other canals.

It is apparent that one of the features of evolution in the darters is the relative completeness of development of some of the characters mentioned above. Independently in many different lines of darters, various primitive characters have been repressed. Thus in the subgenus *Nothonotus, E. tippecanoe* stands out as the most advanced species being the smallest in size, having the belly squamation reduced, and having an incomplete lateral line. *Microperca,* the most advanced subgenus of *Etheostoma,* shows the effects of incomplete development in almost all characters: dorsal spines, anal rays, lateral-line scales, pored lateral-line scales, size, etc. The three species of *Microperca* can be ranked phylogenetically by the amount of development of various characters: the most primitive (*E. proeliare*) has 2-7 pored scales and the preopercle and opercle are scaly. The two more advanced species lack pored scales and scales in those areas. *E. fonticola,* the most advanced species, has the anal spines reduced to one. The same type of situation is shown in *Hololepis* in section VI, evolutionary relationships.

V. Subgeneric Diagnosis

Hololepis Agassiz, 1863

Hololepis Agassiz, in Putnam, 1863: 4 (type species *Boleosoma barratti* Holbrook, 1855, by subsequent designation of Jordan and Gilbert, 1877: 93).

Copelandellus Jordan and Evermann,1896: 1100 (type species *Poecilichthys quiescens* Jordan, 1884, by original designation).

Lateral line arched upward anteriorly and always incomplete; pored lateral-line scales 0 to 45; unpored 12 to 52; total 35 to 66; infraorbital canal complete or incomplete; interorbital pores 0, 1, or 2; supratemporal canal usually complete in adults; coronal pore usually present; preoperculomandibular pores 6 to 12, usually 9 or 10; vomer and palatine toothed; preopercle entire, partially serrate, or serrate, entire in most species; branchiostegal membranes narrowly conjoined; branchiostegal rays usually 6; opercle, preopercle, breast, nape, interorbital, and parietal regions naked to fully covered with imbedded cycloid to exposed ctenoid scales; belly covered at least in part with unspecialized cycloid or ctenoid scales; flesh opaque; body rather compressed and elongate to somewhat stocky; vertebrae 35 to 41; premaxillary frenum broad; first dorsal fin moderately high, with 7 to 13 spines which lack thickened, fleshy tips; anal spines 2 in most species, the first somewhat shorter and thicker than the second, the second equal to one-half to three-quarters of the length of the first anal ray; pelvic fins closely approximated, separated by one-half to three-quarters of the fin base; pectoral rays 10 to 15; second dorsal rays 8 to 17; anal rays 4 to 10; genital papilla of breeding female modified into an elongate and either cylindrical or somewhat flattened and bilobed tube; breeding tubercles present in breeding males on the anal fin rays and the undersides of the pelvic fin rays; maximum size of males equal to or less than that of females; habitat slow-moving waters such as lakes, swamps, and the backwaters of streams.

The subgenus *Hololepis* appears to be most closely related to the subgenus *Microperca,* and to some species of *Oligocephalus* (e.g., *Etheostoma exile*). The subgenus *Hololepis* is distinguished from *Microperca* by a more complete lateral line; more lateral-line scales; the presence of a premaxillary frenum; and the absence of the peculiar flap on the pelvic fins of breeding male *Microperca. Etheostoma* (*Hololepis*) *collis* and *saludae* are the species of *Hololepis* that resemble most the species of *Microperca* in body shape, coloration, male breeding pigmentation, reduced number of pored lateral-line scales, and having forms with both one and two anal spines. *Microperca,* while distinguishable as a subgenus, appears to be further along on the same phyletic line as *Hololepis.*

From the subgenus *Villora, Hololepis* is distinguished by a more highly arched and less complete lateral line; an elongate genital papilla in breeding females as contrasted with the low tube crowned with villi in *Villora;* presence of nuptial tubercles on the pelvic and anal fins of breeding males; lack of a strongly developed black humeral spot; maximum size of males less than that of females; and a habitat of slow, muddy waters (see also diagnosis of *Villora* in Collette and Yerger, 1962).

Etheostoma (*Oligocephalus*) *exile* shows a number of similarities to the species of the subgenus *Hololepis.* These include compressed body form; arching of the lateral line, incomplete development of the lateral line, and slow water habitat. On the other hand, male *E. exile* have much more brilliant breeding colors than do any of the species of the subgenus *Hololepis* and apparently lack breeding tubercles.

I think that the phyletic line that goes from *Hololepis* through *E. collis* and *E. saludae,* culminating in *Microperca,* probably has its origin somewhere in *Oligocephalus,* perhaps near *E. exile.*

VI. Evolutionary Relationships in *Hololepis*

The characters used to delimit subspecies, species, species groups, subgenera, and genera in the darters show many cases of convergent and divergent evolution as noted by Bailey (in Bailey, Winn and Smith, 1954, p. 141). Characters which can be considered as generalized in the darters include: serrate preopercle; conical genital papilla; deep compressed body; relatively large body size; gill membranes separate; most areas of the body covered with ctenoid scales; lateral line complete and not arched; ten preoperculomandibular pores; infraorbital canal complete with eight pores; supratemporal canal complete; interorbital pores present; two anal spines; 41-45 vertebrae; sexual dimorphism and sex recognition weakly developed; females equal to or larger in size than males; non-territorial; eggs scattered over wide area; no parental care; habitat of large streams (modified from Hubbs and Cannon, 1935; Bailey and Gosline, 1955; Winn, 1958; etc.).

Of the species in the subgenus *Hololepis,* *E. serriferum* is the most primitive in virtually all characters. It is the largest species of the subgenus, has a serrate preopercle, interorbital pores present, infraorbital canal complete (although pores reduced to six); and has a more complete lateral line, more dorsal spines and rays, more scales below the lateral line, more lateral-line scales, and a scalier nape, parietal, and interorbital than the other *Hololepis.* Its only real specialization is the bilobed genital papilla of the breeding female although it also shows a reduction in the number of preoperculomandibular pores (to nine) and infraorbital pores.

Etheostoma gracile and *E. zoniferum* share a number of characters which indicate that they are closely related. These include ten preoperculomandibular pores; interorbital pores absent; naked breast, parietal, and interorbital; green vertical bars on the sides in life; rows of red spots in the dorsal fins of breeding males; the presence of accessory breeding tubercles on the chins of breeding males; and territorial behavior. There is a combination of primitive characters (ten POM pores) with specialized ones (INT absent, breast and nape naked, territorial behavior). Most of the characters that differentiate *E. zoniferum* from *E. gracile* indicate that it is an offshoot of *E. gracile.* This is especially true of the most important differentiating character which is the incomplete infraorbital canal in *zoniferum.* *E. zoniferum* also shows a reduction in the number of anal rays, scales above and below the lateral line, pored lateral-line scales, squamation of the breast and preopercle, and usually has the supratemporal canal incomplete. Only in the more extensive opercular squamation does *zoniferum* appear less specialized than *gracile.* Apparently, *zoniferum* differentiated from *gracile* after isolation in the Alabama and Tombigbee Rivers, east of the range of the widespread *gracile.*

Etheostoma fusiforme is the most widespread species of *Hololepis.* It shows a few more advanced characters over the *E. gracile* group such as having the preoperculomandibular pores reduced to nine, and the infraorbital canal interrupted with 1 + 3 or 2 + 3 pores. In several other characters it is slightly more primitive than the *E. gracile* group. It has slightly more lateral-line scales and vertebrae; scalier interorbital, parietal and breast; the occurrence of individuals with partially serrate preopercles; and territoriality is absent. In all respects but one, *E. fusiforme fusiforme* is clearly a specialized offshoot of *E. f. barratti.* It has fewer pored lateral-line scales, a lower percentage of individuals with partially serrate preopercles, and a reduced squamation, especially in the interorbital and parietal regions. *E. f. barratti,* however, has a higher percentage of individuals with 1 + 3 infraorbital pores while *f. fusiforme* usually has 2 + 3. Some of these characters show clinal variations. The extent of squamation and the percentage of individuals with partially serrate preopercles increases toward the south. Other characters have a much more complex variation as discussed at length under geographic variation in *E. fusiforme.*

The *Etheostoma collis* group is the most specialized in the subgenus. Here the pored lateral-line scales are further reduced in number; the supratemporal canal is frequently incomplete; there are fewer vertebrae, fewer lateral-line scales; and one anal spine is frequently absent. The three forms of this group have deserted the lowland habitat characteristic of the other *Hololepis* for backwaters of Atlantic Piedmont streams. *E. saludae* is clearly the most primitive of the three since it retains the interorbital pores and only about a third of the specimens have the anal spines reduced to one. *E. saludae* and *E. collis lepidinion* are scalier than *E. c. collis,* especially in the nape and breast regions. *Etheostoma c. collis* is the most specialized *Hololepis.* It has one anal spine; no interorbital pores; infraorbital 1 + 3; breast, nape, parietal, and interorbital naked. There is still some doubt in my mind as to the taxonomic categories to use for the *E. collis* group. There may be one species with three subspecies, three species, or two species with the Roanoke-Neuse River form a subspecies of *E. collis.* In two respects, *E. saludae* is intermediate between *E. c. collis* and *E. c. lepidinion:* number of infraorbital pores and squamation of the nape. On the basis of one anal spine and the absence of interorbital pores, I have decided to consider the Roanoke-Neuse and Pee Dee-Catawba forms as conspecific, thus making *lepidinion* a subspecies of *E. collis.*

Thus it is apparent that the species of *Hololepis* form four species groups, and within each of these groups there are specialized and generalized characters so that these four lines are offshoots of some more primitive stock. The intra-group relationships are clearer: *E. serriferum* is the most primitive *Hololepis; E. zoniferum* is a specialized derivative of *E. gracile; E. fusiforme fusiforme* has undergone a reduction in squamation and other characters in developing from *E. f. barratti; E. saludae* has given rise to *E. collis lepidinion* which has subsequently differentiated into *E. collis collis,* probably the most advanced of the *Hololepis.*

VIII. Species Accounts

Etheostoma serriferum (Hubbs and Cannon)

Boleichthys fusiformis—Driver, 1942:285 (range in key partly *serriferum*).

Hololepis serrifer—Hubbs and Cannon, 1935:31-36, pl. I, (original description); Fowler, 1945:40, 139 (N.C.), 196 (S.C.); Freeman, 1952a:37 (Congaree and Wateree r., Richland Co., S.C.); Bailey and Frey, 1951:191, 203 (Ellis L., N.C.); Anderson and Freeman, 1957: 106 (Congaree R., S.C.); Randall, 1958:342 (Catawba-Wateree R., S.C.).

Etheostoma serriferum—Bailey and Gosline, 1955:20, 44 (number of vertebrae); Eddy, 1957:219-220; Moore, 1957:197; Collette, 1961:2051.

Misidentifications—*Etheostoma fusiforme barratti* as *Hololepis serrifer,* Fowler, 1945: 252 (Savannah R., Ga.).

Types—Holotype, UMMZ 107053; 52 mm male; N.C., Wake Co., Buffalo Cr.;

VII. Key to the Species and Subspecies of the Subgenus *HOLOLEPIS*

1. Infraorbital canal complete 2
   Infraorbital canal interrupted 3
2. Preopercle strongly serrate; infraorbital pores 6 .... *E. serriferum*
   Preopercle entire; infraorbital pores 8 .... *E. gracile*
3. Preoperculomandibular pores 10; interorbital pores absent; anal spines 2 .... *E. zoniferum*
   Preoperculomandibular pores 9; interorbital pores 0, 1, or 2; anal spines 1 or 2 4
4. Interorbital pores absent; breast squamation 100%; interorbital with 0-37 scales .... *E. fusiforme* 5
   Interorbital pores 0, 1, or 2; breast squamation 0-80%; interorbital naked 6
5. Interorbital with 0-12 scales, usually 0-4; infraorbital pores usually (80%) 2+3 .... *E. fusiforme fusiforme*
   Interorbital with 1-36 scales, usually 5-20; infraorbital pores usually (70%) 1+3 .... *E. fusiforme barratti*
6. Anal spines 1 or 2; interorbital pores present .... *E. saludae*
   Anal spines 1; interorbital pores usually absent .... *E. collis* 7
7. Breast squamation 10-80%; nape squamation 70-100%; infraorbital pores usually 1+4 .... *E. collis* LEPIDINION
   Breast naked; nape squamation 0-40%; infraorbital pores usually 1+3 *E. collis collis*

Wendell; Brimley and Harris; Nov. 19, 1925. Paratypes: all other specimens examined by Hubbs and Cannon (1935:31-33).

Diagnosis—Differs from the other species of *Hololepis* by having a completely serrate preopercle. The female has a flattened bilobed genital papilla. There are two intense black spots at the base of the caudal with a pair of fainter spots above and below them. *E. serriferum* has more second dorsal rays (mode: 14, x̄: 13.6) than other species of *Hololepis* (modes: 11 or 12, x̄: 10.6-12.4) and more scales below the lateral line (mode: 12, x̄: 11.8) than other species of *Hololepis* (mode: 8 or 9, x̄: 8.1-8.9). Both interorbital pores are usually present as in *E. saludae.* Parietal region completely covered with scales. Infraorbital canal complete as in *E. zoniferum* but usually with only six pores instead of eight. Maximum size: males—52.1 mm (CU 29981, Roanoke R.) and females—57.4 (CU 35059, Santee R.).

Coloration—The first dorsal fin of the female is clear or has small melanophores concentrated on or near the spines and between their bases. The second dorsal fin is indistinctly barred and may have pigment at the base of the membranes. The anal either lacks pigment or has melanophores concentrated on the rays in groups, which give a barred appearance. Both pectoral and pelvic fins are clear or have melanophores outlining the rays. The caudal is barred; pigment is also present on the proximal portion of the membranes in some specimens. The belly and breast are usually immaculate, but sometimes have a few scattered large melanophores. The cheek has a few large melanophores. All four orbital bars are present but not especially prominent; the supraorbital extends onto the eye. The pored portion of the lateral line appears as a narrow light line. A pair of intense black spots occur above and below the midcaudal base. Faint spots are found at both the dorsal and ventral bases of the caudal in most specimens. Black lateral blotches are usually fused into a band below the lateral line. Some specimens have uniformly tan sides without lateral blotches. Dorsal saddles and blotches are absent. The genital papilla is usually immaculate but may have some pigment posteriorly. Figure 2 shows a female.

The cheek and first dorsal fin of the nonbreeding male are colored like those of the female but have a few more melanophores. The anal fin has scattered melanophores on the membranes and rays; there are fewer on the rays. The belly and breast vary from

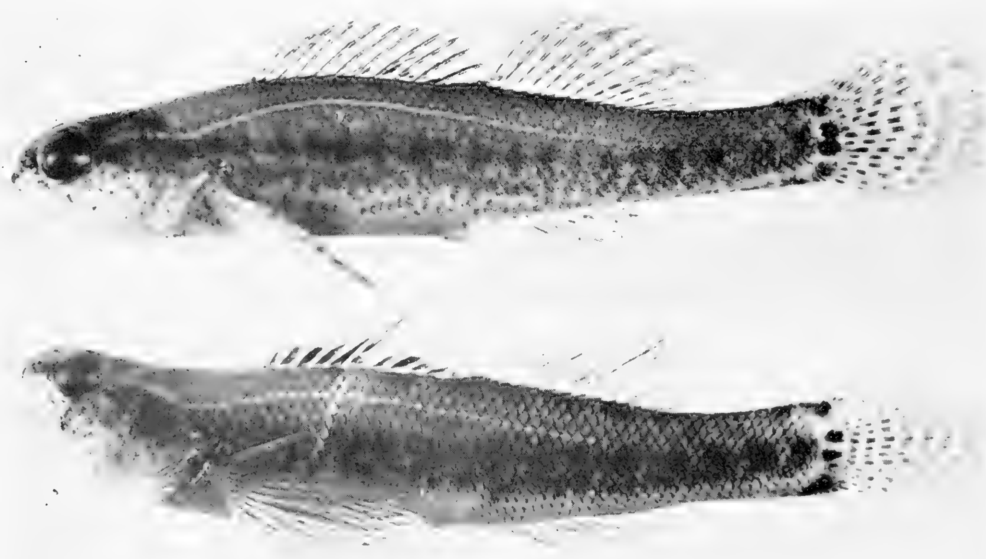

Figure 2. Breeding patterns of *Etheostoma serriferum.* (upper) female; CU 29989; 41.0 mm; S.C., Chesterfield Co., Pee Dee dr.; Mar. 29, 1956. (lower) male; CU 29981; 56.0 mm; N.C., Martin Co., Roanoke dr.; Mar. 24, 1956. (Photographs by Douglass M. Payne)

immaculate to an overall sprinkling of small melanophores. The orbital bars are more prominent in some non-breeding males than in females. The narrow light line along the pored portion of the lateral line appears more prominent in the male because of the darker sides. Melanophores usually form a band that encircles the base of the genital papilla.

In the breeding male the pectoral and caudal fins, basi-caudal spots, sides, dorsal surface, and the genital papilla are similar to the non-breeding male; other areas are darker. The basal portion of the first dorsal fin is almost solid black. A narrow clear band borders the membranes between the last spines. The membranes of the second dorsal fin are covered with large melanaphores which do not form rectangular blotches as they do in *E. saludae* and *collis*. The anal and pelvic fins and the belly and breast are uniformly covered with small melanophores. The suborbital bars are less prominent than in the female because the cheeks are darker. The light line along the pored portion of the lateral line is interrupted by some pigment on the distal parts of the scales. The breeding pattern of a male is shown in Figure 2. Hubbs and Cannon (1935:36) used Jordan's (1890:120) description for life colors. The description mentions red on various areas of the body which does not at all agree with my observations.

Breeding Tubercles—Breeding tubercles are present on the anal rays and the lower surface of the pelvic rays. In a 40.2 mm male taken on March 24-25 (UG 152) from the Ogeechee River, breeding tubercles occur on the distal one third of anal rays one through four, the distal quarter of pelvic rays one through three, and the distal eighth of pelvic ray number four. In a male taken on March 30 (CU 15636, #2) from the Pee Dee River, tubercles are present on the distal two thirds of the anal rays, mostly on the main branches, and on the distal one third of the pelvic rays, mostly on the smaller branches. At maximum development the tubercles are moderately large. Figure 1l shows their distribution on the pelvic fin of a 43.9 mm male taken on March 23 (CU 30122) and Figure 1i shows the tubercles on the anal fin of a 36.0 mm male from the same collection.

Genital Papilla—The other species of the subgenus *Hololepis* have a moderately elongate tube with a sharp or blunt end, but in *E. serriferum* the females have the tip of the tube flattened and bilobed. The long axis of the opening of the papilla is perpendicular to the papilla, while in other species of *Hololepis* the opening is parallel to the papilla. Figure 1d shows the papilla of a female taken on March 24 from the Chowan River (CU 29976). Figure 1e shows the most extreme development of a papilla noted in *E. serriferum*: a female (56.6 mm) from the Cape Fear River taken on March 31 (CU 15614).

Habitat—*E. serriferum* prefers slightly more open, better oxygenated, and less sluggish waters than most species of *Hololepis*. In collections containing both *E. fusiforme* and *E. serriferum*, the former species is limited to the backwaters of streams, while the latter is usually found in clumps of weeds in the middle of the stream. The larger, less compressed body of *E. serriferum* perhaps permits this species to resist the force of the current more efficiently than *E. fusiforme*. However, both species have been taken together in some lakes (*e.g.*, Ellis Lake, N. C.).

At 16 localities where I collected *E. serriferum*, the current was slow (5), slow to moderate (3), and moderate (8); the bottom composed partly of sand in 13 collections, mud and/or silt (8), detritus (4), and clay (3); the vegetation ranged from sparse emergents along the shore to dense stands of aquatic plants (in Ellis Lake); the water was usually clear and stained brown; the width of the streams varied from 5 to 30 feet (also taken in two lakes); and the shore was wooded or open.

Species Associates—Examination of my field notes for 16 North Carolina collections which contained *E. serriferum* shows the following to be frequent associates (number of collections present with *serriferum* given in parentheses): *Aphredoderus sayanus* (11); *Etheostoma f. fusiforme* or *f. barratti* (8); *Esox a. americanus* (8); *Gambusia affinis holbrooki* (7); *Chaenobryttus gulosus* (7); *Enneacanthus gloriosus* (6); *Notemigonus crysoleucas* (6); and *Lepomis macrochirus* (6). All the associated species can tolerate the sluggish, acid, brown-stained waters characteristic of the Atlantic Coastal Plain.

Habits—Specimens kept in aquaria have acted much like *E. fusiforme* (*q.v.*). They rested upon the bottom most of the time and darted forward after food such as white worms, tubificid worms, or pieces of earthworms. Occasionally they swam up into the plants and rested there. As with *E. fusiforme,* there was never any indication of any territoriality.

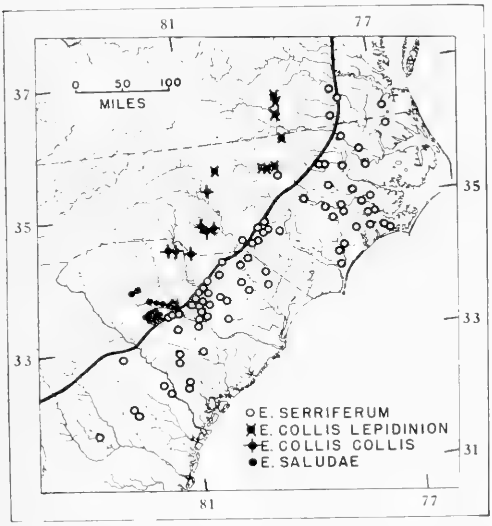

Figure 3. The distribution of *Etheostoma serriferum, E. collis,* and *E. saludae* in relation to the Fall Line. (Based upon specimens examined.

Distribution—Found along the Atlantic Coastal Plain, usually below the Fall Line, from the Dismal Swamp of southeastern Virginia to the Altamaha River of Georgia. This extends the range given by Hubbs and Cannon (1935) south by three river systems. It has been taken above the Fall Line in Mud Creek, a tributary of the Cape Fear River, at Durham, N. C. However, Mud Creek is like a typical sluggish Coastal Plain stream. Another typical Coastal Plain species, *Aphredoderus sayanus,* was also taken here. Figure 3 shows the distribution of *E. serriferum* collections examined.

This distribution coincides with that of *Chologaster cornutus.* Woods and Inger (1957:249-250) commented that there appeared to be no reason why *Chologaster* should not range into the Okefenokee Swamp or west into Alabama. Several species with similar habitat requirements, such as *Gambusia affinis, Aphredoderus sayanus,* and *Elassoma* do range westward on the Gulf side of the former Mississippi Embayment to beyond the Mississippi River. (They also erroneously listed *Umbra pygmaea* in this category. Briggs (1958) and Miller (1958:196) gave the southern distribution as northeastern Florida.) Woods and Inger (1957) concluded that *Chologaster* did once extend west as far as the Mississippi and that during some period of drought during late or even post-glacial times the habitat dried up. The other species named have apparently been able to make their way back into this area but *Chologaster* has not done so. Whether this situation is true for *E. serriferum* is even more problematical than for *Chologaster.*

Geographic Variation—Tables 3-9 give the frequency distribution of the characters examined by river systems. Characters which showed no appreciable variation are presented only in the species comparisons tables. These include: number of anal spines (two except for one Neuse specimen with one); supratemporal canal complete (except one Neuse and two Santee specimens); infraorbital canal complete, pelvic elements I, 5 (except for one Santee specimen with I, 6); opercular and preopercular squamation 100-X-T; coronal pore present; pectoral rays 11-13, usually 12; and branchiostegals 5-7, usually 6.

There seem to be two poorly defined groups based on the number of pored lateral-line scales (Table 3). Populations in the five northern drainages, Nansemond through Neuse-Ellis Lake, have fewer pored scales ($\bar{x}$:30.00-32.39) than the southern eight populations; Cape Fear through the Altamaha ($\bar{x}$:over 33.75). The total lateral-line scales (Table 4) show a similar trend; the northern group has slightly fewer scales than the southern group.

The mode of dorsal spines is eleven except for the Edisto population, which has a mode of ten (Table 5). Seven populations have modal values of 14 rays in the second dorsal fin (Table 5); the Ellis-Neuse population has a mode of 13, as do also the small samples from the Tar, Combahee, Savannah, Ogeechee, and Altamaha. The modal number of anal rays is seven, except for small samples from the Tar, Savannah, Ogeechee, and Altamaha, where the modes are at six (Table 6).

TABLE 3.
Number of pored lateral-line scales in Etheostoma serriferum

Drainage	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	N	x̄
Nansemond									1	1	–	1	1														4	30.00
Chowan							1	1	2	1	2	4	1	1	3	3	–	2	1	1							23	32.39
Roanoke								1	1	–	3	1	4	2	1	2	2	1									18	32.39
Tar				1	–	–	–	1	–	–	1	–	–	1	1	2											7	31.00
Neuse-Ellis L.	1	–	1	–	1	1	1	–	2	5	8	8	1	6	6	6	5	5	1								58	31.95
Cape Fear									1	1	2	2	2	7	5	8	3	2	1	–	2	–	–	1			37	34.24
Pee Dee			1	–	–	–	–	1	3	6	5	7	6	10	14	11	11	7	10	2	6	1	1	–	–	1	103	34.35
Santee						1	1	1	4	5	3	5	3	6	7	6	6	6	10	2	4	2	1	1	–	1	75	34.53
Edisto													1	–	2	–	1	3	1								8	35.63
Combahee											1	–	–	–	–	2	3										6	34.67
Savannah										1	–	–	1	–	1	–	–	–	–	–	1						4	33.75
Ogeechee													1	1	1	–	1										4	33.75
Altamaha																	1										1	

TABLE 4.
Number of total lateral-line scales in Etheostoma serriferum

Drainage	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	N	x̄
Nansemond					1	–	–	1	1	–	1													4	51.25
Chowan					1	–	2	6	2	5	2	4	3	–	1									26	52.96
Roanoke					1	–	2	3	3	1	1	2	2	3										18	53.17
Tar						1	3	1	2															7	50.57
Neuse-Ellis L.				2	3	5	8	10	10	9	7	–	3	1	–	1	1							60	51.87
Cape Fear	1	–	–	–	1	2	1	6	3	4	3	8	4	4	3	–	1							41	53.71
Pee Dee				1	1	2	6	3	14	14	13	20	9	7	11	1	2	–	1					105	54.29
Santee							3	1	3	5	10	8	12	6	13	4	8	1	2	2	1	–	1	80	56.59
Edisto							1	–	–	3	–	1	3	–	–	1								9	54.56
Combahee								1	1	–	1	2	–	1										6	54.00
Savannah						1	–	–	–	1	1	–	–	1										4	53.25
Ogeechee							1	–	1	–	2	1												5	53.00
Altamaha														1										1	

TABLE 5.

Number of first dorsal spines and second dorsal rays in Etheostoma serriferum

Drainage	Dorsal Spines 9	10	11	12	13	x̄	Dorsal rays 11	12	13	14	15	16	17	x̄
Nansemond			3	1		11.25			1	2	1			14.00
Chowan		2	18	6		11.15		1	9	15	1			13.62
Roanoke		2	14	2		11.00			5	12	1			13.78
Tar		2	5			10.71		3	4					12.57
Neuse-Ellis L.	1	9	38	10		10.98	1	10	33	14				13.03
Cape Fear		4	32	6		11.05		2	14	21	4	1		13.71
Pee Dee		7	56	41	1	11.34		6	41	48	10			13.59
Santee	1	13	50	18		11.04			16	46	18	1	1	14.09
Edisto	1	8				9.89			3	4	2			13.89
Combahee			5	1		11.17			4	2				13.33
Savannah			3	1		11.25			3	1				13.25
Ogeechee		1	3	1		11.00			3	2				13.40
Altamaha				1					1					

TABLE 6.

Number of anal rays and of scale rows above and below the lateral line in Etheostoma serriferum

Drainage	Anal rays 5	6	7	8	9	x̄	Above 3	4	5	Below lateral line 10	11	12	13	14	15	x̄
Nansemond		1	1	2		7.25		4		1	2	1				11.00
Chowan	3	9	13	1		6.46	2	24		3	9	10	4			11.58
Roanoke		4	9	5		7.06	1	15	2	1	5	9	3			11.78
Tar		4	3			6.43		4	3	2	—	3	2			11.71
Neuse-Ellis L.	1	22	28	9		6.75	4	38	8	2	22	21	3			11.52
Cape Fear		6	17	17	2	7.36	4	33	4	7	14	14	6	1		11.52
Pee Dee		9	66	29	1	7.21	5	92	8	8	37	44	16			11.65
Santee		12	49	20	1	7.12	1	61	20	1	18	32	28	2	1	12.18
Edisto			6	2	1	7.44		7	2		3	1	5			12.22
Combahee		3	3			6.50		2	4			1	4	1		13.00
Savannah	1	3				5.75		2	2		1	2	1			12.00
Ogeechee	1	3	1			6.00		3	2			1	3			12.75
Altamaha		1						1				1				

The mode of the number of scale rows above the lateral line is four (range three to five) (Table 6); below the lateral line 12 in most populations (range 10-15) (Table 6). The modal number of infraorbital pores is six, of preoperculomandibular pores nine, and of interorbital pores two (Table 7).

The nape, breast and parietal are completely covered with scales with modes of X-T, I-C, and I/PX-C/T, respectively (Table 8). The interorbital squamation in *E. serriferum* shows the greatest geographic variation (Table 9). The northern five drainages (Nansemond, Chowan, Roanoke, Tar, and Ellis-Neuse) have fewer scales in the region ($\bar{x}$:9.50-13.81) than the eight southern drainages ($\bar{x}$:17.00-23.25). This reduced squamation is correlated with the reduced number of pored and total lateral-line scales in the same drainages. This same trend is shown in *E. fusiforme,* except that the geographic break between the subspecies of *E. fusiforme* comes between the Cape Fear and Pee Dee, rather than between the Neuse and Cape Fear. The break between subspecies of *E. collis* also occurs in this region, although I am not yet certain whether it is between the Roanoke and Cape Fear or between the Cape Fear and Pee Dee; the latter seems more likely.

This roughly clinal north-south difference, coupled with the lesser differences in pored and total lateral-line scales, indicates differentiation at the racial level.

Specimens Examined—Complete locality data are listed for the Nansemond drainage (northern limit of range), the Tar drainage (new record), and for the Savannah, Ogeechee, and Altamaha drainages (southern limit of range and new locality records). Other collections are listed by drainage, state,

TABLE 7.
Number of pores in infraorbital (INF), *preoperculomandibular* (POM), *and interorbital* (INT) *canals in Etheostoma serriferum*

	INF					POM				INT		
Drainage	4	5	6	7	8	7	8	9	10	0	1	2
Nansemond			3	1				4				4
Chowan		1	21	4			2	24		1	6	19
Roanoke			15	3				18			1	17
Tar			6					5	2	1	–	6
Neuse-Ellis L.			40	10	1		1	47	2	3	9	37
Cape Fear	1	2	35	4			5	35		1	7	32
Pee Dee		2	87	15	1	2	8	93		15	20	70
Santee		1	63	14	3		8	71	2	12	19	50
Edisto			7	2				9			2	7
Combahee			4	2				6			1	5
Savannah			3	1				4			2	2
Ogeechee			5					5				5
Altamaha			1					1				1

TABLE 8.
Squamation of nape, breast, and parietal regions in Etheostoma serriferum

	Nape				Breast			Parietal				
Drainage	PX-T	PX/X-T	X-T	I-C	I/PX-C/T	PX-C/T	PX X-T	I-C	I/PX-C/T	PX-T	PX X-T	X-T
Nansemond	1	–	3	4					4			
Chowan			10	13	2				12	–	3	
Roanoke			12	12	3				8	4	3	
Tar	2	4	–	6					6			
Neuse-Ellis L.		4	12	18	7				19	5	1	
Cape Fear		1	9	13	7	–	1		10	3	6	3
Pee Dee			12	12	8	2		1	11	3	6	1
Santee		1	10	14	6	1		1	8	6	3	3
Edisto			9	4	5				1	–	1	7
Combahee		3	3	4	2					1	2	3
Savannah			3	3					3	1		
Ogeechee			4	4						4		
Altamaha			1		1						1	

TABLE 9.

Number of interorbital scales in Etheostoma serriferum

Drainage	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	x̄
Nansemond	1	–	–	–	1	–	–	–	–	–	–	–	–	1																	11.67
Chowan			1	–	2	1	1	2	2	2	2	–	1	–	1																13.67
Roanoke	1	–	3	1	2	–	–	1	1	2	2	1	–	–	–	–	1														12.47
Tar	1	1	1	1	–	–	1	–	–	1																					9.50
Neuse-Ellis L.		1	2	3	3	–	–	4	3	1	2	1	3	–	–	1	1	–	1												13.81
Cape Fear							1	2	1	–	2	1	4	2		2	1	3	–	–	1										18.50
Pee Dee										6	1	–	3	1	2	2	2	1	–	1	1										18.95
Santee				1	–	–	1	1	1	1	2	2	2	1	–	–	2	–	1	–	–	1	1	–	1	1	1				20.00
Edisto								2	–	2	–	–	–	1	–	–	1	1	1	–	1										18.89
Combahee								1	–	–	–	2	–	–		–	–	1	–	–	–	–		1	–	–	–	–	–	1	22.33
Savannah													1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	1			23.25
Ogeechee									1	1	–	–	–	–	–	–	1														17.00
Altamaha													1																		

county, and museum number. Complete data on almost all specimens examined are in Collette (1960). A total of 447 specimens from 112 collections was examined.

Nansemond Dr., Va.—Nansemond Co.: CU 9920 (4, 34-41); trib. of Nansemond R., 2 mi. N of Suffolk on US 460· March 29, 1941.

Chowan Dr., 26 specimens, Va.—Dinwiddie Co.: CU 11781. Greensville Co.: CU 20623, 29976. Sussex Co.: CU 16881. N.C.—Gates Co.: CU 9892, 30141.

Roanoke Dr., 18 specimens, N.C.—Bertie Co.: CU 29979. Martin Co.: CU 25241, 29981. Northhampton Co.: CU 17017.

Tar Dr., N.C.—Edgecomb Co.: USNM 179732 (1,26); Fishing Cr., Tarboro; Sept. 19, 1959. Nash Co.: DU uncat. (4, 42-46); Little Sapony Cr., 3.6 mi. W of Nashville on US 64; June 1, 1950. DU uncat. (2, 43-46); Little Sapony Cr., 2.3 mi. S of Nashville on NC 58; June 1, 1950.

Neuse-Ellis Lake Dr., 94 specimens, N.C.—Carteret Co.: DU uncat. Craven Co.: USNM 53041; CU 9878, 9814, 16821, 29982, 29984; out of UMMZ 161986; DU uncat. Johnston Co.: USNM 179730. Lenoir Co.: CU 9723, 9748. Onslow Co.: CU 9752, 30573. Pitt Co.: DU uncat. Wayne Co.: CU 33105. Wilson Co.: CU 10636. Wake Co.: UMMZ 107053 (1, 52); Buffalo Cr., Wendell; Nov. 19, 1925; holotype of *Hololepis serrifer*

Cape Fear Dr., 60 specimens, N.C.—Bladen Co.: CU 34529. Brunswick Co.: CU 4090. Cumberland Co: CU 14100, 30134. Duplin Co.: CU 30557. Durham Co.: DU uncat.; CU 34517. Hoke Co.: CU 15614, 25948, 26109, 33102. Moore Co.: CU 25262, 32170; USNM 93193. New Hanover Co.: USNM 93132, 93133, 86163 paratypes of *Hololepis serrifer*. USNM 170975, 94348. Pender Co.: CU 29986, 30052, 33103, 33104.

Pee Dee Dr., 134 specimens, N.C.—Moore Co.: DU uncat.; CU 11147, 32706, 35134. Richmond Co.: CU 19571. Richmond-Scotland cos.: UG 460. Scotland Co.: CU 25965. S.C.—Chesterfield Co.: CU 15636, 29989, 29990. Clarendon Co.: CU 15202, 15359. Darlington Co.: CU 15721, 28206, 30122. Dillon Co.: CU 15867. Florence Co.: CU 19188. Lee Co.: CU 28220. Marion Co.: CU 25225. Marlboro Co.: ANSP 61027-9. Sumter-Lee cos.: CU 15225.

Santee Dr., 80 specimens, S.C.—Calhoun Co.: CU 35051. Kershaw Co.: CU 35042, 35061, 35056, 35059, 35060, 35064, 35055, 35047. Lexington Co.: CU 35058, 35050, 35063. Richland Co.: CU 35049, 35054, 35046, 35057, 35043, 35053, 35044, 35062, 35052, 35048, 35045.

Edisto Dr., 9 specimens, S.C.—Aiken-Lexington cos.: CU 35041. Bamburg Co.: CU 35065, 35066.

Combahee Dr., 6 specimens, S.C.—Allendale Co.: CU 15322. Bamburg Co.: CU 19194. Hampton Co.: CU 32672. Jasper Co.: CU 32661.

Savannah Dr., Ga.—Richmond Co.: CU 30321 (1,39); Boggy Gut Cr., trib. of Brier Cr., 22.5 mi. SW of Augusta on US 1; March 24, 1950. Screven Co.: CU 30621 (2, 45); trib. of Savannah R., 12.9 mi. SW of Savannah R., Dec. 28, 1949. UG 240A (1, 50); Blue Sp., Black Cr., 6 mi. NE of Newington; Jan. 31, 1952.

Ogeechee Dr., Ga.—Candler Co.: UG 152 (2, 40-44); March 24-25, 1950 and UG 152A (1, 30); March 24-25, 1950 and out of UG 152B (1, 29); Aug. 8, 1958; Canoochee R., 4 mi. W of Metter on Ga 46. Emmanuel Co.: UG 554 (1, 44); Canoochee R., 8 mi. S of Twin City; Aug. 8, 1958.

Altamaha Dr., Ga.—Telfair Co.: CU 17257 (1, 45); Little Ocmulgee R., 1.2 mi. N of McRae on US 319; March 25, 1950.

Etheostoma gracile (Girard)

Boleosoma gracile—Girard, 1859:103 (original description).

Poecilichthys butlerianus—Hay, 1882:61-62 (original description).

Poecilichthys palustris—Gilbert, 1884:209-210 (original description).

Boleichthys fusiformis—Forbes, 1907:281; 287, 291-292, map XV (in part) (ecology, Ill.); Forbes, 1909:390, 401, 403, 417, 421, 425, 432, tables I-VI, map XCVIII, pl. XXV (in part) (ecology and distribution, Ill.); Forbes and Richardson, 1909, 1920:315, map 98 (in part) (description and distribution, Ill.); Forbes, 1914:17, map 48 (in part), fig. 30 (distribution in Ill., not given by Hubbs and Cannon, 1935, in their synonymy); Thompson and Hunt, 1930:33, 45 (ecology, Champaign Co., Ill.); Driver, 1942:285 (in key, in part).

Hololepis fusiformis—Luce, 1933:120 (Ill.); O'Donnell, 1935:489-490 (in part) (Ill.).

Hololepis gracilis—Hubbs and Cannon, 1935; Baker, 1939a:36-37 and 1939b:45 (Reelfoot Lake, Tenn.); Kuhne, 1939:93, fig. 63; Lamb, 1941:45 (San Jacinto R., Tex.); Fowler, 1945:40 (Ala., Pearl, Trinity, Nueces r.), 369-370 (La.); Gerking, 1945:16, 95 (distribution in Ind.); Hubbs, 1946:39 (Okla.); Moore and Poole, 1948:37 (McCurtain Co., Okla.); Baughman, 1950:247 (Tex.); Hall, 1951:17 (Lake Murray, Carter and Love cos., Okla.); Cross and Moore, 1952:409 (Poteau River in Okla. and Ark.).

Boleichthys gracilis—Blatchley, 1938:98-99 (Ind.); Driver, 1950:298 (in key).

Boleichthys fusiformis gracilis—Schrenkeisen, 1938:235.

Etheostoma gracile—Hubbs, 1952:486 (Tex.); Moore, 1952:11 (Okla.); Jurgens and Hubbs, 1953:4 (Tex.); Knapp, 1953:126, 128 (Tex.), fig. 166; Cross, 1954:478-479 (Kan.); Bailey and Gosline, 1955:20, 44 (number of vertebrae); Gerking, 1955:84 (Ind.); Gunning and Lewis, 1955:557 (Ill.); Linder, 1955a:28-29 (in aquaria); Linder, 1955b:176 (Blue R., Okla.); Eddy, 1957:219, fig. 545; Hubbs, 1957a:9 (Tex.); Hubbs, 1957b:93, 98 (distribution in Tex.); Moore, 1957:197-198; Bridges, 1958:3, 9 (poisoned in Ill. farm ponds); Hancock and Sublette, 1958:49 (La.); Hubbs, 1958:11 (Tex.); Blair, 1959 (Okla., distribution, ecology); Boudreaux, Strawn, and Callas, 1959:8, 10 (poisoned in Tex.): Cook, 1959:35, 38, 200, 207-208 (Miss.); Hubbs, 1959:50, 52 (artificial hybridization with *Percina sciera* and *Etheostoma proeliare*); Riggs and Bonn, 1959:167 (Lake Texoma, Okla.); Collette, 1961:2051.

Types—Hubbs and Cannon (1935) selected USNM 1328, 36 mm SL, as lectotype of *Boleosoma gracile;* from Rio Seco, near Fort Inge, Texas, collected by Dr. Kennerly. They listed two extant paratypes: MCZ 113, from the lectotype locality, and USNM 1329, from Leona River, near Fort Inge, Texas, also collected by Dr. Kennerly. The holotype of *Poecilichthys butlerianus* is USNM 32224, 43 mm SL, from a pool along the Big Black River, near Vaughan's Station, Yazoo Co., Mississippi. Hubbs and Cannon selected USNM 34983, 30 mm SL, from Switz City Swamp, Indiana, as lectotype of *Poecilichthys palustris.*

Diagnosis—Similar to *E. zoniferum* in usually having: ten preoperculomandibular pores; interorbital pores absent; naked breast and nape; and green vertical bars on the sides in life. Differs from *E. zoniferum* primarily in having the infraorbital canal complete with eight pores. Also differs in having more anal rays ($\bar{x}$:6.7), more scales above the lateral line (mode:4, $\bar{x}$:3.7) and below the lateral line (mode:9, $\bar{x}$:8.9). Maximum size of males 43.4 mm SL and females 46.4 mm (TNHC 578, Neches River, Tex.).

Coloration—In the non-breeding female, groups of medium sized melanophores are present on the membrane at the base of the first dorsal fin and small melanophores are found on the distal margin of the membranes between the last three dorsal spines. Medium melanophores are scattered on the membranes of the second dorsal fin and do not form the rectangular blotches present in *E. saludae* and *E. collis.* The pectoral fin is clear, but a few small melanophores outline the rays. The pelvic fin varies from clear to having a few melanophores on the last rays and on the membranes between them. The caudal is barred. The belly and breast are immaculate, or have a few scattered melanophores. There are a few scattered medium melanophores on the cheek. The preorbital and postorbital bars are prominent; the supraorbital and suborbital are faint. The pored portion of the lateral line usually is light, although some specimens have a few melanophores under the scales and/or along their distal edge. The median basi-caudal spot is usually prominent. Sometimes there are faint spots at the upper and lower bases of the caudal fin. The pattern of the sides varies within, as much as between, populations. Some specimens have no lateral blotches while others show, more or less clearly, eight to ten which alternate with the dorsal saddles and give the fish a variegated pattern. The eight to eleven dorsal saddles connect at the level of the lateral line and isolate central light areas. There is no pigment on the genital papilla or in an area around it. Figure 4 compares a breeding female *E. gracile* with *E. zoniferum.*

The pectoral and caudal fins, dorsal body surface, and genital papilla in the non-breeding male are colored like the female. The dorsal fins are darker than those of the female. The anal fin is covered with large melanophores which tend to fuse. The pelvic fins have many melanophores between the last two rays and fewer between the anterior rays. The breast and belly usually are covered with small melanophores. The orbital bars and lateral blotches appear less prominent in the non-breeding male because the cheek and sides are darker than in the female. The pored portion of the lateral line has more pigment on the distal than on the proximal parts of some scales. The non-pigmented area around the genital papilla is smaller than in the females and appears more prominent, because of the darker venter.

In the breeding male, the pectoral and caudal fins, pored portion of the lateral line, orbital bars, basi-caudal spots, sides, dorsal surface, and genital papilla are colored like the non-breeding male; the other regions are darker. Most of the basal third of the first dorsal fin is solid black. The second dorsal and anal fins show a lesser tendency toward melanophore fusion. The pelvic fins, breast, and belly are densely speckled with small melanophores. The cheek is usually darker. Figure 4 compares the pattern of breeding male *E. gracile* and *E. zoniferum.*

In life, *E. gracile* and *E. zoniferum* differ from the other species of the subgenus *Hololepis* in having vertical green bars on their sides. Males of both species have a submarginal red-orange band in the first dorsal fin which intensifies at breeding season. Hubbs and Cannon (1935) quoted Jordan and Evermann (1896) to the effect that the spinous dorsal in life is usually bright blue. This is an obvious reference to the color of a breeding male *Etheostoma exile* which Jordan confounded with *E. gracile.*

Breeding Tubercles—At the height of the breeding season, moderately large tubercles are present on the distal half of the anal rays (Fig. 1h), the distal three-quarters of the lower side of the pelvic spine and rays (Fig. 1k), and in two rows of four tubercles on each ramus of the lower jaw (Fig. 1m). The earliest that tubercles were ob-

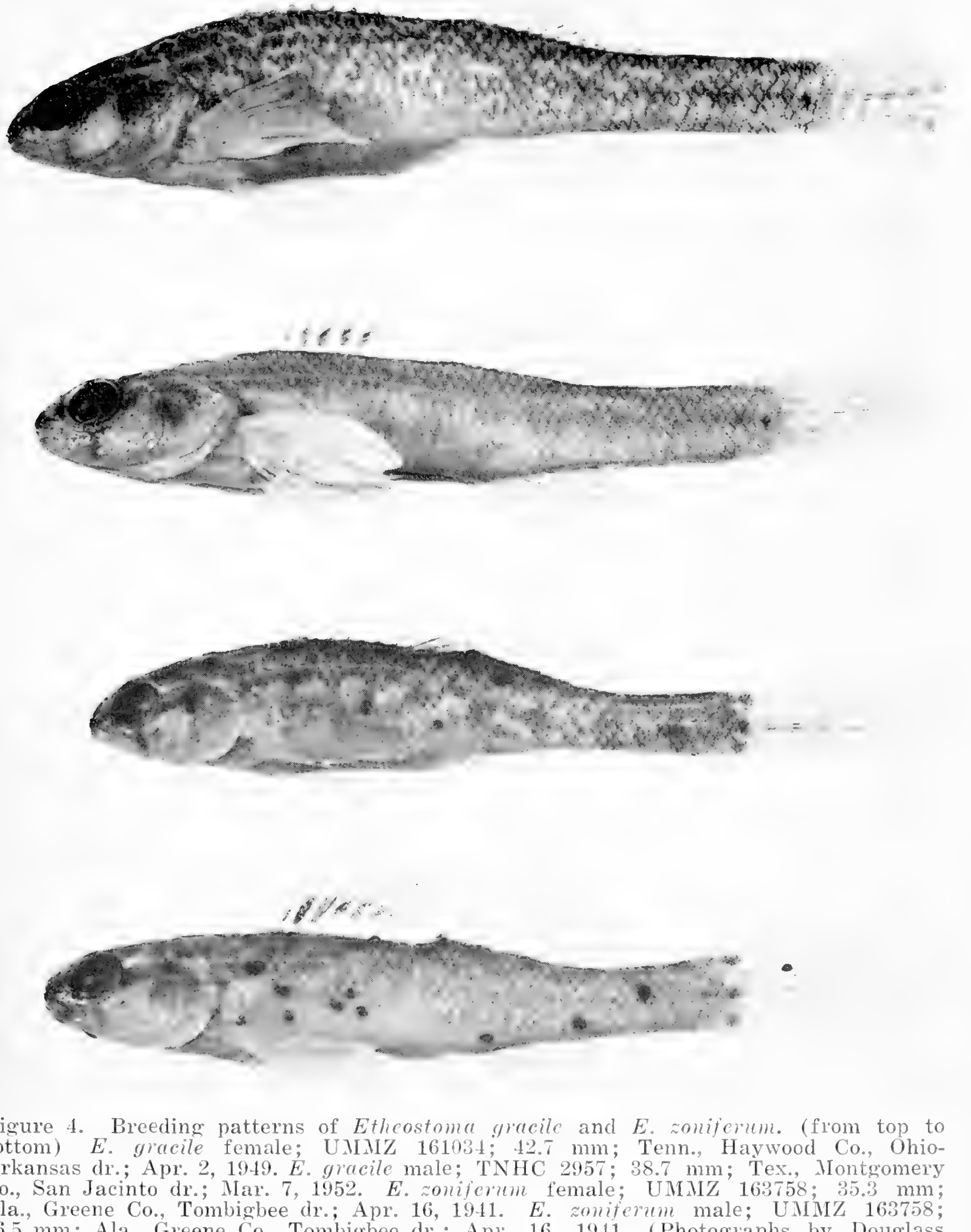

Figure 4. Breeding patterns of *Etheostoma gracile* and *E. zoniferum.* (from top to bottom) *E. gracile* female; UMMZ 161034; 42.7 mm; Tenn., Haywood Co., Ohio-Arkansas dr.; Apr. 2, 1949. *E. gracile* male; TNHC 2957; 38.7 mm; Tex., Montgomery Co., San Jacinto dr.; Mar. 7, 1952. *E. zoniferum* female; UMMZ 163758; 35.3 mm; Ala., Greene Co., Tombigbee dr.; Apr. 16, 1941. *E. zoniferum* male; UMMZ 163758; 36.5 mm; Ala., Greene Co., Tombigbee dr.; Apr. 16, 1941. (Photographs by Douglass M. Payne)

TABLE 10.

Number of pored lateral-line scales in Etheostoma zoniferum and E. gracile

Species and drainage	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	x̄
zoniferum																						
Alabama	1	–	–	1	–	1	2	3	6	2	2	3	2	1								15.21
Tombigbee											2	–	1	1								18.25
gracile																						
Tombigbee										1	–	1	–	–	–	2	3	–	–	–	1	21.75
Pearl														2								20.00
Mississippi																						
Wabash								1	–	3	–	4	7	7	4	5	1	–	1	1		19.85
Ohio								1	–	2	3	5	6	12	5	2	2	3	2			19.95
Wabash-Miss.									1	1	–	3	7	3	9	5	2	2	–	1		20.50
to Missouri										1	4	3	4	2	–	1						18.40
Missouri-Ohio										1	3	2	9	8	6	2	5	3	4	5	1	21.39
Ohio-Arkansas								1	1	1	6	4	3	3	7	2	1	2	1	1	1	19.88
Yazoo-Big Black											3	2	3	–	2	1	–	1				19.33
Red-Ouachita							1	5	10	14	17	29	38	27	23	15	14	5	1	1		19.18
Arkansas									2	–	9	7	8	12	15	8	9	1	1			20.11
Lower Miss.									1	–	–	1	–	1	–	1						18.75
Total Miss.							1	8	15	23	45	60	85	75	71	42	34	17	10	9	2	19.76
West of Miss.																						
Vermilion										1	3	–	1	–	1							17.83
Calcasieu											1	–	2	2	1							19.33
Sabine								2	3	6	4	4	1	2	2							17.08
Neches								7	5	8	6	14	11	10	8	4	–	2	–	2		18.44
Trinity								1	1	2	4	6	6	8	9	1	–	–	1	1		19.33
San Jacinto							1	1	–	1	6	9	12	10	10	3	2	1	2	1		19.61
Brazos								1	–	2	3	5	4	4	1	1	–	1				18.64
Colorado										2	5	1	12	4	13	6	5	2				20.22
Navidad													1									
Guadalupe										2	–	–	3	3	3	1	1					19.77
Nueces										1	1	1	3	2	2	1	–	–	–	1		19.83

served was February 19 (TNHC 4994; 1, 39.4 mm; Red River, Tex.). The latest that breeding tubercles were found was April 19 (UK 2418; 3, 33.6-39.6 mm; Red River, Okla.). The maximum development appears to take place in mid-March in Texas, where collections taken from throughout the year have been examined.

Genital Papilla—The genital papilla of the breeding female is a moderately elongate tube with a somewhat blunt end. A 36.7 mm female (UMMZ 162897) taken from the Yazoo River of Mississippi has a genital papilla which is 1.7 x 0.7 mm. Figure 1c shows the genital papilla of a 40.4 mm female taken on Mar. 7 (TNHC 2750, San Jacinto R.). There is a bulbous enlargement of the base of the papilla in some specimens.

Development—As in *Etheostoma fusiforme,* the supratemporal canal is incomplete in juveniles and the two ends of the canal fuse with age. A series of 25 Mississippi specimens (USNM 129113), ranging from 12.5 to 20.7 mm, all have incomplete supratemporal canals. Again, as in *E. fusiforme,* the transition period from incomplete to complete takes place at different sizes in different populations. This is shown by two groups of collections (UMMZ 107048, Missouri to Ohio Drainage; USNM 172570, 172495, 172523, 172481, 172576, and 172560 from the Red River Drainage). Of the thirty specimens in UMMZ 107048, five (19.4-21.0 mm) have incomplete supratemporal canals, while the other 25 (26.7-34.7 mm) have complete canals. Eight of the Red River specimens (14.6, 14.7, 16.1, 16.5, 16.5, 17.1, 17.4, 23.4 mm) have incomplete canals while the larger specimens (17.7, 17.7, 18.7, 19.1, 25.5, 27.5, 34.1, 35.4 mm) have complete canals.

Development of the pored lateral-line scales is also very similar to that in *E. fusiforme* (*q.v.*) as shown in USNM 129113. Eleven specimens (18.1-20.7 mm) have from 10 to 16 pored lateral-line scales which is below the normal range of 13-27, mean 19.5 (Table 39). Six specimens (17.4-

TABLE 11.
Number of total lateral-line scales in Etheostoma zoniferum and E. gracile

Species and drainage	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	x̄
zoniferum																	
Alabama		2	1	–	–	2	1	6	6	3	1	–	1	1			47.17
Tombigbee									1	2	–	1					49.25
gracile																	
Tombigbee										1	1	2	1	1			51.00
Pascagoula										1							
Pearl								1	1								47.50
Mississippi																	
Wabash					1	4	5	7	4	5	6	3	2				48.03
Ohio			1	–	3	3	6	7	7	7	4	3	1	–	2		47.86
Wabash-Miss.			1	1	2	4	6	8	4	5	2	2					46.97
to Missouri					1	1	1	3	1	1	2	3	–	1			48.50
Missouri-Ohio				1	3	2	5	4	7	6	4	10	1	5	1		48.86
Ohio-Arkansas			2	2	3	1	3	4	3	6	3	4	1				47.41
Yazoo-Big Black		1	–	–	2	3	2	3	1	–	–	1					45.85
Red-Ouachita	1	3	5	7	7	21	24	40	35	18	19	11	6	3	–	1	47.31
Arkansas					2	5	4	6	15	12	6	9	4	2			48.62
Lower Miss.		1	–	–	–	–	1	2									45.25
Total Miss.	1	5	9	11	24	44	57	84	77	60	46	46	15	11	3	1	47.70
West of Miss.																	
Vermilion						1	3	–	1	1							46.67
Calcasieu			1	1	–	1	2	–	–	–	1						45.33
Sabine		2	1	1	–	3	5	5	2	1	1	1	–	1			46.35
Neches	1	4	6	9	3	11	8	12	16	5	3	1					45.77
Trinity		1	2	2	1	8	4	6	11	3	–	1	1	1			46.63
San Jacinto	1	–	2	3	5	6	8	10	10	6	1	3	4	1	–	1	47.11
Brazos						2	3	3	2	3	2	3	2				48.45
Colorado						3	–	1	3	6	12	9	8	7	1		50.40
Navidad								1									
Guadalupe					1	–	1	–	5	1	2	–	1				48.27
Nueces									2	1	1	3	3	2			50.83

TABLE 12.

Number of first dorsal spines and second dorsal rays in Etheostoma zoniferum and E. gracile

Species and Drainage	First Dorsal								Second Dorsal							Abnormal
	7	8	9	10	11	12	13	x̄	9	10	11	12	13	14	x̄	
zoniferum																
Alabama		3	10	7	4			9.50	1	7	13	3	1		10.84	–
Tombigbee			1	1	2			10.25		3	1				10.25	–
gracile																
Tombigbee			6	2				9.25		1	4	2	1		11.38	–
Pascagoula			1							1						–
Pearl			1	–	1			10.00		1	–	1			11.00	–
Mississippi																
Wabash		3	23	11				9.22		5	22	9	1		11.16	–
Ohio		2	26	13	1			9.31			23	17	2		11.50	I, 11; I, 12
Wabash-Miss.		2	17	13	2			9.44		5	21	8			11.09	I, 11
to Missouri		1	5	11				9.59			15	2			11.12	–
Missouri-Ohio		4	34	20				9.28		5	21	29	3		11.52	I, 11
Ohio-Arkansas	1	1	16	13	2			9.42		1	19	12	1		11.39	I, 11
Yazoo-Big Black		1	8	4				9.23		3	6	4			11.08	–
Red-Ouachita		9	121	68	3	1		9.34	1	26	107	58	10		11.25	I, 10; I, 11; I, 11
Arkansas	1	13	48	9				8.92	1	26	38	6			10.69	I, 9; I, 10
Lower Miss.		1	2	1				9.00		2	–	2			11.00	–
Total Miss.	2	37	300	163	8	1		9.28	2	73	272	147	17		11.20	–
West of Miss.																
Vermilion		2	5					8.71		1	3	3			11.29	–
Calcasieu			5	1				9.17		2	3	1			10.83	–
Sabine			12	6	1			9.42		2	15	2			11.00	I, 10
Neches		10	48	17	–	–	1	9.14		7	47	21	1		11.21	–
Trinity		4	25	10				9.15		6	16	14	3		11.36	–
San Jacinto	1	7	35	21	1	–	1	9.27		5	47	13	1		11.15	I, 11
Brazos		3	14	6				9.13		1	11	10	1		11.48	–
Colorado		3	40	9				9.12		1	22	27	1	1	11.60	–
Navidad			1								1					–
Guadalupe		3	8	1				8.83		3	7	2			10.92	I, 10
Nueces			6	4				9.40		2	7	1			10.90	–

(The abnormal specimens with a spine in the anterior part of the second dorsal fin are not included in the frequency distributions or means.)

TABLE 13.
Number of anal rays in Etheostoma zoniferum and E. gracile

Species and Drainage	4	5	6	7	8	9	x̄
zoniferum							
Alabama	1	6	11	7			5.96
Tombigbee		2	2				5.50
gracile							
Tombigbee			3	4	–	1	6.88
Pascagoula		1					
Pearl			2				6.00
Mississippi							
Wabash			8	24	2		6.82
Ohio			6	32	6		7.00
Wabash-Miss.			18	17	1		6.44
to Missouri			7	10			6.59
Missouri-Ohio			10	34	3		6.85
Ohio-Arkansas			6	26	2		6.88
Yazoo-Big Black			6	5	2		6.69
Red-Ouachita		1	93	99	12		6.60
Arkansas		1	35	36	1		6.51
Lower Miss.			2	1	1		6.75
Total Miss.		2	191	284	30		6.67
West of Mississippi							
Vermilion			4	3			6.43
Calcasieu			5	1			6.17
Sabine			10	10			6.50
Neches		2	44	37	2		6.46
Trinity			16	22	1		6.62
San Jacinto		1	24	40	1		6.62
Brazos			8	15			6.65
Colorado			2	34	16		7.27
Navidad				1			
Guadalupe			3	10			6.77
Nueces			1	7	1		7.00

18.0 mm) have 0-13 pored scales. Five specimens (15.9-17.1 mm) have either one or no pored scales, while the three smallest specimens (12.5-14.9 mm) have no pored scales. From 18.0 mm down, all the specimens in this collection have ridges on some of the scales in the lateral line posterior to the completely pored scales. These ridges grow out from the scale and then meet over the center of the scale forming the pored lateral-line scale.

The development of squamation was also studied in this collection. The smallest (12.5 mm) specimen has scales on the sides of the caudal peduncle and extending forward along the lateral line. Scales are absent on the ventral part of the caudal peduncle, nape, pectoral fin base, opercle, preopercle, belly, and dorsally and ventrally from the lateral line anterior to the first dorsal fin origin. At 14.6 mm, a few imbedded scales appear on the opercle and squamation of the ventral half of the belly begins. Between 19.0 and 20.7 mm, squamation of the opercle, preopercle, and the posterior part of the belly is complete. Scales develop on the nape and the base of the pectoral fin some time after this.

The most interesting developmental feature that can be studied in this collection is the infraorbital canal. In adult *E. gracile,* it is complete with eight pores. In all 25 specimens in USNM 129113, this canal is incomplete. The 12.5 mm specimen has two pores in the anterior portion of the canal and only an open groove in the posterior portion of the canal. Most of the middle nineteeen specimens (14.6-19.0 mm) have three pores in the anterior portion and two in the posterior ($2 + 3$ as in *E. fusiforme*) but there are also two specimens with $3 + 3$ and two with $2 + 4$. The largest five specimens in the collection have $3 + 4$. In addition, the 20.7 mm specimen has a groove extending between the anterior and posterior portions of the canal. This groove has lateral ridges along it which will roof over the canal in a manner similar to the development of the

TABLE 14.
Number of scale rows above and below the lateral line in Etheostoma zoniferum and E. gracile

Species and Drainage	Above						Below						
	2	3	4	5	6	x̄	7	8	9	10	11	12	x̄
zoniferum													
Alabama		20	5			3.20	5	11	7	2			8.24
Tombigbee		2	2			3.50	1	1	2				8.25
gracile													
Tombigbee		8				3.00		3	4				8.57
Pascagoula		1						1					
Pearl		1	1			3.50		1	1				8.50
Mississippi													
Wabash		14	21	1		3.64		10	19	6	2		9.00
Ohio		19	14	1		3.47		9	16	9			9.00
Wabash-Miss.	1	23	8			3.22	1	11	17	5			8.76
to Missouri		2	14			3.88		7	9				8.56
Missouri-Ohio		22	29	4		3.67	4	25	17	7	1		8.56
Ohio-Arkansas		20	13			3.39	1	10	13	8			8.88
Yazoo-Big Black		7	5	1		3.54		4	7	1	1		8.92
Red-Ouachita	1	71	121	13		3.71	10	56	80	45	10	1	8.96
Arkansas		28	33	2		3.59		20	30	14	4		9.03
lower Miss.		3	1			3.25		2	–	1	1		9.25
total Miss.	2	209	259	22		3.61	16	154	208	96	19	1	8.90
West of Miss.													
Vermilion		1	2			3.67		1	2				8.67
Calcasieu	1	4				2.80	1	2	2				8.20
Sabine		5	15			3.75		3	13	4			9.05
Neches		24	51	6		3.78	1	26	39	12	1	1	8.86
Trinity		3	29	9		4.15		5	15	15	4		9.46
San Jacinto		16	39	10		3.91		13	26	18	2		9.15
Brazos		10	11			3.52		10	9	3			8.68
Colorado		6	32	13	1	4.17	1	15	28	8			8.83
Navidad			1					1					
Guadalupe			10	1		4.09		3	6	–	2		9.09
Nueces		1	5	5		4.36		1	4	4	1	1	9.73

pored lateral-line scales. It will be noted that development in the infraorbital canal proceeds from the pore just behind the nostril posteriorly *and* from the junction with the lateral canal anteriorly.

Habitat—Data on 50 University of Texas collections made available by Clark Hubbs show that most *E. gracile* were found in slow, moderately flowing, or quiet waters (Table 17). The type of water was about equally divided between muddy and/or murky, clear, and brown. No aquatic vegetation was present at about half the collection localities and most of the rest had only slight to moderate amounts (*Myriophyllum, Potamogeton, Typha,* green algae, and water lilies). Aquatic vegetation was abundant at only four localities and was composed of *Ceratophyllum,* rushes, and filamentous algae. The number of times each of the six elements in the bottom types—mud and/or slit, sand, detritus, gravel, clay, and bedrock—were present is given in Table 17. The most often found bottom type was mud and/or silt (present at 77% of the localities).

All *E. gracile* in 12 collections I made in Illinois, Indiana, Tennessee, Oklahoma, and Texas, were taken from ponds, swamps, or backwaters. Eight localities lacked aquatic vegetation. One had slight amounts of algae, another some emergents, and a third a few aquatics. The north end of Reelfoot Lake, Tennessee, had abundant aquatic vegetation, including *Cabomba, Azolla, Ceratophyllum,* and *Ludwigia.* The water was white and turbid at 11 localities; turbid and slightly stained brown in the other. At all localities, *E. gracile* was taken over mud, silt or detritus.

Blatchley (1938) reported the habitat of *E. gracile* in Indiana as lowland swamps and bayous; Gerking (1945) as sluggish, turbid water on a rather firm bottom of sand (or sand and mud). In Illinois, O'Donnel (1935) reported that *E. gracile* pre-

TABLE 15.

Number of pores in preoperculomandibular and infraorbital canals in Etheostoma zoniferum and E. gracile

Species and Drainage	Preoperculomandibular						Infraorbital										
	8	9	10	11	12	x̄	2+3	2+4	3+4	3+5	2+6	6	7	8	9	10	x̄
zoniferum																	
Alabama		2	19			9.90	2	17	4								2+4
Tombigbee			4			10.00		4									2+4
gracile																	
Tombigbee			6	–	1	10.29							1	5			7.83
Pascagoula			1											1			
Pearl			2			10.00								2			8.00
Mississippi																	
Wabash		1	33			9.97							12	22			7.65
Ohio		1	43			9.98							16	26			7.62
Wabash-Miss.		1	27	1		10.00							5	30			7.86
to Missouri	1	1	12	3		10.00								13	3		8.19
Missouri-Ohio		1	46	1		10.00					1*	1	12	32			7.69
Ohio-Arkansas		3	29	1		9.94						1	5	23	3		7.88
Yazoo-Big Black			13			10.00							1	12			7.92
Red-Ouachita	1	13	186	3		9.94				1*			16	160	22	1	8.04
Arkansas	2	18	51			9.69							6	56	7		8.01
lower Miss.			3	1		10.25								4			8.00
total Miss.	4	39	443	10		9.93						2	73	378	35	1	7.92
West of Miss.																	
Vermilion		1	6			9.86								4	3		8.43
Calcasieu		1	5			9.83							1	5			7.83
Sabine			19	1		10.05							3	14	3		8.00
Neches	1	5	66	1		9.92							9	64	2		7.91
Trinity		4	33	2		9.95							2	37			7.95
San Jacinto		5	57	4		9.98							5	55	4	3	8.07
Brazos		4	19			9.83							1	21			7.95
Colorado		4	45	2		9.96							5	43	4		7.98
Navidad			1											1			
Guadalupe			8	2		10.20							1	10	1		8.00
Nueces		1	7			9.88								9	1		8.10

* Abnormal. Not included in calculation of means.

TABLE 16.
Squamation of preopercle, opercle, and nape in Etheostoma zoniferum and E. gracile

Species and Drainage	Preopercle (100% scaled)				Opercle (100% scaled)				Percent of Nape Scaled											
	I/PX-C/T	PX-T	PX/X-T	X-T	I/PX-C/T	PX-T	PX/X-T	X-T	0	10	20	30	40	50	60	70	80	90	100	Nape x̄%
zoniferum																				
Alabama	4	1	4					10	9	1										1
Tombigbee		3	1					4	3	1										3
gracile																				
Pascagoula				1				1			1									20
Pearl				1				1												–
Mississippi																				
Wabash	2	2	2	5	5	2	4		1	1	1	1	–	–	–	–	1	1	5	66
Ohio				9				9			1	1	–	–	–	–	1	1	5	80
Wabash-Miss.				13	3	3	4	3	1	1	1	3	–	–	–	–	–	1	4	65
to Missouri				3				3						1	–	–	–	1	1	80
Missouri-Ohio			1	4		1	4			2	1	–	–	1	1					30
Ohio-Arkansas				14			6	8		1	–	–	–	2	2	1	–	3	5	76
Red-Ouachita		1	4	9	1	3	1	9	2	1	2	–	1	–	–	–	–	2	5	59
Arkansas		1	2	6	1	–	6	1	4	–	1	–	1	–	–	–	–	2	1	38
lower Miss.			1	1			1	1									2			80
total Miss.	2	4	10	64	10	9	26	34	8	6	7	5	2	4	3	1	4	11	26	62
West of Miss.																				
Calcasieu				4		2	1	1	2	1	–	1								10
Sabine	2	2	4	1		5	5	1		3	1	1	1	–	–	–	2	2	1	51
Neches			5	6		3	6	2		1	–	–	–	–	–	–	1	3	6	87
Trinity				8		2	5	1		1	–	–	–	–	–	–	1	–	6	86
San Jacinto			1	6		2	3	2			1	–	–	–	–	1	–	–	5	84
Brazos				10				10											8	100
Colorado			1	11	1	5	4	1											12	100
Navidad				1				1			1									
Guadalupe			4	5			4	5				2	–	–	–	1	1	–	7	76
Nueces			1	8			1	8		1	–	–	–	–	–	–	2	2	4	83

TABLE 17.
Habitat data for Etheostoma gracile collections from Texas

Water Current	Number of collections	Percent of collections
none	8	19.0
slow	8	19.0
none to moderate	6	14.3
slow to moderate	5	11.8
moderate	4	9.5
none to fast	2	4.8
slow to fast	4	9.5
moderate to fast	2	4.8
fast	3	7.1
total	42	99.8
Water Current	**Present in collections**	**Present in percent of collections**
none	16	38.1
slow	25	59.4
moderate	23	54.7
fast	11	26.2
Aquatic Vegetation	**Number of collections**	**Percent of collections**
none	22	46.8
slight to moderate	21	44.6
abundant	4	8.5
total	47	99.9
Bottom Type	**Present in collections**	**Present in percent of collections**
mud and/or silt	33	76.7
sand	22	51.1
detritus	14	32.6
gravel	10	23.0
clay	7	16.3
bedrock	5	11.6

ferred sluggish water and a mud bottom and Bridges (1958) recorded it from two farm ponds. The information presented by Forbes (1907, 1909, 1914) and Forbes and Richardson (1909, 1920) is not reliable since they confounded *Etheostoma exile,* a species of cooler, cleaner waters, with *E. gracile.* However, both species prefer water with little or no flow. Forbes and Richardson (1920) found 78% of *gracile-exile* collections in areas of sluggish flow and Forbes (1907:303) and Forbes and Richardson (1920) reported that 66% of *gracile-exile* collections were made over muddy bottom. Forbes and Richardson, apparently mistakenly, reported this in their ecological table as 67% over rock and sand. Hancock and Sublette (1958) reported it from a sluggish brown-water bayou in Louisiana. Blair (1959) noted that *E. gracile* and *E. chlorosomum* are fishes of sluggish , muddy, streams and lakes in northeastern Oklahoma.

Species Associates—Forbes (1907) found a large coefficient of association between *Etheostoma chlorosomum* and *E. gracile-exile* in Illinois. However, his figures are not accurate, because he confounded *E. gracile* with *exile.* If the northern collections of the allopatric *exile* could be eliminated the coefficient would be still higher. *Etheostoma chlorosomum* was taken in 6 out of 41 localities in the Poteau River of Oklahoma and Arkansas (Cross and Moore, 1952). At five of these localities, *E. gracile* was also taken. This association was also noted in several of my southern Illinois and Indiana collections. Fishes that are associated with *E. gracile* prefer or tolerate low gradient and/or silty bottoms and turbid water.

Habits—Forbes (1878) and Forbes and Richardson (1920) reported the food of a few Illinois specimens to consist of "larvae of gnats and of may-flies, with a few copepoda."

Forbes and Richardson reported that females taken in Illinois on April 28 contained "full-sized eggs." Hubbs and Cannon (1935) reported the breeding season in Illinois to be late March and April. Moore and Poole (1948) noted that specimens in an Oklahoma collection of *E. gracile* were "in breeding color" on April 19. Breeding tubercles are present in Texas specimens of *E. gracile* from February 19 to April 19 with their greatest development in mid-March. Therefore, the spawning season in Texas appears to be about mid-March.

The breeding behavior of *E. gracile* and *zoniferum* may differ slightly from that of *E. fusiforme* because these two species possess accessory breeding tubercles on the lower jaw rami. Perhaps the male rubs his chin along the nape of the female during courtship. The red in the first dorsal fin of male *E. gracile* and *zoniferum* indicates the presence of territoriality. My aquarium observations of *E. gracile* have indicated this with a dominant male occupying the corner of an aquarium where they were fed. This dominance was indicated by brighter colors and by chasing intruders. Also, pairs of male *gracile* have been observed spreading their dorsal fins at each other in an apparent threat posture. No specimens of *E. fusiforme* or *E. serriferum* have been seen to do this.

E. gracile does well in aquaria, specimens having been kept for several months on a diet of white worms, pieces of earthworms, frozen brine shrimp, and moistened pellets of dry food. Linder (1955a) also reported success in maintaining *E. gracile* in aquaria.

Distribution—Found along the Gulf Coastal Plain from the Tombigbee River in Mississippi west to the Nueces River of Texas and northward in the low lying areas of the former Mississippi Embayment (Fig. 5). Hubbs (1957b:98) reported *E. gracile* as occupying the Texan, Austroriparian, and Tamulipan biotic provinces of Texas, but absent from the Rio Grande drainage of the Tamulipan. In northeastern Oklahoma, Blair (1959) noted that *E. gracile* is found mostly in the sluggish, turbid streams of the Cherokee Prairie biotic province avoiding the clear, faster flowing streams of the Ozark biotic province. In Indiana it is known only from the lowland southwestern corner south of the Wisconsin glaciation (Gerking, 1945:95, map 94).

There is only one collection of *E. gracile* available from the Tombigbee River (UMMZ 113453, Lowndes Co., Miss.). *E. zoniferum* has been taken several times farther south in this river. These two are very similar to each other, so much so that I think they would probably hybridize if they came together. *E. zoniferum* is clearly an offshoot of *E. gracile,* and so they would not be expected to be in the same river system together. Therefore, there is a possibility that a stream capture allowed *E. gracile* to invade the upper part of the Tombigbee River. Tributaries of three different rivers approach this section of the Tombigbee; the Yalobusha, tributary to the Yazoo, the Big Black, and the Pearl. The tributary of the Big Black is the one that approaches closest to the Lowndes County locality and also there are more collections of *E. gracile* from it than from the other two rivers.

A better understanding of factors important in the distribution of *E. gracile* can be obtained by study of a limited area. Illinois was selected because Forbes and Richardson (1920) gave a lengthy account of the topography of the state, and because it has been well covered by collectors (INHS, UMMZ, CU). All known Illinois localities for *E. gracile* were plotted upon a map of glacial geology taken from Forbes and Richardson (1920, Map III). The collections they reported as *Boleichthys fusiformis* from the Rock River district of northeast Illinois refer to the superficially similar *Etheostoma exile,* as pointed out by Hubbs and Cannon (1935). The distribution of *E. gracile* in Illinois is listed below: (names from Forbes and Richardson, 1920: Atlas):

Drainage system	*No. collections*
Galena District, Rock River System, Lake Michigan Drainage, Mississippi Drainage	none
Illinois River System	2
Kaskaskia River System	10
Wabash River System	20
Big Muddy River System	10
Saline River System	10
Cairo District	11

Only two collections of *E. gracile* are from the Illinois River, which drains about three-

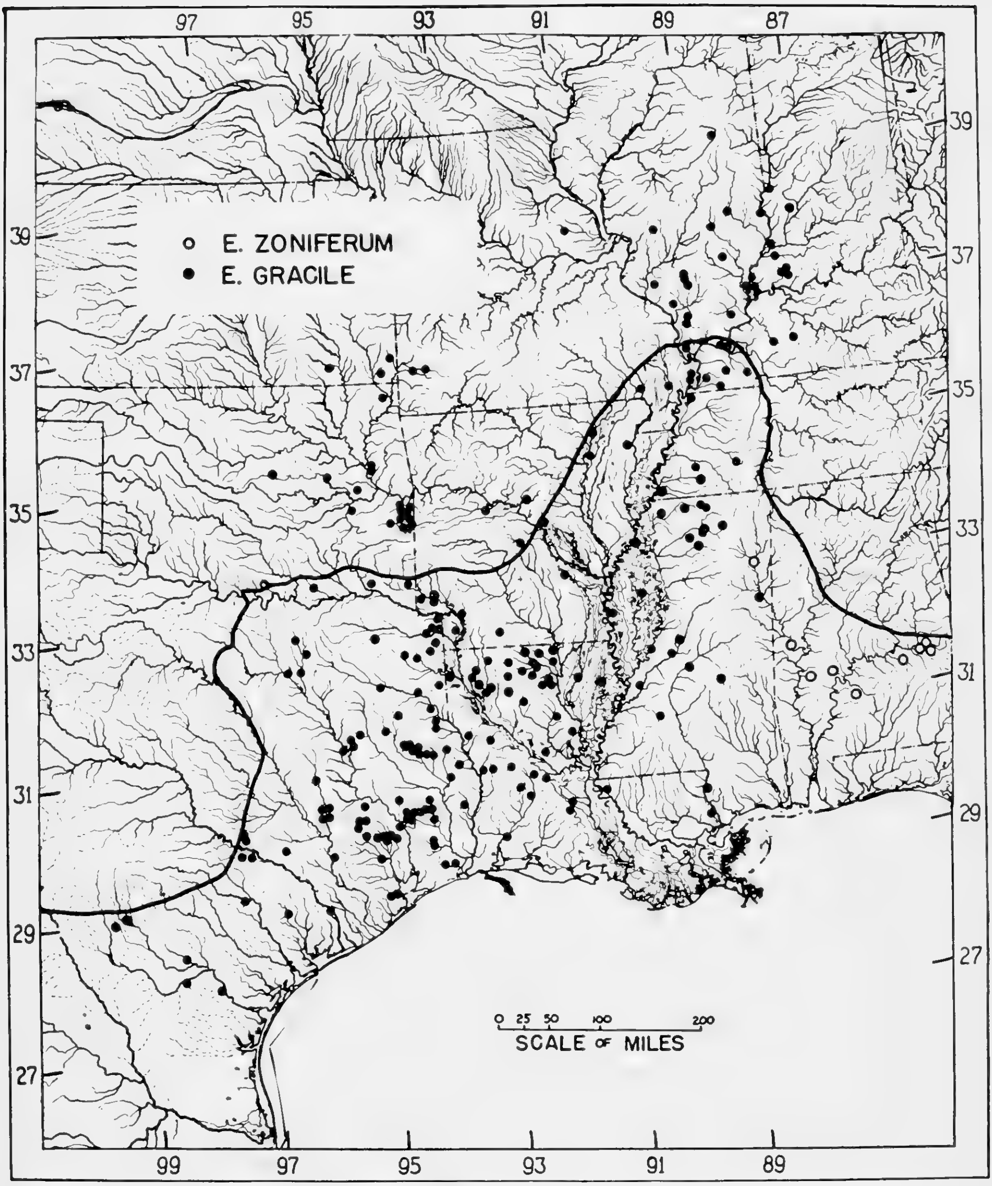

Figure 5. The distribution of *Etheostoma gracile* and *E. zoniferum* in relation to the Fall Line. (Based upon specimens examined)

sevenths of the state. This seems odd because the whole state has been covered thoroughly by collectors. Each collection is represented by only a single specimen. I have verified the identification of the Champaign Co. specimen and although the Christian Co. specimen appears to be lost (P. W. Smith, personal communication), it was examined by Hubbs and Cannon so its actual identification is not suspect. The Champaign Co. specimen was mentioned in Thompson's field notes but no specimens have been taken in more recent collections (P. W. Smith, personal communication);

therefore there is a possibility that the locality for the Christian Co. specimen is erroneous.

With the exception of the two abovementioned specimens and a specimen from a Madison Co. tributary of the Kaskaskia River, the remainder of the *E. gracile* collections are from only three of the nine physiographic areas of Illinois (Forbes and Richardson, 1920, Map III):

	No. collections
1) Unglaciated areas (of southern Illinois only)	6
2) Lower Illinoisan Glaciation	18
3) Bottom lands (of Lower Illinoisan Glaciation only)	36

The two Illinois River specimens came from the Wisconsin and Middle Illinoisan Glaciation area and the Madison Co. specimen came from the Middle Illinoisan Glaciation. Concerning the drainage of Illinois, Forbes (1909:381) pointed out that "... the headwaters and tributaries of its various stream systems so approach and intermingle that in times of flood they formed an interlacing network, through which it would seem that a wandering fish might have found its way in almost any direction and to almost any place." Why then is *E. gracile* so clearly limited to the southern part of the state? The answer lies in the glacial geology which, as Forbes (1909) pointed out, is more diversified than the topography. The Kaskaskia and Embarrass Rivers cut across the Shelbyville moraine which separates the lower Illinoisan and Wisconsin glaciations, but the distribution of *E. gracile* stops south of the moraine, although the bottomlands which are its preferred habitat continue across the moraine into the Wisconsin Glaciation for a short distance. Two physical factors seem important in limiting *E. gracile* distribution: current and turbidity.

Forbes (1909) presented a list of seven species tolerant of muddy bottoms and a list of thirteen species that avoid muddy bottoms. All the species in the former group are freely distributed over the lower Illinoisan Glaciation and all the species in the latter group avoid this area. The streams of the Wisconsin Glaciation are narrow and fast flowing, quickly carrying off any silt load they acquire. Forbes and Richardson (1920) also pointed out that the soil of the lower Illinoisan Glaciation is an extremely fine-grained, light-colored clay which when washed into streams remains in suspension and renders the waters turbid for a long time. The correlation of turbid waters and muddy bottoms with *E. gracile* distribution seems to be due not to a preference of *gracile* for this type of habitat but to the fact that more species of fishes are present in the favorable upland habitat and have become specialized for certain ecological niches. They are therefore able to compete more successfully which leaves the muddy swamps by default to *gracile* and other fishes tolerant of poor conditions.

I have computed the gradient in feet per mile for streams in which *E. gracile* was collected, basing my calculations on the data of Forbes and Richardson (1920) and Luce (1933). In ten streams, the most upstream collection of *gracile* was found in areas having gradients of 1.0 to 6.7 feet per mile ($\bar{x}$:2.9 ft/mi). The gradients that *gracile* avoids in these streams range up to 100 ft/mi ($\bar{x}$:18.3). Of course, most *gracile* were collected in backwaters and so were found at gradients of much less than 2.9 ft/mi. It seems that the upstream spread of *gracile* is limited by fast water in the same way that the Atlantic Coast species of the subgenus *Hololepis* are limited by the Fall Line.

In Illinois and Indiana a number of species have distributions similar to that of *E. gracile.* Gunning and Lewis (1955) noted that *Lepomis symmetricus, Elassoma zonatum, Chologaster agassizi, Gambusia a. affinis,* and *Centrarchus macropterus* have their northern limit in southern Illinois. Four species are limited to the extreme southwestern tip of Indiana, in the area of the Wabash River and Ohio River flood plain (Gerking, 1945): *Gambusia a. affinis, Centrarchus macropterus,* and *Etheostoma chlorosomum,* in addition to *Etheostoma gracile.* Of twenty species of darters for which Gerking (1945) presented distribution maps, only *E. gracile* and *E. chlorosomum* are limited to the southwest corner of the state. *Opsopoeodus emiliae* also has the center of its Indiana distribution in the muddy waters of the southwestern corner of the state.

Geographic Variation—Tables 10-16 give frequency distributions of the characters examined and include *E. zoniferum;* this facilitates comparison between these closely related species. Several characters which showed little or no geographic variation are given only in the species comparisons tables (Tables 38-49); squamation of interorbital, parietal, and breast (naked); condition of preopercle (entire); coronal pore (present); interorbital pores (usually absent, rarely 1-2); pectoral rays (mode usually 13, a few populations with 12); branchiostegals (usually 6, Mississippi to Missouri population with a mode of 5).

The number of pored and total lateral-line scales showed little difference between populations (Tables 10-11). The modal number of dorsal spines was nine in all populations except for an Audrain Co., Mo. collection (UMMZ 149331) which had a mode of ten (Table 12). The modal number of second dorsal rays is 11 in all populations except Missouri to Ohio and Colorado, which have 12 (Table 12). A spine was present in the anterior part of the second dorsal fin more often in *E. gracile* (13 specimens) than in the other species of the subgenus *Hololepis*. Most specimens of *E. gracile* had two anal spines but 22 specimens had only one spine and one specimen had three (Table 42). The modal number for anal rays was either six or seven (Table 13).

By use of the number of scale rows above the lateral line (Table 14), populations of *gracile* may be divided into three groups: Populations east of the Mississippi with a low number (mode of three); the Mississippi, Vermilion, and Calcasieu populations with a moderate number (modes three or four); and a western group from the Sabine through the Nueces, with means greater than 3.75 (except for the Brazos) and a mode of four. In regard to the number of scale rows below the lateral line (Table 14) the Nueces population stands out with a mean of 9.73. The other populations had means from 8.5 to 9.0, with the exception of the Trinity population, which was intermediate with a mean of 9.46.

There were no important differences between populations in the number of head pores. Most specimens had ten preoperculomandibular pores but some individuals had as few as eight or as many as 11 (Table 15). Two anomalous specimens had incomplete POM canals (Missouri-Ohio and Neches systems). Both had counts of 5 + 6, and therefore would have had normal counts of ten if the canal had been complete. The infraorbital pores are typically eight (Table 15) but range from six to ten. The INF canal is typically complete but two individuals had 3 + 5 (Red River) and 2 + 6 (Missouri-Ohio drainage). Both of these would be low counts of seven if the canals were complete. The supratemporal canal is usually complete in adults but in most collections a few specimens had incomplete canals (see development).

The preopercle (POP) and opercle (OP) are completely covered with scales but the character of squamation varies (Table 16). Most specimens had POP covered with exposed ctenoid scales (X-T) but a few had the squamation less well developed. One Sabine River specimen had imbedded cycloid scales and the sample had a mode of PX/X-T. The OP squamation was similar but less well developed. The mode is usually X-T but it varied to I/PX-T in the Wabash population. The extent of the nape that was covered by scales varied from 0-100% within many populations, but the mode was usually 100 I/PX-T (Table 16).

The most interesting result of comparison of populations of *E. gracile* is that although there is a large amount of variation within systems and within collections as in *E. fusiforme,* there is much less difference between populations. This is probably due to less complete isolation, than in fishes living along the Atlantic Coastal Plain.

Specimens Examined—Specimens examined are given by drainage system, state, county, and museum number, except for localities at the margins of the range and type localities of nominal species. A total of 1580 specimens from 309 collections was examined. Complete data for most of the collections are listed in Collette (1960).

Tombigbee Dr., Miss.—Lowndes Co.: UMMZ 113453 (10, 28-36); Tombigbee R., 3 mi. W of Columbus; Aug. 18, 1931.

Pascagoula Dr., Miss.—Newton Co.: CU 33795 (1, 33); trib. of Leaf R. between Lawrence and Lake on US 80; Oct. 25, 1958.

Pearl Dr., Miss.—Pearl River Co.: TU 14423 (1, 30); oxbow of W. Pearl R., 3.2 mi. E of Bogalusa, La.; Nov. 11, 1956. Rankin Co.: USNM 129113 (25, 13-21); borrow pits on Meeks Ferry Rd. along Pearl R.; June 12, 1933. La.—St. Tammany Par.: UMMZ 163687 (1, 40); ditch 1 mi. E of Pearl R. village; Apr. 15, 1951.

Mississippi River

Ohio-Wabash Dr., 40 specimens. Ind.—Gibson Co.: UMMZ 81382. Green Co.: USNM 34983 (1, 31); Switz City Swamp; Aug. 1883; lectotype of

Poecilichthys palustris. Knox Co.: UI 425. Posey Co.: UI 446. Ill.—Crawford Co.: INHS uncat. Cumberland Co.: CU 34586. Effingham Co.: UMMZ 105940. Wayne Co.: INHS uncat. White Co.: CU 32245; TU 19326.

Ohio Dr., 44 specimens, Ind.—Warrick Co.: UMMZ 81406; UI 440, 441; CU 32246. Ky.—Muhlenberg Co.: CU 22186.

Wabash to Mississippi Dr., 38 specimens, Ill.—Massac Co.: INHS 4 uncat. coll.; TU 35155. Saline Co.: INHS uncat. Ky.—Hopkins Co.: USNM 63782. Marshall Co.: UMMZ 168360.

Middle Mississippi

To Missouri Dr., 17 specimens, Ill.—Champaign Co.: INHS uncat. Mo.—Audrain Co.: UMMZ 149331.

Missouri to Ohio Dr., 63 specimen, Ill.—Alexander Co.: UMMZ 111594. Bond Co.: CU 34587. Jackson Co.: UMMZ 107048, 105930. Jefferson Co.: UMMZ 105866, 163066. Madison Co.: UMMZ 131198. Perry Co.: UMMZ 130301. Randolph Co.: UMMZ 163079. Union Co.: CU 3466. Washington Co.: UMMZ 163027.

Ohio-Arkansas Dr., 45 specimens, Ark.—Craighead Co.: USNM 125086. Ky.—Graves Co.: USNM 63783; TU 3018. Hickman Co.: UMMZ 154781. Miss.—Coahoma Co.: USNM 129185. Mo.—Butler Co.: UMMZ 139647. Mississippi Co.: UMMZ 153260, 153237, 153201. New Madrid Co.: UMMZ 153159. Tenn.—Chester Co.: UMMZ 168526. Haywood Co.: UMMZ 161034. Obion Co.: UMMZ 105396; CU 33346. Shelby Co.: USNM 195973.

Lower Mississippi

Yazoo-Big Black Dr., 35 specimens, Miss. — Benton Co.: UMMZ 161444, 162897; UM H51-2. Copiah Co.: UMMZ 170715. De Soto Co.: USNM 129013, 129593. Hinds Co.: UMMZ 170744. Holmes Co.: UMMZ 161108. Lafayette Co.: UMMZ 161392, 162923; UM 50-6, 51-19, 55-4. Marshall Co.: UMMZ 161054; UM 51-2, 55-16. Sunflower Co.: USNM 170978. Union Co.: UMMZ 144722. Warren Co.: USNM 129110. Washington Co.: USNM 129123. Yazoo Co.: USNM 32224 (1, 44); Vaughan's Station, pool along Big Black R., Aug. 20, 1881; holotype of *Poecilichthys butlerianus;* USNM 129140.

Arkansas Dr., 169 specimens, Mo.—Barton Co.: UMMZ 151793, 151815. Ark.—Arkansas Co.: TU 2196. Faulkner Co.: Univ. Ark. uncat. coll. Jackson Co.: UMMZ 123620. Lawrence Co.: USNM 109881. Pulaski Co.: UMMZ 123262. Yell Co.: TU 24466. Okla.—Craig Co.: OAM 5172. Le Flore Co.: UMMZ 109427; OAM 972, 1001, 1136, 1234, 1090, 782, 1182, 1319, 1343, 1357, 1403, 1390, 4473. Lincoln Co.: OAM 4529. McIntosh Co.: TU 10559. Muskogee Co.: OAM 4329, 5054. Okmulgee Co.: UMMZ 107052. Osage Co.: OAM uncat. Ottawa Co.: OAM 5147. Pittsburg Co.: OAM 4961. Kans.—Cherokee Co.: UMMZ 144463 (2, 29-30); Fly Cr., 4 mi. S and 3 mi. W of Hoover at Columbus; July 26, 1946. Crawford Co.: UK 2255 (6, 29-36); Clear Cr. and Second Cow Cr., Sec. 20, T29S, R24E; Apr. 18, 1952. UK 2933 (4, 31-34); Cow Cr., Sec. 20, T29S, R24E; Apr. 10, 1953. Montgomery Co.: UK 6043 (1, 43); Big Elk Cr. between Independence and Elk City on US 160; Mar. 28, 1961.

Red-Ouachita Dr., 717 specimens, Ark.—Columbia Co.: USNM 165848. Hempstead Co.: UMMZ 123169. Howard Co.: TU 10165. Lincoln Co.: UMMZ 127832. Little River Co.: UMMZ 170868. Miller Co.: UMMZ 123135, 123125. Saline Co.: USNM 36470. Sevier Co.: TU 10165. La.—Bienville Par.: UMMZ 170824; USNM 172878. Bossier Par.: UMMZ 170842; USNM 172608, 172661, 172883, 173002. Caddo Par.: CU 32249, 32248. Caldwell Par.: TU 14372. Catahoula Par.: TU 4343. Claibourne Par.: UMMZ 161294. Grant Par.: TU 907, 2096, 4296. Jackson and Bienville par.: USNM 172576. Lincoln Par.: UMMZ 161310; USNM 172495, 172623, 172523, 172745, 172889, 172934. Madison Par.: USNM 172732. Natchitoches Par.: TU 13649. Ouachita Par.: UMMZ 170780, 170804; USNM 172762. St. Landry Par.: TU 961, 1021. Union Par.: TU 14355; USNM 172481, 172560, 172570, 172677, 172692, 172709, 172812, 172833, 172861, 172911, 172953. Webster Par.: TU 1355; USNM 172648, 172988. Okla.—Bryan Co.: OAM 4192. Choctaw Co.: OAM 2108, 4684. Love Co.: OAM 4766. McCurtain Co.: UK 2418; OAM 2165, 3074, 3004, 5169; CU 17890, 33746. Tex.—Bowie Co.: OAM uncat.; TNHC 3529, 3930, 4992. Bowie and Cass cos.: TNHC 3179. Cass Co.: TNHC 3508, 3542, 3952, 4044, 4092. Franklin Co.: TU 14070. Harrison Co.: TNHC 2048. Morris Co.: TNHC 3845. Red River Co.: TNHC 4994.

Calcasieu Dr., 6 specimens; La.—Allen Par.: USNM 172116; TU 14050. Calcasieu Par.: ANSP 55538. Vernon Par.: UMMZ 170594; TU 14090.

Sabine Dr., 34 specimens; La.—Sabine Par.: TU 976, 4564. Vernon Par.: TU 14360. Tex.—Harrison-Panola cos.: TNHC 3217. Newton Co.: TNHC 3300. Panola Co.: CU 34909. Sabine Co.: TNHC 465. Shelby Co.: TNHC 3387. Shelby-Panola cos.: TNHC 3591. Upshur-Smith cos.: UMMZ 170038.

Neches Dr., 129 specimens, Tex.—Cherokee Co.: TNHC 3809. Hardin Co.: TNHC 488, 578; TU 21651, 22214, 21417. Nacogdoches Co.: UMMZ 170469; TNHC 363, 371, 202, 400, 1061, 1231, 1776, 556; TU 14037. Polk Co.: UMMZ 170446; TNHC 2419, 2575, 2696. Rusk Co.: CU 34590. Sabine Co.: UMMZ 170502. San Augustine-Nacogdoches cos.: UMMZ 170480. Tyler Co.: TNHC 2943; TU 14085, 21373, 21464, 21718, 21845.

Sabine Lake Dr. (Neches plus Sabine), 4 specimens, Tex. — Jefferson Co.: TNHC 4181; TU 22295.

Trinity Dr., 44 specimens, Tex.—Anderson Co.: TU 3801. Collin Co.: TNHC 3434, 3739. Freestone Co.: CU 33819. Kaufman Co.: TNHC 4008. Madison-Walker cos.: TU 4899. Polk Co.: TNHC 509, 1345, 1601, 2029, 2720, 2757. San Jacinto Co.: UMMZ 170429.

San Jacinto-Galveston Bay Dr., 68 specimens, Tex.—Harris Co.: UMMZ 86325, 170399, 158845. Liberty Co.: TNHC 1587. Montgomery Co.: UMMZ 147541; TNHC 1165, 1394, 1146, 1204, 1219, 1476, 1517, 2004, 2957; TU 14065. Walker Co.: TNHC 1006, 1793, 2750.

Brazos Dr., 23 specimens, Tex.—Brazos Co.: UMMZ 129938, 129863, 129804, 129749. Robertson Co.: CU 33333. Waller Co.: TNHC 4267.

Colorado Dr., 52 specimens, Tex.—Bastrop Co.: TNHC 1890, 3715, 3796, 5272. Lee Co.: TNHC 2541. Wharton Co.: UMMZ 170310.

Navidad Dr., Tex.—Lavaca Co.: TNHC 1264 (1, 40); Navidad R., 2 mi. NW Seclusion; May 5, 1951.

Guadalupe Dr., Tex.—Gonzales Co.: USNM 166171 (16, 22-41); Guadalupe R., L. Belmont, 2 mi. above Wrights Camp; Apr. 17, 1952.

Nueces Dr., Tex.—Live Oak Co.: Lake Corpus Christi State Park, TNHC 4975 (1, 37); Feb. 1954 and TNHC 4974 (1, 41); Dec. 11, 1956. McMullen Co.: TNHC 1766 (6, 34-38); Nueces R., 10 mi. W Sutton; Dec. 6, 1947. TNHC 3005 (1, 38); 8.6 mi. N Tilden, San Miguel Cr.; Jan. 15, 1952. Uvalde Co.: USNM 1328 (1, 36); lectotype and MCZ 113 (1, 36); paratype; Rio Seco near Ft. Inge; and USNM 1329 (1, 31); Leona R. near Ft. Inge; paratype of *Boleosoma gracile.*

Etheostoma zoniferum (Hubbs and Cannon)

Hololepis zonifer—Hubbs and Cannon, 1935; 47-50, pl. I-III (original description); Fowler, 1945: 40 (Ala. R. after Hubbs and Cannon).

Etheostoma zoniferum—Bailey and Gosline, 1955:20, 44 (number of vertebrae); Eddy, 1947:219; Moore, 1957:198; Cook, 1959:35, 200, 208 (Miss.); Collette, 1961: 2051.

Types—Holotype, UMMZ 88803, 31 mm female; Ala., Pools of Catoma Cr., 5 mi. SW of Montgomery; Sept. 18, 1929; Creaser and Becker. Paratype, UMMZ 88822; Ala., Lowndes Co.; Pools of Big Swamp Cr., 25 mi. SW of Montgomery; Sept. 18, 1929; Creaser and Becker.

Diagnosis—*E. zoniferum* differs from its close relative *E. gracile* primarily in having the infraorbital canal incomplete with 2 + 4 pores. It also has fewer anal rays (mode: 6, $\bar{x}$:5.9), fewer scale rows above the lateral line (mode: 3, $\bar{x}$:3.2) and below the lateral line (mode: 8, $\bar{x}$:8.2). Maximum size of males — 36.6 mm and females 35.0 mm (Tombigbee R., UMMZ 163758).

Coloration—No specimens of non-breeding adult males or females were available. The patterns of breeding *E. zoniferum* are like those of breeding *E. gracile;* the patterns of the non-breeding individuals are probably also similar. The pattern of the non-breeding female *zoniferum* is probably like that of the breeding female *zoniferum,* as is usual in the subgenus *Hololepis.*

There are a few scattered medium-sized melanophores on the first dorsal fin membranes in the breeding female. Small melanophores are concentrated on the distal portions of the posterior membranes. The second dorsal rays are barred and large melanophores are scattered on the membranes, especially on the basal eighth of the fin. Melanophores outline the anal rays, and a few are present on the posterior membranes. The pectoral rays also are outlined. The pelvic fin is clear. The caudal fin is barred. The breast and belly are immaculate, with a few melanophores sometimes present posteriorly on the belly. Large melanophores are scattered on the cheek. All four orbital bars are present; the suborbital is the most prominent; the supraorbital extends onto the eye. The pored portion of the lateral line stands out as a narrow light line, but pigment is sometimes present on the distal margin of the pored scales. The median basi-caudal spot is prominent and indistinct spots are present at the upper and lower bases of the caudal fin. The sides are brown with blotches more or less apparent. The dorsal saddles are indistinct. The genital papilla is unpigmented. Figure 4 compares the patterns of breeding females of *E. zoniferum* and *gracile.*

The pectoral and caudal fins, basi-caudal spots, dorsal body surface, and genital papilla in the breeding male are colored like the respective parts of breeding females; other areas are darker. Melanophores are concentrated in the lower two-thirds of the first dorsal fin except for a narrow light basal area. The barring of the rays of the second dorsal fin is somewhat obscured by the greatly increased number of melanophores on the membranes. The anal and pelvic fins and the belly and breast are uniformly covered with small melanophores. The suborbital bar appears less distinct in the male because the cheek is darker. There is more pigment on the posterior portions of the pored lateral-line scales than in the female. The sides are more uniformly brown. The patterns of breeding males of *E. zoniferum* and *gracile* are compared in Figure 4.

In life, *E. zoniferum* is quite colorful. R. M. Bailey's field notes on UMMZ 158228 described the male as having a sub-terminal orange band on the first dorsal. The top of the head was a greenish-olive. The lower fins were white. The back was cream-colored and barred with brownish-grey. The lateral bands were greyish-blue.

Carl L. Hubbs' field notes on UMMZ 163758 described the male as having red spots forming a series along the light streak in the first dorsal fin. The red was rather indistinct forward and stronger posteriorly, and the spots were smaller posteriorly. There was a trace of these marks in the female. The first dorsal fin of the male was sooty. The body of the male had deep metallic blue-green lateral bars. The color has completely faded out in the preserved specimens.

Genital Papilla.—The genital papilla in the breeding female is like that of *E. gracile* (Fig. 1c).

Breeding Tubercles—Tubercles are present on the anal fin rays and on the rami of the lower jaw. None have been seen on the pelvic fin rays, probably because of lack of material taken at the height of the breeding season. A few small tubercles are present on the distal parts of the anal fin rays, especially on the distal third of the third ray. In a 38 mm male taken on April 16 (UMMZ 163758) from the Tombigbee River, there are four low tubercles in a row on the ramus of the right half of the lower jaw but none are discernible on the left half. This incomplete development of the jaw tubercles is taken as further evidence that the tubercles of this specimen either have not reached, or are past, maximum development. The distribution of tubercles on the chin and anal fin is like that in *E. gracile* (Fig. 1h, m).

Development—There is little information on the change of characters with age in *E. zoniferum.* The supratemporal canal seems to show the same changes as in *E. fusiforme.* Eight specimens smaller than 25.9 mm had incomplete supratemporal canals, sixteen between 26.0 and 29.9 mm were equally divided between complete and incomplete, and the five available specimens 30.0 mm and larger had complete canals. None of the available specimens were small enough to detect any other changes with age.

Habitat—Hubbs and Cannon (1935) described the habitat at the first two localities from which the species was known as pools in creek bed; water: clear, murky; bottom: gravel, mud; depth to four feet; vegetation: sparse *Chara;* temperature: moderate, warm.

Distribution—Found only in the Alabama and Tombigbee Rivers below the Fall Line (Fig. 5). I do not know why it is not distributed still farther south in these two river systems. Both *E. gracile* and *zoniferum* have been taken in the Tombigbee River in the state of Mississippi. Further collecting is desired in order to find out if they occur together.

Geographic Variation—Tables 10-16 compare the Alabama and Tombigbee populations of *E. zoniferum* with the populations of *E. gracile.* On the basis of the small samples now available, there seem to be no differences between the populations of the two rivers. Tables 38-49 compare *E. zoniferum* with the other species of the subgenus *Hololepis.*

Specimens Examined—Alabama R., Ala.—Macon Co.: UMMZ 111223 (2, 22-23); 3 mi. E of Tuskegee; June 3, 1931. UMMZ 124012 (14,24-28) and USNM 117546 (1, 27); Slough Lake, Tuskegee, East Opintoloco Cr., Sept. 13, 1937. UMMZ 124020 (2, 30-34); Big Swamp, Tuskegee; Sept. 13, 1937. API 566 (2, 26); Slough Lake, SE of Tuskegee, Opintoloco Cr.; Sept. 13, 1937. API 567 (1, 37); Watering Br., Tuskegee; Oct. 3, 1939. Montgomery Co.: UMMZ 88803 (1, 30); pools of Catoma Cr., 5 mi. SW of Montgomery; Sept. 18, 1929; holotype of *Hololepis zonifer.* UMMZ 158228 (1, 27); cr. 19 mi. SE of Montgomery on US 231; Sept. 4, 1939. Wilcox Co.: UAIC 526 (1, 26); Chilatchee Cr. near Alberta; Aug. 30, 1956. UAIC 536 (1, 29); Prairie Cr., 13 mi. E of Camden and 0.5 mi. W of Oak Hill near Ala. 10; Aug. 30, 1956.

Tombigbee R., Ala.—Marengo Co.: UAIC 428 (1, 28); Beaver Cr., 10 mi. SW of Linden (near Ala. 79 and 10 mi. N of jct with Ala. 10); Aug. 24, 1954. Greene Co.: UMMZ 163758 (2, 35-37); flood pool in Tombigbee R., 2½ mi. E of Epes: April 16, 1941. Miss.—Monroe Co.: UMMZ 157751 (1, 28); Tombigbee R., 2½ mi. W of Amory; Aug. 16, 1939.

Etheostoma fusiforme fusiforme (Girard)

Boleosoma fusiforme—Girard, 1854:41 (original description).

Hololepis fusiformis—Putnam, 1863:4 (original description of *Hololepis* by Agassiz); Cope, 1864:233 (diagnosis of the species of *Hololepis*); Greeley, 1939:43 (Long Island, N. Y.); Webster, 1942:127, 196, 203 (Pataganset Lake, Conn.); Cronk, 1950:d (Long Island); Everhart, 1950:43-44 (Me.); Raney, 1950:177-178, 186, 190 (James R., Va.); Smith, 1950: (fish fauna of N. J. lakes and ponds); Smith, 1953a: (N. J.); Smith, 1953b:168 (acidwater fishes of southern N. J.); Stroud, 1955:7, 353 (Ames Long Pd., Mass.); Fletcher, 1957:202-203 (N. J. specimens spawned in aquarium); Mullan and Tompkins, 1959:132.

Hololepis erochrous—Cope, 1864:232 (original description); Fowler, 1940:23 (Bucks Co., Pa.); Fowler, 1952:124 (locality records, N. J.).

Boleichthys fusiformis—Smith, 1907:267-268 (in part, N. C.); Fowler, 1911:13 (ecology, Del.); Schrenkeisen, 1938:234 (brief description); Fowler, 1935:6 (in part, general distribution); Driver, 1942: 285 (in key, in part); Driver, 1950:298 (in key).

Copelandellus quiescens—Smith, 1907: 268-269 (in part, ecology and spawning, N. C.).

Hololepis fusiformis erochrous—Hubbs and Cannon, 1935:72-77, pl. I, III (description, range, synonymy); Mansueti, 1951: 301-302 (ecology, Md.); Harmic, 1952:12 (Del.); Mansueti and Elser, 1953:118 (ecology, Chambers Lake, Md.); Truitt, 1953:1 (in Md. pond after rotenone application).

Hololepis fusiformis atraquae—Hubbs and and Cannon, 1935:68-72, pl. I, III (original description); Fowler, 1945:40 (Potomac R.).

Hololepis fusiformis insulae—Hubbs and Cannon, 1935:83-86, pl. I, III (original description).

Hololepis fusiformis metae-gadi.—Hubbs and Cannon, 1935:81-86, pl. I, III (original description).

Hololepis fusiformis fusiformis—Hubbs and Cannon, 1935:77-81, pl. I, III (description, range, synonymy); Gordon, 1937:102, 116 (N. H.); Bailey, 1938:150-151, 156-161, 176-177, 183 (Merrimack River watershed, N. H.); Bailey and Oliver, 1939:152, 179, fig. 78 (N. H.); Cooper, 1939:55 (Me.); Carpenter and Siegler, 1947:77 (N.H.); Harrington, 1947:191 (fry in N. H.).

Hololepis thermophilus—Hubbs and Cannon, 1935:63-67, pl. I, III (original description); Fowler, 1945:40 (Neuse R.); Frey, 1951:9, 37-41 (N. C. Bay Lakes).

Hololepis thermophilus thermophilus—Bailey and Frey, 1951:191-204, pl. 1-8 (comparison with *H. thermophilus oligoporus*).

Hololepis thermophilus oligoporus—Bailey and Frey, 1951:191-204, pl. 1-8 (original description).

Etheostoma fusiforme fusiforme—Bailey and Gosline, 1955:20, 44 (number of vertebrae); Collette, 1961:2051.

Etheostoma fusiforme erochroum—Bailey and Gosline, 1955:20, 44 (number of vertebrae).

Etheostoma fusiformis—Smith, 1957: (N. J.), 125-126 (food of *Esox niger*).

Etheostoma thermophilum—Moore, 1957: 198.

Etheostoma fusiforme—Eddy, 1957:219, 222, fig. 546; Moore, 1957:198; Collette, 1958:77 (ecology, Me.); Behnke and Wetzel, 1960:143 (Conn.).

Etheostoma barratti—Eddy, 1957:220 (range, in part); Knapp, 1953-128 (range, in part).

Types—Hubbs and Cannon (1935) selected USNM 1188, a 33 mm female, as the lectotype from a series of syntypes (USNM 94686) collected by S. F. Baird in a tributary of the Charles River at Framingham, Mass. Other paratypes of the same original lot are MCZ 24589 (4 specimens) and UMMZ 86582 (1 specimen).

Diagnosis—Distinguished from the other species of the subgenus *Hololepis* by a combination of the following characters: two anal spines; interorbital pores absent; usually nine preoperculomandibular pores; infraorbital canal incomplete; breast entirely scaled. Distinguished from *E. f. barratti* by the following: preopercle usually entire (90% of specimens examined); infraorbital usually 2 + 3 (80%); fewer interorbital scales (0-12, x̄:2.0); parietal less completely scaled (usually 0-20%, x̄:9.5%). Maximum size of males 44.1 mm, females 49.3 mm (CU 33194, N. Y., Suffolk Co., Lower Lake Yaphank).

Coloration—The patterns in this form are extremely variable. Much of this variation is associated with the color of the water from which the specimens were taken, darker stained waters generally produce darker fish, etc. The following description is based upon "typical" specimens and the most common variations from the "typical" pattern.

In the female small melanophores are concentrated on the posterior edge of the first dorsal spines and a few scattered melanophores may be present at the base of the membranes. Some large melanophores are scattered over the membranes of the second dorsal fin. The anal rays are barred; some specimens have a few melanophores on the membranes. The pelvic rays bear a few scattered melanophores. The pectoral and caudal fins are barred. The belly and breast vary from being immaculate to having scattered melanophores. The cheek has a few scattered large melanophores. All four orbital bars are present; the suborbital is usually the most prominent; the supraorbital extends onto the eye and the suborbital sometimes does so. The pored portion of the lateral line appears as a narrow light line which is interrupted by some pigment underneath the scales. There is usually a prominent black basi-caudal spot just below the center of the caudal base; the dorsal and ventral basi-caudal spots are usually faint. The sides have 8-13 indistinct dark brown or black blotches below the lateral line, which tend to fuse into a dark lateral band. Some specimens, especially from New Jersey and Delaware, have this lateral band exceptionally prominent in contrast to the upper part of the body which is a light tan. Approximately 12 dorsal saddles alternate with the lateral blotches in some specimens. The genital papilla is usually unpigmented, but small melanophores often encircle the anal region. Figure 6 compares breeding females from five localities.

In the non-breeding male the pectoral, pelvic, and caudal fins, orbital bars, basi-caudal spots, genital papilla and dorsal body

Figure 6. Breeding patterns of female *Etheostoma fusiforme fusiforme*. (from top to bottom) CU 31847; 38.5 mm; N.Y., Suffolk Co., Lake Yaphank; Apr. 19, 1958. CU 32725; 38.0 mm; N.J., Atlantic Co., Great Egg Harbor dr.; May 16, 1959. CU 31640; 37.9 mm; N.C., Northampton Co., Roanoke dr.; Apr. 4, 1958. CU 25304; 28.4 mm; N.C., Bladen Co., Jones Lake; Aug. 24-26, 1947. CU 14302; 35.7 mm; N.C., Columbus Co., Waccamaw dr.; Mar. 29, 1949. (Photograph by Douglass M. Payne)

surface are colored like the female; the other areas are darker. The dorsal and anal fins have varying numbers of melanophores scattered on the membranes. The belly and breast range from immaculate to being covered with small melanophores. The cheek is darker than that of the female. The narrow light line is interrupted more than it is in the females. Most non-breeding males tend to have the body more uniformly pigmented, obscuring the lateral blotches.

In the breeding male the pectoral and caudal fins, pored portion of the lateral line, basi-caudal spots, genital papilla, and dorsal body surface all have the same melanophore distribution as the non-breeding male; other regions are darker. The large number of melanophores present on the dorsal fins coalesce, in specimens from some localities, and form a solid black band (Fig. 7). The pigmentation is most intense on the first three or four interspinous membranes. The anal and pelvic fins have large melanophores scattered over their membranes; these are usually more prominent on the anal. The cheek, belly, and breast are much darker than in the female and non-breeding male. The sides are similar to the non-breeding male, but with lateral blotches obscure in some specimens. Figure 7 shows the pigment pattern of breeding males from five localities.

Genital Papilla—In the breeding female, the genital papilla is an elongate tube with a slit opening on the anterior side (Fig. 1f). The papilla is a conical tube either with or without a bulbous enlargement similar to that usually present in *E. gracile* (Fig. 1h). The tip is more pointed than in the other species of the subgenus *Hololepis*.

Breeding Tubercles—Present on the anal rays (similar to *E. gracile,* Fig. 1j) and on the undersides of the pelvic rays (Fig. 1k). They seem to be less developed in *E. fusiforme fusiforme* than in *E. f. barratti,* and are present for a shorter time. Tubercles have been found on specimens from only fourteen collections and in some series, small tubercles were present on only one or two specimens. This may be because most collections were either made before or after the spawning season. In the southern part of the range, tubercles have been found on: March 25 (Ellis Lake, CU 29983); March 28 and 29 (Waccamaw R., DU B-49-12 and CU 14302); April 4 (Roanoke R., CU 31640); and March 27 (Chowan R., CU 16880). Tubercles have been found on specimens from a number of New Jersey collections made on May 17 and 18, 1958 and 1959 (CU 31083, 32739, 31797, 31787, 31791, 31794, 32744). One specimen taken on March 27 in Lake Yaphank, N. Y., (CU 31850) had tubercles on the anal fin while most males in an April 19 collection (CU 31847) had tubercles on both anal and pelvic fins.

Development—Two characters clearly change with age in *E. fusiforme fusiforme:* the condition of the supratemporal canal and the number of pored lateral-line scales. The supratemporal canal is incomplete in young and juveniles and normally becomes complete by maturity. Table 31 shows the development of this character in a number of *E. fusiforme* populations. The Long Island population may be taken as an example of normal development. In young specimens the supratemporal canal extends only part way up the side of the head, with the two sides of the canal widely separated. The two sides grow toward each other until they join and the only vestige of the former separation is the central pore. All Long Island specimens up to 21 mm have the supratemporal canal incomplete. Some specimens from 21-25 mm have the supratemporal canal complete and others incomplete. Those 25 mm and larger have complete supratemporal canals (incomplete canals in only four adults). The situation is more complex in the North Carolina Bay Lakes and will be discussed under geographic variation, supratemporal canal.

The second character that changes with age is the squamation. As in *Perca flavescens* (Pycha and Smith, 1955), *Micropterus dolomieui* (Everhart, 1949:113) and *Pomoxis nigromaculatus* (Ward and Leonard, 1954), scales first appear on the caudal peduncle at the base of the caudal fin. Later they extend forward along the lateral line and then spread dorsally and ventrally. Sixteen larvae (9.1-11.1 mm) taken on May 16 and 17, 1958 in New Jersey (CU 32725 and CU 32739) completely lack scales. Four specimens (13.3-14.9 mm) from Lake Ronkonkoma, N. Y., taken on July 6, 1956 (CU 30279) also lacked scales. Two specimens (13.4 mm) taken from Lake Ronkonkoma on Aug. 3, 1956 (CU 30347) had

TABLE 18.
Number of total lateral-line scales in Etheostoma fusiforme

Drainage	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	N	x̄	SD	SE
f. fusiforme																												
Ogunquit						1	2	2	—	—	2	3	1	1											12	49.08	2.71	.25
Cape Neddick							1	2	3	1	3	3	1	1	-	1									16	49.75	2.41	.19
North-Isinglass											1	2													3	50.67		
Merrimack					1	1	8	6	6	13	13	15	8	7	10	5	1								94	50.39	2.73	.28
Ipswich								4	5	7	7	5	5	1	1	-	1								34	49.97	2.12	.36
Mass. Bay									1	4	7	3	3	5	2	—	1	-	1						27	51.48	2.33	.45
Neponset								2	3	1	5	4	[illegible]		2	2									22	50.68	2.38	.51
North R.								1	1		3	2	1	1											9	50.22	1.86	.62
Mills R					2	3	3	9	20	17	10	10	4	1	2										81	48.84	2.03	.23
other Cape Cod							1	1	6	12	12	17	21	26	21	5	11	1	2	1	1				138	52.34	2.50	.21
Nantucket	1	1	2	1	3	2	[illegible]	2	—	3															17	44.71	2.59	.63
Weweantic R					1	1	3	3	4	2	2	1	1	2											20	48.35	2.54	.60
Taunton R					1	1	1	-	—	2	2	12	5	6	3	1	-	1							35	51.34	2.57	.43
Seekonk							1	1	-	4	2	7	5	4	1	1									26	51.04	2.05	.40
Pataganset L											1		2	1	3	—	3	1	2						13	54.62	2.47	.68
Ronkonkoma L.											1	1	5	7	5	10	16	14	1	4	3		2		69	55.71	2.43	.29
Yaphank L.							1		3	1	4	11	25	26	29	23	22	13	5	8	2				173	54.13	2.49	.19
Raritan							1		-	[illegible]	[illegible]	7	14	13	8	3	3	-	1						56	52.50	2.02	.27
Coastal N.J.		3	3	7	17	19	23	18	11	11	8	4	4	3	1										132	46.58	2.72	.24
Delaware R			2		3	7	11	9	8	11	7	7	2												67	47.67	2.34	.29
Coastal Del.-Md						2	2	6	10	10	11	5	4	4	2	1	1								58	49.62	2.40	.32
Chesapeake Bay						2	2	2	8	7	16	12	14	11	8	5	2		1						88	51.28	2.40	.26
Potomac				1		3	6	3	3	5	7	[illegible]	2	2	1										31	48.62	2.71	.46
James					2	2	2	[illegible]	4	1															14	46.57	1.60	.43
Nansemond				1				1	2	1	1	4		2	1										13	49.92	2.96	.82
Chowan		1	1	3	5	4	8	11	25	17	13	11	7	3	2										115	48.58	2.53	.24
Roanoke				1	1	5	2	15	19	16	7	15	8	6	-	3									98	49.17	2.44	.25
Neuse			2	1	1	1	6	7	9	9	6	3	2		2	1									50	48.28	2.72	.38
Ellis L				1	2	4	8	4	11	14	6	3	1	2	1										57	48.18	1.46	.19
Singletary L.								2	6	7	12	6	9	7	2		1								52	50.65	1.98	.27
Salters L.					1	—	4	11	4	7	6	7	2	1	2	1		1							47	49.23	2.66	.39
Jones L						1	2	7	11	5	12	14	9	3	2	1	1								70	49.96	2.22	.27
White L.					2	3	11	13	29	24	29	22	19	9	8	2	2		1						174	49.75	2.48	.19
other Cape Fear			2		1	3	4	2	4	4	[illegible]	4	1	1											29	47.86	2.84	.53
Waccamaw				4	[illegible]	2	2	5	7	4	10	13	10	5	5		1								71	49.68	3.09	.37
f. barratti																												
Pee Dee							2	[illegible]	[illegible]	7	7	6	1	2	3	3	4				1				47	51.13	3.11	.46
Santee					2	1	1	5	6	15	4	11	8	8	2	1	1								65	50.11	2.51	.31
Edisto									4	2	1	3	1	1	3		1								16	51.00	2.61	.65
Combahee-Broad									1	3	3	2	2		2	1									14	51.00	2.15	.57
Savannah						2	4	5	15	11	17	21	20	22	16	17	12	25	6	7	3	3	3	1	210	53.16	3.78	.26
Ogeechee							1	2	3	2	6	3	5	1	1		2			1					27	50.85	2.97	.57
Altamaha-Satilla						1	—	4	1	1	11	4	7	8	3		2								42	51.10	2.42	.37
St. Marys				1	2	1	3	5	5	5	4	5	6	4											41	49.10	2.72	.42
St. Johns								1	2	6	9	17	15	15	16	9	5	6	4	2	1				108	52.96	2.66	.26
St. Cloud					1		2	2	7	8	5	4	5	3		1	1								39	49.79	2.47	.40
Orlando					7	9	4	14	13	11	20	10	10	3	1	5	3								108	49.00	2.86	.28
Oklawaha-St. Johns							1		2	[illegible]	4	7	5	7	11	3	5	5	2		1				56	[illegible]	2.90	.39
Okeechobee					1	2	2	1	4	4	9	7	6	6	2		2								46	[illegible]	2.70	.40
S. Fla				2	—	—	4	1	3	4	5		3	2											24	48.71	2.77	.57
Tampa Bay							3	2	4	1	1	4	2		2		1			1					21	50.19	3.49	.76
Withlacoochee-Waccasassa						1		1	4	5	4		4	1	1			1							[illegible]	50.05	2.43	[illegible]
Newnan L					1	—		1	3	4	[illegible]	9	9	9	9	6	7	3	6	2	2				74	53.58	3.27	.37
other Suwannee								3	1	2	4	2	1	2	4										19	50.68	2.49	.57
Crystal L			2	2	1	5	1	4	6				1												25	46.04	2.26	.45
Okefenokee				1	—		1	4	10	9	11	8	5	4	1		2								56	49.89	2.34	.31
Fenholloway-St. Marks										4	3	8	4	6	2	2	1								30	51.80	1.88	[illegible]
Ochlockonee				1	—	3	5	9	11	9	14	11	8	12	8	1	1	1			1				95	50.24	2.96	.30
Apalachicola					1			3	2	3	8	4	8	5	1	2	1	1							39	51.03	2.64	.42
Choctawhatchee-Perdido				1	—	2	1	2	4	9	1	4	2	4		2									35	49.60	2.43	.41
Mobile Bay									1	--		[illegible]	2		1		1				1				8	53.00	3.66	1.30
Miss. Sound									1	—	1	1	—	1	1			1							6	52.17		
Pearl-Pontchartrain											1	2	4	6	6	4	[illegible]	4	4	3					[illegible]	55.30	2.80	.45
Yazoo																			1						1	58.		
Reelfoot L.													1	—		1									2	[illegible]		
Red												1	3	4	1	3	3	4	6	1		—		1	[illegible]	[illegible]	2.59	.46
French Broad						1	1		5	4	6	9	7	2	5	3	2								45	51.78	2.54	.38

TABLE 19.
Number of pored lateral-line scales in Etheostoma fusiforme

Drainage	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	N	x̄	SD	SE
f. fusiforme																																										
Ogunquit										2	1		[illegible]	1	2	2						1																	12	[illegible]	[illegible]	[illegible]
Cape Neddick										1	4	2			1																								16	[illegible]	1.41	[illegible]
North-Isinglass												2		1																										11.67		
Merrimack									1	1	4	11	14	25	15	9	11	1	1				1																94	13.29	2.86	.29
Ipswich											1	[illegible]	[illegible]	5	8	9	3	5																					[illegible]	14.44	1.67	.29
Mass. Bay										1	—		1	[illegible]	10	1	2	1																					27	[illegible]	1.63	[illegible]
Neponset										1	1	1	2	5	8	2	1																						21	[illegible]	2.69	.59
North R.														4	2																								[illegible]	13.89	.93	.31
Mills R									1		3	11	10	15	7	2	1	1																					[illegible]	[illegible]	1.62	.23
other Cape Cod						1	1	3	1	[illegible]	3	[illegible]	20	25	22	21	14	4	1			1																	[illegible]	[illegible]	2.41	.21
Nantucket								1		1	1	5	1																										17	11.20	1.61	.40
Weweantic R										1	—	1	2			5																							18	[illegible]	[illegible]	[illegible]
Taunton R												2	4	8	10	5	1																						[illegible]	[illegible]	[illegible]	[illegible]
Seekonk									2	2	1	2	1	9			1																						[illegible]	12.04	2.01	.41
Pataganset L																1	2	6																					[illegible]	[illegible]	[illegible]	.26
Ronkonkoma L.										1		2	[illegible]	6	15	27	[illegible]	11	4	2	1																		81	[illegible]	1.90	.21
Yaphank L.												1	6	12	[illegible]	[illegible]	42	20	10	5	1	1																	[illegible]	[illegible]	1.44	.11
Raritan													[illegible]	8	8	8	11	8	5	1	1																		56	[illegible]	2.04	.27
Coastal N.J.													5	16	27	22	17	12	7	1	[illegible]			1															[illegible]	[illegible]	[illegible]	.19
Delaware R												[illegible]	1	11	13	21	9	6	2				1																67	14.76	1.78	.22
Coastal Del.-Md												1		[illegible]	[illegible]	15	10	5	5	1	[illegible]	[illegible]	2																56	[illegible]	[illegible]	.32
Chesapeake Bay														3	5	7	11	11	[illegible]	11	12	[illegible]	4	2	1														86	17.88	2.45	.26
Potomac											2	6	6	[illegible]	3	[illegible]																							[illegible]	[illegible]	1.29	.22
James													2	1	2	[illegible]	1	2																					11	14.05	1.66	.41
Nansemond														4	[illegible]			1		1		2																	11	16.00	[illegible]	.92
Chowan												2	[illegible]	21	[illegible]	27	10	10	4	1																			[illegible]	[illegible]	1.69	.16
Roanoke								1		1	[illegible]	9	14	[illegible]	18	7	5	7	2	1		1	1																[illegible]	[illegible]	[illegible]	[illegible]
Neuse													2	2	6	8	9	9	[illegible]	7		2	1																49	[illegible]	[illegible]	[illegible]
Ellis L								1	[illegible]	2		[illegible]	1	6	12	8	[illegible]			—																			18	[illegible]	1.94	[illegible]
Singletary L.				[illegible]	1		[illegible]	1		[illegible]	5	7	7	1	[illegible]	4	1																						[illegible]	10.19	[illegible]	[illegible]
Salters L.				2		2		8	9	9		5	1	1	1																								[illegible]	7.12	.11	[illegible]
Jones L	11	3	8	[illegible]	3	8	15	6	14	11	10	[illegible]	[illegible]	1			1																						[illegible]	6.14	[illegible]	[illegible]
White L.			1				1	1		[illegible]	5	12	[illegible]	7	26	51	[illegible]	[illegible]	21	22	14	6	5	2	2		1												[illegible]	15.54	[illegible]	.17
other Cape Fear									1		[illegible]	2	1	[illegible]	[illegible]	7	2	1			2	1																	28	14.07	[illegible]	.57
Waccamaw								1		1	1	2	11	11	9	6	15	6	5			1																	[illegible]	[illegible]	[illegible]	.29
f. barratti																																										
Pee Dee															1	1	[illegible]	4	9	[illegible]	5	[illegible]	7	1	5	1		1											47	19.98	2.88	[illegible]
Santee									1				1	[illegible]	7	11	4	9	7	1	6	7	[illegible]	4	1	—													67	17.66	[illegible]	[illegible]
Edisto																	1	2	1	2	2	1	2	2	1	1	1												16	[illegible]	[illegible]	.75
Combahee-Broad			1													1		1			1	4	2	1		1	1												[illegible]	19.69	[illegible]	1.68
Savannah												1	1		[illegible]	5	[illegible]	6	14	15	17	14	19	[illegible]	15	14	16	12	6	1	7	[illegible]	1	2	[illegible]	[illegible]	1	1	[illegible]	[illegible]	4.82	[illegible]
Ogeechee																1		[illegible]	1		2	2	2	[illegible]	[illegible]	[illegible]		2	2		1				1			1	26	[illegible]	4.61	.91
Altamaha-Satilla																				1	1	5	4	8	8	2	8	2			1		2						[illegible]	21.14	2.82	[illegible]
St. Marys																	1	[illegible]	1	1	5	2	2	4	3	8	1	[illegible]	1	—									[illegible]	[illegible]	[illegible]	[illegible]
St. Johns																	2	1	6	9	11	9	10	1	5	[illegible]	9	7	4	1	2	2	1		1				102	[illegible]	[illegible]	[illegible]
St. Cloud		1			1		1		[illegible]		3	4	2		[illegible]	10	4	[illegible]	2	1																			[illegible]	[illegible]	.77	.61
Orlando			2	2	1	[illegible]	2	1	1	2	1	7		5	2	8	4	[illegible]	10	[illegible]	5	[illegible]	4	4			4	[illegible]		1			1						97	16.76	6.16	[illegible]
Oklawaha-St. Johns									1					—	1		[illegible]	5	4	2	[illegible]	5	1	6	5	4	4	[illegible]	1		1	1							[illegible]	[illegible]	1.67	[illegible]
Okeechobee						1		1	2	2		1	1	2	[illegible]	4	4		4	1		4	3	—			3	1			1								[illegible]	[illegible]	3.68	.85
S. Fla																		1	1	1	—	[illegible]	6	1	1	[illegible]	[illegible]												[illegible]	21.58	2.48	.50
Tampa Bay																				1	1	2	1	4	1	2	4	4			1		1						22	21.68	[illegible]	.68
Withlacoochee-Waccasassa																2	1	2	4		[illegible]		1	2	1	—	1		1			3							21	20.90	1.12	.97
Newnan L.																1	1	2	2	1	6	6	6	6	1	12	[illegible]	7	1	6	[illegible]	1						1	71	[illegible]	[illegible]	.47
other Suwannee																1			1		1	1	5	5	1	2	1	1											19	[illegible]	[illegible]	[illegible]
Crystal L.	4		2	2				2	2	1	3				1		1																						18	[illegible]	4.86	1.13
Okefenokee																	1	1	3	2	—		7	[illegible]	7	6		7	2	1									[illegible]	[illegible]	[illegible]	[illegible]
Fenholloway-St. Marks													1	1	1	1		1	8	3	2	2	1	—	—		1		—										[illegible]	19.71	4.02	[illegible]
Ochlockonee													1	1	1	1			8	10	[illegible]	10	7	5	5	12	[illegible]		1	2				1					[illegible]	[illegible]	[illegible]	[illegible]
Apalachicola																	—	2	3	5	6	[illegible]	—				5			1									[illegible]	[illegible]	[illegible]	[illegible]
Choctawhatchee-Perdido																1	2	[illegible]	3	1	[illegible]	2	—	—	2	1	1	1											[illegible]	[illegible]	[illegible]	.61
Mobile Bay																1	1	2	1				1	1	1														8	19.00	[illegible]	1.22
Miss. Sound															1			1		1	—			[illegible]		1													6	19.17		
Pearl-Pontchartrain														—		5	[illegible]	—	6	4	[illegible]	6	2	3		1													[illegible]	[illegible]	[illegible]	.50
Yazoo										1																													1	[illegible]		
Reelfoot L.															1					1																			2	[illegible]		
Red										1	-			[illegible]		[illegible]	6	8	4		1		1																[illegible]	[illegible]	2.56	.45
French Broad													—	2	1	4	[illegible]	14	[illegible]	1	6	2	4	3	1														46	[illegible]	[illegible]	.15

TABLE 20.
Number of first dorsal spines in Etheostoma fusiforme

Drainage	8	9	10	11	12	13	x̄
f. fusiforme							
Ogunquit		2	9	–	1		10.00
Cape Neddick		2	3	1			9.83
North-Isinglass		3					9.00
Merrimack		15	53	26	1		10.14
Ipswich		12	18	4			9.76
Mass. Bay		2	20	3	2		10.19
Neponset		3	16	3			10.00
North		2	6	1			9.89
Mills		1	5	6			10.42
other Cape Cod	5	49	66	16	2		9.72
Nantucket	12	4					8.25
Weweantic		14	6	1			9.38
Taunton		9	21	5			9.89
Seekonk		7	19	1			9.78
Pataganset L.		5	8				9.62
Ronkonkoma L.		4	36	10	1		10.16
Yaphank L.		13	19	1			9.64
Raritan	8	21	19	7			9.45
Coastal N. J.	4	34	62	19	2		9.84
Delaware		10	33	15	1		10.12
Coastal Del.-Md.			2	4			10.67
Chesapeake Bay		8	47	20			10.16
Potomac		2	14	1			9.94
James			14				10.00
Nansemond	1	8	3				9.17
Chowan			11	68	34	2	11.23
Roanoke	1	27	46	7	1		9.76
Neuse		13	27	8			9.90
Ellis L.		26	28	3			9.60
Singletary L.	12	23	8				8.91
Salters L.	14	20	2				8.67
Jones L.	12	27	6				8.87
White L.	4	28	29	4			9.51
other Cape Fear		9	10	2			9.67
Waccamaw	3	18	27	15			9.86
f. barratti							
Pee Dee	1	13	23	11	1		9.96
Santee	2	13	42	11	1		9.94
Edisto		1	13	2			10.06
Combahee-Broad			10	4			10.29
Savannah		13	123	64			10.26
Ogeechee	2	2	12	10	1		10.22
Altamaha-Satilla		1	17	15	1		10.47
St. Marys		2	14	11			10.33
St. Johns		6	23	7	1		10.08
St. Cloud		9	24	6			9.92
Orlando		2	14	3			10.05
Oklawaha-St. Johns	2	7	28	12			10.02
Okeechobee	1	12	24	3			9.73
S. Fla.		2	10	3			10.07
Tampa Bay		7	7	2			9.69
Withlacoochee-Waccasassa			15	7			10.32
Newnan L.		3	14	9			10.23
Suwannee		1	15	3			10.11
Crystal L.	1	4	7	3			9.80
Okefenokee		4	29	19			10.29
Fenholloway-St. Marks	1	1	17	11			10.27
Ochlockonee		4	33	22	1		10.33
Apalachicola		2	15	9	2		10.39
Choctawhatchee-Perdido		5	15	14	2		10.36
Mobile Bay		2	4	2			10.00
Miss. Sound			6	1			10.14
Pearl-Pontchartrain		9	14	6	1		9.97
Reelfoot L.		1	–	1			10.00
Red			10	14	1		10.64
French Broad	2	15	27	3			9.66

TABLE 21.
Number of second dorsal rays in Etheostoma fusiforme

Drainage	8	9	10	11	12	13	x̄
f. fusiforme							
Ogunquit			5	7			10.58
Cape Neddick			2	4			10.67
North-Isinglass				3			11.00
Merrimack		7	42	39	7		10.48
Ipswich			20	12	1		10.42
Mass. Bay	1	–	15	11			10.33
Neponset			7	15			10.68
North			4	5			10.56
Mills			4	5	3		10.92
other Cape Cod		1	27	83	25	2	11.00
Nantucket			4	3	1		10.63
Weweantic			3	9	9		11.29
Taunton			16	18	1		10.57
Seekonk			6	18	3		10.89
Pataganset L.			9	4			10.31
Ronkonkoma L.			5	31	12	2	11.22
Yaphank L.			1	16	16		11.45
Raritan		1	21	28	6		10.70
Coastal N. J.		1	26	67	25	2	11.01
Delaware		1	26	33			10.53
Coastal Del.-Md.			1	4	1		11.00
Chesapeake Bay			8	56	10	1	11.05
Potomac			3	12	2		10.94
James			6	7	1		10.64
Nansemond		1	7	3	1		10.33
Chowan		7	60	45	3		10.38
Roanoke			40	35	7		10.60
Neuse		1	19	24	4		10.65
Ellis L.		5	33	17	2		10.28
Singletary L.	1	9	24	9			9.95
Salters L.		1	17	17	1		10.50
Jones L.		13	27	5			9.82
White L.		5	43	17			10.18
other Cape Fear		1	4	16			10.71
Waccamaw		20	30	12			9.87
f. barratti							
Pee Dee	1	19	25	3	1		9.67
Santee			18	36	14	1	10.97
Edisto	1	4	10	1			9.69
Combahee-Broad		2	10	2			10.00
Savannah	1	10	58	91	40		10.80
Ogeechee			5	19	3		10.93
Altamaha-Satilla			6	22	5	1	11.03
St. Marys			11	15	1		10.63
St. Johns		1	11	21	4		10.76
St. Cloud		1	16	19	3		10.62
Orlando			10	8	1		10.53
Oklawaha-St. Johns			11	25	12	1	11.06
Okeechobee			15	14	10	1	10.93
S. Fla.			2	9	4		11.13
Tampa Bay		1	2	11	2		10.88
Withlacoochee-Waccasassa			3	10	8	1	11.32
Newnan L.		1	3	13	9		11.15
Suwannee			7	9	2	1	10.84
Crystal L.			6	9			10.60
Okefenokee			12	27	13		11.02
Fenholloway-St. Marks			5	13	11	1	11.27
Ochlockonee		1	28	27	3	1	10.58
Apalachicola			8	14	6		10.93
Choctawhatchee-Perdido			15	19	2		10.64
Mobile Bay			3	4	1		10.75
Miss. Sound			3	2	2		10.86
Pearl-Pontchartrain		1	10	15	3		10.69
Reelfoot L.			2				10.00
Red			4	16	5		11.04
French Broad			5	29	12	1	11.19

TABLE 22.

Number of scale rows above and below lateral line in Etheostoma fusiforme

Drainage	Above the lateral line						Below the lateral line								
	2	3	4	5	N	x	6	7	8	9	10	11	12	N	x̄	Total
f. fusiforme																
Ogunquit	3	9			12	2.75			6	6				12	8.50	11.25
Cape Neddick		5			5	3.00			1	3	2			6	9.17	12.17
North - Isinglass		3			3	3.00			2	1				3	8.33	11.33
Merrimack	8	87			95	2.92		4	50	32	6	1		93	8.46	11.38
Ipswich	13	20			33	2.61			22	12				34	8.35	10.96
Mass. Bay	1	26			27	2.96			11	16				27	8.59	11.55
Neponset	1	20	1		22	3.00			12	10				22	8.45	11.45
North		9			9	3.00		1	5	3				9	8.22	11.22
Mills		12			12	3.00			10	2				12	8.17	11.17
other Cape Cod	28	106	2		136	2.81		12	75	44	4	1		136	8.32	11.13
Nantucket	2	6			8	2.75		3	4		1			8	7.88	10.63
Weweantic	2	19			21	2.90		2	8	10				20	8.40	11.30
Taunton	7	28			35	2.80		1	22	11				34	8.29	11.09
Seekonk		26			26	3.00		1	16	7				24	8.25	11.25
Pataganset L.		13			13	3.00			11	2				13	8.15	11.15
Ronkonkoma L.	3	41	4		48	3.02			22	25	2			49	8.59	11.61
Yaphank L.		33			33	3.00			22	10	1			33	8.36	11.36
Raritan		49	7		56	3.13		7	38	11				56	8.07	11.20
coastal N. J.	13	102	2		117	2.91	1	24	58	29	3			115	8.08	10.99
Delaware	3	46	3		52	3.00		14	29	9	2			54	7.98	10.98
coastal Del. - Md.		4	1	1	6	3.50			3	2	—	—	1	6	9.00	12.50
Chesapeake Bay	1	59	12		72	3.15			11	54	9			74	8.97	12.12
Potomac	2	15			17	2.88			9	7	1			17	8.53	11.40
James	3	8	3		14	3.00		5	6	3				14	7.86	10.86
Nansemond	4	8			12	2.67		3	7	2				12	7.92	10.59
Chowan	42	67	5		114	2.68	2	43	56	11	1			113	7.70	10.38
Roanoke	19	62	1		82	2.78	3	29	46	2				80	7.59	10.37
Neuse	6	38	6		50	3.00		15	33	2				50	7.74	10.74
Ellis L.	36	21			57	2.37	10	45	2					57	6.86	9.23
Singletary L.	17	24	1		42	2.62		5	28	9				42	8.10	10.72
Salters L.	31	3			34	2.09	2	15	13	4				34	7.56	9.65
Jones L.	27	18			45	2.40		16	17	11	1			45	7.93	10.33
White L.	40	27			67	2.40		21	39	6	1			67	7.81	10.21
other Cape Fear	11	12			23	2.52	5	13	3	1	1			23	7.13	9.65
Waccamaw	42	21			63	2.33	6	23	29	5				63	7.52	9.85
f. barratti																
Pee Dee	14	27	5		46	2.80		1	20	19	6			46	8.65	11.45
Santee	17	49	2		68	2.78		5	34	22	7			68	8.46	11.24
Edisto		13	3		16	3.19			3	4	8	1		16	9.44	12.63
Combahee - Broad	3	10	1		14	2.86		1	6	6	1			14	8.50	11.36
Savannah	14	156	27		197	3.07		1	59	92	37	5		194	8.93	12.00
Ogeechee	2	23	2		27	3.00			6	11	9	—	1	27	9.22	12.22
Altamaha - Satilla		15	9		24	3.38		1	2	16	13	1		33	9.33	12.71
St. Marys	2	22	5		29	3.10			9	11	7			27	8.93	12.03
St. Johns	1	34	2		37	3.03		1	4	23	7	1		36	9.08	12.11
St. Cloud	20	19			39	2.49		11	25	3				39	7.79	10.28
Orlando	17	4			21	2.19	1	13	7					21	7.29	9.48
Oklawaha - St. Johns	7	40	2		49	2.90		3	11	25	8	1	1	49	8.92	11.82
Okeechobee	15	24	1		40	2.65		13	17	9				39	7.90	10.55
S. Fla.		10	5		15	3.33			5	8	2			15	8.80	12.13
Tampa Bay	1	18	3		22	3.09			6	9	7			22	9.05	12.14
With.-Waccasassa	2	13	2		17	3.00			6	7	3	1		17	8.94	11.94
Newnan L.	4	21			25	2.84			6	15	4			25	8.92	11.76
other Suwannee	3	14	1		18	2.89			3	10	6			19	9.16	12.05
Crystal L.	13	1			14	2.07		10	4					14	7.29	9.36
Okefenokee	2	44	5		51	3.06			16	29	5	1		51	8.82	11.88
Fenholloway - St. Marks	3	23	2		28	2.96			1	13	11	2		27	9.52	12.48
Ochlockonee	3	51	5		59	3.03			8	32	16	2		58	9.21	12.24
Apalachicola	3	20	5		28	3.07			5	13	7	2		27	9.22	12.29
Choctawhatchee - Perdido	2	27	5		34	3.09			9	16	6	4		35	9.14	12.23
Mobile Bay		7	1		8	3.13			1	7				8	8.88	12.01
Miss. Sound		7			7	3.00			1	4	1			6	9.00	12.00
Pearl - Pontchartrain	1	25	4		30	3.10			3	14	10	3		30	9.43	12.53
Reelfoot L.		2			2	3.00					1	1		2	10.50	13.50
Red	3	17	2		22	2.95			4	9	8			21	9.19	12.14
French Broad	5	40	1		46	2.91		1	5	29	10	1		46	9.11	12.02

TABLE 23.
Number of anal and pectoral rays in Etheostoma fusiforme

	Anal Rays							Pectoral Rays			
Drainage	5	6	7	8	9	10	x̄	12	13	14	15
f. fusiforme											
Ogunquit		1	8	3			7.17				
Cape Neddick		1	3	2			7.17				
North-Isinglass		1	2				6.67				
Merrimack	3	27	52	13			6.79	1	4	1	
Ipswich		10	21	3			6.79				
Mass. Bay		2	15	10			7.30				
Neponset		2	12	8			7.27				
North		3	4	2			6.89				
Mills			4	7	1		7.75		5	1	
other Cape Cod		4	71	61	2		7.44		10	5	
Nantucket		2	3	3			7.13		4	4	
Weweantic			8	11	2		7.71				
Taunton		5	25	5			7.00	3	6		
Seekonk		1	14	12			7.41				
Pataganset L.		3	8	1	1		7.00		4	1	
Ronkonkoma L.			7	35	9		8.04		4	3	
Yaphank L.			10	13	10		8.00	1	14		
Raritan		8	30	18			7.18		8		
Coastal N. J.		15	53	43	10		7.40		9	3	1
Delaware	1	14	31	13			6.95		5	1	
Coastal Del.-Md.		2	2	2			7.00	1	5	2	
Chesapeake Bay		2	39	32	2		7.45		10		
Potomac		1	8	7	1		7.47	1	6		
James			9	5			7.36		2	1	
Nansemond			7	4	1		7.50		4	1	
Chowan		9	63	39	4		7.33		11	4	
Roanoke		4	40	32	6		7.49		9	1	
Neuse		5	26	18	1		7.30		9	1	
Ellis L.			16	32	9		7.88				
Singletary L.			15	26	2		7.70		3	2	
Salters L.			7	24	5		7.94		3	2	
Jones L.		2	14	25	4		7.69	1	7		
White L.			22	41	2		7.69		4	3	
other Cape Fear		1	14	7			7.27				
Waccamaw		2	33	24	3		7.45	1	9		
f. barratti											
Pee Dee	1	4	25	19			7.27		4	1	
Santee		1	20	38	9	1	7.84	1	9	2	
Edisto			2	12	2		8.00	2	6	1	
Combahee-Broad			3	7	4		8.07		7	2	
Savannah		20	55	90	35		7.70		10		
Ogeechee			6	17	4		7.93		4	1	
Altamaha-Satilla		5	16	9	4		7.35		5	4	1
St. Marys		1	9	17	1		7.64	1	5	1	
St. Johns			14	19	4		7.73	2	2	2	
St. Cloud		1	12	25	1		7.67				
Orlando		2	12	4	1		7.21				
Oklawaha-St. Johns		3	17	21	8		7.69				
Okeechobee			6	24	9	1	8.13		5		
S. Fla.			7	7	1		7.60	7	3		
Tampa Bay		1	5	8	2		7.69	1	3	1	
Withlacoochee-Waccasassa			9	9	4		7.77		3	2	
Newnan L.				9	17		8.65	1	3	1	
Suwannee			10	8	1		7.53	2	5	1	
Crystal L.			8	6	1		7.53			6	9
Okefenokee			17	32	3		7.73		8	1	1
Fenholloway-St. Marks		2	15	9	2		7.39	1	2	6	
Ochlockonee		4	44	12			7.13	1	7	7	
Apalachicola		5	18	4	1		7.04		5		
Choctawhatchee-Perdido		3	24	8			7.14	2	8	4	
Mobile Bay			3	5			7.63		2	2	
Miss. Sound		1	3	3			7.29	1	3	2	
Pearl-Pontchartrain		2	20	7	1		7.23	3	11	1	
Reelfoot L.		1	–	1			7.00		1		
Red		1	10	13	1		7.56	1	4		
French Broad			10	29	8		7.96				

scales along the posterior portion of the lateral line and in others (16.7 mm and larger) squamation is nearly complete. In the July 6 collection, squamation is nearly complete in specimens 15.6 mm and larger.

The pored lateral-line scales do not develop until after the body squamation is nearly complete. Figure 11 shows the change in number of pored lateral-line scales with age in the Long Island population. Small lateral ridges grow higher and higher and finally form the pore by meeting over the middle of the scale. The smallest (15.6 mm) *E. f. fusiforme* with a fully developed pored scale was taken from Lake Ronkonkoma (CU 30279) on July 6. The pored scales form quite rapidly starting at the anterior part of the lateral line. After about 20 mm there is little or no change in the number of pored scales (Fig. 11). The development is similar in White Lake, one of the North Carolina Bay Lakes (Fig. 12) but the dark Bay Lakes show a more complicated situation that will be discussed under geographic variation, pored lateral-line scales.

Habitat—E. fusiforme fusiforme is found primarily in ponds, swamps, and backwaters of streams. I have taken it only rarely in flowing waters, and then not in abundance. In many areas (*e.g.,* in New Jersey), mill ponds and ponds for cranberry bogs provide an ideal habitat for *E. f. fusiforme.* Mansueti (1951) found 1,000 specimens after rotenoning such a pond in Maryland.

The bottom at most *E. f. fusiforme* localities consists of mud or detritus. This is especially true in the realtively few collections in which both *Etheostoma olmstedi* and *E. f. fusiforme* were taken. For example, in Lower Lake Yaphank, Long Island, the southern end of the lake is mostly sand bottomed, with some areas of mud and detritus. Seining in the detritus produced only *E. f. fusiforme* and collecting over the open sand only *E. olmstedi.* Where both species were taken in streams *olmstedi* occupied the central sandy areas while *f. fusiforme* was limited to the weedy, mud-bottomed backwaters. However, in the absence of *olmstedi,* as in some of the acid water ponds of the New Jersey Pine Barrens, *f. fusiforme* may be quite abundant over open sand.

The body of *E. f. fusiforme* is quite compressed, adapted for living in dense aquatic vegetation, while the heavier body of *E. olmstedi,* roughly triangular in cross section, is adapted for living on stream bottoms facing a current. A specimen of *E. f. fusiforme,* dislodged from its protecting weed bed in the outlet stream of Wildwood Lake, Long Island, was carried downstream by the current, while *E. olmstedi* maintained its position on the bottom. *E. olmstedi* also appears to live in more highly oxygenated waters than does *f. fusiforme.*

Although usually reported from acid brown-stained waters, *E. f. fusiforme* is not limited to such habitats, but is found there for two reasons. It avoids currents, and many of the slow waters on the Coastal Plain are acid and brown-stained. Secondly, most fishes are poorly adapted to this type of habitat and the acid-water fishes (see species associates) avoid competition from other species by living there.

In Maine, Everhart (1950) reported that *E. f. fusiforme* was "taken in sluggish, lowland streams and mudholes among the vegetation" and Collette (1958) stated that it "is usually found in muddy, swampy areas." In Delaware, Fowler (1911) noted that it was "abundant in almost all lowland fresh waters, at least above tide." Harmic (1952) found that it was "abundant in mill ponds and sluggish waters" in Delaware. Mansueti (1951) described four millponds and a sluggish stream in Maryland where it was taken. In Connecticut, it has been reported from Pataganset Lake, where it was found over muddy bottom among floating marginal vegetation (Webster, 1942, and personal observation). In New Jersey, Smith (1957) reported that it appeared to seek cover in vegetation and detritus to a greater degree than the Johnny darter (*E. olmstedi*). Smith (1907:269) quoted W. P. Seal to the effect that around Wilmington, N. C., it will "... stand warm and stagnant water better than any other darter I know of." This was also noted by Hubbs and Cannon (1935:67) who referred to a statement by G. S. Myers about *E. f. fusiforme* around Wilmington, N. C. "... it occurs abundantly in very warm, quiet waters reaching summer temperatures of 85° to 90°F. or even more, at the depth of 3 or 4 inches in masses of filamentous algae along banks of 'black water' streams." Bailey (1938:176) seems

TABLE 24.
Number of infraorbital pores and condition of the preopercle in Etheostoma fusiforme

Drainage	0+2	0+3	1+2	1+3	1+4	2+0	2+2	2+3	2+4	3+3	3+4	N	% 1+3 etc.	Condition of Preopercle PS	E	% PS
f. fusiforme																
Ogunquit				1	–	–	–	11				12	8.33	2	10	16.7
Cape Neddick								16				16	0	3	13	18.8
North - Isinglass								3				3	0	2	1	–
Merrimack								88	1	3		92	0	19	76	20.0
Ipswich				1	–	–	–	30	–	1		32	3.13	3	31	8.8
Mass. Bay				7	–	–	–	20				27	25.93	2	25	7.4
Neponset				2	–	–	–	20				22	9.09		22	0
North				1	–	–	–	8				9	11.11	2	7	22.2
Mills				13	–	–	–	47				60	21.67		62	0
other Cape Cod		1	–	19	–	–	–	111	4			135	14.81	10	128	7.2
Nantucket				2	–	–	–	15				17	11.76		19	0
Weweantic				2	–	–	–	18	–	1		21	9.52		21	0
Taunton				5	–	–	–	30				35	14.29	1	34	2.9
Seekonk		2	–	2	–	–	–	17				21	19.05		27	0
Pataganset L.				1	–	–	-	12				13	7.69		13	0
Ronkonkoma L.				6	–	–	–	43				49	12.24	2	49	3.9
Yaphank L.								33				33	0	1	32	3.0
Raritan				7	–	–	–	49				56	12.50	4	52	7.1
coastal N. J.		1	–	14	–	1	3	105				124	12.10	1	125	.1
Delaware				5	–	–	–	48	–	2		55	9.09	19	48	28.4
coastal Del. - Md.				4	1	–	–	51	–	1		57	8.77	13	45	22.4
Chesapeake Bay				2	–	–	1	74	–	4	1	82	2.44	24	65	27.0
Potomac				1	–	–	–	34				35	2.86	11	24	31.4
James				1	–	–	–	13	1			15	6.67	2	12	14.3
Nansemond				4	–	–	–	9				13	30.77		14	0
Chowan				3	1	–	–	110	–	1		115	3.48	13	102	11.3
Roanoke								97	–	1		98	0	15	84	15.2
Neuse				2	–	–	–	47	–	1		50	4.00	12	38	24.0
Ellis L.		1	–	26	–	–	–	30				57	47.37	5	52	8.8
Singletary L.		1	1	42	–	–		13				57	77.19	1	58	1.7
Salters L.				39	–	–	–	8				47	82.98	3	47	6.0
Jones L.		4	2	64	–	–	–	2				72	97.22	2	72	2.7
White L.	1	–	3	13	–	–	2	81	–	1		101	16.83		142	0
other Cape Fear				2	–	–	–	25				27	7.41	8	21	27.6
Waccamaw				7	–	–	–	62	2	3		74	9.46	16	55	22.5
f. barratti																
Pee Dee				44	–	–	–	5				49	89.80	18	31	36.7
Santee		5	–	53	–	–	–	8	1			67	86.57	25	43	36.8
Edisto				14	–	–	–	2				16	87.50	4	12	25.0
Combahee - Broad				11	–	–	–	–	–	1		12	91.67	3	11	21.4
Savannah		1		83	2	–	1	106	3			196	43.88	42	164	20.4
Ogeechee				2	–	–	–	25				27	7.41	20	8	71.4
Altamaha - Satilla				14	–	–	–	25	–	1		40	35.00	18	22	45.0
St. Marys		1	2	26	1	–	–	9				39	76.92	21	19	52.5
St. Johns			1	89	1	–	1	10	2	2		106	85.85	18	90	16.7
St. Cloud			1	37	–	–	–	1				39	97.44	1	38	2.6
Orlando		1	–	86	2	–	–	8				97	91.75	51	56	47.7
Oklawaha - St. Johns				50	1	–	–	5				56	91.07	18	38	32.1
Okeechobee		3	1	38	–	–	–	4				46	91.30	6	40	13.0
S. Fla.				19	–	–	–	1				20	95.00	5	15	25.0
Tampa Bay				14	–	–	–	8				22	63.64	11	11	50.0
Withlacoochee - Waccasassa		1	–	19	–	–	–	7				27	74.07	11	16	40.7
Newnan L.		1	–	58	4	–	–	12				75	84.00	24	52	31.6
other Suwannee				11	1	–	–	9				21	57.14	8	11	42.1
Crystal L.				24	–	–	–	2				26	92.31	1	25	3.8
Okefenokee			2	32	–	–		21				55	61.82	38	19	66.7
Fenholloway - St. Marks				16	–	–	–	14				30	53.33	19	11	63.3
Ochlockonee				66	1	–	1	34	1			103	65.05	53	50	51.5
Apalachicola				24	1	–	–	26	–	1		52	48.08	13	32	28.9
Choctawhatchee-Perdido		1	–	14	–	–	–	21				36	41.67	15	21	41.7
Mobile Bay				8								8	100.00	5	3	62.5
Miss. Sound				6	–	–	–	1				7	85.71	5	2	71.4
Pearl - Pontchartrain		2	–	38								40	100.00	24	17	58.5
Yazoo				1								1	100.00	1		–
Reelfoot L.				2								2	100.00		2	–
Red				41	1							42	100.00	7	35	16.7
French Broad		2	–	44								46	100.00	36	8	81.8

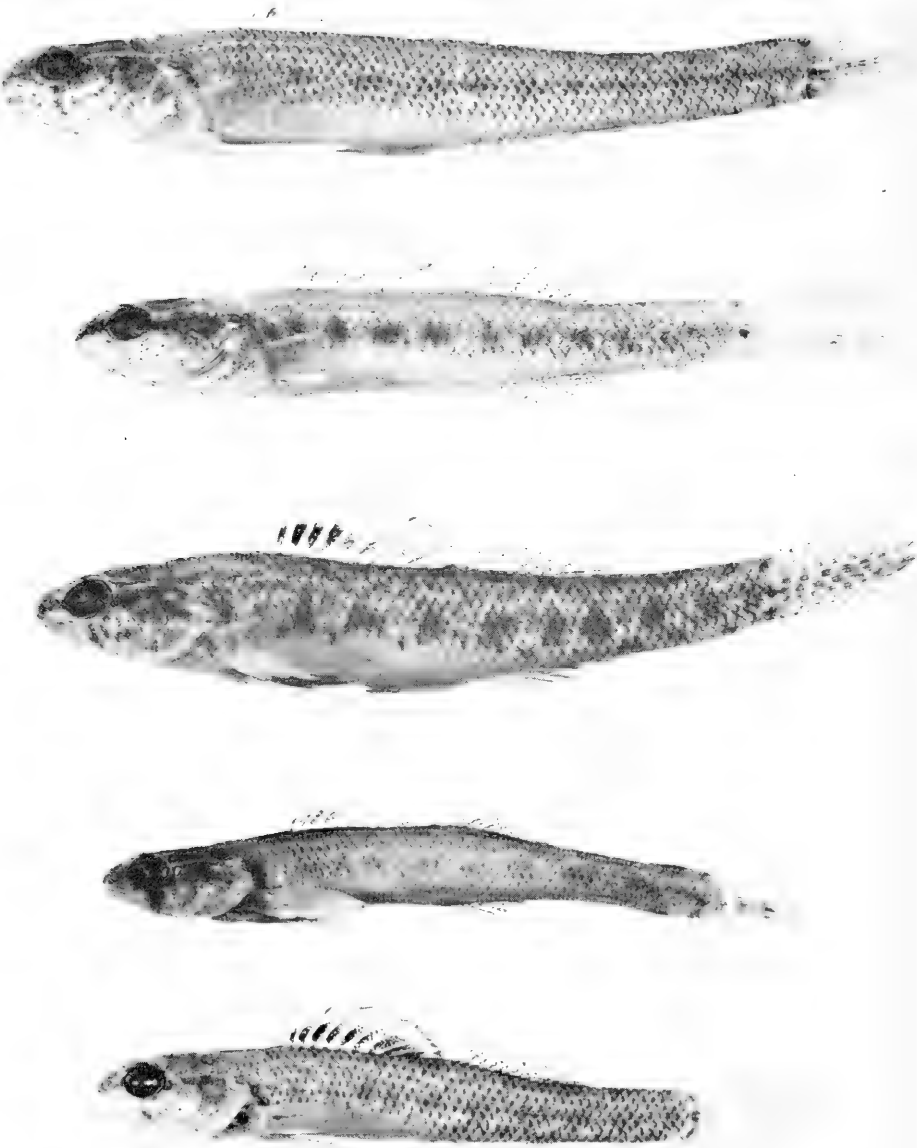

Figure 7. Breeding patterns of male *Etheostoma fusiforme fusiforme*. (from top to bottom) CU 31847; 41.3 mm; N.Y., Suffolk Co., Lake Yaphank; Apr. 19, 1958. CU 32725; 33.6 mm; N.J., Atlantic Co., Great Egg Harbor dr.; May 16, 1959. CU 31640; 37.4 mm; N.C., Northampton Co., Roanoke dr.; April 4, 1958. CU 25304; 30.4 mm; N.C., Bladen Co., Jones Lake; Aug. 24-26, 1947. (past maximum breeding pattern). CU 14302; 30.3 mm; N.C., Columbus Co., Waccamaw dr.; Mar. 29, 1949. (Photograph by Douglass M. Payne)

TABLE 25.
Squamation of the breast in Etheostoma fusiforme

Drainage	I-C	I/PX-C/T	PX-T	X/PX-T	X-T
f. fusiforme					
Ogunquit	5				
Cape Neddick	6				
Merrimack	4	1			
Ipswich	9				
Mass. Bay	5				
Neponset	5				
Mills R.	4	1			
Cape Cod	10	2			
Weweantic	5				
Taunton	6	1			
Pataganset L.	5	2			
Ronkonkoma L.	4				
Yaphank L.	15	3			
Raritan	8	3	1		
Coastal N. J.	7	3	1		
Delaware R.	8	1			
Del.-Md.	7	1			
Chesapeake	5				
Potomac		3	–	3	1
James	2	2	3		
Nansemond	5				
Chowan	3	2	4	1	
Roanoke			3	4	
Neuse	7	3			
Ellis L.	4	5	1		
Singletary L.		1	1	2	1
Jones L.	1	2	1	1	
White Lake	9	9	2	2	4
Other Cape Fear	4	2			
Waccamaw	2	2	1	5	
f. barratti					
Pee Dee	1	1	6	1	2
Santee		5	–	1	6
Edisto		5	–	1	3
Combahee-Broad	8	1			
Savannah	1	4	4	1	
Ogeechee		4	3	1	1
Altamaha-Satilla	2	6	6	1	
St. Marys	3	7	1	2	
St. Johns	2	5	1	–	3
Orlando		2	1	3	
Oklawaha-St. Johns		1	2		
Okeechobee			1	4	5
S. Fla.		3	3		
Tampa Bay					6
Withlacoochee-Waccasassa			2	2	5
Newnan L.		5	4	–	1
Suwannee	3	5			
Crystal L.	2	4			
Okefenokee		5			
Fenholloway-St. Marks		1	6	3	
Ochlockonee		5	–	1	
Apalachicola	1	5			
Choctawhatchee-Perdido		3	2		
Mobile Bay			2	–	2
Miss. Sound			6		
Pearl-Pontchartrain			3	2	8
Reelfoot L.			1		
Red					5
French Broad		2	3	–	5

TABLE 26.
Parietal squamation in Etheostoma fusiforme (percent of parietal covered with scales)

Drainage	0	5-10	15-20	25-30	35-40	45-50	55-60	65-70	75-80	85-95	100	x̄
f. fusiforme												
Ogunquit	6											0
Cape Neddick	6											0
Merrimack	5											0
Ipswich	9											0
Mass. Bay	3	2										3.00
Neponset	5											0
Mills R.	1	4										6.00
Cape Cod	11	1										.63
Nantucket	4											0
Weweantic	3	2										3.00
Taunton	4	3										3.29
Pataganset L.	6	1										1.07
Ronkonkoma L.	6											0
Yaphank L.	7	10										4.41
Raritan	10	3										1.73
Coastal N. J.	2	4										5.00
Delaware R.	4	7										4.77
Del.-Md.	2	5	1									6.88
Chesapeake	2	7	1									7.00
Potomac	4	3										3.21
James		1	4	3								20.00
Nansemond		4	1									9.50
Chowan		5	4	1								13.50
Roanoke			3	2	–	1						25.83
Neuse		9	1									8.50
Ellis L.		6	4									11.50
Singletary L.	5	16										5.71
Salters L.		3										7.50
Jones L.		1	8									16.39
White L.			5	9	2	2	1					29.61
Other Cape Fear		2	2									15.00
Waccamaw		2	9	2								17.50
f. barratti												
Pee Dee			1	3	3	5						37.50
Santee					2	5	2	1	2	1		56.73
Edisto			2	2	5							30.83
Combahee-Broad			2	1								20.83
Savannah				2	1	2	1	1	1	1	1	57.75
Ogeechee			1	1	2	1	2	1	1	1		51.50
Altamaha-Satilla			1	1	4	1	1	–	1	1		46.50
St. Marys		1	2	–	–	1	1	2	4	1		56.67
St. Johns						1	–	–	5	5		79.32
Orlando							4	2				63.33
Oklawaha-St. Johns									1	1		85.00
Okeechobee					3	1	–	–	1	3	1	63.67
S. Fla.					1	1	1	2	1			59.17
Tampa Bay									2	2	2	88.33
Withlacoochee-Waccasassa						2	–	–	3	1	1	73.57
Newnan L.							1	1	1	7		81.50
Suwannee			2	2	3	–	–	1				33.75
Crystal L.		1	–	2	1	–	1					31.50
Okefenokee					2	1	–	–	1	1		57.50
Fenholloway-St. Marks						1	–	3	3	3		74.50
Ochlockonee					1	1	–	–	2	1	1	71.25
Apalachicola					1	–	1	–	2	2		70.83
Choctawhatchee-Perdido						1	1	1	1			67.50
Mobile Bay			1	1	1							27.50
Miss. Sound			2	3	1							25.83
Pearl-Pontchartrain				2	3	3	1	3	2	2		56.25
Red										5		87.50
French Broad			1	1	2	1	2	1	2			50.50

TABLE 27.
Number of interorbital scales in Etheostoma fusiforme

Drainage	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
f. fusiforme																
Ogunquit		4	2													
Cape Neddick	6															
Merrimack	4	7														
Ipswich	3	5	1													
Mass. Bay	4	—	1													
Neponset	3	2														
North	2	3														
Mills R.	3	2														
Cape Cod	1	4	5	1												
Nantucket	3															
Weweantic	2	3														
Taunton	1	4														
Seekonk	1	3	1													
Pataganset L.	5	2														
Ronkonkoma L.	4	1	2													
Yaphank L.	4	3	7	4												
Raritan	9															
coastal N. J.	9	4	4													
Delaware R.	6	3	1													
Del.-Md.	1	2	2	1	1											
Chesapeake	1	6	4	1												
Potomac		4	1													
James		1	4													
Nansemond			3	2												
Chowan		1	5	2	1	1										
Roanoke			1	3	1	3	—	2	—	—	1	—	1			
Neuse				3	6	—	—	1								
Ellis L.			3	2	1	—	3	1								
Singletary L.	2	6	9	3												
Salters L.				2	—	—	—	—	—	1						
Jones L.	2	1	3	8	2	—	1									
White L.			2	5	7	2	2	1								
other Cape Fear		1	1	4	4	2	3									
Waccamaw L.			2	3	1	1	—	1	2							
f. barratti																
Pee Dee							1	—	—	1	2	3	2	—	1	3
Santee							1	—	1	—	—	2	—	—	2	3
Edisto						1	1	1	—	—	1	2	1	—	1	—
Combahee Broad						1	1									
Savannah						1	—	—	2	—	2	2	—	1	—	—
Ogeechee										1	2	2	—	1	1	1
Altamaha-Satilla						2	—	2	2	5	2	1	1	—	2	1
St. Marys										1	1	2	2	—	1	1
St. Johns											3	—	—	—	2	1
Orlando								1	—	2	—	—	—	—	—	—
Oklawaha-St. Johns								1	—	1	—	—	1			
Okeechobee							1	1	2	1	2	1	—	—	1	—
S. Fla.													1	1	3	—
Tampa Bay									1	—	—	—	1	—	—	—
Withlacoochee-Wacasassa							1	—	—	—	2	3	—	—	—	—
Newnan L.												1	1	—	3	1
other Suwannee					1	—	1	—	2	1	2	—	—	—	—	—
Crystal L.		1	1	1	—	1	—	1								
Okefenokee														2	2	1
Fenholloway-St. Marks										2	1	1	—	1	—	1
Ochlockonee									3	2	—	1	3	1	—	—
Apalachicola									1	—	—	—	—	—	1	—
Choctawhatchee-Perdido								1	1	1	1	1	1	1	1	—
Mobile Bay									1	—	1	—	1			
Miss. Sound									1	—	1	1	—	—	—	—
Pearl-Pontchartrain										1	—	1	2	4	2	1
Reelfoot L.															1	
Red														1	—	2
French Broad						1	—	1	—	—	3	1	2	1	—	—

Drainage	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31//37	x̄
f. fusiforme																	
Ogunquit																	1.33
Cape Neddick																	0
Merrimack																	.64
Ipswich																	.78
Mass. Bay																	.40
Neponset																	.60
North																	.40
Mills R.																	.40
Cape Cod																	1.55
Nantucket																	0
Weweantic																	.60
Taunton																	.80
Seekonk																	1.00
Pataganset L.																	.29
Ronkonkoma L.																	.71
Yaphank L.																	1.61
Raritan																	0
coastal N. J.																	.71
Delaware R.																	.50
Del.-Md.																	1.86
Chesapeake																	1.42
Potomac																	1.20
James																	1.80
Nansemond																	2.40
Chowan																	2.60
Roanoke																	5.50
Neuse																	4.00
Ellis L.																	4.10
Singletary L.																	1.65
Salters L.																	5.00
Jones L.																	2.65
White L.																	4.00
other Cape Fear																	3.93
Waccamaw L.																	4.50
f. barratti																	
Pee Dee	2	1	—	1	—	1	—	—	—	—	—	·	—	—	—	— 1	14.58
Santee	—	—	—	—	1	—	—	1									13.82
Edisto	—	—	1														10.44
Combahee Broad																	5.50
Savannah	3	2	—	—	—	—	1	—	—	2							14.38
Ogeechee	1	1	—	1													13.18
Altamaha-Satilla	1	1															10.20
St. Marys	2	1	—	—	1												13.58
St. Johns	—	2	1	1	—	1											15.00
Orlando	1	—	—	—	1	—	—	—	—	1							14.33
Oklawaha-St. Johns																	9.33
Okeechobee	—	—	1														10.10
S. Fla.	1																13.83
Tampa Bay	1	—	—	—	2	—	—	—	—	—	—	1					17.16
Withlacoochee-Wacasassa	1	2															12.11
Newnan L.	—	—	3	—	1												15.40
other Suwannee	1																8.88
Crystal L.																	3.60
Okefenokee	—	1															14.33
Fenholloway-St. Marks	1	—	—	1	1	—	1										14.40
Ochlockonee	1	4	1	1	2	1											14.20
Apalachicola	1	—	1	—	—	1	—	—	—	—	1						17.16
Choctawhatchee-Perdido	—	—	—	—	1	—	1										12.60
Mobile Bay																	10.00
Miss. Sound	—	1															11.50
Pearl-Pontchartrain	—	—	1	1	—	—	—	1	—	—	—	—	—	—	—	1	15.33
Reelfoot L.																	
Red	1	1	1	—	1	—	—	—	—	—	—	—	—	—	1		18.00
French Broad	—	—	—	—	—	—	1										11.20

TABLE 28.

Characteristics of the North Carolina Bay Lakes (based in part on Frey, 1949)

Characters	Black	Jones	Salters	Singletary	White	Waccamaw	Used for Indices?
$\bar{x}$ Secchi disc depth (ft.)	1.8	2.4	1.8	2.5	11+	4.4	Phys.-Chem.
$\bar{x}$ color (p.p.m.)	182	297	299	168	10	160	No
$\bar{x}$ depth (ft.)	5.3	6.1	6.9	7.0	7.5	7.6	No
maximum depth (ft.)	7.1	8.7	10.1	11.8	10.6	10.8	No
area (A.)	1418	224	315	572	1068	8938	No
volume (yd.^{3})	12,197,700	707,100	3,520,200	6,495,300	12,844,100	109,964,800	No
maximum length (mi.)	2.11	.80	.94	1.49	1.81	5.3	No
length of shore line (mi.)	5.91	2.19	2.70	3.92	4.77	14.21	No
shore line development	1.12	1.05	1.09	1.17	1.04	1.07	No
pH	4.40	4.34	4.49	4.50	4.92	6.95	Phys.-Chem.
ml. N/44 H_2SO_4 per liter	1.9	3.0	3.2	2.4	1.6	9.2	Phys.-Chem.
pounds of fish per acre	0.33	2.30	6.37	5.76	53.07	31.37	Biological
number of fish species	10	13	14	15	21	35	Biological
amount of aquatic vegetation	none	none	none	very little	moderate	abundant	Biological

TABLE 29.

Comparison of physical-chemical and biological characters of the North Carolina Bay Lakes by ranking

	Physical-Chemical Factors				Biological Characters						
	light penet.	pH	alk.	total	lbs/A fish	amt. aq. veg.	No. fish species	total	Total Index	$\bar{x}$ Pored Scales	% 1+3 INF pores
Black	1.5	2	2	5.5	1	2	1	4	9.5	—	—
Jones	3	1	4	8.0	2	2	2	6	14.0	6.14	97.22
Salters	1.5	3.5	5	10.0	4	2	3	9	19.0	7.42	82.98
Singletary	4	3.5	3	10.5	3	4	4	11	21.5	10.19	77.19
White	6	5	1	12.0	6	5	5	16	28.0	15.54	16.83
Waccamaw	5	6	6	17.0	5	6	6	17	34.0	14.38	9.46

(1 = *least productive*, 2 = *next productive*, 6 = *most productive*).

to be the only author to report it from fast waters (Merrimack River, N. H.), as follows: "Where found in streams they usually seek the fastest waters and seclude themselves in clumps of aquatic vegetation.... In lakes they are found in protected coves provided with dense growths of aquatic vegetation." Hubbs and Cannon (1935) gave brief descriptions of the habitat for each of their subspecies of *E. fusiforme* which verify what has already been brought out concerning their habitat.

Species Associates—Etheostoma f. fusiforme is found over a large range; species associates, therefore, are discussed by regions. I have collected throughout the range of this form and in addition there are published data for the Merrimack River of New Hampshire (Bailey, 1938) and for the lakes and ponds of New Jersey (Smith, 1950, 1953a, 1957).

Esox americanus, Enneacanthus obesus, and *Etheostoma f. fusiforme* all have similar distributions in New Hampshire: lowland (65-313 feet), brown-stained waters with vegetation at least moderately thick (Bailey, 1938).

An acid-water fish fauna (Smith, 1953b) exists in the brown-stained waters of the Pine Barrens of southern New Jersey. This is composed of *Umbra pygmaea, Ictalurus natalis, Noturus gyrinus, Aphredoderus saya-*

TABLE 30.
Fishes of the North Carolina Bay Lakes and of Crystal Lake, Georgia

Lake Index of Productivity	Black 9.5	Jones 14.0	Salters 19.0	Single-tary 21.5	White 28.0	Wacca-maw 34.0	Crystal L. —
Species							
Esox americanus	x	x	x	x	x	x	x
Erimyzon succetta	x	x	x	x	x	x	x
Ictalurus natalis	x	x	x	x	x	x	
Noturus gyrinus	x	x	x	x	x	x	
Gambusia affinis	x	x	x	x	x	x	x
Aphredoderus sayanus	x		x	x	x	x	
Ennecanthus gloriosus	x	x	x	x	x	x	x
Centrarchus macropterus	x	x	x	x	x	x	
Chaenobryttus gulosus	x	x	x	x	x	x	x
Perca flavescens	x	x	x	x	x	x	
Esox niger		x	x	x	x	x	
Etheostoma fusiforme		x	x	x	x	x	x
Fundulus notti		x	x		x		x
Micropterus salmoides		x	x	x	x	x	x
Notropis chalybaeus				x	x	x	
Lepomis macrochirus				x	x	x	x
Amia calva					x	x	
Anguilla rostrata					x	x	
Lepomis auritus					x	x	
Mesogonistius chaetodon					x	x(?)	
Lepisosteus osseus						x	
Dorosoma cepedianum						x	
Erimyzon oblongus						x(?)	
Notemigonus crysoleucas						x	x
Notropis petersoni						x	
Cyprinus carpio						x	
Ictalurus catus						x	
Roccus americanus						x	
Lepomis gibbosus					x	x	
Lepomis punctatus						x	
Pomoxis nigromaculatus						x	
Acantharchus pomotis						x	
Elassoma zonatum						x	
Fundulus waccamensis						x	
Menidia extensa						x	
Etheostoma perlongum						x	
Notropis maculatus							x
Labidesthes sicculus							x
Lepomis marginatus							x
Totals	10	13	14	15	21	35	13

nus, Acantharchus pomotis, Enneacanthus obesus, Mesogonistius chaetodon, and *Etheostoma f. fusiforme.* For the most part these are fishes found at altitudes of 300 feet or less. Smith (1953b) noted for *E. obesus* that these fishes are found in these areas because competition from other species is greatly reduced or eliminated. In clearer, more alkaline waters of southern New Jersey, other species replace the acid-water fishes: *Ictalurus nebulosus* replaces *I. natalis; Enneacanthus gloriosus* replaces *E. obesus* and *M. chaetodon: Etheostoma olmstedi* replaces *E. f. fusiforme;* species of *Lepomis* replace *Acantharchus,* etc. There are also several wide-ranging species in New Jersey, *e.g., Micropterus, s. salmoides* and *Esox niger* which form part of both the acid-water and the alkaline-water faunas.

Smith (1957) reported a change in species composition (or at least abundance) that seems to be correlated with a change in pH. In 1952, when the pH of Lefferts Lake, New Jersey, was 6.8, *Fundulus diaphanus* and *Notemigonus crysoleucas* were common throughout the lake and both *Ictalurus nebulosus* and *Lepomis gibbosus* were abundant but stunted. In August 1954, the pH was down to 4.4 and *I. nebulosus* and *L. gibbosus* had become less abundant. In June 1955, when the pH was 4.1, *Notemigonus, I. nebulosus,* and *L. gibbosus* were still less abundant, and *Enneacanthus obesus* was taken for the first time. In a rotenone sample taken on August 6, 1956, 478 *E. obesus* and 4 *Etheostoma f. fusiforme* were taken with only 4 *I. nebulosus,* 13 *Notemigonus,* 3 *L. gibbosus,* and 1 *Fundulus.* On the same day I obtained the following in 15 minutes seining: 32 *E. f. fusiforme,* 19 *E. obesus,* 3 *L. gibbosus.* I believe that this is evidence for one of the few times that pH (or effects connected with pH, such as productivity) can be indicated as important in determining species abundance.

Smith (1907:269) quoted a letter from Seal concerning the associates of *E. f. fusiforme* in the vicinity of Wilmington, N. C.: "This species is . . . to be found . . . where *Fundulus, Gambusia, Heterandria, Umbra, Chologaster, Elassoma, Aphredoderus,* and sunfishes abound." In New Hampshire, Harrington (1946) reported that *E. f. fusiforme* was often found on the bottom within an inch or two of foraging bridled shiners, *Notropis bifrenatus,* and that *Enneacanthus obesus* was occasionally found in its immediate vicinity. He also noted (p. 55) that when young *Notropis bifrenatus* first appear they are sometimes found in a chance association with small schools of chub sucker fry (*Erimyzon oblongus*), golden shiners (*Notemigonus crysoleucas*) and northern mud darters (*E. f. fusiforme*). In Delaware, Fowler (1911:13) reported *E. f. fusiforme* "to be usually associated with *Erimyzon, Aphredoderus, Enneacanthus, Mesogonistius* and similar fishes." *Etheostoma f. fusiforme* was taken in 8 of 17 of my collections on the Delmarva Peninsula. Common associates (with number of times taken with *E. f. fusiforme* and total number of times taken) are: *Aphredoderus sayanus* (7/8); *Lepomis gibbosus* (7/14); *Anguilla rostrata* (6/11); *Erimyzon oblongus* (5/8); *Enneacanthus gloriosus* (5/6); *E. obesus* (3/4); *Acantharchus pomotis* (4/4); *Notropis chalybaeus* (3/3); *Mesogonistius chaetodon* (2/2); and *Noturus gyrinus* (3/4).

Predators—Smith (1950) reported *Etheostoma f. fusiforme* from *Esox niger* stomachs in a number of acid southern New Jersey lakes: Lake Absegami, Colliers Mills, Farrington Lake, Hanover Lake, Union Lake, and Barnegat Pines Lake (1953a). He also (1957) presented a table of the food of *Esox niger* from lakes of different acidity for specimens under 6 inches and over 6 inches. *Etheostoma f. fusiforme* formed 25% of the food of the smaller *Esox* in very acid waters (pH 4.0-4.8), 15% in acid waters (pH 4.9-5.5), 2% in slightly acid waters (pH 5.6-6.9) and 0% at pH 7.0 and over. For the larger *Esox,* the figures were 12%, 13%, 2%, and 0% for pH 7.0 and over. Harrington (1946) reported *E. f. fusiforme* from the stomach of a 16-inch *Esox niger* from the Oyster River, New Hampshire.

Smith (1950) reported *E. f. fusiforme* from the stomachs of *Micropterus s. salmoides* (mostly young) in Colliers Mills, Farrington Lake, Parvin Lake, and Union Lake.

Parasites—The only report of parasitism for any species of the subgenus *Hololepis* is that of Harrington (1946) who found that *E. f. fusiforme* from the Oyster River of New Hampshire was heavily parasitized by glochidia. I have also noted glochidia on a number of specimens.

Acanthocephalans were found with their proboscides imbedded in the stomachs of three *E. f. fusiforme* taken on Long Island (CU 31847). One specimen had two, another five, the third specimen had six, and a fourth specimen had none.

Habits—Specimens collected from Lake Ronkonkoma, Long Island, on April 21, 1956, and brought into the laboratory, began pre-spawning behavior almost at once, although none of the females were distended with eggs. There were two phases to this behavior. First, the male approached the female from the rear, mounted her, and began to "beat" her with his pelvic fins. Usually a female "accepted" this but a male so approached immediately moved away from such attentions. A few weeks later the second phase began; after the male started "beating" a female, she "led" him forward into floating plants at the top of the aquarium. With the male close alongside, she pointed her genital papilla forward and up into a mass of plants, and quivered. On a few occasions two males followed a single female. No fighting or display of territoriality was ever noted. Although no eggs were actually seen being laid, spawning is probably essentially the same in the wild. Fletcher (1957) reported similar behavior in specimens collected on March 27, 1957, in New Jersey. Spawning followed and continued for two days. The eggs were deposited singly on leaves of *Myriophyllum* and hatched in eight to ten days. Smith (1907) quoted Seal's observations on some specimens taken near Wilmington, N. C., which spawned on the underside of lilies and other plants in a small still-water aquarium.

My collections from New Jersey on May 17, 1958, in four lakes indicated that some specimens had partially completed spawning. Two collections made in the same areas on May 16 and 17, 1959, by N. R. Foster and J. S. Ramsey contained adults and postlarvae as small as 9 mm. A school of 20 to 30 postlarvae was taken by dipnet while free swimming at the surface in six inches to two feet of water over open sand. No other species were closely associated with them (personal communication and field notes of N. R. Foster). On July 6, 1956, I collected 24 young in Lake Ronkonkoma, Long Island, ranging from 13.3 to 22.0 mm. They were taken about 30 feet out in the lake on an open sandy bottom, in water four to five feet deep. Fletcher's (1957) aquarium specimens were about this size ("3/4 inch") when two months old. Harrington (1947) reported taking "very small fry" of *E. f. fusiforme* on July 2 and 5, in the Oyster River at Durham, New Hampshire.

Although no aging based on scale reading has yet been done, there is evidence to indicate that a large number, if not most, *E. f. fusiforme* live only for one year. Most Long Island collections show only one major size class. On July 6, in Lake Ronkonkoma, the 24 specimens which were taken were postlarvae. In November and April all specimens taken in Lake Yaphank were adults.

Everhart (1950) reported that young and adult *E. f. fusiforme* feed on entomostraca in Maine. This is probably true, but no food studies have yet been made of this subspecies. A 31 mm specimen from New Jersey had over 130 copepods in its stomach. The intestine was filled with copepod exoskeletons. A large number of specimens from many localities had copepod exoskeletons projecting from the anus. In aquaria, *E. f. fusiforme* feeds avidly on daphnia, chasing them around the tank in spurts. They will also readily eat anything else of small size that moves. Strange food is inspected; the darter swims to the item, turns its head and looks down on the object with one eye. The object is then taken into the mouth but rejected if not suitable. They have been trained to eat such non-living food as frozen brine shrimp, frozen daphnia, and dried fish food which has been dampened and formed into small pellets. For moderately large darters a supplementary method of feeding was devised. A few pairs of guppies (*Lebistes reticulatus*) were added to the tanks, and the darters fed on the baby guppies.

A large number of specimens of *E. f. fusiforme* have been kept in aquaria. They are easy to care for, interesting to watch, and one of the easiest species of darter to transport because of their apparently low oxygen requirement. In aquaria, they spend most of their time either on the bottom or among plants. Specimens often swim up to a plant, such as *Elodea,* and balance themselves there, with pectoral and pelvic fins in front of the plant stem and the rest of the body bent down behind.

Distribution—The range of *E. f. fusiforme* extends from the southeastern tip of Maine along the Seaboard Lowland section of the New England Province (Fenneman, 1946) south along the Atlantic Coastal Plain below the Fall Line to the Waccamaw River in North Carolina, south of which it is replaced by *E. f. barratti* (Fig. 8).

The distribution of *E. f. fusiforme* in New Jersey has been analyzed to ascertain the factors important in limiting its distribution. New Jersey was selected because a large amount of information is available from the publications of Smith (1950, 1952, 1953a, 1953b, 1957). The freshwater fish fauna of New Jersey may be divided into three groups: (1) species limited to the sluggish, brown-stained, acid lowland ponds and streams; (2) species of upland, clear, alkaline bodies of water; and (3) species

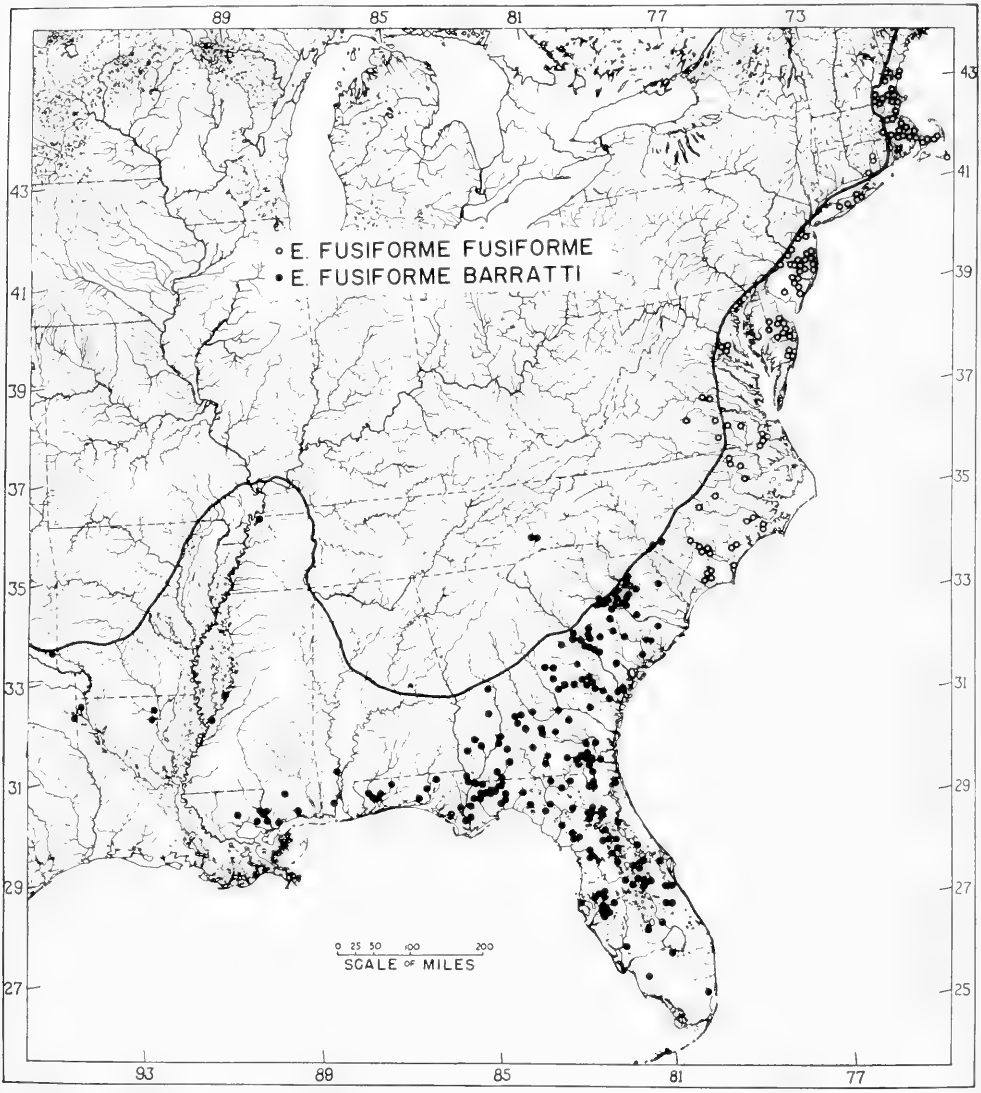

Figure 8. The distribution of *Etheostoma fusiforme* in relation to the Fall Line. (Based upon specimens examined)

found throughout the state in both types of situation. *Etheostoma f. fusiforme* belongs to the acid-water fauna (see species associates) which also includes *Enneacanthus obesus, Acantharchus pomotis, Mesogonistius chaetodon, Ictalurus natalis,* and *Aphredoderus sayanus.* These fishes are found in waters with pH values of 3.7 to 7.6 and usually 4.1 to 5.0 (Smith, 1953b). The average altitudes at which these acid-water species are found in New Jersey are: 52, 51, 98, 54, 64, and 54 feet, respectively. A number of widespread New Jersey species may be found with the preceding six species. These, together with their mean altitudinal ranges and their mean pH values, where known, are: *Erimyzon oblongus* (306, 6.70), *Notemigonus crysoleucas* (352, 7.11), *Ictalurus nebulosus* (366, 7.12), *Noturus gyrinus* (271), *Esox niger* (287, 6.46), *Umbra pygmaea* (266, 5.62), *Anguilla rostrata* (246), *Micropterus s. salmoides* (329, 7.30), *Lepomis gibbosus* (350), *Perca flavescens* (351, 7.13).

Cooper (1939) first reported *E. f. fusiforme* from southeastern Maine in the Ogunquit and Cape Neddick rivers, where I have also taken them. Subsequent collections in more northern parts of the state have not shown it to be present. Gordon (1937) and Bailey (1938) reported it in New Hampshire from the North and Isinglass rivers of the Coastal watershed and the Merrimack River. Hubbs and Cannon reported *f. fusiforme* from one pond on Cape Cod (as *fusiforme metae-gadi*). My collections made in the summers of 1956 and 1957 indicate that *E. f. fusiforme* is found in most of the ponds along the southern coast of Cape Cod but is absent in a number of ponds along the north shore. Hubbs and Cannon also were the first to report (1935) *E. f. fusiforme* from Gibbs Pond, Nantucket Island (as *fusiforme insulae*). They postulated the possible extinction of this form based on Cannon's unsuccessful attempt to collect additional specimens in 1933. I was able to collect eight specimens in a brief visit made in August 1956. Webster (1942) reported *E. f. fusiforme* from Pataganset Lake for the first Connecticut record, but did not find it in any other Connecticut ponds. I collected ten additional specimens from this lake in November 1957. Additional localities from the Thames drainage of Connecticut were reported by Behnke and Wetzel (1960). Greeley (1939) was the first to record *E. f. fusiforme* from Long Island, where the New York Biological Survey obtained it in Lake Ronkonkoma and in two tributaries of the Peconic River: the Little River and Merritt Pond. Further collecting over much of Long Island from the summer of 1956 through 1959 has revealed moderately large *E. f. fusiforme* populations in Lower Lake Yaphank on the Carmans River as well as in Lake Ronkonkoma. Two specimens were also taken in the outlet stream of Wildwood Lake in the Peconic River system. Its presence in the Maryland portion of the Delmarva Peninsula was shown by Mansueti (1951) and Mansueti and Elser (1953). My collections extend the known range south to about six miles north of the Virginia-Maryland border. Hubbs and Cannon (1935) described *fusiforme atraquae* from a Maryland collection from the Potomac River and reported no success in collecting *f. fusiforme* in the area between the Potomac and Neuse rivers. Raney (1950) reported it from the James River where it has been taken well above the Fall Line (Fig. 8). Since then a number of additional specimens have been collected from the James, Nansemond, Chowan, and Roanoke rivers, thus filling in the distributional gap. Frey (1951) and Frey and Bailey (1951) reported *E. f. fusiforme* (as *thermophilum* and *thermophilum oligoporum*) from the Bay Lakes of North Carolina (except Black Lake).

Specimens Examined—Complete locality data are given for only those collections which show range extensions or other significant distributional data. Other collections are listed by drainage, state, county and museum number. Complete data on almost all of the collections may be found in Collette (1960). A total of 3601 specimens from 209 collections was examined.

Ogunquit Dr., Me.—York Co.: UMMZ 129635 (12, 28-32): Ogunquit R., July 17, 1937. CU 31250 (7, 21-32): Ogunquit R. on US 1 in Ogunquit, Sept. 18, 1957.

Cape Neddick Dr., Me.—York Co.: UMMZ 129639 (1, 34); Cape Neddick R., July 17, 1937. CU 31245 (26, 22-36); Cape Neddick R. on US 1, Sept. 18, 1957.

North-Isinglass Dr., 3 specimens, N.H.—Rockingham Co.: UMMZ 163199. Strafford Co.: UMMZ 163198.

Merrimack Dr., 99 specimens, N.H.—Hillsboro Co.: UMMZ 140883, 141243, 141244, 141245, 163218. Rockingham Co.: UMMZ 141241, 141246, 141247. Mass.—Essex Co.: CU 30434, 30428. Middlesex Co.: CU 30444; BU uncat.

Ipswich Dr., 34 specimens. Mass.—Essex Co.: CU 15459, 30438.

Massachusetts Bay Dr., 59 specimens. Mass. Middlesex Co.: USNM 1188 (1, 33) lectotype, USNM 94686 (25, 23-36), UMMZ 86582 (1, 38), and MCZ 24589 (4, 27-36), paratypes of *Boleosoma fusiforme;* trib. of Charles R. at Framingham. CU 30440; BU uncat.

Neponset Dr., 22 specimens. Mass.—Norfolk Co.: CU 30533.

North Dr., 9 specimens. Mass.—Norfolk Co.: CU 30464.

Cape Cod, 386 specimens. Mass.— Barnstable Co.: USNM 77860 (1, 33) holotype and USNM 94683 (36, 27-43) paratypes of *Hololepis fusiformis metac-gadi;* Tempies Pd., Osterville; Nov. 2, 1902. CU 30475, 31602, 30487, 30490, 30503, 30772, 31173, 31254, 31165, 30494.

Mills River, 85 specimens. Cape Cod, Mass.—Barnstable Co.: 0.1 mi. W of jct. of Mass. 28 and 149 on Mass. 28. CU 30481, 31162, 31176, 31601, 31170, 31538.

Nantucket Island, Mass.—Nantucket Co.: Gibbs Pd. MCZ 28274 (1, 24) holotype, MCZ 33547 (8, 16-27), UMMZ 86601 (2, 22-25) paratypes of *Hololepis fusiformis insulae;* Aug. 10, 1893. CU 30462 (8, 21-30).

Buzzards Bay Dr., 21 specimens. Mass. — Plymouth Co.: CU 30517.

Taunton Dr., 35 specimens. Mass.—Bristol Co.: CU 30448. Bristol-Norfolk cos.: CU 20582. Plymouth Co.: CU 30768, 30769.

Blackstone-Seekonk Dr., 27 specimens. Mass.—Worcester Co.: CU 30457.

Pataganset Lake, 13 specimens. Conn.—New London Co.: CU 10182; UMMZ 138515; CU 31006.

Thames Dr., 31 specimens. Conn.—New London Co.: UCF 136-9, 260. New London-Windham cos.: UCF 140-5, 260.

Long Island, N.Y.—Suffolk Co.

Lake Ronkonkoma, 114 specimens. NYSM 2441; CU 6527, 29993, 30265, 30279, 30347, 30529, 31849

Lake Yaphank, 197 specimens: CU 30285, 30352, 31005, 31850, 31133, 31847, 32697, 33194, 34098.

Peconic River, 3 specimens: NYSM 1452, 2410; CU 30258.

Raritan Bay Dr., 56 specimens. N.J.—Middlesex Co.: CU 30363. Monmouth Co.: CU 30371.

Atlantic Coast of N.J. Dr., 484 specimens. Atlantic Co.: USNM 45142; CU 30390, 30398, 31787, 31791, 31797, 32725, 32731, 32739. Burlington Co.: ANSP 20714, 31123; CU 20513, 30382, 30389, 31803, 31794, 31781, 32744. Cape May Co.: USNM 1338; ANSP 40702-8. Ocean Co.: ANSP 55989; CU 27331, 22771, 13163, 30374, 30380, 30381; UMMZ 114413.

Delaware Dr., 111 specimens. N.J.—Burlington Co.: ANSP 32571-2, 78737; CU 30416. Camden Co.: USNM 49085. Mercer Co.: ANSP 32598, 40671-701, 40711-27. Pa.—Bucks Co.: Bristol. ANSP 32557-70, 32573, 40670.

Atlantic Coast of Delmarva Peninsula, 90 specimens. Del.—Kent Co.: ANSP 40728-31; CU 32083. Sussex Co.: CU 30606, 31172, 31168, 31171, 34718, 34719. Md.—Worcester Co.: USNM 85822.

Chesapeake Bay Dr., 92 specimens. Del.—Sussex Co.: ANSP 40668-9; CU 31169. Md.—Caroline Co.: CU 18621, 18375; uncat. Worcester Co.: CU 33927, CU 33097, trib. of Pocomoke R., 10.8 mi. S of Snow Hill.

Potomac Dr., 41 specimens. Md.—Charles Co.: USNM 100244, 103862, UMMZ 100677, 136032. Charles-Prince Georges Cos.: Mattawoman Cr.: May 21, 1933. UMMZ 107090 (1, 31) holotype; UMMZ 107089 (15, 28-32), USNM 117547 (2, 29-31), USNM 92946 (4, 32-34) paratypes of *Hololepis fusiformis atraquae.*

James Dr., 15 specimens. Va.—Goochland Co.: USNM 107470; UR 136, 262, uncat. Prince Edward Co.: USNM 197197.

Dismal Swamp-Nansemond Dr., 15 specimens. Va.—Norfolk Co.: USNM 100307, 100726; CU 30251, 30253, 30255, 24625.
USNM 107197.

Chowan Dr., 134 specimens. Va.—Dinwiddie Co.: CU 30252. Greensville Co.: CU 30254. Sussex Co.: CU 16880, 32090. N.C.—Gates Co.: UMMZ 138483; CU 30143.

Roanoke Dr., 99 specimens. Va.—Greensville Co.: USNM 107554. N.C.—Bertie Co.: CU 29978. Halifax Co.: CU 29977. Martin Co.: CU 29980. Northhampton Co.: CU 17018, 31640.

Trent-Neuse Dr., 232 specimens. N.C.—Craven Co.: UMMZ 138484. Jones Co.: CU 30554. Johnston Co.: USNM 179731. Wilson Co.: USNM 179733.

Ellis Lake, 62 specimens. N.C.- Craven Co.: UMMZ 161986; CU 29983, 29985.

Cape Fear Dr., N.C.

Jones Lake, 193 specimens. Bladen Co.: DU uncat.; UMMZ 161968; CU 25304, 33107, 33715; UMMZ 161969 (1, 26) holotype of *Hololepis thermophilis oligoporus.*

Singletary Lake, 95 specimens. Bladen Co.: UMMZ 158771, 161965; CU 35131, 31951, 33720.

Salters Lake, 108 specimens. Bladen Co.: UMMZ 161973, 161975, 161974; CU 33108, 33707, 15562.

White Lake, 455 specimens. Bladen Co.: CU 25086, 15646, 33109, 31820, 33106, 34748; DU uncat.

Other Cape Fear Dr., 31 specimens. Bladen Co.: CU 33182. New Hanover Co.: Wilmington. USNM 52066, 52071, 86165, 86160, paratypes of *Hololepis thermophilus.* USNM 94687, 49144, 102149. Pender Co.: CU 29987, 33181. Harnett Co.: UMMZ 107072 (1, 33); Kipling, holotype of *Hololepis thermophilus.*

Waccamaw Dr., 92 specimens. N.C.—Brunswick Co.: CU 14257. Columbus Co.: UMMZ 161979, 161980, 161981, 161982, 161983; DU uncat; CU 31023, 14302, 31938, 34370.

Etheostoma fusiforme barratti (Holbrook)

Boleosoma Barratti—Holbrook, 1855:56-57 (original description).

Hololepis barratti—Putnam, 1863:4 (original description of *Hololepis* by Agassiz); Cope; 1864:233 (diagnosis of the species of *Hololepis*); Hubbs and Greene, 1928: 384-385 (*Hololepis* must replace *Copelandellus* confirmed by examination of Agassiz's specimens of *Hololepis "barratti"*); Hubbs and Cannon, 1935:54-62, pl. I, III, (description, range, synonymy); Carr, 1937: 84 (Fla.); Baker, 1939a:36-37 and 1939b: 45 (Reelfoot Lake, Tenn.); Kuhne, 1939: 93; Fowler, 1941:244, fig. 3, not 13 as given, (Suwannee R., Dixie Co., Fla.); Harkness, Pierce, and Lowe, 1941:112 (ecology, Lake Mize, Fla.); Driver, 1942:285 (in key, in part); Meehean, 1942:185 (lakes in Ocala National Forest, Fla.); Goin, 1943: 146 (water hyacinth community, Gainesville, Fla.); Fowler, 1945:40 (distribution table, Pee Dee, Santee, Savannah, Altamaha, St. Johns, Suwannee rivers), 195-196 (synonymy, S. C. records), 252 (Ga. records), 364 (Biloxi, Miss.); McLane, 1948:116-117 (in stomach of young *Micropterus salmoides* from St. Johns R., Fla.); Bailey and Hubbs, 1949:34 (characteristic Floridian species); Dickinson, 1949:26 (two shallow ponds near Gainesville, Fla.); Driver, 1950:298 (in key); McLane, 1950:196-199 (in stomach of rotenoned *Micropterus salmoides,* stomach contents of the *Hololepis,* Buck Pd., Fla.); Reid, 1950:179 (Orange Lake, Fla.); Freeman, 1952a:37 (Congaree R., S. C.); Freeman, 1952b:269 (Barnwell Co., S. C.); Reid, 1952:65 (around floating islands, Orange Lake, Fla.); Freeman and Huish, 1953:39, 44, 91-94, 96-102 (in stomachs of *Micropterus salmoides, Pomoxis nigromaculatus, Lepisosteus osseus, L. productus*); Anderson and Freeman, 1957:106 (Calhoun, Lexington, and Richland cos., Congaree R., S. C.); Randall, 1958:342 (Coastal Plain, Catawba-Wateree R., S. C.).

Poecilichthys quiescens—Jordan, 1884: 478-479 (original description).

Etheostoma quiescens—Woolman, 1892: 294, 297, 299, 300, 302 (description, habitat, Peace R., Hillsboro R., Withlacoochee R., Fla.).

Boleichthys fusiformis—Fowler, 1935:6, 23 (Santee, Cambahee, Edisto, Pee Dee r., Coastal Plain, S. C., in part).

Boleichthys barratti—Schrenkeisen, 1938: 235.

Hololepis barratti barratti—Bailey, 1950: 311-316 (comparison with *H. barratti appalachia*).

Hololepis barratti appalachia—Bailey, 1950:311-316 (original description).

Etheostoma barratti—Hubbs, 1952:486 (Caddo Lake, Texas); Moore, 1952:11 (Okla.); Bick, Hornuff, and Lambremont, 1953:230 (St. Tammany Par., La., misspelled *barrati*); Knapp, 1953:128 (range, in part), 126 (key to Texas fishes), fig. 167; Jurgens and Hubbs, 1953:4 (list of Tex. fishes); Bailey, Winn and Smith, 1954:144-145, 161 (Escambia R., Fla. and Ala.); Freeman, 1954:144, 146, 148, 154 (Salkahatchie and Savannah rivers, S. C.); Bailey and Gosline, 1955:20, 44 (number of vertebrae); Carr and Goin, 1955:31, 102 (description, habitat) pl. 30; Eddy, 1957: 220, fig. 547 (range, in part); Hubbs, 1957a:9 (list of Tex. fishes); Hubbs, 1957b:94 (distribution in Tex.); Moore, 1957:198; Briggs, 1958:275 (Fla.); Crittenden, 1958:217 (Bay Co., Fla.); Hubbs, 1958:11 (list of Tex. fishes); Cook, 1959: 35, 200, 203 (Miss.); Patrick, 1961: 257 (Savannah R.).

Etheostoma barratti appalachia—Bailey, Winn and Smith, 1954:144 (two introduced centrarchids in the pond from where *E. b. appalachia* was taken).

Etheostoma fusiforme barratti—Collette, 1961:2051.

Misidentifications—*E. fusiforme barratti* as *Hololepis serrifer*—Fowler, 1945:252 (Savannah R., Ga., specimens re-examined); as *Villora edwini*—Fowler, 1945:251-252 (two series from Piney Woods Lake, Ware Co., Ga., one series re-examined), 293-294 (seven series from Florida, five of which were re-examined).

Types—MCZ 24571 (5 specimens, 37.0-45.8 mm), from "Florida." The holotype of *Poecilichthys quiescens* is USNM 25509, a 35.5 mm male from a tributary of the Suwanee R. near Nashville, Georgia.

Diagnosis—Distinguished from the other species of the subgenus *Hololepis* by a combination of the following characters: two anal spines; interorbital pores absent; preoperculomandibular pores usually nine; infraorbital canal incomplete; breast completely scaled. Distinguished from *E. fusiforme fusiforme* by the following: preopercle more often partially serrate (36% of specimens examined); infraorbital pores usually 1 + 3 (70%); more interorbital scales (1-37, x̄: 13.2); parietal more completely scaled (usually over 25%, x̄: 57.5%). Maximum size of males 46.2 mm (USNM 99988, Hillsborough Co., Fla.) and of females 46.6 mm (CU 35102, Santee River).

Coloration—The range of variation is generally similar to that of *E. f. fusiforme;* both forms are extremely variable.

In both sexes there is a tendency toward the development at the base of the caudal of a supramedian spot in addition to the submedian spot present in *E. f. fusiforme.* When present, the supramedian spot is not as intense as the submedian. The tendency toward the formation of a median band in the first dorsal fin occurs more often in populations of *f. barratti* than in *f. fusiforme.* This tendency was also noted in the second dorsal and anal fins in some specimens. A male from the Okefenokee Swamp showed the most extreme development of pigmentation (Fig. 10) of any *fusiforme* males that were examined. The patterns of breeding males and females from four localities are shown (Figs. 9 and 10).

As noted by Collette and Yerger (1962),

Figure 9. Breeding patterns of female *Etheostoma fusiforme barratti.* (from top to bottom) CU 29752; 40.2 mm; Ga., Bullock Co., Ogeechee dr.; Feb. 15, 1951. UG 201; 42.3 mm; Ga., Charlton Co., Okefenokee Swamp; Apr. 10, 1951. UG 205; 24.5 mm; Ga., Irwin Co., Crystal Lake; May 5, 1951. DU uncat; 32.8 mm; N.C., Henderson Co., French Broad dr., date unknown but apparently past height of breeding season. (Photograph by Douglass M. Payne)

the drawing in Fowler (1941: Fig. 13) labeled as *Hololepis barratti* is reversed with the one labeled as *Villora edwini* (Fig. 3).

Genital Papilla—The genital papilla of the breeding female is like that in *E. fusiforme fusiforme* (Fig. 1f) and *E. gracile* (Fig. 1c).

Breeding Tubercles—Tubercles are present on the anal and pelvic fin rays as in *E. fusiforme fusiforme,* but are frequently also present on the pelvic and second anal spines. Besides showing a greater development of breeding tubercles than in *E. f. fusiforme,* the tubercles are present for a longer period of time. In the Ochlockonee population, tubercles have been found on specimens taken from December 17 through April 13. Tubercles have been found as early as October 27 (Suwannee to Ochlockonee population, FSU 3273) and as late as May 29 (UG 516, Pee Dee population). In these collections not all males have tubercles, and some specimens have them only on the pelvic fins. Specimens with tubercles on both anal and pelvic fins were taken in the period from March 25 to May 29. The spawning period varies between populations but should be within the period that tubercles are developed to their maximum extent.

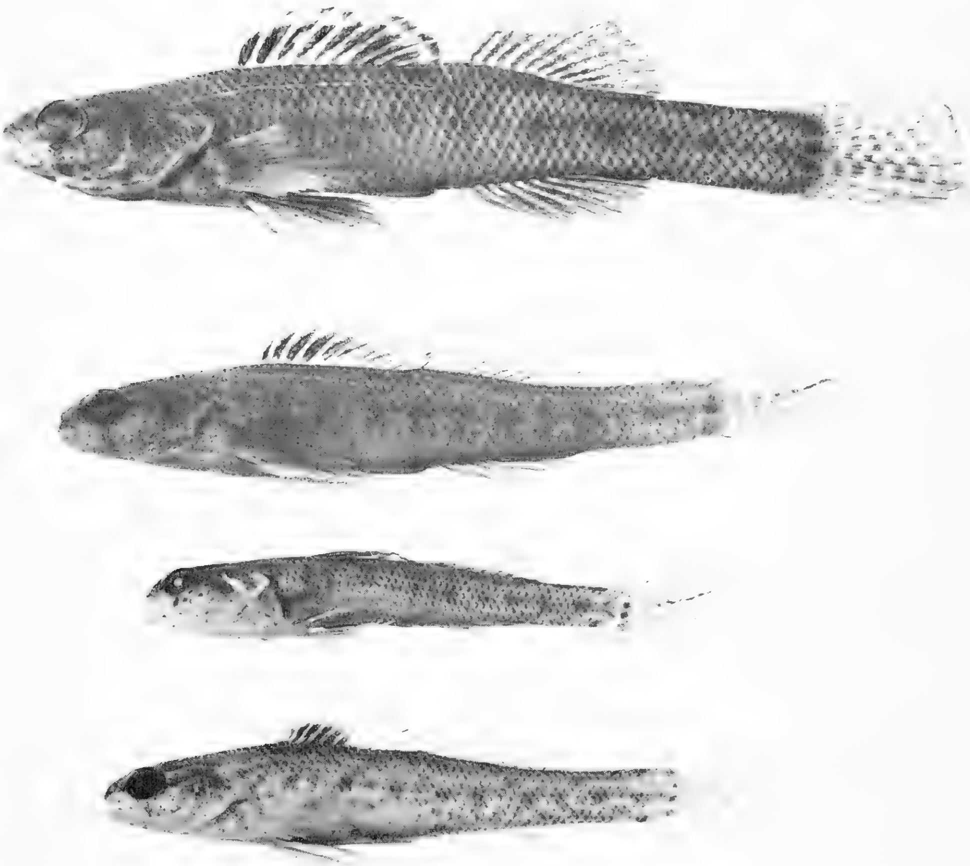

Figure 10. Breeding patterns of male *Etheostoma fusiforme barratti*. (from top to bottom) UG 201; 46.7 mm; Ga., Charlton Co., Okefenokee Swamp; Apr. 10, 1951. TU 7937; 37.8 mm; Miss., Pearl River Co., Pearl dr.; Mar. 21, 1952. UG 205; 28.1 mm; Ga., Irwin Co., Crystal Lake; May 5, 1951. DU uncat; 32.5 mm; N.C., Henderson Co., French Broad dr., date unknown but apparently past height of breeding season. (Photograph by Douglass M. Payne)

The distribution of breeding tubercles on the pelvic fins of male *E. f. barratti* is essentially the same as in *E. gracile* (Fig. 1k). The distribution on the anal fin of a male *f. fusiforme* (Fig. 1j) is similar to the distribution in *f. barratti,* except that in the latter the tubercles are more likely to be on the second anal spine.

Development—As in *E. fusiforme fusiforme,* both the supratemporal canal and the number of pored lateral-line scales change with age. The supratemorpal canal is incomplete in young specimens (16.8 to 20.1 mm) from Crystal Lake, Georgia (UG 205) (Table 31); the transition period extends from 20.5 mm to 22.0 mm; and the supratemporal canal is complete in specimens 22.0 mm and larger. In specimens from the Arlington River, Florida (UF 6945), the juvenile period extends to 21.3 mm, the transition period from 21.5 to 27.4 mm, and the supratemporal canal is complete in specimens larger than 27.4 mm (Table 31). In a series of collections from Lake Fairview, Florida (ANSP) the juvenile period extends to 19.9 mm and the transition period is completed by 24.9 mm (Table 31).

A 12.6 mm specimen from the Okeechobee drainage (CU 35069) has scales on the caudal peduncle and extending forward along the lateral line to a point opposite the rear base of the first dorsal fin. A 16.8 mm specimen in this collection has the body squamation nearly complete but has only four pored lateral-line scales; a 21.6 mm specimen has 11 pored scales, and the other six specimens (22.8 to 27.2 mm) have 15-19 pored lateral-line scales. The incomplete development of pored lateral-line scales in adults from Crystal Lake, Georgia, will be discussed under geographic variation, pored lateral-line scales.

Habitat—Basically the habitat of *E. fusiforme barratti* is the same as that of the nominate form: swamps, backwaters of streams, sloughs and lakes. Goin (1943) listed *E. f. barratti* as part of the lower vertebrate fauna associated with water hyacinths (*Eichornia crassipes*) around Gainesville, Florida. In Orange Lake, Florida, Reid (1950 and 1952) found *E. f. barratti* both in shallow shore zones and around the edges of floating islands composed of arrowhead (*Sagittaria*) and pickerel weed (*Pontederia*) some distance from shore. The characters of a Florida stream containing *E. f. barratti* are contrasted with those of a stream containing *Etheostoma* (*Villora*) *edwini* under the account of the latter species in Collette and Yerger (1962).

Species Associates—J. R. Bailey (1950) listed *Chaenobryttus gulosus, Lepomis m. machrochirus,* and *Lepomis auritus* as associates of his *Hololepis barratti appalachia.* R. M. Bailey, Winn, and Smith (1954) used the presence of *Chaenobryttus* and *L. auritus* at the type locality of *E. b. appalachia* as an indication that it is merely the product of an introduction.

Woolman (1892), in reporting on the fishes of central Florida, found *E. f. barratti* in eleven localities. Species commonly found by him with *f. barratti* and the number of times taken were: *Gambusia affinis* (11); *Chaenobryttus gulosus* (11); *Fundulus chrysotus* (8); *Jordanella floridae* (7); *Lepomis machrochirus* (7); and *Elassoma evergladei* (7).

Predators—From lakes Eustis and Harris, Florida, Freeman and Huish (1953) reported *E. f. barratti* from the stomachs of *Micropterus salmoides, Pomoxis nigromaculatus, Lepisosteus osseus,* and *L. productus.* McLane (1948) reported one *E. f. barratti* from the stomach of a young (47-229 mm) *Micropterus salmoides floridanus* from the St. Johns River. After rotenoning, McLane (1950) also reported 500 *E. f. barratti* from 62 *M. salmoides floridanus* stomachs from Buck Pond, Marion County. One had eaten 47 *f. barratti.* He noted that most of the bass may have taken *f. barratti* during the poisoning operation. It seems likely that any larger fish will feed on *E. f. barratti* if they are available.

Habits—McLane (1950) found 82 *Chaeborus,* 37 *Chydoras,* 15 *Cyclops,* 2 Chironomidae, and 2 Amphipoda in nine stomachs of *E. f. barratti* from Buck Pond, Florida.

Distribution—Found from the Pee Dee River of North and South Carolina south along the Atlantic Coastal Plain below the Fall Line throughout most of peninsular Florida; west along the Gulf Coastal Plain as far as Caddo Lake on the Texas-Louisiana border; and north in the former Mississippi Embayment as far as McCurtain Co., Oklahoma and Reelfoot Lake, Tennessee (Fig. 8). Also known from a few ponds in the vicinity of Asheville, North Carolina, in the French Broad River system, but this population is believed (Bailey, Winn, and Smith, 1954) to be the result of an introduction.

Hubbs and Cannon (1935: pl. III) gave the range of *E. f. barratti* as the Pee Dee River south to the Peace River of Florida and west as far as the Suwannee River drainage of Georgia and Florida. Since then Baker (1939a) reported one specimen from Reelfoot Lake to which I have added another specimen from a collection made in June, 1959. Although Cook (1959) stated that there were no positive records from Mississippi, it has been taken at a number of localities in that state as indicated under the specimens examined.

The presence of *E. f. barratti* in southeastern McCurtain County, Oklahoma, reflects the influence of the Coastal Plain on the fish fauna of this region, as noted by Reeves and Moore (1951) for *Lepomis marginatus, L. symmetricus, Fundulus notti dispar, Centrarchus macropterus,* and *Elassoma zonatum.*

Etheostoma f. barratti has been taken from several other localities in the Red River system: Caddo Lake on the Texas-Louisiana border (Hubbs, 1952) and from various localities in the northern part of Louisiana. Hubbs (1957b) listed several species that occur in the Red River system east of Lake Texoma but are absent from the Sabine and other drainages to the west such as: *Esox niger, Moxostoma erythrurum, Notropis cornutus, N. ortenburgeri, Menidia audens, Stizostedion canadense* and *E. f. barratti.*

A specimen with the locality data of "Spring Creek, Texas," (USNM 118555) must come from west of Caddo Lake and so is the western-most record of *E. f. barratti,* but due to the large number of places with this name in Texas, the exact locality is unknown.

As Briggs (1958) pointed out, only one of the 11 Florida percid fishes *(E. f. barratti)* is found in the southern part of the peninsula. He gave the distribution of *E. f. barratti* as south to Lake Okeechobee. Woolman (1892) reported *f. barratti* as far south as the Peace River on the Gulf Coast. Recent collections have extended the range farther south into Collier Co. on the west coast (TU 20719) and into Dade Co. near Miami on the east coast (USNM 195862).

Figure 8 shows how clearly the Fall Line delimits the range of *E. f. barratti,* particularly in the Congaree watershed of South Carolina, where a large number of collections show *E. f. barratti* (and *E. serriferum,* Fig. 3) below the Fall Line and *E. saludae* above it (Fig. 3). It is also of interest to compare Fig. 5 of the distribution of *E. gracile* with Fig. 8. This comparison will show that although there is a large overlap in the total ranges of *E. gracile* and *E. f. barratti,* there are relatively few localities where both have been taken together (Reelfoot Lake, Tenn.; Caddo Lake, Tex.; SE McCurtain Co., Okla.; Ouachita Parish, La.).

Specimens Examined—Complete locality data are given only for those collections which show range extensions or other significant distributional information. Other collections are listed by drainage, state, county, and museum number with the total number examined for each drainage. Complete data for most of the collections can be found in Collette (1960). A total of 2265 specimens from 339 collections was examined.

Pee Dee Dr., 49 specimens. N. C.—Richmond Co.: CU 19570; UG 516. Scotland Co.: UG 457. S. C.—Florence Co.: CU 19189. Georgetown Co.: ANSP 61023-6. Lee Co.: CU 28217.

Santee Dr., 78 specimens. S. C.—Berkeley Co.: USNM 116236. Clarendon Co.: CU 26250. Kershaw Co.: CU 35104, 35121, 35123, 35110, 35106; USNM 195865, 195866. Lexington Co.: CU 35124, 35122, 35116. Lexington-Calhoun cos.: CU 35102. Richland Co.: CU 35117, 35125, 35112, 35130, 35113, 35127, 35115, 35105, 35129, 35103, 35108; USNM 149254. Sumter Co.: CU 35132.

Charleston Harbor Dr., 13 specimens, S. C.—Charleston Co.: USNM 1143 and 1161. Dorchester Co.: USNM 1185.

Edisto Dr., 16 specimens. S. C.—Bamburg Co.: CU 35114, 35101. Colleton Co.: ANSP 54788. Orangeburg Co.: CU 19080, 30622.

Combahee-Broad Dr., 14 specimens. S. C.—Barnwell Co.: CU 35118, 35109, 35128. Jasper Co.: CU 32662.

Savannah Dr., 336 specimens. S. C.—Aiken Co.: ANSP 73458; UG 247, 270; CU 35107, 35126, 24325, 30882; ANSP 78845, 78494; USNM 195864. Allendale Co.: ANSP 73409, 74263, 78875; UG 252; UMMZ 167889; CU 30897; USNM 162530, 162531, 162532. Barnwell Co.: CU 35120, 35119, 35111, 24396; ANSP 78899, 80401; USNM 195863. Jasper Co.: UMMZ 155201. Ga.—Chatham Co.: ANSP 79858. Richmond Co.: UMMZ 158026; CU 17628, 17209; UG 177; USNM 86194, 82624, 82625.

Ogeechee Dr., 49 specimens. Ga.—Candler Co.: UG 152, 152B. Bryan Co.: CU 30322; TU 16454. Bullock Co.: CU 30627, 30625, 30626, 30623, 30624, 29752, 29762. Jenkins Co.: USNM 43457, 61567.

Altamaha-Satilla Dr., 54 specimens. Ga. —Appling Co.: CU 29756. Brantley Co.: UG 447; TU 21200. Coffee Co.: BU uncat. Dodge Co.: CU 17702. Emmanuel Co.: UMMZ 158045; CU 17686. Irwin Co.: CU 29748; UG 292, 292A. Jeff Davis-Montgomery cos.: UG 259. Johnson Co.: TU 14298. Tattnall Co.: CU 29755. Toombs Co.: UMMZ 158062. Washington Co.: CU 29761.

St. Marys Dr., 69 specimens. Ga.—Camden Co.: ANSP uncat. Charlton Co.: CU 516, 503, 522, 4043, 35136, 35137, 35135; UG 200; TU 21309. Fla.—Baker Co.: CU 12615, 21088; TU 21212.

St. Johns Dr., 188 specimens. Fla.—Brevard Co.: UMMZ 158576. Duval Co.: UF 6945. Flagler Co.: USNM 125479, 170976. Lake Co.: TU 12519; CU 35140. Seminole Co.: ANSP uncat.; CU 24572. Volusia Co.: UF 6940; USNM 133270.

Indian River Dr., 1 specimen. Fla.—Brevard Co.: USNM 25343.

St. Cloud, Fla.—Osceola Co.: UMMZ 158641 (39, 24-38); canal between Alligator and Lizzie Lakes near St. Cloud; Dec. 28, 1939.

Orlando isolates, 204 specimens. Fla.—Orange Co.: USNM 44413, 106941, 133527, 133536, 133509, 133517, 133516; ANSP 4 uncat. coll.

Oklawaha-St. Johns isolates, 90 specimens. Fla. —Clay Co.: CU 35067. Marion Co.: UMMZ 110658, 158125, 166544, 166601; UF 6958; CU 26277. Osceola Co.: UMMZ 158606. Putnam Co.: CU 35068.

Lake Okeechobee Dr., 47 specimens. Fla. —Hendry Co.: CU 35069. Highlands Co.: OAM uncat.; CU 24236. Indian River Co.: UF 6948. Osceola Co.: CU 8614, 10235, 12030, 23951; UMMZ 158555; FSU 2496.

Dade Co., Fla.—USNM 195862 (1, 19); W suburbs of Miami, canal near Milam Dairy Rd. and Ludlum Rd.; Apr. 7, 1960.

South Florida isolate—Collier Co.; TU 20719 (54, 18-38); canal 11.2 mi. E. jct. US 41 and Fla 846, or 21.6 mi. NE of Naples; July 9, 1959.

Charlotte Harbor Dr., Fla.—Charlotte Co.: UMML 4754 (3, 33-39); roadside canal 8.5 mi. E of Punta Gorda on Fla. 74; Dec. 22, 1957.

Tampa Bay Dr., 46 specimens. Fla.—Hillsborough Co.: UMMZ 139251; CU 12731, 21124; TU 208, 3054, 3772, 4626; FSU 1846; USNM 100029, 100050; 99988, 170974, 99956, 106960. Pasco Co.: TU 20737. Pinelas Co.: CU 12246. Polk Co.: CU 26256.

Withlacoochee-Waccasassa Dr., 101 specimens. Fla.—Citrus Co.: TU 9842. Citrus-Marion cos.: FSU 2131. Lake-Polk cos.: CU 35139. Levy Co.:

CU 12796, 24550; UF 2903; TU 15672; USNM 106932, 106939.

Newnan Lake Dr., 84 specimens. Fla.—Alachua Co.: UF 6944; UG 9; CU 12302, 12846, 16035; USNM 88490, 93715.

Suwannee Dr., 68 specimens. Ga.—Berrien Co.: USNM 28509 (1, 37); trib. of Alapaha R. at Nashville; holotype of *Poecilichthys quiescens*. Irwin Co.: CU 29601; UG 208. Lanier Co.: USNM 94893; BU uncat. Lowndes Co.: UG 458. Wilcox Co.: CU 17652, 17411. Fla—Bradford Co.: USNM 63779. Columbia Co.: CU 12500; UF 8301. Dixie Co.: ANSP 69213. Hamilton Co.: UMMZ 163310; TU 24465. Lafayette Co.: UMMZ 166609.

Crystal Lake, Ga.—Irwin Co.: UG 205 (26, 17-28); Crystal L., 4.5 mi. N Irwinville; May 5, 1951.

Okefenokee Swamp, 88 specimens. Ga.—unknown co.: ANSP 55935; USNM 153440. Charlton Co.: CU 8610-3, 257-60, 353-4, 262-5, 129, 320, 340, 535, 6-7 9-10, 325; ANSP 79923; UG 201; USNM 153433. Ware Co.: ANSP 70564; CU 27322; UMMZ 138720.

Fenholloway to St. Marks Dr., 30 specimens. Fla.—Lafayette Co.: CU 12202. Leon Co.: FSU 3273; TU 9763. Madison Co.: CU 12484. Taylor Co.: TU 5056. Wakulla Co.: UMMZ 163428; UF 1887.

Ochlockonee-New Dr., 122 specimens. Ga. — Colquitt Co.: CU 17504. Grady Co.: UG 102, 103; FSU 2887. Thomas Co.: FSU 3970. Fla.—Gadsden Co.: UF 6956, 4889; FSU 306, 2167, 3861; TU 22590. Leon Co.: FSU 400, 67, 74, 259, 1300, 3609, 2091. Liberty Co.: UMMZ 158183; FSU 230, 2267, 3755; TU 1116.

Apalachicola Dr., 102 specimens. Ga.—Baker Co.: UG 31, 27, 36. Crisp Co.: UG 6. Dougherty Co.: UMMZ 164001, 164039; BU uncat. Early Co.: UG 25A. Sumter Co.: UMMZ 163989. Taylor Co.: CU 30319. Fla.—Franklin Co.: FSU 2767. Gadsden Co.: UMMZ 166266. Gulf Co.: FSU 1551; TU 20540, 22453. Jackson Co.: FSU 2679, 2688, 2701, 2733.

Choctawhatchee to Perdido Bays, 64 specimens. Fla.—Bay Co.: UMMZ 163450. Escambia Co.: FSU 2916. Escambia-Santa Rosa cos.: ANSP 72892, 73028, 79004; UMMZ 165074. Holmes Co.: UMMZ 163501; TU 20406. Okaloosa Co.: TU 23694, uncat. Santa Rosa Co.: UMMZ 155507, 165119; ANSP 73060; TU 10489. Walton Co.: TU 311, 20865, 22730, 22775, 23154.

Unknown Fla. Dr., 48 specimens.—USNM 92864, 92896, 106941.

Mobile Bay Dr., Ala.—Mobile Co.: TU 6257 (4, 30-44); Hall's Mill Cr. at Navco, trib. of Dog R., Feb. 11-13, 1938. Washington Co.: UMMZ 163599 (4, 33-38); Bilbo Cr., on US 43 near McIntosh, T3N, R1E, Sec. 7; Apr. 12, 1941.

Mississippi Sound Dr.. Miss.—Hancock Co.: TU 7663 (6, 32-42); Bayou Phillip, trib. to Jordan R., 2.5 mi. E of Waveland on rt. 90; Mar. 9, 1953. Harrison Co.: ANSP 55746 (1, 36); 3 mi. N of Biloxi in cypress cr.; Mar. 15, 1932. Stone Co.: USNM 195873 (1, 36); Red Cr. near US 49, near Wiggins; May 13, 1933.

Pearl R.—Lake Pontchartrain Dr., 41 specimens. Miss.—Pearl River Co.: Hobolochitto Cr., 0.9 mi. N of Picayune on US 11: TU 7937, 14103, 5112, 7670, 16773; UMMZ 166128; CU 31890. La.—St. Tammany Par.: CU 32247 (1, 40); 8 mi. W of Slidell. TU 379 (1, 34); slough at second bridge W of Pearl R. on Hickory Rd. TU 5755 (1, 38) and TU 835 (1, 35); Talisheek Cr., 0.3 mi. N of Talisheek. TU 8159 (1,40); canal along W Pearl R., 13 mi. N of the town of Pearl River. TU 15144 (2, 34-37), TU 17369 (6, 34-40), and TU 17413 (4, 35-38); Talisheek Cr. at Talisheek on La. 41. Tangipahoa Par.: TU 3574 (1, 40); Selser Cr., 3.3 mi. E of Hammond on rt. 7.

Yazoo Dr., Miss.—Warren Co.: USNM 129093 (1, 38); Yazoo R. at bridge on US 61 near Vicksburg; May 1933. Yazoo Co.: USNM 170977 (1, 36); Little and Big Kilby Lakes, Yazoo City; June 2, 1933.

Reelfoot Lake, Tenn.—Obion Co.: UMMZ 105397 (1, 39); stagnant basin at N end of lake; July 26, 1937. CU 33345 (1, 20); N end of lake by Oak Log Lodge near the Reelfoot Biological Station; June 27, 1959.

Red River Dr., La.—Caddo Par.: USNM 172636 (9, 21-26); Black Bayou L., 0.5 mi. above dam on E side of lake, sec. 23, T22N, R15W; July 24, 1956. Ouachita Par.: UMMZ uncat. (2, 30-40); Cheniere Cr. below dam of Cheniere L., Sec. 17 and 20, T17N, R3E; June 6, 1956. Union Par.: USNM 172708 (8, 21-27); Bayou de l'Outre at La. 2. Hattick Lake, sec. 20, T20N, R3E; June 18, 1955. Okla.—McCurtain Co.: OAM 3078 (8, 25-31); Aug. 20, 1948; and CU 33747 (8, 20-25); June 24, 1959; cypress swamp 3 mi. S of Eagletown on dirt road. Tex.—Harrison Co.: OAM 4732 (9, 29-39); 3.5 mi. NE of Kernack on Caddo Lake; Mar. 24, 1951.

Unknown Texas Dr.—USNM 118555 (1, 36); Spring Cr.; Apr. 23, 1940.

French Broad Dr., N. C.—Buncombe Co.: pond S of mouth of Bent Cr., 300 ft. W of the French Broad R., 7 mi. SSW of Asheville. UMMZ 156224 (1, 37) holotype, UMMZ 156225 (49, 17-43) paratypes, July 14, 1947, and CU 18444 (3, 30-40), June 7, 1949, paratypes of *Hololepis barrati appalachia*. Henderson Co.: DU uncat. (12, 28-38); Cane Cr. oxbow, 1 mi. SW of Fletcher, 1 mi. above mouth of Cane Cr. into French Broad R.; 1952.

1. *Geographic Variation in Etheostoma fusiforme*

Variation in the characters examined for the two valid subspecies (*E. fusiforme fusiforme* and *E. fusiforme barratti*) will be discussed in this section (Tables 18-31). Nine names presently apply to segments of this species. From north to south they are: *fusiforme fusiforme* (Girard) from southern Maine through Massachusetts, exclusive of Cape Cod; *f. metaegadi* (Hubbs and Cannon) from Cape Cod; *f. insulae* (Hubbs and Cannon) from Nantucket Island; *f. erochroum* (Cope) from New Jersey and the Delmarva peninsula; *f. atraquae* (Hubbs and Cannon) from the Potomac River; *thermophilum thermophilum* (Hubbs and Cannon) from the Neuse, Cape Fear, and Waccamaw rivers, and White Lake; *t. oligoporum* (Bailey and Frey) from the dark-stained North Carolina Bay Lakes (Salters, Jones, Singletary) in the Cape Fear drainage; *barratti barratti* (Holbrook) from the Pee Dee River south through most of penisular Florida, west to the Red River in Texas and Oklahoma, and north in the Mississippi Embayment as far as Reelfoot Lake, Tenn.; and *b. appalachia* (Bailey) from the French Broad River, near Asheville, N.C. The validity of these nominal forms will be discussed below.

Total Lateral-line scales (Table 18): Hubbs and Cannon (1935:83) gave the number of total lateral-line scales of their *Hololepis fusiformis insulae* from Nantucket as "somewhat fewer than in typical *fusiformis* and much fewer than in *metaegadi*." This was true on the basis of the one Cape Cod collection on which *metaegadi* was based and a few more recent collections. However, at one Cape Cod locality, Mills River, counts are intermediate between *insulae* and *metaegadi* ($\bar{x}$: Nantucket-44.71, Mills River—48.84, and the rest of Cape Cod—52.34). There is also a reduced mean number of total lateral-line scales in some other scattered populations: the Weweantic River just to the west of Cape Cod ($\bar{x}$: 48.35); the coastal streams south of Raritan Bay, New Jersey (46.58); the James River of Virginia (46.57); and Crystal Lake, Georgia (46.04).

Several populations have more total lateral-line scales than *f. metaegadi:* Lake Ronkonkoma, N.Y. ($\bar{x}$:55.71); Pataganset Lake, Conn. (54.62); Lake Yaphank, N.Y. (54.13); Pearl-Pontchartrain, La. (55.10); Red River (55.68).

Pored lateral-line scales (Table 19): The major difficulty with regard to this character is the great amount of variation present (0-37 scales). This is particularly true in a number of natural lakes in North Carolina, known as the Bay Lakes.

Although the Carolina Bays have long been a subject of geological investigations to determine their mode of origin, relatively little is known about the biology of the few lakes that remain in the Bays. Fowler (1942) and Hubbs and Raney (1946) described four endemic species of fishes from Lake Waccamaw, the largest of the southern North Carolina natural lakes. Later (Frey, 1951), *Notropis waccamanus* Fowler was reduced to a synonym of *N. petersoni* Fowler. Frey (1948a, 1948b), Hueske (1948), and Louder (1958, 1959) published a series of popular papers about the lakes and their fauna.

Frey also published a series of scientific papers (1949, 1951) and Bailey and Frey (1951) recognized two subspecies of *Hololepis thermophilum* from the Bay Lakes. They named the form in the dark stained lakes *thermophilum oligoporum* and considered the nominate form to be present in the clearer lakes (White, Ellis, and Waccamaw) as well as in the Cape Fear and Neuse rivers. Bailey and Frey (1951) were aware of the biogeographic difficulties in this allocation of subspecies: lakes White, Waccamaw and Ellis each belong to a separate major Atlantic drainage while the dark lakes (Jones, Salters, Singletary) along with White, are found in the Cape Fear system. Bailey and Frey discussed the possibility of polyphyletic origin of *t. oligoporum.* I believe that taxonomic recognition should be withheld when polyphyletic origin of a subspecies is suspected.

A special search was made for a reasonable explanation for the presence of the different forms in the dark and light Bay Lakes. The explanations proposed are based on an intensive study of the Bay Lakes and their fishes. The best differentiating character lies in the number of pored lateral-line scales, which is considerably reduced in the dark lakes. Frey (1951) noted a similar situation, with the *Perca flavescens* and *Chaenobryttus gulosus* from the darker lakes having fewer total lateral-line scales, but considered these to be cases of ecotypic variation. Bailey and Frey (1951) rejected the possibility that their *thermophilum oligoporum* was an ecotypic variation.

The correlation between water color and number of lateral-line scales might be due, not to color *per se,* but to productivity. Therefore, the productivities of the lakes were compared. Productivity is characterized in many different ways so several methods of estimation were utilized, both physical-chemical and biological.

Increased productivity is frequently correlated with increased carbonate content. Carlander (1955) showed a positive correlation between fish crop and methyl orange alkalinity in trout lakes, warm water lakes, and reservoirs. Moyle (1949) showed a positive correlation between yield of pikeperch and total alkalinity. Frey (1949) presented a summary table of physical and chemical characteristics of the Bay Lakes. He gave the alkalinity in ml. N/44 H_2SO_4 because there is some free sulphuric acid present in some of the lakes. Thus the alkalinity cannot be stated in the usual manner (parts per million of methyl orange alkalinity). However, it is apparent that the lakes fall into two categories (Table 28); a low alkalinity group, the Bladen County Lakes (Black, Jones, Salters, Singletary, White) and a high alkalinity lake (Waccamaw). This high alkalinity is apparently due to the solution of lime and other minerals from the outcrops of the calcareous Duplin formation, and of the older Cretaceous formation along the northeast shore (Clark, *et al.,* 1922).

The pH of lakes is also correlated with

productivity. Smith (1952, 1953b) noted the low productivity of New Jersey waters with a pH below 6.0. Renlund (1950) noted the absence of a number of plants (especially species of *Potamogeton*) from the acid lakes of southern New Jersey. Table 28 shows the pH as taken from Frey (1949). Again there are two distinct groups; the Bladen County Lakes on the one hand and the more alkaline Waccamaw on the other.

Shoreline development is also correlated with productivity (Welch, 1952) since increased irregularity of shoreline results in greater contact of water with land, increased area of protected bays, greater diversification of bottom and margin conditions, increased areas of shallow water for growth of rooted vegetation, and increased opportunity for close super-position of the photosynthetic zone upon the decomposition zone. The last two factors are of no importance here because all the lakes are so shallow. These lakes are all oval with few irregularities, so the figure for shore line development (Table 28) is quite close to 1, the value for a perfect circle. Singletary Lake has an artificial dredged channel, 160 yards long, in the outlet creek and so has the highest value (1.17).

Another factor that limits productivity is the amount of light energy that reaches the phytoplankton; that reaching a certain depth in a lake is due to differences in transparency which in turn varies with three factors: color of the water; amount of organic and inorganic material in the water; and the amount of plankton present (Ruttner, 1953). The first two factors are of importance in the Bay Lakes. Frey (1951) gave the actual color of the water in parts per million of potassium chloroplatinate (Table 28). However, the scattering of the radiation by suspended materials is just as important as the absorptive function of the coloring material in these lakes. Singletary, Black, and Salters lakes have larger quantities of non-living organic materials than do the other lakes. Light penetration, as measured with the Secchi disc, takes into consideration both of these factors. Based on Frey's mean Secchi disc readings, the lakes fall into three groups (Table 28): low light penetration (Black, Jones, Salters, Singletary); moderate penetration (Waccamaw); and high penetration (White).

Table 29 ranks the physical-chemical indices of productivity from 1 to 6 and the totals of these rankings give a physical-chemical index of productivity by means of which the lakes may be arranged in order of increasing productivity namely: Black, Jones, Salters, Singletary, White, Waccamaw.

Certain biological characteristics can be used to measure productivity. One of these is the relative amount of rooted aquatic vegetation. Data from Frey (1948a, 1948b, 1949), Louder (personal communication), and personal observation classify the lakes as follows: 1. no rooted aquatics (Black, Jones, Salters); 2. small amount, especially in the artificial channel (Singletary); 3. moderate amounts (White and Waccamaw). In addition to being a measure of productivity, the amount of aquatic plants present has a direct effect on productivity. One of the reasons that the darker lakes are so unproductive is that there are few aquatics present to provide food, cover, and spawning sites for fishes and other animals. The lack of abundant rooted aquatic vegetation is caused in part by the dark water which prevents photosynthesis at other than very shallow depths.

The number of species of fish (or other animals) present may also be used as an indication of relative productivity. Frey (1951) listed the species of fishes collected during the 1947 survey as follows: Black-8; Salters-11; Jones-12; Singletary-13; White-17; and Waccamaw-25. Since then my collections and those made by Darrell E. Louder (1959 and personal communication) have added to the number of species taken in all of the lakes (Table 30). Frey (1951) pointed out that there is a group of 11 species in almost all of the lakes (Table 30) with *Etheostoma f. fusiforme* and *Esox niger* lacking only in Black Lake. *Aphredoderus sayanus* may now be added to this list and is absent only from Jones Lake. In the various lakes, additional species are found correlated with increased productivity until Waccamaw is reached, which has all but one of the species present in the other lakes. Here *Fundulus notti lineolatus* is replaced by the endemic *F. waccamensis.* Frey noted that probably none of the species of *Lepomis* is native to the Bladen County lakes. Introductions have of course been attempted, from which subsequent re-

TABLE 31.
Development of the supratemporal canal in Etheostoma fusiforme

Size (mm)	*E. fusiforme fusiforme* Long Island com.	inc.	Jones L. com.	inc.	White L. com.	inc.	Singletary L. com.	inc.	L. Waccamaw com.	inc.	Salters L. com.	inc.	*E. fusiforme barratti* L. Fairview com.	inc.	Arlington R. com.	inc.	Crystal L. com.	inc.
12.0-13.9		3		2				2										
14.0-15.9		8		6		17		9				3						
16.0-17.9		8		4		30		6		1	1	14						3
18.0-19.9		9	3	15	6	29		17	3	10	7	17		7		2		2
20.0-21.9	3	14	3	4	21	16	1	11	8	12	6	14	3	8	1	3	3	1
22.0-23.9	12	9	16	5	35	16	3	3	5	3	4	14	3	5	8	5	5	1
24.0-25.9	18	5	10		32	7	2	8	13	—	1	4	4	1	13	3	6	
26.0-27.9	26	—	7		9	7	5	11	4	2		1	2		7	1	1	
28.0-29.9	19	1	1		2		4	7	1	—		—	2		3		1	
30.0-31.9	10	—	1		1		1		6	2		1	—		—			
32.0-33.9	24	—					—		4			1	1		2			
34.0-35.9	27	—					—											
36.0-37.9	36	2					—											
38.0-39.9	23	—					—											
40.0-41.9	10	1					1											
42.0-43.9	20																	
44.0-45.9	7																	
46.0-47.9	4																	
48.0-49.9	1																	
50.0-51.9																		

(The horizontal lines mark the extent of the transition period, with the juvenile condition above the top line and the adult condition below the bottom line. Inc. — incomplete, com. — complete.)

TABLE 32.
Number of pored lateral-line scales in Etheostoma collis and E. saludae

Form and drainage	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	x̄
collis lepidinion																											
Roanoke						1	—	—	4	3	4	4	3*	6	1	1	1	1									16.17
Neuse								1	1	1	2	1															14.17
Cape Fear														1**													—
collis collis																											
Yadkin-Pee Dee					1	—	4	2	4	3	4	3	2	2	—	1	2	1	1	1							15.48
Rocky-Pee Dee						3	1	2	3	2	3	4	1	1	—	—	1	—	—	—	—	—	—	—	—	1	14.86
Catawba	1	—	—	—	2	2	1	1	1	—	—	—	—	1	1												11.60
"Santee"									1	—	—	—	1														15.00
saludae	1	1		—	1	1	5	3	5	7	6	11	7	7	14	3	6	6	3	1	—	—	—	—	1		16.87

* Count of holotype of *E. c. lepidinion.*
** This specimen counted on right side.

captures have been made only in Singletary and White lakes. Based upon present data, the lakes may be ranked with the number of fish species present as the criterion as follows: Black; Jones; Salters; Singletary; White; Waccamaw.

Meager data for a third type of biological estimate of productivity are available. In the course of fishery investigations upon the Bay Lakes made by D. E. Louder, two shore rotenone collections of a half acre each were made during the summers of 1957, 1958 and 1959 in each of the lakes (1959 collections omitted in Black Lake). The mean pounds of fish per acre from these samples is included in Table 28. These values are used with some hesitation for several reasons. Two samples per lake, per year, especially in a lake as large as Waccamaw, can not adequately represent the productivity of the lake. Secondly, the variations between the pairs of collections from Waccamaw are so great as to make the value of these quantities dubious. Nevertheless, ranking the lakes by this method gives the following order: Black; Jones; Singletary; Salters; and Waccamaw and White.

If the three biological characters are ranked in the same manner as the physical-chemical factors, the lakes fall into the same order (Table 29). Plotting the mean number of pored lateral-line scales alongside of the physical-chemical and biological indices of productivity (Table 29) shows them to be correlated. White and Waccamaw appear to be reversed, but the difference between these two (as well as between Jones and Salters) is not of great significance because differences of this magnitude or greater occur between most isolated populations. What is the significance of this correlation? Is this correlation caused by some effect of the environment upon these fishes?

To answer these questions the development of the pored lateral-line scales was studied (see development of *E. f. fusiforme*). The development of pored lateral-line scales in the Long Island population (Fig. 11) and in White Lake (Fig. 12) is similar except that in White Lake there are a few adults 23 and 24 mm long that have retained the juvenile condition of a reduced number of pored scales.

When the data for Jones Lake are ex-

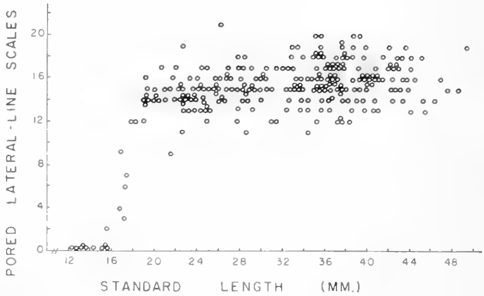

Figure 11. Change in the number of pored lateral-line scales with size in *Etheostoma fusiforme fusiforme* from two ponds on Long Island, New York.

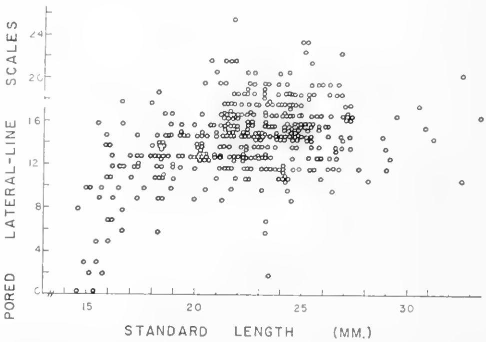

Figure 12. Change in the number of pored lateral-line scales with size in *Etheostoma fusiforme fusiforme* from White Lake, North Carolina.

amined (Fig. 13) a different picture is revealed. The no-pored condition is present until about 16 mm as in the two preceding cases, but here the transition period is never completed. Some of the largest specimens examined lacked pored lateral-line scales. It is apparent that here too the number of pored scales does not change after maturity; the whole range of variation has merely been shifted to lower values. Since this population retains into maturity the juvenile, no-pored condition, or at least a reduced number of pored scales, it can be considered a case of neoteny. In other words, there is a relative retardation in the rate of development of the body as compared with the reproductive organs, so that the body does not go through as many steps in development in the ontogeny of the descendants as it did in that of the ancestor (de Beer, 1951).

What has caused neoteny in the dark Bay Lakes populations of *Etheostoma f. fusi-*

forme? Hubbs (1926) discussed the results of changes in developmental rate and noted that accelerated development might lead to the retention of juvenile characters. In the dark Bay Lakes, under conditions of reduced productivity, selection may have acted to favor populations capable of spawning at a younger age or smaller size because of the relative scarcity of food. If populations could reproduce at smaller sizes they would be favored because of the food economy effected. Thus, selection could gradually reduce the size of the *E. fusiforme* in the dark lakes and result in a reduced number of pored lateral-line scales. Hubbs (1926) noted that degeneration resulting from a change in developmental rate does not primarily or necessarily involve any genetic loss, but involves physiological adaptations which preclude the completion of certain ontogenetic processes. Evidence is not yet available to determine whether or not the reduced number of pored scales in the dark Bay Lakes is genetically controlled or is a direct result of the environment. However, there is no significant difference between the number of pored lateral-line scales between the 1947, 1958, and 1959 year classes (see section IV) indicating that direct environmental control is unlikely. Linder (1958: 205-206) noted that *E. spectabile* and *E. spectabile* x *radiosum* hybrids, raised from eggs laid in the laboratory failed to develop any pored lateral-line scales. It would be interesting to raise *E. fusiforme* from the light and dark Bay Lakes for several generations to discover if there is genetic control for this neotenic character.

There is still more evidence for the neoteny theory. Examination of the variation in the number of pored lateral-line scales in *E. fusiforme barratti* (Table 19) shows that a few populations of this subspecies also have a reduced number of pored lateral-line scales. The over-all mean for *f. barratti* pored lateral-line scales is 20.65, while the mean of a population of *f. barratti* from Crystal Lake, Ga. is only 6.06. This lake is surrounded by the Suwannee River drainage although it lacks both inlet and outlet. The mean number of pored lateral-line scales in the Suwannee population is 22.41. Thus, in the Suwannee drainage, there is an even greater difference than between the dark and light Bay Lakes. Crystal Lake, Ga. is *not* a dark stained lake as are the unproductive Bay Lakes. The only apparent similarity between these lakes is their poor productivity. Donald C. Scott (personal communication) described Crystal Lake as "one of a number of sink hole lakes in Georgia which is filled with beautiful white sand and crystal clear water; the latter would double well for the distilled product. Crystal Lake has no inlet or outlet, its water obviously is rainwater that has percolated through nothing more than clean sand. The water of the lake has no contact with the underlying limestone responsible for the basin. The carbonate content is only about 15 p.p.m., vegetation is sparse, plankton likewise." Two collections (UG 205, 205a) were made on May 5, 1951, and April 26, 1952, and only 13 species of fishes were taken. Interestingly (Table 30) the first six species listed are part of the core of 11 species present in the Bay Lakes. The next three were found in at least one dark and one light lake. *Notemigonus* was taken only in Lake Waccamaw. Only the last three species were not taken in the Bay Lakes. If Crystal Lake is placed in the ranked Bay Lakes series it ranks at about the same level as Salters Lake. (This results from ranking the alkalinity as 1, the aquatic vegetation as 3, the light penetration as 6, and the number of species as 2, for a total of 12 while Salters equals 11.5.) Because Crystal Lake is clear, water color is eliminated as a sole cause of the difference in number of pored lateral-line scales between the dark and light Bay Lakes. However, color is important because of its great effect in reducing productivity by limiting photosynthesis. This is supported by the fact that the *E. f. fusiforme* from Ellis Lake, North Carolina, have a normally high number of pored lateral-line scales ($\bar{x}$:13.31 vs. an over-all mean for *E. f. fusiforme* of 13.96). This, as Bailey and Frey (1951:202) noted, is a dark, shallow lake with a low pH and low concentration of chemically active substances. They also pointed out (p. 192) that "Ellis Lake has large fish populations, and might be even more productive per unit area (or volume) than Waccamaw." Once again it is productivity that is correlated with the number of pored lateral-line scales.

Several other populations of *E. f. barratti* had unusually low numbers of pored lateral-line scales (Table 19). One of these is from a canal between Alligator and Lizzie lakes near St. Cloud, Osceola Co., Florida (UMMZ 158641). These two lakes are connected, by canal only, with the St. Johns River system. The mean of a sample from the St. Cloud population is 13.42, while that of the St. Johns population is 22.68. Collections are available from a number of small isolated lakes in and around Orlando, Florida. These also have a low mean number of pored lateral-line scales ($\bar{x}$: 16.76). However, in this case some lakes seem to have normal populations, others intermediate forms. There are collections from the Lake Okeechobee drainage which also have a reduced number of pored lateral-line scales ($\bar{x}$:17.33). Here the range is 5 to 30 in adult specimens. There is a temptation to cite these cases as additional corroboration of the neoteny theory, but unfortunately no information was available on the productivity of these lakes.

If the low number of pored scales in the dark Bay Lakes has arisen independently through neoteny in each of these lakes, then the populations in the Cape Fear River, which is presumably more productive, should have a higher count similar to the specimens from productive White Lake. I tried to collect specimens in Turnbull Creek, which receives drainage from both Jones and White lakes. The localities seined were moderately fast streams for the Coastal Plain and no *E. f. fusiforme* were collected. However, specimens were available from various localities in the Cape Fear River. The majority of these are paratypes of Hubbs and Cannon's "*thermophilum*" taken from the region around Wilmington, N.C. These specimens plus several small Cornell collections (Table 19) show a count ($\bar{x}$: 14.07) which is closer to that of the White Lake population than that of the dark Bay Lakes populations. Probably the river was originally populated by a form with a normally high number of pored scales. Some individuals were able to make their way into each of the Bay Lakes (except Black Lake?) where populations built up quite rapidly. Then, in each of the dark lakes, the scarcity of food caused selection to favor the development of neotenic populations.

Dorsal Spines (Table 20): The range is eight to thirteen, with the mode usually ten. Six *E. f. fusiforme* populations have a mode of nine and one (Nantucket) has a mode of eight spines. Eight dorsal spines was the primary character of which Hubbs and Cannon (1935:83) based their *f. insulae.* The Nantucket population is quite different from the Cape Cod and other Massachusetts populations in this regard. However, the Weweantic River, which is just west of Cape Cod, has a population with a mode of nine, bridging the gap between nominal *metaegadi* and *insulae*. The other five populations of *E. f. fusiforme* with a modal number of nine are: Raritan, N.J.; Nansemond, Va.; and the three dark N.C. Bay Lakes (Singletary, Salters, Jones). This seems to be a separate system of variation, not connected with neoteny, because both the neotenic and normal populations of *E. f. barratti* have modes of ten dorsal spines (except for the Red River population, which has a mode of eleven).

Dorsal Rays (Table 21): There is a range of eight to thirteen and the mode is either ten or eleven. The variation is slightly different from that in other characters. Populations of *E. f. fusiforme* seem to alternate geographically between modes of ten and eleven. All *E. f. barratti* populations from the Savannah southward have a mode of eleven. The Pee Dee, Edisto, and Combahee-Broad populations have modes of ten like adjacent *E. f. fusiforme*, indicating that the break between the Waccamaw and Pee Dee rivers is not as complete as in other characters.

Scale rows above the lateral line (Table 22): The range is two to four, with one specimen from coastal Maryland having

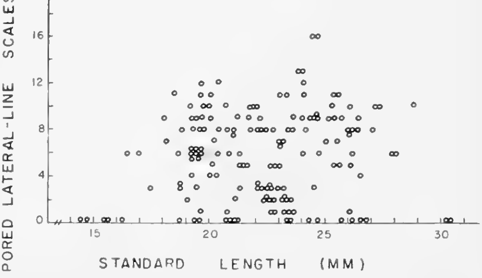

Figure 13. Change in the number of pored lateral-line scales with size in *Etheostoma fusiforme fusiforme* from Jones Lake, North Carolina.

five scales. The mode of most populations of both subspecies is three. The only populations of *E. f. fusiforme* with a mode of two are lakes Ellis, Salters, Jones, White, and Waccamaw. This was one of the characters used by Hubbs and Cannon (1935) in distinguishing *thermophilum.* However, the other North Carolina Bay Lake (Singletary) has a population with the normal mode of three scales. The reason for this is as yet unknown; the more productive Bay Lakes (White, Ellis, and Waccamaw) all have a reduced number.

Several populations of *E. f. barratti* also have a mode of two: St. Cloud, Fla.; Orlando, Fla.; and Crystal Lake, Ga. This is of interest because these populations are neotenic with regard to pored lateral-line scales. The reduction in number of pored lateral-line scales is correlated with the reduction in the number of scales below the lateral line. Perhaps the low productivity in these lakes has led to a reduction in several different characters.

Scale rows below the lateral line (Table 22): The range in *E. fusiforme* is six to twelve scales. The mode in the majority of populations is either eight or nine scales. There are three populations of *E. f. fusiforme* and two of *E. f. barratti* that have a mode of only seven: Ellis, Salters, other Cape Fear, Crystal Lake, Ga., and Orlando, Fla. The other four North Carolina Bay Lakes populations (Singletary, Jones, White, and Waccamaw) all have a more typical mode of eight. St. Cloud, Fla., Lake Okeechobee, Fla., and the Santee River, S.C., are the only populations of *f. barratti* with modes of eight; the first two are neotenic with regard to pored lateral-line scales. This character shows the same trend as the scales above the lateral line. If these two numbers are added together (Table 22) most populations have a total greater than 10.5 in *E. f. fusiforme* and greater than 11.2 in *E. f. barratti.* The populations with the lowest total number are neotenic and partially neotenic ones: Ellis Lake, N.C. (9.23); Salters Lake (9.65); other Cape Fear (9.65); Waccamaw (9.85); and in *E. f. barratti,* St. Cloud (10.28); Orlando (9.48); Lake Okeechobee (10.55); and Crystal Lake (9.36).

Anal Spines (Table 42): There is no significant variation in anal spines; almost all *E. fusiforme* have two. Seventeen specimens of *E. f. fusiforme* and eight of *E. f. barratti* had only one spine while two specimens of *E. f. barratti* had three spines.

Anal rays (Table 23): The range in this character is five to ten with the mode at either seven or eight, except for the Newnan Lake, Fla. population which has a mode of nine. Bailey (1950) gave a modal number of eight anal rays for his *Hololepis barratti appalachia* versus a modal value of seven for other *barratti* populations. However, as Table 23 shows this is hardly the basis for describing a new subspecies.

Pectoral Rays (Table 23): The range is 12 to 15 with the majority of specimens of both subspecies having 13. The Crystal Lake, Ga. population stands out with a range of 14 to 15 and a mode of 15. Perhaps this difference is negatively correlated with the reduced number of pored lateral-line scales present in this population; however, the other neotenic populations typically have the usual mode (13).

Branchiostegal Rays (Table 44): The range of this character was from five to seven with the majority of specimens having six rays. The few Cape Cod specimens examined showed a slight tendency to have more specimens with five rays. There was not sufficient variation in this character to necessitate presenting the frequency distributions by river systems, so summaries of both subspecies are presented in comparison with the other forms studied.

Interorbital Pores (Table 45): All the *E. f. fusiforme* examined lacked interorbital pores, but a few specimens of *E. f. barratti* had one or two pores present.

Infraorbital pores (Table 24): There were 11 different combinations of the pores in this

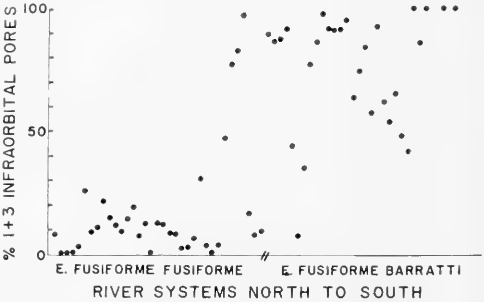

Figure 14. Percent of individuals with 1 + 3 infraorbital pores by river systems from north to south in *Etheostoma fusiforme.*

canal. They have been arranged across the table in the order of increasing numbers of pores in both segments of the canal. Since there were only two major categories (1 + 3 and 2 + 3), the infrequent counts were added to the more similar of the two frequent counts and the percentage of 1 + 3 individuals in each population was computed.

The number of infraorbital pores was used by Hubbs and Cannon (1935:30) to differentiate *fusiforme* and *thermophilum* (2+3) from *barratti* (1 + 3). The present study confirms this with 80% of *E. fusiforme fusiforme* having 2 + 3 pores and 70% of *E. fusiforme barratti* having 1 + 3 pores (Table 24).

Bailey and Frey (1951) used the number of infraorbital pores to distinguish their *thermophilum oligoporum* (1 + 3) in the dark North Carolina Bay Lakes from *thermophilum thermophilum* (2 + 3) in the lighter Bay Lakes. The present study confirms these differences: the dark Bay Lakes have a high percent of individuals with 1 + 3 pores (Singletary-77%, Salters-83%, Jones-97%); the light Bay Lakes a low percentage (White-17%, Waccamaw-9%). If these percentages are plotted against the indices of productivity (Table 29), it can be seen that the two numbers are even more closely correlated than in the case of the pored lateral-line scales. The population of *E. f. fusiforme* in the Cape Fear River proper has a percent (7%) much closer to the White Lake population than to the populations in the dark Bay Lakes. Therefore, it appears that under similarly unproductive conditions in each of the dark Bay Lakes, selection (or the environment?) has acted to produce a form with a reduced number of infraorbital pores as well as a reduced number of pored lateral-line scales. Ellis Lake has 47% of its individuals with 1 + 3 pores and so falls in between the dark and light Bay Lakes in this character. The populations of *E. f. barratti* with reduced numbers of pored lateral-line scales are of less help in this situation because the normal number for this subspecies is 1 + 3. All the populations with reduced numbers of pored lateral-line scales have a higher percent of 1 + 3 pores than do the populations from which they are probably derived: Crystal Lake, Ga., population (92%) compared with the surrounding Suwannee population (57%), St. Cloud, Fla. (97%) and the surrounding St. Johns population (86%), and Orlando, Fla. (91%) and the St. Johns population (86%).

One peculiar population of *E. f. barratti* (Ogeechee, Ga.) has an abnormally low percent (7%) of individuals with 1 + 3 pores. Some of the western populations of *E. f. barratti* (Table 24) have 100% 1 + 3 pores (Pearl-Pontchartrain, La. and Red River) as does also the population from the French Broad (*"barratti appalachia"*).

Condition of Preopercle (Table 24): Hubbs and Cannon (1935:29-30) char-

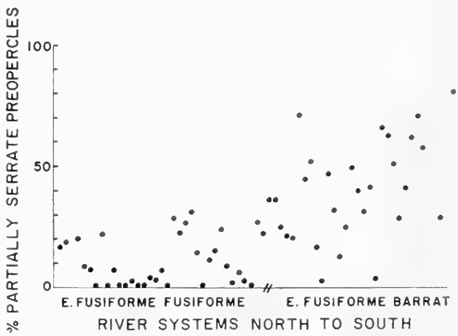

Figure 15. Percent of individuals with partially serrate preopercles by river systems from north to south in *Etheostoma fusiforme*.

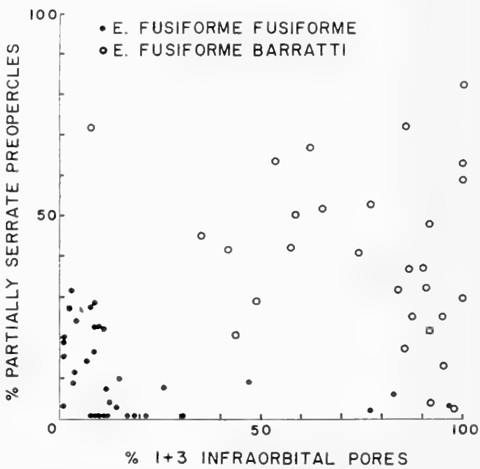

Figure 16. Correlation between percent of individuals with 1 + 3 infraorbital pores and percent of individuals with partially serrate preopercles by river systems in *Etheostoma fusiforme*.

acterized all the species of the subgenus *Hololepsis,* except *serriferum,* as having the "preopercle strictly entire." Bailey (1950: 315) has shown that *E. fusiforme barratti* has some serrae on the preopercle. This was one of the main characters that he used to distinguish his *Hololepis barratti appalachia.* There is a tendency toward a partially serrate preopercle in most populations (Table 24). This character can be used to divide *E. fusiforme* into two subspecies. Most populations of *E. f. fusiforme* have less than 25% of the specimens with serrae present while most populations of *E. f. barratti* have serrae in more than 25%. There is a tendency for the percentage to increase southward, with a break between the Pee Dee and Waccamaw rivers (Fig. 16). There are a number of exceptions that must be discussed.

In all of the North Carolina Bay Lakes except the Waccamaw population (23%) there is a much lower percent than would be expected (0% in White to 9% in Ellis Lake). Several *E. f. barratti* populations also have low percentages. Three of these are at least partially neotenic with regard to the number of pored lateral-line scales: Crystal Lake, Ga. (4%), St. Cloud, Fla. (3%), and Okeechobee, Fla. (13%). The Orlando populations do not show this tendency as they did in the number of pored lateral-line scales. A few typical *E. f. barratti* populations also have a low percentage of individuals with partially serrate preopercles: St. Johns, Fla. (17%), Savannah (20%), Red (17%), and Combahee-Broad (21%). Here is one more case where the North Carolina Bay Lakes are similar to some of the Florida and Georgia populations. It seems unlikely that these similarities are merely coincidental. Somehow the reduced productivity in all these lakes has acted, or is acting to influence these characters.

There is an interesting relationship between the percentage of individuals with partially serrate preopercles and the percent of individuals with 1 + 3 infraorbital pores: both percentages tend to increase to the south (Figs. 14 and 15). Most *E. f. barratti* populations have high percentages in both characters. The populations which have a low percent of partially serrate preopercles have a high percent of 1 + 3 individuals. If one percentage is higher than usual in a population of *E. f. fusiforme* the other is then lower than usual. For example, the dark Bay Lakes have a high percent with 1 + 3 pores (77%, 83%, and 97%) but the partially serrate percent is very low (2%, 6%, and 3% respectively). Some populations have the partially serrate percent relatively high, for example Potomac (31%), Delaware River (28%), other Cape Fear (28%), and Chesapeake Bay (27%) but the values of their 1 + 3 percentages are low: 3%, 9%, 7%, and 2% respectively. The percent of individuals having 1 + 3 infraorbital pores has been plotted by populations against the percent of individuals having partially serrate preopercles in the same drainages. Most populations of *E. f. fusiforme* are found along the edge of Fig. 16, below 25% partially serrate preopercles and extending up to nearly 100% 1 + 3 infraorbital pores while the populations of *E. f. barratti* are limited to the central portion of the figure.

Preoperculomandibular Pores (Table 45): The range in *E. f. fusiforme* is six to eleven; eight to ten in *E. f. barratti,* with the mode always nine. Populations from both Raritan Bay, N. J. and White Lake, N.C. have means (8.30 and 8.34) considerably below the over-all mean (8.9).

Coronal Pore (Table 47): As Bailey and Frey (1951:200) pointed out, this character is difficult to use. They reported that the pore was frequently absent in populations in White and Ellis lakes and present in the other Bay Lakes populations. This appears to be true although in the case of White Lake there were only a few specimens in which the condition could be satisfactorily determined. In most other populations the pore was usually present, although its development varied, sometimes being a rather long posterior-extending tube with an external opening, and other times being just an opening at the junction of the two medial sidebranches of the supraorbital canal. Perhaps further study of this pore would be of value.

Supratemporal Canal (Table 47): This canal is typically complete in adult *E. fusiforme* and incomplete in young and juveniles (see development in *E. f. fusiforme* and *E. f. barratti*). Table 31 shows the normal development in the Long Island population. There are differences between populations. For example, Bailey and Frey (1951:200) cited the incomplete nature of the supratemporal canal in the Singletary and Salters lakes populations as an example of local variation in a character. Development in Jones Lake (Table 31) is like that in the Long Island population except that it is completed at a smaller size. The transition period is longer (ten mm) in both White and Singletary lakes (Table 31); than in the Long Island and Jones Lake populations (six mm). Since there are so few large specimens it is doubtful if the transition is ever completed. The transition period in the Waccamaw population is lengthened to 14 mm. The most extreme condition is present in Salters Lake, where the transition period is entirely enclosed by the juvenile period, the largest specimens having incomplete supratemporal canals.

Since the development of the supratemporal canal is retarded relative to the growth of the gonads in the Salters, Waccamaw, Singletary, and White populations, these populations may be considered neotenic in this character. The Crystal Lake, Ga. population that was neotenic in the number of pored lateral-line scales shows the usual development of the supratemporal canal (Table 31 and development in *E. fusiforme barratti*).

Squamation: The value of squamation as a taxonomic character was indicated by Hubbs and Cannon (1935) in their analysis of the species of *Hololepis.* They gave only general descriptions of squamation characterizing *E. fusiforme* as "interorbital scaleless, or with one or two more or less imbedded scales," *thermophilum* as "interorbital with several ctenoid scales," and *barratti* as "interorbital well covered with ctenoid scales." They further differentiated *barratti* from *fusiforme* and *thermophilum* with the former having "parietals covered well toward or across median line with ctenoid scales" and the other two forms as having "parietals scaleless." Hubbs and Cannon described only the general trends. More quantitative methods were devised, as discused in section III. The squamation of the preopercle, opercle and nape is usually 100-X-T, so frequency distributions for the subspecies are summarized in Table 48. However, there are significant differences in the squamation of the breast, parietal, and interorbital.

Breast Squamation (Table 25): In the northern part of the range of *E. fusiforme* the breast squamation is usually 100-I-C, with the amount of exposure and the tendency to become ctenoid increasing to the south. In the North Carolina Bay Lake populations, specimens were found to have all the intermediate conditions (I/PX-C/T, PX-T, and X/PX-T) between imbedded cycloid scales (I-C) and exposed ctenoid scales (X-T). Most specimens in populations south of the Waccamaw River have the squamation at least I/PX-C/T. West of the Apalachicola River, Fla. the breast is usually PX-T or even X-T in the case of the Pearl-Pontchartrain, La. and Red River populations.

Parietal Squamation (Table 26): This character shows the differentiation between the two subspecies more clearly than does the breast squamation. In the northern part of the range of *E. f. fusiforme,* most specimens have naked parietals. The amount of squamation gradually increases toward the south. Of the North Carolina Bay Lakes, the Singletary Lake population has the parietal squamation the least well developed (mostly 5-10%) and the White Lake population has the squamation the best developed (mostly 25-30%). There is a break between the Waccamaw (15-20%) and Pee Dee (35-40%). The variation in this character is greater in *E. f. barratti* (5-100%) than in *E. f. fusiforme* (0-50%). The range within populations is also considerably greater in the southern subspecies (5-95% in the St. Mary's, based on only 12 specimens) than in the northern subspecies (15-60% in White Lake). This tendency has been noted for a number of other characters, in particular the interorbital squamation *(q.v.).*

Interorbital Squamation (Table 27): The range in *E. f. fusiforme* is 0-12 (mode 0, $\bar{x}$: 1.97), while that of *E. f. barratti* is 1-37 scales (mode 10, $\bar{x}$: 13.15) (Table 46). This difference seems to be sufficient to divide the species into two subspecies but does not seem great enough, because of the wide overlap, to merit specific recognition. The north-south clinal nature of the variation in *E. f. fusiforme* is clearly demonstrated in the table. There is a gap between Waccamaw on the north and the Pee Dee River on the south. There seems to be more intrapopulation and relatively less interpopulation variation in *E. f. barratti.*

2. Taxonomic Conclusions

Etheostoma fusiforme is the most variable species of the subgenus *Hololepis.* There are two ways to treat this variation: to name all distinguishable populations; or to describe the variations and try to understand them without the use of names. Minor differences beween populations should not be formally recognized because of the great plasticity of some characters in fishes. A number of environmental factors effect some meristic characters in some fishes. Perhaps the most important of these is the effect of water temperature on such characters as the number of vertebrae and fin rays (Tåning, 1952; Blaxter, 1956; and others).

There are four patterns of variation in the characters studied in *Etheostoma fusiforme.* First, there are the characters that showed little or no variation; number of anal spines, anal rays, preoperculomandibular pores, interorbital pores, pectoral rays, pelvic rays, caudal rays, branchiostegals, and the squamation of the preopercle, opercle, and nape. In the second type, characters vary from population to population in an apparently random fashion (total lateral-line scales, dorsal spines, and dorsal rays). The third type is clinal; the breast, parietal, and interorbital show increasing development of squamation from north to south. The percent of individuals with 1 + 3 infraorbital pores and with partially serrate preopercles also increases from north to south. The fourth type is the most interesting: the incomplete development of some characters (neoteny) in populations in the unproductive North Carolina Bay Lakes and in a few Florida and Georgia lakes. This has been noted in the greatly reduced number of pored lateral-line scales, the failure of the supratemporal canal to become closed, the reduced number of scales above and below the lateral line, and the percentage of individuals with 1 + 3 infraorbital pores.

The major taxonomic problem was to decide which populations merit nomenclatorial recognition. I believe the differences between Hubbs and Cannon's three species, *fusiforme, thermophilum,* and *barratti,* are due to clinal variations (squamation, infraorbital pores, development of the pored lateral line) and to developmental variations (infraorbital pores and pored scales in *thermophilum*). The subspecies of *fusiforme* recognized by Hubbs and Cannon (1935) were based on a combination of: random variations (total lateral-line scales in *fusiforme insulae* and *f. metaegadi* and dorsal spines in *fusiforme insulae*) and clinal variations (interorbital squamation in three groups: *f. atraquae* and *f. erochroum; f. fusiforme* and *f. metaegadi; f. insulae*). This was coupled with the improper presentation of counts from both sides of individuals (see section IV) and inadequate sampling between the ranges of the forms they recognized. J. R. Bailey's *barratti appalachia* is almost certainly based upon an introduced population (Bailey, Winn, and Smith, 1954). It is slightly different in having a higher percentage of specimens with partially serrate preopercles. The most interesting case is surely *thermophilum oligoporum.* It seems clear that the form in the dark North Carolina Bay Lakes has differentiated independently in each lake, probably as a result of the unproductive conditions in these lakes. Thus all the subspecies of *E. fusiforme* and of *E. thermophilum* are reduced to synonymy under *E. fusiforme fusiforme* while *E. barratti* and *E. barratti appalachia* become *E. fusiforme barratti.*

Etheostoma saludae (Hubbs and Cannon)

Hololepis saludae—Hubbs and Cannon, 1935:50-52, pl. I-III (original description); Fowler, 1945:40, 196 (Saluda Co., S. C.); Freeman, 1952a:37 (Broad R., Richland Co., S. C.).

Etheostoma saludae—Bailey and Gosline, 1955:20, 44 (number of vertebrae); Eddy, 1957:220; Moore, 1957:198; Collette, 1961: 2051.

Types—Holotype, UMMZ 107079; 21 mm juvenile; S. C., Saluda Co., Richland Cr., trib. to Lake Murray, 10 mi. SE of Saluda; June 21, 1933; E. M. Burton. Paratypes, the other 16 specimens examined by Hubbs and Cannon (1935:50).

Diagnosis—One or two anal spines; both interorbital pores usually present; infraorbital pores either 1 + 4 or 1 + 3; nape squamation usually less than 60% ($\bar{x}$: 15%);

TABLE 33.
Number of total lateral-line scales in Etheostoma collis and E. saludae

Form and drainage	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	x̄
collis lepidinion																	
Roanoke					3	1	7	5	2	5	2*	3	4				43.00
Neuse	1	2	1	–	2	–	1										37.57
Cape Fear												1**					–
collis collis																	
Yadkin-Pee Dee						1	1	1	6	8	3	5	4	–	1		44.50
Rocky-Pee Dee						1	–	2	3	4	4	1	2	3	1		44.86
Catawba			1	–	1	1	1	1	1	–	2	1					42.00
"Santee"								1	1								42.50
saludae		1	2	8	8	11	12	10	17	9	7	1	1	1	1	1	41.78

* Count of holotype of *E. c. lepidinion.*
** This specimen counted on right side.

breast naked. Maximum size of males 42.5 mm SL. (CU 35019) and females 43.5 mm (CU 35029).

Coloration—Hubbs and Cannon's (1935: 51-52) description was based entirely upon immature specimens (17-22 mm). No adult non-breeding males were available to me, but they probably are similar to the females. The pigmentation of *E. saludae* is similar to that of *E. collis.*

The spinous dorsal fin of the non-breeding female has few to a moderate number of small to medium sized melanophores scattered on the membrane. The soft dorsal fin is barred on the rays and rectangular blotches composed of 10-15 melanophores are present on the membranes. The anal fin is clear or has a few small melanophores on the proximal portion of the membranes. The pectoral fin membranes are clear, but melanophores outline the rays. The pelvic fin, belly, and breast lack pigment. The caudal is barred. There are large and small melanophores scattered on the cheek. The suborbital, preorbital, and postorbital bars are all prominent. The pored portion of the lateral line is light. The median basi-caudal spot is prominent; dorsal and ventral spots are sometimes present. The sides are irregularly mottled with brown; up to eight lateral blotches may be present. The genital papilla is unpigmented. Most specimens have about seven dorsal saddles, two before the first dorsal fin, two under each dorsal fin and one posterior to the second dorsal fin.

Some breeding females have more melanophores on the second dorsal fin membranes than do non-breeding females. The anal fin pigmentation varies, even within a single collection, from immaculate to a moderate number of melanophores scattered over the membrane. Figure 17 shows the pattern of a breeding female *E. saludae* compared with *E. collis.*

Most parts of the body and fins of the breeding males are colored like the females; other areas are darker. The spinous dorsal has more melanophores; they are concentrated on the first two or three membranes, and there is a tendency toward a median band. The second dorsal fin has about 30-40 melanophores in each rectangular blotch. The anal and pelvic fins and the belly and breast are uniformly covered with small to medium melanophores. The cheek is darker in the male than in the female. The suborbital bar is more prominent in some breeding males. There is more pigment on the distal edges of the pored lateral-line scales. Dorsal saddles and blotches are usually absent. Figure 18 compares the patterns of breeding males of *E. collis* and *E. saludae.*

Genital Papilla—A moderately elongate blunt tube in breeding females. A specimen taken on April 1 (CU 25982) has a genital papilla 1.5 mm long and 0.9 mm thick at the base. The genital papilla is like that of *E. f. fusiforme* (Fig. 1f).

Breeding Tubercles—Present on anal and pelvic fins. Males taken on April 16 (CU 35019) have tubercles on most of the ventral surface of pelvic rays one to four and along the distal seven-eighths to three-quarters of the anal rays. The tubercles on the anal rays are somewhat larger than those on the pelvic rays. Another collection taken on March 14 (CU 35036) contains a male with large tubercles on the distal three-quarters of anal rays one and two

TABLE 34.

Condition of supratemporal canal and the number of pores in the infraorbital, interorbital, and preoperculomandibular canals in Etheostoma collis and E. saludae

Form and drainage	Infraorbital				Interorbital			Preoperculomandibular						Supratemporal	
	2+4	1+4	1+3	2+3	0	1	2	6	7	8	9	10	11	Incomplete	Complete
c. lepidinion															
Roanoke		29*	3		31*	1				2	27*	1	1	23*	8
Neuse		5	2		6	1				1	6				7
Cape Fear		1			1						—			1	
c. collis															
Yadkin-Pee Dee		2	28	1	23	1	2	1	—	3	19	3		20	11
Rocky-Pee Dee		1	28		24					1	22			5	19
Catawba			11		11						10	1		9	2
"Santee"		1	1		2						2			1	1
saludae	1	59	34			3	90			3	85	2		53	41

* Count of holotype of *E. c. lepidinion.*

TABLE 35.

Number of anal rays and of scale rows above and below the lateral line in Etheostoma collis and E. saludae

Form and drainage	Anal Rays					Above			Below lateral line						
	6	7	8	9	x̄	2	3	4	6	7	8	9	10	11	x̄
c. lepidinion															
Roanoke	1	7	20*	4	7.84	8	23*	1		1	11*	11	7	2	8.94
Neuse	1	3	3		7.29		7			1	3	3			8.29
Cape Fear		1			—			1			1				—
c. collis															
Yadkin-Pee Dee		2	20	9	8.23	6	24	1		7	12	12			8.16
Rocky-Pee Dee		13	10	1	7.50	3	13	2			12	7	3		8.59
Catawba		3	7	1	7.82	2	5	1			5	4	—	1	8.70
"Santee"			2		8.00		2						2		10.00
saludae	1	18	64	10	7.89	25	67		1	19	37	29	6		8.22

* Count of holotype of *E. c. lepidinion.*

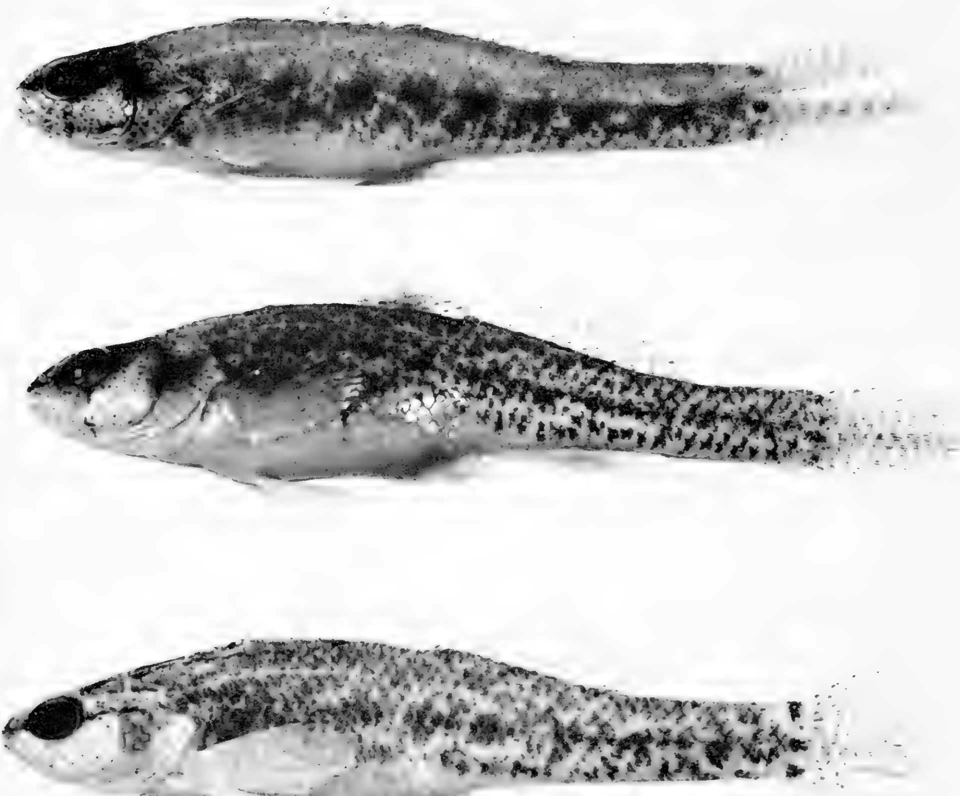

Figure 17. Breeding patterns of female *Etheostoma collis* and *E. saludae.* (upper) *E. collis* LEPIDINION, paratype; CU 29992; 38.6 mm; Va., Charlotte Co., Roanoke dr.; Mar. 31, 1956. (middle) *E. collis collis;* CU 11988; 41.3 mm; N.C., Davidson Co., Yadkin-Pee Dee dr.; Mar. 22, 1958. (lower) *E. saludae;* CU 35030; 40.7 mm; S.C., Saluda Co., Saluda dr.; Apr. 16, 1954. (Photograph by Douglass M. Payne)

and on the distal three-quarters of all the pelvic rays where the tubercles are scattered and smaller. This is essentially the same distribution as found in *E. collis collis* (Fig. 1g).

Habitat—Field notes of E. C. Raney for four spring collections (CU 17542, 25966, 25982, 26061) indicate the habitat to be small woodland streams, 5-15 feet wide, 2-4 feet deep, with a flow of 5-10 cubic feet per second, current slow to moderate, and the bottom consisting of sand, gravel, and bedrock.

Distribution — Limited to Piedmont streams of the Saluda and Broad Rivers, which are tributaries of the Congaree, the southern branch of the Santee River in South Carolina. Figure 3 shows the distribution of the collections examined.

Specimens Examined—Saluda-Broad Dr., S.C.—Laurens Co.: CU 19745 (1, 39): Bush Cr. 1.5 mi. SW of Kinards on SC 560; March 28, 1951. Lexington Co.: CU 35035 (3, 30-41); Kinley Cr. 2 mi. S of Irmo, ½ mi. W SC 36; March 18, 1954. CU 35024 (6, 25-38); CU 35026 (6, 25-37); SC 36 1 mi. W of US 76; March 27, 1954. CU 35027 (1, 37); SC 20, 1 mi. S of Little Mt.; March 27, 1954. CU 25966 (1, 32); Rawl Cr., 2 mi. S of Kino on SC 107, trib. ½ mi. from Saluda R.; April 1, 1954. CU 25982 (12, 25-39); trib. of Saluda R. about 1 mi. from Saluda R., 2 mi. S of Irmo on SC sec. 36; April 1, 1954. Newberry Co.: CU 35029 (1, 44); Timothy Cr. SC 42, 2 mi. W of Prosperity; Feb. 20, 1954. CU 35037 (1, 42); Garrison Cr. SC 58, 6 mi. SW Kinards; Aug. 5, 1954. Richland Co.: CU 26061 (14, 28-42); Nicholas Cr. trib. of Broad R. 4.5 mi. S of Broad R., 6 mi. SE Ballentine on SC sec. 129; April 1, 1953.

Figure 18. Breeding patterns of male *Etheostoma collis* and *E. saludae.* (upper) *E. collis* LEPIDINION, holotype; USNM 179847; 37.6 mm; Va., Charlotte Co., Roanoke dr.; Mar. 31, 1956. (middle) *E. collis collis;* CU 31663; 39.5 mm; N.C., Stanly Co., Rocky-Pee Dee dr.; Mar. 31, 1958. (lower) *E. saludae;* CU 35030; 34.9 mm; S.C., Saluda Co., Saluda dr.; Apr. 16, 1954. (Photograph by Douglass M. Payne)

Saluda Co.: UMMZ 107077 (4, 17-21); Moore's Cr., trib to Lake Murray, 6 mi. SE of Saluda; June 21, 1933; paratypes. UMMZ 107078 (2, 20-22), USNM 94685 (1, 22), Chicago Nat. Hist. Mus. 38331 (1, 17), out of Charleston Mus. 33.149.1, paratypes and UMMZ 107079 (1, 21) holotype of *Hololepis saludae;* Richland Cr., trib. to Lake Murray, 10 mi. SE of Saluda; June 21, 1933. CU 17542 (15, 28-40); trib. of Little Saluda R., 2.1 mi. N of Saluda on rt. 19; March 23, 1950. CU 35023 (1, 32); 1 mi. NE Cherry Hill School, 7 mi. E of Saluda on SC 192; Oct. 16, 1953. CU 35033 (2, 29-31); Richland Cr., 4 mi. E of Saluda on SC 43; Oct. 16, 1953. CU 35032 (2, 37-38); Moore's Cr., 3 mi. W of Batesburg on SC 57; Mar. 14, 1954. CU 35031 (1, 40); Clouds Cr., 3 mi. N of Ridge Spring on SC 57; Mar. 14, 1954. CU 35036 (3, 32-40); Mine Cr., 6 mi. S of Saluda on SC 193; March 14, 1954. CU 35022 (3, 31-36); S branch of Red Bank Cr., 5 mi. SW of Saluda on SC 84; April 6, 1954. CU 35034 (1, 36); S branch of Big Cr. on SC 83 at Trinity Church, 5 mi. NW of Saluda; April 6, 1954. CU 35021 (1, 37); Ready Cr., ½ mi. E of Ready Cr. School, 5 mi. N of Ward; April 16, 1954. CU 35019 (3, 33-43); N branch of Mine Cr., 3 mi. N of Ward on SC 193; April 16, 1954. CU 35030 (6, 33-43); S. branch of Red Bank Cr., on SC 186, 5 mi. SW of Saluda; April 16, 1954. CU 35020 (2, 25-28); a south branch of Red Bank Cr., SC 84 at Salem Church, 5 mi. W of Saluda; April 16, 1954. CU 35028 (1, 39); Big Cr., 5 mi. NW of Saluda Shiloh Church on SC 39; April 6, 1954. CU 35025 (2, 31-36); Little Saluda R., 5 mi. NE of Saluda on SC 39; Oct. 16, 1954.

Etheostoma collis ***lepidinion*** *subsp. nov.*

Etheostoma collis new subspecies—Collette, 1961:2051.

Types—Holotype, USNM 179847; 37.6 mm male; Va., Charlotte Co., trib. of Horsepen Cr., 2.4 mi. NW of Wylliesburg on Va. 607; March 31, 1956; Raney, Collette, New, Cole, Robins; ECR 2787 and BBC 160. One of a series of nine specimens (CU 29992). Paratypes are all the other specimens examined except for CU 25187 from the Cape Fear River.

TABLE 36.

Squamation of the nape, breast, preopercle, and opercle in Etheostoma collis and E. saludae

Form and drainage	Percent of Nape Scaled												Percent of Breast Scaled									
	0	10	20	30	40	50	60	70	80	90	100	x̄	0	10	20	30	40	50	60	70	80	x̄
c. lepidinion																						
Roanoke									2	4	26*	97.5		3	5	5	6*	6	3	3	1	40.3
Neuse								1	–	3	3	91.4		2	–	1	–	1	2		1	42.9
Cape Fear										–		–										–
c. collis																						
Yadkin-Pee Dee	26	1	1									1.1	28									0
Rocky-Pee Dee	18	5	–	1								3.3	24									0
Catawba	6	1	1	1								6.7	9	1								1.0
"Santee"	–											–	2									0
saludae	32	30	14	10	1	2	1	–	1	3		15.2	91	2								.2

Form and drainage	Percent of Preopercle Scaled									Percent of Opercle Scaled											
	30	40	50	60	70	80	90	100	x̄	0	10	20	30	40	50	60	70	80	90	100	x̄
c. lepidinion																					
Roanoke								32*	100.0											32*	100.0
Neuse								7	100.0											7	100.0
Cape Fear								1	–											1	–
c. collis																					
Yadkin-Pee Dee			1	1	–	1	2	19	94.6	2		–	1	–		–	1	2	1	20	87.0
Rocky-Pee Dee								24	100.0										2	16	98.9
Catawba								8	100.0				1	–	1	–	–	–	1	4	81.4
"Santee"									–												–
saludae	1	2	–	1	–	–	6	74	96.5				1	1	–	1	1	8	27	30	90.9

* Squamation of holotype of *E. c. lepidinion*.

Diagnosis—Similar to *E. collis collis* in having one anal spine and usually lacking both interorbital pores. Differs from *E. c. collis* and *E. saludae* in having the breast at least partially covered with scales ($\bar{x}$: 41%). Differs from *E. c. collis* by usually (88%) having 1 + 4 rather than 1 + 3 infraorbital pores. Differs from both *E. saludae* and *E. c. collis* in having the nape well scaled (80-100%, $\bar{x}$: 96%), while *E. c. collis* has less than 20% of the nape scaled and *E. saludae* usually has less than 60% scaled. Maximum size of males 37.7 mm, females 40.1 mm (both from CU 34544, Roanoke R.).

Counts of the holotype (with one asterisk) and paratypes are given in Tables 32-36 in comparison with *collis collis* and *saludae*. The three forms are compared in Table 37.

The relationships of this form with *E. collis collis* and *E. saludae* are discussed above in Section VI.

Etymology—The name *lepidinion* is derived from the Greek (*lepis*, scale) and (*inion*, nape) in allusion to the diagnostically scaly nape.

Coloration—The female has a few scattered melanophores on the first dorsal fin, mostly on the spines. The second dorsal fin has a few large melanphores on the membranes. The anal fin is clear in most specimens; sometimes with a few melanophores scattered on the rays. The pelvic fin is clear. The caudal fin membranes are clear; large brown or black chromatophores are present on the rays. The belly, breast and usually the lower sides are free of melanophores. The cheek has a few large scattered melanophores. The preorbital and postorbital bars are well developed; the suborbital is usually faint; the supraorbital is usually absent. The pored portion of the lateral line is clear. There is usually a median spot at the division of the upper and lower caudal rays, and faint spots at the base of the upper and lower portions of the caudal fin. About eight lateral blotches are present and are most distinct posteriorly. The genital papilla is immaculate. Figure 17 compares the pattern of a breeding female *E. collis lepidinion* with *E. collis collis* and *E. saludae*.

The anal, pectoral, pelvic and caudal fins, orbital bars, basi-caudal spots, and the pored portion of the lateral line in the non-breeding male are colored like the female; other areas are darker. Many small melanophores form a median band on the membrane of the first dorsal fin. The second dorsal fin differs from that of the female in having rectangular patches of small melanophores on the membranes. Both the belly and breast are covered with slight to moderate numbers of small melanophores. The cheek is darker. The lateral blotches are slightly more distinct in some males than in the females. There is a narrow band of small melanophores around the base of the genital papilla.

In the breeding male the pectoral and caudal fins, orbital bars, and genital papilla are colored like the non-breeding male; the other areas are darker. The entire spinous dorsal fin is covered with small melanophores. These are concentrated medially and form a band which is especially prominent on the first three membranes. The rectangular blotches in the soft dorsal fin are each composed of about 25 (15-50) melanophores, and these blotches tend to form bands across the fin. The anal and pelvic fins, belly, breast and cheeks are completely covered with small melanophores. The pored portion of the lateral line is prominent because of the dark sides; some pigment is present on the distal portions of the pored lateral-line scales, in-

TABLE 37.
Differential characters of the forms of Etheostoma collis and E. saludae

Form	*collis lepidinion*	*collis collis*	*saludae*
River system	Roanoke, Neuse	Pee Dee, Catawba	Saluda, Broad
Infraorbital pores	1+4 (90%)	1+3 (95%)	1+4 (65%) 1+3 (35%)
Interorbital pores	0 (95%)	0 (95%)	2 (95%)
Nape (% scaled)	80-100%	Less than 20%	Usually less than 60%
Breast (% scaled)	10-80%	naked	naked
Anal spines	always I	always I	II (70%) I (30%)

terrupting the narrow light line. The median basi-caudal spot is prominent; the dorsal and ventral ones diffuse. The sides usually show less distinction between the darker blotched portion below the lateral line and the lighter upper portion. Figure 18 is a comparison of the pattern of a breeding male with *E. collis collis* and *E. saludae.*

Genital Papilla—The genital papilla of the breeding female is a moderately elongate tube like that of *E. fusiforme* (Fig. 1f).

TABLE 38.
Number of total lateral-line scales in the species of the subgenera Hololepis and Villora

Species	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Hololepis																			
serriferum													1	—	—	3	8	11	27
gracile									3	12	21	27	34	79	91	123	130	89	70
zoniferum										2	1	—	—	2	1	6	7	5	1
f. barratti											2	8	16	28	39	72	121	132	165
f. fusiforme									1	5	12	20	46	64	118	152	226	220	229
saludae					1	2	8	8	11	12	10	17	9	7	1	1	1	1	1
c. lepidinion				1	2	1	—	5	1	8	5	2	5	2	4	4			
c. collis						1	—	1	3	2	5	11	12	9	7	6	3	2	
Villora																			
okaloosae	1	6	24	34	13	1													
edwini			4	12	79	217	189	91	35	14	3								

Species	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	N	x̄
Hololepis																		
serriferum	32	40	42	41	46	36	24	28	7	12	1	3	2	1	—	1	366	54.05
gracile	68	33	24	4	2												810	47.60
zoniferum	1	1	1														28	47.46
f. barratti	165	158	138	102	66	60	51	29	17	10	5	3	2				1389	51.37
f. fusiforme	234	198	160	124	65	66	31	14	13	6	—	2					2006	50.18
saludae																	90	41.78
c. lepidinion																	40	42.13
c. collis																	62	44.19
Villora																		
okaloosae																	79	34.70
edwini																	644	37.67

TABLE 39.
Number of pored lateral-line scales in the species of the subgenera Hololepis and Villora

Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Hololepis																			
serriferum																			
gracile														2	20	24	49	78	101
zoniferum								1	—	—	1	—	1	2	3	6	2	4	3
f. barratti	4	1	5	4	2	3	3	4	7	7	7	13	12	24	32	61	57	89	106
f. fusiforme	11	7	12	11	8	14	23	23	34	46	53	113	182	300	300	320	235	172	92
saludae						1	1	—	—	1	1	5	3	5	7	6	11	7	7
c. lepidinion											1	—	1	5	4	6	5	3	7
c. collis						1	—	—	—	3	5	6	5	9	5	7	7	4	4
Villora																			
okaloosae																			
edwini																			

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Hololepis																			
serriferum		1	—	2	1	1	2	3	5	14	20	25	28	21	34	41	40	33	26
gracile	140	120	121	61	45	23	13	14	3										
zoniferum	3	2																	
f. barratti	74	116	111	105	107	84	84	76	58	24	23	17	11	6	3	5	—	1	3
f. fusiforme	68	42	21	15	5	3	—	1											
saludae	14	3	6	6	3	1	—	—	—	—	1								
c. lepidinion	1	1	1	1															
c. collis	1	1	3	1	1	1	—	—	—	—	—	1							
Villora																			
okaloosae												3	4	19	27	19	6	2	
edwini		2	5	9	23	48	62	101	112	97	48	40	22	20	5	4			

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	N	x̄
Hololepis																	
serriferum	24	5	13	3	2	2	—	2								348	33.66
gracile																814	19.53
zoniferum																28	15.64
f. barratti																1349	20.65
f. fusiforme																2111	13.96
saludae																89	16.87
c. lepidinion																36	15.89
c. collis																65	14.66
Villora																	
okaloosae																80	33.01
edwini																598	27.02

Breeding Tubercles—Present on the pelvic and anal fins of breeding males. Specimens taken on March 31 (CU 29992) have moderately large tubercles on the lower side of the spines and rays of the pelvic fins and on all the anal fin rays. Their distribution is similar to that in *E. collis collis* (Fig. 1g).

Habitat—Field notes for two Roanoke River localities (CU 29992 the type locality, and CU 34544) show the habitat to be backwater pools of small streams with a depth of 2-4 feet, width of 10-20 feet, flow of about three cubic feet per second, banks partly wooded, current slow to moderate, bottom sand overlain with some mud and with thin to thick layers of detritus.

Distribution—Like its relatives, *E. collis collis* and *E. saludae, E. c. lepidinion* is limited to Atlantic Piedmont streams. This is the most northern of the three forms and is found in the Roanoke and Neuse Rivers. The juvenile specimen from the Cape Fear River is referred to this subspecies with some question so it remains to be determined whether the range extends that far south. Figure 3 shows the distribution of the collections of this form that have been examined.

Specimens Examined—All specimens are designated as paratypes except for the single specimen from the Cape Fear.

Roanoke, R., Va.—Charlotte Co.: USNM 100215 (3, 29-31); Wards Fork, trib. to Roanoke R., S of Madisonville; April 23, 1935. USNM 101330 and 101334 (12, 22-29); Wards Fork, Roanoke Cr., below mill dam, between Madisonville and Cullen; Sept. 15, 1935. USNM 179847 (1, 38) holotype and CU 29992 (8, 30-38); trib. of Horsepen Cr., 2.4 mi. NW of Wylliesburg on Va. 607; March 31, 1956. CU 34544 (7, 29-40); Wards Fork Cr., 6.7 mi. SSW of Madisonville on Va. 47; Sept. 16, 1959. N.C.—Granville Co.: DU uncat. (1, 38); Beech Cr., 3 mi. NNE of Cornwall (this area now flooded by Kerr Dam); Spring 1952.

Eno-Neuse R., N.C.—Durham Co.: DU uncat. (5, 30-35); 4.5 mi. E Oak Grove, Lick Cr. on rt. 264; April 9, 1950. Orange Co.: DU uncat. (1, 36); Eno R. 2 mi.

TABLE 40.
Number of unpored lateral-line scales in the species of the subgenera Hololepis and Villora

Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Hololepis																			
serriferum													2	5	4	14	18	30	36
gracile																			2
zoniferum																			
f. barratti																	1	2	4
f. fusiforme																			
saludae																			2
c. lepidinion																			
c. collis																	1	—	—
Villora																			
okaloosae	5	33	26	12	4														
edwini					5	10	11	24	50	97	95	121	70	50	56	17	9	5	1

Species	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Hololepis																			
serriferum	39	44	33	25	24	15	25	10	13	2	1	2	—	—	2	1	—	—	1
gracile	1	2	4	9	17	32	64	88	123	118	113	76	49	36	30	12	7	2	
zoniferum							1	1	1	—	3	3	3	5	1	6	1	1	1
f. barratti	8	6	12	16	41	51	53	77	83	101	120	103	100	108	95	70	56	65	41
f. fusiforme					2	3	1	4	16	26	35	65	84	111	132	155	181	190	183
saludae	2	3	10	2	14	9	14	8	7	4	2	4	3	1	—	—	1	—	1
c. lepidinion			2	2	3	2	5	6	4	5	2	3	—	1	1				
c. collis	—	—	—	1	—	5	1	1	5	3	6	13	8	4	—	4	6	2	
Villora																			
okaloosae																			
edwini																			

Species	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	N	x̄
Hololepis																	
serriferum																346	20.51
gracile																785	28.02
zoniferum	1															28	31.82
f. barratti	20	22	20	19	11	12	4	3	2	3	2	1	—	—	1	1333	30.71
f. fusiforme	150	144	119	103	54	32	25	13	12	2	9	5	2	3	1	1862	36.17
saludae																87	24.83
c. lepidinion																36	26.25
c. collis																60	29.77
Villora																	
okaloosae																80	1.71
edwini																621	10.68

TABLE 41.

Number of first dorsal spines and second dorsal rays in the species of the subgenera Hololepis and Villora

Species	Spines									Rays											
	7	8	9	10	11	12	13	N	x̄	8	9	10	11	12	13	14	15	16	17	N	x̄
Hololepis																					
serriferum			3	48	227	88	1	367	11.10				1	22	137	167	37	2	1	367	13.62
gracile	3	69	506	240	11	1	2	832	9.24		2	106	454	244	25	1				832	11.22
zoniferum		3	11	8	6			28	9.61		1	10	14	3	1					29	10.76
f. barratti		12	141	605	288	12		1058	10.14	3	41	324	503	177	9					1057	10.79
f. fusiforme		76	418	689	251	45	2	1481	9.85	2	73	563	686	141	7					1472	10.62
saludae		12	68	12				92	9.00				5	48	37	2				92	12.39
c. lepidinion		7	28	5				40	8.95				4	19	16	1				40	12.35
c. collis	1	3	55	9				68	9.06			1	21	38	8					68	11.78
Villora																					
okaloosae		2	31	4				37	9.05			3	32	40	5					80	11.59
edwini		52	368	149	4			573	9.18		7	175	296	89	7					574	10.85

TABLE 42.

Number of anal spines and rays in the species of the subgenera Hololepis and Villora

Species	Spines					Rays								
	1	2	3	N	x̄	4	5	6	7	8	9	10	N	x̄
Hololepis														
serriferum	1	368		369	2.00		6	77	196	85	5		369	7.02
gracile	22	817	1	840	1.98		6	313	468	51	1		839	6.68
zoniferum	3	26		29	1.90	1	8	13	7				29	5.90
f. barratti	8	1057	2	1067	1.99		1	57	400	472	124	2	1056	7.63
f. fusiforme	17	1445		1462	1.99		4	127	691	578	75		1475	7.40
saludae	28	68		96	1.71			1	18	64	10		93	7.89
c. lepidinion	40			40	1.00			2	11	23	4		40	7.73
c. collis	68			68	1.00				18	39	11		68	7.90
Villora														
okaloosae		37	1	38	2.03			8	65	7			80	6.99
edwini	5	541	1	547	1.99		5	195	286	58	3		547	6.74

TABLE 43.
Number of scale rows above and below the lateral line in the species of the subgenera Hololepis and Villora

	Above the Lateral Line						
Species	2	3	4	5	6	N	x̄
Hololepis							
serriferum		17	286	55		358	4.11
gracile	3	289	453	66	1	812	3.72
zoniferum		22	7			29	3.24
f. barratti	157	776	100			1033	2.94
f. fusiforme	362	1042	48	1		1453	2.79
saludae	25	67				92	2.73
c. lepidinion	8	30	2			40	2.85
c. collis	11	44	4			59	2.88
Villora							
okaloosae		10	70			80	3.88
edwini	5	304	245	8		562	3.46

	Below the Lateral Line												
Species	5	6	7	8	9	10	11	12	13	14	15	N	x̄
Hololepis													
serriferum						25	111	140	75	4	1	356	11.79
gracile			19	238	356	160	29	3				805	8.94
zoniferum			6	12	9	2						29	8.24
f. barratti		1	61	286	456	200	26	2				1032	8.85
f. fusiforme		28	299	723	361	35	2	1				1449	8.06
saludae		1	19	37	29	6						92	8.22
c. lepidinion			2	15	14	7	2					40	8.80
c. collis			7	29	23	5	1					65	8.45
Villora													
okaloosae	5	74										79	5.94
edwini	7	150	246	114	36	8	1					562	7.09

TABLE 44.
Number of branchiostegals and pectoral rays in the species of the subgenera Hololepis and Villora

	Branchiostegals				
Species	5	6	7	N	x̄
Hololepis					
serriferum	3	138	9	150	6.04
gracile	10	177	8	195	5.99
zoniferum		11	2	13	6.15
f. barratti	15	134	4	153	5.93
f. fusiforme	31	150	3	184	5.85
saludae	1	30	2	33	6.03
c. lepidinion		30	2	32	6.06
c. collis		34	1	35	6.03
Villora					
okaloosae		10		10	6.00
edwini	1	98	7	106	6.06

	Pectoral Rays							
Species	10	11	12	13	14	15	N	x̄
Hololepis								
serriferum		13	118	26			157	12.08
gracile			2	158	13		173	13.06
zoniferum			3	17	2	1	23	13.04
f. barratti			26	125	47	11	209	13.21
f. fusiforme			9	155	36	1	201	13.14
saludae		40	47				87	11.54
c. lepidinion		2	28	3			33	12.03
c. collis	1	29	31	1			62	11.52
Villora								
okaloosae			16	52	6		74	12.86
edwini		2	45	91	3		141	12.67

TABLE 45.
Number of preoperculomandibular pores and interorbital pores in the species of the subgenera Hololepis and Villora

	Preoperculomandibular pores								
Species	6	7	8	9	10	11	12	N	x̄
Hololepis									
serriferum		2	24	322	6			354	8.94
gracile			5	64	718	22	1	810	9.94
zoniferum				2	23			25	9.92
f. barratti			37	919	20			976	8.98
f. fusiforme	5	21	149	1201	20	2		1398	8.87
saludae			3	85	2			90	8.99
c. lepidinion			3	33	1	1		38	9.00
c. collis	1	—	4	53	4			62	8.95
Villora									
okaloosae			1	46	4			51	9.06
edwini			11	163	366	7		547	9.67

	Interorbital Pores					
Species	0	1	2	3	N	x̄
Hololepis						
serriferum	33	67	255		355	1.63
gracile	786	15	3		804	.03
zoniferum	29				29	0
f. barratti	1026	3	2		1031	.01
f. fusiforme	1427				1427	0
saludae		3	90		93	1.97
c. lepidinion	38	2			40	.05
c. collis	65	1	2		68	.07
Villora						
okaloosae	1	2	44		47	1.91
edwini	7	33	493	1	534	1.91

W of Hillsboro; March 20, 1949. DU uncat. (1, 38); Eno R. at ford N of Hillsboro near Skipper Wright's; April 21, 1955.

Cape Fear R., N.C.—Guilford Co.: CU 25187 (1, 20); Haw R., 3.5 mi. S of Stokesdale on rt. 68; June 24, 1946.

Etheostoma collis collis
(Hubbs and Cannon)

Hololepis collis—Hubbs and Cannon, 1935: 52-54, pl. I-III (original description); Fowler, 1940:40 (Santee R.); Randall, 1958: 342 (Piedmont of S. C., Catawba-Wateree R.).

Etheostoma collis—Bailey and Gosline, 1955: 20, 44 (number of vertebrae); Moore, 1957:198.

Etheostoma colle—Eddy, 1957: 220.

Etheostoma collis collis—Collette, 1961: 2051.

Types—Holotype, UMMZ 94560; 40 mm male; S. C., York Co., creek near York; Nov. 11, 1931; Donald Ameel, Paratypes, UMMZ 107085; same data as holotype and UMMZ 94546; S. C., York Co., Steele Cr., trib. to Catawba R., Rock Hill; Nov. 11, 1931, Donald Ameel.

Diagnosis — One anal spine (erroneously given as two on the types by Hubbs and Cannon, 1935:53); interorbital pores usually absent; usually (93%) 1 + 3 infraorbital pores; nape squamation usually less than 20% (x̄: 3%); breast naked. Maximum size of males 43.1 mm SL (CU 31663, Rocky-Pee Dee R.), females 43.0 mm (CU 33052, Yadkin-Pee Dee R.).

Coloration—All the available collections contain specimens with at least a vestige of breeding color. There are no important differences between the breeding patterns of *E. collis collis* and *E. collis lepidinion.* There are probably few differences between the patterns of non-breeding individuals. Hubbs and Cannon's (1935) description of males taken in November indicated the breeding pattern. Breeding males do not have a red submarginal band in the first dorsal fin as postulated by Hubbs and Cannon (1935).

The breeding female has small melanophores scattered on the anterior spines, and has large and small melanophores on the posterior spines of the first dorsal fin. The second dorsal has rounded patches of me-

TABLE 46.

Number of infraorbital pores and interorbital scales in the species of the subgenera Hololepis and Villora

Species	Complete Infraorbital							Interrupted Infraorbital										N	Usual Number	
	4	5	6	7	8	9	10	0+2	0+3	1+2	1+3	1+4	2+2	2+3	2+4	3+3	3+4			
Hololepis																				
serriferum	1	6	290	56	5													358		6.16
gracile			2	101	648	53	4											808		7.95
zoniferum														2	21	—	2	25	84%	2+4
f. barratti									18	7	976	15	3	364	7	5		1395	70%	1+3
f. fusiforme								1	10	6	298	2	6	1381	8	19	1	1732	80%	2+3
saludae											34	59	—	—	1			94	63%	1+4
c. lepidinion											5	35						40	88%	1+4
c. collis											63	4	—	1				68	93%	1+3
Villora																				
okaloosae				2	39													41		7.95
edwini			1	39	480	24	1											545		7.97

Species	Interorbital Scales																																						N	x̄
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37		
Hololepis																																								
serriferum							3	2	7	6	8	1	4	13	9	16	11	7	15	6	4	5	10	6	3	1	3	1	1	1	1	1	1	1		1			148	16.6
gracile	116																																						116	0
zoniferum	14																																						14	0
f. barratti		1	1	1	1	7	7	9	17	19	26	25	19	14	24	16	18	17	10	6	11	4	4	2	—	3	1	1	—	—	1	1	—	—	—	—	—	1	267	13.2
f. fusiforme	76	72	64	43	24	7	9	6	2	1	1	—	1																										306	2.0
saludae	46																																						46	0
c. lepidinion	13																																						13	0
c. collis	35																																						35	0
Villora																																								
okaloosae	10																																						10	0
edwini	85																																						85	0

TABLE 47.
Supratemporal canal and coronal pore and condition of preopercle in the species of the subgenera Hololepis and Villora

Species	Coronal Pore		Supratemporal Canal	
	Present	Absent	Complete	Incomplete
Hololepis				
serriferum	47		346	3
gracile	455	2	715	48
zoniferum	6		8	21
f. barratti	342	24	1201	84
f. fusiforme	305	55	1047	122
saludae	45		41	53
c. lepidinion	32		15	24
c. collis	37		33	35
Villora				
okaloosae	46		43	3
edwini	259		516	20

Species	Condition of Preopercle			
	Entire	Partly serrate	Serrate	N
Hololepis				
serriferum			304	304
gracile	772			772
zoniferum	29			29
f. barratti	900	515		1414
f. fusiforme	1620	194		1814
saludae	96			96
c. lepidinion	35	5		40
c. collis	68			68
Villora				
okaloosae	3	14*	28*	45
edwini	518	2		520

* The preopercle is crenulate instead of serrate in *E. okaloosae.*

lanophores that tend to form bands across the fin. The anal fin is clear in most specimens, while others have concentrations of small melanophores. The pectoral fins of both males and females have melanophores on the rays. The pelvic fin lacks melanophores. The caudal is barred. The breast, belly and lower sides lack melanophores. There are scattered large melanophores on the cheek. In both sexes there are usually three orbital bars present; suborbital, preorbital, and postorbital. The first two are the most prominent and some specimens lack the postorbital as well as the supraorbital. The pored portion of the lateral line stands out as a narrow light line although it may be interrupted by some pigment under the distal third of the scale. The median basi-caudal spot is the most prominent although it is diffuse in some specimens. The dorsal and ventral spots vary in intensity, and are sometimes almost as prominent as the median spot. Most females have variegated brown sides and lack lateral blotches. The genital papilla lacks pigment. The patterns of breeding females of *E. collis collis, E. collis lepidinion* and *E. saludae* are compared in Figure 17.

As in *E. collis lepidinion,* the breeding male is colored like the female, but darker in some regions. The membranes of the first dorsal fin are covered with small melanophores concentrated on the anterior three membranes. Some specimens have the first membrane almost entirely black. Four to five sets of quadrangular blotches give the second dorsal a banded appearance. The anal fin, belly and breast are uniformly covered with small melanophores. There are more small melanophores on the membranes than on the rays of the pelvic fin. The cheek has more melanophores than that of the female. Males usually have seven to eight lateral blotches which extend from the caudal base to the middle of the first dorsal fin. These blotches are more prominent in the smaller adults. There is pigment on the posterior ventral side of the genital papilla in large males. Some small specimens have a band of pigment encircling the papilla. A specimen

TABLE 48.
Squamation of breast, nape, parietal, preopercle and opercle in the species of the subgenera Hololepis and Villora

Breast

	Percent 0	10-20	30-40	50-60	70-80	90-100	Almost entirely 100% I-C	I/PX-C/T	PX-C/T	PX/X-T	X-T	N	x̄
Hololepis													
serriferum							107	41	3	1		152	70% I-C
gracile	129											129	0
zoniferum	14											14	0
f. barratti							23	78	57	23	52	233	33% I/PX-C/T
f. fusiforme							156	49	18	18	6	247	63% I-C
saludae	91	2										93	.2%
c. lepidinion		10	12	12	5							39	41%
c. collis	63	1										64	.2%
Villora													
okaloosae			1	10	4							15	59%
edwini	2	1	9	22	16	52						102	76%

Nape

	Percent 0	10-20	30-40	50-60	70-80	90-100	Almost entirely 100% I-C	I/PX-C/T	PX-C/T	PX/X-T	X-T	N	x̄
Hololepis													
serriferum									3	13	88	104	85% X-T
gracile	10	24	12	7	14	93						160	70%
zoniferum	12	2										14	1%
f. barratti								3	19	46	111	179	62% X-T
f. fusiforme								12	39	57	70	178	39% X-T
saludae	32	44	11	3	1	3						94	15%
c. lepidinion					3	36						39	96%
c. collis	50	9	2									61	3%
Villora													
okaloosae							5	26	1			32	81% I/PX-C/T
edwini							3	43	23	13	18	100	43% I/PX-C/T

Preopercle

	Percent 30-40	50-60	70-80	90-100	Almost entirely 100% I-C	I/PX-C/T	PX-C/T	PX/X-T	X-T	N	x̄
Hololepis											
serriferum									99	99	100% X-T
gracile					1	3	6	26	126	162	78% X-T
zoniferum						4	4	5		13	38% PX/X-T
f. barratti							1	6	155	162	96% X-T
f. fusiforme						4	6	59	113	182	62% X-T
saludae	3	1	–	80						84	97%
c. lepidinion				40						40	100%
c. collis		2	1	53						56	98%
Villora											
okaloosae						23	5	2		30	77% I/PX-C/T
edwini						7	13	30	53	103	51% X-T

Opercle

	Percent 0	10-20	30-40	50-60	70-80	90-100	Almost entirely 100% I-C	I/PX-C/T	PX-C/T	PX/X-T	X-T	N	x̄
Hololepis													
serriferum											99	99	100% X-T
gracile							1	10	28	55	68	162	42% X-T
zoniferum											14	14	100% X-T
f. barratti								4	1	25	139	169	82% X-T
f. fusiforme								4	9	23	158	194	81% X-T
saludae			2	1	9	57						69	91%
c. lepidinion						40						40	100%
c. collis	2	–	2	1	3	44						52	90%
Villora													
okaloosae										1	31	32	97% X-T
edwini								16	17	17	53	103	51% X-T

Parietal

	Percent 0	5-20	25-40	45-60	65-80	85-100	Almost entirely 100% I-C	I/PX-C/T	PX-C/T	PX/X-T	X-T	N	x̄
Hololepis													
serriferum							2	82	27	26	17	154	53% I/PX-C/T
gracile	129											129	0
zoniferum	14											14	0
f. barratti		17	57	47	55	46						222	57.5%
f. fusiforme	105	144	19	4								272	9.5%
saludae	46											46	0
c. lepidinion	12											12	0
c. collis	36											36	0
Villora													
okaloosae	10											10	0
edwini	83	2										85	0

TABLE 49.
Number of vertebrae in the species of the subgenera Hololepis and Villora (based in part on data presented by Bailey and Gosline, 1955)

Species	33	34	35	36	37	38	39	40	41	N	x̄
Hololepis											
serriferum						3	14	7	1	25	39.24
gracile				4	15	13	2			34	37.38
zoniferum				1	3	4	2			10	37.70
f. barratti					3	13	16	1		33	38.45
f. fusiforme					5	25	15	8		53	38.49
saludae				3						3	36.00
c. lepidinion			2	7	5	2				16	36.44
c. collis			1	1	1					3	36.00
Villora											
okaloosae	1	10	13	2						26	34.62
edwini		1	3	4	10	3				21	36.52

as small as 27.4 mm has full breeding pigmentation and tubercles. A comparison of the breeding pattern of male *E. collis collis, E. collis lepidinion* and *E. saludae* is presented in Fig. 18.

Genital Papilla—The genital papilla of the breeding female is an elongate tube like that of *E. fusiforme* (Fig. 1f).

Breeding Tubercles—Present on the anal and pelvic fins of breeding males. Specimens taken on March 22 (CU 11988) have moderately large tubercles on the lower side of the pelvic spine and rays and on all the anal fin rays (Fig. 1g).

Habitat—Field notes for five late March collections (CU 29832, 29991, 31663, 31717, 33052), show the habitat to be small to medium-sized streams, shore wooded or partly wooded and partly pasture, width 5-40 feet, depth 2-3 feet, current slow to moderate, aquatic vegetation absent, bottom sand, mud, or rubble covered with silt and/or detritus. All specimens were taken either in backwater pools or near stream banks in slow-moving water. Most of the specimens in one collection (CU 31663) were taken from the shallow water along the banks of a pool at a cattle crossing; here a number were resting in depressions made by cows' hoofs, sheltered from the current. In Waxhaw Creek Creek (CU 31717) three out of nine specimens were taken near the banks of the main stream over mud, while the other six were collected in a small backwater pool less than two feet wide.

Habits—Little is known of its habits. In the spring of 1958, specimens from the Yadkin River were brought back alive to the laboratory. Although they survived a week-long collecting trip, they all died after being left in the laboratory for a few hours. Members of the *E. collis-saludae* complex live in the cooler and presumably more oxygenated waters of the Piedmont, so perhaps their oxygen requirements are higher than those of the lowland species of *Hololepis,* which are frequently taken in very warm stagnant situations. A few *E. serriferum* taken on this trip also died, but all the *E. fusiforme fusiforme* survived.

Courtship and spawning have not been observed. However, judging from the pigment pattern of the breeding males and the location of the breeding tubercles, it seems likely that the courtship patterns are similar to those of *E. f. fusiforme (q.v.).* Eggs were extruded by a female collected on March 31 (CU 31663) when held in my hand, confirming the evidence from the breeding tubercle development that the spawning season is near the end of March.

Distribution—Restricted to the Piedmont streams of North and South Carolina. Taken only in two tributaries of the Pee Dee River (the Rocky and Yadkin rivers) and in the Catawba-Wateree branch of the Santee River (Fig. 3). The holotype and one of the paratypes were listed from an indefinite locality between the Catawba and Broad rivers (part of the Congaree-Santee system) but it is felt that these specimens must have come from the Catawba because the Saluda-Broad is inhabited by the closely related *E. saludae.*

Specimens Examined—Yadkin-Pee Dee R., N. C. Davidson Co.: all collections from the same locality which is: trib. of Yadkin R., 0.4 mi. W jct NC 109 and sec. rd., 1 mi. N of Cid: UMMZ 138569 (2, 31-33); UMMZ 138568 (1, 39); and CU 11988 (12, 27-41); March 22, 1948. Also CU 29991 (7, 31-38); March 30, 1956; and CU 33052 (9, 33-43); March 30, 1958.

Rocky R.-Pee Dee R., N. C.—Caborrus Co.: CU 19324 (1, 20); Rocky R. 5 mi. S of Odell; Oct. 13, 1946. Stanly Co.: CU 29832 (2, 35-36); trib. of Long Cr., 3.7 mi. N of Aquadale on sec. rd.: March 29, 1956. CU 31663 (21, 25-43): trib. of Rocky R. on dirt rd. between Red Cross and Locust (not NC 27); March 31, 1958.

Catawba-Santee R., N.C.—Union Co.: CU 35133 (1, 36); where a paved rd. from Waxhaw to NC 200 crosses Waxhaw Cr., 3.5 mi. SSE of Waxhaw; June 15, 1956. Same locality, CU 31717 (9, 22-38); March 31, 1958. S. C.—York Co.: UMMZ 94546 (1, 37); paratype; Steele Cr., trib. to Catawba R., Rock Hill; Nov. 11, 1931.

"Santee R." (Almost certainly Catawba-Santee), S.C.—York Co.: UMMZ 94560 (1, 40) holotype and UMMZ 107085 (1, 40) paratype; cr. near York; Nov. 11, 1931.

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X. ABSTRACT

The subgenus *Hololepis*, genus *Etheostoma*, includes eight forms of small specialized darters: four are found in the swamps, lakes, and backwaters of the Coastal Plain of eastern North America (*fusiforme fusiforme, fusiforme barratti, serriferum,* and *zoniferum*); one in the lowlands of the Mississippi Basin *(gracile);* and three in the backwaters of Atlantic Piedmont streams *(collis collis, collis* LEPIDINION new subspecies, *saludae). Etheostoma edwini* was replaced in the subgenus *Villora* Hubbs and Cannon.

E. serriferum is the most primitive species in the subgenus in virtually all characters: size, preopercular serrations, presence of interorbital pores, complete infraorbital canal, fairly complete lateral line, more fin rays, more complete squamation. It is divided into a northern and a southern race based on the number of interorbital scales, pored and total lateral-line scales.

E. gracile and *E. zoniferum* share a number of characters which show their close relationship: ten preoperculomandibular pores; interorbital pores absent; reduced squamation; green bars on the side; red spots in the dorsal fins and accessory breeding tubercles on the chins of males. The characters which differentiate *E. zoniferum* from *E. gracile* show that it is a specialized offshoot which has the squamation reduced and the infraorbital canal incomplete. *E. gracile* has as much variation inherent in each population as in the other species of *Hololepis,* but there has been little differentiation between populations.

The most variable species of the subgenus, and the one studied most intensively, is *Etheostoma fusiforme.* There are three types of variation in this species: (1) Variation from population to population in an apparently random fashion (*e.g.,* total lateral-line scales); (2) clinal variation shown in the increased development of squamation, the increased percent of individuals with 1+3 infraorbital pores and partially serrate preopercles; (3) variation in the retention of juvenile characters (neoteny). Neoteny was particularly evident in the greatly reduced number of pored lateral-line scales in the dark North Carolina Bay Lakes and in clear Crystal Lake, Georgia, both areas of low productivity. It was also noted in the failure of the supratemporal canal to become closed, in the reduced number of scales above and below the lateral line, and in the reduced number of infraorbital pores.

Etheostoma fusiforme, barratti, and *thermophilum* are shown to be conspecific; the differences between them are of clinal and developmental nature. The subspecies of *fusiforme* recognized by Hubbs and Cannon (1935) were based upon a combination of random variation, developmental variation, and clinal variation so *f. insulae, f. metaegadi, f. erochroum,* and *f. atraquae* are synonymized with *f. fusiforme. Etheostoma thermophilum oligoporum* (J. R. Bailey and Frey) is considered to be based upon neotenic populations that have been produced independently in three of the dark North Carolina Bay Lakes. *Etheostoma thermophilum thermophilum* and *E. thermophilum oligoporum* are synonymized with *f. fusiforme. Etheostoma fusiforme fusiforme* differs from *E. f. barratti* in having fewer interorbital scales, less developed squamation of the breast and parietal, and fewer individuals with 1+3 infraorbital pores and partially serrate preopercles. *Etheostoma barratti appalachia* (J. R. Bailey) is considered a slightly differentiated introduced population of *f. barratti* not worthy of subspecific recognition.

The *E. collis* group is the most specialized in the subgenus as shown in the reduction in number of pored and total lateral-line scales and vertebrae. *E. saludae* is more primitive than *E. collis*

in retaining the interorbital pores and having only about a third of the specimens with one anal spine. *E. collis* LEPIDINION is described from the Roanoke, Neuse, and Cape Fear rivers. It is more primitive than the nominate subspecies in having a scalier nape and breast and 1+4 instead of 1+3 infraorbital pores.

The paper includes a diagnosis of the subgenus *Hololepis;* keys to all forms; synonymies; pigmentation descriptions; range maps; photographs of all forms; drawings of breeding tubercles and genital papillae; discussions of habitat, associated species, habits, geographic variation, development, and evolutionary relationships.

THE AMERICAN PERCID FISHES OF THE SUBGENUS *VILLORA*

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I. Introduction

The aims of this paper are threefold: to define the subgenus *Villora,* to resurrect and define *Etheostoma (Villora) okaloosae* (Fowler), and to examine intra-specific variation in *E. (Villora) edwini. Villora* was described as a new genus by Hubbs and Cannon (1935) on the basis of the new species *edwini.* Bailey (1951), in Bailey Winn and Smith (1954), and in Bailey and Gosline (1955) reduced the many nominal genera of darters to three: *Percina, Ammocrypta* and *Etheostoma.* In 1955 (Fig. 1), Bailey and Gosline arranged the darters in order of increasing specialization and some former genera were utilized as subgenera. *Etheostoma edwini* was listed under the subgenus *Hololepis,* without further comment. We cannot subscribe to this view. During his study of the subgenus *Hololepis,* the senior author (Collette, 1960) became convinced that *Villora* should be regarded as distinct from *Hololepis.* Through extensive collecting in western Florida, the junior author (Yerger, 1960) discovered that *Etheostoma okaloosae* (Fowler) is a valid species referable to the subgenus *Villora,* and concluded that it must be removed from the synonymy of *E. swaini* (Jordan) where it was placed by Bailey, Winn and Smith (1955).

The methods of this study are similar to those of Collette (1962). However, here we present the counts of the unpored (Table 3) as well as the pored and total lateral-line scales. This character is unimportant in the subgenus *Hololepis,* but proves most useful in *Villora.* Measurements were made following the technique described by Hubbs and Cannon (1935). In the course of this study, more than 1100 specimens of *E. edwini* and nearly 200 of *E. okaloosae* were examined. For purposes of comparison, summary counts for the two species of *Villora* are being presented along with those for the species of *Hololepis* in another paper (Collette, 1962, Tables 38-49).

II. Acknowledments

The section on *Etheostoma edwini* is based on part of a doctoral dissertation presented to Cornell University by the senior author. Professor Edward C. Raney, who served as chairman of the committee, provided, in addition to constant interest, support for the study through National Science Foundation Grants 2893 and 9038.

The section on *E. okaloosae* is part of a study on the fishes of the Florida panhandle undertaken by the junior author with support from a National Science Foundation Grant G-6260 and from the Research Council of the Florida State University. The many contributions to this project by Ardith B. Cochran are gratefully acknowledged, as are the services rendered by W. Bruce Walden and Robert F. Christensen, graduate students at Florida State University. Colonel John N. Reynolds, Commander, Eglin Air Force Base, Florida, granted permission to collect on the military reservation and extended many courtesies. James E. Böhlke compared the type of *E. okaloosae* with several specimens sent to him by the junior author.

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III. Subgenus *Villora*

Villora Hubbs and Cannon, 1935:11-13 (type species *Villora edwini* Hubbs and Cannon, 1935, by original designation).

Lateral line slightly arched upward, incomplete to complete; pored lateral-line scales 20 to 36, unpored 0 to 18, total 32 to 42; infraorbital canal always complete, usually with 8 pores; supratemporal canal usually complete in adults; coronal pore present; interorbital pores usually 2; preoperculomandibular pores usually 9 or 10; vomer and palatine toothed; preopercle entire or crenulate; branchiostegal membranes separate or narrowly conjoined; branchiostegal rays usually 6; breast naked to entirely covered with scales; nape, preopercle, and opercle completely covered with imbedded cycloid to exposed ctenoid scales; parietal and interorbital regions naked; belly covered with unmodified ctenoid scales; flesh opaque; body rather stocky and somewhat compressed; vertebrae 33 to 38; premaxillary frenum broad; first dorsal fin moderately high, with 8 to 11 spines that lack thickened fleshy tips; second dorsal fin somewhat higher than first dorsal, with 9 to 13 rays; anal spines usually 2, the first thicker than the second; anal soft-rays 5 to 9; pectoral rays usually 12 or 13; segmented caudal rays: upper 8 to 13, lower 7 to 10, total 15 to 22; genital papilla of breeding female a low tube crowned with villi; pelvic fins closely approximated, separated by a distance equal to about one-half the pelvic base; dark humeral spot behind the opercle and above the pectoral fin origin usually prominent; breeding tubercles absent; males reaching a larger maximum size than females; habitat moderately fast, clear streams with patches of vegetation; range northern and western Florida and below the Fall Line in southwestern Georgia and in Alabama.

Hubbs and Cannon (1935) placed *Villora* between *Hololepis* and the catch-all *Poecilichthys*. They felt that many of the features of *Villora* were primitive and suggested that it may have evolved from an ancestor of *Hololepis.* The relationships of *Villora,* however, do not seem to lie with *Hololepis* (see Collette, 1962). The rediscovery of *E. okaloosae,* which is obviously closely related to *E. edwini* and more different from *Hololepis* than *edwini,* gives support to our view that *Villora* should stand as a subgenus separate from *Hololepis.* In a number of characters *E. okaloosae* is somewhat intermediate between *E. edwini* and E. *(Oligocephalus) swaini* (Jordan). There seems to be a trend toward a shorter genital papilla (Fig. 7), a more highly arched lateral line, a slenderer caudal peduncle, and fewer pored lateral-line scales as one moves from *E. (O.) swaini* through *E. (V.) okaloosae* to *E. (V.) edwini.* In the last three characters the evolutionary trend parallels that of the subgenus *Hololepis,* resulting in a superficial similarity between the *Villora* and *Hololepis* lines. *Villora* differs from the subgenus *Hololepis* by lacking breeding tubercles and by having a nearly complete lateral line, extending past the origin of the second dorsal fin (occasionally complete in *E. okaloosae*); a much less arched lateral line; the genital papilla in the form of a low tube crowned with villi (Collette, 1962: Fig. 1); and a dark humeral spot. The species live in clear, moderately fast-flowing, sandy-bottomed streams. *Villora* differs from many of the species of the subgenus *Oligocephalus* in having a somewhat arched lateral line and in the shape of the genital papilla. We have not studied thoroughly the differences between *Oligocephalus* and *Villora.* This matter deserves further study.

IV. Species of *Villora*

The two species that we refer to the subgenus *Villora* differ in a number of respects (Table 1). Frequency distributions of the more important characters are presented in

Tables 2-8. Table 9 compares the proportional measurements of the two species.

Etheostoma (Villora) edwini
(Hubbs and Cannon)

Villora edwini—Hubbs and Cannon, 1935:13-16 (original description); Carr, 1937:83 (Fla.); Fowler, 1941:242, fig. 13 (not 3 as given) (Fla.); Bailey and Hubbs, 1949:10 (*edwini* one of a group of endemic species, probably relicts, in sinkhole region of N. Fla.).

Etheostoma edwini—Bailey, Winn, and Smith, 1954:144, 156 (range extension W to Perdido R., and N into S Ala.); Bailey and Gosline, 1955:20, 43-44 (number of vertebrae); Carr and Goin, 1955: 31, 101-102, pl. 30 (description, Fla.); Eddy, 1957: 220, 223, fig. 552; Moore, 1957:197; Neill, 1957:196 (distribution in Fla. stops at the Suwannee Straits, although habitat continues); Briggs, 1958: 275 (distribution); Crittenden, 1958:218 (Bay Co., Fla.); Yerger, 1960:41 (comparison with *E. okaloosae*); Collette, 1961: 1051.

Fowler's reports (1945: 251-252, 293-294) of *Villora edwini* from Ware County, Georgia and from Florida were based on *E. fusiforme barratti.*

Types—Holotype UMMZ 87892; 38 mm male; Fla., Santa Fe R., at Poe Springs; Feb. 8, 1928; E. T. Boardman. Paratypes, the rest of the specimens examined by Hubbs and Cannon (1935:13).

Coloration—The first dorsal fin of the female varies from almost clear to having four rows of rectangular blotches on each interspinous membrane. The second dorsal fin is colored like the first dorsal but has additional pigment on the rays, producing a barred appearance. Melanophores usually outline the anal and pectoral rays; the anal membranes are clear or have a few pigment cells. The pelvic fin is clear, with occasional melanophores on the rays. The caudal rays are barred; the membranes sometimes have pigment. Both belly and breast vary from being immaculate to having scattered large melanophores. The cheek has small and medium melanophores. All four orbital bars are developed; the suborbital is the most prominent; the supraorbital and suborbital both enter the eye. The pored portion of the lateral line is light, with pigment underneath some scales. Most specimens lack distinct basi-caudal spots; some have blackish median spots and vestiges of dorsal and ventral spots. Eight to twelve lateral blotches are sometimes present along the sides; they may extend down to the underside of the caudal peduncle. There are usually about nine dark brown dorsal saddles. Melanophores on the sides below the lateral line are generally arranged in a prominent X-pattern as described by Hubbs and Cannon (1935). Chromatophores below the lateral line are mostly black; those above the lateral line are brown. The genital papilla is usually devoid of pigment, but the dorsal surface of the distal portion is sometimes pigmented. Figure 1 shows the pattern of a breeding female.

In the non-breeding male the pectoral and caudal fins, orbital bars, basi-caudal spots and sides of the body are colored as in the female. The first dorsal fin is similar to but darker than that of the female. Small melanophores occur between the blotches on the second dorsal fin. The proximal three-fourths of the anal fin and and the proximal seven-eighths of the pelvic fin membranes are covered with small melanophores. Both belly and breast are covered almost entirely with small melanophores. The cheek is darker than that of the female. The light, pored portion of the lateral line stands out more sharply against the dark sides of the male. The lateral blotches and the dorsal saddles are usually more prominent in the male. The genital papilla is free from pigmentation and there is no pigment on the belly dorsal to it.

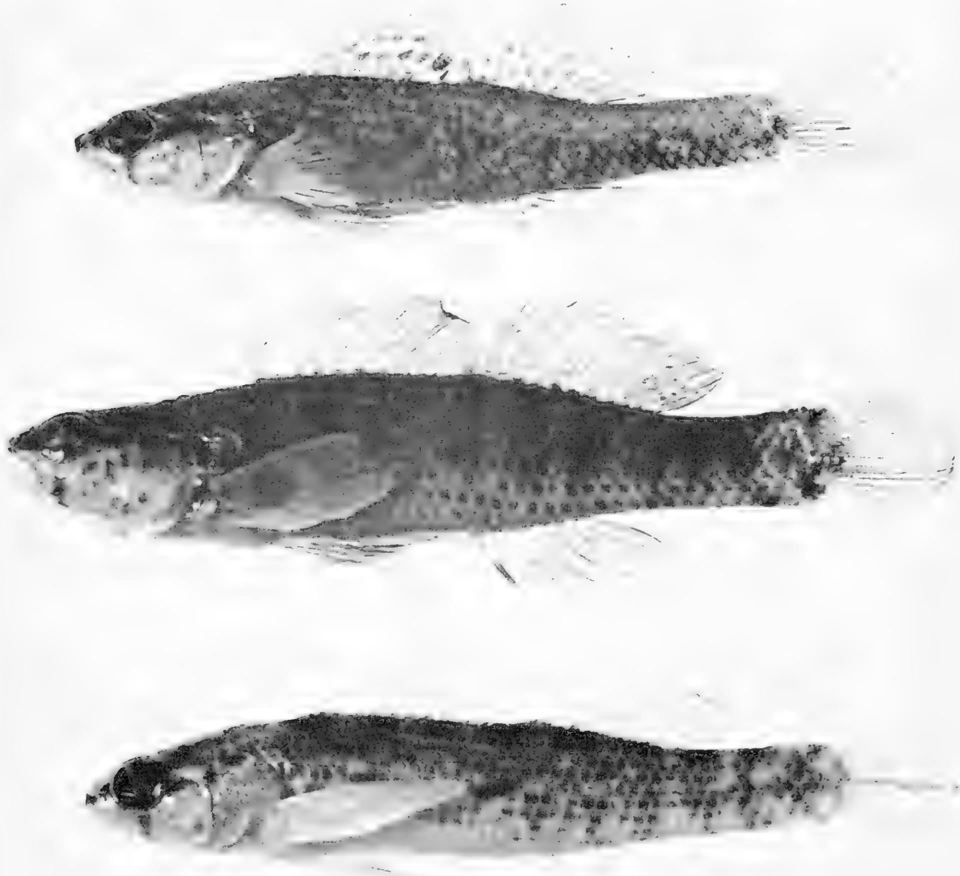
The basi-caudal spots, orbital bars, cheek and genital papilla of the breeding male are colored as in the non-breeding male. The blotches in the dorsal fins have orange centers. Most breeding males have three or four rows of such spots on the membranes of the first dorsal fin and three to five rows on the membranes of the soft-dorsal. Black pigment is concentrated anterior and posterior to the last dorsal spine. The anal fin also has orange spots which are usually arranged in one or two rows, and the entire fin is darkened by melanophores. The pelvic fin is covered with small melanophores. The pectoral fin differs from that of the species of the subgenus *Hololepis* in having at least the basal half of its membranes covered with small melanophores. In addition to the barring of the caudal rays there are small mel-

Figures 1-3. Females of three species of *Etheostoma*. 1. (Upper) *E. edwini*, FSU 6178, Mar. 25, 1960, 35.4 mm. **2.** (Middle) *E. okaloosae*, FSU 6078, Jan. 25, 1960, 40.0 mm. **3.** (Lower) *E. swaini*, FSU 1632, Mar. 5, 1954, 35.8 mm.

anophores on the interradial membranes. The belly, breast and branchiostegal membranes are uniformly sprinkled with small melanophores. The narrow light streak along the lateral line is not prominent. There are light (orange in life) spots on the sides, both above and below the lateral line. The dorsal saddles are sometimes indistinct. Figure 4 shows the pigment pattern of a breeding male compared with males of *E. okaloosae* and *E. swaini*.

Fowler (1941) presented a drawing labeled as *Villora edwini* (Fig. 3), and another labeled as *Hololepis barratti* (Fig. 13). The labels on these drawings were apparently reversed, since the scale on Figure 3 indicates a fish of about 26 mm total length (close to the stated length of the specimen of *barratti*, 29 mm) and that on Figure 13 indicates a fish of about 41 mm (close to the stated length of the specimen of *edwini*, 44 mm). Figure 13 is clearly intended to represent *Villora edwini* since the pored portion of the lateral line extends behind the end of the second dorsal fin and there are no prominent basi-caudal spots. The pored portion of the lateral line in Figure 3 extends only to the end of the first dorsal fin, and there are three prominent basi-caudal spots, characters indicative of *barratti*. However, there are too few lateral-line scales in the figure to portray *Etheostoma fusiforme barratti* accurately.

The colors of *E. edwini* in life are very striking, and the presently accepted common name, brown darter, does not portray adequately the distinctive characters of this species. A more descriptive common name is redspot darter. The following descriptions are based on a composite of field notes (by Yerger) on series collected from January through April. Males in full breeding color have orange-red spots scattered over the body from the back of the oper-



Figures 4-6. Males of three species of *Etheostoma*. **4.** (Upper) *E. edwini*, FSU 6154, Mar. 26, 1960, 36.8 mm. **5.** (Middle) *E. okaloosae*, FSU 6078, Jan. 25, 1960, 43.4 mm. **6.** (Lower) *E. swaini*, FSU 6071, Jan. 23, 1960, 39.6 mm.

culum to the caudal fin, above the lateral line, and extending halfway from the lateral line to the ventral contour of the body. The largest spots, about the size of the pupil, are immediately above and below the lateral line. Each spot consists of a central red portion surrounded by a yellow ring. The spinous dorsal fin has a prominent basal row and a sub-marginal row of orange-red spots, with two irregular rows between them. A large black blotch is present on the posterior part of the membrane, centered between the last two spines. The second dorsal fin has four similar rows of slightly smaller orange-red spots, and lacks the black area. There are two incomplete rows of reddish spots on the anal fin, best developed on the posterior third of the membrane. The caudal has three to six vertical bands of elongate reddish or reddish-brown blotches, most prominent on the base of the fin. The pelvics are dusky. The general body color is tan to yellow brown, with irregular darker blotches below the lateral line. Males with less brilliant coloration and younger males are generally more yellow and possess fewer spots on the body and on the dorsal and anal fins. Neither *E. okaloosae* nor any species of the subgenus *Hololepis* has red spots on the body.

Females lack the brilliant orange-red spots on the fins, but have several rows of very small reddish spots just above and parallel to the lateral line. The caudal fin is like that of the male, but has smaller and more numerous reddish to yellowish spots. The pelvics are clear. The black coloration below the lateral line contrasts more strikingly with the tan coloration above the lateral line than in the males.

Genital Papilla — Hubbs and Cannon (1935:14) described the genital papilla of *E. edwini* as follows: "In the breeding female scarcely developed as such, represented by matted villi surrounding the oviducal opening; some villi long enough to reach anal fin; in the non-breeding female shrunken but preserving the villous appearance." Examination of a large number of specimens

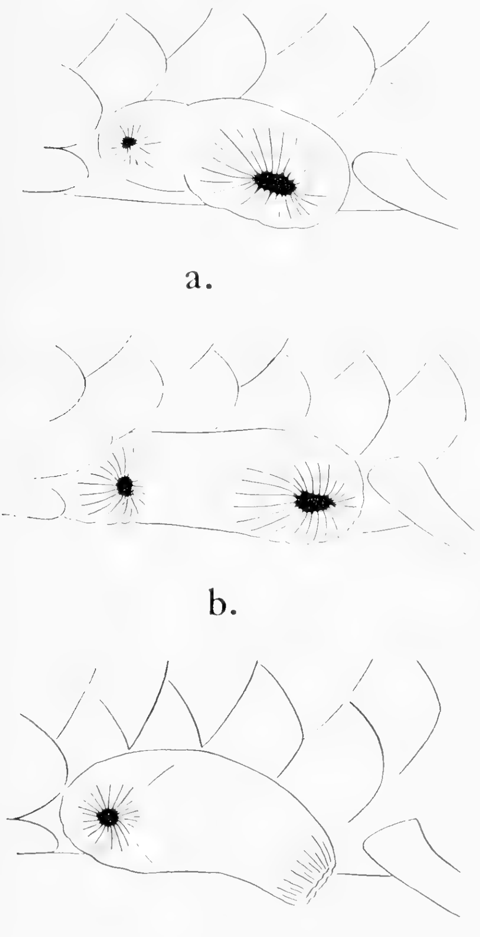


Figure 7. Genital papillae of breeding females of three species of *Etheostoma*. **a.** (Upper) *E. edwini*. **b.** (Middle) *E. okaloosae*. **c.** (Lower) *E. swaini*.

indicates the need for modifying this description. The papilla of the breeding female is a short tube, containing rugae which form villi at the terminus of the papilla. The thin membrane connecting these rugae tends to break from excessive probing or from the use of an air jet; the ends of the rugae then appear as free villi. Figure 7a shows the genital papilla of a typical female in breeding condition.

Development — Little information is available on the development of *E. edwini*. One collection (UF 6962) from the Apalachicola River system contains specimens as small as 11 mm SL. Plotting pored lateral-line scales against standard length for this collection (Fig. 8) gives about the same picture for their development as found in *E. fusiforme fusiforme* (Collette, 1962: Figs. 12 and 13). An 11.3 mm specimen lacked scales on the anterior portion of the body while another, 11.0 mm long, had the body completely scaled. The pored scales begin developing at about 12-13 mm. Figure 8 shows an intermediate group from about 15-21 mm which indicates that the definitive number of pored lateral-line scales may not be formed until a length of about 22 mm has been attained.

The same collection furnishes data on the size at which the supratemporal canal becomes complete. Specimens from 36.6 mm to 21.7 mm long are about equally divided between those with the canal complete and those with the canal incomplete, but all from 21.7 to 11.0 mm long have incomplete canals. A 12.0 mm specimen has only a shallow groove and completely lacks a roofed-over supratemporal canal. Adults of *E. edwini* typically have this canal complete, but individuals in a number of collections retain the juvenile incomplete condition.

Habitat — *E. edwini* usually lives in clear to slightly turbid streams varying in depth from six inches to two or three feet. The current is usually moderate. The bottom consists chiefly of sand with an occasional light overlay of fine silt, or some gravel, and occasionally rock outcrops. The vegetation varies from sparse to dense. The list of plants is long, and varies to some extent from one locality to another, but frequently consists of species of *Ludwigia, Scirpus, Orontium, Nitella,* and *Batracho-*

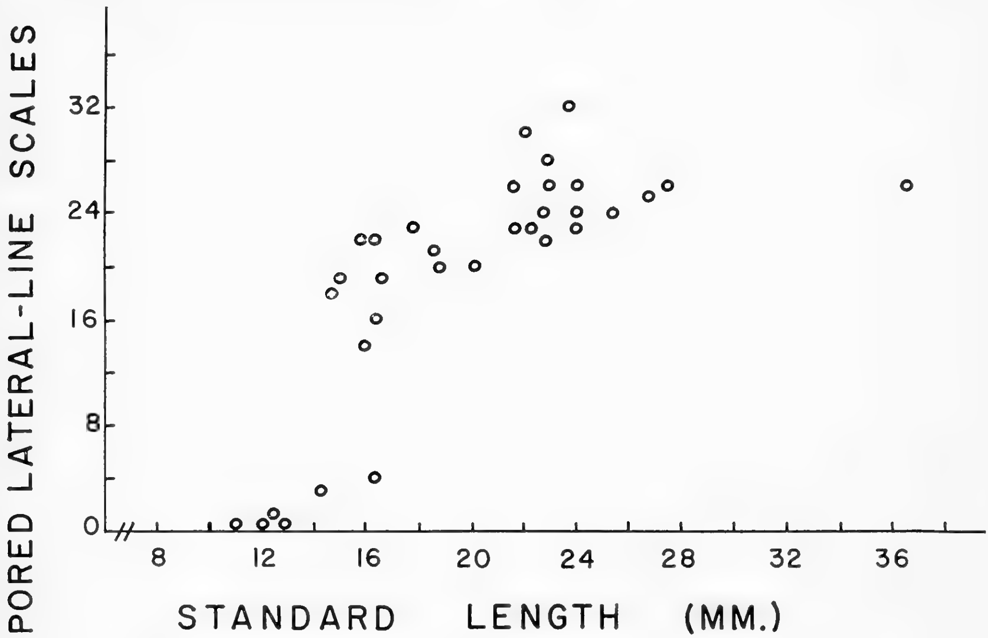


Figure 8. Change in number of pored lateral-line scales with size in *Etheostoma edwini*. (UF 6962, Fla., Apalachicola Dr., Dec. 2, 1939).

spermum. The pH varies from 6.4 to 7.8, the more alkaline readings having been recorded in spring runs with limestone outcrops.

Both species of the subgenus *Villora* prefer faster, clearer and more alkaline situations than do the species of the sugenus *Hololepis.* Crittenden (1958) gave some of the physical and chemical characters of two streams in Bay Co., Fla., one of which is inhabited by *Etheostoma edwini* and the other by *Etheostoma (Hololepis) fusiforme barratti.* The stream with *E. edwini* — Econfina Creek—"is spring-fed, clear, fast-flowing fresh water creek over most of its course; depths are three to ten feet near the mouth; and the bottom is of sand and limestone in its upper reaches." The pH was 7.5-7.8 and the methyl orange alkalinity was 45.5-56.0 p.p.m. The stream containing *E. f. barratti*—Cedar Creek—"is a sluggish slow-moving stream with currents noticeable only at low tide; the sand and mud bottom had a vegetable detritus overlay; depths vary from three to ten feet and the water is stained." The pH was 7.3 and the methyl orange alkalinity 35.0 p.p.m.

Habits—These darters are most frequently found beneath the leaves of scattered clumps of vegetation toward the margins of the streams rather than in the main current. Nothing is known about their spawning behavior, but since the genital papilla and the ecological requirements of *E. edwini* are so similar to those of *E. okaloosae*, it is highly probable that in behavior the two species are very much alike.

Examination of the ovaries of females and the development of breeding color in males indicates that the breeding season is at its height in February, March, and early April. Ripe ova occasionally observed in specimens collected as late as June indicate that the spawning season may be prolonged. Specimens as small as 11.0 mm SL. (UF 6962, Chipola R., Florida) were collected by William MacLane on December 2 in dense clumps of filamentous algae. The presence of fry in the beginning of December indicates that some individuals may spawn in the fall, at least in some years. Since this river originates from springs, its ecological conditions may differ from those in neighboring streams.

The males of *E. edwini* are considerably larger than the females. The largest male examined is 48.8 mm long (FSU 3404, Ochlockonee R.) and the largest female

39.9 mm (FSU 2218, Apalachicola R.). In the subgenus *Hololepis* the females are larger or the sexes are of equal size. Males of *E. edwini* have much brighter colors than do the males of the species of *Hololepis*. These characters would seem to be of advantage only to territorial species. Winn (1958:172) stated that for the darters he studied: "The male is larger than the female in all the species studied that have a well-developed territory . . ." with the exception of two species in which sex recognition and territoriality are easily disrupted. Hubbs and Cooper (1936), Noble (1938) and Raney and Lachner (1943) have also noted correlations between territorial behavior and degree of sexual dimorphism in color, size, or structure in various groups of freshwater fishes.

Distribution—Etheostoma edwini is limited to the Coastal Plain from the St. Johns River in northeastern Florida, west to the Perdido River of western Florida and southern Alabama, and north into Georgia as far as the Fall Line (Fig. 9). It is replaced by its relative *E. okaloosae* in several small streams tributary to Choctawhatchee Bay (Fig. 10).

Neill (1957) listed *E. edwini* as one of a group of species that has not crossed the Suwannee Straits to penetrate peninsular Florida. However, since the range of *E. edwini* does extend into Marion and Putnam counties in the St. Johns drainage, *edwini* should be added to Neill's list of species that barely penetrate the peninsula.

On the basis of present knowledge it is impossible to determine where or when *E. edwini* differentiated. Its wide range east to west and northward to the Fall Line would indicate that it probably was in existence before the Pleistocene. Periodic encroachments of the sea must have forced it to retreat toward the headwaters, where it survived only in those larger river systems along the Gulf Coast that were not completely inundated by salt water. As sea-level receded, it moved downstream to occupy all suitable habitats, and surrounded the restricted range of *E. okaloosae*. At the

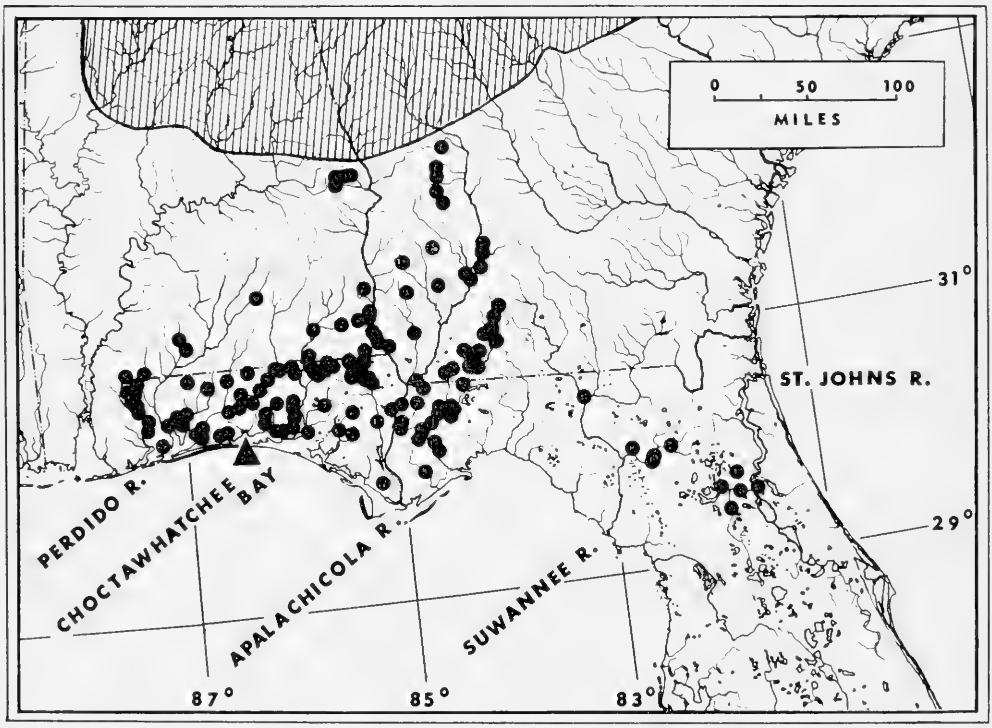


Figure 9. Distribution of *Etheostoma edwini* (dots) and of *E. okaloosae* (two streams at end of triangle) with reference to the Fall Line (taken from Fenneman, 1938 and 1946). (Based on specimens examined.)

present time, at several localities, streams occupied by *okaloosae* originate less than one mile from the headwaters of streams inhabited by *edwini,* but since the two species have never been taken together, there is no possibility of interbreeding under present conditions.

Geographic Variation — Since there is no appreciable variation in the number of pectoral rays (11-14, modes 13), condition of supratemporal canal (usually complete), number of interorbital pores (0-3, usually 2), or the squamation of the preopercle, opercle, and breast, summed frequency distributions have been presented in comparison with the data for *E. okaloosae* and the species of the subgenus *Hololepis* elsewhere (Collette, 1962: Tables 38-49).

The three easternmost populations (St. Johns, Suwannee, and Ochlockonee) have slightly more pored lateral-line scales ($\bar{x}$: 28.0, 29.9, 28.3) than the other populations ($\bar{x}$: 24.6 to 27.8) (Tables 2). This difference is correlated with the difference in number of total lateral-line scales. Populations in the St. Johns and Suwannee have higher means ($\bar{x}$: 38.1, 39.3); the westernmost population, the Perdido, also has a high mean (38.1); in the other populations the means vary from 37.1-37.6 (Table 4). The modal number of the scale rows above the lateral line is usually 3; the Suwannee and Ochlockonee populations have a mode of 4; the numbers are of about equal frequencies in the Flint system (Table 5). Most populations have a mode of 7 scale rows below the lateral line; the Suwannee population has a mode of 8; the westernmost populations, Pensacola Bay and Perdido drainage, have a mode of 6 (Table 5).

The modal number of first dorsal spines in most populations is 9 ($\bar{x}$:9.40 or less); the St. Johns and Suwannee populations again stand out with a modal number of 10 spines ($\bar{x}$: 9.69 and 9.55) (Table 6). The modal number of second dorsal rays is 11 in most populations; 10 in the Chipola and Choctawhatchee; 12 in the Chattahoochee population (Table 6). The modal number of anal soft-rays is 7 in all but two populations; the Chipola and Choctawhatchee populations have a mode of 6 rays (Table 8).

Most populations have modes of 10 preoperculomandibular pores but the three easternmost show a tendency toward fewer pores that is especially evident in the Ochlockonee population which has a mode of 9, thus resembling *E. okaloosae* (Table 7).

There is no evident geographic variation in extent of squamation except in the nape region. The eastern populations, through the Apalachicola, have the nape mostly I/PX-C/T to PX/X-T,* while the populations west of the Apalachicola (Choctawhatchee, Pensacola, Perdido) have modes of X T (Table 8).

Three slightly differentiated races of *edwini* may be distinguished: (1) an eastern race (St. Johns and Suwannee) with more pored lateral-line scales, more total lateral-line scales, and more dorsal spines; (2) an Ochlockonee race with a modal number of nine preoperculomandibular pores and a high number of pored lateral-line scales; and (3) a western race (Pensacola, Perdido, Choctawhatchee) having more scales on the nape. The Apalachicola River is inhabited by a population lacking any differentiating characters. If other characters are used, these races may be further subdivided. The Suwannee population has on the average more scale rows above and below the lateral line than does the St. Johns population. The Choctawhatchee population has fewer dorsal and anal soft-rays, and more scale rows below the lateral line than do the Pensacola and Perdido populations. Even the Apalachicola populations can be subdivided: the Chipola population has more total lateral-line scales and fewer second dorsal rays; the Chattahoochee population has more second dorsal rays; the Flint population has an intermediate number of second dorsal rays.

Specimens Examined—Full locality data are given only for collections from the St. Johns River (range extension) and for the type locality. For the other collections, drainage, state, county, and museum number are listed. Complete data for most of the collections are contained in Collette (1960).

St. Johns Drainage, Fla.—Marion Co.: UF 6963 (6 specimens, 32-43 mm. in standard length), small spring cr., 5¾ mi. NE Bruceville on Salt Springs Rd., Oct. 13, 1948. Oklawaha R. at Davenport Landing, 6-7 mi. upstream from mouth; UF 6968 (22, 22-38), Mar. 26, 1949; UF 6966 (7, 25-27), Oct. 2, 1949; and UF 6967 (2, 27-28),

* Squamation designation follows Collette, 1962. I, PX, X refer to the relative imbedding of the scales (imbedded, partially exposed, exposed respectively); C and T stand for cycloid and ctenoid.

Oct. 7, 1949. CU 35138 (1), Oklawaha R. just E of Eureka on Fla. 316, Mar. 27, 1960. Putnam Co.: Acosta Cr., 1.5 mi. N Welaka on Fla. 309; UF 6969 (4, 33-39), Dec. 28, 1946; and UF 6970 (1, 34), Mar. 24, 1947. UF 1911 (11, 25-37), 9 mi. W Palatka on Keystone Heights Rd., Mar. 24, 1947. UF 99 (1, 38), Little Orange Cr., 6 mi. S Johnson, May 22, 1947.

Suwannee Drainage, 131 specimens. Fla. — Alachua Co.: Santa Fe R. at Poe Springs, type locality: USNM 94684 (1, 33) and UF 2674 (2, 32-33), Feb. 8, 1928, paratypes; UF 209 (2, 33-38), Mar. 19, 1934; CU 10198 (1, 34), Apr. 6, 1940; UF 2910 (5, 29-35), May 8, 1947; UF 52 (13, 24-35), Oct. 13, 1947; UF 6964 (35, 22-38), July 27, 1947; UF 298 (6, 22-36), July 15, 1952. Columbia Co.: ANSP 69160; UMMZ 166571; TU 8441; UF 2676, 8091, 8087, 8106, 8100, 8095, 8074, 8125, 8078, 8131, 8115, 8116, 8126, 8122, 8123, 8030. Gilchrist Co.: UF 6960, 8028. Hamilton Co.: UF 2675. Suwannee Co.: FSU 1742. Union Co.: UF 2677.

Ochlockonee Drainage, 125 specimens. Ga.—Colquitt Co.: CU 17768; FSU 4447, 4069. Decatur Co.: FSU 2979, 3011. Grady Co.: CU 29759; FSU 2885, 2863, 4201, 4191, 4489. Thomas Co.: FSU 3990, 3969. Fla.—Franklin Co.: FSU 4865. Gadsden Co.: UF 6959; FSU 1657, 1637, 2524, 2205, 3404, 4431. Leon Co.: UF 6935; FSU 654, 5174, 3927. Liberty Co.: UMMZ 158182; UF 6965; FSU 228, 166, 2797, 3754, 3872. Wakulla Co.: FSU 3851.

Apalachicola River

Flint-Apalachicola Drainage, 110 specimens. Ga.—Calhoun-Dougherty cos.: UMMZ 164083. Decatur Co.: UF 595, 4493; FSU 1736, 2218. Dougherty Co.: CU 17322; UMMZ 163969, 164033; BU uncat. coll.; Early Co.: CU 18235. Miller Co.: CU 23794. Randolph Co.: CU 17752. Schley Co.: CU 29751, 29754. Seminole Co.: UF 4560. Sumter Co.: CU 29757. Taylor Co.: CU 21147, 29750. Terrell Co.: CU 15795. Worth Co.: UMMZ 164013; BU 2 uncat. coll. Fla.—Gadsden Co.: FSU 4029, 6272.

Chattahoochee-Apalachicola Drainage, 34 specimens. Ga.—Early Co.: CU 29745; FSU 6627. Ala.—Henry Co.: CU 17487; TU 2560; FSU 6572. Houston Co.: TU 2542, 2338, 2325. Lee Co.: UMMZ 128786; CU 15995; FSU 6649. Russell Co.: API 551; CU 15600, 13977; TU 10716; FSU 6586, 6655.

Chipola-Apalachicola Drainage, 125 specimens. Ala.—Houston Co.: CU 17676, 17667; TU 2406; UAIC 381. Fla.—Calhoun Co.: FSU 3814. Jackson Co.: UMMZ 158204, 163469, 163478; UF 6936, 6962, 4896; CU 29749; TU 127, 2292, 2380; FSU 1698, 2826, 4090, 4174.

Other Apalachicola Drainage, 19 specimens. Fla.—Calhoun Co.: TU 2042. Gadsden Co.: UF 4916, 4941. Gulf Co.: FSU 3298. Liberty Co.: UF 6971, 6972.

St. Andrews Bay Drainage, 4 specimens. Fla.—Bay Co.: FSU 552, 5766; TU 21449.

Choctawhatchee Bay Drainage, 197 specimens. Fla.—Holmes Co.: UMMZ 163502; CU 12116; TU 183, 1091, 1598, 2283, 2485, 2461, 2304, 2309, 20409; UMMZ 166327; FSU 1702, 1619, 2805, 4129, 4408, 6309. Holmes-Jackson Cos.: FSU 4168. Okaloosa Co.: FSU 5165, 6048. Walton Co.: TU 1073, 310; CU 21773; TU 1694, 1610, 22750; FSU 368, 4154, 5378, 5411, 6026, 6178, 6125, 6154. Washington-Bay Cos.: TU 3643. Washington Co.: FSU 5053. Ala.—Dale Co.: TU 4037, 2520. Geneva Co.: TU 1703, 14286, 16383. Houston Co.: CU 29758; TU 2512.

Pensacola Bay Drainage, 249 specimens. Ala.—Conecuh Co.: UMMZ 155518. Crenshaw Co.: TU 14194. Escambia Co.: TU 14177; UAIC 417, 420. Fla.—Okaloosa Co.: UF 6961, 3359; UMMZ 166239; FSU 4732, 4744, 4996, 6094, 6183. Santa Rosa Co.: UF 1456; UMMZ 155506, 166220, 165134; TU 4590, 20535; UF 7879; FSU 4670, 4940, 4950. Walton Co.: UMMZ 166246, 166351; FSU 6060.

Perdido Drainage, 76 specimens, Ala.—Escambia Co.: CU 15603; TU 14183, 16366, 23978, 21188. Fla.—Escambia Co.: UMMZ 134605, 166173, 166188; FSU 2958, 4799, 4761, 4726, 5956, 5843, 5799, 5862, 5880.

Etheostoma (Villora) okaloosae (Fowler)

Villora okaloosae—Fowler, 1941:242, 244 (original description), fig. 12 (holotype); Fowler, 1945:40, 294 (reference to holotype).

Etheostoma okaloosae — Carr and Goin, 1955:100 (characters and range mixed with that of *E. swaini*); Neill, 1957:185 (endemic in Florida panhandle); Yerger, 1960: 41 (validity of species, range).

Etheostoma swaini—in part; Bailey, Winn, and Smith, 1954: 143-144 *(E. okaloosae* synonymized with *E. swaini);* Moore, 1957:195 *(E. okaloosae* included under *E. swaini).*

Type—Holotype ANSP 69159; 24.4 mm female; Fla., Okaloosa Co., Little Rocky Cr., 7 mi. NE of Niceville on rt. 218 (now Fla. 285); June 20, 1939; F. Harper.

Since Fowler (1941:242) omitted counts of the cephalic pores, the following should be added to the original description (from examination of the holotype by the senior author): supratemporal canal complete, infraorbital with 8 pores, preoperculomandibular with 9 pores, both interorbital pores and coronal pore present. Counts of the lateral-line scales differ from Fowler's account of 30+3=33; there are 33+3=36 on the left and 35+2=37 on the right.

Comparisons—*Etheostoma okaloosae* is compared with *E. edwini* in Table 1. As previously indicated, it appears to be somewhat intermediate between *E. edwini* and *E. (Oligocephalus) swaini,* with which it has been confounded. *E. okaloosae* differs from *E. swaini* in the much shorter and more rugose genital papilla of the female (Fig. 7); in the higher arch in the lateral line, in the slenderer caudal peduncle, in the smaller number of unpored lateral-line scales, and in various details of pigmentation (Figs. 1-6); in having the preopercular margin at least slightly crenulate; and the prepectoral area at least partly scaled. *E. okaloosae* usually has 9 preoperculomandibular pores while both *E. edwini* and *E. swaini* usually have 10.

Coloration—On the first dorsal fin of the non-breeding female small to medium-sized melanophores are arranged in two or three irregular bands. The membrane of the soft dorsal fin is clear, with dark spots in four to six (usually four) rows. On the anal fin a few small melanophores are scat-

TABLE 1.
Comparison of Etheostoma edwini and E. okaloosae

Character	*E. edwini*	*E. okaloosae*
Branchiostegal membranes	Separate	Narrowly conjoined
Unpored lateral-line scales	4-18 (usually 7-15)	0-4
Pored lateral-line scales	20-34 (usually 23-32)	30-36 (usually 32-34)
Total lateral-line scales	34-42 (usually 36-40)	32-37 (usually 34-35)
Preoperculomandibular pores	Usually 10 (but often 9, and usually 9 in the Ochlockonee drainage)	Usually 9
Preopercular margin	Entire	At least slightly crenulate
First anal spine	Shorter than second	Longer than second
Red spots on body of males in life	Conspicuous	Lacking

tered, chiefly on the basal portion, occasionally on the rays. The rays of the pectoral fins are indistinctly outlined with pigment cells, which may also be scattered on the rays. The pelvic fins are similar to the pectoral fins. The caudal fin is indistinctly barred with five dark bands. The interradial membranes are clear or have a few melanophores on their distal portions. The belly and breast are usually immaculate white, but may possess a few brownish chromatophores. The cheek, throat, chin and branchiostegal membranes are usually white with numerous freckles formed by clusters of medium to large melanophores. All four orbital bars are developed. The supraorbital enters the eye. The suborbital is slightly to moderately developed and rarely enters the eye. The snout is almost uniformly pigmented. A single, median black spot is present at the base of the caudal fin and diffuse, brownish spots usually occur dorsal and ventral to the median spot. A well defined black spot covers one to two and one-half scales in the humeral region. Lateral-line scales are pigmented like the scales above and below, but the pores are unpigmented and appear as a thin, light-colored line. Excluding the humeral and basi-caudal spots, a series of 9-11 (usually 9) rectangular lateral blotches, wider than high, are located immediately below the lateral line. Dorsal spots or saddles are absent or indistinct; if present, two are on the nape, three under the first dorsal, two to four under the soft dorsal, and one, rarely, at

TABLE 2.
Number of pored lateral-line scales in Etheostoma edwini and E. okaloosae [1]

Species and Drainage	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	N	x̄
E. edwini																			
St. Johns							3	10	7	4	5	1						30	28.03
Suwannee							4	5	10	15	13	10	11	4	3			75	29.87
Ochlockonee			1	—	—	2	7	18	20	8	8	6	5	1				76	28.30
Apalachicola																			
Flint				1	4	9	12	27	14	7	—	2	2					78	27.00
Chattahoochee				1	3	5	6	3	2	3								23	26.09
Chipola	1	4	6	13	26	14	18	3	5	—	2	—	1					93	24.62
Total Apalachicola	1	4	6	15	33	28	36	33	21	10	2	2	3					194	25.75
West of Apalachicola																			
Choctawhatchee	1	1	2	8	13	27	40	25	12	3	1	—	1					134	25.79
Pensacola Bay					2	5	10	17	21	7	11	3	—	—	1			77	27.79
E. okaloosae							1	4	6	1								12	27.58
Perdido											3	4	19	27	19	6	2	80	33.01

[1] To eliminate developmental variation, counts on specimens below 22 mm. have not been used.

TABLE 3.
Number of unpored lateral-line scales in Etheostoma edwini and E. okaloosae

Species and Drainage	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	N	x̄
E. edwini																					
St. Johns								1	4	4	6	12	2	1	—	—	1			31	10.32
Suwannee					1	3	6	11	15	19	13	4	1	1						74	9.41
Ochlockonee					4	6	3	8	12	23	10	5	3	1	1					76	8.43
Apalachicola																					
Flint						2	—	1	10	16	19	13	7	4	3	2				77	10.16
Chattahoochee								1	1	7	3	8	1	2	5	2				30	11.13
Chipola								2	1	1	2	12	14	20	29	9	7	2		99	13.11
Total Apalachicola						2	—	4	12	24	24	33	22	26	37	13	7	2		206	11.72
West of Apalachicola																					
Choctawhatchee							1	—	2	7	19	42	29	20	15	4	1	3	1	144	11.81
Pensacola Bay					1	1	4	5	9	21	13	12	9	1	2					78	9.49
Perdido										3	4	4	1							12	10.25
E. okaloosae	5	33	26	12	4															80	1.71

the origin of the first caudal ray. The sides of the body are marked with longitudinal rows of dark dots, which extend from head to tail. There are two or three rows above and three to five rows below the lateral line. The center of each scale bears a pigment spot which is darker than the remainder of the scale. The genital papilla is usually immaculate, but occasionally a patch of melanophores appears posterior to its base. In breeding females there is a general increase in the number of small melanophores over most of the body and fins, and the submarginal orange-red band in the first dorsal becomes brighter. Figure 2 illustrates a female in breeding condition.

In the non-breeding male the pigmentation of the pectoral fins, orbital bars, snout, basi-caudal spots, humeral spot, lateral blotches, and longitudinal rows of dots is very similar to that of the female. Melanophores are more numerous on the first dorsal, anal, pelvic, and caudal fins. One-half to seven-eighths of the anal and pelvic fin membranes are darkened by these melanophores. The second dorsal fin is dark with light spots, just opposite to the condition in the female. The belly, breast, cheek, throat, and branchiostegal membranes possess numerous small melanophores. The genital papilla is immaculate, except for a few small melanophores around the base posteriorly.

The pigmentation of the breeding male is characterized by an enormous increase in the number of small melanophores over the entire body and fins. The submarginal orange-red band on the first dorsal fin is more vivid. Numerous melanophores are concentrated between spines VIII and IX to form two dark blotches. The anal fin is darkened by numerous melanophores, and one or two blotches are frequently evident between the first and second or between the second and third soft-rays. Melanophores are present on the basal one-third to one-half of the pectoral fin membranes. The pelvic fins are dusky, with an occasional blotch. The barring on the caudal fin may be indistinct, and the entire membrane is speckled with tiny melanophores. The presence of more melanophores on the lateral line renders the pores less distinct than in non-breeding individuals. The lateral blotches usually become more promi-

TABLE 4.
Total number of lateral-line scales in Etheostoma edwini and E. okaloosae

Species and Drainage	32	33	34	35	36	37	38	39	40	41	42	N	x̄
E. edwini													
St. Johns						7	18	6	1	1		33	38.12
Suwannee					2	1	13	27	22	8	3	76	39.34
Ochlockonee				5	25	44	5	4	1			84	36.77
Apalachicola													
Flint			3	5	13	30	24	8	1			84	37.13
Chattahoochee					4	12	4	3	2			25	37.48
Chipola					9	40	46	15	.	2		112	37.67
Total Apalachicola			3	5	26	82	74	26	3	2		221	37.44
West of Apalachicola													
Choctawhatchee				1	15	53	46	14	5	2		136	37.59
Pensacola Bay			1	1	11	25	29	10	3			80	37.53
Perdido						5	4	4	....	1		14	38.14
E. okaloosae	1	6	24	34	13	1						79	34.70

TABLE 5.
Number of scale rows above and below the lateral line in Etheostoma edwini and E. okaloosae

	Above the lateral line						Below the lateral line								
Species and Drainage	2	3	4	5	N	x̄	5	6	7	8	9	10	11	N	x̄
E. edwini															
St. Johns		16	5		21	3.24		2	15	4				21	7.10
Suwannee		22	40	1	63	3.67		4	11	24	20	4		63	8.14
Ochlockonee		15	56	5	76	3.87		10	40	23	3	1		77	7.29
Apalachicola															
Flint		38	39	2	79	3.54		21	42	15	1			79	6.95
Chattahoochee	2	13	10		25	3.32	1	6	15	3				25	6.80
Chipola		44	20		64	3.31	1	8	19	20	11	3	1	63	7.71
Total Apalachicola	2	95	69	2	168	3.42	2	35	76	38	12	3	1	167	7.22
West of Apalachicola															
Choctawhatchee	2	86	50		138	3.35	1	43	75	19				138	6.81
Pensacola Bay	1	58	23		82	3.27	4	42	29	6	1			82	6.49
Perdido		12	2		14	3.14		10	3	1				14	6.36
E. okaloosae		10	70		80	3.88	5	74						79	5.94

nent, increase in size, become deeper than wide, and extend above the lateral line to within one or two scale rows of the dorsal fin, as well as below the lateral line. In some specimens these lateral blotches are barely discernible. The darkened appearance of the fish in breeding color renders the longitudinal rows of dots on the sides of the body less distinct. Melanophores are formed on the margins of the upper and lower surfaces of the genital papilla, as well as on the basal portion. Other areas are similar but darker than in the non-breeding male. Figure 5 shows the pattern of a male in breeding condition.

In life, the colors are far less striking than in *E. edwini.* The general color of the adult male is reddish-brown to yellow-brown, becoming lighter on the lower flanks and yellow-white to dusky white on the throat. An olive-green cast is especially prominent below the lateral line and on the caudal peduncle. The areas around the bases of the pectoral and pelvic fins are golden-yellow. The margin of the first dorsal is dusky with a bright submarginal orange-red stripe. The basal two-thirds of the fin is dusky. The membranes of the dorsal and pelvic fins are dusky with a papilla of a typical female of *E. okaloosae* is fin is usually barred with vertical bands of light and reddish brown, the dark bands are the broader. Females generally resemble the males, but the fins and body are lighter, and the orange-red stripe in the spinous dorsal is less bright.

Genital Papilla—In breeding females, the genital papilla is very similar to that of *E. edwini,* except that the tube is somewhat longer. Misuse of an air jet or excessive probing will create the appearance of free villi, as in *E. edwini.* The genital papilla of a typical female *E. okaloosae* is compared with that of *E. edwini* and *E. swaini* in Figure 7.

Development—Development in *E. okaloosae* is probably similar to that in *E. edwini.* Two 15 mm specimens have only 22 and 28 pored lateral-line scales while all specimens over 20 mm long have at least 32. Both 15 mm specimens have incomplete supratemporal canals, ten specimens 17.5-20.0 mm long are equally divided between incomplete and complete, and almost all specimens over 20 mm long have complete canals.

Habitat—The terrain in that portion of Okaloosa and Walton counties inhabited by *E. okaloosae* is sandy, deeply dissected, and covered by pines, scrub oaks and mixed hardwoods. Stream valleys are marked by the presence of alder, titi, wax myrtle, black-gum, and pines and oaks. The clear streams are small to medium-sized, with a moderate to swift current. The bottom consists chiefly of clean, light-colored sand, with some mud and detritus around patches of vegetation in areas with reduced circulation. Depths vary from six inches to four feet, and widths from five to 40 feet. The water is nearly neutral or slightly acid (pH 6.6-6.9). Vegetation is absent in some areas, sparse and scattered where clumps of bullrushes *(Scirpus etuberculatus)* are found, or dense with *Mayaca, Orontium, Nuphar, Nitella,* and *Potamogeton capillaceus.* The red alga, *Batrachospermum,* is present throughout the year, and occasionally forms thick concentrations. Other common fishes in these streams included: *Ichthyomyzon gagei, Esox americanus, Erimyzon sucetta, Notropis hypselopterus, N. petersoni, Hybopsis harperi, Noturus leptacanthus, Gambusia affinis, Aphredoderus sayanus, Micropterus salmoides, Ambloplites rupestris ariommus, Lepomis punctatus,* and *Percina nigrofasciata.*

Habits—The two species of darters in this stream system occupy different niches. *Etheostoma okaloosae* is most common around clumps of the bullrush *(Scirpus)* over a clean sandy bottom in areas with reduced current. It is usually in water from six inches to two feet deep and has rarely been collected at depths of three feet or greater. Few specimens have been taken from sections of the stream where *Mayaca* and other aquatic plants provide dense cover. Apparently this species avoids the large amounts of silt and organic sediments that accumulate in these heavily vegetated areas.

The other darter, *Percina nigrofasciata,* frequents the swifter areas of the stream, in the channels and deeper pools where vegetation is sparse or absent, but where logs or brushy cover are available. Only occasionally is it taken in areas with little water movement.

E. okaloosae was observed spawning by W. Bruce Walden and Ray Birdsong in Tom's Creek on March 25, 1961, in the swiftest part of the stream in water 12 to

TABLE 6.
Number of first dorsal spines and second dorsal rays in Etheostoma edwini and E. okaloosae

	First dorsal spines						Second dorsal rays						
Species and Drainage	8	9	10	11	N	x̄	9	10	11	12	13	N	x̄
E. edwini													
St. Johns		9	16	1	26	9.69		1	19	6		26	11.19
Suwannee	1	27	33	1	62	9.55		6	34	20	2	62	11.29
Ochlockonee	2	47	34	1	84	9.40		18	59	7		84	10.87
Apalachicola													
Flint	9	53	17		79	9.10	1	14	39	23	2	79	11.14
Chattahoochee	6	17	2		25	8.84	1	4	8	11	1	25	11.28
Chipola	5	44	15		64	9.16	4	35	22	3		64	10.38
Total Apalachicola	20	114	34		168	9.08	6	53	69	37	3	168	10.87
West of Apalachicola													
Choctawhatchee	15	98	22	1	136	9.07	1	72	58	6		137	10.50
Pensacola Bay	14	60	9		83	8.94		22	49	10	2	83	10.90
Perdido		13	1		14	9.07		3	8	3		14	11.00
E. okaloosae	2	31	4		37	9.05		3	32	40	5	80	11.59

TABLE 7.
Number of pores in the infraorbital and preoperculomandibular canals in Etheostoma edwini and E. okaloosae

	Infraorbital pores							Preoperculomandibular pores					
Species and Drainage	6	7	8	9	10	N	x̄	8	9	10	11	N	x̄
E. edwini													
St. Johns			12	3		15	8.20	1	7	11	1	20	9.60
Suwannee		2	38	2	1	43	8.05	1	26	33	1	61	9.56
Ochlockonee		4	75	4		83	8.00	3	70	5		78	9.03
Apalachicola													
Flint		8	75	1		84	7.92	2	14	62	1	79	9.78
Chattahoochee		1	21	2		24	8.04			24		24	10.00
Chipola		5	55	5	1	66	8.03		2	57		59	9.97
Total Apalachicola		14	151	8	1	174	7.98	2	16	143	1	162	9.88
West of Apalachicola													
Choctawhatchee	1	6	124	6	1	138	8.00	1	24	108	4	137	9.84
Pensacola Bay		12	69	1		82	7.87	3	18	54		75	9.68
Perdido		1	13			14	7.93		2	12		14	9.86
E. okaloosae		2	39			41	7.95	1	46	4		51	9.06

TABLE 8.
Number of anal soft rays and squamation of nape in Etheostoma edwini and E. okaloosae

	Anal soft-rays							Nape squamation*				
Species and Drainage	5	6	7	8	9	N	x̄	I-C	I/PX-C/T	PX-T	PX/X-T	X-T
E. edwini												
St. Johns		4	14	3		21	6.95					
Suwannee		13	29	3		45	6.78	1	6	2	1	
Ochlockonee	1	31	43	3		78	6.62		7	1	3	
Apalachicola								1	5	7	2	
Flint		8	41	29	1	79	7.29	1	15	3		
Chattahoochee	1	4	13	6	1	25	7.08		7	6	1	
Chipola	1	34	25	3	1	64	6.52		1	3	5	2
Total Apalachicola	2	46	79	38	3	168	6.96	1	23	12	6	2
West of Apalachicola												
Choctawhatchee	2	70	62	4		138	6.49		1	—	1	7
Pensacola Bay		31	49	3		83	6.66		1	1	—	9
Perdido			10	4		14	7.29					3
E. okaloosae		8	65	7		80	6.99	5	26	1		

* See Text, page 223.

18 inches deep over a sandy bottom at the edge of clumps of *Nitella.* The male mounted the back of the female. Then, while remaining in a horizontal position, both moved forward a short distance, paused, and moved again. The pair spawned a few moments later, while lying side by side. Both male and female rotated their bodies slightly until their ventral surfaces were opposed, and quivered for several seconds. Examination of the vegetation revealed that several eggs had been deposited singly within the branches of *Nitella.* The vegetation and eggs were taken to the laboratory where one 5.5 mm larva hatched on March 27.

Several mature adults captured on March 25 were placed in aquaria in the laboratory. Although spawning behavior was not witnessed, six eggs were discovered on April 1, individually attached to masses of *Nitella.*

This spawning behavior is quite different from that observed by Winn (1958: 173) for other darters, where species with flattened, flower-like genital papillae demonstrated a complex, inverted spawning behavior and laid their eggs on the underside of rocks.

Examination of adult females collected in January, March, August, September, and October revealed that large ova were present from late January to early August. The smallest young (15 mm SL.) in existing collections were taken August 11 and September 9. Breeding coloration appears to be most highly developed in January and March collections. It seems likely that this species has a rather long breeding period, probably from midwinter through early summer. The onset of spawning may vary from year to year, for temperature conditions in January and February in western Florida are mild in some years and severe in others.

Males are larger than females but the difference appears to be less than in *E. edwini.* The largest male of *okaloosae* examined is 43.5 mm long and the largest female 40.0 mm (both FSU 6078, Tom's Cr.). Differences in sexual coloration are likewise less pronounced. Although these differences in size and coloration are slight, limited observations both in the field and in aquaria indicate that this species exhibits territorial behavior to some extent. Studies on the reproductive behavior of both species of *Villora* are being continued by the junior author.

Distribution—*E. okaloosae* is confined to those streams of Okaloosa and Walton counties in west Florida that empty into Rocky and Boggy bayous near the western end of Choctawhatchee Bay, in the vicinity of Niceville. From east to west these streams are known as Rocky Creek, Lone Creek, Swift Creek, Turkey Creek, Tom's Creek, and their various tributaries. Although several of the streams inhabited by *E. okaloosae* originate less than a mile from the headwaters of streams inhabited by *E. edwini,*

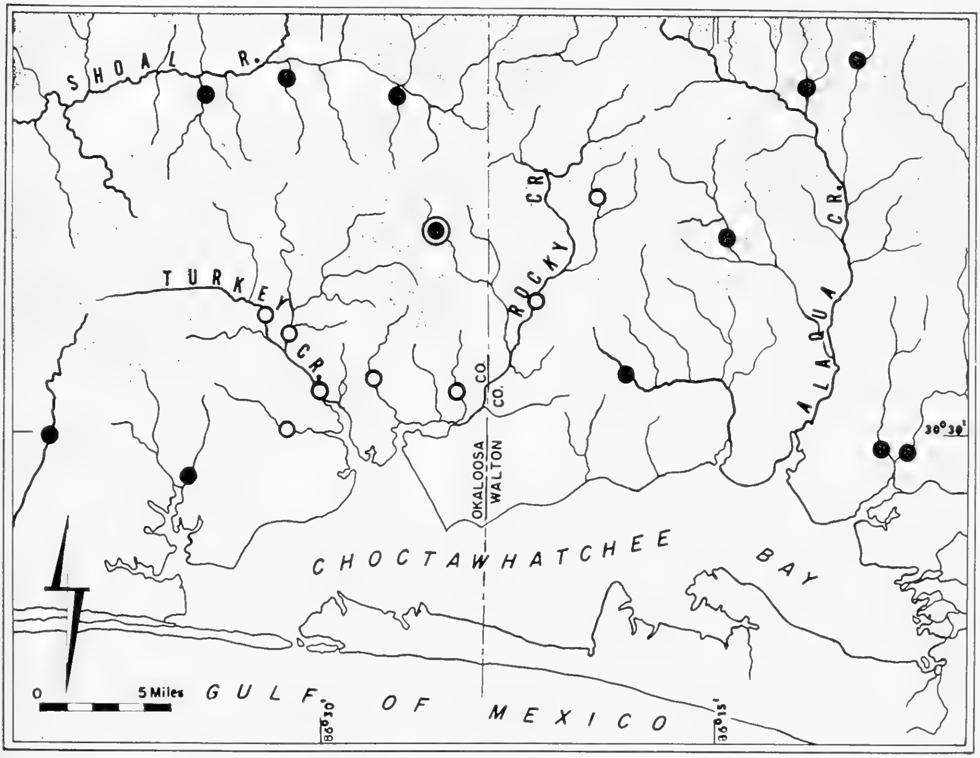


Figure 10. Distribution of *Etheostoma edwini* (dots) and of *E. okaloosae* (open circles; encircled dot is the type locality) in the Choctawhatchee Bay region of western Florida. The stippling indicates the area of the hypothetical Pleistocene peninsula or island (see text) above the 150-foot contour line.

the two species are allopatric. The greatly restricted range of *E. okaloosae* is encircled by the range of the much more widely distributed *edwini* (Figs. 9 and 10). The collection sites for the specimens examined in this study together with the distribution of adjacent populations of *E. edwini* are shown in Fig. 10.

A slight lowering of sea level during Pleistocene glacial stages would have resulted in the conjoining of all the creeks inhabited by *E. okaloosae* into a single stream system originating in a highland area a few miles north of the Gulf of Mexico. The stippling on Fig. 10 indicates the land areas above the 150-foot contour line, which according to MacNeill (1957), is the maximum height to which sea-level rose during Pleistocene interglacial stages. It is likely, then, that during maximum inundation of the Coastal Plain, a peninsula with a very narrow connection to the mainland, or possibly an island, with freshwater drainage would have remained above the sea, and served as a refuge for *E. okaloosae* and other freshwater and terrestrial species. Cooke (1945) postulated a maximum rise of the sea to the present 270-foot contour. Even if this were the case, some land would have been emergent, for elevations up to 294 feet occur along this high ridge. Under these conditions, an island would have been cut off from the mainland to the north. Since erosion has continuously lowered this land mass, elevations in the Pleistocene were undoubtedly considerably higher, and consequently the highlands would have been greater in area than at present.

During one of the oscillations of sea-level in the Pleistocene, the *Villora* population in the stream system now inhabited by *okaloosae* may have been cut off from other *Villora* populations in the Choctawhatchee River drainage. During this period of isolation, a series of mutations may have occurred and may have spread rapidly through this small inbred population. Since the headwaters of this stream system would have remained above the sea, differentiation might have been completed prior to the subsequent lowering of sea-level to the point where the differentiated population may again have come in contact with older *Villora* populations. In the meantime, the ancestral *Villora* stock would have been forced into the headwaters of adjacent streams, and with the lowering of sea-level, could have moved downstream into newly emerged habitats to the west, north, and east (in the Yellow, Shoal, and Choctawhatchee rivers), and thereby have surrounded the range of *E. okaloosae.*

TABLE 9.

Proportional measurements of adults of Etheostoma edwini and E. okaloosae in thousandths of standard length

Catalog Number, FSU	*E. edwini* 4799 (5 females) 6178 (3 males) 4950 (2 males)		*E. okaloosae* 5135 (3 males, 1 female) 5138 (2 males, 1 female) 6214 (3 females)	
Measurement	Range	x̄	Range	x̄
Standard length, mm	29.7 - 43.6	36.3	28.7 - 39.9	33.4
Head length	256 - 302	280 6	268 - 323	292.6
Greatest depth	197 - 228	212.7	200 - 235	215.2
Least depth	95 - 115	105.8	109 - 153	123.5
Body width	128 - 157	143.4	131 - 164	146.3
Caudal peduncle length	280 - 350	299.7	245 - 272	260.2
Highest dorsal spine	109 - 158	131.3	106 - 135	123.2
Highest dorsal soft-ray	140 - 174	153.0	137 - 153	145.7
Caudal length	221 - 249	231.3	205 - 221	213.4
First anal spine	71 - 93	79.6	85 - 120	94.5
Second anal spine	76 - 95	86.7	70 - 105	84.4
Highest anal soft-ray	135 - 194	151.0	132 - 155	142.8
Longest pectoral ray	241 - 269	255.4	246 - 273	255.1
Pelvic length	196 - 212	206.4	194 - 223	205.7
Pelvic base	26 - 35	29.6	30 - 37	32.8
Interpelvic distance	11 - 17	14.5	12 - 18	14.6
Head depth	165 - 185	162.8	163 - 186	172.1
Head width	139 - 167	155.0	151 - 173	162.2
Snout length	41 - 60	50.2	48 - 64	57.6
Orbit length	71 - 90	79.5	72 - 81	75.9
Fleshy interorbital width	51 - 60	55.0	46 - 62	55.4
Upper jaw length	70 - 79	74.7	64 - 88	80.2
Distance from tip of jaw to union of gill membranes	104 - 139	117.9	137 - 161	150.0
Distance from union of gill membranes to insertion of pelvic fin	146 - 191	165.1	135 - 165	150.5

However, a comparison of primitive and specialized characters in the two species of *Villora* indicates that *E. okaloosae* is the more primitive species. It has a more nearly complete lateral line and a deeper body, the genital papilla of the breeding female is not quite as specialized, and the male lacks red spots on the body. If it evolved at an earlier date than *E. edwini,* it is reasonable to assume that it formerly occupied a wider range, which was later restricted by changes in sea-level during the Pleistocene, and that today it persists only as a relict. Its presence in only one stream system tributary to Choctawhatchee Bay is definitely believed to be related to the Pleistocene peninsula or island conditions described previously.

The unusual distributional patterns of many plant and animal species in the Florida panhandle have been discussed by Neill (1957). The occurrence of a number of endemics and "northern disjuncts" in Okaloosa and Walton counties on or in proximity to the Pleistocene peninsula or island emphasizes the unusual ecological conditions prevailing there. Recent unpublished investigations have added several species to this list. Further investigations on these problems are in progress by the junior author.

Specimens Examined—Since *E. okaloosae* was heretofore known only from the type locality, complete data are given. All series are from the Choctawhatchee Bay drainage system of western Florida.

Rocky Creek—Walton Co.: FSU 6101 (6 specimens, 24-32 mm. in standard length), E. Rocky Cr., 11.2 (airline) mi. NE Niceville, on Eglin Air Force Base rd. 201, Jan. 24, 1960. FSU 6032 (2, 27-30), Rocky Cr., 7.75 (airline) mi. NE Niceville on EAFB 200, Jan. 24, 1960. Okaloosa Co.: Little Rocky Cr., 7.5 mi. NE of Niceville on Fla. 285, type locality; ANSP 69159 (1, 24), holotype, June 20, 1939; FSU 6045 (25, 23-39), Jan. 23, 1960. UF 6937 (2, 23), Big Rocky Cr. near Niceville, Nov. 13, 1938.

Lone Cr.—Okaloosa Co.: FSU uncat. coll., Lone Cr., 4 mi. E Niceville, Feb. 4, 1961.

Swift Creek—Okaloosa Co.: FSU 5158 (7, 26-40), Swift Cr., 1.2 mi. NE Niceville on Fla. 285, Sept. 9, 1959.

Turkey Creek-Okaloosa Co.: FSU 5135 (26, 15-35), Turkey Cr., 5.4 mi. NW Niceville on EAFB 232, Sept. 9, 1959. Tenmile Cr., 3.5 mi. NW Niceville on Fla. 85; USNM 196136 (10, 23-39), Oct. 19, 1960; TU 18364 (3, 27-34), May 31, 1958. Turkey Creek, at W edge of Niceville on Fla. 85; FSU 1937 (1, 28), May 24, 1953; FSU 6214 (21, 15-33), Aug. 11, 1959; TU 4716 (1, 25), Nov. 14, 1952.

Tom's Creek - Okaloosa Co.: Tom's Creek approx. 2 (airline) mi. W Valparaiso on Fla. 85; FSU 6078 (50, 30-44), Jan. 25, 1960; FSU 6138 (11, 31-43), Mar. 26, 1960; FSU 6748 (10, 25-40), Oct. 19, 1960; TU 2079 (3, 28-38), May 26, 1951.

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VI. ABSTRACT

The subgenus *Villora* Hubbs and Cannon is removed from *Hololepis* Putnam where it has been placed by some authors. This decision is based upon the belief that *Villora* constitutes a separate phyletic line running somewhat parallel to *Hololepis* and probably originating from the subgenus *Oligocephalus.* Important differentiating characters of *Villora* include lack of breeding tubercles, moderately arched lateral line, genital papilla of breeding female a low tube crowned with villi, a prominent humeral spot and a somewhat incomplete lateral line.

Variation in a number of meristic characters between populations of *Etheostoma (Villora) edwini* (Hubbs and Cannon) is considered. Three slightly differentiated races of *edwini* may be distinguished using lateral-line scales, preoperculomandibular pores and squamation of the nape. This species occurs in nothern and western Florida and below the Fall Line in southwestern Georgia and in Alabama.

E. okaloosae (Fowler) is resurrected from the synonomy of *E. swaini* (Jordan). It differs from *E. (Oligocephalus) swaini* in number of preoperculomandibular pores, shape of the genital papilla of breeding females, arching of the lateral line, squamation of the breast, nape, and prepectoral area, and in habitat. Several of these characters show that *E. okaloosae* is most closely related to *E. edwini* and belongs to the subgenus *Villora.* Possible reasons for the isolation of *E. okaloosae* in several small streams tributary to one arm of Choctawhatchee Bay are discussed and it is concluded that this is a relict species.

Photographs of both species and figures of the genital papillae are presented along with those for *E. swaini.* Discussions of habits, habitat, and relationships are included.

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TULANE STUDIES IN ZOOLOGY

TULANE STUDIES IN ZOOLOGY

Volume 9, No. 5 April 16, 1962

VIOSCA MEMORIAL NUMBER

TULANE UNIVERSITY
NEW ORLEANS

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TULANE STUDIES IN ZOOLOGY

Volume 9, No. 5 April 16, 1962

CONTENTS

PERCY VIOSCA, JR. — NATURALIST

The death of Percy Viosca, Jr. on August 27, 1961 marks the passing of one of the last of America's great naturalists. Viosca, unlike the vast majority of today's highly specialized biologists, was a man whose uncanny ability to observe and interpret all manner of diversified natural phenomena, and whose dedicated interest to the whole glorious world of the great outdoors, ranks him inevitably with such great naturalists as Audubon, Rafinesque, Say, Agassiz, Cope, and Jordan.

Born in New Orleans sixty-nine years ago, Viosca was one of a large family whose modest means early instilled in him as a youth, and in his brothers and sisters, the knowledge that all would have to work hard for what they wanted in life. Percy and his brother, Civil District Judge René Viosca, knew that they would go to college, and they did by the hardest.

From early childhood, these two with family and friends, had fished and seined for the shrimp and crabs that are such an important part of a Louisianian's diet. Thus, naturally the two turned their love of the outdoors to practical application. For many long years the two brothers arose before dawn, bicycled from their home on what was then the swampy eastern fringe of New Orleans, to the shore of Lake Pontchartrain. There they would fish and seine with nets they had knited themselves. From this early morning activity the next stop was the French Market where their catch was sold to Covington and Mandeville resort owners who catered to the vogue of steamboat excursionists. Each day, by the time the brothers arrived for classes at Tulane University, they had completed, in addition to their commercial fishing chores, thirty to forty miles of rough peddling over cobblestone and other rough streets.

Such was the spirit of Percy Viosca, the youngster and the man, an ebullient personality, indefatigable despite the handicap of a bad knee suffered in an automobile accident in his young manhood. He could never be slowed down. Under the guidance of George E. Beyer, then chairman of biology at Tulane University, Viosca's restless energy was channelled into a formal morphological and taxonomic knowledge of the local animals and plants, and most importantly their ecology. Later his interests turned primarily to the fields of herpetology and marine biology in which he received his widest recognition.

At Tulane in 1913 he was awarded the B.S. degree, and then instructed undergraduate classes under Beyer for two years. He received the M.S. degree in 1915. At the age of 23 in 1915, seeing the practical possibilities of commercially sending Louisiana's vast store of animal life all over the world, he established the Southern Biological Supply Company (still in existence), and was its president many years.

From here on Viosca's life was a potpourri of interests and activities. In 1915, almost simultaneously with his first commercial venture, he became curator of reptiles, amphibians and fishes at the Louisiana State Museum. In 1917 he added to these other activities the duties of biologist for the Louisiana Department of Conservation. This associaton with the state lasted until his death, although it was never permanent. He was in and out dependent upon the turbulent clime of Louisiana politics. During one short period, from 1923 to 1926, he returned to Tulane as an instructor. Coincident with this he served as entomologist for the New Orleans Board of Health in 1923 and 1924. In 1939 he conceived, organized, and directed Ganivory Crafts, which was a small business carried on in his home and employing several workers fashioning clever costume jewelry and other artistic articles from Louisiana garfish scales. For a few years, beginning in 1942, he worked independently as a consulting biologist. This work was mostly for industries having stream pollution problems. When he quit this and last returned to the Louisiana Wildlife and Fisheries Commission as its marine biologist he admitted that although this venture had been lucrative it involved entirely too much of his time serving as an expert witness in the courts.

Being in a conservation department of a state that year by year was becoming more conscious of its potential of vast untapped biological resources, Viosca had ample opportunity to delve at length into many problems. His research interests ranged greatly, he

PERCY VIOSCA, JR.
(1892 - 1961)

was not known as a specialist. His diligence and constant search for truth was all the more amazing in view of the fact that his position as biologist in the state conservation effort was one that all too often had been awarded as a political plum.

Describing himself as a "field naturalist" he was an observer, not a mere collector. He was widely recognized as an authority on the biology of shrimp, crawfish, oysters, fish, and mosquitoes, but his first love was for frogs and salamanders. Viosca poured out countless articles for scientific journals, conservation magazines, and newspapers. Despite this productivity those who bemourn his passing know that he stored countless treasures of natural observations in his fertile brain that are forever lost. As one example, he was particularly fascinated by the incredible migration of the fragile monarch butterflies and the timing of their departure from the northernmost part of the country early enough that their arrival in Louisiana coincided with the arrival of the non-stop-flying geese. Unfortunately these data remain unpublished, although popularly circulated via news interviews.

Viosca was also an authority on the wild flowers of Louisiana; particularly the ecology and hybridization of irises which reach a breathless profusion of beauty in the southern part of the State. In 1935 he published a lengthy article straightening out the taxonomic jumble in which hitherto a multitude of species had been described in Louisiana. After years of crossbreeding and countless observations in the wetlands his deduction that there were only four species of Louisiana irises was surprising, but remains undisputed by taxonomic botanists.

The reasons for the reduction of the last several years' take of commercial shrimp in the Gulf of Mexico was a far-reaching research program he was engaged in at the time of his death. This study, when completed, will stand as yet another monument to his perception. Ironically, had his data on the life history of the white shrimp, published in 1920, been recognized then, the shrimp decline might well have been avoided and the shrimp fishery could have been forty years ahead of the present situation.

Although Percy Viosca was never able to afford a pursuit of the Ph.D. degree, he had been initiated into Phi Beta Kappa at Tulane. In the year of his death he received two honors that he was deeply proud of. He was selected "Conservationist of the Year" by the Louisiana Outdoor Writers Association, and he was proclaimed "Tulane Biologist of the Year" by the Department of Zoology at Tulane. He was always in demand for lectures before scientific societies, sportsman's groups, and garden societies; all of his lectures were profusely illustrated with slides made from pictures he had taken in the field with a variety of cameras. Of himself, he often said that he received his highest degree from the "University of Hard Knocks" for studies in the unique wilds and waters of the Gulf Coast, but particularly in the vicinity of Lake Pontchartrain.

Raconteur par excellence, one of his typical stories involved an incident in 1948 (when he was 56) in which he wrestled a five-foot alligator in the Honey Island Swamp near New Orleans for the benefit of a visiting biologist from Holland. The visitor had expressed a desire to see a Louisiana alligator, and as Viosca put it, "Rather than take him to Audubon Park I thought he would enjoy seeing them in their native haunts. After waiting several hours for a large enough alligator we finally spotted one. I was so glad that I jumped out of the boat, landed on his back, and caught him between the shoulders with both hands so he couldn't bite me."

Despite his serious scientific dedication, Viosca's personal spirit and gaiety always showed through as when he won a crawfish eating contest at the old French Market in New Orleans; he was triumphant, although some of his irate competitors claimed that sometimes he ate shells and all! Just before his long drawn out and painful death, an amusing little personal vignette was revealed about the true story of the Louisiana crab that won the world's speed championship race. Favored to win was the personal entry of the Governor of Maryland, but Viosca had selected a fleet-footed male fiddler crab, fastest of the thousands scurrying at night across the sand beach of Grand Isle. The race was not even a contest for Louisiana's standard bearer.

The writer, too, remembers countless examples illustrating both the warm, gentle man that Viosca was, and the biologist. On a fishing trip in Lake Pontchartrain when I was a stripling some twenty years ago, he claimed he could catch just about anything he wanted to with his casting rod simply by adjusting the length of the leader, distance from hook to sinker, and variations of these. I had been for some time without even a nibble and questioned these claims. Twice in succession he made the necessary adjustments, stated what he would catch and did so: a gaff-topsail catfish and a speckled trout. Dismayed, I demanded a sheepshead. He said, "This is not just the right place; how about a croaker?" And you can guess the result—a beauty of a croaker!

Viosca for several years had a radio program, a jambalaya of Louisiana nature lore, current to the season, accurate as to content, and spliced with his inimitable personality. Typically Viosca, the program signature was a series of frog calls recorded by him in the Louisiana wetlands.

The list of his many technical and popular articles is an impressive one. In addition he wrote several books, the more important of which were *Louisiana Out-of-Doors* (1933) and *Pondfish Culture* (1937). He held membership in a number of scientific societies, took the responsibility of an officer in several, and was a Fellow in the AAAS since 1933. He was vice-president of the American Society of Ichthyologists and Herpetologists (1939), vice-president (1947) and president (1948) of the Louisiana Academy of Sciences, president of the New Orleans Botanical Society (1955), and served on important committees of a number of other biological organizations.

As an indication of the esteem in which he was held, several animals were named for him by his colleagues. These include: the salamander *Pseudotriton ruber vioscai* Bishop, 1928; the turtle *Pseudemys vioscana* Brimley, 1928 (now relegated to synonomy with *P. floridana mobilensis*); the shrimp *Solenocera vioscai* Burkenroad, 1934; and the crawfish *Procambarus vioscai* Penn, 1936. Viosca also named a few species. These are: the frog *Hyla avivoca* (1928); the rockbass *Ambloplites ariommus* (1936); and the salamanders *Necturus alabamenis, Necturus beyeri, Necturus lodingi* (1937); and *Necturus louisianensis* (1938).

Percy Viosca, Jr. will long be remembered, not only by those with whom he personally shared his knowledge of biology, but by innumerable others who must consult his publications. Because of his contributions toward a knowledge of the biology of the Gulf Coast area, and as an inspiration to students, this special issue of *Tulane Studies in Zoology* is dedicated to him.

GEORGE HENRY PENN,
Department of Zoology,
Tulane University,
New Orleans

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(with a few annotations)

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Department of Zoology, Tulane University, New Orleans, Louisiana

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OBSERVATIONS ON THE BIOLOGY OF THE LEECH *PHILOBDELLA GRACILE* MOORE IN SOUTHEASTERN LOUISIANA

PERCY VIOSCA, JR.[1]

In Louisiana *Philobdella gracile* is found almost exclusively in the cypress and tupelo swamps and freshwater marshes. It also occurs in the bayous, canals, and ditches that are the natural or artificial drainage channels of these regions. As *P. gracile* does not remain permanently associated with its hosts (or, victims), observations in the field are difficult unless numbers of the hosts are handled. The water where this species occurs is generally of a dark or reddish-brown transparency, hence these black leeches when swimming or stationary are difficult to see. The following notes are the result of an accumulation of observations and experiences extending over a period of about ten years.

Hosts.—Individuals of this species have been taken by the writer attached to or feeding on quite a number of amphibians and reptiles, including the frogs *Rana catesbeiana, R. grylio, R. clamitans*, and *R. pipiens,* the alligator, the water snakes *Ancistrodon piscivorous, Natrix cyclopion,* and *N. sipedon fasciatus,* and the turtles *Chelyrda serpentina* and *Kinosternon subrubrum hippocrepis.* This does not mean that this leech shows a preference for the species named above; these animals are the most abundant members of the aquatic society with which this leech is associated in southeastern Louisiana. If preference is shown at all it is for the bullfrog, *Rana catesbeiana.* This may be more apparent than real, however, the writer having caught, purchased, or otherwise handled greater numbers of bullfrogs than any other of the leech's hosts in the early spring when the leeches come out of hibernation and show their greatest appetite.

The greatest harm done by this leech is the destruction of large quantities of frog eggs. The eggs of *Rana pipiens* suffer in particular because they are the first to be laid in the spring. I have made no observations that would show that this leech feeds on fishes, or on invertebrate animals other than perhaps water snails and certain crawfish. On several occasions while digging in the bottoms of dry sloughs and ditches near Pearl River (St. Tammany Parish, La.) I found specimens of this leech in the shallow burrows of the dwarf crawfish *Cambarellus shufeldti.* In each instance that a leech was found there was a dead crawfish in the same burrow. This suggests at least that the leech had fed on the crawfish; however, I have never seen a leech attached to a crawfish.

These leeches, if carefully looked for, sometimes may be found in the mud or under logs at the edge of bodies of water. When not feeding or swimming usually they are buried in the mud at the bottom of shallow swamps, marshy ponds, and other aquatic habitats. If one wades with bare legs in places where they occur, only a few individuals will attach to the legs unless the mud is vigorously stirred with the feet or sticks, when every leech within the immediate area may be induced to attach to one's legs. Yet, never has one leech actually taken or attempted to take blood from the writer, or in fact to my knowledge from any other human being. I think that if they did, this would be a well known fact as hunters, trappers, moss pickers, fishermen, and crawfish netters are constantly exposed to them; and, the public has a tendency to exaggerate rather than suppress facts.

From boyhood I had been under the impression that these leeches lived on the blood of cows, but would not bite human beings. During that time many of the New Orleans dairies were located at the borders of the swamps where land was cheap. Here, during wet spells or high water, marshy meadows were formed. In such places the leeches were abundant, but I do not recollect whether I actually found them attached to the legs of the cattle. Certainly I did not observe them taking blood. There may have been no relation of their abundance to the presence of cattle, except perhaps that the mud was kept slushy and afforded them excellent places for concealment. Most of these dairy lands have now been reclaimed so I have had little opportunity to make further observations on this point in recent years.

[1] This brief note was written in 1922 and is published posthumously. Editor.

Habits.—Normally, during the day, these leeches are buried in the soft alluvium under or at the edge of the water. At night they may be found in the water on top of the mud or swimming, but they are particularly abundant at the edge of the water where they often rest with the anterior half out of water and the posterior below the surface; often they sway in this location with an undulating motion. If they are in a current, their heads are upstream and their undulations assist the flow of the water. When a number of leeches are placed in a globular aquarium they may produce a current by their motions; eventually all leeches in the bowl face against the flow so that the water may continue to circulate in one direction for a considerable length of time due to the action of the leeches. During times of high water or heavy rain they leave the mud (day or night) and head against the currents; and, if currents are produced in a pond by wind action they will swim to and accumulate at the leeward shore. They will not descend to the bottom in deep water; thus, they are usually found in water about 6 to 18 inches deep as such places usually retain their water or sufficient moisture, to tide the leeches over an average summer drought. During hot weather they are active only at night; and, in moderate mild temperatures that occur in spring and autumn in this area, they may be active day or night.

Large specimens have been found in our concrete frog pens (Southern Biological Supply Co.) where they evidently had been since late summer, we having obtained no frogs between October and March when the leeches were removed from the pens. The leeches must have been small and thus unnoticed or they would have been removed when the frogs were counted into the pens. This would suggest a rather rapid rate of growth under favorable conditions.

DISTRIBUTION AND VARIATION OF *BRANCHIOSTOMA CARIBAEUM* IN MISSISSIPPI SOUND

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The only lancelet known from the Gulf of Mexico is *Branchiostoma caribaeum* Sundevall. The first account of *Branchiostoma* in the Gulf was made by Garman (*in* Kingsley, 1885, p. 64), who mentioned "Specimens at hand from the Gulf of Mexico . . ." but gave no precise location. The first account of a collection from a specific locality in the Gulf was that of Wright (1890), who took lancelets from Tampa Bay, Florida. Adams and Kendall (1891) reported several in dredges at two stations made by the schooner *Grampus* off Cape Romano and Sanibel, Florida. Andrews (1893) recorded additional material from Tampa Bay. Evermann and Kendall (1900) extended the distribution to the Snapper Banks off Pensacola. Large numbers of Gulf lancelets were unknown until Wells (1926) collected some 5,000 on the west coast of Florida. Fowler (1941, 1945) listed a total of 14 specimens in three collections from Sanibel, Florida, and Longley and Hildebrand (1941) reported three near Tortugas. Hutton *et al.* (1956) took 63 specimens in Boca Ciega Bay and Springer and Woodburn (1960) caught 3 in Tampa Bay at salinities ranging from 24.8 to 25.5. Baughman (1950) recorded lancelets from Texas collected by T. E. Pulley, the first known west of Pensacola, Florida. Subsequent small Texas collections were reported by Gunter and Knapp (1951) and by Hoese (1958). Hefley and Shoemaker (1952) took lancelets from Mississippi and Louisiana, and Boschung and Mallory (1956) found them in Alabama. Dawson (1961) also collected lancelets in Louisiana.

Up to the present, amphioxus has been reported in large numbers on the beaches of West Florida, but the literature indicates that its distribution on the northern Gulf is spotty and thin. Statements in the literature also generally indicate that this little animal is most abundant on pure sand bottom. However, it seems to be uncommon along that thousand miles of sand beach between Sabine Pass and Tampico, possibly because of the fine, packed sand.

Distribution and Abundance In Mississippi Waters

Investigations on amphioxus were begun at the Gulf Coast Research Laboratory several years ago (Cf. Hefley and Shoemaker, 1952), but were carried on in a more or less disorganized manner by class and student groups digging for the animals around the shores of the offshore islands, where they are taken every summer. In some cases a thousand and more specimens have been taken by a student group.

In the spring of 1960, the Pan American Petroleum Company sent a research team to Ocean Springs which worked out of the Laboratory and made several hundred corings of Mississippi Sound and adjacent Gulf bottoms. Samples were also taken with a modified Petersen grab. Samples covering one-eighth of a square meter were collected and it was soon noted that *Branchiostoma* was being taken. Figure 1 shows the map of these samplings with the *Branchiostoma* catches distinguished by the large closed circles. The Pan American data give some quantitative information on the numbers and abundance of lancelets which is of considerable interest because such information is lacking in the literature. The figures are minimal because the geologists were not searching for lancelets. They gathered what they could when the Petersen grab was

[1] The first author was enabled to work on this problem through a grant of the National Science Foundation to the Gulf Coast Research Laboratory.

dumped—as a courtesy to this Laboratory. Their data show that there was an average of 72 *B. caribaeum* per square meter in the areas where they were found (see Figure 1), or about 290,000 individuals per acre. Since the area where these animals are taken extends from Mobile Bay to Cat Island, and is about 75 by 5 miles in extent, the lancelets in the area would seem to be numbered in billions.

The greatest depth at which lancelets were taken in the Petersen grab was about 90 feet at a station approximately 20 miles south of Mobile Bay. They are sometimes exposed by low tide. The bottom salinity range at 32 stations where the lancelets were caught was 15.4 to 33.1 *per mille,* and the mean salinity was 24.3. The lancelets are one continuous population and we have noted no differences between low and high salinity populations or any division equivalent to the lagoon and marine forms of *B. nigeriense* which Webb (1956a) reported.

Amphioxus was associated with the infauna commonly found in the bays and shallow Gulf at medium to high salinities. There was often broken shell mixed with the sand and silt, varying in size from fine particles to single valves of *Donax variabilis, Ensis minor, Mulinia, Dosinia, Tagelus* and occasional whole specimens. The lancelets are also associated with various annelid and nemertean worms and at times with *Saccoglossus* sp. Small specimens of the echinoid, *Mellita quinquiesperforata,* were also commonly found on the bottom. The invertebrate crawlers and creepers and bottom swimming fishes, of much greater abundance than the infauna, are too numerous to mention and they need further description and characterization.

Where amphioxus was dug for in shallow water it was noted that they were not abundant on clean sand, but on sand with dark streaks of silt and bottom debris consisting of plant materials (bits of wood) and shell.

Dr. Charles Upshaw, of the Pan American Petroleum Corporation supplied us with a very fine colored map showing the relative entropy isopleths of the sediments, by the usual triangular approximation of sediment grain size, ranging from silt and clay at less than 62 microns diameter up to sand at greater than 250 microns. This map and Figure 1 showed that about nine out of ten times amphioxus was found on coarse sand or mixtures of coarse sand and silt. It was rarely found on fine sand and not at all on clay.

Miscellaneous Observations

In laboratory aquaria *B. caribaeum* swims about vigorously at times, and it is not surprising that both immature specimens and adults have been taken several times in the upper layers of water and at the surface. Rice (1880) reported collecting 20 young from surface tows near the Chesapeake Biological Station at Fort Wool. Wright (1890) reported many lancelets taken in dipnets, "far offshore," at Tampa, and Andrews (1893) reported "small miniature" specimens at the surface of Kingston Harbor, Jamaica. Four specimens from the Aransas Pass ship channel of Texas (Gunter and Knapp, 1951) were taken in plankton tows. We believe they were swimming naturally and were not stirred up by a ship as suggested by Dawson (1961), who also reported a specimen from a plankton tow off Grand Isle, Louisiana.

Various species of *Branchiostoma* are reported to swim both backward and forward and they are also known to burrow quickly into the sand, entering either by the head or tail with equal ease. We have also observed a third method by which *Branchiostoma* buries itself, which has not been mentioned in any of the accounts we have read. Sometimes the animals will lie flat on the surface of the sand and give convulsive little wiggles much like the swimming pattern and thus settle in the sand. This action is somewhat like that of a flounder settling into its bed.

During the months of July and August large individuals were seen with gonads. Smaller individuals had gonads at immature stages of development.

The Mississippi population of amphioxus has associated with it an interesting commensal protozoan, which is a more or less bell-shaped ciliate attached singly along the buccal cirri. Counts in 1960 show that 72 of a hundred specimens were carrying the Protozoa. In August 1961, only two of 50 specimens were found with this commensal.

Variation of Taxonomic Characters

Several meristic characters and measurements have been used by previous authors (Kirkaldy, 1895; Franz, 1922; Hubbs, 1922;

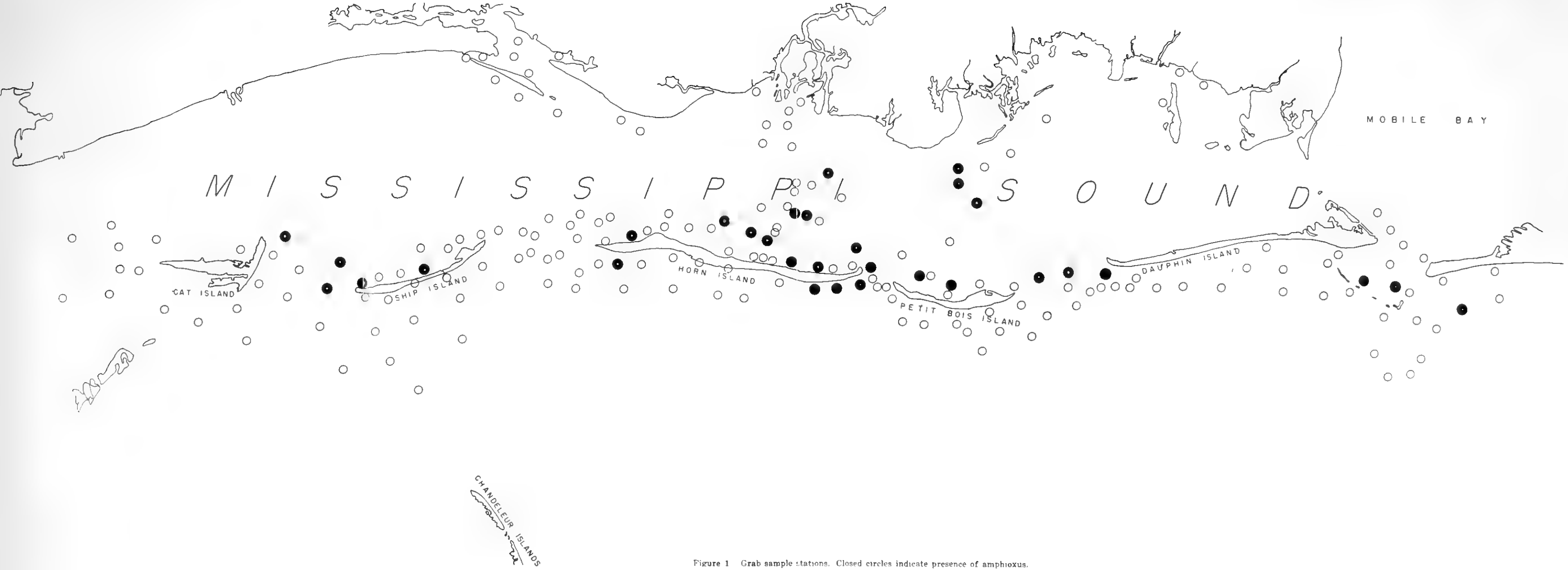
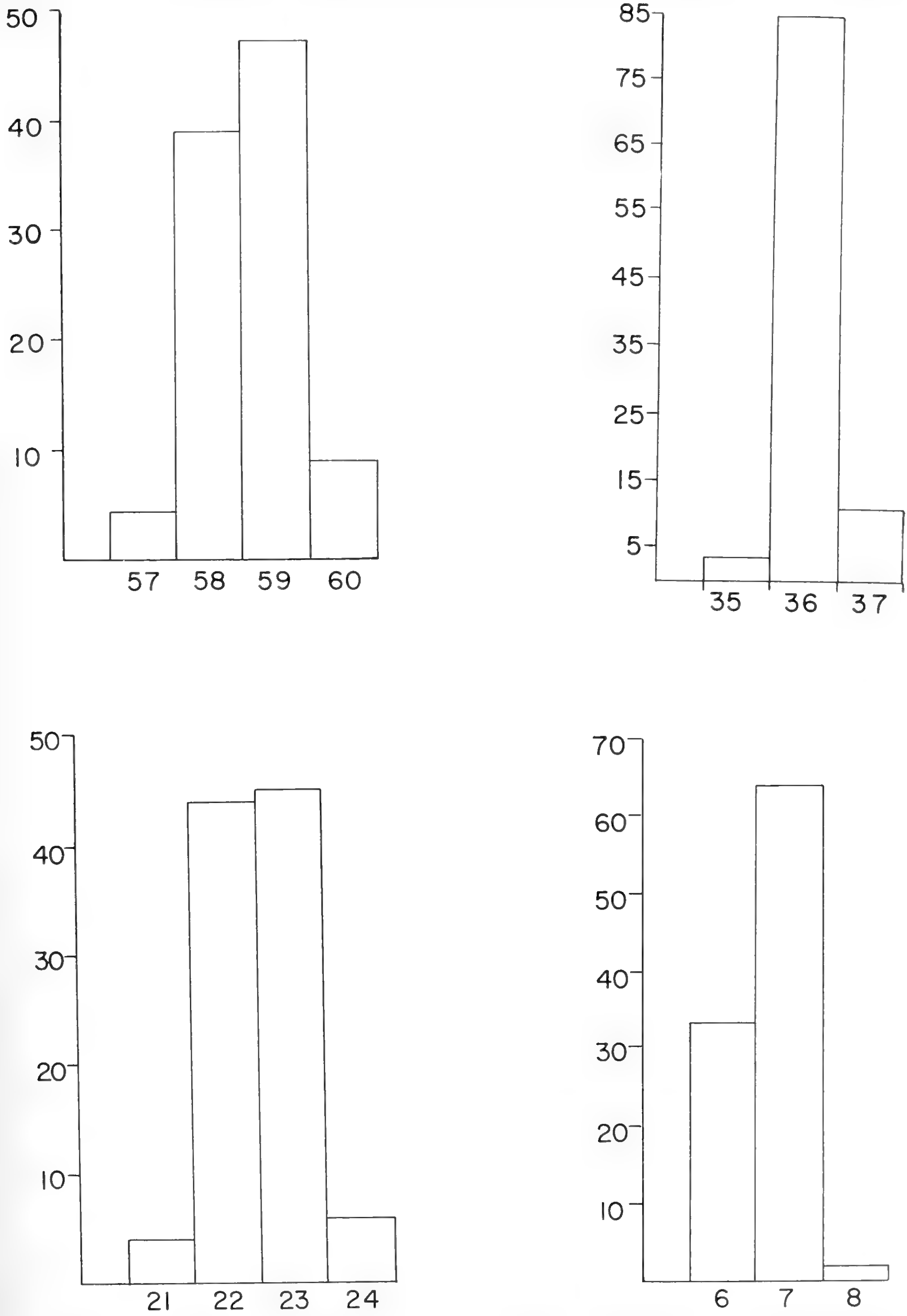


Figure 1 Grab sample stations. Closed circles indicate presence of amphioxus.



Figures 2-5. Mississippi lancelets. **2.** (top left) Frequency distribution of total myotomes. **3.** (top right) Frequency distribution of preatriopore myotomes. **4.** (bottom left) Frequency distribution of postatriopore myotomes. **5.** (bottom right) Frequency distribution of postanal myotomes.

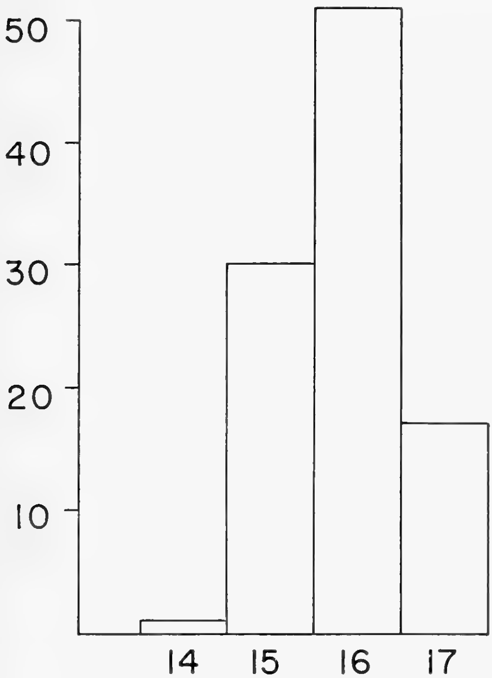


Figure 6. Frequency distribution of myotomes between atriopore and anus of Mississippi lancelets.

Bigelow and Farfante, 1948; Webb, 1956) for the description and identification of lancelets. In addition to the usual characters we have included body depth, caudal fin length, postatriopore length, postanal length expressed as percentage of total length, and the number of oral cirri. Counts and measurements were made on 100 specimens selected at random from the material collected in Mississippi Sound during the spring and summer of 1960. Almost all characters examined showed considerable variation.

Myotomes.—Total myotomes varied from 57 to 60, with 87 per cent of the specimens possessing 58 or 59 (Fig. 2). The number of preatriopore myotomes varied from 35 to 37, with 86 per cent having 36 (Fig. 3). The postatriopore myotome number varied from 21 to 24, with 90 per cent having either 22 or 23 (Fig. 4). The number of postanal myotomes varied from 6 to 8, with 97 per cent of the specimens possessing 6 or 7 (Fig. 5). The number of myotomes between the atriopore and the anus varied from 15 to 17, with the exception of a single specimen whose count was 14 (Fig. 6). The formula for expressing the ranges in myotome counts would seem to be 35 to 37 + 14 to 17 + 6 to 8 = 55 to 62; however, since the minimum and maximum total number of myotomes were 57 to 60, respectively, the theoretical limits of 55 to 62 were not reached. It is evident then that the variation in preanal and postatriopore myotomes were not additive. The variation in the postatriopore numbers was as great as that of the total count, and one of its components, the number of myotomes between the atriopore and anus, showed equal variation. The variation in the number of myotomes of the two components of the postatriopore count was not additive, and where the total myotome counts vary from the mode (59) it is more likely a function of the variation in postatriopore count. The myotome formula for this population is, 35 to 37 + 14 to 17 + 6 to 8 = 57 to 60, or typically 36 + 16 + 7 = 59.

The myotome count is the least variable character of the Mississippi Sound lancelets. Based on works of Andrews (1893), Hubbs (1922) and Bigelow and Farfante (1948) and disregarding Andrews' Jamaican specimen reputed to have had only 48 myotomes,

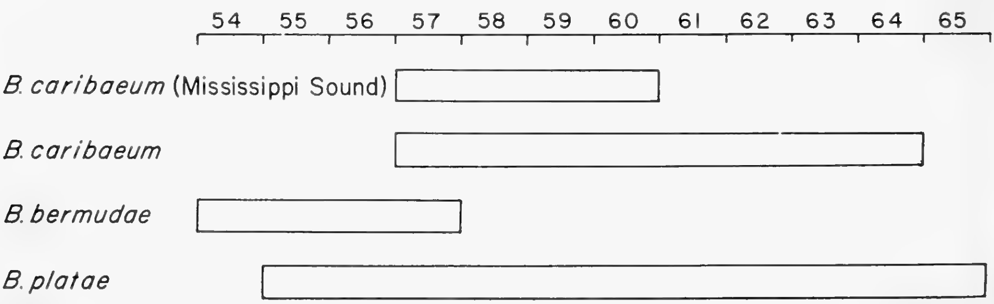


Figure 7. The range of total myotome number of Mississippi specimens compared with other western Atlantic lancelets.

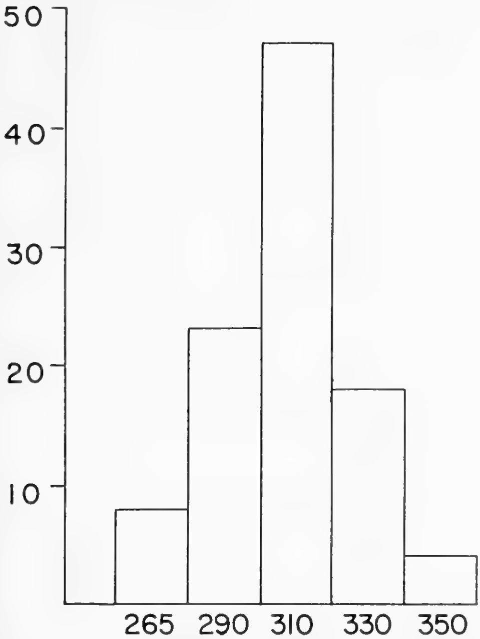


Figure 8. Frequency distribution of dorsal fin-ray chambers of Mississippi lancelets.

the known range of myotomes for *caribaeum* (including *floridae* and *virginiae*) is 57 to 64. The range of total myotomes of *platae* (55 to 65, Samaya and Carvalho, 1950) encompasses the range of *caribaeum* and broadly overlaps that of *bermudae* (Fig. 7). The myotome count of our study material as well as other *caribaeum* reported in the literature overlaps *bermudae* by only one; however, the variation of all *caribaeum* reported in the literature is great enough to encompass the range known for *haekelii* and *minucauda* and overlaps that of *bazarutense* and *belcheri* as well as *bermudae*.

Fins.—The number of dorsal fin-ray chambers varied from 252-359, with 84 per cent of the specimens possessing 281-330 chambers (Fig. 8). Bigelow and Farfante (1948) gave a minimum count of 227 chambers for specimens from Puerto Rico and a maximum count of 330 for specimens from Florida. Thus, the now known range of dorsal fin-ray chambers in *caribaeum* is 227 to 359, giving a variation of 133 chambers for the species. However, the variation of 108 chambers in the Mississippi Sound lancelets is unparalleled by any known population of *Branchiostoma.* The dorsal fin-ray chamber variation of *caribaeum* narrowly overlaps that of *bermudae* and encompasses that of *platae* (Fig. 9).

The preanal (ventral) fin-ray chambers varied from 35 to 61, with 81 per cent of the specimens possessing 41 to 55 (Fig. 10). Previously reported low and high counts for *caribaeum* were 15 and 18 for specimens from Puerto Rico and Florida respectively to 42 for those from Virginia and North Carolina (Bigelow and Farfante, 1948). The number of preanal fin-ray chambers in *caribaeum* is now known to vary from 15 to 61, giving a variation of 47 chambers for the species. The preanal fin-ray chamber variation of *caribaeum* overlaps well that known of *bermudae* and encompasses that of *platae* (Fig. 11). The ventral fin-ray chambers become progressively smaller towards the anus and are difficult to see in opaque specimens.

The caudal fin varied in shape, and several selected from the study material are shown in Figure 12. No attempt to categorize shapes was made since there is no sharp line of demarcation between the types studied. Caudal fin A shows the upper lobe

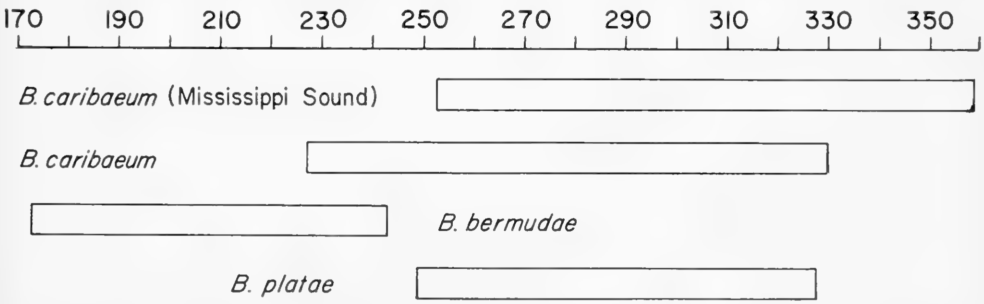


Figure 9. The range of numbers of dorsal fin-ray chambers of Mississippi specimens compared with other western Atlantic lancelets.

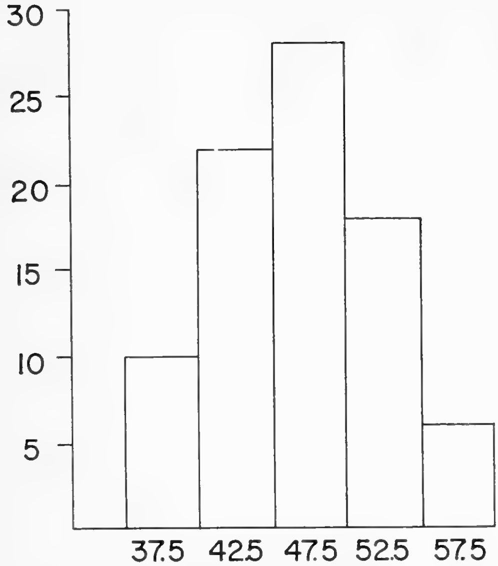


Figure 10. Frequency distribution of preanal fin-ray chambers of Mississippi lancelets.

of the caudal fin considerably posterior to the lower lobe. This shape when compared with the figures of Bigelow and Farfante (1948, Fig. 2, A and F) is seen to be similar to that of *bermudae,* and to some extent *platae*. Fins B and C are most typical of our study material, C being more characteristic of the larger specimens. In fin D the upper lobe extends as far anteriorly as does the lower.

The caudal fin length, measured from the anterior-most part of the lower lobe to the tip, varied from 11.6 to 17.5 per cent of the total body length (Fig. 13). There is a direct correlation between caudal length and body length.

Body proportions.—The study material varied in total length from 9.9 to 52.3 mm. Seventy per cent of the specimens fell into the 35 to 45 mm. class. The mean size was 38 mm. The body depth varied from 7.3 to 11.7 per cent of the total length, with 78 per cent being in the 7.5 to 8.5 per cent class

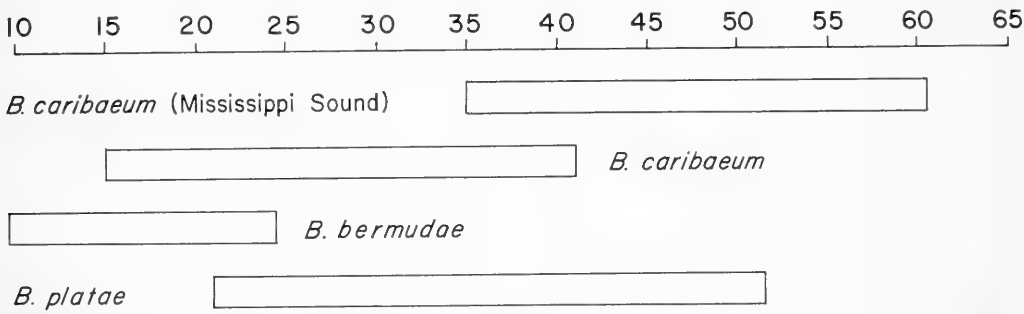


Figure 11. The range of number of preanal fin-ray chambers of Mississippi specimens compared with other western Atlantic lancelets.

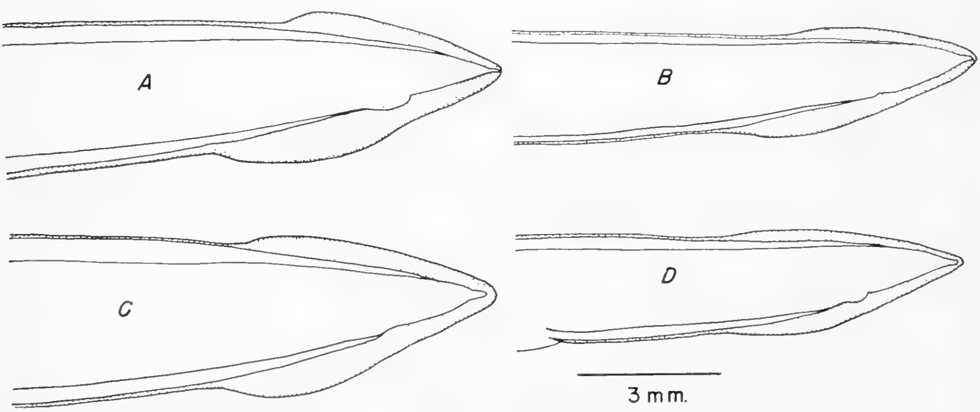
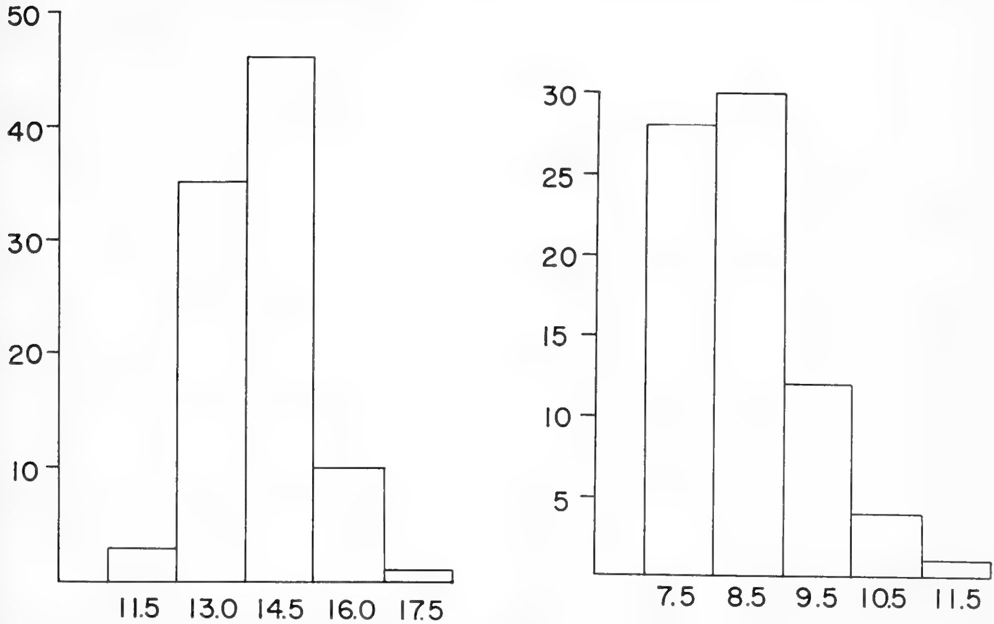


Figure 12. Variations in caudal fin shapes of Mississippi lancelets.



Figures 13-14 Mississippi lancelets. 13. (left side) Frequency distribution of per cent caudal fin length of total body length. 14. (right side) Frequency distribution of per cent body depth of total length.

(Fig. 14). The postatriopore length varied from 27.4 to 32.4 per cent of the total length, 61 per cent falling into the 29 to 30 per cent class (Fig. 15). Both the depth and postatriopore length are more or less directly proportional to total length (Figs. 16 and 17).

The dorsal fin-ray chamber height-breadth ratio is quite variable, the height being from 3 to 5 times the breadth. These limits are equal to those of *bermudae* and overlap those of *platae*. The height of the dorsal fin is contained in the body depth (at deepest point) from 6 to 10 times. There is no correlation of number of dorsal fin-ray chambers and total length. In fact, two relatively small specimens measuring 19.4 and 20.8 mm. in total length possessed 252 and 359 dorsal chambers, respectively. Although the fin-ray chamber measurements were made with an ocular micrometer, we consider the measurements not too reliable since such measurements are affected by the opaqueness of the specimen. Other workers have used this characteristic but we feel that it is not of much value.

The position of the anus varies within the genus *Branchiostoma* from in advance of the center of the caudal lobe to far behind the center. Previous writers have stated that in *caribaeum* the anus is near the center

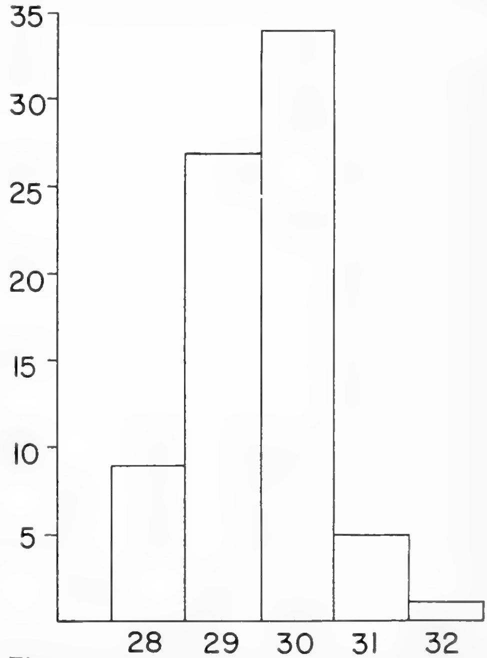


Figure 15. Frequency distribution of per cent postatriopore length of total length of Mississippi lancelets.

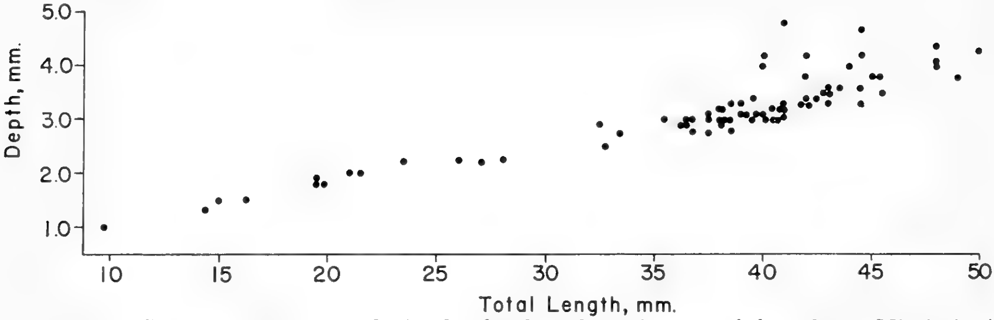


Figure 16. Scatter diagram of body depth plotted against total length of Mississippi lancelets.

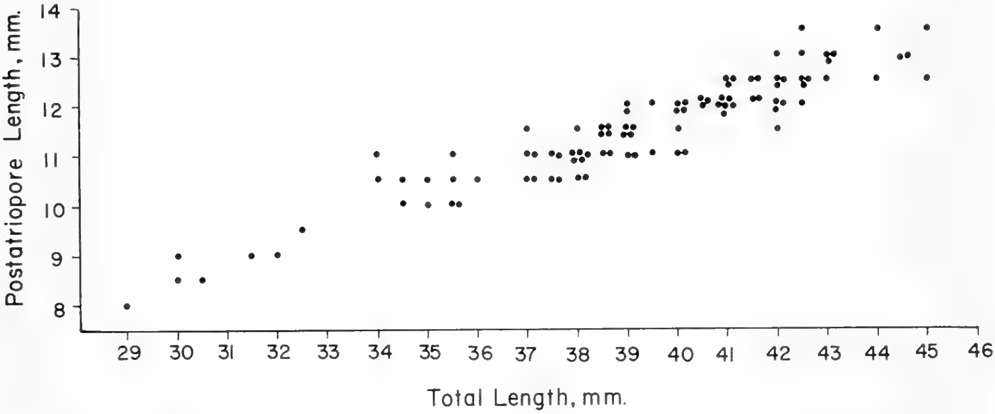
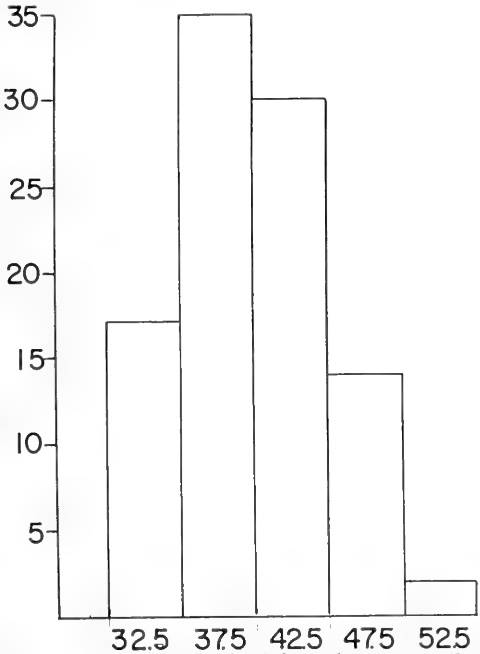
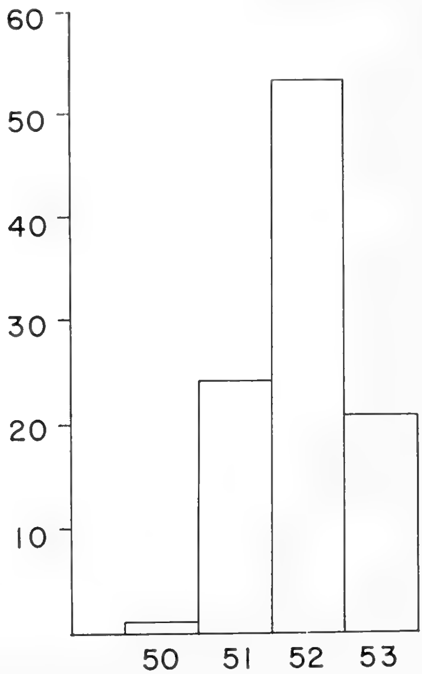


Figure 17. Scatter diagram of postatriopore length plotted against total length of Mississippi lancelets.





Figures 18-19. Mississippi lancelets. **18.** (left) Frequency distribution of per cent postanal length of lower caudal fin lobe. **19.** (right) Frequency distribution of position of anus by myotome number.

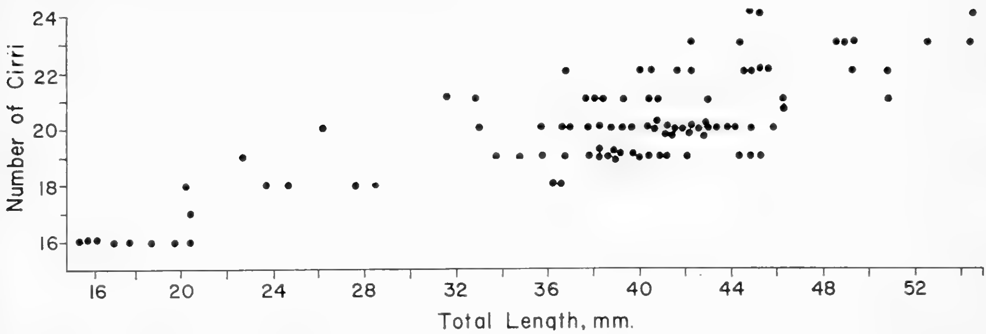


Figure 20. Scatter diagram of number of cirri on left side of oral hood plotted against total body length of Mississippi lancelets.

but have not placed it by actual measurements. We have found in the Mississippi Sound specimens that the anus is almost always behind the center of the lower caudal lobe, the postanal length varying from 30 to 53 per cent of the lower caudal lobe. The mean postanal length is 40 per cent of the lower caudal lobe (Fig. 18). The position of the anus by myotome number varies from myotome 50 to 53, with the mode 52 (Fig. 19).

Cirri.—Oral cirri were counted on the left side only. They varied from 16 to 24, the number increasing proportionally with body length (Fig. 20). The diameter of the cirri varied from 0.04 to 0.09 mm., this too having some correlation with total length of the lancelet. The cirri of the Mississippi Sound lancelets all have lateral knob-like projections, varying in number and position. They are best developed on larger specimens and are most dense on the longer, lateral cirri.

Gonads.—The position of the gonads relative to myotomes may have some taxonomic significance. The modal formula for this character is 9—25—1, where 9 is the number of myotomes anterior to the first gonad; 25, the number of myotomes within the gonadal region, and 1, the number of myotomes between the last gonad and the atriopore. Counts on 50 specimens, without regard to sex, varied as follows: 6 to 11 — 20 to 28 — 0 to 3. These figures were established from counts made on the left side of the animal.

Gonad counts were made on 100 mature specimens ranging in size from 32 to 52 mm. The total number of gonads varied from 46 to 57, with a mean of 51.4 and mode of 52. There was a slight difference between right and left sides. The left side

TABLE 1.
Statistical table of 12 characters in Branchiostoma caribaeum *

Character	Number	Range	Mean	Standard Deviation	Standard Error	Coefficient of Variation	Rank
1	100	57–60	58.6	0.76	0.07	1.3	2
2	100	35–37	36.1	0.14	0.01	0.39	1
3	100	21–24	22.5	0.45	0.04	2.0	4
4	100	14–17	15.8	0.69	0.07	4.4	6
5	100	6–8	6.7	0.50	0.05	7.5	9
6	100	252–359	306.9	18.84	1.88	6.2	7
7	84	35–61	47.2	5.75	0.63	12.2	12
8	95	11.6–17.5	14.1	0.99	0.10	7.1	8
9	100	30.2–53.2	39.8	4.62	0.46	11.7	11
10	74	7.3–11.7	8.4	0.85	0.99	10.1	10
11	100	50–53	51.95	0.70	0.07	1.4	3
12	100	27.4–32.4	29.4	1.0	0.1	3.4	5

*(1) Total myotomes; (2) Preatriopore myotomes; (3) Postatriopore myotomes; (4) myotomes between atriopore and anus; (5) Postanal myotomes; (6) Dorsal fin-ray chambers; (7) Preanal (ventral) fin-ray chambers; (8) Per cent caudal fin length of total body length; (9) Per cent postanal length of caudal fin length; (10) Per cent body depth of body length; (11) Position of anus, myotome number; (12) Per cent atriopore length of total length.

varied from 23 to 29, with a mean of 25.1 and mode of 27, whereas the right side varied from 22 to 30, with a mean of 26.3 and a mode of 26. There was no correlation between number of gonads and size of the animal.

Discussion of Taxonomic Characters

A statistical analysis of 12 meristic counts and measurements is shown in Table 1. The coefficient of variation was calculated to give an index to the reliability of each character. The characters are accordingly ranked in order of increasing variation or decreasing taxomonic significance. Myotomes, especially preatriopore myotomes, are the least variable among the characters, but as we have seen, they alone cannot be used to separate *B. caribaeum* from the other western Atlantic species, or indeed, several other species of the world. In fact, a statistical analysis of populations of lance-

TABLE 2.

Comparison of seven taxonomic characters of six species of Branchiostoma

Species	N	Total Myotomes				Preatriopore Myotomes			
		Range	Mean	S.D.	C.V.	Range	Mean	S.D.	C.V.
B. caribaeum (Mississippi Sound)	100	57–60	58.6	0.76	1.3	35–37	36.1	0.14	0.39
B. platae [1]	64	55–65	59	0.65	1.1	34–42	37	0.53	1.4
B. nigeriense [2]	100	65–71	67.8	1.4	2.6	39–44	41.8	1.29	3.1
B. senegalense [2]	40	67–71	68.6	0.86	1.3	39–41	40.2	0.6	1.5
B. leonense [3]	25	66–73	69.2	1.92	2.8	40–45	43.2	1.33	3.1
B. lanceolatum [4]	27	61–65	62.6	1.04	1.67	35–37	36	0.71	1.42

Species	N	Myotomes between Atriopore and Anus				Postanal Myotomes			
		Range	Mean	S.D.	C.V.	Range	Mean	S.D.	C.V.
B. caribaeum (Mississippi Sound)	100	14–17	15.8	0.69	4.4	6–8	6.7	0.5	7.5
B. platae [1]	64	9–17	15	0.47	3.1	5–9	6.8	0.23	3.3
B. nigeriense [2]	100	14–16	15.2	0.35	2.3	10–12	10.9	0.3	2.8
B. senegalense [2]	40	16–18	17	0.63	3.7	10–12	11.4	0.57	5.0
B. leonense [3]	25	14–16	15.5	0.59	3.8	10–12	10.4	0.65	6.2
B. lanceolatum [4]	27	13–16	14.3	0.71	5.0	11–14	12.4	0.75	6.0

Species	N	Dorsal Fin-Ray Chambers				Preanal Fin-Ray Chambers			
		Range	Mean	S.D.	C.V.	Range	Mean	S.D.	C.V.
B. caribaeum (Mississippi Sound)	100	252–359	307	18.8	6.2	35–61	47	5.8	12.2
B. platae [1]	64	249–310	278	14.7	5.2	22–53	35	11.4	32.5
B. nigeriense [2]	100	330–376	346	9.7	2.8	50–58	55	2.0	3.7
B. senegalense [2]	40	267–325	292	13.4	4.6	45–59	52	3.2	6.2
B. leonense [3]	25	355–418	382	15.2	4.0	51–64	58	3.2	5.4
B. lanceolatum [4]	27	210–270	238	15.0	6.3	30–48	39	4.1	10.5

Species	N	Per cent postatriopore length of preatriopore length			
		Range	Mean	S.D.	C.V.
B. caribaeum (Mississippi Sound)	100	38–48	42	2.1	5.0
B. platae [1]	64	—	—	—	—
B. nigeriense [2]	100	40–45	42.4	1.5	3.5
B. senegalense [2]	40	44–54	50	2.3	4.6
B. leonense [3]	25	33–41	38	2.1	5.5
B. lanceolatum [4]	27	43–51	47	1.9	4.1

[1] Sawaya and Carvalho, 1950
[2] Webb, 1955
[3] Webb, 1956a
[4] Webb, 1956c

TABLE 3.

Comparison of the Mississippi Sound lancelets with the other species of the western Atlantic *

Species	Taxonomic Characters										
	1	2	3	4	5	6	7	8	9	10	11
B. caribaeum (Mississippi Sound)	57–60	35–37	14–17	6–8	252–359	35–61	6–10x	3–5x	.38–.48	22–30	Behind midpoint of lower caudal lobe
*B. caribaeum*** (Previously reported)	57–64	35–38	13–17	6–9	227–320	15–42	8x	5–8x	–	22–29	In advance of midpoint of lower caudal lobe
*B. platae***	55–65	34–42	9–17	5–9	249–327	19–53	4–8x	4x	.28–.32	26–31	Near midpoint of lower caudal lobe
*B. bermudae***	54–57	35–36	12–14	5–7	172–242	9–24	6–7x	3–4x	.31–.43	22–28	Little behind midpoint of lower caudal lobe

* The characters are numbered 1-11: (1) Total myotomes; (2) Preatriopore myotomes; (3) Myotomes between atriopore and anus; (4) Postanal myotomes; (5) Dorsal fin-ray chambers; (6) Preanal (ventral) fin-ray chambers; (7) Number of times height of dorsal fin is contained in depth of body; (8) Height of dorsal fin-ray chamber times its breadth; (9) Postatriopore region as a proportion of the length of the preatriopore region; (10) Gonads, one side; (11) Position of anus.

** Data based on works cited in text.

lets would be necessary in order to separate them unequivocally. Too, a character that varies widely in one species does not necessarily do so in another. Webb (1955) assessed the value of various taxonomic characters in *B. senegalense* and *nigeriense* and found that although both species were equally variable as a whole, the degree of variation for a given character was not necessarily the same in both species. Comparison of present data on *B. caribaeum* (Table 2) with that of several other species of lancelets of the world gives further weight to Webb's conclusion.

Table 3 compares the Mississippi Sound lancelets to others of the western Atlantic. In some ways *B. caribaeum* is more similar to *platae* than to *bermudae,* and vice versa, but in general it seems to be a bit more similar to *B. platae.*

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Abstract

The known distribution of *Branchiostoma caribaeum* Sundevall in the Gulf of Mexico is from Cape Romano, Florida to Port Aransas, Texas. The literature indicates that this lancelet is abundant on parts of the western Florida coast, but it has not been recorded in abundance along the northern Gulf coast. Quantitative collections by the use of a modified Petersen grab showed that this species is present in numbers up to 73 per square meter in Missis-

sippi Sound and a little way outside the barrier islands from Mobile Bay to Louisiana, an area of about 350 square miles. The total numbers in this region must be in the order of several billions. The lancelet is sometimes exposed by low tides, and the greatest depth at which it was taken was 15 fathoms, 20 miles south of Mobile Bay. In shallow water *B. caribaeum* was taken in greatest numbers where shell and plant debris was common on the bottom. Hundreds of sediment samples collected in Mississippi Sound and the adjacent Gulf show that about nine times out of ten amphioxus was taken in coarse or medium coarse sand, or coarse sand mixed with silt, and was taken rarely on fine sand and not at all on clay. The salinity at 32 stations where amphioxus was taken ranged from 15.4 to 33.1 *per mille* and the mean salinity was 24.3. (This does not include the outside stations, where the salinity was certainly up to 36.0). Lancelets were taken with *Saccoglossus*, the echinoid *Mellita*, and various nemertean and annelid worms, as well as several pelecypods. It was observed that lancelets lying on the bottom would wriggle their way into the sand, a manner of burial which has not been recorded before. Analysis of meristic characters confirms Webb's dictum that a character which varies widely in one species does not necessarily do so in another. Some meristic characters overlap those of the other species of the western Atlantic to a considerable extent, and even other species of lancelets of the world. In meristic characters *B. caribaeum* is more similar to *B. platae* than to *B. bermudae* but this generalization does not hold for all characters. Statistical analyses of populations of lancelets are necessary for their unequivocal separation as species.

JAMES TRUDEAU AND THE RECENT DISCOVERY OF A COLLECTION OF PAINTINGS OF EGGS OF NORTH AMERICAN BIRDS

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Though it has generally escaped the notice of the several commentators who have reviewed the paintings of John James Audubon, very few of his drawings include representations of birds' eggs. There is a scattering of plates among his *Birds of America* where the eggs comprise accessories to the bird portrait but nowhere does Audubon focus our attention on a nest with eggs as the center of interest. Herrick (1917, 1:374 and 2:387) records the intention of Audubon to illustrate "the eggs of most of the species," but that with the many new birds discovered in the West when the great work was drawing to its close there was a necessity for abandoning the figures of the eggs, which Audubon had planned for the final fascicles, to permit the inclusion of these late additions from the travels of Townsend and Nuttall. Can it be that this illustrated account of eggs was to have been carried out in cooperation with his New Orleans friend, James de Berty Trudeau (1817-1887), "physician, surgeon, artillery officer, painter, and sculptor"?[1]

In the course of reorganization of the collections of the Louisiana State Museum, Mr. Clive Hardy, Archivist and historical consultant, recently brought to light an overlooked parcel of 80 water color drawings of unknown provenance but named, and some longer holographs in several different hands. Through the cooperation of the Museum's Manager, Mr. C. E. Frampton, and at the suggestion of Mr. Hardy, I have examined these materials and offer the present explanation of their nature.

The first group of drawings of birds' eggs with full dates associated with them were noticed by Mr. Hardy to carry the inscription "Labrador. 4. 6. July 1833." Thinking that these drawings might relate to Audubon's Labrador trip, Mr. Hardy checked the dates in the Labrador Journal and found indeed that this was so. However, I believe that these egg paintings are not the work of Audubon, but of his friend Trudeau who drew them from collections Audubon brought back from Labrador. Four egg drawings are associated as part of this Labrador origin, and must be directly due to Audubon's interest. These four are: "Sylvia striata" [Blackpoll Warbler], "Anthus spicolata" [Horned Lark], "Fringilla savanna" [Savannah Sparrow], and "Fringilla leucophyrus" [White-crowned Sparrow]. A drawing of an egg of undoubted Labrador source is labelled "Clangula barrovii" [Barrow's Goldeneye]. Another labelled "Phalacocorax dylophus. June. Labrador" represents the egg of the double-crested cormorant. Certainly these may be traced to Audubon's expedition of 1833. The egg drawing of "Little Auk," now known as Dovekie, and well known from Labrador coast, is not dated, but the birds were not drawn until 1836 (Plate 339, *Birds of America*), and so the egg collection may have a later and different origin.

Watermarks have been of limited use in identification. Whether the scaup duck egg dates from the 1833 Labrador trip is unrecorded; in any event Audubon's label "Marila" is inscribed on Whatman Turkey Mill paper watermarked 1837. Another drawing, Audubon's "Red-necked Grebe" [i.e. Holboell's grebe, Plate 298], inscribed "Grebe rubricollis" is drawn on Whatman paper watermarked 1838. It may be noted that these dates suggest Trudeau's active period when he was in correspondence with Audubon, Bachman, and other naturalists.

Beside these materials of Labrador origin and surely dating from Audubon's trip of 1833, there is a group of egg paintings without doubt originating with Trudeau. One is labelled "Common Buzzard. Grand Saline, May, 1840," accompanied by two paragraphs of notes in a thin delicate hand. These paragraphs, evidently written in the field, read:

"The common Buzzard is the most common hawk in the plains of this district of

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[1] See Postscriptum.

Missouri. This Bird is not positively as shy as its congeners. Its note differs from the European buzzard as well as the nest and eggs. Those 3 in number were roundish (in 5 nests I found) of a dirty white without any dots nor Blotches. All the nests I have seen were on high isolated trees; never on the ground. (June 20th 1840).

"This egg I figure here was taken by me in a nest placed in a cotton tree (platanus) 2 miles from the Grand Saline. They were all perfectly alike. The mother was watching the boy climbing up the tree, at little distance but out of the reach of my gun. As he arrived close to the nest she made a swoop at him which afforded me a chance of bringing her on the ground, and thereby ascertain positively to what species the eggs belonged. (June 27th)."

Trudeau's field note on the burrowing owl, reproduced here, (Fig. 1) reads:

"[The Burrowing Owl is very abundant in all the Prairie dogs or marmots villages.] It has been stated that these birds inhabited in desert villages and in ancient holes deserted by the marmots: the fact may be true but in all the deserted villages which abounds in the Prairies of the S. W. Missouri I have never seen a bird. On contrary they are common in all villages w[h]ere the marmots are to be found. Do they inhabit the same holes? Why should the birds follow the quadrupeds if they were on unfriendly terms? The fact is this: the Bird occupies in the burrow a kind of vestibulum about 2 or 3 feet from the entrance. Its eggs 2 in number are laid there in some cases on the ground, in others on a few dry sticks. This burrow is so deep that with our poor means we were not enabled to find its termination. But often I have seen the owl and the marmot enter the same Burrow (perhaps frightened by my approach). Hiding myself, I could see with a spy glass, the Bird emerging out first, then the marmot would be seen cautiously taking a peep, and being certain that no enemy is present run out and bark to call the others. This seems to me to be in favour of the opinion of those

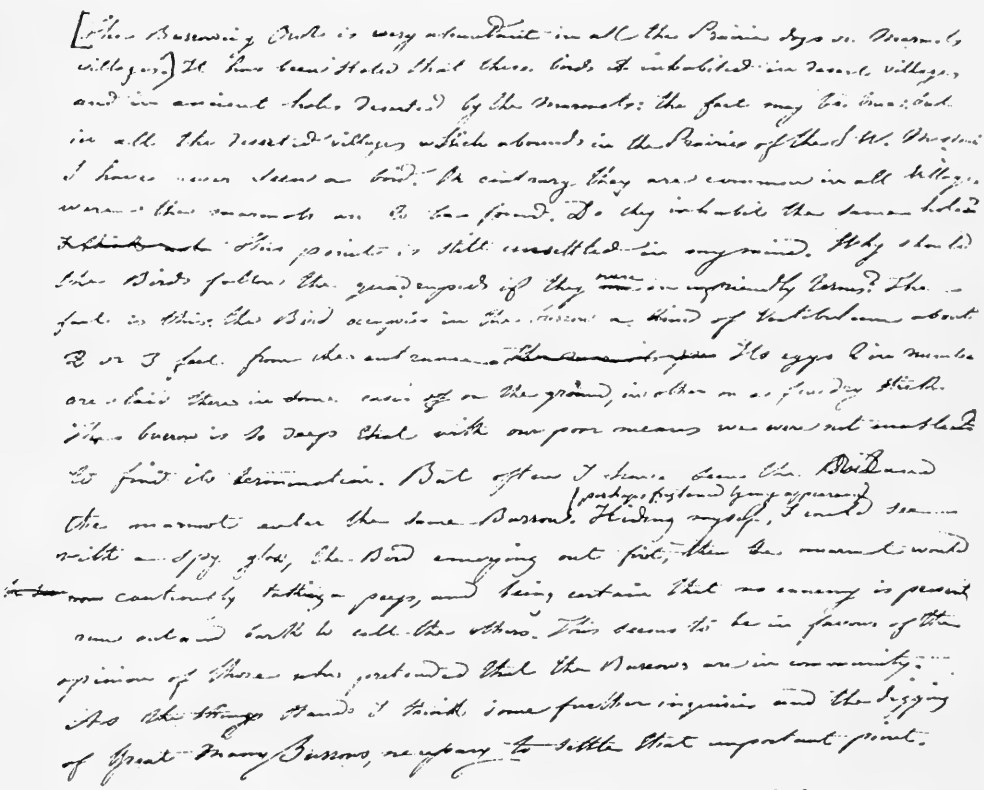

Figure 1. Trudeau's field notes on the Burrowing Owl.

who pretended that the Burrows are in community. As the thing stands I think some further inquiries and the digging of great many Burrows necessary to settle that important point."

The handwriting has been identified as that of Dr. Trudeau who accompanied Charles Tixier on a trip to the Osage country in 1840 (McDermott, 1940, map opp. p. 272). A letter from Trudeau, dated New York, Jan. 17, 1846, to Audubon's friend and patron, Edward Harris (Harris Papers, Alabama State Archives, Montgomery) confirms this. The letter does not mention Trudeau's egg painting activities.

James Trudeau's son, Edward Livingston Trudeau, M.D., says in his *Autobiography* (1916, p. 9) that a sister-in-law, Miss Félicie Bringier, wrote him that his father "often helped Audubon with the anatomy of his ornithology work, and drew illustrations of birds and eggs for him." It was this statement, perhaps more than other leads, that suggested the provenance of these paintings as Trudeau's. We know that Dr. James Trudeau returned to New Orleans in 1858 after practicing medicine in New York city for many years. At about this time he sold his library, but he must have retained a few favorite books and acquired others of a natural history character later because several of his books appeared in 1956 at the annual book fair sponsored by the New Orleans Symphony Society, and these are now in my library. My recollection of Trudeau's inscription on the title page of the second volume of C. D. Degland's *Ornithologie Européenne* (Paris, 1849) established the association of this little collection of egg drawings with Audubon's friend. This second volume of Degland's account of European birds would have had peculiar interest for Trudeau since it described the terns. Audubon named Trudeau's Tern (*Sterna trudeaui* Aud.) in 1838 and it is illustrated in his *Birds of America* as Plate 409.

Dr. Trudeau also owned a copy of L. F. Alfred Maury, *La Terre et l'Homme* (Paris, 1857) and the sixth edition of Michelet's *l'Oiseau* (Paris, 1859) a popular work on birds of that period. When the present drawings came to the State Museum is not known; Dr. Trudeau died in New Orleans on May 25, 1887.

The collection of birds' egg drawings include other memoranda than those identified as either Audubon's or Trudeau's, but these cannot now be placed with certainty. A drawing of the egg of the Red-shouldered Hawk is signed "L. Marchisio 1839" and some drawings carry numbers, e.g., "88 Tetrao cupido" [Prairie Chicken], "89 Tetrao obscura [Dusky Grouse], and others, the highest number noted being 102. The significance of these numbers has not been determined. The earliest dated drawing is of the egg of the Orchard Oriole, June 20, 1821. However, this date may represent the collection date of the egg, and not the year the drawing was executed. Audubon was at the Pirrie Plantation, "Oakley," five miles from St. Francisville, on June 20, 1821, having arrived on the 18th as tutor to Miss Eliza Pirrie, accompanied by his assistant John Mason. Audubon's drawing of the Orchard Oriole, Plate 42 in his *Birds of America,* is dated 1828, and includes an empty nest!

Examination of documents and published accounts of Trudeau has revealed contradictions and some egregious errors, and so to summarize our information on "one of the most learned, accomplished and many sided men that Louisiana ever produced" I offer the following chronology:

1817

Sept. 14. Born, second child, eldest son of M. and Mme. Rene Trudeau, at the family sugar plantation in Jefferson Parish.

ca. 1827

Sent to College of Louis-le-Grand, Paris. Because of failing health transferred to a military school in Switzerland to complete his primary education.

before 1835

Returned to Paris for medical education.

ca. 1836

Enrolled as medical student at University of Pennsylvania under Dr. Joseph Pancoast.

1837

March. Received M.D. degree. Subject of thesis: apoplexy.

June 27. Read a paper before the Academy of Natural Sciences, Philadelphia, on a presumed new species of woodpecker (*Picus auduboni* [proved to be a form of *P. villosus,* hairy woodpecker]). This paper was later published in the Academy's *Journal* 7: 404-

406. 1837. Sometime during the year moved to New York City and there entered medical practice.

Sometime during 1837-38 visited Great Egg Harbor, N.J., and collected the skin of *Sterna trudeaui* described by Audubon.

1838

Oct. 7. Resident at No. 12 Rue de Lancy, Paris, whence came Rev. John Bachman and his companion Christopher Happoldt, the three then proceeding to the residence of the Prince of Messina to examine his natural history cabinet.

Audubon published Trudeau's Tern *(Sterna trudeaui)* as Plate 409 in *Birds of America.*

Dec. 19. Audubon wrote to Edward Harris that Trudeau had been "commissioned" to buy books for him in Paris, but he had received "neither books nor promise of them from Trudeau as yet." He mentions Trudeau's having examined the bird skins of J. K. Townsend, presumably in Philadelphia, and of Frederick Ward.

1839

June 4. Read a paper before the Academy of Natural Sciences, Philadelphia, on a presumed new species of tanager *(Pyranga leucoptera).* This paper was later published in the Academy's *Journal* 8: 160. 1839.

1840

May. Left New Orleans in company of Victor Tixier on the *Grand Pratte* for St. Louis.

May 12. Reached St. Louis. Left for Osage country on 15th.

May 20. Left Independence, Missouri, for Nion-Chou [Neosho River].

June 20. Collected eggs of "Common Buzzard" [Swainson Hawk] and others at Grand Saline, Osage country, which were later painted.

Osage tribe presented Dr. Trudeau with Indian costume in which John Woodhouse Audubon later painted him.

Aug. 25. Arrived in St. Louis en route to New Orleans, as Tixier left for New York via Pittsburgh.

1841

Jan. or Feb. John Woodhouse Audubon painted Trudeau in Osage costume.

1843

Removed to New York City and reestablished his medical practice there.

Married Céphise Berger (b. 1825) of New York.

June 19. John G. Bell, member of Audubon's trip up the Missouri River, took nest and eggs of Lark Bunting. Edward Harris, also a member of the expedition, wrote in his journal of this date: "we hope [they] will be an acquisition for our friend, Dr. Trudeau."

1844

Aug. 4. Wrote to Edward Harris, Morristown, N.J., relative to sales offer of European bird skins.

1845

Feb. S. F. Baird, then a resident of Carlisle, Pa., visited Trudeau in New York city and saw a "splendid collection of birds' eggs and drawings of eggs."

1846

Jan. 17. Wrote to Edward Harris, Morristown, N. J., relative to medical experiments he had been carrying out with carotid artery of sheep.

1847

A Founder of New York Academy of Medicine, established this year.

1847-48

Active as artist and sculptor, particularly of medical colleagues.

1848

Oct. 5. Edward Livingston Trudeau (d. 1915) born, the youngest of three children.

1851

Divorced Céphise Berger Trudeau.

1852

March 8. Trudeau's "entire professional library . . . also a fine assortment of medical instruments" sold at auction.

[1857

See Postscriptum.]

1858 (?)

Removed to New Orleans.

1860

Commissioned Brigadier-General of artillery in Confederate Army.

1861

Published *Considérations sur la Défense de l'état la Louisiana, et sur l'organisation de ses milices* (New Orleans, 1861), 82 pp. Copy in Howard Tilton Memorial Library.

Severely wounded at Battle of Shiloh.

1863

Married Louise Bringier and settled at

plantation La Maison Blanche, St. James Parish, on the Mississippi River.

1864

Oct. Taken prisoner.

1882-84

Chief Editor of *Medical Review according to the Dosimetric Method of Dr. Ad. Burggraeve,* published in New Orleans, extending through vols. 1-3.

1887

May 25. Died in New Orleans.

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Postscriptum

Thomas Mayo Brewer, 1814-1880, M.D., "America's first oölogist," close personal friend of Audubon and of Spencer Fullerton Baird while the latter was living at Carlisle, Pennsylvania, as well as later when Baird was associated with the Smithsonian Institution, published *North American Oölogy* (Washington, 1857, reissued in 1859). In his preface Brewer substantiates our prophecy that a work on North American birds' eggs was planned. However, instead of Audubon and Trudeau as coauthors, we learn it was to have been Brewer and Trudeau. Though Brewer does not admit as much, it is within the realm of possibility that this project was spurred by Audubon's having to abandon his inclusion of the drawings of birds' eggs in his *Birds of America,* as announced in his Prospectus, and noted above. That Brewer was deeply indebted to Audubon there can be no doubt, and his characterization is outstanding in a welter of critiques of the American woodsman. Here is Brewer's tribute:

> "To John James Audubon, the gifted artist, the ardent and enthusiastic devotee alike of art and nature, the warm-hearted and kindly impulsive man, we must give credit for having been the first to warm into a permanent and enduring aim the earlier germs of interest in this subject. It is to his prompt and opportune sympathy, his generous contributions of materials and of many valuable specimens which would be irreplaceable if lost, that he is indebted for the foundation of his present knowledge, and many of the materials for his task."

Brewer then remarks that where he has found it necessary to correct errors—

> "It is hardly possible even for the exact and cautious to avoid falling into mistakes,"—

but that he speaks of them "without imputation of censure."

Then Brewer continues with an explanation of the Trudeau material in hand:

"To Dr. James Trudeau, hardly less than to Mr. Audubon, acknowledgments must be made for valuable co-operation and assistance. Many years since, almost coincident with his earliest investigations, the design was entertained of a joint work illustrative of American Oölogy. It has been abandoned in consequence of the continued absence of Dr. Trudeau from the country, the want of knowledge of his present address, and, above all, the fact that no use could be made of the materials jointly collected for the illustrations. To Dr. Trudeau the writer is indebted for a large number of valuable and rare specimens, and for a much larger number of drawings, which are often referred to in the text, but which cannot be made use of in illustrating the present work."

It only remains to report that the high cost of the color plates forced Brewer's project to be discontinued after the appearance of Part One. The Museum of Comparative Zoology, Harvard, received Brewer's oölogical collection by his will and details relative to this present series of paintings should be sought there.

RESTRICTED MOVEMENTS OF THE AMERICAN EEL, *ANGUILLA ROSTRATA* (LeSueur), IN FRESHWATER STREAMS, WITH COMMENTS ON GROWTH RATE[1]

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Introduction

The European eel, *Anguilla vulgaris* Turton, has been studied extensively. Bertin (1956) summarized the pertinent literature on this species. The American eel in comparison, has received little attention. Carlander (1950) compiled existing data on the latter.

The results discussed here were derived as a side-line of more extensive studies on the home range of sunfishes (Centrarchidae) and suckers (Catostomidae); a report on the first phase of this work will appear in the near future (Gunning and Shoop, *In Press*). Home range is defined as the area over which an animal normally travels. Gerking (1959) listed 33 species of fishes which exhibit restricted movement or occupy home ranges. The American eel has not been investigated in this regard.

Methods

Home range studies in stream environments are generally conducted by arbitrarily dividing a continuous stream section into several segments, marking the fish in each segment distinctively, and subsequently sampling the segments, as well as adjacent areas upstream and downstream, to determine how restricted fish movements are (Gerking, 1953; Gunning, 1959; Gunning and Shoop, *In Press*). In the present study, the streams were sampled with an electrical shocker; the details of the sampling procedure will be given elsewhere (Gunning and Shoop, *In Press*). The eels were marked distinctively either by removing one of the pectoral fins or attaching a monel-metal strap tag (fingerling size). Tags were attached dorsally a short distance in front of the posterior end of the vertebral column, in such manner that the hold-fasts of the tags penetrated the musculature. This tagging method is considered to be unsatisfactory, since many tags were lost from the fish judging by the number of recaptured eels possessing scars and notches in the tagging location. Fin-clipping is the better of the two methods we used. However, with only two pectoral fins one can have only two clipping combinations per segment of stream studied. Vladykov (1957) found monel-metal strap tags to be unsatisfactory for eel tagging. He designed ring-shaped strap tags and another type designated "split ring and plate tag." The latter were attached to the lower jaw of eels; they were considered to be satisfactory.

Two study areas (Figs. 1-3) at Talisheek Creek, St. Tammany Parish, Louisiana, and one study area (Figs. 3-4) at Big Creek, Grant Parish, Louisiana, were utilized. Talisheek Creek is 10-20 feet wide at the study areas used, with a few expansions of greater width. Big Creek is 25-35 feet wide at the point of our investigation. In Talisheek Creek, eels are generally collected in pools over a mud bottom, or at obstructions in riffle areas. In Big Creek, where the largest specimens were taken, eels are generally collected under overhanging banks, which afford cover, or at obstructions such as log jams. All study areas were located in the headwaters of the streams where water depth was not prohibitive to successful collection of fishes.

Results

Talisheek Creek

The movements of 15 eels in Talisheek Creek are shown in Table 1. Numerical designations are given to facilitate discussion. Multiple recaptures (eels 1, 11, and 12) resulted in a total of 19 recorded move-

[1] This study was aided in part by research grants from the National Institutes of Health (RG-7125), Sport Fishing Institute (Washington, D. C.), and National Science Foundation (G-10697).

ments for the 15 eels. The first stream segment in which a given eel was first captured is taken as an assumed home area. All subsequent statements concerning extent of movement are thus based on this assumed home area. Hence, an eel marked and subsequently recaptured in the expanded pool region at the upper end of section A, Study Area I, Talisheek Creek (Fig. 1) would be recorded in our field notes as having moved 0-50 feet. Extent of movement of the 19 recaptures may be summarized as follows (Table 1): 1) four eels moved 0-50 feet, 2) seven eels moved 51-100 feet, 3) six eels moved 101-150 feet, and 4) two eels moved 151-200 feet.

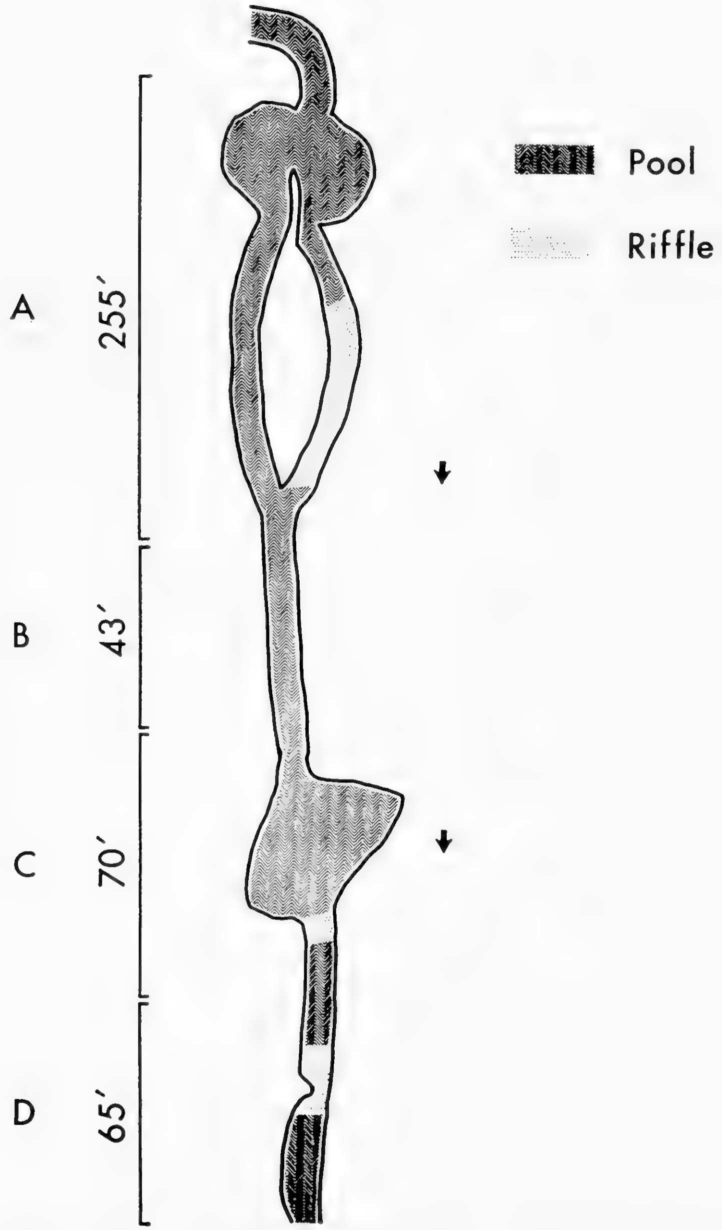

Figure 1. Diagram of Study Area I, Talisheek Creek. Section A is not drawn to scale. Direction of stream flow is indicated by arrows.

All eels were individually recognizable except numbers 9, 10, 14, and 15. All four of these were marked on July 21, 1960, by removing the left pectoral fin. Limited duplication of recaptures was thus possible with regard to these four eels.

The size range of eels 9, 10, 14, and 15 when marked was 305-360 mm, total length. For purposes of determining approximate increases in length from July 21, 1960, to July 26, 1961, for eels 14 and 15, the larger length (360 mm) was used. Eel 14 thus grew at least 138 mm/year. Eel 15 grew at least 325 mm/year, which means that it almost doubled in total length during one year of growth. The writers are not aware of any growth rate data for the American eel derived from the mark-recapture method.

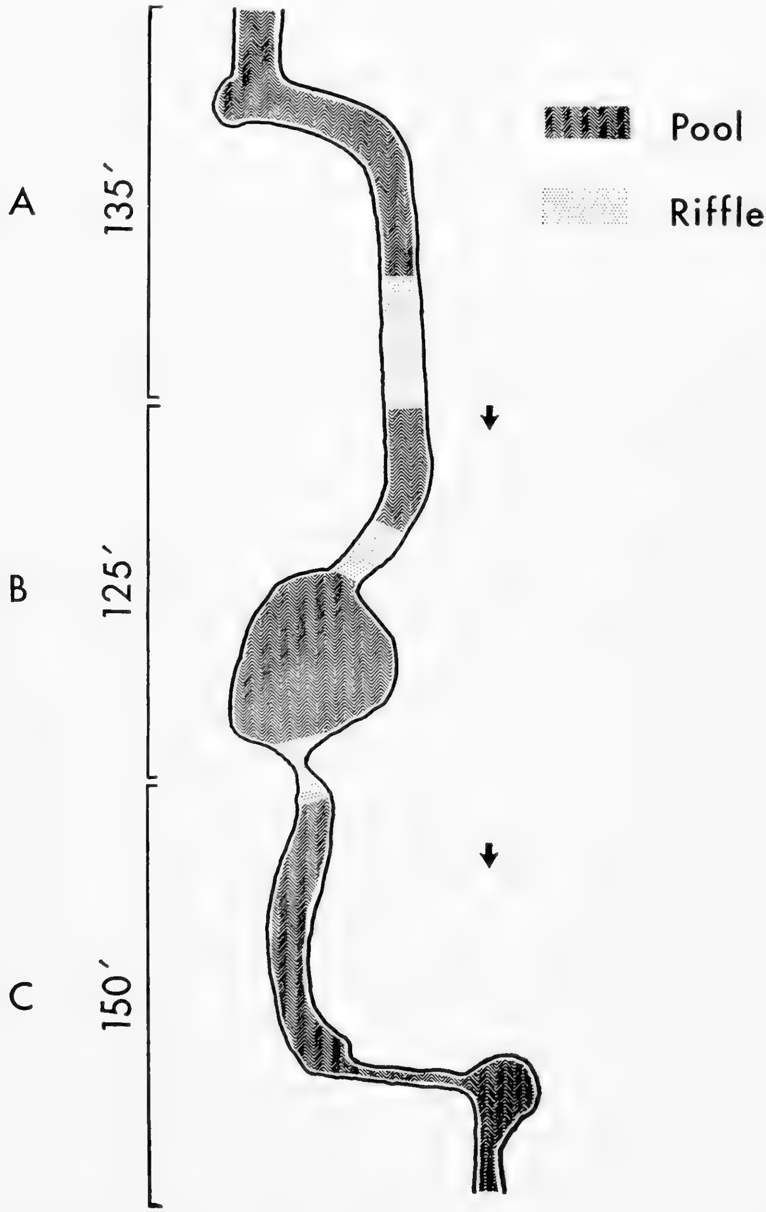

Figure 2. Diagram of Study Area II, Talisheek Creek.

For this reason we record the present observations. The growth rates for our American eels (14 and 15) are considerably higher than growth rates reported for American eels studied in Canada (Smith and Saunders, 1955). The latter authors determined the number of annuli on the scales of a large sample of eels; data on eels believed to be in their fourth to twelfth year of freshwater life were included. Maximum growth derived from scale analysis appears to be 77 mm/year, compared with at least 138 mm/year and 325 mm/year for our two specimens. Although our growth data are extremely limited, the mark-recapture method is far superior to scale analysis in the determination of growth rate. Bertin (1956) states that eel scales should not be used as a measure of the passage of time, and presents data to support his contention. Otoliths are considered to be more reliable as age indicators. One would expect slower growth in Canada than in Louisiana due to latitudinal differences. To reconcile a discrepancy of this degree however, otolith readings or mark recapture data for Canadian specimens are needed. Smith and Saunders (1955) realized the limitations of the scale method of age and growth analysis.

Bertin (1956) reported that the growth of the European eel is extremely irregular. He reached this conclusion after reviewing data on several thousand eels. Bertin (1956: 42-43) emphasized that the dimensions and weight of one individual may be five times as great as those of another individual of the same age. He reported that an eel of 45 cm could belong to any one of age groups VI-X.

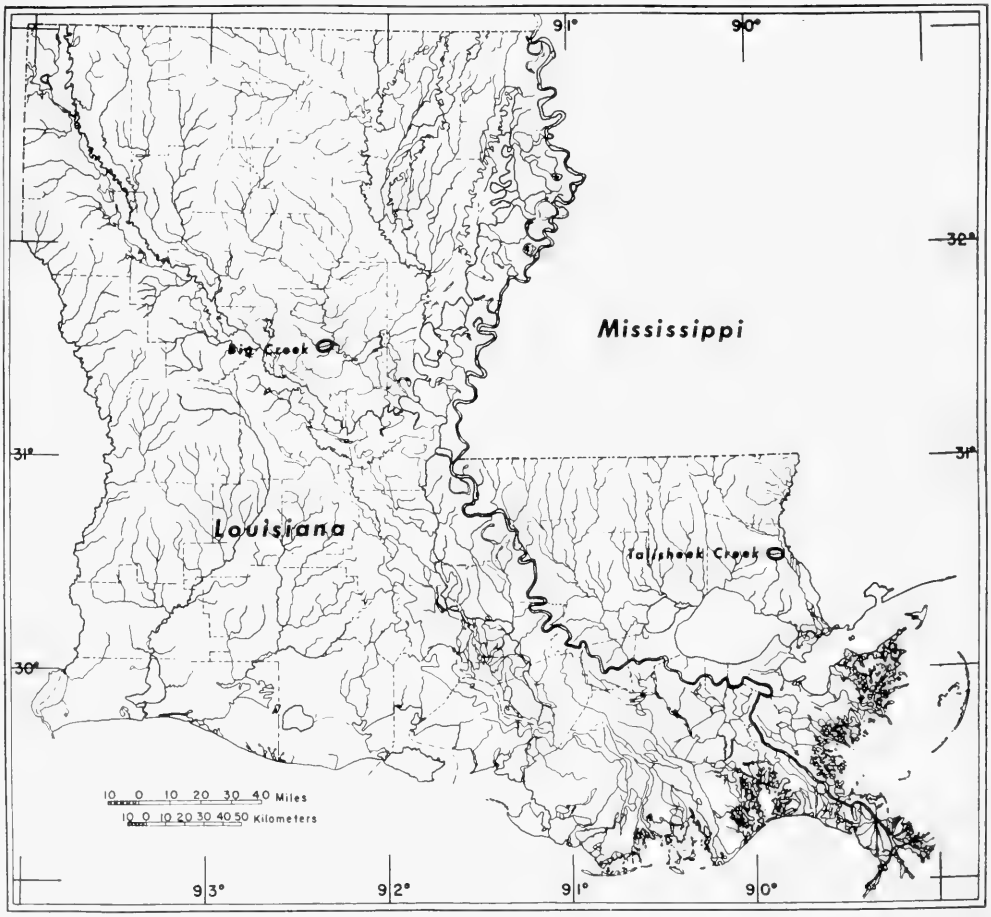

Figure 3. Geographic location of the study areas on Talisheek Creek and Big Creek.

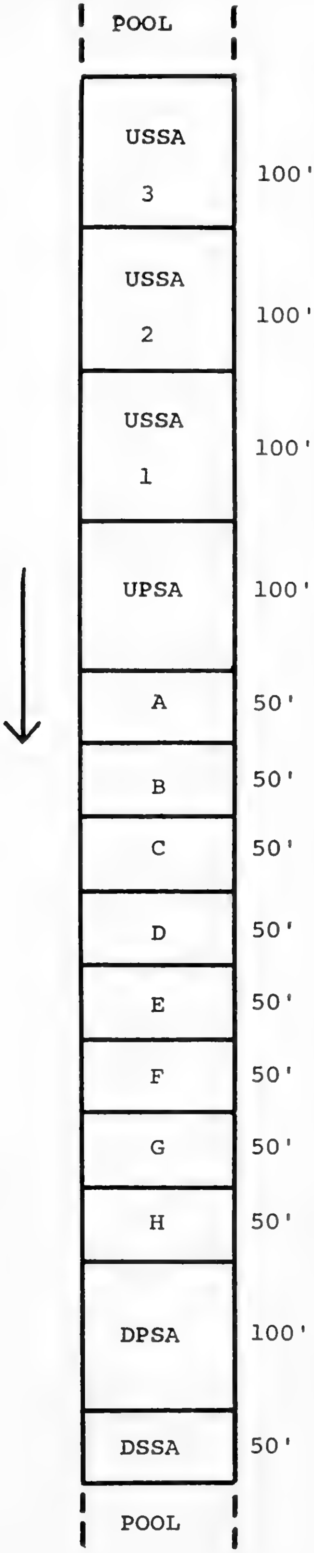

Figure 4. Schematic representation of the study area on Big Creek. The stream segment is actually S-shaped. USSA, Upstream Secondary Stray Area; UPSA, Upstream Primary Stray Area; DPSA, Downstream Primary Stray Area; DSSA, Downstream Secondary Stray Area.

TABLE 1.
Movements of American eels in Talisheek Creek, Louisiana

Eel Number	Date Marked*	Date Recaptured	Total Length in mm.	Distance Travelled (In Feet)
1	9/7/60	....	390	....
		9/30/60	......	0–50
		10/28/60	......	0–50
		11/18/60	......	0–50
2	11/18/60	....	310	....
		12/9/60	310	0–50
3	9/7/60	....	255	....
		9/30/60	......	51–100
4	9/7/60	....	355	....
		9/30/60	......	51–100
5	10/28/60	....	280	....
		12/9/60	285	151–200
6	9/7/60	....	560	....
		10/28/60	......	51–100
7	9/7/60	....	305	....
		10/28/60	......	51–100
8	9/30/60	....	390	....
		10/28/60	......	101–150
9	7/21/60	....	305	....
		7/28/60	......	51–100
10	7/21/60	....	360	....
		7/28/60	......	51–100
11	8/9/60	....	......	....
		9/7/60	321	101–150
		11/4/60	......	101–150
12	10/7/60	....	567	....
		11/4/60	......	51–100
		12/2/60	......	101–150
13	8/10/60	....	360	....
		10/7/60	......	151–200
14	7/21/60	....	360	....
		7/26/61	498	101–150
15	7/21/60	....	360	....
		7/26/61	685	101–150

* All eels were identified by metal tags except numbers 9, 10, 14, and 15; these were fin-clipped.

Big Creek

Four eels were marked in the study area at Big Creek (Figs. 3-4). No other unmarked eels were taken in the 950 foot segment of stream during the period it was studied; a single eel was captured in a basket trap in a large pool below the study area (Fig. 4), however. One of the four eels (610 mm total length) was tagged with a monel-metal strap tag on November 25, 1960; it was never taken again. A second eel (Table 2, eel 3) was tagged in the same manner on September 1, 1960. It was subsequently recaptured in the same stream segment on November 25, 1960, but was not taken again. The remaining two eels (Table 2, eels 1-2) were fin-clipped; these were taken repeatedly.

Eel number 1 was recaptured six times between July 7, 1960, and May 6, 1961. During this 10-month period, the eel probably remained within a home range consisting of 450 linear feet of stream (Table 2; Fig. 4).

TABLE 2.
Recapture data for three American eels marked in Big Creek, Louisiana

Eel Number	Date Marked*	Stream Segment Marked In	Date Recaptured	Stream Segment Recaptured In	Total Length in mm.
1	7/7/60	Section A	....	....	......
			7/8/60	USSA #2	......
			10/21/60	USSA #3	660
			11/25/60	USSA #3	......
			3/25/61	UPSA	678
			4/22/61	USSA #1	685
			5/6/61	UPSA	......
2	4/14/60	Section D	....	....	760
			6/7/60	D	......
			6/8/60	A	......
			7/7/60	F	......
			8/2/60	D	......
			5/30/61	C	......
3	9/1/60	USSA #3	....	....	915
			11/25/60	USSA #3	......

* Eel number 3 was marked using a monel-metal strap tag; the other two were fin-clipped.

Eel number 2 was recaptured five times between April 14, 1960, and May 30, 1961. During this 13-month period the eel presumably remained within a home range consisting of 300 linear feet of stream (Table 2; Fig. 4).

Eel number 1 grew 25 mm between October 21, 1960, and April 22, 1961. Since a full year's growth was not recorded, no comparison is made with other data.

DISCUSSION

On the basis of the recapture data presented here, we conclude that eels occupying the headwater regions of streams exhibit restricted movements. The eel recaptures from Talisheek Creek indicate, mostly on the basis of short-term observations (one week to three months, except numbers 14-15; Table 1), that the home range of the eel is probably 200 linear feet of stream or less. The Big Creek recaptures, covering longer time periods of 10-13 months, indicate that these eels were restricted to home ranges of 300-450 linear feet of stream. The home range of smaller fishes, sunfishes for example, generally ranges from 100-200 feet (Gerking, 1953; Gunning, 1959; Gunning and Shoop, *In Press*). Sufficient recapture data were not available to compare home ranges of young versus older eels.

One factor detracts from the home range hypothesis. Twenty-seven eels tagged in Study Areas I and II, Talisheek Creek, were not recaptured. Tag loss is known to be significant, hence this factor should be considered. Although our field notes are not complete in this regard, nine instances were recorded wherein eels lost tags. Scars and notches were clearly visible at the tagging location. Nevertheless, critics of the home range hypothesis would point out that a considerable percentage of the 27 eels that were marked but not subsequently recaptured may have left the study areas.

Fortunately, a limited check on the relative amounts of straying from study areas on Talisheek Creek was feasible. The two study areas utilized were 0.4 mile apart. We have collected marked longear sunfish *(Lepomis megalotis)*, bluegill *(Lepomis macrochirus)*, and spotted bass *(Micropterus punctulatus)* that have traversed the distance between the two study areas in whole or in part. We have not, however, taken eels that have strayed from the study areas, although equal opportunity was afforded to do so.

Vladykov (1957) recorded eel movements of 200 miles extent in the St. Lawrence River and other waters of Quebec. The maximum time recorded between tagging of an eel and its recovery was five years and eleven months. Movements of 200 miles are not spectacular, considering that eels are presumed to travel from a spawning area in the Sargasso Sea to inland streams of North America. Smith and Saunders (1955) described runs of the American eel from various lakes in New

Brunswick, Canada, which represented the beginning of their return trip to the ocean. The movements of eels must be considered with respect to the specific environment they occupy and the phase of their life history being completed.

Eels entering the mouth of the Pearl River, of which Talisheek Creek is a tributary (Fig. 3), could travel a minimum of 30 miles to reach the study areas on Talisheek Creek. The present configuration of Talisheek Creek differs somewhat from that shown in Figure 3 due to the construction of a canal. Those eels entering the mouth of the Mississippi River would normally travel 250-350 miles if their destination should happen to be the study area on Big Creek. One must keep in mind the fact that many alternate routes would be possible, since eels can travel overland to a limited degree if the ground is moist (Eddy and Surber, 1947; Bertin, 1956).

Eels are catadromous; thus the primary recruitment of freshwater eel populations is by elvers from the ocean. One might anticipate that the distance of a habitat from salt water would affect the number of young eels that reach it (Smith and Saunders, 1955). The effect of distance alone is often obscured, however, since it is modified by man-made obstructions, mortality during extended journeys, and so forth. Smith and Saunders (1955) showed that the smaller standing crops of eels per unit area in New Brunswick lakes were associated with greater distances from the sea and with obstructions to eel movements.

The composition of the eel population of Talisheek Creek differed greatly from that of Big Creek, which is much farther from the Gulf of Mexico (Fig. 3). The smallest eel taken in Big Creek measured 610 mm total length. On the other hand, 13 of the 15 eels taken in Talisheek Creek measured less than 400 mm total length when first captured (Table 1). The general impression gained from studying both streams was that Talisheek Creek has a dense eel population. One of us (G.E.G.) has sampled some 30 streams in midwestern United States, mostly in Illinois, without seeing an eel population as dense as the one in Talisheek Creek. Further studies are needed in order to determine if other streams tributary to the Gulf of Mexico have such dense eel populations.

It has been assumed for some time that only female eels travel very far inland. The males, which are smaller in size, are believed to remain near the various river mouths in brackish water.

Acknowledgments

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Abstract

Movement of the American eel was studied in two headwater streams in Louisiana. Eels were marked using metal tags or by fin-clipping. Short-term experiments in Talisheek Creek yielded home range estimates of 200 linear feet of stream. Long-term observations, though limited, indicated home ranges up to 450 linear feet of stream for larger specimens. Limited growth data based on observation of marked eels showed that growth is quite irregular, a fact well-established for the European eel.

NOTES ON THE AFFINITIES OF THE MEMBERS OF THE BLANDINGII SECTION OF THE CRAYFISH GENUS PROCAMBARUS
(Decapoda, Astacidae)

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The last comprehensive work in which the relationships of the members of the Blandingii Section were treated was that of Ortmann (1905). Subsequent studies involving segments of the Section include those of Hobbs (1942b, 1958c), Williams (1954), Villalobos (1953, 1955, 1959), and Penn (1956a). Ortmann (1905: 101-102) included 15 species in the Blandingii Section, assigning: *spiculifer, versutus, pubescens, angustatus,* and *lecontei* to his "Group of *C. spiculifer*"; *acherontis,*[1] *blandingii, hayi,* and *fallax* to his "Group of *C. blandingii*", *clarkii* and *troglodytes* to his "Group of *C. clarki*"; and *evermanni, barbatus, weigmanni,* and *alleni* to his "Group of *C. alleni*". Of these, *barbatus* was removed to the Barbatus Section and *acherontis* to the Acherontis Section by Hobbs (1942b: 35 and 91), and *weigmanni* was declared a *nomen nudum* by Villalobos (1950: 383). Since 1905, some 42 species and subspecies assignable to the Blandingii Section have been described, and are listed following the diagnoses of the several groups below.

Before entering into a discussion of the inter-relationships of the members of the Blandingii Section, it seems advisable to discuss briefly the position of the Section within the genus, and to do so, it will be helpful to consider the probable characteristics of the ancestral procambarid and to emphasize certain morphological features which have not been thoroughly considered, although Villalobos has mentioned and illustrated some of them beautifully for the Mexican crayfishes.

The Ancestral Procambarid

Although certain non-secondary-sexual characteristics have been found to be of taxonomic importance, evidence exists which indicates that many, if not most of them, might often better be associated with environmental factors than with phylogeny. It is not implied that such characteristics have *no* phylogenetic significance. For example, such features as spination, which is frequently strongly developed in crayfishes living in open water and obsolete in burrowing forms, can only be useful when used in combination with other characters which are not so affected. On the other hand, all of the members of the Spiculifer Group (see below) possess two or more lateral spines on the carapace, a characteristic which is shared only by the members of the Pilosimanus Group of the Mexicanus Section, distant relatives at best of the members of the Spiculifer Group—the first pleopods of the males of the two groups are morphologically far removed. It is maintained that within each group the presence of multiple spines *is* of phylogenetic significance, and it is at least possible that in the advanced Pilosimanus Group the two spines represent a primitive retention, but all students of the crayfish will agree that there are many other species of crayfishes with only a single spine (or without any) which are more closely related to members of the Spiculifer Group than is any member of the Pilosimanus Group.

In contrast to those characteristics which appear to be influenced by environmental factors are the secondary sexual ones which seem not to have been strongly influenced in their form by other than genetic factors—suffice it to say that no particular secondary sexual characteristic may be associated with any particular type of environment. These secondary sexual characteristics associated with the female will undoubtedly provide, when adequately studied, additional evidence upon which an understanding of the phylogeny of the group is ultimately to be realized. Presently, no comparative studies have been made of them. Therefore, our present understanding is based primarily on the secondary sexual characteristics of the

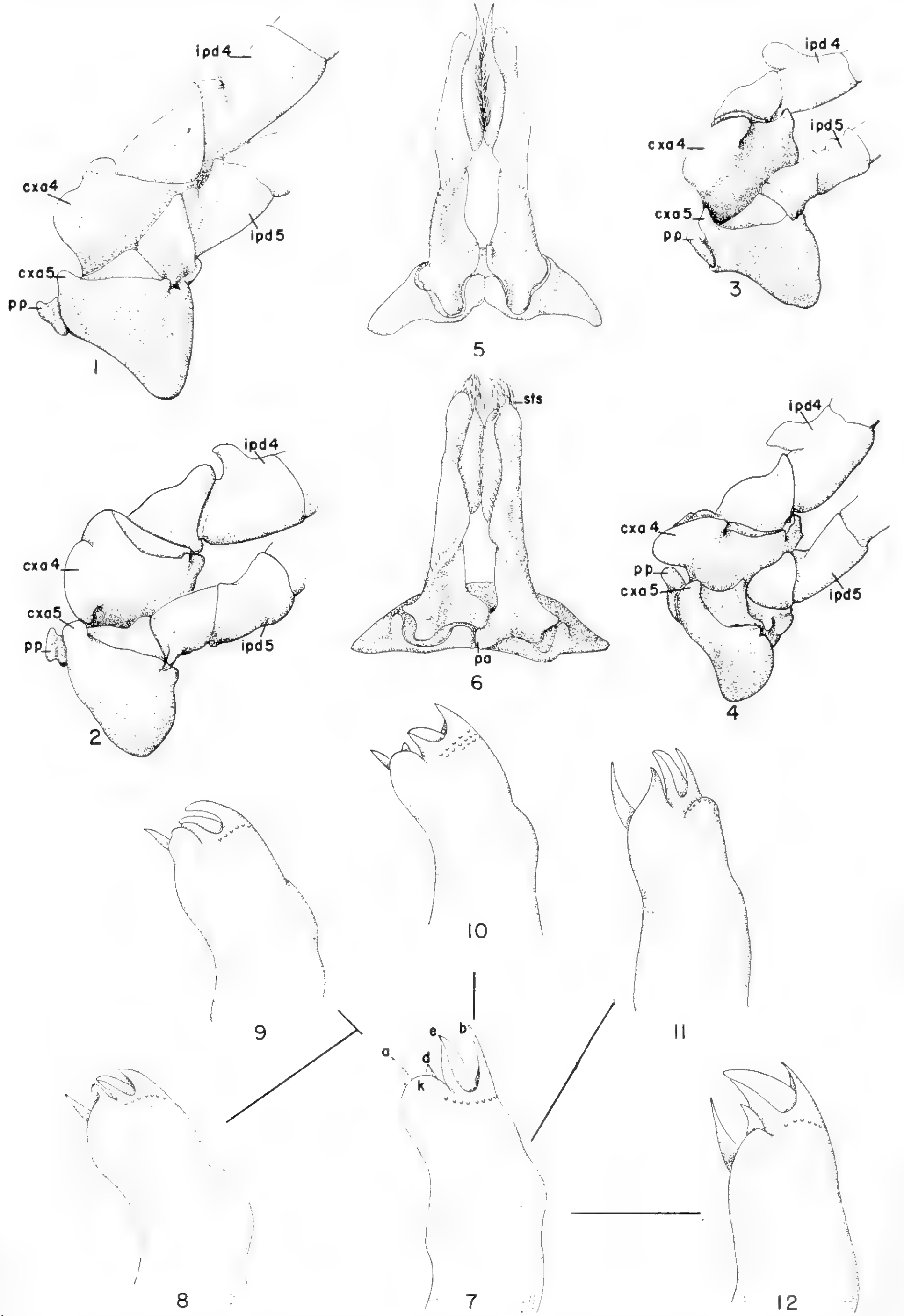
[1] This designation was based on *acherontis* Faxon (not Lönnberg) which is a synonym of *lucifugus lucifugus* (Hobbs).

male augmented by such characteristics as spination, body proportions, color, etc.

Ortmann (1905: 93-96) outlined what he considered to have been the primitive facies of the genus *Cambarus* [equivalent to the subfamilies Cambarinae (Hobbs 1942a) and Cambarellinae (Laguarda 1961)]. These features may be summarized as follows: (1) *General shape of the carapace* ". . . seems to be more or less ovate, generally depressed". (2) *Areola* ". . . rather broad and short". (3) *Rostrum* ". . . rather long . . . with more or less parallel margins, with a marginal spine on each side, and a rather long acumen". (4) *Copulatory hooks of the male* were considered by Ortmann but no concrete generalization was made; it does seem apparent that he considered an increase in number of hooks a more advanced condition. (5) *Chelae*—"Among the more primitive species the shape of the chelae seems to be more or less subcylindrical, and rather elongated." (6) Ortman discussed the *"Sexual Organs"* (= first pleopods) of the male, and emphasized their importance in that their study "gives us a standard by which to judge the other characters that are of systematic value, and as we shall presently see, there is hardly another structure that has the same value for revealing the affinities within the genus, that is to say, the characters generally develop independently in different groups, being clearly subject to parallelism, presumably under the influence of similar external conditions." He did not characterize the generalized pleopod but stated, "The most primitive sexual organs are found in species of the first section [Section of *C. digueti*], where there is only one tooth at the end of the outer part." (Ortmann, loc. cit., p. 98).

Hobbs (1940c) depicted a hypothetical generalized pleopod, and while stating that "*Cambarus pubescens, Cambarus lucifugus,* and *Cambarus pallidus* may be cited as species which most nearly approximate the hypothetical pleopod in their structure", he indicated that the pleopod of *Cambarus digueti* "most nearly approaches that of the prototype appendage . . ." The latter statement is not at all in line with my present views, and in making it, I was most certainly influenced by Ortmann's contention that the Section of *C. digueti* represents the most primitive of the cambarids. In discussing the evolutionary history of the Pictus Group Hobbs (1958c) treated four characteristics and the conclusions were similar to those of Ortmann. "A *broad, short areola* (not more than four times as long as broad, and its length not exceeding thirty per cent of the total length of the carapace) in contrast to a narrow long one is here deemed more generalized" . . . "a *rostrum with subparallel or convex margins and bearing a pair of marginal spines* . . . is a more generalized type than one in which the margins converge or are lacking spines altogether" . . . *"the first pleopod of the first form male terminating in four distinct elements* is considered to be more primitive than one terminating in fewer elements" . . . and a *"color pattern . . . which includes a U-shaped 'saddle' on the thoracic portion of the carapace* is considered to be more generalized than one that has only portions of the saddle." The above generalizations are maintained here.

Hooks on the ischiopodites of the pereiopods of the males are employed in amplexus in holding the females. They occur in a variety of forms with their apices either simple or bituberculate, and they may or may not be opposed by a tubercular prominence on the corresponding coxa. Not only is there variation in form of the hook but variations also occur in their presence or absence on the second through the fifth pereiopods. Among the nearctic and oriental crayfishes the following combinations of hooks are present: (1) only on the third —*Procambarus, Orconectes,* and *Cambarus;* (2) only on the fourth—*Procambarus* and *Paracambarus;* (3) on the second and third —*Cambaroides* and *Cambarellus;* (4) on the third and fourth—*Procambarus, Troglocambarus, Orconectes* and *Cambarus dissitus* Penn (1955); (5) on the third and fourth and occasionally on the fifth—*Procambarus latipleurum* Hobbs (1942b); (6) absent—*Pacifastacus.* It is at least possible that the primitive stock from which the cambaroids, cambarellids, and cambarids were derived exhibited serially homologous hooks on the ischiopodites of the second through fifth pereiopods of the males and that the derived condition has been reached through the loss of hooks with two main lines having developed: (1) retention of hooks on the second and third—*Cambaroides* and *Cambarellus,* and (2) retention



Figures 1-12. **1-4.** Caudalventral views of proximal podomeres of fourth and fifth periopods of first form males. **1.** *P. gracilis.* **2.** *P. pictus.* **3.** *P. latipleurum.* **4.** *P. riojae.* **5-6** Caudal view of the first pleopods of first form males. Pleopods in the normal resting position. **5.** Symmetrical pleopods of *P. gracilis.* **6.** Asymmetrical pleopods of *P. pictus.* **7-12.** Lateral views of hypothetical pleopods of first form males. **7.** Generalized Procambarid. **8.** Proclarkii. **9.** Proplanirostris. **10.** Propictus. **11.** Problandingii. **12.** Prospiculifer. Abbreviations—a, mesial process; b, cephalic process; cxa4 and cxa5, coxal apophyses of fourth and fifth pereiopods; d, caudal process; e, central projection; ipd4 and ipd5, ischiopodites of fourth and fifth pereiopods; k, caudal knob; pa, proximal apophysis of first pleopod; pp, penis papilla.

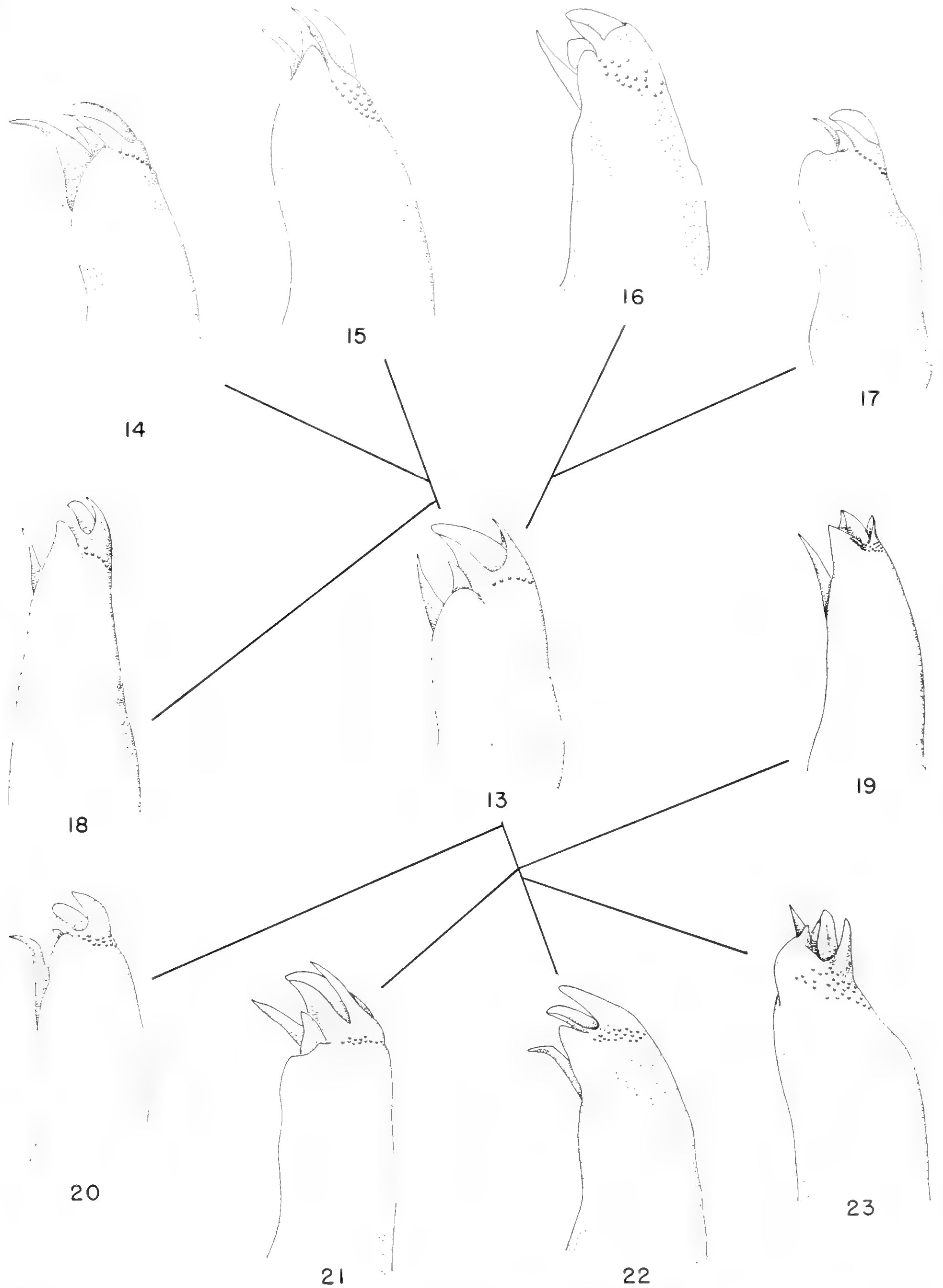
of hooks on the third and fourth. Adhering to the second derived condition are many members of the genus *Procambarus,* a few members of *Orconectes*, one member of the genus *Cambarus,* and the monotypic *Troglocambarus*. Deviating from the second derived condition are (a) those which retained hooks only on the third pereiopods —some members of *Procambarus*, most members of *Orconectes*, and all but one member of *Cambarus;* and (b) those which retained hooks only on the fourth pereiopods—some Mexican members of *Procambarus* and the two species (also Mexican) of *Paracambarus*. The possession of hooks on the fifth pereiopod of some members of *P. latipleurum* is considered to be an atavistic tendency. Following this explanation, one must conclude that the absence of such hooks in *Pacifastacus* (as well as in the European Astacines) must be explained as a loss from primitive stock, or that hooks appeared in the ancestral stock after the Astacines had been separated from it, or that there was an independent origin, presumably from marine ancestors, of the two stocks of holarctic crayfishes. In light of the absence of cyclic dimorphism in the adult males of the Astacinae (including *Pacifastacus*) and its occurrence in the remaining subfamilies (Cambaroidinae, Cambarinae, and Cambarellinae) one of the latter two alternatives seems more probable.

Heretofore not considered are the apophyses which occur on the coxae of the third, fourth, and fifth pereiopods of the male, particularly those of the fourth and fifth. These are most prominently developed in *Paracambarus, Cambarellus, Troglocambarus*, and most members of *Procambarus* but are poorly developed or absent in most members of the genera *Orconectes* and *Cambarus*. There is scarcely a trace of them in *Cambaroides*. What is believed to be the generalized condition of the fourth and fifth pereiopods is depicted in Figure 2 where the apophysis on the fourth pereiopod is a vertically expanded prominence, flattened in the longitudinal axis of the body, projecting ventrally from the caudomesial rim of the coxa. The evolutionary trends are believed to have been in two directions: (1) a shifting of the apophysis on the fourth from the vertical to the horizontal axis (Figs. 3, 4) and (2) a reduction of the apophysis to form a globular prominence on the fourth coxa and a tuberculiform projection on the fourth (Fig. 1)—this tendency culminating in the absence of one or both apophyses.

Not previously taken into account also are the articulations of the first pleopods (of the male) and the subterminal setae that are present on many of them. The first pleopods may be *symmetrical* (Fig. 5), or *asymmetrical* (Fig. 6). If symmetrical, the *bases* of the two pleopods, when viewed ventrally, lie in essentially the same horizontal plane, and have similar configurations. If asymmetrical, the base of one of the pleopods (the left in all specimens examined) lies in a plane posterior to the other, and frequently their proximomesial apophyses overlap. The distinct asymmetrical condition appears only in the genera *Procambarus* (where it is a characteristic of the majority of the species), *Paracambarus,* and *Troglocambarus*. The symmetrical arrangement is considered to be more primitive.

The presence of terminal setae on the pleopods of holarctic crayfishes must be assumed to be a derived condition; however, in the genus *Procambarus* a row of them across the anterolateral surface at the base of the terminal elements must be viewed as a generalized feature; likewise in both paracambarids, and *Troglocambarus*. The major trends from the generalized setiferous condition are: (1) an elevation of the part of the pleopod bearing the row to form a knob—Blandingii Group—and the shifting of this knob caudally along the lateral surface of the appendage (Figs. 44, 45); (2) a duplication of the row to form several rows or a cluster (Figs. 13, 21, 15); and (3) a reduction in the number of setae culminating in a total loss of them (Gracilis and Mexicanus sections and certain members of other sections).

To summarize, the ancestral Procambarid is considered to have had the following characteristics: (1) carapace subovate, somewhat depressed, and bearing several lateral spines on each side of its carapace; (2) areola not more than four times as long as broad, and its length not exceeding 30 per cent of the total length of the carapace; (3) rostrum with subparallel or convex margins and with marginal spines delimiting the base of an acumen about one-third the total length of the rostrum; (4)



Figures 13-23. Lateral view of terminal portions of first pleopods of first form males. **13.** Hypothetical Prospiculifer. **14.** *P. raneyi.* **15.** *P. spiculifer.* **16.** *P. ouachitae.* **17.** *P. suttkusi.* **18.** *P. versutus.* **19.** *P. penni.* **20.** *P. vioscai.* **21.** *P. echinatus.* **22.** *P. natchitochae.* **23.** *P. dupratzi.* [dark semicircles represent positions of subterminal setae.]

color pattern with a U-shaped "saddle" on the thoracic portion; (5) chelae that are elongate, subovate, and slightly depressed; (6) simple hooks on the ischiopodites of the third and fourth pereiopods; (7) coxae of the third, fourth, and fifth pereiopods provided with apophyses—that on the fourth elongate in the vertical axis, and that on the fifth smaller and compressed in the longitudinal axis of the body; (8) symmetrical first pleopods bearing a row of terminal setae on the cephalolateral surface of the appendage at the base of the terminal elements; tip terminating in four distinct parts disposed as illustrated in Figure 7 and with a *caudal knob* (k) at the base of the *caudal process* (d).

The Composition of the Genus Procambarus

As presently understood, the genus *Procambarus* consists of some 108 species and subspecies which have been assigned to *Sections, Groups,* and *Subgroups.* Hagen (1870), in the first monograph of the American Astacidae, initiated the practice of employing infrageneric categories, "Groups", for the purpose of expressing relationships between certain species. Ortmann (1905) proposed a supergroup category which he designated the "Section". Subsequent authors have found it convenient to continue to utilize both categories, and Hobbs (1942b), Penn (1953a), and Villalobos (1955) employed a third one, "Subgroup". (The latter is not utilized in the proposed groupings in this study.)

While there has been some rearrangement of the groupings and shuffling of species within them from time to time, it does not seem appropriate here to summarize such changes. With full acknowledgment of the contributions of those authors listed in *References Cited,* the infrageneric categories herein recognized within the genus *Procambarus* are summarized in Table 1. Following each, the number of species and

TABLE 1.
Subdivisions of the Blandingii Section of the Genus Procambarus [1]

Sections	Groups
Blandingii (55) Ortmann 1905: 98	Spiculifer (10) Ortmann 1905: 100 Pictus (10) Hobbs 1942b: 129 **Seminolae (6) Hobbs 1942b: 142 **Lucifugus (3) Hobbs 1942b: 134 Blandingii (10) Ortmann 1905: 100 **Planirostris (7) Penn 1953a: 75 Clarkii (5) Ortmann 1905: 100 Disjunct members (4)
Tenuis (1) Here designated.	
Riojae (6) Villalobos 1955: 94	Riojae (3) Villalobos 1955: 96 Erichsoni (3) Villalobos 1955: 130
Digueti (2) Ortman 1905: 98	
Advena (8) Hobbs 1942b: 73	Advena (4) Hobbs 1942b: 73 Rogersi (4) Hobbs 1942b: 88
Acherontis (1) Hobbs 1942b: 91	
Hinei (2) Penn 1953c: 67	
Barbatus (12) Hobbs 1942b: 33	Barbatus (7) Hobbs 1942b: 35 Alleni (3) Ortmann 1905: 100 Disjunct members (2)
*Gracilis (5) Ortmann 1905: 98	
Mexicanus (16) Villalobos 1955: 159	Mexicanus (8) Villalobos 1955: 160 Pilosimanus (4) Villalobos 1955: 160 Cubensis (4) Here designated.

[1] Following each category the number of species and subspecies assigned to it is enclosed in parentheses, and this is followed by the author of the category.
* Originally proposed as a group.
** Originally proposed as a subgroup.

subspecies assigned to it is enclosed in parentheses.

As is indicated in Table 1, more than half of the species and subspecies within the genus are placed within the Blandingii Section, the most heterogeneous, but which nevertheless appears to contain the most generalized members. The characteristics of the Section and the inter-relationships of the groups within it are discussed below. Excluding introductions by man (see Penn, 1954), the range of the Section extends from southern New England, east of the Appalachian mountains to Florida, northwest along the southern Great Lakes to Minnesota, and south into Veracruz, Mexico.

The Tenuis Section, represented by a single species, *Procambarus tenuis* Hobbs (1950: 194), is undoubtedly one of the most disjunct of the genus. Its range is restricted to eastern Oklahoma and western Arkansas. Although its affinities are questionable, it seems probable that it is more closely allied to the members of the Blandingii Section than to the other species.

The Riojae Section, restricted to the Gulf slopes in Hidalgo, Puebla, and Veracruz, Mexico, consists of two distinct groups. The more generalized Riojae Group shows, in the first pleopods of *P. riojae* (Villalobos 1944a: 162) and *P. Hoffmani* (Villalobos 1944a: 169), distinct affinities with members of the generalized Spiculifer and Pictus groups of the Blandingii Section, while the third member, *P. hortonhobbsi* Villalobos (1950: 402), possesses a pleopod which is quite similar to those of the three members of the Erichsoni Group. *P. contrerasi* (Creaser 1931: 1) is probably the most divergent member of the Section.

The Digueti Section, comprising only two species that themselves are not strikingly similar, is restricted to streams of the Pacific slope in Jalisco and Michoacan, Mexico. These two morphologically and geographically disjunct species *P. digueti* (Bouvier 1897: 225) and *P. bouvieri* (Ortmann 1909: 159) are perhaps best linked to the other sections through the Simulans Section.

The seven members of the Advena Section, confined to the coastal plain of Georgia and Florida, constitute a closely allied morphological and ecological assemblage. In both respects, the Section represents, as a whole, the most specialized segment of the genus. Except for *P. pygmaeus* Hobbs (1942b: 83), all of its members are primary burrowers, very probably deriving early from a stock not greatly unlike *P. spiculifer* (LeConte 1856: 401), a member of the Blandingii Section.

The monotypic Acherontis Section is restricted to subterranean waters in peninsular Florida, and while not obviously related to any other particular species, exhibits certain characteristics of the Spiculifer Group of the Blandingii Section.

The Hinei Section, comprising two species found in lentic and sluggish lotic habitats in the coastal areas of Louisiana and Texas, like the Acherontis Section is morphologically somewhat disjunct. It is probably best linked to the other sections through the Pictus Group of the Blandingii Section.

There seems to be little reason to question the origins of the three remaining Sections, Barbatus, Simulans, and Mexicanus, from a common stock. The three sections are allopatric, occupying respectively the coastal plain from South Carolina to Alabama; Alabama to Wisconsin southwest to Tamaulipas, Mexico and Veracruz to Honduras, Cuba and the Isle of Pines. While obvious similarities occur between the first pleopods of the members of these three sections, it is decidedly difficult to link them with the remaining sections, except as pointed out above, possibly with the Digueti Section. At present, our best clue is seen in *P. rathbunae* (Hobbs 1940a: 414) and the supposedly disjunct *P. alleni* (Faxon 1884: 110), the pleopods of which resemble respectively those of *P. shermani* Hobbs (1942b: 61), a disjunct member of the Barbatus Section which approaches the Blandingii Section, and *P. bivittatus* Hobbs (1942b: 96) a member of the Blandingii Section.

The foregoing treatment is so brief as to seem almost useless; however, a fuller documented manuscript on the Sections of the genus exclusive of the Blandingii Section is in progress, and the evidence upon which the above statements of relationships are made will be presented therein. If, for the present, these statements be granted, it be-

Key to Sections of *Procambarus*

1	Hooks present on ischiopodites of fourth pereiopods only, occasionally with a rudimentary hook on that of third	2
1′	Hooks present on ischiopodites of third, third and fourth, or third, fourth, and fifth pereiopods; hook on third always well developed	3
2(1)	First pleopod with subterminal setae, mesial process decidedly the most conspicuous terminal element; apophysis on coxa of fourth pereiopod not prominent	Barbatus Section
2′	First pleopod without subterminal setae, mesial process never the most conspicuous terminal element; apophysis on coxa of fourth pereiopod strongly developed and expanded horizontally	Riojae Section
3(1′)	Hooks on ischiopodites of third and fourth pereiopods bituberculate	Acherontis Section
3′	Hooks on ischiopodites of third, third and fouth, or third, fourth and fifth pereiopods, but never those on third and fourth (both) bituberculate	4
4(3′)	First pleopods asymmetrical (fig. 6)	5
4′	First pleopods symmetrical (fig. 5)	9
5(4)	First pleopods extend forward between bases of second pereiopods	6
5′	First pleopods extend forward between bases of third pereiopods	8
6(5)	Hooks present on ischiopodites of third and fourth pereiopods	*P. shermani* (Barbatus Section)
6′	Hooks present on ischiopodites of third pereiopods only	7
7(6′)	Cephalic process of first pleopod forming a rounded plate across cephalic side of tip	*P. bouvieri* (Digueti Section)
7′	Cephalic process present or absent but never forming a rounded plate across cephalic side of tip	Advena Section
8(5′)	Cephalic process of first pleopod arising *distinctly* from mesial side of appendage; palm of chela often barbate; two lateral spines never present on each side of carapace	Barbatus Section
8′	Cephalic process of first pleopod seldom arising *distinctly* from mesial side of appendage (only in *P. suttkusi* and occasionally in *P. ouachitae*, both of which possess two lateral spines on each side of carapace); one of two lateral spines may be present on each side of carapace; palm of chela never barbate	Blandingii Section
9(4′)	Hooks present on ischiopodites of third and fourth pereiopods	10
9′	Hooks present on ischiopodites of third pereiopods only	11
10(9)	Dactyl of chela longer than inner margin of palm	Tenuis Section
10′	Dactyl of chela much shorter than inner margin of palm	Hinei Section
11(9′)	Cephalic process of first pleopod spiniform, directed distally and although sometimes small, always clearly recognizable; prominent caudal process corneous and distally somewhat lamellate	Gracilis Section
11′	Cephalic process of first pleopod never spiniform, either broad and corneous, acute, vestigal or absent; caudal process mostly absent, if present never lamellate	12
12(11′)	Caudal process present; cephalic process a transversely broad corneous element	Digueti Section
12′	Caudal process absent; cephalic process usually absent (small and acute in *P. acanthophorus*)	Mexicanus Section

comes apparent that the Blandingii Section has served as a focal point, suggesting both diversity of its members and the probable generalized nature of at least some of them.

BLANDINGII SECTION (*Ortmann* 1905: 98)

Diagnosis.—(Based on the first form male.) Palm of chela never barbate. Hooks present on ischiopodites of third and fourth pereiopods and occasionally also on fifth. Coxae of fourth pereiopods with prominent vertically disposed apophyses (Fig. 2). First pleopods asymmetrical (except in *P. jaculus*,[2] a member of the Planirostris Group) and reach the coxopodites of the third pereiopod when the abdomen is flexed; subterminal setae present except in the disjunct *bivittatus* and *lewisi;* pleopod terminating in three or four distinct parts (cephalic or caudal processes may be lacking); cephalic process never *arising distinctly* from mesial face of appendage except in *suttkusi* and sometimes in *ouachitae* (both of which have two lateral spines on each side of carapace).

Relationships.—The inter-relationships of the several groups of this Section are depicted in Figures 7 through 12 in which five secondary prototype appendages radiate from the prototype of the Blandingii Section. The secondary prototype appendages (Figs. 8 through 12) are reproduced again in the following plates where the relationships of the members of each group are indicated by lines diverging from the prototype. It will be noted that the Pictus, Seminolae, and Lucifugus groups are postulated to have arisen from the same prototype (Figs. 25-43).

[2] There is only one first form male of this species known, and one of the pleopods had been removed before it was determined whether or not they are symmetrical. In a recent examination of this specimen, the pleopods appear to be symmetrical.

Key to the Groups and Disjunct Members of the Blandingii Section

1	Albinistic, eyes reduced	Lucifugus Group
1′	Pigmented, eyes well developed	2
2(1′)	Two lateral spines present on each side of carapace	Spiculifer Group
2′	A single lateral spine present or absent on each side of carapace	3
3(2′)	Cephalic surface of first pleopod always bearing a prominent angular or tuberculiform shoulder some distance proximal to tip (figs. 59-63)	Clarkii Group
3′	Cephalic surface of first pleopod entire or bearing a distinct hump, but never is the latter angular or tuberculiform	4
4(3′)	Subterminal setae present	5
4′	Subterminal setae absent	10
5(4)	Tip of cephalic process of first pleopod lying in a plane caudal to terminal third of main shaft of pleopod (fig. 57)	*P. toltecae*
5′	Tip of cephalic process of first pleopod lying cephalic to caudal surface of distal third of main shaft of pleopod	6
6(5′)	Caudal process of first pleopod in the form of a corneous longitudinal ridge along caudodistal surface of appendage (fig. 64)	*P. gonopodocristatus*
6′	Caudal process of first pleopod variable in form; if present, never in the form of a corneous longitudinal ridge	7
7(6′)	Subterminal setae of first pleopod borne on a knob on cephalodistal or laterodistal surface	Blandingii Group
7′	Subterminal setae of first pleopod never borne on a distinct knob	8
8(7′)	Cephalic process arising from cephalic side of central projection; caudal process prominent, compressed laterally, arising distinctly from caudolateral surface of pleopod; caudal knob never well defined (figs. 66-72)	Planirostris Group
8′	Cephalic process arising from cephalic or lateral side of central projection; caudal process seldom prominent (sometimes absent) and arising distinctly mesial to caudal knob except in *P. lepidodactylus* which possesses a laterally situated cephalic process (fig. 33)	9
9(8′)	Areola 4.7 to 9.0 times as long as broad (if less than 5.0 then caudal process of first pleopod always lacking) and constituting 28 to 35.5 percent of entire length of carapace (mostly greater than 30 percent)	Seminolae Group
9′	Areola 2.5 to 5.2 times as long as broad (if greater than 4.9 then caudal process of first pleopod always present) and constituting 25 to 30.5 percent of entire length of carapace (mostly less than 30 percent)	Pictus Group
10(4′)	Cephalic process of first pleopod cephalic to base of central projection (fig. 56)	*P. bivittatus*
10′	Cephalic process of first pleopod lateral to base of central projection (fig. 55)	*P. lewisi*

Spiculifer Group (*Ortmann* 1905: 100)[3]
(Figures 14-23)

Diagnosis.—Rostrum with marginal spines. Areola two to five times as long as broad and constituting 23-29 percent of entire length of carapace. Two or more lateral spines present on each side of carapace. First pleopod of first form male terminating in three or four distinct parts (cephalic process sometimes absent); subterminal setae in anterolateral rows or clusters, dense or relatively sparse, but never arising from the surface of a knob; corneous caudal process always present but caudal knob sometimes absent; cephalic surface of pleopod always lacking a prominent angular or tuberculiform shoulder some distance proximal to tip. Female with a tuberculate sternum immediately cephalic to annulus ventralis; tubercles frequently projecting over ventral face of annulus.

[3] A detailed study of the Spiculifer Group is presently being conducted by Dr. George H. Penn, Jr. He has read this section of the manuscript and has kindly added several range extensions.

Species and Ranges

P. dupratzi Penn (1953b: 1) Trinity, Red, Neches, Sabine, and Calcasieu drainages (La. and Tex.).

P. echinatus Hobbs (1956: 117) Salkehatchie and Edisto drainages (S.C.).

P. natchitochae Penn (1953b: 5) Red, Calcasieu, and Bayou Teche drainages (La. and Tex.).

P. ouachitae Penn (1956b: 109) Ouachita and Arkansas drainages (Ark.).

P. penni Hobbs (1951: 273) Pearl and Pascagoula drainages (La. and Miss.).

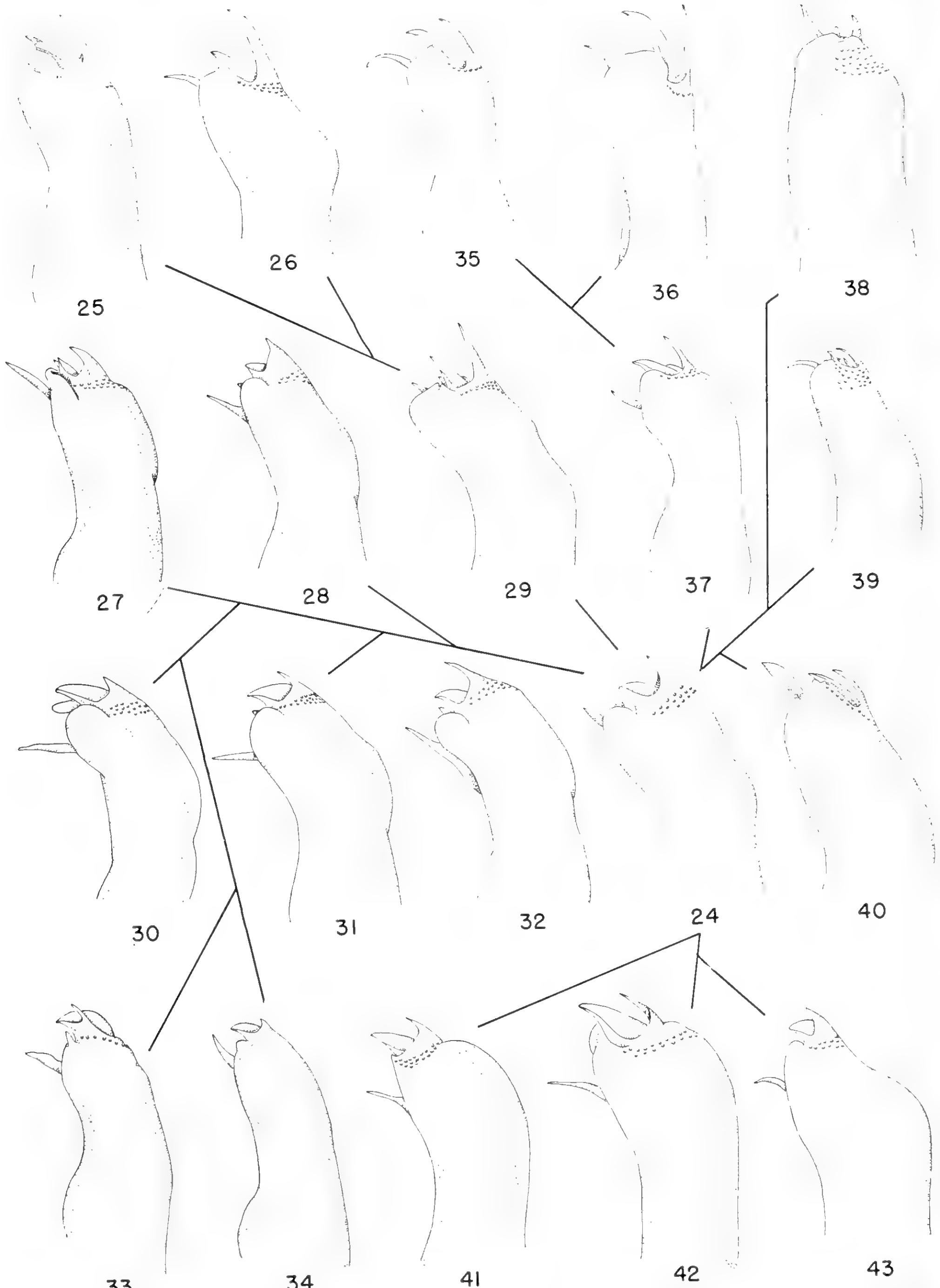
P. raneyi Hobbs (1953b: 412) Upper Savannah and Ocmulgee drainages (Ga. and S.C.).

P. spiculifer (LeConte 1856: 401) Savannah Drainage (S.C.) to Escatawpa Drainage (S.E. Ala.).

P. suttkusi Hobbs (1953a: 173) Choctawhatchee Drainage (Ala. and Fla.).

P. versutus (Hagen 1870: 51) Chattahoochee Drainage (Ga. and Fla.) to Escatawpa Drainage (S.E. Miss.).

P. vioscai Penn (1946: 27) Red Drainage to Tombigbee Drainage (La. and Miss.).



Figures 24-43. Lateral view of terminal portions of first pleopods of first form males. **24.** *Hypothetical Propictus.* **25.** *P. youngi.* **26.** *P. hirsutus.* **27.** *P. litosternum.* **28.** *P. chacei.* **29.** *P. pubescens.* **30.** *P. epicyrtus.* **31.** *P. enoplosternum.* **32.** *P. pictus.* **33.** *P. lepidodactylus.* **34.** *P. angustatus.* **35.** *P. ancylus.* **36.** *P. seminolae.* **37.** *P. lunzi.* **38.** *P. pycnogonopodus.* **39.** *P. leonensis.* **40.** *P. fallax.* **41.** *P. lucifugus lucifugus.* **42.** *P. lucifugus alachua.* **43.** *P. pallidus.* [Dark semicircles represent positions of subterminal setae.]

As a group the range extends from the Salkehatchie and Edisto systems in South Carolina to the Trinity and Red systems in Texas and Arkansas.

Habits.—All of the members of the Spiculifer Group frequent lotic habitats where they may be found among vegetation and debris, under logs or stones, or in shallow burrows in the banks of the streams. [Further details may be found in Hobbs (1942b, 1953b) and Penn (1946, 1953b, 1956a, 1956b)].

Relationships.—There is no reason to question the close affinities of the crayfishes assigned to the Spiculifer Group, and there are a number of reasons for postulating that, as a group, these crayfishes closely approximate, in their anatomy, the ancestral procambarid stock. All of the members are so similar except in certain of their secondary sexual characteristics that a discussion of their relationships must be based largely on the first pleopods of the male. The diagnostic feature of sharing two or more lateral spines on each side of the carapace occurs elsewhere only in certain members of the Mexicanus Section.

Procambarus vioscai (Fig. 20) retains more nearly than do any of the other species the primitive facies of the pleopod of the postulated Prospiculifer stock (Fig. 13). Its caudal process arises from the mesial base of the caudal knob, and the other terminal elements are disposed much as they are in the prototype. With a straightening of the terminal portion of the appendage, *dupratzi* (Fig. 23) has also remained little altered. In *penni* (Fig. 19) and *natchitochae* (Fig. 22) the caudal knob has been imperceptibly fused with the caudal process, and the former has approached *dupratzi* in the straightening of the terminal elements. In *echinatus* (Fig. 21), the caudal knob has been almost completely suppressed, and the cephalic process has been shifted laterally to arise primarily from the lateral base of the central projection. In *versutus* (Fig. 18), the entire distal portion of the appendage has been attenuated, and in many populations there is hardly a trace of the caudal knob, although the caudal process remains distinct. In *suttkusi* (Fig. 17), the emphasis of change is seen in the tremendously enlarged and caudally removed caudal knob leaving the caudal process at the caudolateral base of the central projection; too, the cephalic process has been shifted to a mesial position (not visible in Fig. 17) to arise at the mesial base of the central projection close to the cephalic base of the mesial process, thus departing markedly from the prototype appendage. The most striking deviations from the postulated ancestral appendage are seen in *spiculifer* (Fig. 15), some specimens of *ouachitae* (Fig. 16), and *raneyi* (Fig. 14) in which the cephalic process is lacking. The former two have retained the caudal knob which is absent in the latter. In *ouachitae,* the caudal process is strongly developed and arises from a generalized caudal knob, and in some specimens (Penn 1956b: 116) the cephalic process is present, arising on the cephalomesial side of the central projection, thereby approaching the disposition of this process in *suttkusi.* In *spiculifer* the caudal knob is elongated and bears a comparatively small caudal process.

With reference to the pleopods, the more generalized forms, *vioscai, penni, natchitochae, dupratzi,* and *echinatus* occupy the western and eastermost portion of the range of the group, while the more divergent members are found in the eastern half and *ouachitae* near the westernmost limit of the range.

One of the most striking features of the females of the Spiculifer Group is the tuberculate sternum immediately cephalic to the annulus ventralis. Among the generalized members it is most prominent in *dupratzi* and *echinatus* but is also well developed in *penni* and *vioscai* and to a lesser degree in *natchitochae.* Among the more divergent species, *versutus* and *suttkusi* exhibit this feature to an extent surpassing that of any other member of the group. In *raneyi* it is prominent as it is also in some populations of *spiculifer.*

Pictus Group (*Hobbs* 1942b: 129)
(Figures 2, 6, 25-34)

Diagnosis. — Rostrum with marginal spines. Areola 2.5 to 5.2 times longer than broad (if greater than 4.9 then caudal process of first pleopod always present) and constituting 25 to 30.5 percent of entire length of carapace. A single lateral spine present on each side of carapace. First pleopod of first form male terminating in three or four distinct parts (caudal process sometimes absent, but if so, areola never more than 3.5 times longer than wide); subterminal setae in rows or clusters on cephalolateral surface of appendage (very sparse in *youngi,* and their disposition is not known in *angustatus*); caudal knob well developed, or clearly evident, except in *lepidodactylus;* cephalic surface of pleopod lacking a prominent angular or tuberculiform shoulder some distance proximal to tip although some of the more generalized species exhibit a hump in the corresponding position. Female with or without a tuberculate sternum immediately cephalic to annulus ventralis.

Species and Ranges

P. angustatus (LeConte 1856: 401) Known only from the type specimen which was reported to have been collected "*Habitat in Georgia inferiore, in aquae purae rivalos que inter colloculos arenosus* [sand-hills] *currunt.*"

P. chacei Hobbs (1958a: 5) Wateree, Congaree, Edisto, and Savannah drainages (S.C.) and from isolated localities in the Ogeechee and Ocmulgee drainages (Ga.).

P. enoplosternum Hobbs (1947a: 5) Ohoopee Drainage (tributary of the Altamaha River) (Ga.).

P. epicyrtus Hobbs (1958b: 1) A single stream tributary of the Ogeechee River in Screven Co., Ga.

P. hirsutus Hobbs (1958a: 160) Edisto, Salkehatchie, and Savannah drainages (S.C.).

P. lepidodactylus Hobbs (1947b: 25) Pee Dee, Black, and Wateree drainages in the lower piedmont and coastal plain of S.C. and extreme southeastern N.C.

P. litosternum Hobbs (1947a: 9) Canoochee, Ogeechee, and Newport drainages (Ga.).

P. pictus (Hobbs 1940a: 419) Black Creek drainage (tributary of the St. Johns River) in Clay Co., Fla.

P. pubescens (Faxon (1884: 109) Savannah and Ogeechee drainages, and a single locality in the Altamaha drainage (Ga.).

P. youngi Hobbs (1942b: 131) St. Marks River, Leon Co., and from a tributary of the Chipola River and Wetappo Creek, Gulf Co. (Fla.).

Habits.—"The ecological requirements of all of them seem to be satisfied in streams (mostly sand-bottomed) of the lower piedmont and coastal plain. The size of the stream, as well as the condition of the water, whether clear, silt-laden, or coffee-colored, appear to have no effect on the subgroup [=Group] as a whole. Whether or not certain species may be limited by these factors remains to be demonstrated. There seems to be little doubt that a lotic habitat is necessary. These species occur abundantly in beds of *Vallisneria* and other aquatic plants. They are also found in litter and roots along the undercut banks of streams." (Hobbs 1958c: 76).

Relationships.—The intra-group relationships of the members of the Pictus Subgroup [equivalent to Group here] have been discussed in some detail by Hobbs (1958c), and there seems little reason to modify conclusions set forth therein. These are depicted in Figures 24 through 34. The inter-group relationships are mentioned above.

Seminolae Group (Here designated as a Group)[4]
(Figures 35-40)

Diagnosis.—Rostrum with or without marginal spines, margins often entire. Areola 4.7 to 9.0 times as long as broad (if less than 5.0 then caudal process of first pleopod always lacking) and constituting 28 to 35.5 percent of entire length of carapace (mostly greater than 30 percent). A single lateral spine or tubercle on carapace present or absent. First pleopod of first form male terminating in three of four parts (caudal process always reduced or absent); subterminal setae in a row or cluster at, or near, base of cephalic process and central projection; caudal knob greatly swollen or almost imperceptibly fused with shaft of appendage; cephalic surface of pleopod lacking a prominent angular or tuberculiform shoulder some distance proximal to tip. Female with or without a tuberculate sternum immediately cephalic to annulus ventralis.

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4 Previously treated as the Seminolae Subgroup of the Pictus Group (Hobbs 1942b: 142; Hobbs 1958c) and the Fallax Subgroup of the Blandingii Group (Hobbs 1942b: 111); united here as the Seminolae Group.

Species and Ranges

P. ancylus Hobbs (1958b: 164) "From Columbus and Bladen counties, North Carolina, in the lowermost portions of the piedmont and in the coastal plain to the Santee River system in South Carolina." (Hobbs 1958c: 80).

P. fallax (Hagen 1870: 45) From the Suwannee and St. Mary drainages (Ga.) south to DeSoto, Highlands, and Palm Beach counties, Fla.

P. leonensis Hobbs (1942b: 114) Between the Apalachicola and Suwannee rivers (Fla.).

P. lunzi (Hobbs 1940b: 3) Hampton and Beaufort counties, S.C.

P. pycnogonopodus Hobbs (1942b: 117) Between the Apalachicola and Choctawhatchee rivers (Fla.).

P. seminolae Hobbs (1942b: 142) Coastal plain from the Altamaha River (Ga.) south to Marion County, Fla.

Habits.—The members of the Seminolae Group have habits markedly similar to those of the Clarkii Group, frequenting swamps, ponds, lakes, roadside ditches, springs, and streams. Not infrequently, they also dig simple burrows—even when standing water is available. *Procambarus fallax* is particularly abundant among the roots of floating mats of water hyacinths. (See Hobbs 1942b: 113-119, 145.)

Relationships.—Two previously recognized subgroups of the Blandingii Section are here united, for while *fallax* (Fig. 40), *leonensis* (Fig. 39), and *pycnogonopodus* (Fig. 38) appear to be more closely allied to one another than either is to *ancylus* (Fig. 35), *lunzi* (Fig. 37), and *seminolae* (Fig. 36), I now believe that all of them have arisen from a common ancestor. Previously, my opinion was that *evermanni* (Fig. 72) represented a possible link between the Fallax Subgroup and the Clarkii Subgroup; however, in light of the discovery of the several other species of which the Planirostris Group is composed, the relationships of *evermanni* seem clearer and it is highly unlikely that *fallax* and its obvious relatives should be linked closely with it, but rather to *lunzi*.

This Group is confined to the coastal plain from the Choctawhatchee Drainage in Florida to the lakes region in southeastern North Carolina. Here, the ranges of only two of them, *fallax* and *seminolae*, overlap—in extreme southern Georgia and northern Florida.

On the basis of the first pleopods, the most generalized members of the Group appear to be *lunzi* and *ancylus*, with *leonensis* and *fallax* not far removed. The greatest divergence is seen in the accentuated terminal elements of *seminolae* and the reduced ones in *pycnogonopodus*. In the structure of the areola, *seminolae*, in contrast, has both the broadest and shortest, approaching that of the generalized members of the Pictus Group. Conspicuous in this Group is the tendency toward a reduction of the caudal process of the first pleopod. Only in *fallax* and *leonensis* is there a vestige of it remaining.

Hobbs (1958c: 88) discussed the possible origin of *ancylus*, *lunzi*, and *seminolae*, and the addition of the other three species to the Group does not alter his conclusions. In this discussion *P.* sp. D is *ancylus*.

Lucifugus Group (Here designated as a Group)[5]

(Figures 41-43)

Diagnosis.—Albinistic, eyes reduced. Rostrum with marginal spines. Areola 10 to 36 times as long as broad and constituting 37 to 43 percent of entire length of carapace. Lateral surface of carapace strongly tuberculate with a row of them along caudal margin of cervical groove, occasionally one somewhat larger than the others—corresponding to the lateral spine of other crayfishes. First pleopod of first form male terminating in four distinct parts although caudal process is not evident in lateral aspect; subterminal setae arising from cephalolateral base of the terminal elements in the form of an arc consisting of two or more rows; cephalic surface lacking a prominent angular or tuberculiform shoulder some distance proximal to tip. Female with or without a tuberculate sternum immediately cephalic to annulus ventralis.

Species and Ranges

P. lucifugus alachua (Hobbs 1940a: 402) Western part of Alachua County, Fla. [Intergrades between the two subspecies occur in Marion Co., Fla.]

P. lucifugus lucifugus (Hobbs 1940a: 398) Citrus and Hernando counties, Fla.

[5] Previously treated as the Lucifugus Subgroup of the Pictus Group (Hobbs 1942b: 134; Hobbs 1958c).

P. pallidus (Hobbs 1940a: 154) North-Western part of Alachua Co. to Leon Co., Fla.

Habits.—These three crayfishes are confined to subterranean waters where they are found in caves and sinkholes wandering about over muddy or rock-littered bottoms of pools. While the animals appear to avoid bright light, they are often found in large numbers in diffuse light in sinkholes or at the mouths of caves.

Relationships.—The members of the Lucifugus Group have their closest affinities with the generalized members of the Pictus Group. As was shown by Hobbs (1958c), a common ancestry of the two seems almost certain. Of the three, *lucifugus alachua* (Fig. 42) is probably the most generalized—the first pleopod of the male resembles that of the primitive members of the Pictus Group more closely than do those of typical *lucifugus* (Fig. 41) and *pallidus* (Fig 43). The areola is slightly shorter and distinctly broader than in the latter two, and it is only one of the three that has retained (?) pigment in the eyes. A discussion of the origin of the Group may be found in Hobbs (1958c).

Blandingii Group (Ortmann 1905: 100) (Figures 44-54)

Diagnosis.—Rostrum with or without marginal spines or tubercles, but if without, then margins always interrupted near apex except in *viae-viridis* and *caballeroi*. Areola four to twenty times as long as broad and constituting 25 to 38 percent of entire length of carapace (30 to 38 percent excluding *lecontei*). A single lateral spine present or absent on each side of carapace. Apophysis on coxa of fourth pereiopod somewhat reduced in *viae-viridis*, otherwise typical of the Section. First pleopod of first form male terminating in four distinct parts; subterminal setae always arising from the surface of a knob (not always clearly distinct in *verrucosus*); cephalic surface of pleopod always lacking a prominent angular or tuberculiform shoulder some distance proximal to tip. Female with or without a tuberculate sternum immediately cephalic to annulus ventralis, but only in *caballeroi* do the tubercles approximate the sizes characteristic of certain members of the Spiculifer Group *(e.g., versutus and suttkusi)*.

Species and Ranges

P. acutissimus (Girard 1852:91) Tombigbee, Alabama, and Choctawhatchee drainages (Ala. and Miss.).

P. blandingii acutus (Girard 1852: 91) Florida to Texas and Minnesota to Ohio. [The ranges of the subspecies of *blandingii* are not accurately determined.]

P. blandingii blandingii (Harlan 1830: 464) Coastal plain and piedmont from Massachusetts to Georgia. [See note under *blandingii acutus* above.]

P. blandingii cuevachicae (Hobbs 1941: 1) Puebla and San Luis Potosi, Mexico.

P. caballeroi Villalobos (1944b: 175) Villa Juárez, Puebla, Mexico.

P. hayi (Faxon 1884: 108) Tallahatchie and Tombigbee drainages (Miss.)

P. lecontei (Hagen 1870: 145) Pascagoula, Escatawpa, and Chickasaw drainages (Miss. and Ala.).

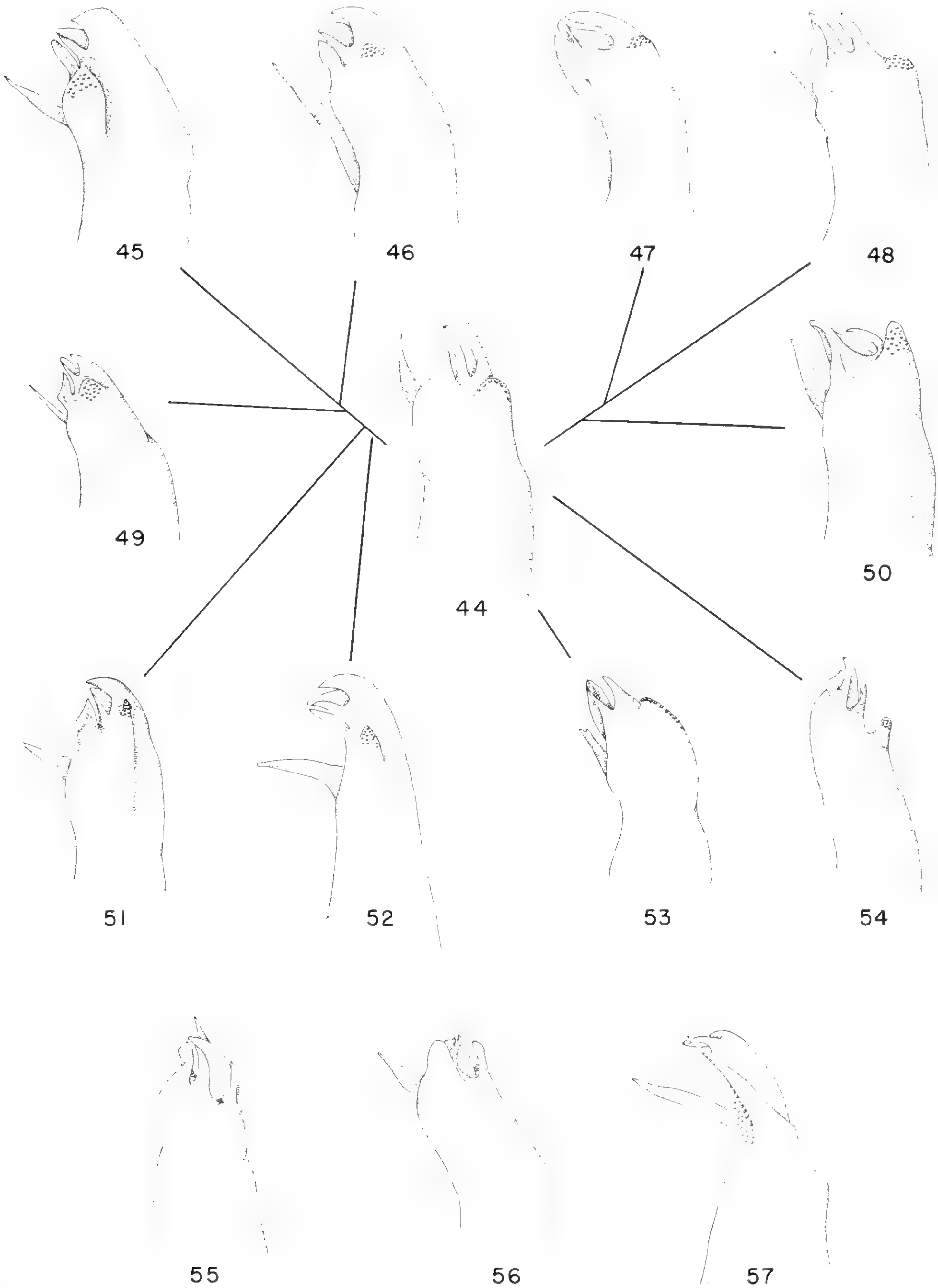
P. lophotus Hobbs and Walton (1960: 123) Alabama drainage in Lowndes, Montgomery and Wilcox counties, Ala.

P. verrucosus Hobbs (1952b: 212) Chattahoochee and Tallapoosa drainages (Ala.).

P. viae-viridis (Faxon 1914: 370) Southeastern Arkansas and northeastern Louisiana, western Tennessee, northern Mississippi and northwestern Alabama.

Habits.—The members of the Blandingii Group, with the possible exception of *lecontei,* occur in all types of epigean lotic and lentic habitats, and frequently they are found in simple burrows. *Procambarus lecontei* has been found only in sand and silt bottom streams.

Relationships.—The characteristics which unite this assemblage of crayfishes are a pleopod (1) terminating in four parts which, for the most part, are similarly disposed and (2) bearing a setiferous knob along the distal cephalic (or lateral) surface of the appendage. The most generalized pleopod is probably that of *blandingii blandingii* (Fig. 48) with the setiferous knob situated on the cephalic surface at the base of the cephalic process. In *blandingii acutus* (Fig. 50) the terminal elements and the setiferous knob are similarly disposed but the latter is much accentuated. In *blandingii cuevachicae* (Fig. 47), the knob has shifted caudally on the lateral side of the



Figures 44-57. Lateral view of terminal portions of first pleopods of first form males. **44**. Hypothetical Problandingii. **45**. *P. hayi.* **46**. *P. lophotus.* **47**. *P. blandingii cuevachicae.* **48**. *P. blandingii blandingii.* **49**. *P. caballeroi.* **50**. *P. blandingii acutus.* **51**. *P. acutissimus.* **52**. *P. lecontei.* **53**. *P. verrucosus.* **54**. *P. viae-viridis.* **55**. *P. lewisi.* **56**. *P. bivittatus.* **57**. *P. toltecae.* [Dark semicircles represent positions of subterminal setae.]

appendage, a tendency which is slightly more accentuated in *lophotus* (Fig. 46), caballeroi (Fig. 49), *acutissimus* (Fig. 51), and *lecontei* (Fig. 52), and reaches the extreme in *hayi* (Fig. 45) where it lies in a caudolateral position at the base of the caudal process. Accompanying the shifting of the setiferous knob is a tendency of the cephalic process to form a hood-like element over the central projection; the extreme of this condition is seen in *lecontei,* although it is clearly evident in *lophotus, acutissimus,* and *hayi.* The two most divergent members of the group are *verrucosus* (Fig. 53) and *viae-viridis* (Fig. 54). In the former, the setiferous knob is not so well defined as in the other members of the group, and the terminal setae are dispersed along a longitudinal ridge rather than in a cluster. In *viae-viridis,* not only is the setiferous knob much withdrawn from the terminal elements, but the mesial process is also displaced cephalically so as to lie only slightly cephalomesial to the cephalic process (in Fig. 54 it may be seen lying between the cephalic process and the central projection).

In the rostrum and the areola, *lecontei* is the most generalized. It is the only member of the group in which the areola constitutes less than 30 percent of the entire length of the carapace and is less than 7 times as long as broad. In this connection, it is worthy of note that this is the only species which is known to occur only in lotic habitats—approaching both ecologically and morphologically the members of the Spiculifer and Pictus groups.

The ranges of only two members of the group, *caballeroi* and *blandingii cuevachicae,* do not extend into the Mississippi-Alabama-Georgia area, and the ranges of five of them (*hayi, lophotus, acutissimus, lecontei,* and *verrucosus*) are limited to this region. It seems, therefore, highly possible that the Problandingii stock took its origin in this region.

Planirostris Group (Here designated as a Group)[6]
(Figures 65-72)

Diagnosis--Rostrum with or without marginal spines or tubercles, margins usually entire. Areola 30 to 37.5 percent of entire length of carapace and from 3.7 to 24 times longer than broad. A single lateral spine or tubercle present or absent on each side of carapace. First pleopod of first form male terminating in three or four distinct parts (cephalic process lacking in *mancus*); subterminal setae linearly arranged except in *evermanni* and *jaculus* in which they are more irregularly arranged—never, however, arising from a distinct knob; caudal process corneous, compressed laterally and always well developed; caudal knob; if recognizable, always imperceptibly fused with caudal process; cephalic surface of pleopod lacking a prominent angular or tuberculiform shoulder some distance proximal to tip, although a weak shoulder present in *pearsei plumimanus* and a rounded prominence in *planirostris, hybus, mancus,* and *jaculus.* Female with, or more usually without, a tuberculate sternum immediately cephalic to annulus ventralis.

Species and Ranges

P. evermanni (Faxon 1890: 620) Okaloosa County, Fla. west to Jackson County, Miss.

P. hybus Hobbs and Walton (1957: 39) Green County, Ala. and Kemper, Lowndes, and Noxubee counties, Miss.

P. jaculus Hobbs and Walton (1957: 48) Known only from the type locality, one mi. W. of Scott-Rankin County line on U.S. Hwy. 80, Rankin County, Miss.

P. mancus Hobbs and Walton (1957: 44) Known only from the type locality, five mi. S. of Meridian, Lauderdale County, Miss.

P. pearsei pearsei (Creaser 1934: 1) Johnson and Pitt counties, N.C. south to Horry County, S.C.

P. pearsei plumimanus Hobbs and Walton (1958: 8) Craven and Duplin counties, N.C.

P. planirostris Penn (1953a: 71) Florida parishes of southeastern Louisiana and Perry and Pearl River counties, Miss.

Habits.—For the most part, the members of the Planirostris Group are secondary burrowers, frequenting temporary bodies of water and burrowing during dry seasons. They occur in shallow ponds, roadside ditches, swamps, and sluggish streams. Penn (1956a: 412) summarized the habits and life history of *planirostris,* and these observations are in

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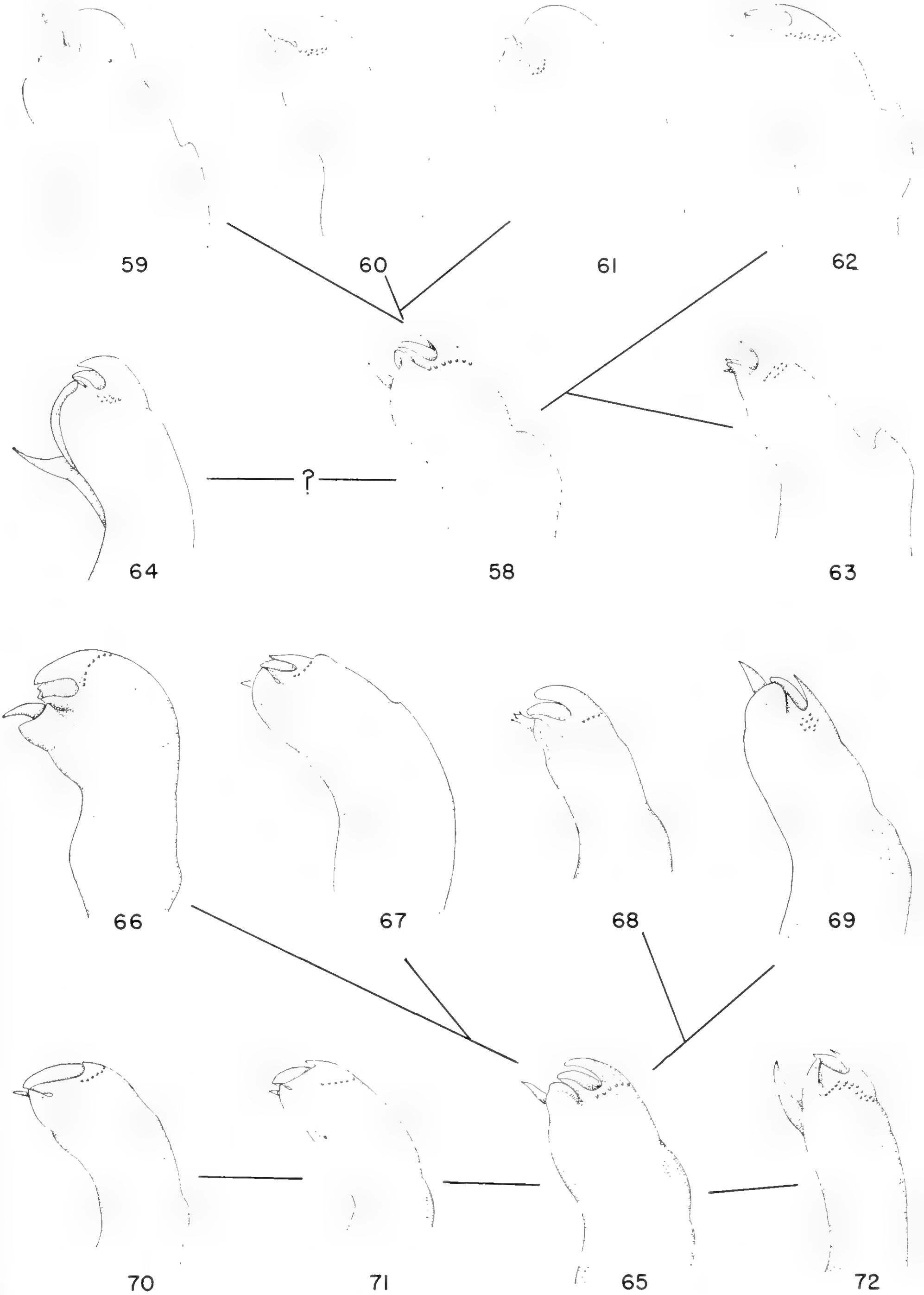
[6] Originally proposed as the monotypic Planirostris Subgroup of the Blandingii Section (Penn 1953a: 75).



Figures 58-72. Lateral view of terminal portions of first pleopods of first form males. **58.** Hypothetical Proclarkii. **59.** *P. clarkii.* **60.** *P. okaloosae.* **61.** *P. troglodytes.* **62.** *P. paeninsulanus.* **63.** *P. howellae.* **64.** *P. gonopodocristatus.* **65.** Hypthetical Proplanirostris. **66.** *P. pearsei pearsei.* **67.** *P. pearsei plumimanus.* **68.** *P. hybus.* **69.** *P. jaculus.* **70.** *P. mancus.* **71.** *P. planirostris.* **72.** *P. evermanni.* [Dark semicircles represent positions of subterminal setae.]

accord with the few data available for the other species.

Relationships.—The generalized members of the Planirostris Group have much in common with those of the Clarkii Group. Hobbs and Walton (1957) originally assigned *jaculus* to what they called the Clarkii Subgroup, and Penn (1953a), in discussing the affinities of *planirostris,* indicated the close relationships existing between it and the members of the same subgroup.

As to intra-group relationships, the most generalized species are probably *hybus* (Fig. 68), *planirostris* (Fig. 71), *jaculus* (Fig. 69), and *evermanni* (Fig. 72) and with *pearsei plumimanus* (Fig. 67) not far removed. The specialized members are *mancus* (Fig. 70) in which the cephalic process of the first pleopod is lacking, and *pearsei pearsei* (Fig. 66) in which the entire group of terminal elements is strongly recurved.

The generalized species are found in the Mississippi-Alabama coastal plain, as are all of the members except the two subspecies of *pearsei,* which are widely separated from the other members. There is a gap in the range of the Group which extends from western Alabama almost to the North Carolina-South Carolina line. Apparently vicariating for the Planirostris Group in most of this region are members of the Barbatus Section. Insofar as is known, the ranges of none of the species of the Planirostris Group overlap.

Clarkii Group (Ortmann 1905: 100)
(Figures 58-63)

Diagnosis.—Rostrum with marginal spines or tubercles except in some older animals; in them, margins always interrupted near apex. Areola six to an infinite number of times as long as broad (usually obliterated in *clarkii*) and constituting 23 to 38 percent of entire length of carapace (excluding some specimens of *paeninsulanus,* 31 to 38 percent). A single lateral spine present or absent on each side of carapace. First pleopod of first form male terminating in four distinct parts; subterminal setae sparse *(clarkii)* or abudant but never arising from the surface of a knob; cephalic surface of pleopod always bearing a prominent angular or tuberculiform shoulder some distance proximal to tip (shoulder on right pleopod frequently bent caudally to lie against mesial surface of appendange); corneous caudal process present, but a distinct caudal knob always absent. Female with or without a tuberculate sternum immediately cephalic to annulus ventralis.

Species and Ranges

P. clarkii (Girard 1852: 91) From eastern Ala. to western Tex. and up the Mississippi Valley to Dunklin County, Mo. and Hickman County, Ky. [Introductions: Calif., Fla., Nev., Va., Hawaii, and Japan.]

P. howellae Hobbs (1952a: 167) Tributaries of the Altamaha River in Bibb, Emanuel, and Telfair counties, Ga.

P. okaloosae Hobbs (1942b: 100) Between the Yellow and Perdido rivers in Ala. and Fla.

P. paeninsulanus (Faxon 1914: 369) From the Choctawhatchee River to the Atlantic Ocean, and from southern Ga. to Hillsborough County, Fla.

P. troglodytes (LeConte 1856: 400) North of the Altamaha River in Ga. and S.C. (piedmont and coastal plain).

Habits.—Like the members of the Blandingii Group, these crayfishes occur in lotic and lentic habitats, and are frequently found in burrows. *Procambarus clarkii* is also known to inhabit brackish water. Both *clarkii* and *paeninsulanus* have been observed walking across land some distance from a body of water. Penn (1943:3) gives an excellent summary of the habits of *clarkii* in his study of its life history. Also see Hobbs (1924b: 103, 106).

Relationships. — As noted above, the Clarkii Group consists of five allopatric species which, as a group, occupy an almost unbroken range from Texas to South Carolina. In addition to similarities in their habits and body conformation, the first pleopod of the male has an angular prominence on its cephalic margin — the only members of the Blandingii Section which possess an angular shoulder or hump. An examination of the accompanying figures will disclose the presence of *rounded* prominences in members of the Pictus and Planirostris groups but here the humps are neither so prominent nor are they distinctly angular.

It seems probable that the most generalized member of the group is *paeninsulanus,* for not only is the first pleopod of the male more similar to that of the generalized appendages in the other groups, but also in this species is found the broadest, shortest areola. On the basis of the same characteristics, *howellae* (Fig. 63) is more closely related to *paeninsulanus* (Fig. 62) than are the other three. The close affinities of *clarkii* (Fig. 59), *okaloosae* (Fig. 60), and *troglodytes* (Fig. 61) are seen primarily in the expanded cephalic process which reaches the extreme condition in *troglodytes.* In this Group, therefore, the generalized members are found in the Alabama-Georgia-Florida area, and the more divergent members at the western and eastern limits of the range of the Group.

The Disjunct Members of the Blandingii Section

(Figures 55-57, 64)

Four species which seem properly associated with the members of the Blandingii Section are not, on the basis of present definitions, readily assignable to one of the above seven groups, nor are they closely related to one another. Rather than erect four additional monotypic groups, they are here grouped as disjunct members of the Section.

Species and Ranges

P. bivittatus Hobbs (1942b: 96) Escambia Drainage (Fla.) and Pearl Drainage (La.)

P. lewisi Hobbs and Walton (1959: 39) Lowndes, Montgomery, and Macon counties, Ala.

P. gonopodocristatus Villalobos (1958: 279) Known only from two localities in the State of Veracruz, Mexico.

P. toltecae Hobbs (1943: 198) Vicinity of Tamazunchale, San Luis Potosi, Mexico.

Procambarus bivittatus (Fig. 56) has its closest affinities with the members of the Pictus and Blandingii Groups but is not readily assignable to either. There are no subterminal setae on the first pleopod, and the caudal knob, bearing the caudal process on its cephalodistal surface, sets it apart from both groups. In the elongation of the caudal knob, it approaches *P. alleni* (Faxon 1884: 110) and it also has bituberculate hooks on the ischiopodites of the fourth pereiopod, another characteristic which is shared with *alleni.*

Procambarus lewisi (Fig. 55) is most closely related to the members of the Planirostris Group but, like *bivittatus,* lacks subterminal setae on the first pleopod. Furthermore, the cephalic process lies at the lateral base of the central projection, whereas in the Planirostris Group this process occupies a cephalic position but shows a tendency to migrate toward a mesial position. Also, its range lies on the eastern boundary of the range of the Group. It might well be considered a disjunct member of the Planirostris Group.

Procambarus gonopodocristatus (Fig. 64) is almost certainly allied to the members of the Clarkii Group. Neglecting the absence of the cephalic angular shoulder and the greatly expanded (elongated) ridge-like caudal process, its other characteristics are those of this Group (*c.f.* Figs. 64 and 58-63). Supporting this view are the obliterated areola, the somewhat flattened ventral face of the annulus ventralis, and the arrrangement of the subterminal setae. All of these are characteristic of *clarkii.* There seems to be little doubt that *gonopodocristatus* had a common origin with the members of the Clarkii Group.

Procambarus toltecae (Fig. 57), because of its twisted first pleopod, is difficult to place in the above scheme of classification. That portion which corresponds to the lateral surface of the pleopods of other members of the Section has been displaced caudomesially so that the cephalic process lies in the position usually occupied by the caudal process, and the latter is situated caudomesially. If it could be imagined that the displaced elements were shifted to the usual position, then the pleopod would assume the appearance of that somewhat typical of the members of the Blandingii Section. Probably *toltecae* is most closely related to the members of the Blandingii and Pictus groups although there is a distinct shoulder on the cephalic surface of the appendage. As pointed out above, however, although the members of the Clarkii Group have the best developed shoulder, it is by no means restricted to these crayfishes. It is likely that *toltecae* was derived from a stock that also gave rise to the modern members of the Pictus and Blandingii groups.

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POTENTIAL RESEARCH BENEFITS TO BE DERIVED FROM ESTUARINE HETEROGENEITY [1]

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Introduction

Estuaries are notoriously rigorous habitats. Chemical and physical variables present shocking and formidable conditions for those organisms that enter, by predilection or obligation, the forbidding confines of river mouths. For many species the rewards of life in these turbulent areas transcend the dangers. As a result, we find a rich and valuable fauna—capable of coping with the rigors and receiving the benefits.

Because of their economic importance and relatively easy accessability, the faunal and floral species of estuaries have received abundant attention from shore based biologists. Most of this interest has been in recent years, during the time that most biological and physical sciences were expanding.

But the work has been piecemeal. Almost all of the projects were directed toward a very narrow aspect of the total habitat, most of them centering about one species or one group of organisms. In a few cases, studies were carried out on one or two hydrographic features, but these were rarely correlated in detail with the animals and plants of the area.

Consequently, we now have a vast accumulation of miscellaneous information about estuaries and the animals and plants that live in them, very little of which provides broad ecological interpretations or makes possible any correlations with other naturally occurring phenomena. This is wasteful research because the same studies carried out under a different system could, for the same effort, provide a much greater understanding.

We are all familiar with the limitations of experimental studies, usually conducted upon an isolated mechanism or function under laboratory conditions. The complexity of organisms and their surroundings are difficult to synthesize under artificial conditions. This problem has recently been discussed (Redfield, 1958).

Estuaries, with their easily available transient conditions, can provide experimental situations on a grand scale. These facilities will not have the deficiencies inherent in laboratory procedures.

The Plan

A type of program is now suggested that might be called *Selective Concentration.* (The idea is not entirely original. It was suggested by Dr. George Rounsefell and his group, from Galveston, Texas, in March, 1961, at the meeting of the Gulf States Marine Fisheries Commission in Biloxi, Mississippi. The present paper is an expansion and prospectus of this plan of action.)

Under this plan, several prominent estuaries would be selected for comprehensive use of all the myriad scientific disciplines that are available. Chemistry, physics, zoology, botany, fisheries biology, geology, parasitology, meteorology and the many derived specialties would find a place. All data obtained would be stored on IBM cards or other records suitable for later analysis by machines and computers.

It seems unlikely that all of the studies of potential value could be pursued simultaneously. There would doubtless be a continuous procession of various projects and investigators through the institution established at each estuary.

But many of the undertakings would proceed with no planned termination. These would include:

water temperature
salinity
weather
fishery landings
turbidity
plankton

All would be studied over a wide geographical area about each river mouth.

Such other short term investigations as might seem desirable or for which personnel might be available would be laced into the over-all program. The results of these would be interpreted in the forms and with the

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[1] Contribution No. 63.

background of the long term studies listed above.

All plankton samples would be kept. Any investigator wishing to study a particular animal or group would have a long series of samples instantly available. There would be no need to wait several years for the acquisition of suitable material.

Present Status

Although the institutions recommended are, at this time, hypothetical, certain existing laboratories and groups along our coasts are in some respects carrying out the functions outlined.

Small laboratories have been established along the shore for various reasons. Some were founded to begin investigations on valuable indigenous fisheries; some were established because of a prevailing local manifestation such as red tide; others were adjuncts to university training programs; a few were organized to serve a particular industrial concern or branch of the armed forces.

Whatever their origin, these installations became loci toward which gravitated many different types of investigators, each one providing a new facet of information. Because of the agglutination over the years, these already existing facilities represent the best opportunity for the *Selected Concentration* being proposed.

In some areas, multiple installations exist in reasonable proximity. Here, the program will be accordingly more easily instigated.

Very few of the existing stations have long range sampling programs. Even where such data is available, there are usually long gaps during which no samples were taken or observations made. The methods, sampling stations and conditions are not standardized.

In summary, there exist laboratories and organizations near estuaries with suitable equipment for long term sampling. It only remains for the leadership of these institutions to establish the necessary policies.

Discussion and Recommendations

No attempt will be made here to anticipate all of the possible benefits likely to be derived from the suggested plan of action. But a few examples will illustrate the type of knowledge that can be developed.

Multiple estuaries.—Because of their amenability to cultivation, oysters have been the subject of long and serious study over the world. In our own country, and Canada, more effort has probably been expended on this animal than any other in salt water.

Although most of the studies were directed towards local habitats and growing conditions, the printed reports give information on a wide spectrum of environmental conditions from Newfoundland to Texas.

A synthesis of this material provides insights into the basic physiology of oysters that would not be possible from any one of the individual areas. Where previously it was thought that one species of oyster occupied the entire range, we now know that physiological subspecies or species occur in various localities. Temperature requirements for Florida oysters are so high that they do not reproduce in the colder waters of Long Island Sound. Characteristic hibernation of northern populations does not occur in the Gulf of Mexico. Southern oysters cannot endure the cold winter temperature of Connecticut waters. Growth rates are more rapid and are continuous throughout the year in the South. Spawning proceeds for most of the year in Florida but is limited to a few weeks in New England. In many cases, quantitative values have been established for these functions.

Practical implications from all of this are at once apparent. For any area, oyster spawning, growth and vigor may vary predictably from one year to the next because of a variation in temperature regime.

Actually, a system of prognostication exists now in Long Island Sound which takes into account (in addition to temperature) the presence of microscopical plankters suspected as being inimical to oyster larvae. This forecasting also involves the estimation of spawning success of known predators.

As the many chemicals, physical and biological differences between estuaries are further identified and measured, and these are correlated with differences in oyster activities in each place, more detailed understanding will be available.

Several years ago, Albert Collier, Sammy Ray and their groups worked on organic compounds in the waters around Pensacola that showed a possible influence on oyster pumping. References pertinent to this are included in two of Colliers later papers (Collier, 158; Collier, 1959).

It may be that valuable experiments are presently being performed fortuitously, and naturally, in the various estuaries of this country that will help to further resolve the importance of the compounds Collier found (as well as others). Chemical investigations correlated with oyster survival and well-being should demonstrate identifiable differences in individuals subjected to various concentrations of the presumptively important compounds in separate river mouths.

The critical values of various ecological factors for a particular organism can be established in many cases where an animal or plant is living under marginal conditions. This has been discussed earlier for temperature (Hutchins, 1947).

In some areas the temperature required for spawning is present for a very short period of the year. In colder years, only a very minor or negligible reproduction may take place. The needed temperature can, in most cases, be confirmed by a study of spawning and temperature in the regions having longer periods of high temperatures. By using the critical temperatures so established it may be possible to predict spawning success and the year class abundance in quite distant habitats by the simple expedient of taking water temperatures.

A few examples of the use of this method will suffice. It has been shown in a recent work (Phillips, 1960) that *Thalassia* reproduces sexually in Tampa Bay but such flowerings are not aboudant. Other observers (Hilary Moore, pers. comm.; Gilbert Voss, pers. comm.) indicated a much more abundant florescence in the Florida Keys. Phillips concluded that "Possibly the Tarpon Springs area represents the northern limit of the flowering condition in *Thalassia*."

There may be other factors which are more important than temperature. Phillips mentions photoperiodicity, a factor whose potency is well established in plant physiology. A careful study of these elements in several widely separated estuaries would help to define the relative importance of any particular parameter. The particular problem of *Thalassia* reproduction would be greatliy improved by studies in the northern Gulf if such studies were correlated with the monitoring of basic hydrographic and meteorological regimes.

Although a substantial amount of research has been done on shrimp, and abundance appears to be related to rainfall in two of the common species (see below), the effects of temperature have received but little attention.

Using scattered temperature data, landings statistics and a few providential studies in various parts of the range of *Penaeus duoarum,* it has been possible recently to make a few speculations concerning the role of temperature in spawning and resulting year class abundance (Eldred *et al,* 1961). These authors theorize a spawning temperature of 75° F. which may help to explain the diminished abundance of this species in the northern Gulf. The length of time each year that water temperature might be expected to rise above 75° F. would be presumably less in Texas than in Tortugas, for instance. It is also suggested that the relative and absolute abundance of the other two species may, to some extent, be dependent upon temperature.

Population density, distribution and fishing success have already been shown to be dependent upon temperature in the case of certain Mediterranean shrimp species (Ghidalia and Bourgois, 1961). Similar observations have been made on penaeids of southeastern United States. (Mr. Harvey Bullis, personal communication).

The *selective concentration* studies I suggest will be an invaluable aid in establishing the roles of temperature, salinity and other factors in success of year classes. Detailed temperature studies should throw light on the importance of winter minima, rate of warming, length of time above the critical spawning temperature, rate of cooling not only on spawning but on growth and survival as well.

Due to intensive gathering of shrimp production figures since 1956, a broad picture of abundance is available for each locality of southeastern U. S. from North Carolina to Texas. These data comprehend sizes of shrimp, species, and depth of water in which they are found.

Recently, using this information, a summary of shrimp landings was prepared for the first half of 1961 (Gunn 1961a).

Since the period covered was that during which the brown shrimp, *P. aztecus,* production might be expected to predominate in the western Gulf, a relatively small abundance was evident for this species over a wide geographical area. One ecological parameter that might account for this widespread phenomenon, and which would be general enough to account for the shortage is temperature.

It is remarkable, therefore, to know that with the small amount of temperature data extant from various incidental studies along the Gulf, and without the strong supporting data that could be available, there was an opinion on the part of several biologists concerned that temperature might well have been the critical factor (Gunn, 1961b).

Had temperature monitoring been pursued over the area, as presently recommended, these landings data might be subject to greater interpretation and understanding than they are now. For the present we can only hypothesize.

A similar situation existed in the case of the pink spotted shrimp, *P. duorarum,* in 1959. After the coldest winter of record in Florida in 1957-58, the catch of shrimp in the spring of 1959 was a complete failure along the west coast of that state and Tortugas landings were the poorest of record for the same species (Eldred, *et al, op. cit.*).

But here again, water temperatures sufficient to suport a detailed analysis were not available. It would appear, then, that one of the elements of the suggested monitoring is present now in the form of accurate landings, but that supporting hydrographic surveys must yet be added to complete the picture.

Single estuaries.—While conclusions can be drawn from estuarine differences of geographical origin (e.g., temperature averages due to latitude and chemical aberrances due to geologically different water sheds), other dissimilarities may be found in any one estuary temporally and locally. Thus, information on temperature and salinity tolerances can be obtained for many organisms by a careful recording of changes in abundance in parts of a river mouth; by a careful monitoring of selected habitats over a period of several years; and comparing abundance, growth and spawning with hydrographic conditions.

Here again, the easiest examples to mention are oysters and shrimp.

Those of us who have had the opportunity to observe oyster growing habitats over a considerable number of years are acquainted with the fact that cycles of wet years result in a high productivity of the reefs lying in peripheral regions. During a series of dry years these reefs are decimated by snails, disease and noxious associated organisms such as sponges. The average salinity values of such periods are much more meaningful in establishing ecological limits of the organisms concerned than those of a short term basis.

Similar findings exist for shrimp. During the great drouth of 1948-1956, brown shrimp, *Penaeus aztecus* largely replaced the white shrimp, *P. setiferus,* in the estuaries of the western Gulf of Mexico. When rainfal returned to normal, the white shrimp again achieved a greater abundance.

Abundance of shrimp as demonstrated by landings has also been shown to be correlated with rainfall (Hildebrand and Gunter, 1953; Gunter and Hildebrand, 1954).

In the present connection, the following quotation from the latter work is worth repeating:

> "In view of the general paucity of long term hydrographic work in estuarine areas over the world, it goes without saying that salinity data, adequate for relation to the shrimp catch, even in one bay let alone the whole Texas coast for the 26 year period, is completely absent. For that reason the writers have utilized rainfall, which is one step removed from the probably effective factor, salinity, in this analysis."

As implied above, definite salinity studies in selected nursery and growing areas should elucidate the salinity requirements of the white and brown shrimp more quantitatively and meaningfully.

Under the plan of investigation being here recommended, the same information can be developed for those animals and plants not now so well understood.

Another example of the use of single estuaries is in the oportunity afforded for the evaluation of osmoregulatory abilities of various animals. These can be established under definitely measurable chemical and physical parameters. Then, as in the case of the St. Johns River (Odum, 1953), and the Homosassa River (Herald and Strickland, 1949), both of Florida, a comparison is possible in which one or more of the chemical constituents is altered (Ferguson *et al,* 1947). Laboratory experimentation on such a scale would, of course, be unthinkable.

Summary and Recommendations

1. The heterogeneity of estuaries is discussed. Inasmuch as change and difference are useful qualities in experimentation, the diverse qualities of river mouths offer splendid experimental situations for research if properly utilized.

2. The need for *selective concentration* of estuarine studies is asserted. Those estuaries already possessing laboratories, especially where these installations have been in existence for a relatively long duration, offer the most favorable sites. In those cases, the suggested program could be effected by merely extending, expanding and standardizing activities that are presently underway in a more or less haphazard fashion and by integrating them with similar studies over a wide range of brackish water habitats.

3. Examples of the type of benefit to be derived from suggested studies are provided, using only a few common organisms of southeastern U.S. and the Gulf of Mexico that have already received extensive studies over a relatively wide range. Although others could be mentioned, only a small percentage of organisms has received attention. Proposed studies would bring out salient physiological and ecological factors not now comprehended.

4. Inasmuch as estuarine animals and those of the offshore waters intermingle and are not, in many cases, restricted to either habitat, the proposed studies should embrace, besides the river mouths, the waters nearby for a considerable distance offshore.

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FOUR ECHINOSTOME TREMATODES FROM LOUISIANA BIRDS INCLUDING THE DESCRIPTION OF A NEW SPECIES *

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In connection with life history studies of trematodes encysted in Louisiana crayfishes and poeciliid fishes, various birds and mammals were collected and examined for trematodes at the Goodhope oil field, near Norco, Pass Manchac, and Grand Terre Island, Louisiana. Trematodes from some mammals in the Goodhope oil field have been reported in another paper (Lumsden and Zischke, 1961). The Goodhope and Pass Manchac localities are cypress-tupelo swamps bordering the southern and western shores of Lake Pontchartrain respectively. The Goodhope oil field is located approximately 20 miles west of New Orleans, Louisiana, on U. S. Highway 61; Pass Manchac, on Louisiana Highway 51, 15 miles north of LaPlace, Louisiana, at the junction of Lake Pontchartrain and Lake Maurepas. Grand Terre Island lies approximately one mile east of Grand Isle, Louisiana, in the Gulf of Mexico.

A single adult trematode of the genus *Patagifer* Dietz, 1909, was recovered from the intestine of an ibis taken at the Goodhope oil field. Two specimens of the same species, one a preadult and one containing a few immature uterine eggs, were found in the intestine of another ibis collected at Pass Manchac. These three specimens apparently represent a new species of *Patagifer,* for whcih the name *Patagifer vioscai* is proposed, in honor of the late Percy Viosca, biologist, Louisiana Wildlife and Fisheries Commission.

Specimens were fixed in aceto-formol-alcohol (AFA) under slight coverslip pressure, stained in Van Cleave's combination-hematoxylin and mounted in piccolyte. Measurements cited in the diagnosis of *P. vioscai* were taken from the holotype and are given in millimeters.

The author gratefully acknowledges the technical assistance of Miss Carol Ann Winkler. This study was done under the direction of Dr. Franklin Sogandares-Bernal.

Patagifer vioscai, sp. nov.

(Figures 1 to 4)

Host.—*Eudocimus albus* (Linn.), white ibis.

Location.—Small intestine.

Locality.—Goodhope oil field, near Norco, and Pass Manchac, Louisiana.

Holotype.—U. S. Nat. Mus. Helm. Coll. No. 39099.

Diagnosis.—*Patagifer:* Body elongate 8.567 long and 1.699 wide at level of acetabulum. Forebody 1.381 long. Anterior and posterior ends of body and sides of forebody curved ventrally; sides of hindbody parallel, posterior end of body tapering abruptly to a prominent conical tip. Cuticle rugate, spinose to posterior margin of acetabulum. Circumoral collar well developed, 1.557 wide, distinctly bilobed by dorsal and ventral indentations, bearing a total of 52 to 56 stout, tapered spines. Twenty-three to 25 crown spines arranged in single marginal row on each collar lobe; three spines on corner of each collar lobe not in series with marginal row crown spines; 1 pair of spines on each ventromedial corner distinctly posterior to marginal row crown spines. Ventral corner spines largest, 0.154 to 0.166 long by 0.041 to 0.047 wide; ventro-lateral marginal spines 0.128 long by 0.034 wide; lateral marginal spines 0.100 to 0.115 long by 0.031 to 0.034 wide; dorsal marginal spines 0.065 to 0.090 long by 0.014 to 0.022 wide. Cuticle extending out along sides of each spine from base to apex, forming a continuous web. Oral sucker subterminal, 0.142 long by 0.230 wide. Prepharynx short, pharynx in contact with oral sucker in holotype. Pharynx larger than oral sucker, 0.243 long by 0.230 wide. Esophagus 0.496 long. Ceca two, one on each side of body, bifurcating just anterior to fore margin of acetabulum, terminating blindly near posterior extremity. Acetabulum protruding ventrally in anterior third of body, 1.451 long by 1.522 wide. Sucker ratio approximately

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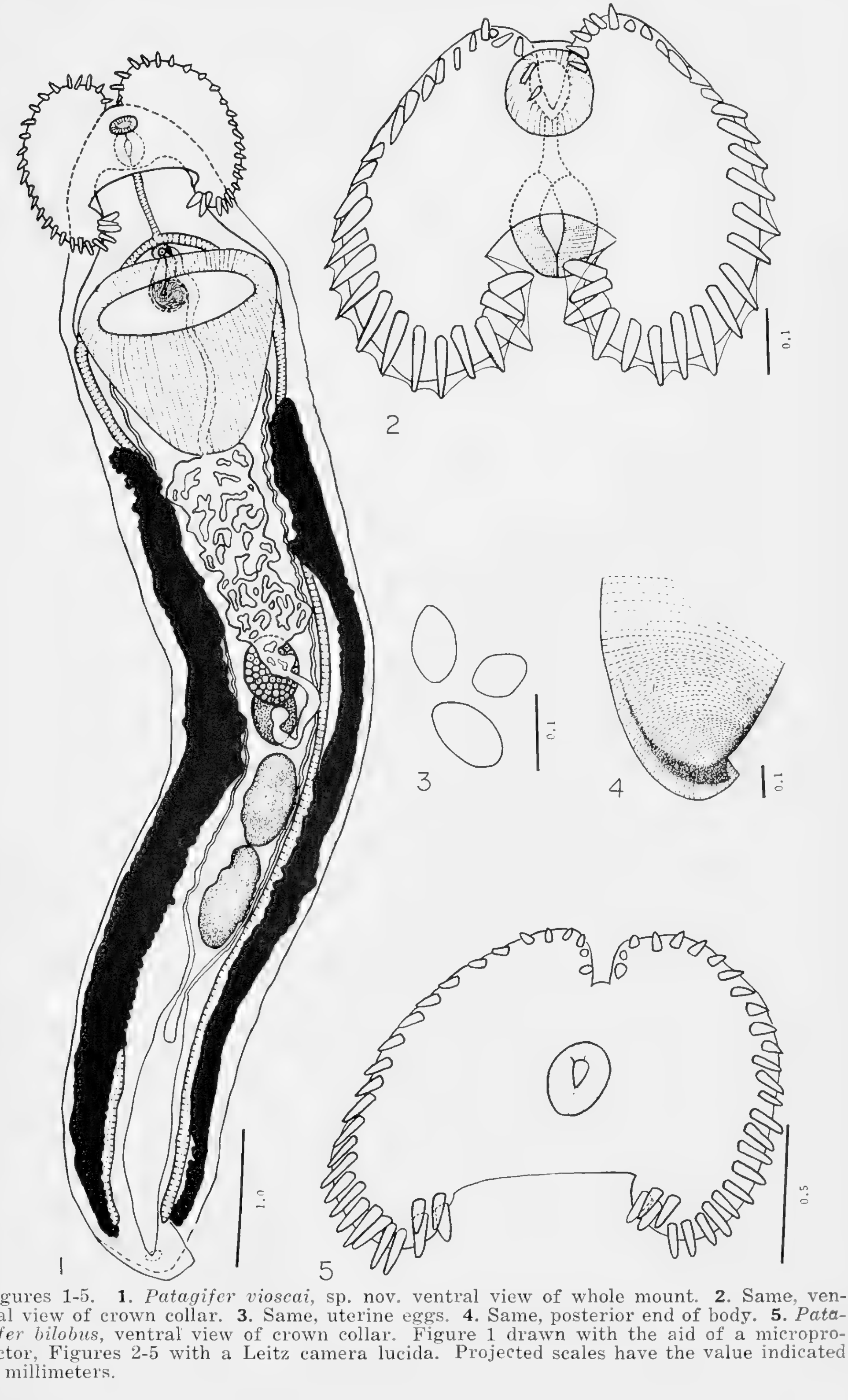
1:7. Genital pore median, immediately preacetabular and posterior to cecal bifurcation, followed by shallow genital atrium. Testes intercecal, tandem, in middle third of body, elongate with irregular margins; anterior testis 0.602 long by 0.333 wide; posterior testis almost in contact with anterior testis, 0.708 long by 0.333 wide. Cirrus sac curved, dorsal to acetabulum, extending 0.512 behind genital pore, inserting into right side of genital atrium; posterior two thirds of sac containing large seminal vesicle; anterior third containing prostate gland cells; cirrus not observed. Ovary mesial, equatorial, pretesticular, 0.486 long by 0.409 wide, separated from anterior testis by oval Mehlis' complex. Mehlis' complex 0.281 long by 0.307 wide. Laurer's canal opening dorsally on midline of body at level of Mehlis' complex. Uterus arising ventrally from Mehlis' complex, enlarged proximally as a *receptaculum seminis uterinum,* then turning anteriorly; uterine coils in transverse loops between level of ovary and hind margin of acetabulum, distally forming weakly differentiated metraterm lying sinistral to cirrus sac and perforating left side of genital atrium. Eggs 0.084 to 0.112 long by 0.050 to 0.064 wide. Vitelline follicles extending from posterior margin of acetabulum to posterior end of body, lateral to or overlapping ceca on ventral surface, nearly confluent on dorsal surface of body. Excretory vesicle elongate, Y-shaped, bifurcating midway between posterior margin of hind testis and posterior end of body. Collecting tubules ascending one on each side of midline mesial to ceca to midlevel of acetabulum where they are no longer observable. Excretory pore subterminal, dorsal.

Discussion.—Patagifer vioscai is the tenth species of the genus to be described, and is the first record of *Patagifer* from North America. *P. acuminatus* Johnston, 1917, and *P. fraternus* Johnston, 1917, are indigenous to Australia; *P. bilobus* (Rud., 1819) Dietz, 1909, the type species, has been reported from Europe, Africa, and Australia; *P. consimilis* Dietz, 1909, from Brazil; *P. parvispinosus* Yamaguti, 1933, from China and Japan; *P. sarai* Saksena, 1957, *P. simarai* Nigam, 1944, and *P. wesleyi* Verma, 1936, from India; and *P. skrjabini* Hilmy, 1949, from Egypt.

Egrets, *Casmerodius albus* (Linn.), and boat-tailed grackles, *Cassidix mesamexicanus* (Gmelin), collected at Pass Manchac were found uninfected with *P. vioscai,* although another echinostome, *Echinostoma revolutum* (Froelich, 1802) Looss, 1899, was recovered from one of the latter hosts. Sogandares-Bernal (personal communication) collected *E. albus* in Florida, but did not recover *Patagifer* from these ibises.

P. vioscai most closely resembles *P. bilobus,* differing from this and other species of the genus primarily in the arrangement of the crown spines. Dietz (1910) noted that the number of crown spines on one side of the collar varied from 26 to 29 in *P. bilobus.* Mendheim (1940) reported that, in one specimen of *P. bilobus* examined, there were 27 spines on each collar lobe, but, in another specimen, there were 27 spines on one side and 26 spines on the other. Odhner (1911) observed a difference of 3 or 4 spines on either side of the collar in some specimens of *P. bilobus.* Dr. Emile A. Malek, of the Tulane School of Medicine, has kindly provided the author with a specimen of *P. bilobus* from the sacred ibis in Egypt. This specimen possesses a total of 58 crown spines (29 on each collar lobe). The holotype of *P. vioscai* bears 26 spines on the left collar lobe and 27 on the right; no scares, possibly indicating loss of spines, were observed. The paratypes possess 28 spines on each half of the collar. In *P. bilobus* there are four spines arranged in overlapping pairs on each ventral corner of the collar not in series with but anterior to the marginal row of crown spines. In *P. vioscai,* however, there are only three spines on each corner not in series with the marginal spines; two of the former are posterior to the marginal row. In *P. bilobus* the ventral marginal spines are larger than the corner spines; in *P. vioscai* the ventral corner spines are larger than the ventro-lateral spines of the marginal row. In addition to the arrangement of the crown spines, *P. vioscai* differs from *P. bilobus* in having a pharynx larger than the oral sucker and a sucker ratio of 1:7, in contrast to a sucker ratio of 1:4 in the latter species. The forebody of *P. vioscai* appears to be somewhat longer than the forebody of *P. bilobus.* The ratio of forebody: hindbody in *P. vioscai* is 1:5.2; in *P. bilobus,* 1:6.6 to 7.2 (as computed from data reported by Dietz (1910)).

P. accuminatus and *P. fraternus,* with 25 and 28 spines respectively on each collar



Figures 1-5. **1**. *Patagifer vioscai*, sp. nov. ventral view of whole mount. **2**. Same, ventral view of crown collar. **3**. Same, uterine eggs. **4**. Same, posterior end of body. **5**. *Patagifer bilobus*, ventral view of crown collar. Figure 1 drawn with the aid of a microprojector, Figures 2-5 with a Leitz camera lucida. Projected scales have the value indicated in millimeters.

lobe, differ from *P. vioscai* in the position of the genital pore, which is anterior to the cecal bifurcation in those two species. There are three corner spines in *P. accuminatus* and four in *P. fraternus*. *P. consimilis* bears 26 to 29 relatively small spines, arranged as in *P. bilobus*. on each side of the collar. The collar of *P. consimilis* is considerably narrower than the body, which is spindle-shaped, the oral sucker is larger than the pharynx, and the sucker ratio is approximately 1:4. *P. parvispinosus* has 26 spines on each half of the collar, with four spines in two oblique rows on each ventral angle not in series with the marginal spines. The cuticle is entirely smooth (spinose to the posterior margin of the acetabulum in *P. vioscai*) and the acetabulum is four times larger than the oral sucker. *P. skrjabini* bears 20 marginal and 5 corner spines on each side of the collar. *P. wesleyi* possesses a total of 60 to 62 crown spines. Nigam (1944) distinguished *P. simarai* from *P. bilobus* on the position of the cirrus sac, which in *P. simarai* lies in front of, not overlapping, the fore margin of the acetabulum. Saksena (1957) separated *P. sarai* from *P. bilobus* on the basis that the cirrus sac was "only partly overlapped by the ventral sucker" in the former species. *P. bilobus, P. simarai* and *P. sarai* do not appear to differ significantly in any other respect. *P. simarai* possesses 27 spines on each collar lobe; *P. sarai*, 30. Some variation in the relative position of the cirrus sac and acetabulum was noted in specimens of *P. vioscai*, apparently due to twisting of the forebody and degree of curvature of the cirrus sac. *P. sarai* and *P. simarai* are probably synonyms of *P. bilobus*.

Himasthla alincia Dietz, 1909
(Figures 6 to 8)

Host.—*Totanus flavipes* (Gmelin), lesser yellowlegs, [new host record].

Location.—Small intestine.

Locality.—Grand Terre Island, Louisiana, [new locality record].

Diagnosis.—based on 4 mature specimens)—*Himasthla:* Body elongate, 18.266 to 20.532 long. Maximum width of body at level of anterior testis, 0.390 to 0.531; width at level of acetabulum 0.354 to 0.425. Forebody 0.461 to 0.743 long. Cuticle spinose to level of acetabulum. Circumoral collar 0.248 to 0.319 wide, bearing a total of 28 to 31 spines; 20 to 23 spines arranged in single dorsally uninterrupted marginal row; 4 spines in overlapping pairs on each ventral corner. Posterior corner spines largest, 0.050 to 0.053 long by 0.014 to 0.017 wide; anterior corner spines 0.034 to 0.039 long by 0.011 wide; marginal spines 0.041 to 0.047 long by 0.008 to 0.014 wide. Oral sucker subterminal, 0.070 to 0.100 long by 0.062 to 0.065 wide. Prepharynx 0.041 to 0.098 long. Pharynx 0.090 to 0.098 long by 0.065 to 0.084 wide. Esophagus 0.192 to 0.205 long. Ceca two, one on each side of the body, bifurcating just anterior to foremargin of acetabulum, terminating blindly near posterior extremity. Acetabulum 0.307 to 0.333 long by 0.256 to 0.307 wide. Sucker ratio approximately 1:3. Genital pore median, immediately preacetabular and posterior to cecal bifurcation. Testes tandem, intercecal, near posterior end of body, oval with smooth margins; anterior testis 0.743 to 0.779 long by 0.283 to 0.354 wide; posterior testis 0.089 to 0.204 behind anterior testis, 0.708 to 0.850 long by 0.283 to 0.390 wide. Cirrus sac elongate, dorsal to acetabulum, 2.042 to 2.148 long by 0.112 to 0.153 wide at base, containing seminal vesicle, prostate gland cells and spined cirrus. Ovary mesial or slightly dextral to midline, 0.166 to 0.192 long by wide. Mehlis' gland between ovary and fore margin of anterior testis, 0.205 to 0.269 long by wide. Laurer's canal opening on dorsal surface of body at level of Mehlis' gland. Uterus arising at Mehlis' complex, ascending in transverse coils between vitellaria, becoming straighter anteriorly. Metraterm dorsal to cirrus sac, entering genital atrium anterior to male duct. Eggs 0.103 to 0.123 long by 0.065 to 0.078 wide. Vitelline follicles lateral, extending from a point 6.407 to 8.531 posterior to hind margin of cirrus to near posterior end of body. Excretory pore terminal.

Discussion.—*Himasthla* spp. are usually parasites of sandpipers (Scolopacidae), though gulls, herons and oystercatchers have also been reported as hosts for certain members of this genus. A single case of human parasitism was reported by Vogel (1933), who described *H. muehlensi* from the feces of the host. Reports of *Himasthla* from fishes (*H. tensa* Linton, 1928, *H. annulata* (Diesing, 1850) and *H. piscicola* Stunkard, 1960) probably represent accidental or incidental infections.

Various pelecypods serve as second intermediate hosts for these echinostomes. Stunkard (1934) exposed *Mya arenaria, Mytilus edulis, Modiola modiolas, Cumingia tellinoides, Pecten irradians, Ensis americana* and *Crepidula fornicata* to cercariae of *H. quissetensis* (Miller and Northrup, 1926) Stunkard, 1938. Metacercariae obtained from the gills, foot and mantle of each of these experimental hosts were fed to laboratory raised gulls, in which the worms developed to maturity. *H. ambigua* Palombi, 1934, was described from metacercariae encysted in *Tapes decussalus* from the Gulf of Naples. Lebour (1907) reported metacercariae of *H. secunda* Dietz, 1909, in *Mytilus*, sp., as did Palombi (1925). Stunkard (1960) reported that *Mya arenaria* harbors the metacercariae of *H. compacta* Stunkard, 1960. In Vogel's (1933) report of human parasitism by *H. muehlensi,* the suspected vector was the edible clam, *Venus morienaria.* Eight species of *Himasthla* have been reported from North America: (1) *H. compacta* Stunkard, 1960; (2) *H. elongata* (Mehlis, 1831) Dietz, 1909; (3) *H. incisa* Linton, 1928; (4) *H. mcintoshi* Stunkard, 1960; (5) *H. muehlensi* Vogel, 1933; (6) *H. quissitensis* (Miller and Northrup, 1926) Stunkard, 1938; (7) *H. tensa* Linton, 1940, reported from *Gadus morrhua* at Woods Hole, Massachusetts, was suppressed as a synonym of *H. elongata* by Stunkard (1960); (8) *H. alincia,* until just recently known only from Brazil, has been reported from Massachusetts by Stunkard (1960).

H. alincia most closely resembles *H. rhigedana* Dietz, 1909, *H. mcintoshi* Stunkard, 1960, and *H. leptosoma* (Creplin, 1829) Dietz, 1909. In these three species the vitellaria are present only in the posterior two-thirds of the body, whereas in other species of *Himasthla* the vitelline follicles extend to the level of the cirrus sac. The length of the cirrus sac distinguishes *H. alincia* from *H. leptosoma* and *H. rhigedana.* The cirrus sac in *H. alincia* is 6 to 7 times longer than the acetabulum, compared with a cirrus sac only 2 to 3 times as long as the acetabulum in *H. leptosoma* and *H. rhigedana. H. mcintoshi* possesses 35 crown spines 28 to 31 in *H. alincia*) and the cirrus sac is tightly coiled, extending behind the acetabulum a distance approximately equal to the diameter of the ventral sucker.

Dietz (1910) described *H. alincia* as bearing a total of 31 crown spines. Some specimens recovered from Louisiana sandpipers possessed only 28 spines, and all of the worms were larger (mean length 19.301) than Dietz's material (10.5 long) from *Ereunetes (Tringa) pusilla* in Brazil. Dietz did not describe the cirrus in the type material, which in the Louisiana specimens is covered with small, closely set spines.

Stephanoprora denticulata (Rud., 1802) Odhner, 1910 (Figue 9)

Host.—*Thalasseus maximus* (Boddaert), royal tern, [new host record].

Location.—Small intestine.

Locality.—Grand Terre Island, Louisiana, [new locality record].

Discussion. — Linton (1928) reported specimens identified as *Mesorchis psuedoechinatus* (Olsson), actually *S. denticulata,* from *Larus argentatus, L. atricilla, L. delawarensis, L. marinus, L. philadelphia, Colymbus auritus, C. holbolli* and *Gavia immer* at Woods Hole, Massachusetts. Price (1932) reported *S. denticulata* from a California sea lion, *Zalophus californianus,* which had died in the National Zoological Park (Washington, D.C.). Hutton and Sogandares-Bernal (1960) recovered a single specimen of *S. denticulata* from *Larus argentatus smithsonianus* in Florida.

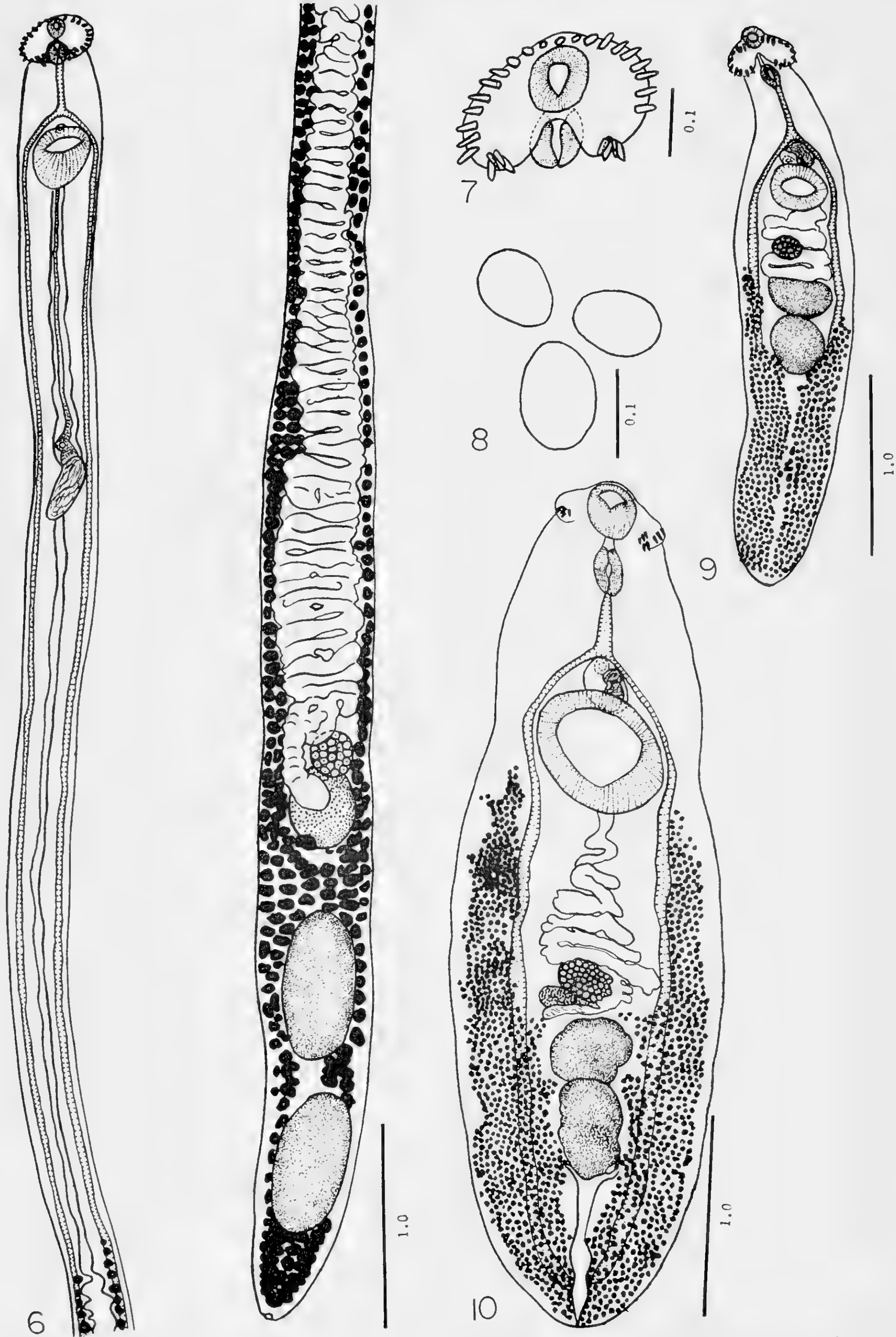
Echinostoma revolutum (Froelich, 1802) Looss, 1899 (Figure 10)

Host.—*Cassidix mesamexicanus* (Gmelin), boat-tailed grackle [new host record].

Location.—Small intestine.

Locality.—Pass Manchac, Louisiana.

Discussion. — One of three boat-tailed grackles, *Cassidix mesamexicanus,* collected at Pass Manchac, Louisiana, was infected with 24 *E. revolutum.* Most of these worms were sexually mature. The posttesticular portion of the body in these specimens appears shorter than normal for *E. revolutum,* but the worms agree in all other respects with the diagnosis by Beaver (1937) for this species. *E. columbae* Zunker, 1925, (which according to Beaver (1937) is a synonym of *E. revolutum*) similarly possesses a short posttesticular region. Morphological variation, particularly in body size and shape, apparently can be induced by such factors as host species and host diet.



Figures 6-10. **6.** *Himasthla alincia*, ventral view of whole mount, showing anterior and posterior ends of body. Portion of midbody omitted. **7.** Same, ventral view of crown collar. **8.** Same, uterine eggs. **9.** *Stephanoprora denticulata*, ventral view of whole mount. **10.** *Echinostoma revolutum*, ventral view of whole mount. All drawings made with the aid of a Leitz camera lucida. The projected scales have the value indicated in millimeters.

Lumsden and Zischke (1961) observed reduction of the hindbody in some specimens of *Rhopalias macracanthus* Chandler, 1932, recovered from a heavily infected opossum, possibly attributable to abnormal location of the worms in the host's intestine imposed by overcrowding. Furthermore, artifacts may be produced in fixation. Body shape may also be dependent on the age of the worm. The author concurs with Beaver (1937) that the arrangement of the collar spines is the most reliable diagnostic character for members of this group of trematodes. Specimens recovered from Louisiana *Cassidix mesamexicanus* bear a total of 37 crown spines, the arrangement of which corresponds to that typically found in *E. revolutum*: 5 spines on each corner of the collar, 6 spines on each lateral margin and 15 alternating spines on the dorsal surface.

Babero and Lee (1961) reported Louisiana nutria, *Myocastor coypus*, infected with *E. revolutum*, adding that snails, *Heliosoma* sp., were occasionally found in the intestines of these hosts. One of eight *Heliosoma trivolvis lentum* collected by the author at Pass Manchac released echinostome cercariae closely resembling the cercaria of *E. revolutum* as described by Beaver (1937). Beaver (1937) noted that *H. trivolvis* could serve as both first and second intermediate host for *E. revolutum*.

Summary

Patagifer vioscai, n. sp., from the white ibis, *Eudocimus albus*, appears distinct from other members of the genus primarily in the arrangement of the crown spines. The new species constitutes the first record of *Patagifer* from North America.

Himasthla alincia, formerly known only from *Ereunetes pusilla* in Brazil and Massachusetts, is reported from Louisiana lesser yellowlegs, *Totanus flavipes*. The original description of this echinostome is amended to include variation in the total number of crown spines (28 to 31) and a spined cirrus.

Stephanoprora denticulata is reported for the first time from Louisiana. Its occurence in the royal tern, *Thalasseus maximus*, is a new host record for this trematode.

Echinostoma revolutum was recovered from a boat-tailed grackle, *Cassidix mesamexicanus*, a new host record. *Heliosoma trivolvis lentum* may serve as both a primary and secondary host for *E. revolutum* in Louisiana.

Abstract

Patagifer vioscai, n. sp., from the white ibis, *Eudocimus albus* (Linn.), is described. *Himasthla alincia* Dietz, 1909, and *Stephanoprora denticulata* (Rud., 1802) Odhner, 1910, are reported for the first time from Louisiana. New host records include *S. denticulata* in the royal tern, *Thalasseus maximus* (Boddaert), *H. alincia* in the lesser yellowlegs, *Totanus flavipes* (Gmelin), and *Echinostoma revolutum* (Froelich, 1802) Looss, 1899, in the boat-tailed grackle, *Cassidix mesamexicanus* (Gmelin). The original description of *H. alincia* is amended.

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CRASPEDACUSTA IN THE SOUTHEASTERN UNITED STATES[1]

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The freshwater medusa *Craspedacusta sowerbii* Lankester has been reported from approximately one hundred localities in the United States and southern Canada. Evidence has been presented by Kramp (1950) and by Lytle (1960) that this medusa is an exotic, introduced into the United States and other parts of the world in recent times from the Yangtze River basin in central China.

Most American records for *C. sowerbii* have come from the northeastern United States and it has been suggested that this apparent concentration of medusa records is a reflection of the greater density of the human population and more intensive biological investigations in that portion of the country. Relatively few records of freshwater medusae have been published from the southeastern quarter of the United States and it is the purpose of the present report to summarize the records of medusae in the Southeast and to supplement these records with a report of several recent occurrences in this area.

I wish to express my appreciation to the several persons who contributed specimens and observations on medusae in this area. I am particularly indebted to Dr. Charles Cutress of the United States National Museum and to Dr. Fritz Haas of the Chicago National History Museum for their generous cooperation and the loan of specimens. Dr. William R. Murchie of Flint College, University of Michigan, very kindly made available to me some papers and several lots of specimens from the collection of the late Dr. Frank Smith of the University of Michigan. Among the several other donors was the Carolina Biological Supply Company, Elon College, North Carolina, which made a gift of specimens collected in North Carolina.

Specimens from the following locations were examined during the present study (source of borrowed specimens indicated in parentheses); *Alabama:* Lake Purdy (Smith Collection), Lake Wilson (TVA collection), *Georgia:* pool in Augusta (USNM), lake near Sonoraville (CNHM). *Kentucky:* Benson Creek (Smith Collection), Kentucky River near Cottonburg (USNM), Indian Lake (USNM). *Maryland:* rocky pool near Cabin John (USNM). *North Carolina:* Lake Jeanette (Carolina Biological Supply Co.). *West Virginia:* lake near Athens (USNM); Cheat Lake (USNM).

The previous records of medusae in the Southeast are summarized by state in Table 1 with the excpetion of records for Maryland, Virginia, and the District of Columbia. This latter area has previously been studied more intensively than other portions of the Southeast and previous records of medusae in these states are listed in a recent paper (Lytle, 1960).

Freshwater medusae have been collected and/or observed in ten new locations in the Southeast; these ten new records are listed by state in Table 2. Information regarding the appearance of medusae was received from many different sources and was often fragmentary in nature. Nevertheless, this information has proved valuable to us in locating *Craspedacusta* for experimental purposes and should prove useful in future analysis of the distribution and ecology of this form. In each case of a report of medusae from a new locality we endeavored to secure specimens and accurate data on the habitat. Several new reports which lacked sufficient data to be authoritative were omitted from this report.

New Records

Alabama: The late Dr. W. E. Snow, formerly a biologist on the staff of the Tennessee Valley Authority at Wilson Dam, Alabama, reported medusae in Lake Wilson, a large TVA impoundment on the Tennessee River in northeastern Alabama on July 1 and 4, 1958. A few medusae were observed at several scattered points on the lake and a total of 17 specimens were collected. Subsequent examination of the alcohol-pre-

[1] This investigation was supported in part by a research grant (RG 8140) from the Division of General Medical Sciences, Public Health Service.

served specimens revealed four male medusae and 13 female medusae, ranging in diameter from 11 to 15 mm. No medusae were observed in the lake during the summer of 1959 as reported by Dr. Gordon E. Smith of the TVA.

Georgia: During August of 1957 medusae were reported in Lake Sidney Lanier, a large impoundment near Gainesville, Georgia, by Mr. T. S. Callaway of Greensboro, Georgia. Dr. W. D. Burbanck reported that several medusae were collected and kept in an aquarium at Emory University during the summers of 1957 and 1958.

A single male specimen collected during August 1946 in "a lake near Farmville, Georgia", was found in the collection of the Chicago Natural History Museum. No further collection data was available.

Professor R. E. Ware of Clemson College,

TABLE 1.
Previous records of freshwater medusae in the southeastern United States

Location	Nature of Habitat	Date Observed or Collected	Reference	Notes
Alabama				
Stallworth Lake, near Tuscaloosa	impoundment of Warrior River	Sept. 14-Oct. 9, 1928	White, 1930	males
Lake Purdy, near Birmingham	impoundment on Cahaba River	Aug. 1-28, 1933	Breder, 1937; papers of the late Dr. Frank Smith	females; disappeared after copper sulfate treatment of the lake
Arkansas				
near Prescott	Blue Lake	1927	Causey, 1938	
near Stamps	mill pond	1937	Causey, 1938	....
Florida				
Little Lake Elbert in Winter Haven	natural lake	Aug. 1-15, 1943; also seen in 1942	Byers, 1944	males (about 24 specimens collected; mostly immature)
Silver Springs, near Ocala	natural spring	1954	Odum, 1957	hydroids only collected
Georgia				
Churchyard pool in Augusta	small concrete pool	Sept. 16, 1918	Hargitt, 1923 Payne, 1924	USNM No. 40794 USNM No. 40795 males
Kentucky				
Benson Creek, near Frankfort	near mouth of creek just above impoundment of Kentucky River	Sept. 26-27, 1916; Sept. 1924	Garman, 1916, 1922, 1924	USNM No. 40053 USNM No. 42797 males
		July 30-Aug. 20, 1925	Payne, 1925, 1926	hydroids only
Kentucky River				
at High Bridge	river	1917	Payne 1926	....
near College Hill	river	Sept. 1925	Payne 1926	males and females
at Valley View	river	1922	Payne 1926	......
Three locations on the river between College Hill and Valley View	. . . . .	1925	Payne 1926	.
Indian Lake, near Owensboro	unknown	Aug. 1927	Schmitt, 1927	USNM No. 42195 USNM No. 42198
Louisiana				
Monroe	small concrete tank	June 1935; also seen 1932 or 1933	Viosca and Burkenroad, 1936	males
Mississippi				
Belhaven College in Jackson	small concrete pool	Aug. 14-31, 1944	Fincher and Buchanan, 1944	males
Tennessee				
Jackson Lake, 12 mi. west of Knoxville	50-60 acre impoundment	July 15-Aug. 3, 1938; also seen 1936 and 1937	Powers, 1938	females
Mouth of Burton's Creek on Kentucky Lake, near Tennessee 100	impoundment	July 24, 1952	Chadwick and Houston, 1953	females
West Virginia				
near Athens (Wood County)	unknown	1930	Schmitt, 1939	USNM No. 42674 one female
Cheat Lake 7 mi. NE of Morgantown	impoundment of Cheat River	Sept. 1939	Reese, 1940	USNM No. 52323 two females
Mercer County	unknown	unknown	Reese, 1940	....
Fayette County	unknown	unknown	Reese, 1940	....

TABLE 2.
New records of freshwater medusae in the southeastern United States

Location	Dates	Body of Water	Notes	Source of Record
Alabama				
Wilson Dam	July 1-4, 1958	Lake Wilson	Large impoundment on Tennessee River, medusae scarce; both males and females present	W. E. Snow, E. Pickard G. E. Smith
Georgia				
Gainesville	Aug. 1958; 1959	Lake Sidney Lanier	Large reservoir completed 1956	T. S. Callaway, W. D. Burbanck
near Sonoraville	Aug. 1946	artificial lake	Lake 10-12 years old near Farmville (2 mi. SW Sonaraville) (CNHM No. 2808)	J. H. Cocks, F. Haas
near Toccoa	1942 and 1953	Lake Louise	USNM No. 52324	R. E. Ware
near Roswell	Sept. 1961	artifical lake	small impoundment near Chattahoochee River; close to Lake Sidney Lanier	R. P. Gravely, Jr.
Kentucky				
near Cottonburg	about Sept. 9, 1937	Kentucky River	Medusae collected at Camp Daniel Boone (Boy Scouts); about 18 mi. S. Lexington (USNM No. 51425)	E. Lotsfitch, D. W. Dunham, E. J. Karlin
Maryland				
Cabin John	Aug. 15-Sept. 5, 1959	rocky pool	5 mi. W. Cabin John; 2-3 acre pool on an island located just below The Great Falls, near the Maryland shore (USNM No. 51332)	J. Atkins, C. F. Lytle, C. E. Cutress
North Carolina				
near Greensboro	Aug. 20-Oct. 1, 1957; summer 1958	Lake Jeanette	Large impoundment about 20 years old; brief notice with photograph appeared in *Carolina Tips* 21(5):20, 1958.	V. M. Cutter, Jr., Carolina Biological Supply Company
Virginia				
Philpott Reservoir 25 mi. NW of Martinsville	July, 1960	impoundment	Lake 20 years old, located at headwaters of Smith River	R. P. Gravely, Jr.
Pocahontas State Park 25 mi. SW of Richmond	1959; also reported present 1957, 1958	impoundment of Swift Creek	males and females present	N. E. Rice

South Carolina, observed freshwater medusae in Lake Louise, near Toccoa, Georgia, in September, 1942 and again in 1953. One male specimen collected in 1942 is deposited in the United States National Museum.

Mr. R. P. Gravely, Jr. of Martinsville, Virginia, observed numerous medusae in a small artificial lake south of Rosewell, Georgia, in September 1961. This lake is located just a few hundred yards from the Chattahoochee River which is itself impounded at this point.

Kentucky: Five small male specimens were collected in the Kentucky River at Camp Daniel Boone (a Boy Scout Camp) located 18 miles south of Lexington, Kentucky by Mr. Edward Lotsfitch on September 9, 1937. These specimens were discovered in the collection of Bowling Green State University, Bowling Green, Ohio, and were subsequently deposited in the United States National Museum by Prof. Edward J. Karlin.

Maryland: Freshwater medusae appeared in a rocky overflow pool in the bed of the Potomac River just below The Great Falls during August and September of 1959. The pool was approximately two to three acres in size at the time of a collection on September 5, 1959. The medusae appeared restricted to a small portion of the pool at the time of collection; several hundred were preserved for study and a sample deposited in the United States National Museum. All specimens examined from the pool were female.

North Carolina: Medusae appeared in Lake Jeanette, located just outside the city limits of Greensboro, North Carolina, during the summers of 1957 and 1958. In 1957 the medusae were abundant and were observed by Dr. Victor M. Cutter, Jr. of the Women's College of the University of North Carolina, from about August 20 to October 1. The following year only a few scattered medusae were seen. Lake Jeanette is a twenty-year-old impoundment about three miles in length, formed by damming a small winding creek valley. A sample of 257 specimens collected in the summer of 1957 were provided by the Carolina Biological Supply Company. All the specimens were found to be males. This is the first record of freshwater medusae in North Carolina.

Virginia: Specimens were collected in July 1960 in Philpott Reservoir, an impoundment 25 miles northwest of Martinsville, Virginia, by Mr. R. P. Gravely, Jr. This reservoir is located at the headwaters of Smith River, a tributary of the Roanoke River in southwestern Virginia. The medusae were observed in large numbers in one small cove of the lake.

Dr. Nolan E. Rice of the University of Richmond collected medusae in an impounded portion of Swift Creek in Pocahontas State Park, about 25 miles southwest of Richmond, Virginia, during the summer of 1959. Two collections totalling 180 specimens contained both male and female medusae in approximately equal numbers (89 males and 91 females). A large number of embryos were preserved for histological study. An attendant at the park stated that the medusae were also present in the lake during the summers of 1957 and 1958.

Figure 1. The known distribution of *Craspedacusta sowerbii* in the southeastern United States.

Discussion

The known distribution of *C. sowerbii* in the southeastern United States is illustrated in Figure 1. A major feature of the distribution is the paucity of records from the Coastal Plain south of the Virginia-North Carolina border. The significance of this pattern is unknown. The disttribution of an exotic species, such as *C. sowerbii* is limited by two major factors: its introduction into new habitats and the actual availability of suitable habitats. In the case of *C. sowerbii* there is little evidence which suggests that its distribution is limited by habitat availability in this area, since the medusae have previously been found in such a wide variety of habitats. Although *C. sowerbii* does seem to occur most frequently in man-made bodies of water (Pennak, 1956; Lytle, 1960), the list of different types of aquatic habitat in which the species has been found is long and varied. Present evidence indicates that the species is highly eurytropic and not likely to be limited in the Coastal Plain by a lack of suitable habitats.

Pennak (1956), Rice (1958), and other authors have commented on the predominance of medusa populations which appear to consist of only one sex. Only two previous records from North America have been published of populations in which both sexes were present (Payne, 1926; Rice, (1958). Payne (loc cit.) found the two sexes present in Benson Creek, Kentucky, in approximately equal numbers, citing a collection of 110 in which there were 52 females and 58 males. Rice (1958), however, sampled a population in Southampton Quarry in Richmond, Virginia, several times during the summer and early fall of 1956, and found the sex ratio changed markedly during the course of the season. At times the population contained males and females in approximately equal numbers, but at other times there was a heavy predominance of females, and for one two-week period males appeared to be completely absent from the population. These results clearly indicate that caution must be exercised in drawing conclusions from a single collection or from any small sample from a medusa population.

An examination of the literature reveals many reports in which the sex of the medusae was not determined and many other cases in which the sex of only one or a few medusae was determined. There are, however, a few cases in which large samples have been collected and examined and found to consist of only males or only females. The data on sex of the medusae as indicated in Figure 1 must be considered in view of these limitations. Many of the collections examined were small and merely establish the presence of the sex indicated; not that the population consisted exclusively of that sex.

Two new populations reported in this study were found to contain both sexes. As noted above, the sexes were present in approximately equal numbers in the collection of Rice from Pocahontas State Park, Virginia, but females predominated in the small sample available from Lake Wilson, Alabama.

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Since this manuscript was submitted for publication, an additional reference to *Craspedacusta* in the southeastern United States has come to my attention. Price (1957) reported the medusae in Broad Creek, Harford County, Maryland, on September 16, 1956. Broad Creek is a tributary of the Conowingo River in northeastern Maryland.

ABSTRACT

The distribution of the freshwater medusa *Craspedacusta sowerbii* in the southeastern United States is reviewed and extended by ten new locality records. Specimens from twelve localities were studied to determine the sex of the medusae; collections from two of the new localities reported were found to include both male and female medusae. *C. sowerbii* is reported for the first time from North Carolina.

NOTES ON THE BREEDING BEHAVIOR OF EUBRANCHIPUS HOLMANI (RYDER)[1]

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and
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INTRODUCTION

The breeding behavior of the branchiopod Anostraca has received little mention, especially that of species occurring in the New World. Except for the cosmopolitan *Artemia* (which is atypical in many respects) there is virtually no literature on the subject other than some notes by Gissler relating principally to *Eubranchipus vernalis* (Verrill) (see Packard, 1883), the more detailed observations of Pearse (1912) on *Eubranchipus serratus* Forbes, and a few notes by Johansen (1922) on the Arctic species, *Artemiopsis stefanssoni* Johansen. A useful review of the subject which deals with the European literature has been published by Mathias (1937) and includes a summary of his own important observations on *Branchipus stagnalis* (L) and *Chirocephalus diaphanus* Prévost.

In the course of studies by the junior author dealing with thermal thresholds in *Eubranchipus holmani* (Ryder) certain stimuli were evidently produced which initiated a breeding response in the shrimp. The initial studies, based on 5 series of observations by Ogren in 1960, were supplemented by 10 additional series by the senior author in 1961. The following descriptions are a summary of the activities noted by both observers.

CONDITIONS OF STUDY

E. holmani is a stenothermal species occurring only during the winter months in certain heavily-shaded temporary ponds on the pine flatlands of southeastern St. Tammany Parish, Louisiana. Field collected specimens were brought to the laboratory in plastic buckets of habitat water and stored in a Precision Low Temperature Incubator at 12-13°C (approximately the habitat temperature at time of collection) until used, a period of a few hours to no more than 6 days. In 1961 some observations were made on shrimp which had been segregated as to sex immediately upon return to the laboratory and stored in glass battery jars under similar conditions. Observations were carried out under conditions of normal room illumination on specimens in the stock buckets, in 2 liter battery jars, and (when photographs were being made) under the light of 2 No. 1 Photoflood bulbs in small, flat-sided museum jars. Temperatures were determined by a recently calibrated mercury thermometer; intervals were timed with a stopwatch.

OBSERVATIONS

When brought from the constant temperature box at 12-13°C shrimp of both sexes swam at random in the usual inverted position, with the horizontal axis of the body approximately parallel to the water surface except when they were moving from one depth to another. Under normal circumstances, occasional bodily contacts with one another were followed by a quick jerk of the abdomen and a rapid change of swimming direction by one or both shrimp.

A deviation in this normal swimming pattern was usually shown when the water temperature reached 13.5°C and it continued sporadically until the water had warmed to about 19°C. Above this temperature normal random swimming was again the rule. The first indication of sexual receptivity occurred in certain females which would assume a more or less stationary position at any depth, with the long axis of the body inclined at an angle of 35° to 45° with respect to the water surface. Such females would maintain this position for some time during which a male might approach from the rear and below, with his head at about her mid-body region. The pair would hold their positions, the male following any changes in the course of the female, for 1-5 seconds (see Figure 1).

[1] These observations were made during the course of investigations supported by a research grant (G-8692) from The National Science Foundation.

[2] Present address: Louisiana Wild Life and Fisheries Commission.

One instance of a pair holding their positions for 16 seconds was recorded, during which the male followed several turns by the female. This "station taking" by the male, as it will be referred to hereafter, was preliminary to one of several courses of action:

1. The male would abruptly break off and turn aside (see Figure 2).

2. The male would attempt to seize the female about her thorax just anterior to the egg sac with his sickle-shaped II antennae. On occasion this would be followed by copulation. Frequently the female would avoid the clasping attempt and both she and the pursuing male would swim in tight vertical circles for a short period (see Figure 3). Again, the male might succeed in clasping an unresponsive female and a short, violent struggle would ensue while she freed herself. The duration of these precopulatory struggles rarely exceeded 1-3 seconds.

3. In cases where copulation took place the responsive female did not struggle after being clasped but continued to swim slowly about carrying the male. His II antennae were firmly clasped about her thorax just anterior to the ovisac; his long antennal appendages, normally carried coiled corkscrew-fashion, were laid out along the female's back.

Contact of the genitalia was effected by the male's efforts. He would twist his posterior thorax and abdomen over and around the side of the female's body in such a fashion as to bring their genitalia in contact. The precise alignment and introduction of the male's intromittant organ into the opening of the female's ovisac was not observed. His position in amplexus was similar to that shown in Figure 4, with his

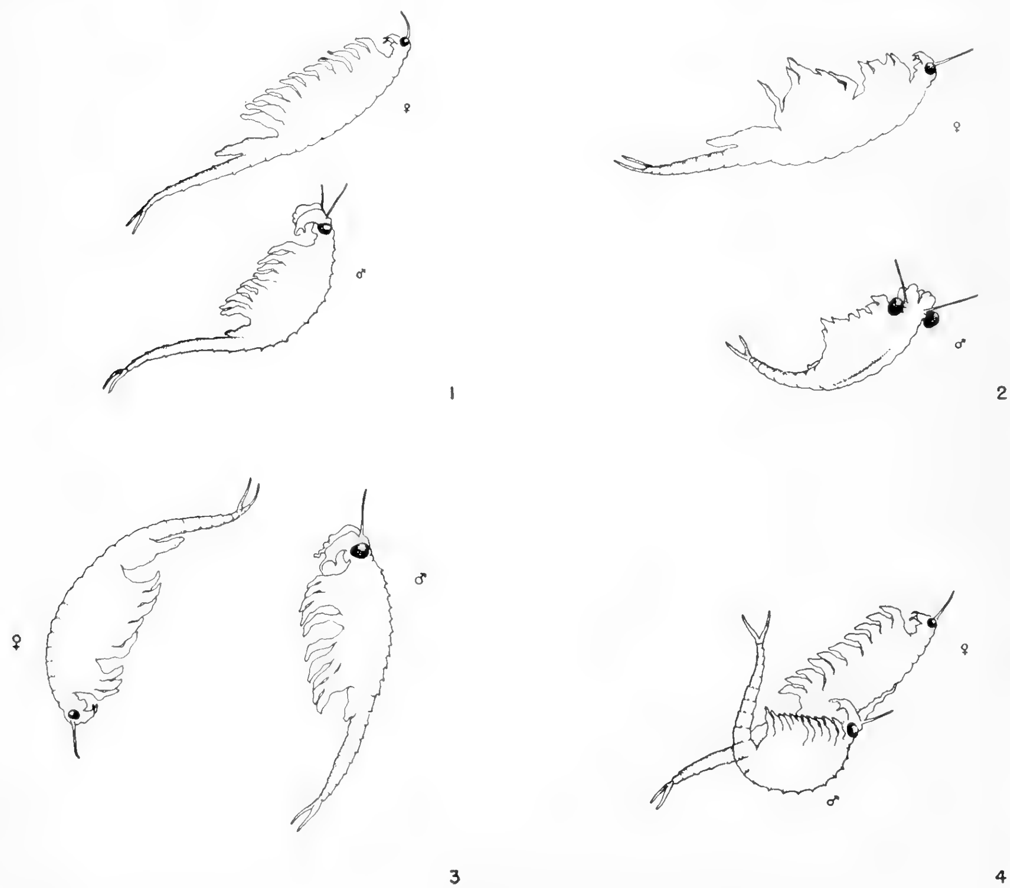

Figure 1-4. Breeding behavior of *Eubranchipus holmani*. For details see text.

anterior body nearly parallel, and his posterior thorax and abdomen carried vertically and at right angles, to the long axis of the female's body. In two cases in which copulation actually took place the duration of the act was timed at 1 minute, 10 seconds and 2 minutes, 10 seconds respectively, both preceded by a preliminary period of clasping lasting as long as 10 seconds. During copulation the female swam slowly about carrying the male, in the first case just above the bottom of the container, in the latter case near the surface. At the termination of the act a brief struggle of 2-3 seconds duration took place as the male disengaged his intromittant organ. It was not determined whether both, or only one, of the penes were involved in the contact. In a third instance, in which the male experienced difficulty in introducing his penes, the pair lay on the bottom in amplexus for 1 minute, 25 seconds before terminating an unsuccessful copulatory attempt.

Unfortunately no females involved in successful copulations were recovered for study. However four females which had been clasped for 3 to 5 seconds before they struggled free were captured and examined. Two of these had white, unshelled eggs in the lateral oviductal pouches, the third carried brown, shelled eggs in the median ovisac, and the fourth had an empty ovisac from which shelled eggs had recently been discharged. Presumably only the first two individuals were carrying eggs capable of being fertilized.

Certain instances of aberrent behavior were noted, one of the more interesting being the preliminary "station taking" of one male below a second (see Figure 1). As many as three males were seen taking station on each other simultaneously. The participants usually broke off without attempting to clasp (Figure 2), but occasionally one male would attempt to clasp a second. In such cases the passive participant struggled free immediately.

The influence of light intensity on behavior was also notable. In the shaded basins, which constitute the natural habitat, light intensity is low and all aspects of breeding behavior observed in the laboratory (except some preliminary "station taking") occurred under conditions of limited and diffuse illumination. When Photoflood lights were switched on to permit photography all the shrimp responded by sinking to the bottom of the container. Preliminary courting behavior started in dim light usually terminated abruptly when the bright lights were switched on.

Discussion

The breeding behavior of *E. holmani* conforms in general pattern to that reported for other Anostraca. Pearse (1912) did not record for *E. serratus* any activity resembling the preliminary "station taking" noted in the present instance. Mathias (1937), however, reported that in *Chirocephalopsis grubii* (Dybrowski) the male swims parallel to and under the female for a few seconds before attempting to clasp; he noted similar behavior in the case of *Branchipus stagnalis*. These two species are also reported as copulating in bright light, unlike *Chirocephalus diaphanus* in which copulation was observed (as in the present instance) to take place under dim illumination.

The period of clasping preceding copulation is usually only a few seconds duration but *Artemia* may clasp and swim in tandem for several hours or days, and *Branchipus stagnalis* is said to maintain union for as long as 60 minutes (Mathias, 1937, p.47). We have observed that the long antennal appendages of the male *E. holmani* are laid out along the female's back; this does not conform strictly to Gissler's statement (in Packard, 1883) "Having observed them often in copulation I can state . . . the frontal tentacles do not come into play as auxiliary organs". Actual sexual contact appears to be rather brief in all anostracans; Mathias (1937) reported it to be from a few seconds to as long as one minute in various Old World species. In the present instance, it will be recalled, sexual union of over 2 minutes duration was noted.

The position of the male during sexual contact is apparently somewhat more variable, a condition attributed by Mathias (1937) to the different lengths of the ovisac in various species. *E. holmani* resembles *Chirocephalus diaphanus* in this regard, both having ovisacs of intermediate length. The male's position has been observed to be somewhat different in species such as *Branchipus stagnalis* which has a very short ovisac, and the planes of symmetry of the anterior regions of the two conjugants are presumed to be almost parallel in the genus

Streptocephalus (which has a very long ovisac) although there does not appear to be any published observations relating to the latter genus.

Conclusions

The courtship-breeding behavior of *E. holmani* appeared to be a series-succession of stereotyped events. Full knowledge of the cues involved and the environmental conditions necessary for courtship to be initiated is incomplete. However the most obvious condition, aside from sexual maturity of the participants, was a gradual warming of the surrounding water. Breeding activity usually occurred when the temperature ranged from 13.5° to 19°C; outside this range little or no such activity took place.

The female seemed to play a nearly passive role in the preliminaries although she may have initiated a response in the male by the angled, nearly stationary posturing that was so frequently observed. This response of the male took the form of "station taking" from below and to the rear of the female. However the fact that such females frequently resisted clasping attempts suggested that such posturing did not necessarily indicate sexual receptivity.

It has been repeatedly observed (Packard, 1883; Mathias, 1937; Pearse, 1912) that only females with eggs in the lateral oviductal pouches accepted copulation, although the last-named noted several instances in *E. serratus* in which males attempted to copulate with females carrying shelled eggs in the median ovisac. Since the females which actually accepted males were not recovered in the present study no evidence on this point can be provided. However clasping attempts on mature females in all stages of egg formation were observed indicating that highly stimulated males will attempt to clasp any female or even other males. The role of the female is positive to the extent that she accepts or rejects a male depending upon the condition of her eggs.

Acknowledgments

The assistance of Mr. Bernard Manale is gratefully asknowledged.

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Abstract

Breeding activities of *Eubranchipus holmani* are described and the environmental factors, especially water temperature, known to be associated with such activity, are reviewed. Various aspects of breeding behavior including preliminary positioning, clasping attempts, and successful and unsuccessful copulation are described and compared with published accounts of other species of Anostraca.

MICROPHALLUS PROGENETICUS, A NEW APHARYNGEATE PROGENETIC TREMATODE (MICROPHALLIDAE) FROM THE DWARF CRAYFISH, *CAMBARELLUS PUER*, IN LOUISIANA.[1]

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It is with great pleasure that I contribute this paper for the number honoring the memory of the late Percy Viosca, a noted Louisiana biologist who studied extensively the crayfishes of his native state.

In connection with studies of trematodes encysted in Louisiana crayfishes, specimens of a progenetic terematode were observed, through the shell of the affected crayfishes, moving about within the cephalothorax. The following is a preliminary report of this trematode.

Acknowledgements are extended to Dr. G. H. Penn for identification of some crayfish hosts and to Mr. Joseph Fitzpatrick, Mrs. Lucy McAlister Sogandares, and Miss Carol Winkler for technical assistance.

Unless otherwise specified all measurements are in millimeters.

Microphallus progeneticus, sp. nov.
(Figures 1-8)

Host.—*Cambarellus puer* Hobbs, 1945; dwarf crayfish; family Astacidae.

Incidence of infection and numbers.—In 4 of 4: 4, 30, 33, 43.

Location.—On surface of viscera in cephalothorax.

Locality.—Maringuoin, Iberville Parish, Louisiana.

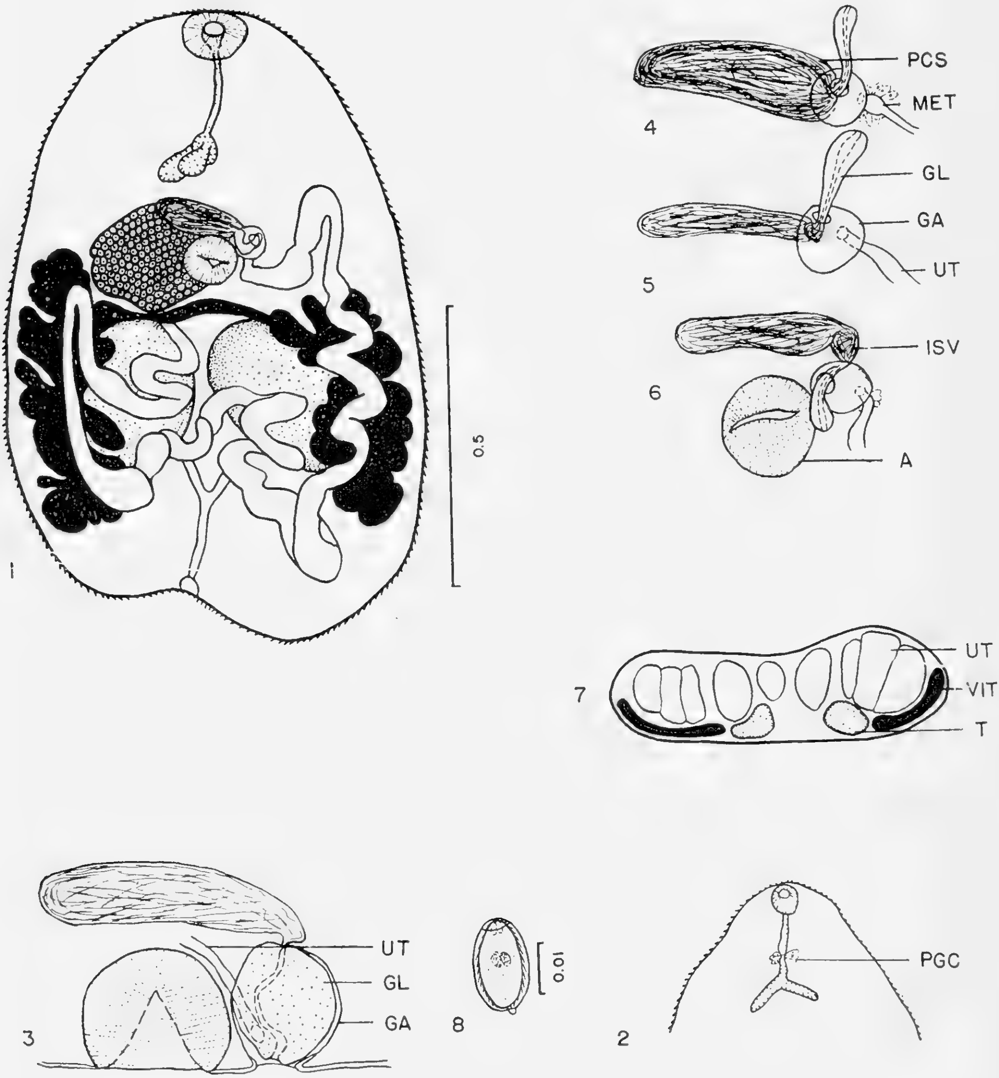
Holotype.—U. S. Nat. Mus. Helm. Coll. No. 59649.

Diagnosis (based on thirty specimens).—*Microphallus.* Body pyriform with posterior notch, 1.150 to 1.750 long by 0.630 to 1.225 wide. Forebody 0.329 to 0.445 long. Cuticle completely spined. Oral sucker subterminal, 0.053 to 0.095 long by 0.053 to 0.106 wide. Muscular pharynx absent, instead pharyngeal gland cells surrounding small area of anterior 1/2 to 3/4 esophagus. Esophagus extending from oral sucker to approximately anterior 1/4 body. Cecae two, rudimentary, extending short distance from cecal bifurcation at posterior end of esophagus. Acetabulum unornamented, preequatorial, mesial, 0.074 to 0.127 long by 0.085 to 0.106 wide. Sucker ratio 1:0.81 to 1.65. Genital pore at left anterior border of acetabulum, followed by genital atrium approximately ¾ diameter of acetabulum. Testes two, side by side, approximately in posterior ¾ body, edges smooth, oval in shape; dextral testis 0.170 to 0.226 long by 0.085 to 0.170 wide; sinistral testis 0.150 to 0.226 long by 0.106 to 0.91 wide. Seminal vesicle preacetabular, transverse to longitudinal axis of body; connecting with intra-atrial unornamental muscular genital lobe perforated by sperm duct. Prostate cells surrounding tip of seminal vesicle adjacent to genital lobe. Genital lobe varying from almost ball-like (Fig. 3) to club-like (Figs. 4-6) in shape. Ovary dextral, dorsally overlapping acetabulum on right side; oblong in shape, edges sometimes notched; 0.170 to 0.212 long by 0.074 to 0.212 wide. Uterus descending from posterior mesial border of ovary, forming double-loop *receptaculum seminis uterinum* short distance from ovary, extending posteriorly to mid-dextral testis, ascending on ventral right border of dextral testis to level of ovary, descending to posterior border of dextral testis, transversing body to posterior level of sinistral testis, descending to halfway between posterior border of sinistral testis and posterior end of body, ascending along left border of sinistral testis to perforate posterior border of genital atirum through short metraterm surrounded by gland cells. Vitellaria composed of coarse follicles, extending on each side of body from level of acetabulum to posterior 1/5 body. Uterine eggs with an antiopercular spine (Fig. 8), containing fully developed miracidia, 20 to 29 microns long by 11 to 17 microns wide. Excretory vesicle short Y-shaped; mainstem extending anteriorly from mesial excretory pore at apex of posterior body notch, forking at level of posterior border of testis; anterior extent of collect-

[1] This study was supported in part by a research grant (E-3386) from the National Institutes of Health, U. S. Public Service.

ing ducts of excretory vesicle disappearing at level of acetabulum in serial cross section. Flame cell pattern 2 [(2+2) + (2+2)]=16.

Discussion: — *Microphallus progeneticus* is closely related to *M. opacus* (Ward, 1894) Ward, 1901, (type species of *Microphallus*) originally described from the bowfin, *Amia calva* Linn., in North America. Now *M. opacus* is known to be a polyxenous trematode. Experimentally it is capable of developing to maturity in several verte-



Figures 1-8. **1.** *Microphallus progeneticus,* ventral view of young adult specimen. **2.** Same, sketch of ventral view of anterior end of body showing variation in shape of ceca, and pharyngeal gland cells. **3.** Same, composite sketch of terminal genitalia from serial cross sections. **4-6.** Same, sketches of ventral views of terminal genitalia showing various shapes assumed by male genital lobe. **7.** Same, sketch of cross section showing relation of vitellaria to uterus and testes in a specimen swollen by large numbers of eggs in the uterus. **8.** Same, uterine egg showing antiopercular spine and miracidium inside. Unless otherwise specified drawings were made with the aid of a camera lucida and the projected scales have the value indicated in millimeters. Abbreviations used: A, acetabulum; GA, genital atrium; GL, genital lobe; ISV, internal seminal vesicle; MET, metraterm; PCS, pseudo-cirrus sac; PGS, pharyngeal gland cells; T, testis; UT, uterus; and VIT, vitellaria.

brates of widely differing classes (Rausch, 1947). *M. progeneticus* differs from *M. M. opacus* by consistently lacking a pharynx, and by its progenetic nature.

Ward (1901) redescribed the genital terminalia of *M. opacus* and Wright (1912) supplemented Ward's description. Strandine (1943) studied the morphological variation of *M. ovatus* Osborn, 1919 and concluded that, at best, this species could be regarded as a variety of *M. opacus.* Rausch (1947) reported the host relationships of *M. opacus* and supported Strandine's view that *M. opacus* and *M. ovatus* are conspecific. He did not report egg production by metacercariae of *M. opacus* encysted in crayfishes. To my knowledge none of the published studies of adult *M. opacus* report the absence of a pharynx. However, Fantham and Porter (1948) pictured (Plate III, Figure 12), but did not describe, an apharyngeate species of *Microphallus* from *Perca flavescens* Mitchell in Lake Memphremagog, Canada. These authors apparently were not sure of their identification because on page 623 they stated, "and *Microphallus* sp. near *opacus* (Plate III, Fig. 12) in one female fish." However, on page 626 they observed: "The only member of the Microphallinae [represented in the collection] was *Microphallus opacus,*" (Plate III, Fig. 12), and in the explanation of figures for Plate III (Page 649) they stated, "*Microphallus opacus* (or near)." In any event their figure of this species does not show a pharynx. Dr. Allen McIntosh (personal communication) informed me that he has studied Ward's (1849) material of *M. opacus* and stated, "in his material the pharynx at best is very small and in one specimen I could not be certain that it had a pharynx." There is little doubt that most morphological characters of adult *M. opacus* from vertebrate hosts may overlap those of adult *M. progeneticus* from the crayfish. There is, however, doubt about the physiological requirements of the two species. None of the published studies on *M. opacus* remotely suggest that this species is progenetic, living unencysted in crayfishes. When two species are isolated from each other, for example, as *M. opacus* and *M. progeneticus* are in their respective hosts, no gene flow could occur between the two populations even if the species existed together in the same locality. In exceptional circumstances the two species might accidentally come together in a vertebrate intestine.

Mechanically excysted metacercariae of *M. opacus,* of small size and still bearing a stylet, had an anlagen of cells which could be identified as the precursor of the pharynx. This pharyngeal anlagen could not be observed in several live immature specimens of the smallest *M. progeneticus* collected. The encysted Metacercariae of *M. opacus* were found in many *Procambarus clarki* from localities where *M. progeneticus* was collected.

Three mechanically excysted *M. opacus* metacercariae kept in 0.7% NaCl at 27°C produced abnormal eggs after 24 hours. In another trial two recently mechanically excysted large metacercariae of *M. opacus* were introduced into an oxalted suspension of human erythrocytes (1:1:1-0.85% NaCl, potassium monohydrogen phosphate/potassium dihydrogen phosphate buffer at pH 7.6, 66.7% oxalted whole blood) kindly supplied by my assistant, Mr. R. D. Lumsden. One worm produced eggs which appeared normal after 36 hours at room temperature (27°C). The other worm appeared to be dead (flame cells not beating), lacked sperm in the seminal vesicle and had produced no eggs.

Despite the fact that *M. progeneticus* lacks a pharynx, and the larval stages are unknown, the species resembles members of the genus *Microphallus* in certain structural details: (1) spined cuticle; (2) short Y-shaped excretory vesicle, and a flame cell pattern of $2[(2+2)+(2+2)]$; (3) testes side by side and posterior to the acetabulum; (4) lack of a true seminal receptacle; (5) presence of an unornamented muscular genital lobe perforated by the sperm duct which connects with a free seminal vesicle; (6) metraterm opening separately into genital atrium which also contains the male genital lobe; (7) vitellaria in region of testes and composed of coarse follicles; and (8) short ceca.

The absence of a muscular pharynx in *M. progeneticus* is not particuarly surprising since cercariae of the "Ubiquita" type are sometimes apharyngeate and also lack an acetabulum. Both structures usually become well developed in the metacercariae. Cable *et al.* (1960) suggested that the development of the acetabulum in microphallids is delayed until the metacercarial stage, ". . . perhaps in adaptation to the modifications of the copulatory apparatus adjacent to that sucker." There is possibly an encystment dependent factor triggering the full development of a pharynx in microphallids with no pharynx or a rudimentary structure in the cercarial stages. *M. progeneticus* has a prominent acetabulum but lacks a pharynx. One explanation may be that *M. progeneticus* does not pass through an encysted metacercarial stage or does so for a relatively short period of time, not allowing development of a pharynx. Serial cross and longitudinal sections of *M. progeneticus* show that a cluster of cells similar to those observed surrounding the pharynx of many different trematode species apparently replaces the muscular pharynx. Since *M. progeneticus* is progenetic, perhaps the acetabulum is developed, as Cable *et al.* (1960) suggest, in adaptation to the modifications of the copulatory apparatus adjacent to that sucker.

One dwarf crayfish was kept alive in the laboratory for a period of three months after collecting. *M. progeneticus* from this crayfish were examined alive under the microscope, but no pharynx was visible except for the pharynngeal gland cells mentioned in the description and discussion above. This observation suggests that the species is permanently apharyngeate after attaining maturity in its crayfish host.

The following Louisiana crayfishes have been examined but found uninfected with *Microphallus progeneticus: Cambarellus shufeldti* (Faxon, 1884); *Orconectes clypeatus* (Hay, 1899); *Orconectes lancifer* (Hagen, 1870); *Procambarus blandingi acutus* (Girard, 1852); *Procambarus clarki* (Girard, 1852); *Procambarus penni* (Hobbs, 1951). Eleven specimens of *Orconectes lancifer* and one specimen of *Procambarus clarkii* found with the infected *Cambarellus puer* were not infected with *Microphallus progeneticus.*

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Abstract

Microphallus progeneticus, new species, (Trematoda: Microphallidae) is described from an astacid decapod, *Cambarellus puer* Hobbs, 1945, in Louisiana. *M. progeneticus* differs from other microphallids by its progenetic nature, by lacking a discrete muscular pharynx and by possessing eggs with an antiopercular spine. It is probably a sibling species of *Microphallus opacus* (Ward, 1894). The following astacid decapods from Louisiana were examined and found uninfected with *M. progeneticus: Cambarellus shufeldti* (Faxon, 1884); *Orconectes clypeatus* (Hay, 1899); *Orconectes lancifer* (Hagen, 1870); *Procambarus blandingi acutus* (Girard, 1852); *Procambarus clarki* (Girard, 1852); and *Procambarus penni* (Hobbs, 1951). Metacercariae of *M. opacus* were found in *Procambarus clarki* from localities in which *M. progeneticus* was collected.

RECORDS OF FRESHWATER FISHES IN FLORIDA

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Since the publication of the first statewide checklist of Florida fishes (Evermann and Kendall, 1900), each subsequent publication concerning the ichthyofauna of the state has added to the total number of species recorded from its freshwaters (Carr, 1937; Carr and Goin, 1955; Briggs, 1958; Kilby, Crittenden, and Williams, 1959). Our collections during the last ten years disclose the presence of nine additional species not included in the latest checklist. Of these nine species, six have been collected for the first time, two have been resurrected from synonomies as valid species, one has been parenthetically mentioned as occurring in Florida in a paper describing a new cyprinid. In addition, several undescribed minnows and darters are known to occur in the state. The widespread interest in ichthyological problems in the southeastern states prompts us to record these findings in this manner, since a more extensive treatise on the distribution of the fishes in this region is still incomplete.

Persons who have assisted in the collection or identification of these fishes are acknowledged under the accounts of species. We are especially indebted to James M. Barkuloo of the Florida Game and Fresh Water Fish Commission, whose tireless efforts and cooperation have furnished many valuable specimens and data. His scientific interests and awareness of biological problems have contributed immeasurably to our knowledge of Florida fishes. We also wish to acknoweldge the many contributions of Ardith B. Cochran during the two-year period that he was associated with the senior author.

Species accounts include the catalog number (FSU - Florida State University, USNM - United States National Museum, TU - Tulane University, and UF - University of Florida, CU - Cornell University fish collections), in parentheses the number of specimens followed by the range of standard length in millimeters, locality, county, date of collection, and names of collectors. In addition to standard compass directions, with the following "of" deleted, these abbreviations are used: Co.=County, Cr.=Creek, mi.= mile(s), R.=River, trib.=tributary (of).

Moxostoma duquesnei (LeSueur)
Black redhorse

Apalachicola River System.—Apalachicola R. at Chattahoochee, from Jim Woodruff Dam to 3 mi. downstream, Gadsen - Jackson Cos. FSU 4900 (1, 390), June 5, 1959, James M. Barkuloo. FSU 5680 (4, 292-374), Aug. 19-20, 1959, Barkuloo and Ernie Grover. TU 22380 (3, 281-324), Aug. 26, 1959, Barkuloo and Grover. FSU 5268 (3, 314-342), Oct. 1, 1959, Barkuloo, Grover, B. Corbin, and J. Willis. TU 22694 (5, 306-380), Nov. 6, 1959, Royal D. Suttkus, Barkuloo, Grover, Donald Stone. TU 22847 (31, 248-417), Dec. 15, 1959, Barkuloo and Grover. TU 22899 (9, 313-384), Mar. 28-29, 1960, Suttkus, Barkuloo and Grover. TU 23655 (17, 163-388), July 7-8, 1960, Suttkus, John Ramsey, Barkuloo, Grover, Phil Hester.

The recent use of electrical shocking gear in western Florida by Game and Fresh Water Fish Commission personnel has revealed the presence of a species of *Moxostoma* which we tentatively refer to as *M. duquesnei.* Robins and Raney (1956: 14) found that meristic data of five yearling *M. duquesnei* (CU 17128) from the Apalachicola River system (Chattahoochee River in Georgia) did not conform with other populations. In some respects the Apalachicola specimens are similar to *M. erythrurum;* however, with regards to meristic data the Apalachicola material seemingly "falls-in" nicely with *M. duquesnei,* as the southern end of a typical north-south cline. Morphometric data, scale and fin ray counts are presented in tables I, II and III respectively

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for specimens of *Moxostoma* from the Apalachicola River in Florida.

The lateral line scale count of 15 specimens of *M. duquesnei* from Pennsylvania, West Virginia and New York ranges from 45 to 50, but is usually 46 or 47. The pelvic fin ray counts for these same specimens are as follows: 2, 9—10: 2, 10—9 and 11, 10—10. The dorsal fin ray counts are as follows: 1, 12; 12, 13 and 2, 14. The body circumference scale counts are: 1, 33; 4, 34; 2, 35; 2, 36; 2, 37; and 1, 38. Caudal peduncle scale counts are: 7, 5—2—5; 4, 6—2—5; 2, 6—2—6; 1, 7—2—5 and 1, 7—2—7. The ranges and average values for these various meristic characters are higher for the northern specimens which typifies a usual north-south cline; however, data of northern and adjoining populations are too few to be dogmatic about a cline or even to be positive about the species identification of the Apalachicola form.

Proportional measurements were determined for the *M. duquesnei* (15 specimens —CU 820: 1,242mm. in standard length; CU 4559: 1,117; CU 5637: 1,220; CU 5639: 3,191-243; CU 5733: 1,201; CU 8152: 1, 221; CU 10347: 4,36-183; CU 28473: 1,207; CU 32406: 1,232; CU 32557: 1,200) from Pennsylvania, West Virginia and New York, and for two samples of *M. erythrurum* from Ohio and Arkansas (16 specimens—CU 30830: 12, 64-177; TU 10285: 4,116-129) and for 66 specimens of *Moxostoma duquesnei* from the Apalachicola River in Florida and for 7 specimens of *Moxostoma*

TABLE 1.
Proportional Measurements of Nine Specimens of Moxostoma duquesnei *from the Apalachicola River in Florida*
All Proportions Are Expressed in Thousandths of the Standard Length

Measurement	TU 22899										
	Females					Males					
					Range						Range
Total length in mm.	420	429	453	470	420–470	386	387	417	445	457	386–457
Standard length in mm.	341	342	370	384	341–384	313	314	343	357	373	313–373
Dorsal origin to snout	495	502	515	533	495–533	507	486	500	532	527	486–532
Dorsal origin to caudal base	556	551	529	512	512–566	545	546	529	532	517	517–546
Dorsal origin to occiput	304	303	318	332	303–332	325	302	314	333	326	302–333
Pelvic insertion to snout	544	511	550	535	511–550	539	521	549	557	554	521–557
Anal origin to caudal base	234	211	216	225	211–234	236	238	232	215	225	215–238
Body, greatest depth	271	266	292	281	266–292	287	260	272	290	255	255–290
greatest width	179	189	187	194	179–194	181	185	184	208	179	179–208
Caudal peduncle, length	144	125	125	140	125–144	149	133	136	129	140	129–149
least depth	99	96	99	105	96–105	102	100	102	106	99	99–106
Head, length[1]	239	261	240	256	239–261	227	230	225	238	245	225–245
depth at occiput	182	190	184	196	182–196	176	168	172	185	198	168–198
width	154	165	162	166	154–166	148	148	145	156	163	145–163
Interorbital, least fleshy	114	123	122	119	114–123	115	109	109	116	126	109–126
Snout, length	126	140	127	145	126–145	125	122	124	124	134	122–134
Orbit, length	37	34	40	39	34– 40	37	37	36	42	39	36– 42
Postorbital, from orbit to upper opercular margin	73	81	73	78	73– 81	67	66	65	73	72	65– 73
Dorsal fin, origin to tip of anterior lobe	184	208	171	192	171–208	190	193	180	190	183	180–193
Dorsal fin, depressed length	249	243	240	259	240–259	270	272	255	273	270	255–273
Anal fin, depressed length	205	214	189	213	189–214	226	246	236	247	248	226–248
Caudal fin, length to tip of upper lobe	231	257	225	242	225–257	238	251	224	245	227	224–251
Pectoral fin, length	162	212	154	191	154–212	194	188	178	197	192	178–197
Pelvic fin, length	140	157	138	141	138–157	166	165	161	171	175	161–175
Distance from insertion of pectoral fin to insertion of pelvic fin	312	268	311	271	268–311	301	293	320	318	304	293–320

[1] Measured from tip of snout to bony margin of opercle

duquesnei from the upper Apalachicola River system in Georgia (TU 12217: 6,112-181; TU 12139: 1,149). Table 1 contains values for numerous proportional measurements of nine of the 66 specimens from the Apalachicola River in Florida. Most of these specimens were spawning at the time of capture (March 28-29, 1960); eggs streamed from the females and milt from the males during handling from the dip net to the container in the boat. Several other fishes taken along with *M. duquesnei* were ripe; spotted sucker, *Minytrema melanops;* carp, *Cyprinus carpio;* quillback, *Carpiodes cyprinus;* and Alabama shad, *Alosa alabamae.* The ripe males of *M. duquesnei* have large tubercles on all anal rays. There are large tubercles also on lower caudal rays but small to medium-size tubercles on upper caudal rays. The lower surface of the caudal peduncle is rough and the entire peduncle is angled upward as is characteristic of most male spawning suckers. The lack of tubercles on the head is in agreement with *M. duquesnei* of northern waters, whereas male *M. erythrurum* have tubercles on the head as well as on the posterior parts of body. The ripe females of the March 28-29 collection also had tubercles on caudal and anal fins; however, these tubercles are smaller and fewer than on males. The skin on the lower surface of the caudal peduncle is rough and thickened. The males in the December 15, 1959 collection (TU 22847) have small tubercles only.

Certain ratios have been used by various workers to distinguish *M. duquesnei* from *M. erythrurum,* e.g. caudal peduncle depth in caudal peduncle length; eye in snout;

TABLE 2.
Scale Counts in Sixty-six Specimens of Moxostoma duquesnei *from the Apalachicola River in Florida*

Predorsal scales

15	16	17	18	19	20	21	22	Mean
3	3	29	22	7	1	0	1	17.53

Lateral line scales

41	42	43	44	45	46	47	Mean
1	9	31	22	2	0	1	42.28

Circumferential scales

29	30	31	32	33	Mean
20	30	10	4	2	30.06

Circumference of peduncle scales

4—2—5	5—2—5	6—2—5	6—2—6	7—2—5	7—2—7
1	49	10	1	4	1

TABLE 3.
Fin Ray Counts in Sixty-six Specimens of Moxostoma duquesnei *from the Apalachicola River in Florida*

Dorsal Rays				Anal Rays		
11	12	13	Mean	6	7	Mean
3	47	16	12.19	1	65	6.98

Pelvic Rays

9—6	9—9	9—10	10—9	10—10	10—11
1	40	4	8	12	1

and postorbital distance in snout. These ratios are useful but one must be certain that specimens of comparable size are being compared. Table 4 is a comparison of four grouped samples with respect to the three ratios mentioned above. The largest specimens are from the Apalachicola River in Florida, the smallest from the upper reaches of the same system. The means for these three ratios indicate that both large and small specimens of *Moxostoma* from the Apalachicola River are in better agreement with typical *M. duquesnei* than with *M. erythrurum.*

The means for the ratios of the three samples of *M. duquesnei* are evidence that at least some proportional measurements change considerably with increase in size. The caudal peduncle deepens, and the snout lengthens in relation to both length of eye and postorbital distance.

Since tubercle patterns, meristic characters and proportional measurements of the Apalachicola material agree favorably with typical *Moxostoma duquesnei* of the north, we tentatively use the name *duquesnei* for the Apalachicola material. Perhaps a thorough study of Alabama and Tennessee river specimens will indicate the need for a change in name.

Moxostoma carinatum (Cope)
River redhorse

Escambia River System.—TU 15946 (3, 97-346) Conecuh R., 3 mi. SE Flomaton, Escambia Co., Ala., July 18, 1957, Suttkus, Jack Dendy, Homer S. Swingle, et al. TU 15966 (4, 89-267) Conecuh R., 3 mi. E Flomaton, Escambia Co., Ala., July 18, 1957, Suttkus, Dendy, Swingle, et al. FSU 3763 (1, 264) Conecuh R., 7 mi. above bridge on Rt. 4 E Century, Escambia Co., Alabama, Aug. 27, 1958, Barkuloo, Keith Byrd, Joe Burgess, and Henry Carpenter.

During rotenone surveys of the Conecuh River in the vicinity of the Alabama-Florida state boundary, members of the Florida and Alabama survey teams collected many redhorse suckers. Most of these were *Moxostoma poecilurum,* the blacktail redhorse which is common from the Choctawhatchee River in west Florida west along the Gulf Coast to eastern Texas. Several specimens as noted above were *M. carinatum.* Although the exact point along the river from which these specimens were collected is not known, obviously the species occurs on both sides of the state boundary, i.e., in both Alabama and Florida. Actually some of the pick-up of fishes was within the state of Florida.

The data for these specimens are as follows: dorsal rays: 3 specimens with 12 and 5, 13; anal rays: 8, 7; pectoral rays: 1, 12—16; 4, 16—16; 3, 17—17; pelvic rays: 1, 8—8; 7, 9—9; predorsal scales: 1, 16;

TABLE 4.
Comparison of three ratios of samples of Moxostoma

	Number of specimens / Range in size–mm. / Mean size–mm.	Caudal peduncle length / Caudal peduncle depth: Range	Mean	Snout / Eye: Range	Mean	Snout / Postorbital: Range	Mean
Apalachicola, Fla. *M. duquesnei*	66 163–417 336	1.2–1.5	1.35	2.7–4.1	3.24	1.5–1.9	1.73
Pa., W. Va., N. Y. *M. duquesnei*	11 183–243 213	1.4–1.9	1.59	2.2–2.8	2.49	1.6–1.8	1.70
Upper Apalachicola, Ga. *M. duquesnei*	7 112–181 132	1.4–1.6	1.54	2.1–2.4	2.23	1.5–1.7	1.61
Ohio, Ark. *M. erythrurum*	7 147–177 161	1.2–1.4	1.25	1.9–2.1	2.01	1.3–1.5	1.42

4, 17; 1, 18; 1, 19; 1, 20; lateral line scales: 3, 42; 3, 43; 2, 44; body circumference scales: 5, 13—2—15; 1, 13—2—17; 2, 14—2—16; scales around caudal peduncle: 8, 5—2—5. The upper caudal lobe is typically longer than lower lobe and is pointed rather than rounded as is the lower lobe. The caudal fin is bright red in life and usually has a narrow black margin. The anal, margin of dorsal, and upper surface of pectoral and pelvic fins, are orange-red.

These records are a notable extension of the range of this little known species. Moore (1957:83) described its range as from Iowa east to Michigan, Ohio, and Pennsylvania, south to Georgia and Alabama, and west to Oklahoma. Robins and Raney (1957:154) reported two specimens (TU 2051) from the Pearl River, Louisiana, and indicated that it could be expected through the lower Mississippi River system and other Gulf rivers as far east as the Pearl. Since their paper, several additional specimens have been obtained from the Pearl River system, and because the fauna of the Choctawhatchee River appears to be similar to that of the Escambia (Bailey, Winn and Smith, 1954:155), *Moxostoma carinatum* may be expected to occur in the Choctawhatchee River.

Hybopsis aestivalis (Girard)
Speckled chub

Escambia River System.—TU 15948 (6, 31-48) Conecuh R. 3 mi. SE Flomaton, Escambia Co., Ala., July 18, 1957, Suttkus, Dendy, Swingle et al. FSU 3534 (2, 36 and 38) and FSU 4366 (4, 34-37) Escambia R., 5-6 mi. (by river) upstream from highway bridge on Rt. 4 E Century, Escambia Co., Aug. 26, 1958, Barkuloo, Byrd, and Burgess.

Choctawhatchee River System.—TU 20811 (28, 20-34), Choctawhatchee R., 3 mi. S Browns on Hwy. 2, or 6 airline mi. S Geneva (Ala.), Holmes Co., July 24, 1959, Suttkus, Barkuloo, Grover, and Byrd. FSU 5457 (21, 21-37), same locality, September 11, 1959, Ralph W. Yerger and Ardith B. Cochran.

Formerly recorded from the Rio Grande and other Gulf Coast rivers of Texas and the Mississippi River, the speckled chub now is known to occur east along the Gulf Coast to the Choctawhatchee River in the Florida Panhandle (Suttkus, 1961:234). Here is another example which bears out the conclusion by Bailey, Winn, and Smith (1954) that the Choctawhatchee and Escambia rivers have similar faunas, and together represent a distinct faunal break in western Florida.

As in the case of *Moxostoma carinatum*, the speckled chub in the Escambia River was taken on one side or the other of the Alabama-Florida line, but unquestionably occurs in the Florida sections of the river.

The specimens in the Escambia River collection of July 18, 1957 and those in the Choctawhatchee River collection of July 24, 1959 were in spawning condition. The females contain large ova and the males are tuberculate.

Both Escambia and Choctawhatchee river specimens have the tetranemus condition. The anterior pair of barbels is well developed in all specimens; i.e. there are no rudimentary or intermediate conditions. This tetranemus condition is common to the populations of *H. aestivalis* in the Arkansas region but not so in the Pearl River population. Although hundreds of specimens from the Pearl River were examined, none has four barbels. Specimens of *H. aestivalis* from the Cahaba River of the Alabama River system have only one pair of barbels like those in the Pearl River. In addition, the Cahaba specimens differ from the other mentioned populations in their darker coloration.

Notropis welaka (Evermann and Kendall)
Bluenose shiner

St. Johns River System.—Type, USNM 48786 (1), St. Johns River near Welaka, Fla., Feb. 19, 1897, W. C. Kendall. TU 12467 (24, 23-44), Wekiva R. under bridge Fla. Hwy 46 at (Seminole-Lake) county line—R 29 E, T 19 S, No. 21, April 7, 1956, S. T. Tucker, Spence, Bateman. UF 6251 (4, 20-28), Alexander Spring run, Astor Park, Lake Co., D. L. Taber and Melvin T. Huish. UF 6252 (28, 17-38), Alexander Spring run below Fla. 445 bridge, Lake Co., Dec. 13, 1949, William McLane. UF 6253 (1, 25), Alexander Spring boil and adjacent run area, 6 mi. SW Astor Park, Lake Co., Sept. 7, 1949, McLane. UF 6254 (3, 21-25), Oklawaha R. at Davenport Landing, approx. 6 mi. upstream from mouth, Marion Co., Oct. 7, 1948, McLane and Giovannoli. McLane (1955) listed these additional localities: Oklawaha R. at Wells Landing, 25 mi. upstream from mouth of river: Wekiva R., Seminole Co.; and mouth of Juniper Springs Creek, Lake Co.

Apalachicola River System.—FSU 1563 (27, 32-50) fish hatchery landing, Dead Lakes near Wewahitchka, Chipola R. drainage, Gulf Co., May 8, 1953, F. Gerry Banks and G. W. Nelson.

Choctawhatchee River System.—FSU 674 (4, 34-45), Holmes Creek, 4.6 mi. W Chipley, on Rte. 90, Washington-Holmes Cos., May 4, 1952, Yerger and ichthyology class. TU 22257 (10, 24-43), trib. of river, ½ mi. upstream from Ebro, Washington Co., July, 1959, Byrd.

Yellow River System.—FSU 7037 (3, 32-36), trib. of Yellow R., 6 (airline) mi. SSE Milton, Santa Rosa Co., May 16, 1961, Byrd and Hester. FSU 7123 (100, 23-45), Nichols Creek, approx. 9 (airline) mi. SSE Milton, Santa Rosa Co., June 22, 1961, Yerger, Carter Gilbert, Byrd, Hester, William Weaver, Louis Prevatt.

The strikingly beautiful bluenose shiner, which occurs from the St. Johns River in eastern Florida along the Gulf coast westward to the Pearl River in Mississippi and Louisiana, was for a long time considered to be an undescribed species. While examining type specimens of cyprinids in the U. S. National Museum in March 1957, Suttkus discovered that the bluenose shiner was conspecific with *Notropis welaka* Evermann and Kendall, a name which Bailey, Winn, and Smith (1954:129) included in the synonmy of *N. maculatus* (Hay).

The wide gap in the range of this species, from the St. Johns River in Central Florida to the Chipola River in the Panhandle, may reflect inadequate collecting in this region, or may be another example of disjunct populations.

Notropis zonistius (Jordan)
Bandfin shiner

Apalachicola River System.—FSU 4035 (6, 39-72), trib. Flint R., 2.4 mi. N. Mt. Pleasant, Gadsden Co., Jan. 26, 1959, Yerger, Cochran, Rhodes Holliman. TU 20641 (5, 23-29), Flat Creek about 10 mi. S Chattahoochee, on Hwy. 269, Gadsden Co., July 22, 1959, Suttkus and Barkuloo. UF 4940 (157, 25-62), S Mosquito Cr. at iron bridge 2 mi. S Oak Grove, Gadsden Co., April 8, 1955, John D. Kilby et al. UF 4925 (32, 24-66), Flat Creek 4 mi. SE river junction, Gadsden Co., Apr. 8, 1955, Kilby et al. UF 4719 (3, 32-46), pond on Butler Rd., 3.6 mi. N U.S. 90, Jackson Co., Mar. 26, 1954, Fred Berry and Wilder.

Earlier records of the bandfin shiner were restricted to the Chattahoochee River of Georgia and Alabama (Moore, 1957:126). These recent collections reveal, as might have been suspected, that the species occurs in tributaries of the Flint River and also of the main or lower division of the Apalachicola system. The tributary of the Flint River from which one of these series was collected originates in Gadsden County, Florida, flows northwestward into Decatur County, Georgia, where the species has also been collected, and enters the Flint River between Recovery, Georgia, and Chattahoochee, Florida.

Notropis leedsi (Fowler)
Ohoopee shiner

Ochlockonee River System.—FSU 1261 (1, 56), trib. Ochlockonee R., 0.4 mi. E Quincy on Fla. 12, Gadsden Co., Mar. 28, 1952, Yerger and ichthyology class. FSU 1633 (11, 35-57), Rocky Comfort Cr., 3.2 mi. ENE Wetumpka, Gadsden Co., Mar. 5, 1954, Yerger and ichthyology class. FSU 3400 (1, 53), same locality, Mar. 31, 1958, Yerger and ichthyology class. FSU 3576 (90, 33-70), Ochlockonee R. at Rocky Bluffs, Leon Co., Sept. 28, 1958, Yerger, Cochran, and William Ragsdale. FSU 3808 (5, 45-60), Ochlockonee R. 1.8 mi. downstream from Lake Talquin Dam, Leon Co., Oct. 10, 1958, Yerger and Cochran. FSU 4416 (2, 30-33), Ochlockonee R., on U.S. 27, 9 mi. NW Tallahassee, Leon Co., Dec. 19, 1958, Yerger and Cochran. TU 22630 (6, 47-69), Ochlockonee R. at Jackson Bluff, Hwy. 20, Leon Co., Dec. 14-15, 1959, Suttkus, Barkuloo, and Grover.

In a strict sense, this is not the first report of the Ohoopee shiner from Florida. In the introduction to their original description of *Notropis callitaenia,* Bailey and Gibbs (1956) mentioned the distribution of *Notropis leedsi* from the Savannah River southward to the Ochlockonee in Georgia and Florida. The unpublished portion of Gibbs dissertation dealing with *Notropis leedsi* lists a single Florida specimen from Liberty County, and two collections from Georgia in the Ochlockonee drainage.

Prior to the fall of 1958, single specimens had been collected for the FSU collection but never identified. Beginning in October 1958, several large series were taken from the main river channel below Lake Talquin Dam. A combination of factors permitted seining operations in areas which normally would be inaccessible to collectors. Part of the dam had been destroyed by spring floods, and after repairs were completed in September, the gates were closed to allow the refilling of the lake. A severe drought was in progress, with the result that for several miles below the dam the river channel at many places was less than three feet deep.

This species appears to frequent the channel in the main river and its larger tributaries. It has been taken only from areas with a sandy bottom devoid of vegetation, and with a moderate current.

It has been collected in the Alapaha River (Lanier County) and in the Withlacoochee River (TU 16069 [1, 50], 12.1 mi. W. Valdosta, Brooks Co., July 29, 1957, R. D. and J. S. Suttkus), Georgia, and therefore may be expected to occur in the Suwanee River System in Florida as well as in the Ochlockonee River.

Etheostoma histrio (Jordan and Gilbert)
Harlequin darter

Escambia River System.—FSU 5911 (4, 27-35), Mitchell Cr., trib. Escambia R., 0.4 mi. N McDavid on Rte. 29, Escambia Co., Aug. 14, 1959, Yerger and Cochran. TU 15942 (1, 32), Conecuh R., 3 mi. SE Flomaton, Escambia Co., Ala., July 18, 1957, Suttkus, Dendy, Swingle, et al.

Previous records of the harlequin darter extended eastward to Louisiana and Mississippi, and these new collections extend the range to the Escambia River of western Florida (Suttkus, 1961:234). Although the Tulane series is labeled "Alabama", it is another instance of a collection made very close to the state line, and the species may appropriately be recorded in the faunal lists of both Alabama and Florida.

Dr. Reeve M. Bailey verified the identification of the series in the FSU collection.

Etheostoma parvipinne (Gilbert and Swain)
Goldstripe darter

Choctawhatchee River System.—FSU 5128 (1, 46), Hurricane Cr. (trib. Pea R.), 1 mi. W Sweet Gum Head, Holmes Co., Feb. 23, 1958, Byrd and Barkuloo FSU 5326 (1, 48), trib. Holmes Cr., just N Vernon, Washington Co., Mar. 23, 1958, Byrd and Barkuloo. FSU 4678 (2, 47-53), trib. Holmes Cr., 14.1 mi. N Ebro, on Rte. 79, Washington Co., Jan. 12, 1958, O. V. and J. M. Barkuloo.

Bailey, Winn, and Smith (1954:144) cited records of this fish in the Escambia River in Alabama, and as far east as the Flint River in Georgia. The Choctawhatchee River is approximately midway between these two drainages. Dr. Reeve M. Bailey kindly verified the identification of these specimens.

Etheostoma okaloosae (Fowler)
Okaloosa darter

Northern Gulf Coast Drainage (tributaries of Choctawhatchee Bay).

The validation, description, distribution, and relationships of this darter are discussed in a recent paper by Collette and Yerger (In press). It is restricted to several small streams (Rocky, Swift, Turkey, and Toms creeks) in the vicinity of Niceville, in Okaloosa and Walton counties.

Discussion

Since the earliest days of exploration in North America, naturalists have been attracted to Florida to study its varied flora and fauna. Many ichthyologists have made state-wide collections, and one might surmise that the freshwater fishes of the region have been adequately known for a long time. This idea can quickly be dispelled by a resume of ichthylogical investigations during the last 60 years. Almost as many species of freshwater fishes have been added to the state list in the last six years as were added in the period from 1900 to 1955.

In the original checklist of Florida fishes, Evermann and Kendall (1900) recorded 61 species from the freshwaters of the state, but since some of these are euryhaline, and others have been reduced to synonomy, only 45 species may be recognized as freshwater types. (It is not always a simple matter, especially in Florida waters, to designate a species as belonging to a freshwater, marine, or euryhaline category, and ichthyologists cannot always agree on the proper placement. In discussing these publications on Florida fishes, we arbitrarily have followed the categorization of Briggs [1958], although we do not necessarily agree in every case.)

Carr (1937) included 102 species in his key, but of these only 59 were freshwater forms, the others were euryhaline or marine invaders of freshwater streams. In their guide to the cold-blooded vertebrates of Florida, Carr and Goin (1955) recorded 154 species in freshwater, of which we consider 77 as belonging in the freshwater category. Three years later Briggs (1958) compiled the most recent checklist and recognized 88 species of "true" freshwater fishes.

But the list continues to expand. Six more species were recorded from western Florida by Kilby, Crittenden, and Williams (1959). Our present paper adds nine more, for a total of 103 species of freshwater fishes known from Florida at the present time. While additional species undoubtedly will be added to this list, it is unlikely that the number will be very great.

Two facts of considerable interest should be noted from this list of fishes newly reported from Florida. First, all of the species are limited to western Florida, or the Panhandle region as it is commonly called. Furthermore, of the 26 additions to the state list since 1955, all but two are restricted to the Panhandle. This is not surprising, however, for this region offers the greatest diversity of habitats to be found anywhere in Florida, and it is an area where many species belonging to the Mississippi Valley fauna reach their eastern limits of distribution. Many of these species have simply gone unnoticed, for until recent years, collections in this area have been few.

The other obvious fact is that earlier collections have inadequately sampled the faunas in the larger rivers. Recent surveys in the Apalachicola and Conecuh rivers have revealed the presence of two additional suckers belonging to the genus *Moxostoma,* whereas for many years only one member of this genus had been known from Florida. More surveys of this kind are needed, and very likely would yield several more unrecorded species.

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Abstract

Extensive collections in western Florida have added nine species of freshwater fishes to the faunal list of the state: *Moxostoma duquesnei, M. carinatum, Hybopsis aestivalis, Notropis welaka, N. zonistius, N. leedsi, Etheostoma histrio, E. parvipinne,* and *E. okaloosae.* All but one *(Notropis welaka)* are restricted to the Panhandle. Although they do not agree in all respects with populations in northern states, specimens of *Moxostoma* from the Apalachicola River are tentatively identified as *M. duquesnei.* Considered as synonyms for many years, both *Notropis welaka and Etheostoma okaloosae* are now recognized as valid species. The present total of 103 species of primary freshwater fishes in Florida will likely be increased by further surveys in the larger rivers.

VARIATION IN SHELL MORPHOLOGY OF NORTH AMERICAN TURTLES
I. THE CARAPACIAL SEAM ARRANGEMENTS

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This study is the first of two papers devoted to variations in the arrangements and relative size of the laminae of North American turtles, and in the position of seams between some of the carapacial laminae. These studies have been supported by a grant from the American Philosophical Society to which I express my appreciation. I am also indebted to many individuals and institutions for permitting me to examine their research collections, particularly to Archie Carr and Walter Auffenberg at the University of Florida, Fred R. Cagle and Harold Dundee at Tulane University, Doris Cochran at the United States National Museum, and Norman Hartweg, at the University of Michigan. The terminology for carapace and plastral structures are those of Carr (1952) to which the reader is referred for details.

Tinkle (1958) demonstrated that the positions of the contacts of the seams between the lateral laminae of the carapace with the marginal laminae, or with the seams between the latter were variable and sometimes could be used to indicate divergence of turtles *(Sternothaerus)* at the infrasubspecific level. Because the number of laminae of the trutle shell is so constant, there are few morphological characters that can be used to show such divergence. Therefore, our knowledge of variation below the species level in turtles is not as detailed as in many reptiles in which scutellation is more variable than in turtles.

This study was undertaken to determine the extent of variation in carapace characters in several species of North American turtles to show how these data might be useful as taxonomic criteria at several taxonomic levels, as indications of genetic divergence at an infrasubspecific level, and as an aid to paleontologists who sometimes use these characters in studies of fossil turtles without sufficient information of the extent of their variation in recent species.

Only turtles without obvious abnormalities such as supernumerary laminae or obviously malformed ones were used. Several studies on abnormalities in the turtle shell have appeared (Newman, 1906; Coker, 1910; Zangerl and Johnson, 1957) with various interpretations of the increase or decrease in number or of the odd arrangements. In each turtle examined, note was made whether the seams between lateral laminae contacted the anterior half of a marginal, the posterior half, or the midline, as determined with dividers. In some instances the interlateral seam contacted an intermarginal seam. For a more thorough discussion of these conditions see Tinkle *(op. cit.)*. The sex, carapace length plastron length, number of "annuli", and the length of each plastral lamina was determined. The data on plastral morphology will appear in another paper.

Interlateral Seam Contacts

The five carapacial seams contacting the marginal laminae were designated from anterior to posterior as A, B, C, D, and E. If the A seam contacted a marginal in the anterior one-half, at the midpoint, or in the posterior one-half, these contacts would be designated 1<, 1½ and 1>, respectively. The data for the contacts of each of the five seams are shown in Tables 1 to 5; the tables are discussed below.

The position of contacts of seam A, which lies between the precentral lamina and the first lateral lamina, shows striking similarity in most species (Table 1). The kinosternids (*sensu* Williams, 1950) are the most divergent from the other species; of these, *Chelydra and Macroclemmys* may be the most primitive. At least, the fossil record of these extends further back than that of the other kinosternids. Sufficient data are lacking for *Macroclemmys,* but *Chelydra* has a seam A contact with its highest frequency at 2>, a position found in only 5 of 2177 non-kinosternid turtles. *Chelydra* also has a high frequency (40%) of contacts between seam A and 2<, a contact relatively infrequent in most turtles, but common in some kinosternids and in *Chelonia.*

TABLE 1.
Seam A contacts in turtles *

Species	1<	1½	1>	s2	2<	2½	2>	s3	3<
Chelonia mydas (31)					100				
Chelydra serpentina (110)			1		40	6	54		
Macroclemmys temmincki (10)					100				
Kinosternon subrubrum (164)	3	1	87	8	1				
Kinosternon flavescens (43)			19	16	65				
Kinosternon sonoriense (23)				4	96				
Kinosternon bauri (52)	2	4	90	4					
Sternothaerus odoratus (847)	26	10	63	1					
Sternothaerus minor (422)	62	21	18						
Sternothaerus depressus (41)	63	32	5						
Sternothaerus carinatus (87)	61	20	20						
Gopherus polyphemus (36)			94	3	3				
Terrapene carolina (144)			99	1					
Terrapene ornata (63)			100						
Emys blandingi (44)			2		96		2		
Clemmys guttata (33)			49	42	9				
Clemmys muhlenbergi (13)			92	8					
Clemmys insculpta (19)	11	11	79						
Clemmys marmorata (5)				20	80				
Malaclemmys terrapin (34)			62	21	18				
Graptemys geographica (25)			56	40	4				
Graptemys pseudogeographica (168)	1	1	95	2	1				
Graptemys kohni (158)	5	3	91	1					
Graptemys versa (64)	9	5	83	3					
Graptemys barbouri (139)	1	1	99						
Graptemys pulchra (146)	6	5	89						
Graptemys oculifera (100)	1		99						
Graptemys flavimaculata (64)			100						
Graptemys nigrinoda (87)	1	3	95						
Pseudemys scripta (347)	12	2	86						
Pseudemys floridana (190)	3	6	89	2					
Chrysemys picta (212)	1	1	62	28	8	1	1		
Deirochelys reticularia (53)	4				91	2	2		
Totals 3975	16	6	66	4	7	0	2		

* Numerals at top indicate marginal laminae; the letter s denotes a seam. Figures in the table are percentages. Number of specimens examined is shown after species name. Figures may not add to 100% because all were rounded to nearest whole per cent.

Kinosternon flavescens and *K. sonoriense* are divergent from the other *Kinosternon* and show closer relationship to each other than to *K. subrubrum* and *K. bauri,* as should be expected. The contact percentages are much the same for *Sternothaerus* species except *S. odoratus* which is considerably different from the other species in the genus in having a low percentage of contacts at 1<. Most emydid species show more than 75% of the individuals with a seam A contact at 1>. Exceptions are *Emys blandingi*[1] *with* 96% at 2< and *Dierochelys reticularia* with 91% at the same point. *Clemmys guttata* (49%), *Malaclemmys terrapin* (62%), *Graptemys geographica* (56%) and *Chrysemys picta* (62%) have less than 75% of the contacts at 1>. Most *Pseudemys* and *Graptemys* are much the same in percentage contacts.

In 66% of the 3824 turtles studied, seam A contacts 1>, and in 88% of all specimens the contact is in the first marginal. The contact most frequent in 3 species (9%) is at 1<, at 1> in 22 (67%), at 2< in 7 (21%), and at 2> in 1 (3%).

Chelydra serpentina is the most divergent species in seam B contacts; there is no overlap with any other species studied (Table 2). The contacts of seam B are between 4> and 5> in 98% of the 3962 specimens examined and in 97% of the species. In 26 (82%) species the contact is somewhere on the fifth marginal. Seam

[1] The author has retained this combination throughout the paper because of its familiarity. Loveridge and Williams (1957) have indicated that *Emys blandingi* should be restricted to the monotypic genus *Emydoidea.*

B most commonly contacted 4> in 2 species (6%), seam 5 in 3 (9%), 5< in 22 (69%), 5> in 4 (13%), and 6< in 1 (3%). The emydid turtles are not so uniform in this contact as in seam A contacts. Fifteen species have the most common contact at 5<, two at 5>, three at s5 and one at 4>. The kinosternids, except *Chelydra* and probably *Macroclemmys*, are fairly uniform with six of eight species having the most common contact at 5< and two at 5>.

Seam C contacts were studied in 3945 specimens (Table 3). In 90% of these, the contacts were on the seventh marginal, with about equal numbers of contacts on the anterior (41%) and posterior (46%) portions. Of the 32 species examined, 88% had the most common point of contact on the seventh marginal. Two species were conspicuously divergent: *Gopherus polyphemus* shows 32 (91%) of the specimens with the most frequent contact of seam C at 6< and *Chelydra serpentina*, at the other extreme, has 95% of 104 specimens with contact at 8>. The kinosternids, exclusive of *Chelydra* and probably *Macroclemmys*, are fairly consistent with 6 of 8 species having 7> as the most frequent point of contact and two of eight with 7< most frequent. The emydid turtles were less consistent with 6>, s7, 7< and 7> the most common contact points in one, one, 14 and five species, respectively. Seam C most frequently contacted 6< in 1 (3%) of the species studied, 6> in one, s7 in one, 7< in 16 (50%), 7> in 12 (38%) and 8> in one.

The contact of seam D with the marginals was examined in 3957 specimens (Table 4). Ninety-one percent had a seam D contact at the ninth marginal. In 88% of the 33 species studied, the ninth marginal was the most frequently contacted.

TABLE 2.
Seam B contacts in turtles *

Species	3>	s4	4<	4½	4>	s5	5<	5½	5>	s6	6<	6½	6>
Chelonia mydas (31)	3				3	13	77		3				
Chelydra sepentina (110)											93	4	4
Macroclemmys temmincki					no analysis possible								
Kinosternon subrubrum (164)							48	6	46	1			
Kinosternon flavescens (43)							98		2				
Kinosternon sonoriense (23)							70	13	17				
Kinosternon bauri (52)							96	2	2				
Sternothaerus odoratus (845)							71	8	22				
Sternothaerus minor (422)							61	20	19				
Sternothaerus depressus (41)							12	34	54				
Sternothaerus carinatus (87)							28	31	41				
Gopherus polyphemus (35)			11	3	86								
Terrapene carolina (143)							22	10	69				
Terrapene ornata (63)					2		5	5	89				
Emys blandingi (44)						2	91		7				
Clemmys guttata (35)							57	14	29				
Clemmys muhlenbergi (13)						15	85						
Clemmys insculpta (19)							100						
Clemmys marmorata (5)							60	40					
Malaclemmys terrapin (34)					9	3	88						
Graptemys geographica (25)							100						
Graptemys pseudogeographica (169)					2	10	88						
Graptemys kohni (158)					1	14	85						
Graptemys versa (64)					22	38	41						
Graptemys barbouri (139)		1			33	39	27						
Graptemys pulchra (146)					44	38	18						
Graptemys oculifera (99)					30	56	14						
Graptemys flavimaculata (62)					10	32	58						
Graptemys nigrinoda (88)					35	47	18						
Pseudemys scripta (347)							99		1				
Pseudemys floridana (192)						4	95	1					
Chrysemys picta (211)						1	90	4	5				
Deirochelys reticularia (53)							100						
Totals 3962					6	8	63	6	15		3		

* Numerals at top indicate marginal laminae; the letter s denotes a seam. Figures in the table are percentages. Number of specimens examined is shown after species name. Figures may not add to 100% because all were rounded to nearest whole per cent.

The most divergent species are *Gopherus polyphemus* in which 77% of 35 individuals had a contact at 8>, and *Chelydra serpentina* and *Macroclemmys temmincki* in which 84% and 91%, respectively, had the most frequent contact at 10>. The kinosternine species are quite uniform. The most frequent contact is at 9< in seven of eight species and at s9 in the other. The emydid turtles, likewise, are extremely uniform with 20 of the 21 species having the most frequent contact at 9<. Of 33 species studied, one (3%) had 8> as the most frequent seam D contact; one (3%) had s9, 28 (85%) had 9<, one (3%) had 9> and two (6%) had 10>.

Seam E contacts were analyed in 3947 specimens (Table 5). Sixty-seven percent had a contact at 11< and an additional 23% at the s11 seam preceding that lamina. *Chelydra serpentina* and *Macroclemmys temmincki,* once again, were widely divergent from the other species with 84% of 107 specimens and 100% of 11 specimens, respectively, having a 12> contact. The kinosternids show considerable variability, with the most frequent contact at 10>, s11, and 11< in two, four, and two species respectively. Of the other species, *Gopherus* is unusual in having the most frequent contact of seam E on the tenth rather than the eleventh marginal. The emydids are, again, uniform with all species having the most frequent contact on the anterior half of the eleventh marginal. Of 33 species studied the most frequent contact was at 10>, s11, 11< and 12> in three (9%), four (12%), 24 (73%) and two (6%) species, respectively.

Discussion of Modal Formulae For Seam Contacts

The modal formula for seam contacts can be determined by the most frequent

TABLE 3.
Seam C contacts in turtles *

Species	6<	6½	6>	s7	7<	7½	7>	s8	8<	8½	8>	s9
Chelonia mydas (31)			3				97					
Chelydra sepentina (110)									5	1	95	
Macroclemmys temmincki					No analysis possible							
Kinosternon subrubrum (163)					26	2	70	2				
Kinosternon flavescens (43)					9	12	77	2				
Kinosternon sonoriense (23)					48	22	30					
Kinosternon bauri (52)					62	6	33					
Sternothaerus odoratus (839)					4	2	89	4				
Sternothaerus minor (421)					2	5	92	2				
Sternothaerus depressus (41)					5	20	76					
Sternothaerus carinatus (87)					8	23	69					
Gopherus polyphemus (35)	91		10									
Terrapene carolina (142)					11	3	85	1				
Terrapene ornata (63)						2	98					
Emys blandingi (44)					5		95					
Clemmys guttata (35)					31	3	66					
Clemmys muhlenbergi (13)					92	8						
Clemmys insculpta (19)					100							
Clemmys marmorata (5)					60		40					
Malaclemmys terrapin (34)					100							
Graptemys geographica (25)					100							
Graptemys pseudogeographica (169)			2	11	88							
Graptemys kohni (158)			1	4	94							
Graptemys versa (64)				3	97							
Graptemys barbouri (139)				2	98							
Graptemys pulchra (147)				10	90							
Graptemys oculifera (99)			3	39	58							
Graptemys flavimaculata (61)			8	51	41							
Graptemys nigrinoda (83)			60	34	6							
Pseudemys scripta (346)					95	2	3					
Pseudemys floridana (192)				2	98		1					
Chrysemys picta (211)					45	6	49					
Deirochelys reticularia (52)					75	8	17					
Totals 3945	1		2	4	41	3	46	1			3	

* Numerals at top indicate marginal laminae; the letter s denotes a seam. Figures in the table are percentages. Number of specimens examined is shown after species name. Figures may not add to 100% because all were rounded to nearest whole per cent.

TABLE 4.
Seam D contacts in turtles *

Species	8<	8½	8>	s9	9<	9½	9>	s10	10<	10½	10>
Chelonia mydas (31)			3		74		23				
Chelydra serpentina (109)									10	6	84
Macroclemmys temmincki (11)									9		91
Kinosternon subrubrum (162)				2	97		1				
Kinosternon flavescens (43)					91	5	5				
Kinosternon sonoriense (23)					96	4					
Kinosternon bauri (51)					100						
Sternothaerus odoratus (842)				2	96		1				
Sternothaerus minor (422)			2	31	67						
Sternothaerus depressus (41)			24	54	22						
Sternothaerus carinatus (87)				7	91	1	1				
Gopherus polyphemus (35)	20	3	77								
Terrapene carolina (145)					65	10	25				
Terrapene ornata (63)					91	3	6				
Emys blandingi (44)					18	5	77				
Clemmys guttata (35)					74	11	14				
Clemmys muhlenbergi (12)					92	8					
Clemmys insculpta (19)					95		5				
Clemmys marmorata (5)					60	20	20				
Malaclemmys terrapin (32)					66	9	25				
Graptemys geographica (25)					100						
Graptemys pseudogeographica (169)				1	97	2					
Graptemys kohni (158)					99		1				
Graptemys versa (64)					100						
Graptemys barbouri (139)				1	94	4	1				
Graptemys pulchra (147)					97	2	1				
Graptemys oculifera (100)					96	3	1				
Graptemys flavimaculata (64)			2	3	95						
Graptemys nigrinoda (87)				6	94						
Pseudemys scripta (342)					83	6	11				
Pseudemys floridana (192)			1		82	7	10				
Chrysemys picta (209)					63	7	30				
Deirochelys reticularia (51)			2	2	57	14	26				
Totals 3957			1	5	82	3	6				3

* Numerals at top indicate marginal laminae; the letter s denotes a seam. Figures in the table are percentages. Number of specimens examined is shown after species name. Figures may not add to 100% because all were rounded to nearest whole per cent.

point of contact of each interlateral seam with a marginal or intermarginal seam. The modal for all turtles studied is shown in Table 6.

Similarly, a modal formula can be devised for each genus. These formulae obviously cut across taxonomic lines with two genera in the same family having widely differing modal formulae (Table 7). Thus, although four genera of emydids have the same modal formula, another shares a different formula with *Sternothaerus*, while others have unique formulae. Therefore, it is not possible to choose a formula except in *Gopherus, Chelydra,* and *Macroclemmys* which will show little overlap with other species; not even in these genera would such a formula have taxonomic value. However, a *particular* seam contact does have taxonomic value at the generic or species level in indicating degree of divergence in such closely related genera as *Pseudemys* and *Graptemys, Sternothaerus* and *Kinosternon* and between the species of these genera.

Taxonomic Consideration of Specific Seam Contacts

Refer to the list of species and their respective modal formulae for the percentage of each contact and for a listing of the number of individuals of each species examined (Table 8).

Seam A Contacts: *Chelydra serpentina* is unique in having most of the seam A contacts at 2>. Ninety percent of *Kinosternon bauri* and 87% of *K. subrubrum* have this contact at 1>, while only 19% of *K. flavescens* and no *K. sonoriense* show this contact. Also, 65% of *flavescens,* 96% of *sonoriense* have a contact at 2< which

TABLE 5.
Seam E contacts in turtles *

Species	10>	s11	11<	11½	11>	s12	12<	12½	12>
Chelonia mydas (31)			97	3					
Chelydra serpentina (107)							9	7	84
Macroclemmys temmincki (11)									100
Kinosternon subrubrum (150)	8	88	4						
Kinosternon flavescens (42)	76	21	2						
Kinosternon sonoriense (22)	55	45							
Kinosternon bauri (51)	25	63	12						
Sternothaerus odoratus (833)	1	29	70						
Sternothaerus minor (422)	1	58	41						
Sternothaerus depressus (41)	5	61	34						
Sternothaerus carinatus (87)		14	85	1					
Gopherus polyphemus (35)	77	6	17						
Terrapene carolina (142)	2		89	3	6				
Terrapene ornata (63)	13	6	79	2					
Emys blandingi (44)			91	5	5				
Clemmys guttata (35)		9	91						
Clemmys muhlenbergi (12)		8	92						
Clemmys insculpta (19)	5	5	79	11					
Clemmys marmorata (5)		20	80						
Malaclemmys terrapin (34)	3	3	85		9				
Graptemys geographica (25)			92	4	4				
Graptemys pseudogeographica (169)	9	21	68	1	1				
Graptemys kohni (158)	1	10	88		1				
Graptemys versa (64)	2	2	91	2	5				
Graptemys barbouri (139)		5	94		1				
Graptemys pulchra (150)	1	15	80	3	2				
Graptemys oculifera (100)		1	83	11	5				
Graptemys flavimaculata (64)		6	91	2	2				
Graptemys nigrinoda (87)		3	87	2	7				
Pseudemys scripta (344)	7	6	86	1					
Pseudemys floridana (192)	9	9	81		2				
Chrysemys picta (210)	5	12	81	1	1	1			
Deirochelys reticularia (49)	2	10	86	2					
Totals 3947	5	23	67	1	1				3

* Numerals at top indicate marginal laminae; the letter s denotes a seam. Figures in the table are percentages. Number of specimens examined is shown after species name. Figures may not add to 100% because all were rounded to nearest whole per cent.

occurs in one percent of *K. subrubrum,* not at all in *K. bauri.*

Among sternothaerine turtles, only *S. odoratus,* probably the oldest phylogenetically of this group (Tinkle, 1958), shows considerable overlap in position of seam A contacts with species of *Kinosternon. Sternothaerus minor, S. depresssus* and *S. carinatus* have, respectively, 83%, 95% and 81% of the contacts at 1< or 1½; i.e. at or anterior to the midpoint of the first marginal. Contact is in similar positions in a maxmum of 6% of any species of *Kinosternon* in which the majority of contacts are at 1> or posterior to this point. The usefulness of these contacts for distinguishing between species of *Sternothaerus* are quite limited and have been discussed previously in sufficient detail (Tinkle *op. cit.*). *Sternothaerus odoratus* has not been discussed previously, but on the basis of this contact further reason exists for considering *S. odoratus* divergent from other species of the genus. It shows at 1> a frequency of 63% compared to a high of 20% in any other species of *Sternothaerus.*

TABLE 6.
Modal formula for seam contacts in 33 species of turtles

	% of species	% of individuals
A - m 1 (>½)	67	66
B - m 5 (<½)	69	63
C - m 7 (<½)	50	41
D - m 9 (<½)	85	82
E - m 11 (<½)	73	67

Among the species of *Graptemys,* the percentage of contacts at 1> are above 83% in all species except *Graptemys geographica* (56%) which is most divergent from the other species.

TABLE 7.
Modal formula for each genus

Modal formula	Genus
1> 5< 7< 9< 11<	Clemmys (68) Malaclemmys (34) Graptemys (952) Pseudemys (537)
1> 5< 7> 9< 11<	Chrysemys (213) Sternothaerus (1397)
1> 5< 7> 9< s11	Kinosternon (281)
1> 5> 7> 9< 11<	Terrapene (207)
1> 4> 6< 8> 10>	Gopherus (36)
2< 5< 7< 9< 11<	Deirochelys (53)
2< 5< 7> 9> 11<	Emys (44)
2< 5< 7> 9< 11<	Chelonia (31)
2> 6< 8> 10> 12>	Chelydra (110)

* Modal formulae (as in Table 6) for each genus of turtle studied. Numbers in parentheses are numbers of specimens examined in each group.

The genera *Emys* and *Deirochelys* which are similar in many other aspects have 96% and 91% of their contacts, respectively, at 2<. Such a contact occurs at most in 18% of any other emydid turtle (excluding *Clemmys marmorata* in which the sample size is too small for conclusions), and supports the conclusions reached by Loveridge and Williams (1957) of the close relationships of *Emys* and *Deirochelys*.

Seam B Contacts: In all specimens of *Chelydra,* the seam B contact is on the sixth marginal. This contact occurs in no other species of turtle examined and is hence diagnostic at the generic level. Among the other species of chelydrid turtles there are no diagnostic differences in seam B contacts. On the basis of this contact, a closer relationship exists between *Sternothaerus odoratus* and *S. minor* than between these two and other *Sternothaerus*.

Gopherus polyphemus with 86% of the contacts on 4> is fairly distinctive and overlaps to any extent only with *Graptemys pulchra.*

Among the emydid turtles, seam B contacts typically the fifth marginal anterior to the middle or contacts the fifth intermarginal seam. The contact at 5< is about twice as common or more in *Graptemys geographica G. pseudogeographica* and *G. kohni* than in the other species of *Graptemys.* Otherwise, the seam contacts reinforce concepts of relationship of *Graptemys* species based on other characters. The major exception to this statement is the big (58%) percentage of contacts at 5< in *Graptemys flavimaculata* compared with 14% in *G. oculifera* and 18% in *G. nigrinoda,* the two other members of the distinct narrow-headed (and presumably closely related) complex of *Graptemys* species in the southeastern United States (see Cagle, 1954).

Seam C Contacts: There is no overlap in seam contacts of *Chelydra serpentina* with any other species studied, so a seam C contact on the eighth marginal can be considered a diagnostic generic character. Among the other chelydrids, the seam contacts are virtually limited to the seventh marginal, but there is great variability in the position of this contact in the seventh marginal so that no generalization can be made concerning them, except that in both *Kinosternon* and *Sternothaerus* the point of contact is in the middle or posterior part of the seventh marginal.

Gopherus polyphemus shows almost no overlap with any other turtle with regard to this seam contact. Ninety-one percent have a seam C contact on the anterior one-half of the sixth marginal. This contact occurs in no other species studied.

The emydid turtles are fairly consistent in having most seam C contacts at 7< or anterior to this point. The major exceptions are the two species of *Terrapene* (85% and 98% at 7>), *Emys blandingi* (95% at 7>), *Clemmys guttata* (66% at 7>) and *Chrysemys picta* (49% at 7>). This contact is found in only three other species for which sufficient numbers were available, and at most in 17% of the individuals *(Deirochelys reticularia)*. The high frequency (60%) of contacts between seam C and 6> in *Graptemys nigrinoda* is unusual. The greatest percentage shown by another *Graptemys* is eight percent by *G. flavimaculata,* a species closely related to *nigrinoda.* As a matter of fact, none of the other emydids shows a higher (than 8%) frequency of occurrence at this contact. This may be taken as evidence additional to that presented by Cagle (1954) to demonstrate the divergence of this species *nigrinoda* from others in the genus. The high frequency (49%) of seam C contacts at 7> that occurs in *Chrysemys picta* is interesting because this contact is found in only 3% of any species of *Pseudemys* examined.

Seam D Contacts: In *Chelydra* and *Macroclemmys,* the seam D contacts are on the tenth marginal, a contact not found in any specimen of other turtle species. Most of the remaining chelydrids are much alike in having 90% or more of the seam D contacts at 9<. A partial exception is *S. minor* with 67% and *S. depressus* with a low 22% showing additional evidence of the distinctiveness of this form, but a closer relationship to *S. minor* than to other sternothaerine turtles. Most of the emydid turtles have over 90% of the seam D contacts at 9<. Notable exceptions are *Emys blandingi* with only 18% and *Deirochelys* with 57%. All others are 60% or above. The *Graptemys* species all show at least 94% of the contacts at 9<.

Seam E Contacts: Chelydra and *Macroclemmys* have most of their contacts at 12> and all of them on the twelfth marginal. No other turtle was seen with this contact. In the other chelydrids the seam E contacts are almost always at 10>, s11, or 11<, but there is little consistency in which of these three contacts is most frequent. In *Kinosternon subrubrum* 88% of the specimens have an s11 contact, while in *K. flavescens* this contact occurs in 21% of the specimens. *Kinosternon flavescens* and *K. sonoriense* show closer relationship to one another in this contact, as do *K. subrubrum* and *K. bauri. Sternothaerus odoratus* and *S. carinatus* show close relationship in this character, as do *S. minor* and *S. depressus.* However, none of these contacts has a high enough frequency to be diagnostic.

Seventy-seven percent of *Gopherus polyphemus* have seam E contacts at 10>. This contact occurs in a maximum frequency of 13% of other turtles, exclusive of those of the genus *Kinosternon.*

The emydid turtles consistently have 80% or more seam E contacts at 11< with the exception of *Terrapene ornata* (79%), *Clemmys insculpta* (79%) and *Graptemys pseudogeographica* (68%). None of the contacts in emydid turtles is diagnostic.

Discussion of Taxonomic Value of Seam Contacts. Consistency of Relationships as Revealed by Percentage Contacts

With the exception of seam A contacts in which *Chelydra* shows considerable overlap with other chelydrid and emydid turtles, all other contacts of *Chelydra* are unique. The scant information available on *Macroclemmys* indicates that it, too, has the same contacts as *Chelydra.*

Chelonia is not unusual in its seam contacts and shows close relationship in this character to the emydid and kinosternid species.

In the genus *Kinosternon,* these contacts do not consistently indicate the same taxonomic relationships. Seam A contacts indicate a close relationship between *K. subrubrum* and *K. bauri* while in seam B contacts *bauri* and *flavescens* are most closely related. In seam C contacts, *bauri* and *sonoriense* are most alike. If the modal seam formula (Table 8) is considered, however, it is clearly evident that *K. subrubrum* and *K. bauri* show more likeness to one another than to *flavescens* and *sonoriense.*

TABLE 8.

Modal formulae for each turtle species for which 10 or more specimens were studied *

	N	A	B	C	D	E
Chelonia mydas	(31)	2<(100);	5< (77);	7> (97);	9< (74);	11<(97).
Chelydra serpentina	(110)	2> (54);	6< (93);	8> (95);	10> (84);	12>(84).
Kinosternon subrubrum	(164)	1> (87);	5< (48);	7> (70);	9< (97);	s11 (88).
Kinosternon flavescens	(43)	2< (65);	5< (98);	7> (77);	9< (91);	10>(76).
Kinosternon sonoriense	(23)	2< (96);	5< (70);	7< (48);	9< (96);	10>(55).
Kinosternon bauri	(51)	1> (90);	5< (96);	7< (62);	9<(100);	s11 (63).
Sternothaerus odoratus	(847)	1> (63);	5< (71);	7> (89);	9< (96);	11<(70).
Sternothaerus minor	(422)	1< (62);	5< (61);	7> (92);	9< (67);	s11 (58).
Sternothaerus depressus	(41)	1< (63);	5> (54);	7> (76);	s9 (54);	s11 (61).
Sternothaerus carinatus	(87)	1< (61);	5> (41);	7> (69);	9< (91);	11<(85).
Gopherus polyphemus	(36)	1> (94);	4> (86);	6< (91);	8> (77);	10>(77).
Terrapene carolina	(144)	1> (99);	5> (69);	7> (85);	9< (65);	11<(89).
Terrapene ornata	(63)	1>(100);	5> (89);	7> (98);	9< (91);	11<(79).
Emys blandingi	(44)	2< (96);	5< (91);	7> (95);	9> (77);	11<(91).
Clemmys guttata	(33)	1> (49);	5< (57);	7> (66);	9< (74);	11<(91).
Clemmys muhlenbergi	(13)	1> (92);	5< (85);	7< (92);	9< (92);	11<(92).
Clemmys insculpta	(19)	1> (79);	5<(100);	7<(100);	9< (95);	11<(79).
Malaclemmys terrapin	(34)	1> (62);	5< (88);	7<(100);	9< (66);	11<(85).
Graptemys geographica	(25)	1> (56);	5<(100);	7<(100);	9<(100);	11<(92).
Graptemys pseudogeographica	(169)	1> (95);	5< (88);	7< (88);	9< (97);	11<(68).
Graptemys kohni	(158)	1> (91);	5< (85);	7< (94);	9< (99);	11<(88).
Graptemys versa	(64)	1> (83);	5< (41);	7< (97);	9<(100);	11<(91).
Graptemys barbouri	(139)	1> (99);	s5 (39);	7< (98);	9< (94);	11<(94).
Graptemys pulchra	(146)	1> (89);	4> (44);	7< (90);	9< (97);	11<(80).
Graptemys oculifera	(100)	1> (99);	s5 (56);	7< (58);	9< (96);	11<(83).
Graptemys flavimaculata	(64)	1>(100);	5< (58);	s7 (51);	9< (95);	11<(91).
Graptemys nigrinoda	(87)	1> (95);	s5 (47);	6> (60);	9< (94);	11<(87).
Pseudemys scripta	(347)	1> (86);	5< (99);	7< (95);	9< (83);	11<(86).
Pseudemys floridana	(190)	1> (89);	5< (95);	7< (98);	9< (82);	11<(81).
Chrysemys picta	(213)	1> (62);	5< (90);	7> (49);	9< (63);	11<(81).
Deirochelys reticularia	(53)	2< (91);	5<(100);	7< (75);	9< (57);	11<(86).

* Number after the name is the number of specimens examined. The numbers after the contacts are the percentages of individuals of that species with such a contact.

There are two species groups recognizable in the genus *Sternothaerus,* the *carinatus* complex composed of the species *carinatus, minor* and *depressus* and the *odoratus* group consisting of a single recognized species. Seam A contacts (Table 1) reinforce this grouping as do B and C contacts, in general. Contacts of B and C seams show, in addition, a closer relationship between *odoratus* and *minor* than between *odoratus* and other species, a relationship that appears likely for many other reasons (Tinkle, 1958). However, seams C and D do not reinforce our concept of relationships because on the basis of these, *carinatus* and *odoratus* are most closely related to one another. The modal formulae for sternothaerine turtles is no more helpful in indicating the probable relationships of the species.

Terrapene carolina and *Terrapene ornata* have the same modal formulae and there are only minor differences between the two in percentage of contacts at any point.

The genera *Emys* with 96% and *Deirochelys* (92%) are the only emydid turtles with the majority of seam A contacts on the second marginal. This may indicate a close relation between the two or may indicate convergence in shell morphology not necessarily indicative of close taxonomic relationship.

With the exception of seam E contacts, the percentages of individuals of the species of *Clemmys* with a certain contact show a closer relation of *C. muhlenbergi* to *insculpta* than to *guttata.* The modal formulae for all three is very nearly the same with only seam C contacts in *guttata* showing a difference from the other two species.

The species of the genus *Malaclemmys* are probably closely related to those of the genus *Graptemys* and the percentage of each seam contact strengthens this supposition. However, it is impossible to pick one or more species of *Graptemys* to which *Malaclemmys,* on the basis of these contacts alone, can be said to be most closely allied.

The taxonomic arrangement of Cagle (1954) based on examination of large numbers of turtles of the genus *Graptemys* is followed in this paper. The reader is referred to these papers for critical evaluation of relationships. The contacts are not consistent in indicating relationships among the species or even of groups, such as the broad-head complex or the narrow-head species. The modal formulae for members of the genus *Graptemys* are not more instructional.

The two species of *Pseudemys* have the same modal formula and the percentages of contacts at each seam show remarkable similarity and consistency.

Chrysemys has a similar modal formula to that of *Pseudemys* and the percentage contacts in the painted turtles shows close relationship to *Pseudemys* in most instances, although in some contacts, particularly of seam C, the relationship is closer to some of the narrow-head members of the genus *Graptemys*.

It must be concluded that the seam contacts are not consistent in indicating a particular taxonomic relation or in strengthening those established on other bases. With

TABLE 9.
Summary of dominance of a particular seam contact in turtles

Seam	Contacts	No. of species in which dominant	Percentage of species in which dominant
A	1<	3	9
	1>	22	67
	2<	7	21
	2>	1	3
B	4>	2	6
	s5	3	9
	5<	22	69
	5>	4	13
	6<	1	3
C	6<	1	3
	6>	1	3
	s7	1	3
	7<	16	50
	7>	12	38
	8>	1	3
D	8>	1	3
	s9	1	3
	9<	28	85
	9>	1	3
	10>	2	6
E	10>	3	9
	s11	4	12
	11<	24	73
	12>	2	6

TABLE 10.
Variability in seam contacts at different places on the carapace *

Seam	Range of contacts of seam with different areas of marginals or intermarginal seams	Number of units in range of contacts (see text for explanation)	Per cent of contacts at the three most common point of contacts in the range shown at left
A	1< to 2>	4	71, 16, 10
B	3> to 6>	7	74, 15, 7
C	6< to s9	6	50, 40, 3
D	8< to 10>	6	90, 3, 3
E	10> to 12>	5	85, 11, 4

* The three figures in the far right column are the three highest percentages. In seam A, for example, 71% of the species studied had the most frequent contact (modal contact) at one point in the range shown at the left.

the exception of such genera *Chelydra* and *Macroclemmys,* there are seldom contacts that are of diagnostic value at either the specific or generic levels.

The usefulness of this character is in establishing the extent of individual variation in animals with few meristically variable parts and, perhaps, in studying geographic variation as will be discussed later.

Considering all 33 species studied and all the seam contacts, there is obviously strong selection for certain contacts. Coker (1920) has pointed out that the proper adjustment between carapacial laminae may be more important than actual number of laminae because supernumerary laminae are more frequently found than are maladjustments. Table 9 shows the number and percentage of species having a particular seam contact in the majority of individuals.

It is readily seen that with the exception of seam A, most species (50-85%) have contacts in the anterior portions of the marginals. In all except seam C, there is a tendency for all species to have a single dominant contact. In seam C 50% are on 7< while 38% are on 7>.

Some difference appears in the range of variability of contacts in different portions of the carapace. This is seen by assigning each possible contact, with the exception of intermarginal seams, a unit value. Thus, if in a series of specimens seam A contacted marginals one and two at points varying from 1< to 2>, the possible contacts would be between s1 and 1½, between 1½ and s2, between s2 and 2½ and between 2½ and s3, for a total of four units. However, along with this must be considered the fact that in some contacts, the total range of variation in position of contact may be high, but most contacts may still be concentrated at one point. Table 10 shows the ranges in units and the percentage concentration at certain points within the range.

From the table, it appears that considering unit spread only, the most anterior and posterior portions of the carapace are least variable with the mid-section most variable. However, from a consideration of the three largest percentages of contacts, seam C shows the greatest variability because almost one-half of the species examined fall into each of two different contact units. The rank in order of decreasing variability being C-B-A-E-D. This arrangement also takes into consideration the proportion of all turtles examined that fell into the three highest percentages. For example, seam A is considered slightly more variable than seam E because the three contacts in E comprised 100% of all species of turtles examined, while 97% were included in the three highest percentage of A contacts.

Thus, the anterior one-half of the carapace seems more variable than the posterior one-half. The studies of abnormalities in the shells of turtles made by Newman (1906), Coker (1910) and Zangerl and Johnson (1957) indicated that the posterior one-half of the carapace was more variable than the anterior half, but most of the abnormalities considered by the above authors were in the form of supernumerary laminae.

Phylogenetic Aspects of Seam Contacts

Most United States turtles have 12 marginal laminae, but members of the subfamily Kinosterninae (*sensu* Williams, 1950) have only 11. The larger number seems to be primitive and it is characteristic of the relatively primitive forms *Macroclemmys, Chelydra* and *Chelonia.* Newman (1906) pointed out that the more recently a certain scute has been lost phylogenetically, the more common it should be as a supernumerary element in turtles with the reduced number. In turtles studied by him, the frequency of occurence of supernumerary scutes diminished in anterior direction on the carapace. From this he concludes that the earliest losses of scutes occurred at the anterior end of the carapace, the most recent at the posterior end.

It should be instructive then to compare the frequencies of contacts of interlateral seams with the marginal laminae in turtles with 12 marginals with the percentages in turtles with only 11. Also, obviously primitive turtles with 12 marginals (such as *Chelydra)* will be compared with other turtles with 12 marginals, but presumably more recently evolved (such as *Graptemys).* For study, the turtles were divided into three groups—turtles with 11 marginals, those with 12-advanced and those with 12-primitive (*Chelydra, Macroclemmys,* and *Chelonia*). The results are shown in Table 11 which includes all species shown in Tables 1-5 except *Gopherus polyphemus* and *Clemmys marmorata.*

I will first compare the primitive turtles with 12 marginals with advanced ones. With the exception of seam A, the seam contacts for primitive species show a bimodal distribution, which is eliminated by excluding *Chelonia* from consideration. If this exclusion is made, it is clear that compared with the contacts in *Chelydra and Macroclemmys,* the other species with 12 marginals show contacts that are shifted anteriorly. Too, the difference between the contacts in primitive and advanced species increases as one passes from anterior to posterior on the carapace. Thus, in seam A the mode of seam contacts in primitive species is at 2<, in advanced species at 1>; in B the same contacts are 6< and 5<; in C, 8> and 7<; in D, 10> and 9<; in E, 12> and 11<. The unit differences between the modes of primitive and advanced species in seam A contacts is 1; between the two groups in seam B contacts is 1; in C, 2; in D, 3; in E, 3.

If *Chelydra* is assumed to represent the primitive condition of scute arrangement in turtles, and all of the other turtles with 12 marginals are advanced over *Chelydra,* then it is evident that there has been a movement forward of all seam contacts, a movement more pronounced posteriorly. Accordingly, it might be possible to detect primitive members of the other 12-marginal species by considering which of these show the closest approach to the *Chelydra* condition.

In *Chelydra* almost all individuals have seam A contacts at 2< or farther posterior. Other species in which the majority of contacts are at 2< and posterior to this point are *Chelonia mydas, Kinosternon flavescens* and *K. sonoriense, Emys blandingi,* and *Deirochelys reticularia.* In other seam contacts there is no overlap of the other species with *Chelydra* and there is no consistency in which of the other species tend toward the contacts dominant in

TABLE 11.
Average percentage contacts of each interlateral seam and marginal lamina in three groups of turtles *

Seam A Points of Contact	1<	1½	1>	s2	2<	2½	2>
11 (8 species)	27.1	11.0	37.8	4.1	20.3	0.0	0.0
12 primitive (3 species)	0.0	0.0	0.3	0.0	80.0	2.0	18.0
12 advanced (20 species)	2.8	1.9	76.4	7.4	11.4	0.2	0.3

Seam B Points of Contact	3>	s4	4<	4½	4>	s5	5<	5½	5>	s6	6<	6½	6>
11	0.0	0.0	0.0	0.0	0.0	0.0	60.5	14.3	25.4	0.1	0.0	0.0	0.0
12 primitive	1.5	0.0	0.0	0.0	1.5	6.5	38.5	0.0	1.5	0.0	46.5	2.0	2.0
12 advanced	0.0	0.1	0.0	0.0	9.4	15.0	64.1	1.7	10.0	0.0	0.0	0.0	0.0

Seam C Points of Contact	6>	s7	7<	7½	7>	s8	8<	8½	8>
11	0.0	0.0	20.5	11.5	67.0	1.3	0.0	0.0	0.0
12 primitive	1.5	0.0	0.0	0.0	48.5	0.0	2.5	0.5	47.5
12 advanced	3.7	7.8	66.2	1.6	20.7	0.1	0.0	0.0	0.0

Seam D Points of Contact	8>	s9	9<	9½	9>	s10	10<	10½	10>
11	3.3	12.0	82.5	1.3	1.0	0.0	0.0	0.0	0.0
12 primitive	1.0	0.0	24.7	0.0	7.7	0.0	6.3	2.0	58.3
12 advanced	0.3	0.7	82.9	4.6	11.7	0.0	0.0	0.0	0.0

Seam E Points of Contact	10>	s11	11<	11½	11>	s12	12<	12½	12>
11	21.4	47.4	31.0	0.1	0.0	0.0	0.0	0.0	0.0
12 primitive	0.0	0.0	32.3	1.0	0.0	0.0	3.0	2.3	61.3
12 advanced	3.0	6.6	85.7	2.5	2.6	0.1	0.0	0.0	0.0

* Average percentages were obtained by dividing total percentage by all species in each group, not just by those in which some individuals actually had the contact.

Chelydra, so it is doubtful if these contacts are of value as measures of primitiveness in other turtles.

Chelonia, of which only 31 juvenile individuals were studied, is also possibly nearer the ancestral condition of turtles than other species studied. *Chelonia* is more like the advanced 12 marginal species than it is like *Chelydra* or *Macroclemmys* and this may indicate the early establishment of the scute pattern characteristic of recent species, whereas the nearly unique arrangement found in *Chelydra* may be off the main path of evolution.

A comparison of the figures in Table 11 shows that the seam contacts in those species with only 11 marginals are quite different from *Chelydra* with 12, but very similar to other species with 12 marginals. Compared to *Chelydra,* the contacts in species with 11 marginals are shifted far anteriorly, as they are in the advanced 12-marginal species. In fact, there are only slight differences in percentage contacts between species with 11 marginals and those with 12, if the chelydrine turtles are excepted.

Assuming that the eleven marginal condition of kinosternine turtles arose by loss of one marginal from an ancestral type like *Chelydra,* to which the Kinosterninae are most closely related, I attempted to determine from which part of the shell the loss of a marginal occurred by comparing the points of contact in *Chelydra* (tables 1-5) with those in the kinosternine species (table 11). In most individuals of species with eleven marginals the contacts of seams A, B and C are shifted at least one unit anteriorly to the most frequent point of contact in *Chelydra;* in seam D and E, the shift is even further anteriorly. The fact that the shifts in turtles with eleven marginals are toward the anterior portion of the carapace seems to indicate that the phylogenetic loss of a shield was there, forcing a readjustment of seams. If Newman (1906) is correct in his conclusions that the earliest loss of scutes occurred at the anterior end of the carapace, as appears the case here, this loss may have occurred quite early in the evolution of kinosternine turtles.

In *Gopherus polyphemus* in which the last marginal shield in the carapace is common to both sides, most seam contacts are shifted slightly anterior to those seen in most other species of turtles.

In general, it seems that the change in number of marginals has not significantly influenced the positioning of seams between the lateral laminae. In fact, there are greater differences within the group of turtles with 12 marginals (including *Chelonia*) than between those with 11 and those with 12.

Geographic Variation in Seam Contacts

The discussion up to now has been concerned with pooled samples of species from several portions of their range. Tinkle (1958) has shown that in some species of *Sternothaerus* differences exist in these contacts between populations occupying different river drainage systems.

Samples were chosen of *Pseudemys floridana, Terrapene ornata, Pseudemys scripta, Chrysemys picta, Graptemys pulchra, Graptemys nigrinoda* and *Sternothaerus odoratus* from different parts of the range of these species. In some of these, the samples encompass the range of more than one geographic race, in some the samples are widely spaced, in others close together so that variation in species under various conditions can be compared. Each species will be discussed separately with regard to the percentage contacts for each of the interlateral seams.

Pseudemys floridana

Fifty-one specimens from the Black Warrior River of Alabama, 45 from the Flint River in Georgia and 28 from the Pearl River between Louisiana and Mississippi were compared (Table 12).

In seam A, B and C contacts the percentages of the three populations are quite similar, but some contacts do occur in one population that are absent or much less common in another. For example 8% of the Black Warrior turtles have a seam A contact at s2, but this contact does not occur in any of the other population samples. Such situations may indicate genetic divergence of the populations if these contacts are genetically determined, but they might be due to chance. If these contacts are genetically determined, the turtles in the Flint and Black Warrior Rivers should show closer relationship to one another than to those in the Pearl. This

TABLE 12.
Comparison of seam contacts in three populations of Pseudemys floridana *

Seam	Position	Pearl River	Black Warrior River	Flint River
A	1<	3 (11)	1 (2)	0 —
	1½	2 (7)	0 —	2 (4)
	1>	22 (81)	45 (90)	43 (96)
	s2	0 —	4 (8)	0 —
B	s5	3 (11)	1 (2)	2 (4)
	5<	25 (89)	49 (96)	43 (96)
	5½	0 —	1 (2)	0 —
C	s7	1 (4)	0 —	2 (4)
	7<	27 (96)	51 (100)	43 (96)
D	8>	1 (4)	0 —	0 —
	s9	0 —	0 —	0 —
	9<	26 (93)	48 (94)	30 (67)
	9½	1 (4)	1 (2)	6 (13)
	9>	0 —	2 (4)	9 (20)
E	10>	4 (14)	8 (16)	0 —
	s11	4 (14)	8 (16)	0 —
	11<	20 (71)	34 (67)	44 (98)
	11½	0 —	0 —	0 —
	11>	0 —	1 (2)	1 (2)

*Figures in parentheses are percentages; others are number of specimens.

TABLE 13.
Comparison of seam contacts in five populations of Pseudemys scripta *

Seam	Position	Sabine River	Ouachita River	Pearl River	Black Warrior River	Coosa River
A	1<	1 (1)	3 (11)	2 (11)	5 (22)	8 (26)
	1½	1 (1)	1 (4)	0 —	1 (4)	1 (3)
	1>	79 (98)	24 (86)	16 (89)	17 (74)	22 (71)
B	5<	81 (100)	28 (100)	18 (100)	23 (100)	31 (100)
C	7<	70 (86)	28 (100)	18 (100)	23 (100)	29 (100)
	7½	3 (4)	0 —	0 —	0 —	0 —
	7>	8 (10)	0 —	0 —	0 —	0 —
D	9<	58 (72)	25 (96)	16 (89)	22 (96)	28 (90)
	9½	7 (9)	0 —	1 (6)	1 (4)	3 (10)
	9>	16 (20)	1 (4)	1 (6)	0 —	0 —
E	10>	2 (3)	0 —	4 (22)	2 (9)	0 —
	s11	5 (6)	3 (11)	1 (6)	4 (17)	0 —
	11<	73 (90)	25 (89)	13 (72)	17 (74)	28 (100)
	11½	0 —	0 —	0 —	0 —	0 —
	11>	1 (1)	0 —	0 —	0 —	0 —

*Figures in parentheses are percentages; others are number of specimens.

situation is generally true with regard to the first three contacts, but with D and E the closest relationship is between the Pearl and Black Warrior populations.

Clearly there are no consistent clines or indication of relationship in this character in this species.

Pseudyemys scripta

Samples of *Pseudemys scripta* from the Coosa and Black Warrior rivers of Alabama, from the Ouachita in Arkansas, the Pearl between Louisiana and Mississippi, and the Sabine between Louisiana and Texas were examined. These samples included specimens from the ranges of the subspecies *P. s. scripta* and *P. s. elegans*. The zones of intergradation between these two races are apparently wide, but most individuals in the Black Warrior and Coosa populations show predominantly *s. scripta* characteristics, while those in the Ouachita, Sabine and Pearl show mostly *s. elegans* characteristics. It is not uncommon, particularly in the Pearl River, to find individuals showing tendencies in color pattern toward *s. scripta.*

Thirty-one specimens from the Coosa, 23 from the Black Warrior, 28 from the Ouachita, 18 from the Pearl and 81 from the Sabine rivers were compared (Table 13).

As was true in *Pseudemys floridana,* the percentage seam contacts show geographic variation but it is largely non-clinal and probably not indicative of relationships at the subspecies level.

Chrysemys picta

The samples used in this study represent the races *p. picta, p. marginata,* and *p. dorsalis.* Forty specimens were examined from des Allemands and Paradis, Louisiana; 24 from Talladega Co., Alabama; 27 from Monroe Co., Tennessee; 33 from Alexander Co., Illinois; 50 from Lake Geneva, Wisconsin; and 40 from New Haven, Connecticut. Comparative data on these are shown in Table 14.

It is impossible to discern consistent geographic trends, but the data do indicate major differences in the populations. There are no conspicuous differences that are consistent enough to distinguish subspecies on the basis of seam contacts.

Terrapene ornata

Twenty-eight specimens of *Terrapene ornata* from one locality in Colorado and 30 from several in western Texas were

TABLE 14.
Comparison of seam contacts in six populations of Chrysemys picta *

Seam	Position	Louisiana	Tennessee	Alabama	Illinois	Wisconsin	Connecticut
A	1½	0 —	1 (4)	0 —	0 —	0 —	0 —
	1>	5 (13)	22 (81)	13 (54)	24 (73)	30 (61)	38 (95)
	s2	25 (66)	2 (7)	8 (33)	8 (24)	14 (29)	2 (5)
	2<	7 (18)	2 (7)	3 (13)	1 (3)	5 (10)	0 —
	2½	1 (3)	0 —	0 —	0 —	0 —	0 —
B	s5	0 —	0 —	1 (4)	0 —	0 —	1 (3)
	5<	29 (73)	27 (100)	23 (96)	27 (84)	46 (94)	38 (97)
	5½	5 (13)	0 —	0 —	2 (6)	2 (4)	0 —
	5>	6 (15)	0 —	0 —	3 (9)	1 (2)	0 —
C	7<	15 (38)	13 (48)	23 (96)	10 (31)	8 (16)	27 (68)
	7½	4 (10)	1 (4)	0 —	0 —	4 (8)	4 (10)
	7>	21 (53)	13 (48)	1 (4)	22 (69)	37 (76)	9 (23)
D	9<	18 (45)	17 (65)	19 (79)	12 (38)	27 (55)	39 (98)
	9½	6 (15)	3 (12)	2 (8)	3 (9)	1 (2)	0 —
	9>	15 (38)	6 (23)	3 (13)	17 (53)	21 (43)	1 (3)
	s10	1 (3)	0 —	0 —	0 —	0 —	0 —
E	10>	2 (5)	3 (12)	1 (4)	1 (3)	1 (2)	3 (8)
	s11	7 (18)	3 (12)	2 (8)	4 (13)	2 (4)	8 (21)
	11<	29 (73)	20 (77)	21 (88)	27 (84)	45 (92)	28 (72)
	11½	0 —	0 —	0 —	0 —	1 (2)	0 —
	11>	1 (3)	0 —	0 —	0 —	0 —	0 —
	s12	1 (3)	0 —	0 —	0 —	0 —	0 —

*Figures in parentheses are percentages; others are number of specimens.

TABLE 15.
Comparison of seam contacts in Texas and Colorado Terrapene ornata *

Seam	Position	Colorado	Texas
A	1>	28 (100)	30 (100)
B	4>	0 —	1 (3)
	s5	0 —	0 —
	5<	3 (11)	0 —
	5½	2 (7)	1 (3)
	5>	23 (82)	28 (93)
C	7½	1 (4)	0 —
	7>	27 (96)	30 (100)
D	9<	22 (79)	30 (100)
	9½	2 (7)	0 —
	9>	4 (14)	0 —
E	10>	3 (11)	4 (13)
	s11	1 (4)	2 (7)
	11<	23 (82)	24 (80)
	11½	1 (4)	0 —

*Figures in parentheses are percentages; others are number of specimens.

TABLE 16.
Comparison of seam contacts in three river system populations of Graptemys pulchra *

Seam	Position	Pearl River	Pascagoula River	Escambia River
A	1<	3 (7)	2 (7)	3 (4)
	1½	0 —	3 (11)	4 (6)
	1>	42 (93)	23 (82)	64 (90)
B	4>	17 (38)	27 (96)	19 (27)
	s5	21 (47)	0 —	33 (47)
	5<	7 (16)	1 (4)	18 (26)
C	s7	3 (7)	5 (18)	7 (10)
	7<	42 (93)	23 (82)	64 (90)
D	9<	45 (100)	27 (96)	68 (96)
	9½	0 —	0 —	3 (4)
	9>	0 —	1 (4)	0 —
E	10>	1 (2)	0 —	0 —
	s11	15 (33)	1 (4)	5 (7)
	11<	29 (64)	26 (93)	63 (89)
	11½	0 —	0 —	1 (1)
	11>	0 —	1 (4)	2 (3)

*Figures in parentheses are percentages; others are number of specimens.

TABLE 17.
Comparison of seam contacts in Graptemys nigrinoda *from two different localities on the Black Warrior River of Alabama* *

Seam	Position	17 miles ssw of Tuscaloosa	3 miles east of Eutaw
A	1<	0 —	1 (3)
	1½	2 (4)	1 (3)
	1>	45 (96)	38 (95)
B	4>	17 (37)	14 (35)
	s5	25 (54)	16 (40)
	5<	4 (9)	10 (25)
C	6>	28 (62)	22 (58)
	s7	16 (36)	12 (32)
	7<	1 (2)	4 (11)
D	s9	4 (9)	1 (3)
	9<	43 (91)	39 (98)
E	s11	3 (6)	1 (3)
	11<	40 (85)	36 (90)
	11½	2 (4)	0 —
	11>	2 (4)	3 (8)

*Figures in parentheses are percentages; others are number of specimens.

compared (Table 15). With the exception of minor discrepancies in seam B contacts, few differences exist. In the first three seam contacts, Texas specimens show a slightly higher percentage of contacts on the posterior portion of the marginals, while in the last two contacts the reverse is true.

These specimens of *Terrapene ornata* do not represent more than a single recognized geographic race — a fact that may partially explain the greater consistency in these data than in those of the preceding species.

Graptemys pulchra

Forty-five specimens of this turtle from the Pearl River between Louisiana and Mississippi, 28 from the Pascagoula River of eastern Mississippi, and 71 from the Escambia River of western Florida were compared (Table 16).

These data show consistent population relations, although not, perhaps, those that would be expected on a geographic basis. If the modal contact for each interlateral seam is considered, the Escambia populations show in every case closer relation to the Pearl populations than either of these do to the Pascagoula turtles.

Graptemys nigrinoda

Eighty-seven of these turtles from Alabama were studied. The samples were chosen from two areas on the Black Warrior

River with no physiographic or ecological barriers to gene exchange between them. The localities are 17 miles SSW of Tuscaloosa (47 specimens) and 3 miles east of Eutaw (40 specimens). The data appear in Table 17.

The differences between the two populations are obviously minor ones. The largest difference is in seam B contacts in which the s5 and 5< contacts of seam B show differences in percentages of 14% and 16%, respectively. The fact that samples drawn from the same river at different points show such similarities strengthens the idea that these contacts are genetically determined.

Sternothaerus odoratus

This species of turtle occurs in many ecological situations and, unlike most of the species of *Graptemys* studied, is not limited to river drainages. Thus, the possibilities of gene exchange are greater over wide areas. Fifty-five specimens from Texas, 58 from Florida and 72 from Michigan were compared (Table 18).

Seam A and B contacts show greater divergence in the three samples than do the posterior three contacts. The first two show closer relation between Texas and Michigan material. The last three show consistent geographic trends; in each the mode percentage is smallest in the Michigan sample, greatest in the Texas material.

Ontogenetic Changes in Seam Contacts

The failure of most of the seam contact percentages to show consistent differences between populations or to show geographic trends could be due to unequal distribution of size groups in the populations studied if seam contacts were subject to ontogenetic changes, or if there were selection against certain contacts in young turtles which would alter the frequency of these contacts in the adults. Both type changes are included under the term ontogenetic change in the following discussion.

To study such changes, seams B and C were chosen because these contacts generally are representative of the variation in different populations. Large samples for study of geographic variation were compared.

The specimens were arbitrarily divided into size groups. Wherever possible, only individual turtles from the same population were utilized for this study to eliminate possible geographic differences. The same size groups could not be used for comparisons of every species, either because of the nature of the samples or because of the size differences between different species.

Pseudemys floridana (Table 12) shows little difference of seam B and C contacts in three populations studied. There are no ontogenetic changes in this species in these seam contacts. The same is true of *Pseu-*

Table 18.
Comparison of Texas, Michigan, and Florida Sternothaerus odoratus *from several localities in those states* *

Seam	Position	Texas	Florida	Michigan
A	1<	18 (33)	4 (7)	18 (25)
	1½	11 (20)	3 (5)	10 (14)
	1>	26 (47)	51 (88)	44 (61)
B	5<	31 (57)	49 (86)	37 (54)
	5½	7 (13)	3 (5)	3 (4)
	5>	16 (30)	5 (9)	29 (42)
C	s8	0 —	0 —	8 (11)
	7<	2 (4)	2 (3)	0 —
	7½	0 —	5 (9)	0 —
	7>	52 (96)	51 (88)	62 (87)
	8<	0 —	0 —	1 (1)
D	s9	1 (2)	3 (5)	1 (1)
	9<	53 (96)	54 (95)	66 (94)
	9½	0 —	0 —	1 (1)
	9>	1 (2)	0 —	2 (3)
E	10>	0 —	2 (4)	0 —
	s11	20 (38)	14 (25)	15 (21)
	11<	33 (62)	41 (72)	55 (79)

*Figures in parentheses are percentages; others are number of specimens.

demys scripta. In *Chrysemys picta* there is considerable variability in seam B and C contacts. The Louisiana specimens are the most divergent from the other five populations studied. In this sample there is a lower percentage of contacts of seam B at 5< and a higher percentage posterior to this point than in other populations. This is precisely what should be expected if a sample contained mostly small individuals. The Louisiana sample is predominently of juvenile individuals under 50 mm in carapace length, a size almost completely absent in other samples. It could be argued that the difference is *still* geographic because most individuals used in a study of ontogenetic differences were from Louisiana. However, if this much difference did exist between Louisiana and other populations, differences of a similar magnitude should occur between some of the other populations since they are from widely separated regions of the United States. It is more reasonable to attribute discrepancies to the difference in size group representation in the six populations.

Seam C contacts in *Chrysemys* show no consistent character. The only strongly evident change is the tendency of larger individuals to have a higher percentage of contacts at 7<. Here the differences existing between populations cannot be correlated directly with differences in size composition of the samples.

In *Terrapene ornata* the two major differences between the two populations studied was a higher percentage of 5> and 9< contacts in the Texas specimens than in those from Colorado. These differences are probably reflective of actual differences between the populations. Differences of the magnitude indicated are not explicable on an ontogentic basis.

The most significant difference between the three populations of *Graptemys pulchra* studied is the high (96%) percentage of contacts at 4> in the Pascagoula River sample. The same population also shows a slightly lower percentage of contacts at 7< than in the other two populations. Both of these differences could be partially explained on an ontogenetic basis if the percentage of individuals in the Pascagoula River sample in the 51-100 and 101-150 mm size classes is greater than in the Pearl or Escambia River samples.

On this basis, too, the Escambia River sample should show closer relation to the Pascagoula than to the Pearl sample. That this is not the case probably indicates that genetic differences, as well as ontogenetic ones are involved.

The differences in *Graptemys nigrinoda* in the two size groups studied are probably negligible. However, almost no large specimens of this little known species are available for study because adults are difficult to capture. Ontogenetic differences may exist and may be shown when more large specimens become available for study. The differences that do exist between the two populations studied are slight and may be genetic or due to chance sampling, but probably not to differences in size distribution of the individuals comprising the samples.

Sternothaerus odoratus, of which the greatest number of specimens was examined, shows very little ontogenetic change in percentage of seam contacts. Contacts at 5< are slightly higher in turtles of a carapace length between 51 and 75 millimeters. The only major geographic difference in the populations studied is the high 5< contacts in Florida samples compared to Texas and Michigan material. This, too, could be partially explained on an ontogenetic basis if a greater percentage of Florida specimens were in the 51-75 mm size group. The percentage of specimens in this group in Texas, Florida, and Michigan samples are 19, 46 and 7 per cent, respectively.

Thus, the difference could be partly accountable to ontogenetic differences. However, Florida *Sternothaerus odoratus* are smaller than those from other areas and the difference in size groups found originally is partly attributable to the smallest size groups being predominantly of Florida turtles, so the differences may still be primarily genetic.

Conclusions

1. The contacts of the seams between the lateral laminae with the marginal laminae or the intermarginal seams vary considerably, but only a few of the variations are divergent enough or consistent enough to be useful as taxonomic

characters. There is obviously strong selection operating for certain shield and seam arrangements.

2. The species most different from all others studied are *Gopherus polyphemus*, *Chelydra serpentina* and *Macroclemmys temmincki*. Most turtles studied were of the family Emydidae, of which the most divergent were the genera *Deirochelys* and *Emys*.

3. In some instances one or more of the five contacts studied indicate one relationship among species in a large genus, while another contact indicates entirely different relationships.

4. Different portions of the carapace show differing degrees of variability, with the anterior one-half being more variable than the posterior one-half. Studies by other authors show that the posterior one-half of the carapace has a higher number of abnormalities.

5. In the turtles with only 11 marginal shields instead of the typical 12, the contacts are shifted forward when compared to primitive turtles such as *Chelydra*. However, in advanced groups with 12 marginals the same shift has occurred. That the number of marginals has not greatly influenced the position of seam contacts is apparent from the fact that there are greater differences in contacts between species with 12 marginals than between those with 12 and those with 11.

6. The loss of a marginal shield to yield the 11 marginal condition of the kinosternine turtles probably occurred from the anterior part of the carapace.

7. Geographic variation occurs in seam contacts, but this variation is largely nonclinal. This variation is useful in showing divergence at the population level in some species, but not in others.

8. Ontogenetic changes in seam positions must be considered when interpreting geographic differences that do occur, but all differences cannot be explained on an ontogenetic basis, so it is likely that many contacts are genetically determined.

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