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BIODEMOGRAPHIC STUDIES OF THE CLAM *RANGIA CUNEATA* GRAY

LAURENCE D. FAIRBANKS,
*DEPARTMENTS OF ZOOLOGY AND MEDICINE, TULANE UNIVERSITY,
NEW ORLEANS, LOUISIANA*

PROXIMAL RETINAL PIGMENT RESPONSES AND THEIR RELATIONSHIP TO TOTAL PHOTOMECHANICAL ADAPTATION IN THE DWARF CRAYFISH, *CAMBARELLUS SHUFELDTI*

MILTON FINGERMAN
and
R. NAGABHUSHANAM,
*DEPARTMENT OF ZOOLOGY, NEWCOMB COLLEGE, TULANE UNIVERSITY,
NEW ORLEANS, LOUISIANA*

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

J. F. FITZPATRICK, JR.,
*DEPARTMENT OF BIOLOGY, UNIVERSITY OF VIRGINIA,
CHARLOTTESVILLE, VIRGINIA*

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.

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(New genera, species, and subspecies in boldface)

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LAURENCE D. FAIRBANKS,
Departments of Zoology and Medicine, Tulane University,
New Orleans, Louisiana

CONTENTS

I. Introduction

Rangia cuneata Gray, 1831, a pelecypod mollusk of the Family Mactridae, is commonly found in brackish water regions of the northern coast of the Gulf of Mexico. Synonyms of this species are given by Dall (1894), Maury (1920), and Abbott (1956). Its range according to Abbott is northwest Florida to Texas. Dall (1894) described it as "living in Mobile Bay, Alabama, and westward on the north shore of the Gulf to Vera Cruz, Mexico, in shallow water, either brackish or perfectly salt". The geological distribution of *Rangia cuneata* includes the Pliocene of the Carolinas and Florida. It is also known from Pleistocene deposits along the Atlantic coast of North America, ranging from Chesapeake Bay southward to cover the entire northern Gulf coast, as well as the northern coast of South America (Dall, 1894; Richards, 1939). The abundance of *Rangia* in Neocene fossiliferous deposits of the Mississippi embayment, particularly in the prairie regions of southern Louisiana, indicates the importance of this animal in the stratigraphic formation of this part of the country (Harris, G. D., 1902: 32, 36, 265-266). References to *R. cuneata* in the literature are generally limited to mention only in species checklists (Johnson, 1934; Behre, 1950; Pulley, 1952; Moore, 1961) and ecological reports (Strecker, 1935; Hedgpeth, 1950, 1953; Ladd, 1951; Gunter and Shell, 1958). *R. cuneata* apparently is restricted to waters of low salinity, occurring landward of the oysters (Hedgpeth, 1953; Ladd, 1951) and its abundant occurrence in the extensive brackish water regions of Louisiana and Texas are well known to biologists familiar with this part of the Gulf coast (Gunter, 1952; Hedgpeth, 1953; Gunter and Shell, 1958). The biology of *Rangia*, other than a cursory knowledge of its limits of salinity, appears poorly understood.

Quantitative or semi-quantitative studies of the abundance of pelecypods are few in the literature. In the absence of precise methods in the study of population density of animals, investigators seeking quantitative estimates of clams have used various methods. According to Moore (1958: 303) Petersen defined ecological bottom communities on the basis of "relatively small grab samples" from the shallow waters of the Danish coasts where the communities were made up generally of echinoderms or mollusks of species that were present in large numbers. Pratt (1953) and Bader (1954) used tow-type dredges for set periods of time and at set speeds of the towing vessel. Since their interests were in comparative abundance on bottom types the results were not expressed in terms of population density per unit area. Petersen's results, as represented by Moore, were expressed in number per one-fourth square meter. Manning and Pfitzenmeyer (1958) used a hydraulically operated "20 square foot sampler"; taking one to 30 samples at a location and seven samples at any one location were not uncommon. Their results were expressed in number of individuals per acre. Among the variety of mechanisms that have been used in quantitative bottom sampling the Petersen and Ekman dredges, of the "clam shell" type, have probably been most extensively employed on all types of bottom (Welch, 1948; Sverdrup *et al.*, 1942).

Complexities involved in a study of populations and difficulties encountered in mathematical treatment of biological data are well known to ecologists (*cf.* Hutchinson, 1948: 221, 222; Allee *et al.*, 1949: 386).

The principal objectives of the present investigation concerning *Rangia cuneata* were: (1) to describe the habitat in terms of some of the pertinent physical and biological factors; (2) to ascertain environmental factors correlated with population density and sizes of individuals; and, (3) to describe reproduction in terms of seasonal events concerning the breeding cycle.

II. Materials and Methods

A. *Study Areas*

Two limited localities in Lake Pontchartrain were chosen for habitat and population study areas because of the abundance of *Rangia* and accessibility to the writer. Many of the physical features of Lake Pontchartrain were described by G. D. Harris (1902), R. A. Harris (1902), and Steinmayer (1939). Some of its flora and fauna

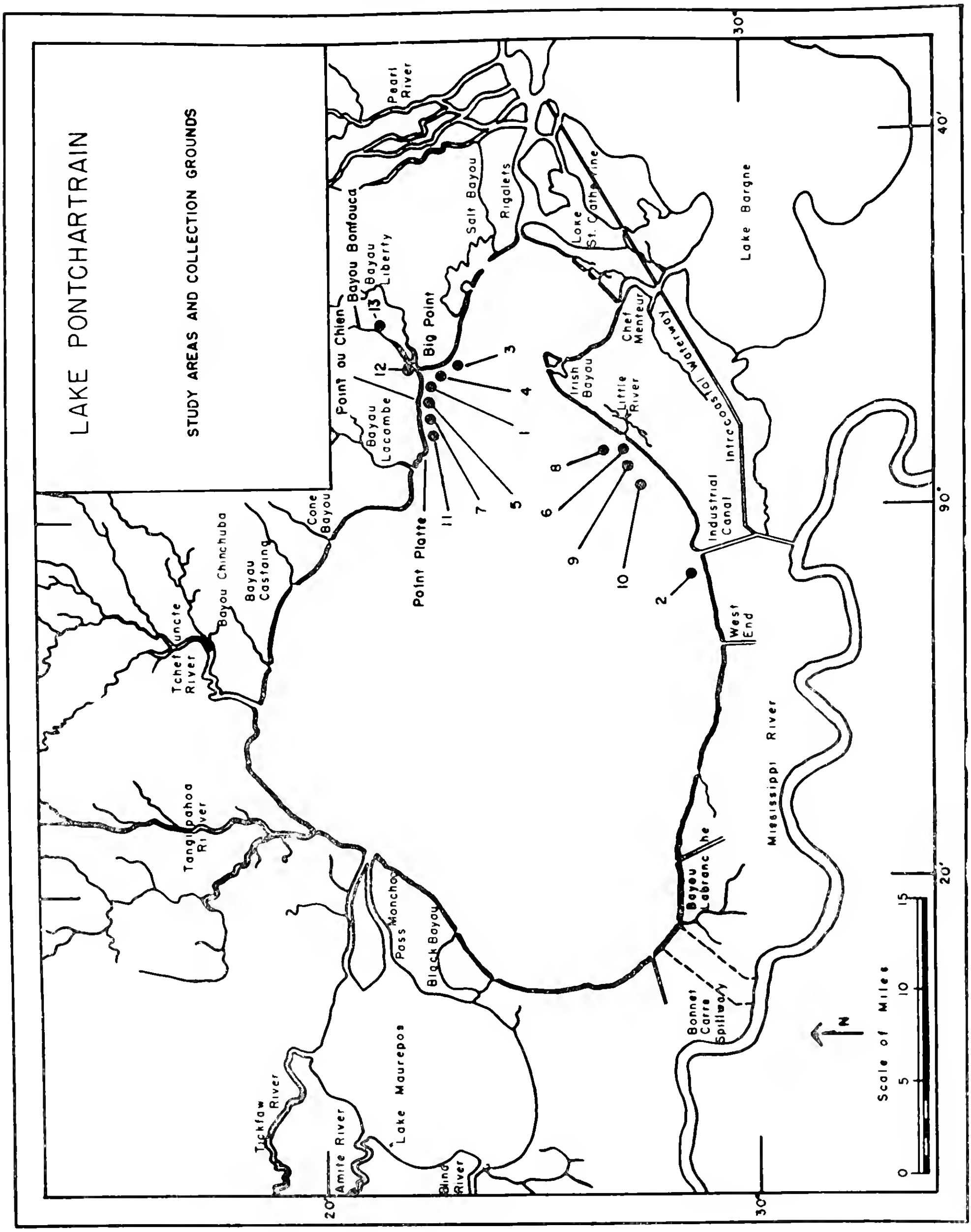


Figure 1. The study areas in Lake Pontchartrain.

were described by Suttkus, Darnell and Darnell (1953-54). Because of potentially variable and heterogeneous conditions in Gulf coast brackish water environments (Ladd, 1951: 135; Gunter, 1952: 138; Gunter and Shell, 1958: 19-28) and a possible wide range of tolerance of *Rangia* to changing conditions, two areas were selected that were expected to be different throughout any one year. Consistent or conclusive biological differences found between two parts of the population were considered likely attributable to certain local and consistent differences in environment.

One of the two areas chosen extends along the northeast shore of the lake from Point

Platte eastward to Big Point (fig. 1) including the mouth of Bayou Bonfouca, a distance of approximately 3.5 nautical miles. Bayou Bonfouca is navigable to small industrial barges up to Slidell, Louisiana and a permanently marked channel from deeper water in the lake is kept open to the mouth of the bayou. The other area extends along the southeast shore of the lake from the mouth of Little River westward to the lake-shore "camps" at the junction of Hayne Boulevard and Paris Road, a distance of about one nautical mile (fig. 1), (U. S. War Dept., 1936, 1939 maps, and U. S. Dept. Commerce, 1956 chart 1269).

For the most part the water and bottom samples were taken within an estimated one thousand yards offshore in these two areas. The area identified along the north shore will be referred to hereafter as the "north shore area" while "south shore area" will refer to the identified area along the southeast shore.

A broad band of marshland averaging about one and one-fourth miles in width extends landward from the north shore area which receives considerable drainage from Bayous Liberty and Bonfouca from the north and east and Bayou Lacombe from the north and west, as well as directly from the marsh itself. When the water level in the lake is high, the marsh is flooded by flow across low points along the shore. There may be a rapid reciprocal influx of water from the marshland into the lake when the latter is low. This is somewhat in contrast with the south shore area which receives only slight drainage in comparison, although likewise joined landward by natural marshland. The shore in this area is modified and interrupted by a railroad embankment extending along the shore several miles in both directions so that exchange between the lake and marsh is greatly limited or even prevented. The flow across the inlet of Little River has been confined to a shallow channel little more than three feet deep and about thirty feet wide. The direction of flow has depended chiefly on the level of the lake: landward when the lake is high and *vice versa* when the latter is low. Natural flow through this channel was terminated in the spring of 1958 by the installation of a control valve. Much of the south shore in other areas has been separated from the lake by a protective levee and communication with water outside the lake is controlled by valves, pumps, or locks.

In the north shore area the bottom consists of irregular reefs, flat or sloping alluvial deposits, and to some extent of a compact base of clay soil. The reefs, probably of quaternary origin, and alluvial deposits are composed of a mixture of sand, highly eroded shell, and copious proportions of dark mud apparently high in organic material (G. D. Harris, 1902; Steinmayer, 1939). The bottom is overlain by a thin cover of shifting sand generally less than half an inch thick. In the south shore area the bottom is typified by ridges approximately 30 to 40 feet wide and two to three feet high. These ridges are composed essentially of sand and shell, probably thrown up by wave action, and are situated more or less parallel to the shore. Depth appears to increase more rapidly with distance from the shore in the south shore area than in the north shore area. Few bottom samples were taken from a depth greater than eight feet in either area.

B. *Collection of Bottom Samples*

Field work was carried out between February 10, 1957 and September 15, 1958, except investigations done in 1960 and 1961 to be explained later. Trips to the north and south shores were made at least once monthly to one or both areas with the exceptions of March, May, and December of 1957 and August of 1958. More attention was given to the north shore area chiefly because the population in this area seemed likely to yield more information concerning the general biology of the species.

A fourteen foot fishing skiff equipped with a small outboard motor, and an anchor, was used in transporting equipment and samples to and from the areas where collections were made. The benthic population of *Rangia* was sampled quantitatively and qualitatively as regularly as practicable to better estimate population densities of the various sizes and to collect material for observation of the gonadal condition. Seasonal information concerning changes in density of the smaller individuals together with the changes accompanying gametogenesis were expected to indicate the time and duration of spawning. Also, higher densities of similar size classes were expected to indicate the spawnings of previous seasons and permit an estimate of growth rate and age, at least for the younger clams. This essentially follows the method used by Coe (1947) on the Pismo clam. Many unsuccessful attempts were made to collect pelagic larvae. The early embryonic development to a veliger stage was, however, observed in the laboratory after artificial fertilization of eggs taken from mature females.

Water and air temperatures were recorded regularly in F. Water samples were taken as regularly as possible and later analyzed in the laboratory for salinity, total phosphorus, organic matter, and phytoplankton pigment. These particular environmental measurements were made with the hope of contributing to a more precise description of the habitat of *Rangia* and to ascertain if these factors or combinations of them were limiting or conducive to biological productivity. The organic matter and phytoplankton pigment determinations were carried out to give a rough estimate of available food and the effect of seasonal change on available food. Field notes were kept concerning the weather, water level in the lake, air and water temperatures, approximate location and depth from which bottom samples were taken, type of dredge used, locations from which water samples were taken, observations concerning the behavior of animals, and quantity of water used in sampling for larvae.

Quantitative samples.—Two Ekman dredges, six and nine inches in size, were used in collecting quantitative bottom samples. For convenience in handling when loaded, the nine inch dredge was suspended by a small plastic coated steel cable and was lowered and raised by a portable hand-operated hoist for small boats, similar to that described by Welch (1948: 179). From six to twenty samples were taken on each collecting trip. Difficulty was sometimes experienced in obtaining large numbers of samples because of rough water, inefficient anchoring, the rather slow procedure in operating the hoist, and tripping and setting the nine-inch dredge. Since few samples were taken from depths greater than eight feet, and the majority were taken from depths of three to six feet, depth was not consistently recorded. In most situations the nine inch dredge proved to be more effective because of its deeper "bite". In bottom predominantly of shell or submerged vegetation neither dredge could pick up samples because of incomplete closure of the jaws. A bottom of shell and sand was troublesome only occasionally. Fortunately there were few places within the two areas that were difficult to sample. However, the quantitative samples are somewhat biased. In case of incomplete closure of the jaws the sample was discarded and another taken at a new location. Thus difficult areas were avoided. Each sample was dumped from the dredge onto several thicknesses of newspaper in the bottom of the boat.

The samples were allowed to remain in storage in freely circulating air until thoroughly dry, a period of three to five weeks. At the end of this time the samples frequently were found congealed into a single mass depending upon the proportion of sand to organic matter in the sample. For analysis, each dry sample was removed from the paper, pulversized by hand and passed through a screen having meshes one millimeter in diameter. The fine material passing through the screen was collected, poured into a gallon-size glass jar and thoroughly homogenized by mixing with a paddle or shaking and turning. It was then measured volumetrically in a 500 cc graduate cylinder and the total volume recorded on an analysis sheet together with the number, date and location of the collection and individual sample. From 50 to 300 cc, depending on the total screened volume, were poured in single portions of 10 cc each into a shallow flat-bottomed petri dish. The petri dish was shaken and rotated to spread the fine material out uniformly to a depth of about one to two mm. The shaking and rotating action rapidly worked the lighter dried whole or half shells of young clams to the surface of the material. At the surface of the sand the clam shells could be noticed and identified easily under the low power of a stereoscopic microscope and often without the aid of a microscope if a bright light was used and the correct angle of reflection was caught by the eye, depending for contrast upon the color of the background material. The probability existed that certain shells may have represented clams dead at the time of collection and these were not counted if possible. Only intact, (*i. e.* whole shells, having the valves tightly closed but with tiny particles of sand stuck to the ventral edges) were counted. The sticky material indicated dried body fluid from the dying clam after being out of water (death after collection). The ventral edge of the shell (opposite the hinge) is the natural course for escaping fluids from dying clams undergoing cytolysis. Half shells soiled on the inside, indicating death before collection, had no sand particles clinging to the ventral edges. Half shells or gaping shells were not counted and were actually quite rare. All the small shells from each 10 cc portion, some as small as 0.35 mm, were identified and counted, using the 2X objective (20 diameters), and measured by an ocular micrometer. The greatest length, (*i. e.*, anterior to posterior), was used in all size measurements of *Rangia* in this study. The number of 100 cc portions from each sample was not consistent but depended on the size of the screen sample and number of small clams (shells) found. The total volume actually inspected was recorded and the ratio of volume inspected to the total volume of screened sample was used to obtain the density estimate per area sampled by the dredge. A sample analysis sheet with a list of possible sizes was used; tally marks were made adjacent to the appropriate size thus automatically dividing the shells into size classes. Both measurement and counting were aided by first removing all the tiny shells with a moistened camel's hair brush from the surface of the sand to a small watch glass that was then placed on a black background. This was also helpful in distinguishing *Rangia* from other small shells such as that of *Polymesoda*, whose shell has distinct concentric rings about the protoconch and an external ligament, and *Macoma* which is thin and elongate. The shape and proportions of specimens of *Rangia* smaller than 4 mm are not greatly different from the adult; also the ligament is internal.

The material retained by the screen, eroded shell, compact chunks of mud and bits of partly decayed vegetation, together with intact shells, was spread out on a white enameled tray and placed under sufficient light for the detection of small clam shells about one mm and larger. All intact shells (valves closed tightly and with sand stuck tightly to the ventral edges, particularly the siphonal ends) were removed and measured by laying them on a millimeter rule. The size and count were tallied on the sample analysis sheet.

Some small shells may have been overlooked by being embedded in chunks of compact dried mud; although small *Rangia* are generally confined to the thin layer of surface sand covering the bottom. The incidence of small *Rangia* in dried portions of mud was investigated by breaking many small and large portions in the samples under analysis. Only in one set of samples, having what appeared to be a considerable proportion of dried colloidal material, were small shells found embedded.

Size classes of three different intervals, increasing with size of the clams, were assigned to better differentiate the smaller sizes in which density was particularly high. For convenience in grouping from the recorded measurements the class intervals were limited fractionally. Sizes up to 1.75 mm were placed in classes with an interval of 0.25 mm. Sizes between 1.75 mm and 14.75 mm were classed in intervals of 1.0 mm. Sizes about 14.75 mm were classed in 2.0 mm intervals. Population density for each size class was converted from density per sampled area (depending on the size dredged used) to density per square foot by multiplying by the reciprocal of the ratio, square inches taken by the sampler to the number of square inches in a square foot. For each group of samples collected on any one date the mean density was calculated for each size class represented, giving the estimated density by size classes. The results were plotted on a histogram with density expressed logarithmically to differentiate small densities and to partly offset seasonal increases of high densities.

Qualitative Samples.—A long-handled rake-type dredge with a wire retaining-basket with meshes approximately 3 mm square was used for collecting living specimens to be inspected in the laboratory. The dredge was equipped with a thin sharp-edged steel plate for cutting into the bottom. However, because of the light weight of the dredge, the writer had to wade out into the water and exert a fair amount of pressure downward on the handle to obtain a section of bottom without disturbing the natural position of the clams. *Rangia* were not found to burrow deeply. Specimens were also collected directly by hand since their siphonal ends can be felt easily when the hand is passed lightly over the surface of the bottom. The clams were taken to the laboratory in a bucket of environmental water and opened the following day for inspection of the gonads. The anterior and posterior adductor muscles were cut separately by inserting a knife blade between the valves at the anterior and posterior ventral edges respectively and cutting toward the muscle. The mantle was pulled away from the right valve and the latter was removed. An incision was made with a razor blade in the right wall of the visceral mass thus laying open the gonad. A few drops of fluid were withdrawn from the incision and one drop was placed on a slide for microscopic observation at a magnification of 430X. The sex of each animal was determined and recorded only when mature gametes were present. Also, the presence of parasites and the color of the gonadal tissue of each animal were noted and recorded. Early in the period of the investigation, slides were made of the fixed and sectioned gonadal tissue of clams whose sex had been determined by inspection of gonadal fluid to establish the presence or absence of gametes. The slides satisfactorily confirmed this method of sex identification although the gonadal condition as revealed by the sections of clams at that particular time of the year could not be expected to be the same at other times of the year.

C. *Analysis of Lines of Growth Interruption*

Although the lines of growth interruption, or "growth lines", have been used to determine or indicate age, the method cannot be relied upon to determine conclusively the age of an individual, particularly in southern latitudes (*cf.*, Coe, 1947: 9-13; Haskin, 1954). The record of past winters may be observed easily as narrow indented bands located in concentric rings on the shell. These bands apparently occur when seasonal low temperatures bring about near complete cessation of growth. The greatest objection to using these rings or bands for estimation of age is that factors other than cold temperatures may cause growth interruptions. Local disturbances such as storms, heavy sedimentation, or seasonal high concentrations of plankton may cause withdrawal of siphons and mantle and cessation of pumping, feeding, and growth. Consequent differences in size for any one age might result. Notwithstanding, 40 right valve specimens of *Rangia* from each study area were analyzed for frequency of growth interruption lines. Since the temperature in Lake Pontchartrain during the winter recedes in reasonably close conformity with the air temperature (U. S. Weather Bureau, New Orleans Station, 1956-58) a somewhat consistent pattern of lines, or growth bands between the lines of growth interruption, might be expected, on the average, to occur in the shells of *Rangia*. At least three lines of growth interruption are consistently situated on the shell of *Rangia*: these are the three smallest and proximal to the umbone. The first is generally obliterated by erosion on older, *i.e.* larger specimens, since it is so closely associated with the umbone, the oldest part of the shell. In smaller and younger shell, nevertheless, the first line is quite distinct. The greatest diameter (corresponding to original length at the time of the formation) of each easily observable line of growth interruption on each shell was measured, including lines out to the periphery. These were recorded together with the length of the shell. The percent frequency distribution of the different sizes of growth interruption line diameters was plotted giving a polymodal curve facilitating the analysis.

D. *Plankton Analysis*

A Wisconsin plankton net was used in sampling for the pelagic larvae. Generally about forty liters of lake water were sampled. No particular station within either area was chosen for sampling. However, most samples were taken in the local area where bottom samples were also obtained. Since most depths concerned in the investigation were less than eight feet the water samples were taken consistently from two feet beneath the surface. On several occasions the net was towed at the surface behind the boat at a standard rate of speed for a standard time. The plankton concentrates were preserved in about 10 per cent formalin and analyzed three weeks to three months later. The method of analysis used was essentially that described by Welch (1948: 279-283) using a Sedgewick-Rafter counting cell and Whipple micrometer.

E. *Observation of Early Embryonic Development*

In October and November, 1957 adult clams bearing mature gametes were brought into the laboratory and specimens of eggs and active spermatozoa were isolated in separate containers of environmental water for 30 minutes, following the method of Awati and Rai (1931: 92-93), and then mixed. A small portion of the mixed fluid was placed in a watch glass where fertilization and early cleavages were observed at a magnification of 430X. The room temperature varied between 73° and 80° F. The times required for attainment of major developmental stages were recorded. Although many embryos developed abnormally, as Coe (1947) noted for other species, there were many individuals that appeared to be normal and the latter are reported.

F. *Salinity*

Owing to the shallowness of the study areas, which were relatively close to the shore, and subject to mixing by prevalent wind action, samples from the surface only were routinely analyzed for salinity. In February, 1957 several samples were taken in the south shore area from both the surface and the bottom in about 12 feet of water. The greatest difference found between surface and bottom was 0.5 ‰. The greatest difference between surface and bottom reported by Suttkus *et al.* was 0.3 ‰. Their samples on which bottom salinity determinations were made were taken from several stations in the eastern half of Lake Pontchartrain in February, 1954.

Glass-stoppered bottles (250 ml size) were used for collection, transport, and storage until the analyses could be made. The determinations were made by titration using silver nitrate (0.05 N solution periodically checked against a standard 0.08 N sodium chloride solution).

G. *Total Phosphorus*

That phosphorus concentration, particularly total phosphorus, is of primary importance in indicating fertility and productivity of natural waters appears to be universally recognized by both marine and freshwater biologists (*cf.*, Sverdrup *et al.*, 1942; Welch, 1952: 109; Ruttner, 1953: 79-81; Hutchinson, 1957: 727).

Water samples to be analyzed for total phosphorus were collected in four-liter size glass-stoppered carboys. Immediately after the samples were brought into the laboratory from the field each sample was thoroughly homogenized by stirring and inverting and one liter was poured into a liter-size tightly stoppered bottle for storage. To minimize loss of phosphates to bacteria that adhere to the inside of the storage bottle (Harvey, 1948: 357; Stephenson, 1949; 378-379), about 2 ml of an aluminum hydroxide precipitate solution was added to each sample before storage. The precipitate provided extensive surface area for the development of the bacteria (Harvey, 1948) so that in running the determinations the aliquot poured off for analysis from a thoroughly homogenized stored sample would contain a reasonably correct proportion of the original phosphorus, even though tied up in bacteria. The determinations were made after all samples had been collected for the period of the investigation. The method used was that of Hansen and Robinson (1953) employing perchloric acid oxidation of organic phosphorus to phosphates and is described concisely by these authors. The quantitative determination depends upon the formation of a blue color by the reaction of ammonium molybdate with phosphates in the presence of stannous ions. The blue color produced by the sample phosphates was compared with that of a standard by the use of a spectrophotometer (Coleman Jr. Model No. 6 A) at a wave length of 410 mu. Blank solutions of sodium chloride having the same chlorinity as the samples were treated throughout the oxidation process simultaneously with the samples; their readings were subtracted from the sample readings. In practice a curve was drawn on semilog paper from plotted readings, in percent transmission, corresponding to several dilutions of a standard made by using potassium dihydrogen phosphate and containing 0.0250 microgram atoms (μg at) phosphate phosphorus per ml. The sample concentration values were read directly from the curve. After some initial determinations were made, inconsistency of results made necessary the use of metallic tin freshly dissolved in 12 N hydrochloric acid in place of the reagent stannous chloride (dissolved in hydrochloric acid) as recommended by Hansen and Robinson. The difficulty apparently lay in the instability of the stannous chloride even though the solution was freshly made. Stannous chloride cannot be allowed to become oxidized to the stannic condition as it must act as a reductant (*cf.*, Deming, 1944: 681-682; Harvey, 1948: 356). The metallic tin (1.131 gm in 20 ml 12 N hydrochloric acid) was allowed to dissolve overnight and used only during the next day; before use it was diluted 1:24 with freshly boiled distilled water. This modification of the method gave consistent results.

H. *Phytoplankton Pigment*

A variety of methods has been used in determining the concentration of phytoplankton pigment for the purpose of measuring phytoplankton concentration in natural waters as well as for the study of the kind and proportional relationships of the different pigments. These pigments include chlorophyll and some yellow substances which seem to be the most important (*cf.,* Kozminski, 1938; Manning and Juday, 1941; Creitz and Richards, 1955; Korringa, 1956). Pigment concentration alone is not intended to be regarded as an index of productivity. According to Ruttner (1953: 144-145) cultures of algae have demonstrated that chlorophyll content, quantity of substance, and cell multiplication are to a certain extent independent of one another. The analysis used here was carried out in a manner similar to that of Korringa (1956: 310).

Water samples to be analyzed for phytoplankton pigment were collected in two four-liter size glass carboys. The samples were obtained with a four-liter Kemmerer sampler from two feet beneath the surface immediately before leaving the field. The pigment extraction was begun approximately two hours later after arriving in the laboratory. From two to eight liters were filtered by suction through Aloe filter paper (No. 42700) 9 cm in diameter. The same type filter paper was used throughout the period of investigation as a standard for seasonal and regional comparison. The number of liters filtered depended chiefly upon the concentration of material in the water as determined by the time required to filter a certain quantity, although, within limits the number of liters used was not important. The time required was later found to be directly proportional to the amount of pigment extracted. The filter paper containing the phytoplankton as well as various particles of detritus was folded several times and inserted into a 30 ml test tube. The tube and filter paper were placed in a boiling water bath for about one minute to destroy the chlorophyllase. Then 8-9 ml of methyl alcohol was added covering the folded filter paper; the tube was stoppered securely and placed in a covered container in absolute darkness for storage until the determinations could be made conveniently, from three weeks to six months later. For determination of the pigment the filter paper was removed carefully from each tube containing the extracted pigment in alcohol, the paper being pressed to the side of the tube to allow as much alcohol as possible to drain back. The extract was transferred to a 15 ml graduated tube and made up to 10 ml with additional methyl alcohol. The extracts were then centrifuged to settle the insoluble detritus and the supernatant carefully poured off into cuvettes for comparison with a standard using a spectrophotometer (Coleman Jr. Model 6 A) at 410 mu. The standard was prepared according to Korringa's method (1956: 310) using a solution of 25 mg potassium chromate and 430 mg nickel sulfate made up to one liter with distilled water. A curve was drawn through points established by readings in percent transmission corresponding to dilutions of the standard and the sample readings were converted to values of the corresponding concentration of the standard divided by the number of liters filtered.

I. *Organic Matter*

The method often employed in determinations of organic matter in natural waters has usually involved oxidation by potassium permanganate either under acid or alkaline conditions at 100° C for a stated arbitrary time. Oxalic acid is then added and the excess back-titrated with standard permanganate (American Public Health Association, 1936: 136-139; Hutchinson, 1957: 878-879). A modification is necessary, however, for samples of sea water (Atkins, 1923: 160-163; Korringa, 1956: 310). These methods give no direct measure of organic carbon since only partial oxidation occurs and this depends upon the state of oxidation of the matter in solution (*cf*., Ruttner, 1953: 84). The permanganate test has been used to estimate the biologically oxidizable organic matter, approximating the biochemical oxygen demand method (*cf*., Korringa, 1956: 310-311). According to Korringa (*loc. cit.*) the test is believed to give an estimate of the readily oxidizable organic matter that can be "mineralized by bacteria, or, without previous transformation, be used as food by filter feeders and the like". Ruttner (*loc. cit.*), in referring to the work of Birge and Juday, stated that "pure" lake waters contain considerable amounts of dissolved organic matter "exceeding by several times that in particulate form (which is chiefly plankton)".

The method used here was that of Korringa (*loc. cit.*). The water samples were collected in four-liter carboys immediately before leaving the field. Upon arrival in the laboratory the collections were thoroughly homogenized and samples were stored in liter-size bottles. One hundred mg of mercuric chloride was added to each storage bottle to preserve the organic matter until the determinations could be made (from one to fifteen months later).

III. ENVIRONMENTAL FACTORS

The dates and locations of collections of water and bottom samples are given in Table I together with the associated air and water temperatures, estimates of salinity, total phosphorus, phytoplankton pigment concentrations, and organic matter. The locations are represented by numbers, in parentheses, referring to points on the map of the study areas (fig. 1).

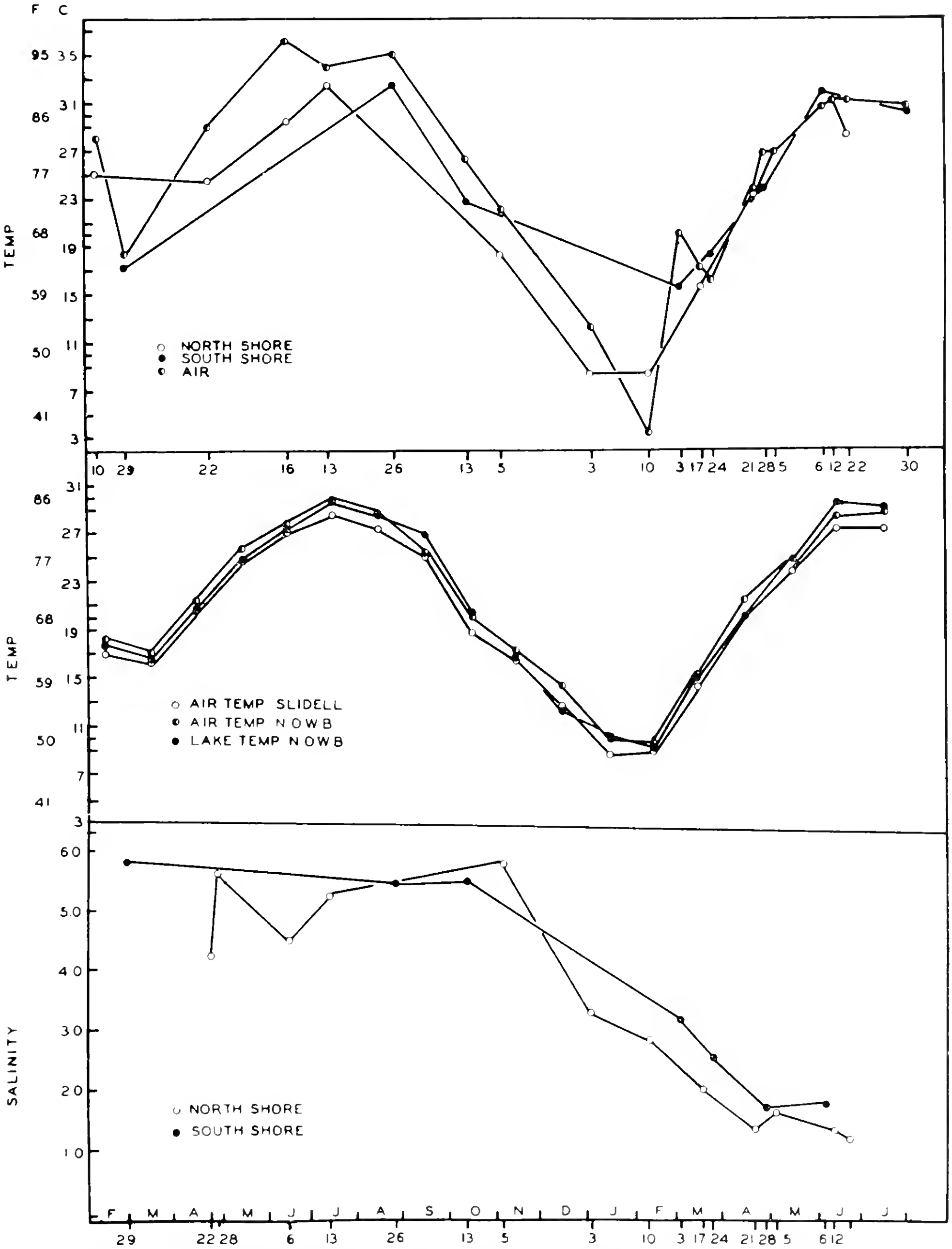
A. *Temperature*

The distributions of air and water temperatures on collection dates are plotted in Figure 2. Monthly mean air temperatures as recorded by the U. S. Weather Bureau at stations nearest the study areas and monthly mean lake temperatures, recorded by the New Orleans Weather Bureau, are plotted in Figure 3. The influence of air temperature upon the lake is readily apparent. The range in monthly mean lake temperatures for the period of the investigation was 48.2° - 85.1° F while the ranges of monthly mean air temperatures were 47.3° - 83.1° for the north shore area (Slidell station) and 48.9° - 85.2° for the south shore area (NO WB station). The lake obviously has a low heat budget. This is understandable in con-

TABLE 1.

Physical and biological estimates at times and locations of collections.
(Bottom locations represented only in part).

Date	Location (nos. in parenthesis refer to fig. 1)	Bottom Sample Locations	Temp. °F air	water	Salinity o oo	P µg at ml	Phyto-plankton Pigment Index	Organic Matter (mg. KMn04/L)
1957								
10 Feb.	NS (1)		82	77				
29 Feb.	SS (2)		65	62	5.77			
22 April	NS (3)		84	76	4.20	.0064		22.9
	(1)					.0078	.105	23.7
28 April	NS (3)				5.59		.075	23.3
	(1)				4.55	.0058	.071	
	(12)					.0062	.121	24.4
16 June	NS (4)	X	97	85	4.43	.0084	.011	23.7
	(3)				4.44			
	(12)					.0091		26.9
13 July	NS (5)	X	93	90	5.20	.0103	.236	22.6
26 Aug.	SS (6)	X	95	90	4.72	.0088		
	(9)				4.99			
	(10)				5.07		.065	21.9
13 Oct.	SS (6)	X	79	73	5.45	.0079	.209	20.8
5 Nov.	NS (11)(7)	X	72	65	5.63	.0105	.198	20.8
	(1)				5.56		.257	
1958								
3 Jan.	NS (11)(7)	X	51	47	3.29	.0077		23.7
	(1)				3.19	.0064	.200	25.8
10 Feb.	NS (11)(7)	X	38	47	2.82	.0053	.072	24.1
3 Mar.	SS (8)	X	68	60	3.16	.0065	.227	23.3
17 Mar.	NS (1)					.0091	.183	29.4
	(3)		63	60	2.01			
	(12)				1.60			
24 Mar.	SS (8)		61	65				
	(9)				2.52			
21 April	NS (1)	X	75	71	1.34	.0100	.485	26.5
	(12)				0.78	.0113		
	(13)				0.09			
28 April	SS (8)		80	75				
	(6)				1.69	.0037	.385	24.8
5 May	NS (11)(7)	X	80	80	1.47	.0060	.544	24.1
	(12)				1.62	.0045		25.8
6 June	SS (6)		87	89	1.77	.0035	.160	23.7
12 June	NS (1)		88	88	1.33	.0045	.112	23.7
23 June	NS (7)	X	88	83	1.18	.0035	.268	23.7
	(1)						1.207	
0 July	SS (6)	X	87	86	0.33		.763	



Figures 2-4. **2.** (Top) Distributions of air and water temperatures at times of collection; F = °F., C = °C. **3.** (Middle) Distributions of monthly mean air and lake temperatures computed from temperatures recorded by the U. S. Weather Bureau; N.O.W.B. = New Orleans City Weather Bureau station. **4.** (Bottom) Distributions of salinity (‰) at times of collection from within the lake only.

sideration of its mean depth of about 14 feet. The range of lake temperatures recorded on collection dates (Table 1), 47°-90 F, represents extremes probably due to the relative shallowness of the areas and again reflects the immediate influence of air temperature.

B. *Salinity*

The distributions of salinity (fig. 4) within the lake itself (salinities in Bayou Bonfouca are not plotted) show a consistent decline between November 5, 1957 and April 21, 1958. A combination of several possible factors may be responsible for this. Precipitation in watershed areas that drain into the lake, mean tide level, and wind direction seem to be most important in determining salinity. Unpublished data recorded by The Corps of Engineers, U. S. Army, (New Orleans District) including total inflow to the lake based on combined monthly runoff in acre feet for the period, 1946 through 1956; chlorides (1946 through 1958), and mean monthly lake level (1940 through 1957) show annual cycles with peak chlorides occurring consistently in the fall and lows in early summer. The annual chloride peaks steadily increased, converted to terms of salinity, from 2.56 ‰ in 1949 to 9.78 ‰ in 1954. The greatest variation within any one year occurred in 1954 following a period of considerable runoff in December and January when the low in February was 1.47 ‰ and the high in October was 9.78 ‰ succeeding and accompanied by the lowest annual runoff of any year recorded in the data. The salinity lows succeeded periods of heavy runoff with a lag of about one month. As runoff is in the increasing phase, generally during the first few months of the year, salinity apparently decreases until mid-summer when the situation is reversed. Following the peak salinity in 1954 the yearly peaks decreased to 1958. The second highest peak was in November, 1956. The mean for August, 1957 was 4.63 ‰, and 1.20 ‰ for July, 1958 illustrating a stepwise decline from the peak in November, 1956.

The data indicate that monthly mean lake level is not primarily influenced by runoff. Annual peaks in mean lake level consistently occur in the fall, matching if not slightly preceding peaks of salinity concentration. One factor seemingly responsible for this is tidal influence. Annual tidal peaks occur in the fall (U. S. Coast and Geodetic Survey, Tide Tables, 1957, 1958; Marmer, 1954: 115). Predicted monthly mean tide levels for Long Point in Lake Borgne are plotted in Figure 5. The average of the monthly means for February through July of 1957, 0.47 ft., is considerably higher than the average for the comparable period in 1958, 0.11 ft. Mean lake level was higher in September of 1957 than it had been since October of 1949. This suggests that mean tide level increased as did peak chlorides following 1949.

Variations in lake levels in relation to velocities and directions of winds associated with highs and lows (below and above mean sea level) for the period 1932 to 1947 inclusive also have been recorded for the south shore area of the lake by the Corps of Engineers. A cursory inspection of these data reveals that winds are of primary importance in determining temporary levels of a few days duration or perhaps longer. Average wind velocities and directions are recorded for only 24 hour periods preceding extreme fluctuations. Highs approaching three feet or more above mean sea level more often occur in the spring and fall (April, May, September, and October) with the peaks succeeding 24 hour periods of east wind variable by north or south having average velocities of 9 to 15 miles per hour. The peaks occurring in the fall are generally superimposed upon a rise of nearly one foot above mean sea level. The duration of the rise appears to be about three months, although this is highly variable. Mean tide level at this time of the year probably supports the rise. Lows approaching one foot below mean sea level are rare, occurring occasionally in December, January, March, and July. They succeed 24 hour periods of west wind variable by north or south having average velocities of 11 to 14 miles per hour. The data indicate a mean lake level somewhat above that of mean sea level which is not surprising in view of the large runoff areas draining into Lake Pontchartrain.

Salinity in the north shore area (fig. 4) was slightly lower and more variable than in the south shore area. In April, May, and June in the north shore area apparently this was more variable than at any other time during the entire period. The proximity of bayous draining into the area more heavily at this time of the year is probably responsible. However, currents from the Rigolets Pass, influenced by the Pearl River drainage, may have had some influence.

C. *Total Phosphorus*

All of the total phosphorus values are given in Table 1 while values for samples taken only from the lake itself are plotted in Figure 6. The lowest of these values, 0.0035 μg at/ml, is higher than values reported by Harvey (1955: 8) for the north Atlantic below 600 M, 0.0013 μg at/ml (phosphorus as inorganic phosphate in solution), or below 150 M in the Antarctic, 0.0029 μg at/ml. Total phosphorus values under the same conditions would have been higher. Concentrations of total phosphorus reported by Korringa (1956: 311-313, 340-343) for coastal and estuarine areas along the southeast coast of Africa ranged from 0.00025 to 0.00141 μg at/ml. The higher value represented a sample from a bay entrance. An average total phosphorus value for western Lake Erie reported by Curl (1959: 68) was 93.0 μg/L (0.0030 μg at/ml). The values reported by Curl were positively and significantly correlated with turbidity originating in tributary streams of western Lake Erie. Hutchinson (1957: 728, 729) stated that total phosphorus varies greatly in lake waters, up to 78 g/M^3 (2.51 μg at/ml), or as much as 208 g/M^3 in saline lakes in closed basins. He quoted a mean value of 77 mg/M^3 (0.00248 μg at/ml) soluble phosphate phosphorus for lakes of Baltic Germany and stated that there was a clear tendency for the waters of brown lakes rich in peaty material to contain more phosphate than the clear-water lakes. The maximum value for these lakes was 600 mg/M^3 (0.019 μg at/ml).

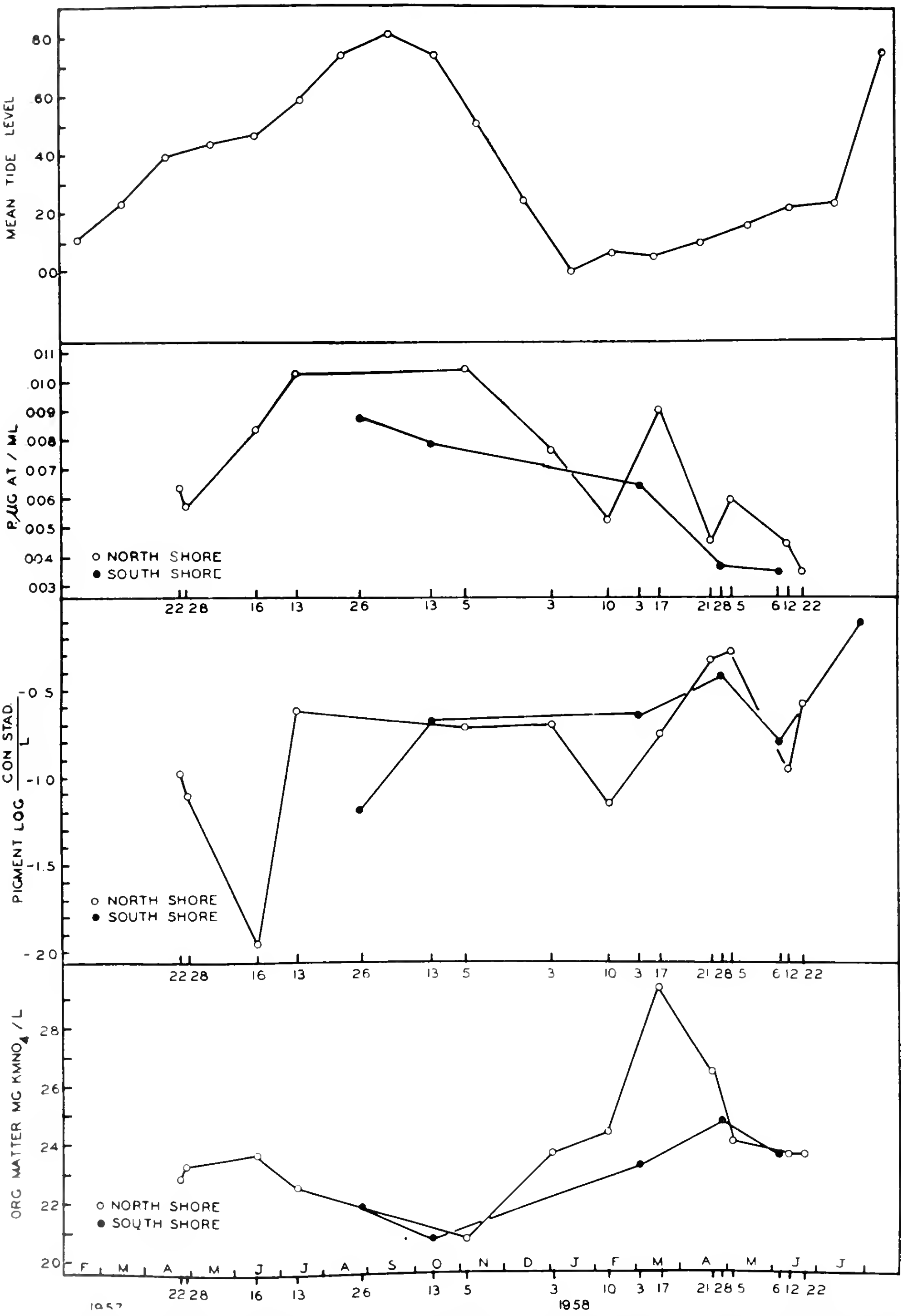
If brownish coloration in the waters of bayous flowing into Lake Pontchartrain has any positive correlation with total phosphorus then the concentration of this element must be relatively high at times. The highest values obtained (Table 1) were from samples taken near the mouth of Bayou Bonfouca and within the bayou. However, the lake values show seasonal lows during the early summer months (fig. 6), probably resulting from dilution with the high runoff occurring at this time of the year. In general the pattern seems to follow that of salinity (fig. 4). That the south shore values are lower than those for the north shore area is remarkable and may indicate that the lake is dependent upon its tributary streams (chiefly along the north and west shores) for phosphorus, although at times and in different areas it may be diluted by high influx of fresh water. The values for the south shore area were less variable than those for the north shore area. In view of the phosphorus concentrations reported for either the ocean or some freshwater lakes by the authors mentioned above, none of the values reported here can be regarded as an indication that phosphorus concentration in Lake Pontchartrain limits biological productivity.

D. *Phytoplankton Pigment*

All the values for phytoplankton pigment concentration are listed in Table 1 and only values for samples from the lake itself or parts of the areas farthest out into the lake away from the inlets are plotted in Figure 7. In general the production of phytoplankton may be inferred as having been greater in the spring and summer of 1958 than during the previous season in 1957. Decreasing salinity with the parallel seasonal influx of freshwater may have had some bearing on an increase in phytoplankton. Major increases in production during June and July of both years may have occurred as indicated, thus accompanying or immediately succeeding the period of high runoff. Suttkus, *et al.* (1953-54: 28-30) stated that "thick scums" of the alga *Anabaena* sp. were observed during late summer and early fall with the heaviest blooms occurring in the western half of the lake. *Anabaena* was referred to as one of the freshwater genera of the lake. Variability in concentration may have been no greater in one study area than the other (fig. 7) but the high value for the north shore area on June 22, 1958 from a sample at the mouth of Bayou Bonfouca and the relatively low value on the same date from a sample taken about two miles west of the mouth seem to indicate a greater variability for the north shore. Greater variability could be expected here if chiefly freshwater species of phytoplankton are involved.

E. *Organic Matter*

The estimates of oxidizable organic matter are listed in Table 1 and the lake values represented by samples taken farthest from inlets on collection dates are plotted in Figure 8. The latter figure shows summer highs for



Figures 5-8. **5.** (Top) Distributions of predicted monthly mean tide levels (1957-1958) for Long Point, Lake Borgne (in feet above mean low water). **6.** (Second) Distributions of estimates of total phosphorus from within the lake only. **7.** (Third) Distributions of phytoplankton pigment concentration from within the lake only. **8.** (Bottom) Distributions of organic matter from within the lake only.

both years with the highest values representing the spring and early summer of 1958. These high values do not seem to be necessarily dependent upon phytoplankton since the north shore peak values in 1958 slightly preceded peak pigment values for that year. The south shore peak values did, however, coincide. Concentration of organic matter reasonably could be expected to depend partly on phytoplankton. Perhaps a reasonable assumption concerning the origin of spring and summer highs is that they are more directly dependent upon allochthonus material carried in by yearly high runoff which precedes or coincides with high content of organic matter.

Estimates reported by Korringa (1956: 311-313, 340-343) for estuarine areas along the African shores of the Indian Ocean ranged from 6.5 to 70.4 mg potassium permanganate per liter (with the same method of analysis used in this investigation). Generally for areas having salinities of 33.0 0/00 or greater the estimates of organic matter were below 12.0 mg. The three highest values reported by Korringa were 31.8 mg representing an up-river sample (1.0 0/00 salinity) from "clear brown water", 50.6 mg and 70.4 mg representing samples from two different landlocked bodies of water with salinities of 1.0 0/00 and 17.0 0/00 respectively. In comparison to the majority of Korringa's estimates, the estimates for Lake Pontchartrain are high.

As far as the north shore area of the lake is concerned, high concentration of organic matter might be expected in view of the proximity of inlets from the marshland where organic matter, both in particulate form and in solution, must be high. The brownish coloration of bayou waters is undoubtedly associated with organic matter in one form or another.

IV. THE POPULATION STRUCTURE

In collecting qualitative bottom samples during the investigation several differences between the clams of the two areas soon became apparent.

A. *Size and Abundance*

Clams were found much more easily in the north shore area than in the south shore area. Near the mouth of Bayou Bonfouca as many as 100 could be dredged or picked up by hand in 30 minutes, whereas near the mouth of Little River dredging 60 clams might have required as much as three hours or more. Specimens from the north shore area were always conspicuously smaller than those from the south shore.

B. *Color*

The periostracum of the north shore clams was generally charcoal or black in those near the bayou but lighter turning to chestnut brown streaked with green and black in specimens collected between Point Platte and Point au Chien west of the bayou. The gills of the dark specimens were often streaked dorso-ventrally with a deep-lying grayish substance. Streaking of the gills in chestnut colored specimens was rusty red. *Rangia* from the south shore area were of a chestnut brown to greenish yellow color with red streaking of the gills.

C. *Shell Erosion*

The umbones of the north shore specimens were conspicuously more eroded than those of the south shore. Erosion of the shell and black appearance of the periostracum may be due to high concentration of organic matter in the bottom sediments with consequent bacterial liberation of carbon dioxide, and immediate formation of carbonic acid responsible for erosion, although many other sources may contribute toward acidity in an environment such as that of the north shore (*cf.*, Welch, 1952: 102, 118-119). A high residue of carbonaceous breakdown products of decay could be responsible for the black shell. The concentration of dead and decaying plant material, apparently in great part from the adjacent marsh areas along the north shore, is observable as black mud and gross particulate plant material mixed with sand in the bottom deposits, and as smaller black particulate plant matter in suspension in the water of the Bayou Bonfouca region and near Bayou Lacombe. Since the erosion is confined to the umbonal and anterior regions of the shell, acid formation could take place beneath the surface of the bottom and reach a considerable concentration before being removed by agitation of the water or by chemical combination.

D. *Movement and Behavior*

The apparent natural position of adult *Rangia* on the bottom is with the anterior end pointing directly downward, the siphonal end vertical with its tip just above the surface so that the umbones, lunule, and greater part of the shell are completely buried. *Rangia* in aquaria with sand bottoms apparently move about rarely. Among several specimens kept for nearly a year in the laboratory the only movements observed were those for the ostensible purpose of burying themselves in the sand, movement of the shells allowing protrusion and withdrawal of the siphons, movement associated with pumping and pressure ejection of feces and pseudofeces from the mantle cavity, and movement toward the surface after being covered by the addition of sand to the aquaria. Many specimens collected from the lake had living barnacles and mussels as well as growths of algae adhering to different parts of the shell, chiefly on the siphonal end in which cases the lake bottom surface lines were obvious, indicating that the clams remain stationary for long periods. Also, such attached organisms have been found on the umbonal and anterior regions of the shell, particularly on those individuals from sand and shell bottoms in which "digging-in" may have been difficult. Frequently individuals of *Rangia* are found in groups of about 3-7, often with no more than a few inches of space between any two individuals. The clams within large groups, however, may be spread out more with perhaps 8-12 inches separating them. A more general aggregation of animals seems to occur with clumped areas of many small groups and relatively few isolated individuals. This was evident in parts of both study areas, but more obvious in the south shore area where some time was spent occasionally searching for places that would yield more clams per dredge haul in qualitative sampling.

E. *Sizes of Adults*

The distributions of sizes (antero-posterior shell lengths) of clams collected from the two study areas for gonadal analysis are shown in Figure 9. Since no clams below size class 25 (23.75 mm) were found whose gonads contained recognizable gametes, sizes larger than this were considered as representing potentially sexually mature adults. The distribution for the north shore area represents 651 right valve measurements with a mean length of 38.5 mm. The distribution for the south shore area represents 427 right valve measurements having a mean length of 42.4 mm. The individuals represented here were collected throughout the period of the investigation. From the appearance of the distributions the difference in mean length may be considered significant. The differences in shape and proportions of the distributions seem conclusive without the application of a statistical test.

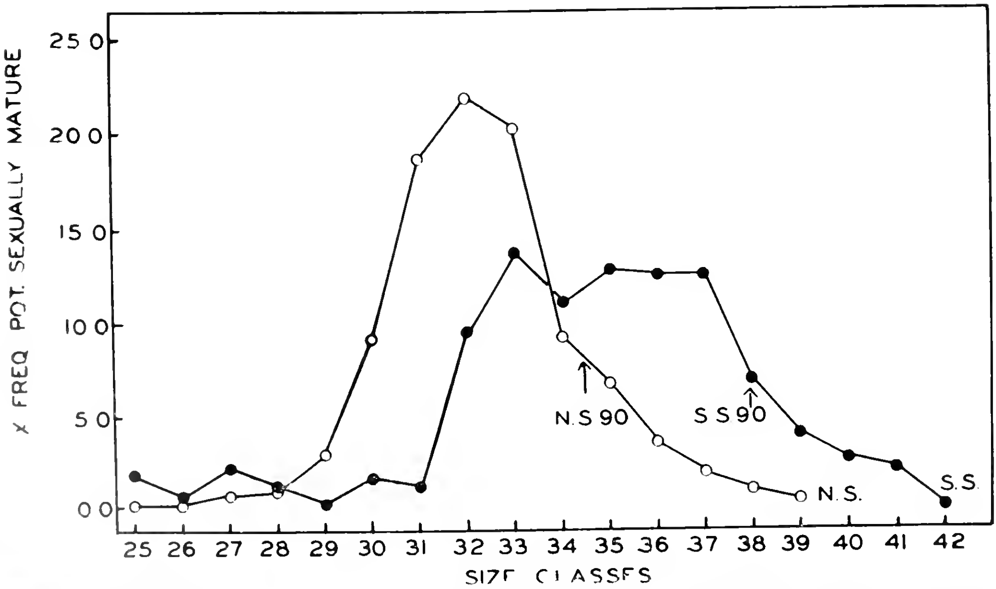


Figure 9. Distributions of size classes of adult clams; Pot.=potentially sexually mature adults, NS 90=90th percentile of the north shore distribution, SS 90=90th percentile of the south shore distribution (see Table 2 for actual sizes represented by size classes).

In regard to mean size and proportions of sizes, the adult population is different in one study area from the other.

F. *Relation of Shell Length to Shell Weight*

To determine whether or not differences existed in shell weight of the clams from the two areas the right valves of specimens collected from the north shore area on May 5, 1958 and from the south shore area on July 30, 1958 were cleaned and allowed to dry thoroughly and then weighed and measured. The north shore area was represented by 230 specimens and the south shore area by 216. The ratio of length to weight (L W) for each shell was computed and the values grouped in classes according to shell size, with 2 mm intervals for each class. The mean ratio value for each class was computed and the means were plotted against size (fig. 10). From one to 56 specimens are represented for each size class from either of the two areas. The smaller numbers are represented only at the ends of the distributions.

The differences between mean ratio values of north and south shore clams for some of the matching size classes were tested for significance by application of the *t-test*. The associated probabilities are listed opposite the size classes tested. The differences in intra-class means are conclusive up to 39 and 40 mm (size class 33) at the 0.01 level. Beyond this size where the differences are reversed with the north shore clams having higher ratio values, only the ratio difference for clams of 45 and 46 mm (size class 36) is conclusive (0.02 level). The reversal can be regarded as conclusive. The irregularity occurring in the distribution of the north shore ratios affects clams well above the average size for that area. Where size is constant a lower ratio value indicates greater weight in proportion to length. Evidently with increasing size the more horizontal deflection of the curve indicates a greater increment in shell length in proportion to increment in shell weight.

G. *Population Density, Growth, and Survival*

The size classes referred to concerning the data that follow are listed together with their intervals and mid-points in millimeters in Table 2. The estimates of population density of the different sizes of *Rangia* for each collection date are represented in Figure 11 (a-m). The densities of size classes 1-16

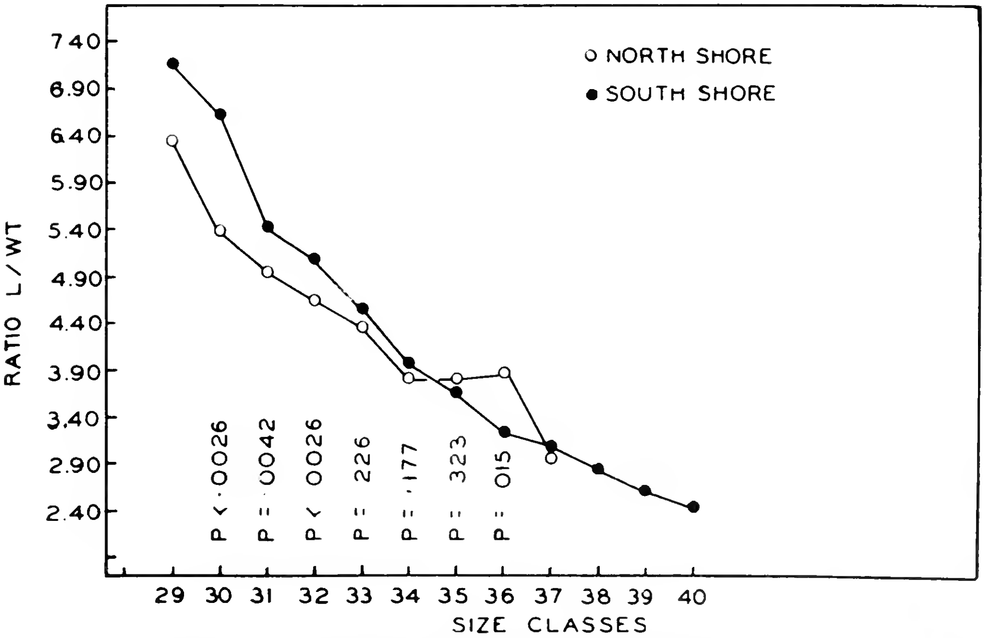


Figure 10. Distributions of length-weight relationship according to size class; P = probabilities derived from tests concerning the differences between the two mean ratio values for size classes indicated (see Table 2 for actual sizes represented by classes).

TABLE 2.
Size classes with intervals and mid-points in millimeters.

Size Class	Interval	Mid-point
1	00.00-00.25	00.125
2	00.25-00.50	00.375
3	00.50-00.75	00.625
4	00.75-01.00	00.875
5	01.00-01.25	01.125
6	01.25-01.50	01.375
7	01.50-01.75	01.625
8	01.75-02.75	02.250
9	02.75-03.75	03.250
10	03.75-04.75	04.250
11	04.75-05.75	05.250
12	05.75-06.75	06.250
13	06.75-07.75	07.250
14	07.75-08.75	08.250
15	08.75-09.75	09.250
16	09.75-10.75	10.250
17	10.75-11.75	11.250
18	11.75-12.75	12.250
19	12.75-13.75	13.250
20	13.75-14.75	14.250
21	14.75-16.75	15.750
22	16.75-18.75	17.750
23	18.75-20.75	19.750
24	20.75-22.75	21.750
25	22.75-24.75	23.750
26	24.75-26.75	25.750
27	26.75-28.75	27.750
28	28.75-30.75	29.750
29	30.75-32.75	31.750
30	32.75-34.75	33.750
31	34.75-36.75	35.750
32	36.75-38.75	37.750
33	38.75-40.75	39.750
34	40.75-42.75	41.750
35	42.75-44.75	43.750
36	44.75-46.75	45.750
37	46.75-48.75	47.750
38	48.75-50.75	49.750
39	50.75-52.75	51.750
40	52.75-54.75	53.750
41	54.75-56.75	55.750
42	56.75-58.75	57.750
43	58.75-60.75	59.750

represented in Figure 11 and other figures based on the same data may be overestimated to some extent because of the inadvertent inclusion of an undescribed species of *Rangia* (*Rangianella*) unknown to the investigator during 1957 and 1958. Investigations pertinent to this species were made in 1960 and 1961 and are reported later in this paper. Density estimates for some of the associated mollusks are given in Figure 12 (a-o). Counts of the latter were not made for every collection.

The mean densities for each size class representing the entire investigational period are plotted in Figure 13. To elucidate the spawning period the seasonal densities of the three smallest size classes are replotted in Figures 14 and 15 for the north shore and south shore areas respectively.

The data represented in Figures 11, 14 and 15 indicate that spawning may occur almost continuously beginning sometime in the summer or fall and continuing through the winter and spring into early summer. The actual beginning and end of spawning cannot be established from these data alone since duration of the larval period, size at metamorphosis, and growth rate of the "spat" or "set" after metamorphosis and settling are not known. These factors are variable and may depend chiefly on food and temperature. The latter two factors are thought to be most important in affecting the size of larvae and duration of their pelagic period in many mollusks (Thorson, 1946: 452; Loosanoff, 1954: 620-621). In January and February of 1958, the two coldest months, the smallest juveniles, 0.375 mm (size class 2), found during the investigation were more abundant in the samples than any other size. Juveniles of size class four (0.875 mm) were the least abundant of the three smallest size classes in the north shore collections (fig. 14).

Density estimates are conspicuously rare for clams between size classes 20 and 25 (14.25 - 23.75 mm). Specimens in this size range were found only with difficulty in the qualitative samples. Finding them only in the summer months is probably significant. A large qualitative sample of 314 individuals, both juvenile and adult, from the north shore area (fig. 16) was collected on September 15, 1958 to verify the results of quantitative sampling in regard to the scarcity of individuals of the sizes 14.25 to 23.75 mm. Only four specimens within this size range were found. Possibly they actually are few in number and their growth rate is probably high so far as annual increment in length is concerned. Growth rate for clams under size class 20 can be inferred by comparing the shift in position of modal peaks from one collection to the next [figs. 11 (j-m), 16]. As the shift proceeds to the right representing increase in size, density decreases sharply. The modal peak at size class 13 (midpoint, 7.25 mm) in September [fig. 16 (frequency is not plotted logarithmically)] most likely represents juveniles spawned in March or April, about six months of age. The small group at the right of the modal peak may be a few months older. Since growth rate declines with age, individuals of size class 13 could not reasonably be expected to reach size class 25 (midpoint 23.75 mm) during the six months following September 15th and probably not before the end of another year because of

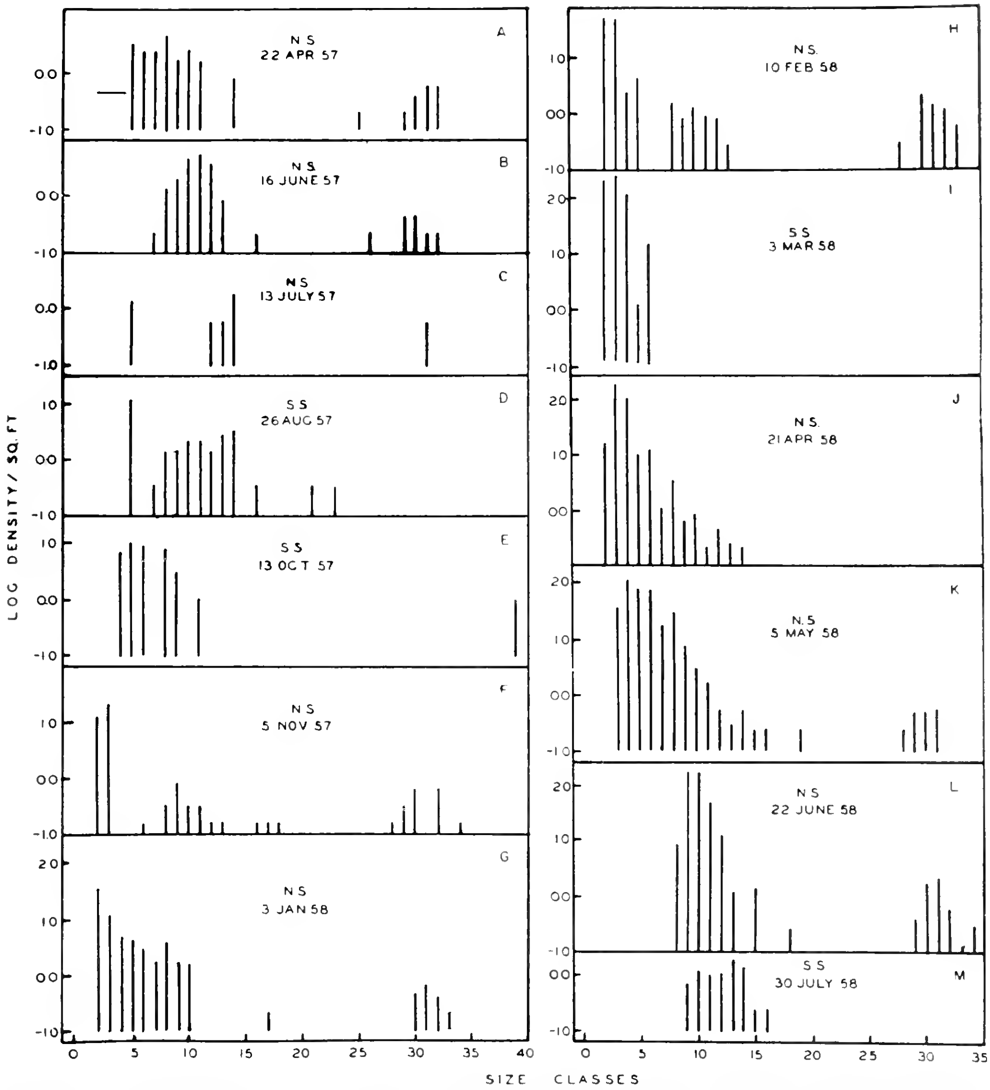


Figure 11. Distributions of population density by size classes; NS = north shore area, SS = south shore area, horizontal line in A indicates no estimates were made for size classes below size class 5 (see Table 2 for actual sizes).

the intervening period of storms, low temperature, and scarcity of food. If average growth rate remained nearly the same for the next six months they might be expected to have attained a length of 15 mm (size class 20) in one year depending upon environmental conditions. In the meantime the numbers of individuals (density) of this age would have declined greatly as is indicated by Figure 11. Any survivors of this size (15 mm) would have had seven months of warm growing season ahead in which possible rapid growth could effect an increase from approximately 15 mm (size class 20) to 24 mm (size class 25). The chances of picking up juveniles in this size range (14.25 - 23.75 mm) would be small because the relatively few clams represented would not be expected to stay within the size range for any length of time.

For further information concerning growth rate in *Rangia* the percent frequency of lines of growth interruption of 40 specimens collected in the north shore area on

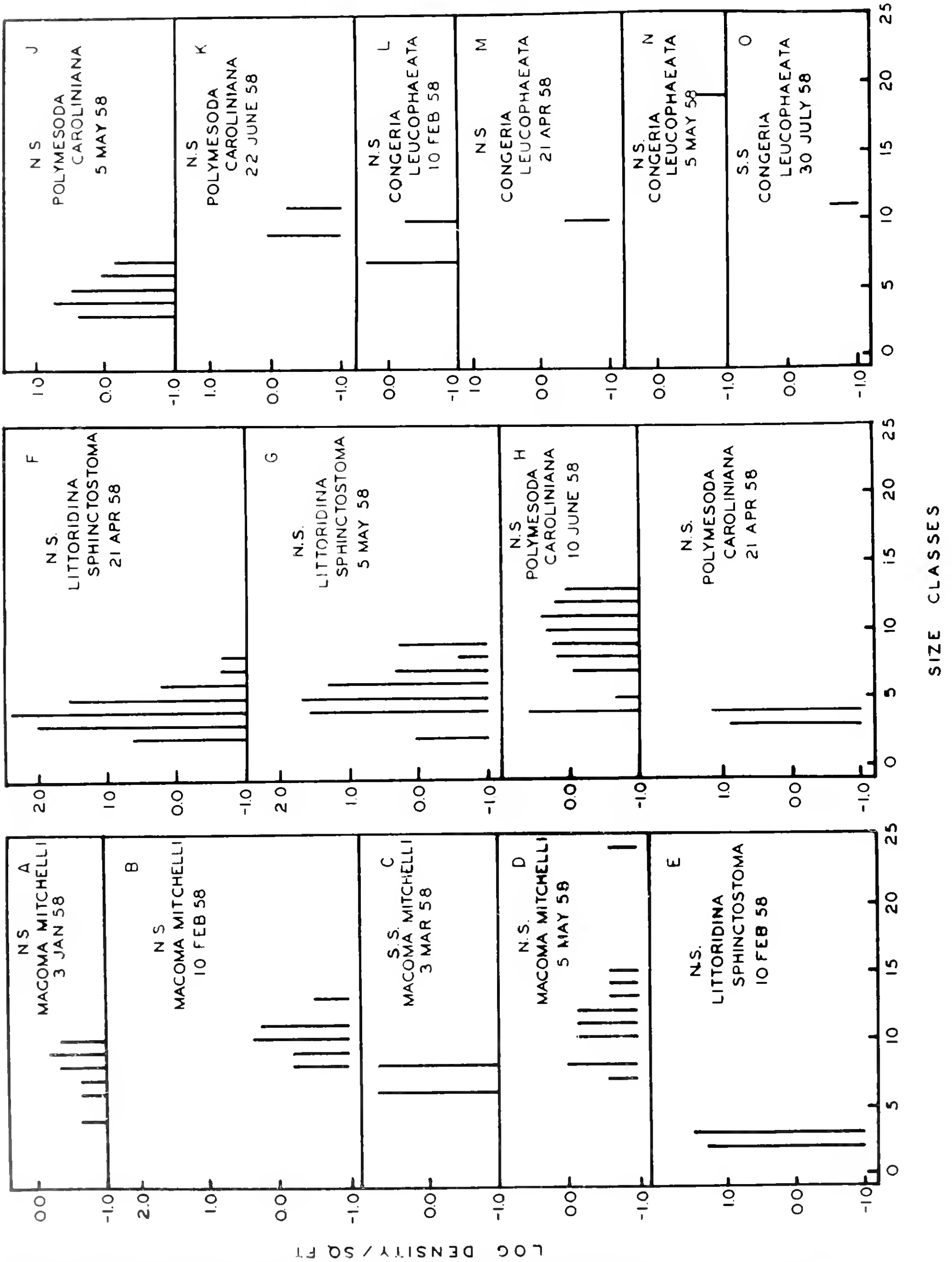
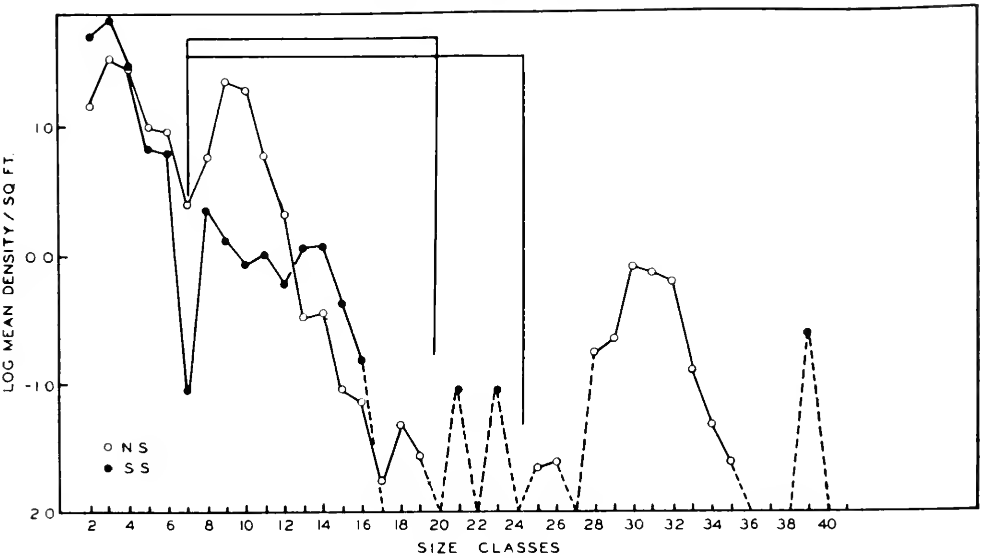
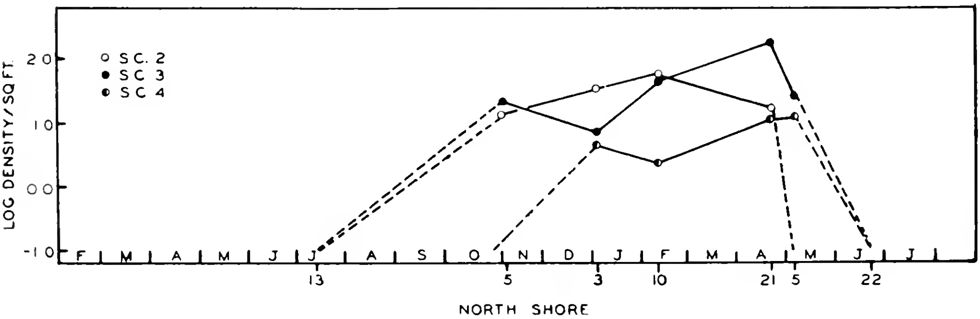
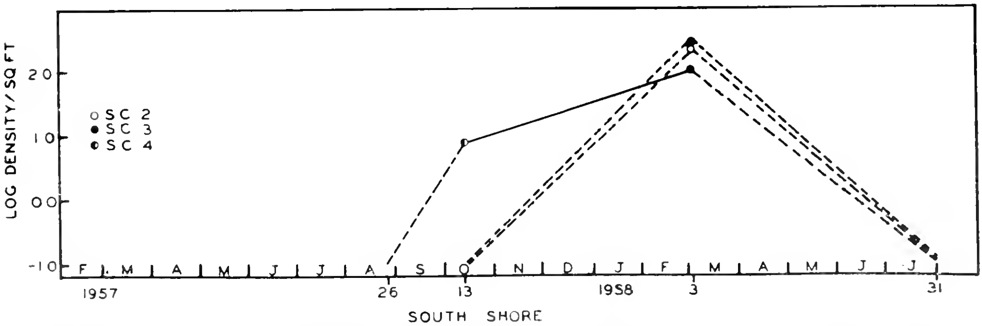


Figure 12. Distributions of population densities of associated mollusks; NS = north shore area, SS = south shore area (see Table 2 for actual sizes).

September 15, 1958 and 60 specimens taken from the south shore area on July 30, 1958 were plotted (figs. 17, 18). The peaks in these distributions were assumed to indicate: (a) the sizes at which shell growth was most frequently interrupted; and (b) that the space between the peaks generally indicated most frequent size intervals in which growth increment occurred. There were growth interruption lines at nearly all diameters above







Figures 13-15. **13.** (Top) Distributions of mean density of size classes; dashed lines indicate size classes having densities estimated to be no greater than the antilog of -2.0 (0.1 sq. ft.), NS = north shore area, SS = south shore area; right angle lines delimit size classes involved in testing the density estimates of juveniles (see text). **14.** (Middle) Seasonal distributions of density of the three smallest size classes of the north shore area; dashed lines indicate dates for which densities were estimated to be no greater than the antilog of -1.0 (0.1 sq. ft.), SC = size class (see Table 2 for actual sizes). **15.** (Bottom) Seasonal distributions of density of the three smallest size classes of the south shore area (symbols as in fig. 14).

7 mm. Mid-winter interruptions due to cold temperatures seem to be responsible for the majority of the modal peaks although spring and fall interruptions caused by stormy periods may have been recorded (*cf.,* Coe, 1947). In the north shore specimens (fig. 17) the first major peak occurred at 15 mm (size class 21) and probably indicates the end of the first year's growth, as indicated by the rate of shift in modes of Figure 11 and the modal positions in Figure 16. The second major peak occurs at 20 mm (size class 23) but is flanked on either side by smaller peaks at 17 mm and 22 mm. This second major peak probably indicates the average increment at the end of the second year's growth. The flanking minor peaks may indicate the end of the second year depending upon whether the interruptions occurred in the fall or the spring stormy periods. (The flanking peaks may also depend upon whether the individual had arisen from spawn in fall or spring). A period of interruption in the fall would be followed by an immediate delay, if not interruption, by winter cold temperature, producing a lesser increment by the end of the second year. On the other hand, since these individuals were of different sizes and had experienced different seasons, a relatively mild fall and winter but with severe conditions in the spring could produce an interruption to be followed shortly by warm temperatures and increase in available food resulting in a greater increment than 20 mm for the same period of time. To what extent the timing of these interruptions affects the total increment in yearling juveniles is impossible to determine from these data. However, the higher growth rate of yearlings makes reasonable an expectation of an increment of 15 mm for their first year. The peaks beyond 23 mm (size class 25) appear more regularly spaced but cannot be relied upon to indicate age of the animal at the time of their formation because of preceding variable growth and variously prolonged interruptions. The same difficulty is met in plotting the frequencies of actual lengths for older year classes; a greater spread of sizes is sometimes shown with overlapping of classes and complete obscuring of the modes (Haskin, 1954: 300). Additional factors affecting growth rate of pelecypods is the energy required by the gametogenic cycle, extent of spawning and resorption of unspawned gametes, and timing of the cycle in the individual (*cf.*, Orton, 1928: 365; Coe and Turner, 1938: 99; Coe, 1947: 13).

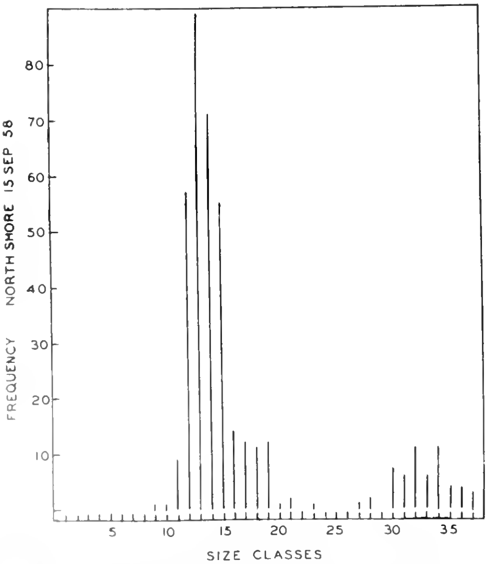


Figure 16. Size distribution of 314 individuals collected on September 15, 1958 in the north shore area (see Table 2 for actual data).

The distribution of frequencies for clams from the south shore area (fig. 18) similarly indicates the age of the smaller clams. A greater annual increment is indicated for these clams at least during their first two years and possibly for the third. The first major peak is at 20 mm (size class 23) indicating the end of the first year's growth. The peak is flanked on the left by a smaller peak at 16 mm which may also indicate the end of the first year's growth or the end of the growing season for some individuals. Absence of the 16 mm peak in association with the presumed first year peak of the north shore shells may be due directly to the difference in growth rate, regardless of what the causes are. The obtuse peak centering on 29 mm (size class 28) seems to indicate the average increment by the end of the second year. Like the distribution for the north shore this second major peak is flanked on either side by minor peaks which probably have the same possible causes as those for the north shore. The separation of the second major peaks of both distributions from the third major peaks, by dips representing much lower frequencies than for adjacent sizes, must indicate that a high proportion of the clams was undergoing rapid continuous growth during the time they were in the respective size intervals. On the average the clams could be in their third summer of growth when these frequencies are low.

The inferred average annual increment for the first three years for the clams from the two areas is as follows:

Year	North Shore	South Shore
1st	15 mm	20 mm
2nd	5 mm	9 mm
3rd	4 mm	5 mm

Accordingly the growth rate in terms of increment in shell length for *Rangia* from the south shore area is initially much greater than for individuals from the north shore but by the end of the third year the rates become nearly equal. The difference in average length for the two areas by the end of the presumed third year is thus 10 mm.

The 90th percentile of the north shore distribution (fig. 9) indicates that 90 percent of the adult population in that area is below 43.0 mm (size class 35) while that of the south shore distribution indicates that 90 percent is below 50.00 mm (size class 38). The difference in these two percentile sizes is 7.0 mm. The shapes of the distribution curves above the 90th percentile are similar and may indicate that growth rate and survival are similar for adults in the two areas only for the upper 10 percent in size. The ages of these clams would be of interest, but data are lacking. The deflection in the distribution of the north shore length weight relationship (fig. 10), in progress when the 90th percentile in size (size class 35) has been attained, is also interesting but not explainable on the basis of present evidence.

The second mode (fig. 13) for the south shore clams, including the mean density estimates for size classes 7-24 (1.62 - 21.75 mm), is considerably in advance of the second mode for the north shore clams, including size classes 7-20 (1.62 - 14.25 mm) supporting the indications of the growth interruption frequencies. (Growth rate is indicated to be greater for south shore clams during the first year at least.) The density estimates for south shore clams in size classes 21 and 23 probably involve clams of about the same age as those in size classes 17-19 of the north shore. The densities of size classes 8-24 inclusive represent clams collected, for the most part, in spring and summer while the densities of size classes 2-7 inclusive are represented in the collections of winter and spring. Comparatively low densities for size class 7 appearing for both areas are probably artifcial, owing to change in size class interval. High densities of size class 7 occur in January, April, and May (fig. 11 a, g, j, k) possibly marking intervals between spawning periods.

The similarity in shape of the distributions of Figure 9 to the distributions of mean densities for size classes 7-24 in Figure 13 is notable and probably means that a differential growth rate exists between the clams of the two areas, regardless of age of the juveniles and bulk of the adult population, *i.e.*, below the 90th percentile of a size frequency distribution.

The estimated density for the north shore adult clams (above size class 24) was 2.88 per square foot while that for the south shore was 0.25 per square foot. Since the distribution of adult *Rangia* in either of the two areas is not believed to be either random or uniform but is clumped in varying degrees, particularly in the south shore area, the difference cannot be tested satisfactorily by statistical analyses without further extensive and careful sampling. The distribution of juveniles in the two areas may be more uniform but occasionally single samples from a collection yielded extremely high or low density estimates. The highest density estimates of juveniles in size classes two and three, for example, came from one sample of the collection of March 3, 1958 from the south shore area. This caused the means of these two classes to be about four times higher for this collection than for the same two classes of any other collection. The bottom material brought up in the sample contained a high proportion of black organic material, rare for the south shore area. This suggests that the pelagic larvae tend to select a bottom high in organic matter for settling and supports the contention of Thorson (1946: 464, 465) that pelagic larvae exercise some selection of substrate for settling rather than simply drifting by chance to any type of bottom. The overall mean density for juveniles (size classes 2-24 inclusive) in the north shore area was 167.95 per square foot and for the south shore, 175.42. The difference is not significant when the data are tested by Student's *t-test* ($p > .50$). The mean densities for size classes 2-7 inclusive were 17.00 per square foot for the north shore and 27.72 for the south shore ($p > .40$). For size classes 8-16 inclusive (delimited by right-angle lines in fig. 13) mean densities were 6.45 for the north shore and 0.99 for the south shore area ($p < .10$). If the difference between the density estimates of the adults in the two areas is tested it may be regarded as conclusive ($p < .02$). Although the results of testing data of this kind may be misleading, there is a tendency for the observed increasing differences between the two areas (fig. 13) to become significant with increasing size from class 2 to adult sizes of class 25 and above. The density data, as such, support the empirical differences found in the qualitative sampling of the adults and suggest that the settling of newly metamorphosed juveniles is no different in one area from the other but that mortality is greater, or survival less, in the south shore area during growth to reproductive size.

If the animals represented by the mean density estimate of size classes 25 and 26 (0.047) for the north shore (fig. 13) were added to the adult (reproducing) population near the end of their third year, as indicated by the data concerning growth rate, then hypothetically about 1.62 percent can be estimated as the mean yearly addition to the north shore adult population, and if the population tends to be stable the same figure could represent yearly mortality. If the frequencies representing size classes 27 and 28 (fig. 16) represent new additions to the adult population following a summer of apparently favorable growth conditions they represent 5.45 percent of the total. That the adult population is stable from year to year is unlikely and whether 1957 and 1958 were representative years for *Rangia* in Lake Pontchartrain, in so far as unknown environmental conditions are concerned, is not known.

The proportions (in different collections) of probably new recruits to the adult population sampled in 1960 and 1961 are listed in the last column of Table 6 and indicate an average yearly recruitment of about 11 percent.

The seasonal mean lengths, as computed from the density data, of adults (above 23.75 mm) from the north shore area and juveniles from both areas are plotted in Figure 19. A discrepancy occurs between the mean length (38.5 mm) of the north shore adults as computed for the specimens from the qualitative samples (fig. 9), collected chiefly for gonadal analysis, and the mean length as computed from the quantitative samples (34.9 mm) in Figure 19. This is probably attributable partly to bias in the earlier qualitative samples in which some smaller specimens were ignored to insure the inclusion of potentially sexually mature individuals in the gonadal inspections. Also the qualitative samples were consistently collected from north shore locations 1 and 7 (fig. 1) which may not have been representative for size in the general north shore area. Another possibility is that the quantitative dredging may have failed to yield a representative sample of larger specimens because of clumping in distribution over the bottom.

Mean length of the adults (fig. 19) fluctuates sharply above and below the overall mean during the late spring and early summer of both 1957 and 1958. The mean lengths of individuals in qualitative samples having relatively large numbers of specimens seem to show the same thing for both the north shore and the south shore:

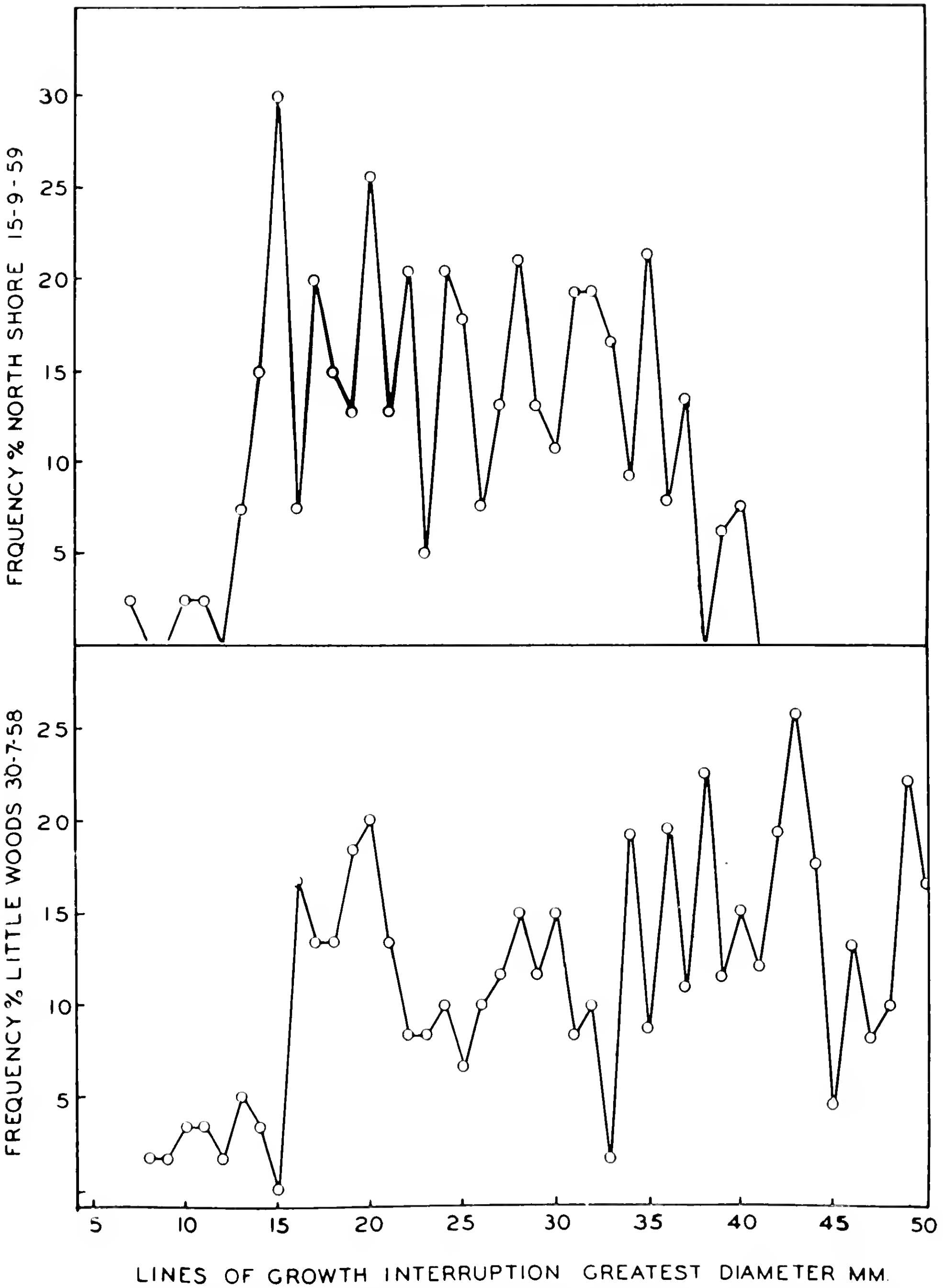
North Shore
Mean = 38.5 mm

Date	Mean	Sample Size
Nov. 5, 1957	38.57 mm	39
Feb. 10, 1958	37.92	48
April 21, 1958	37.54	227
May 5, 1958	38.91	159
June 12, 1958	41.97	90

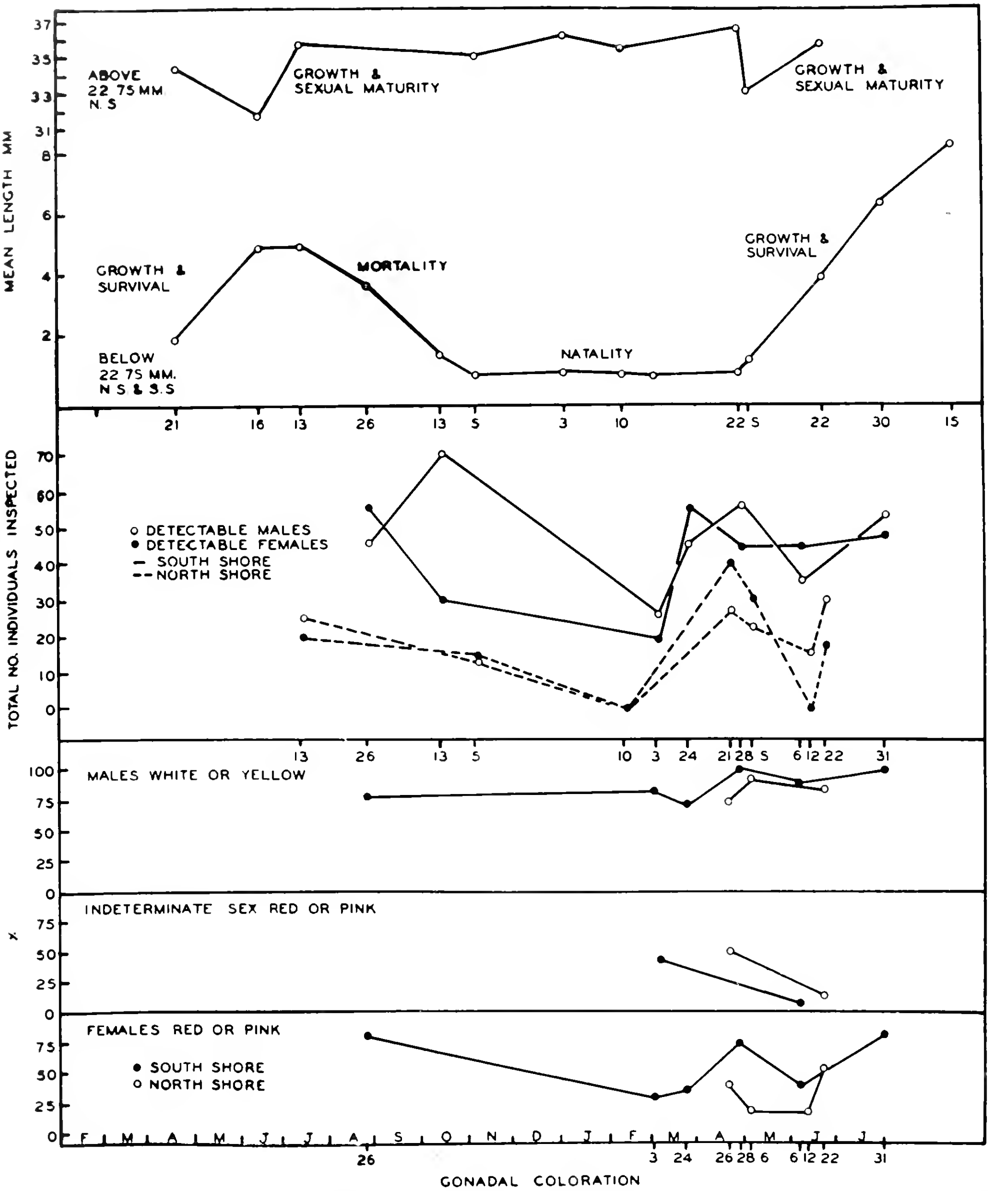
South Shore
Mean = 42.4 mm

Date	Mean	Sample Size
Aug. 26, 1957	44.13 mm	58
March 3, 1958	44.68	60
March 24, 1958	41.44	52
April 28, 1958	41.82	111
June 6, 1958	44.77	82

If the seasonal differences for both areas are significant they are indicative of a slightly higher mortality rate for the larger adults (above the mean) coinciding with the end of the spawning season, a higher growth rate for adults of all sizes, particularly for those below the mean, and the addition of younger members to the adult population coinciding with high temperature and more available food during summer. If the fluctuations in mean length occur annually,



Figures 17-18. **17.** (Top) Frequency of lines of growth interruption in 40 specimens from the north shore area. **18.** (Bottom) Frequency of lines of growth interruption in 60 specimens from the south shore area.



Figures 19-21. **19.** (Top) Distributions of seasonal mean length of north shore adults and of combined north and south shore juveniles; NS = north shore area, SS = south shore area. **20.** (Middle) Seasonal distributions of determinable sexes in the study areas; detectable = determinable. **21.** (Bottom) Seasonal distributions of gonadal coloration according to sex; indeterminate = non-determinable.

possibly they may have been greater for the interval between the springs of 1957 and 1958 than for previous years particularly in view of the trend toward higher amounts of available food indicated by the data concerning pigment and organic matter (figs. 7, 8).

Mean length of juveniles of both areas (fig. 19) was greater in the summer of 1958 than in the summer of 1957. (The curve is an expression of survival or mortality as well as of growth.) By far the greater part of the annual increment in shell length of the adults appears to occur within a period of about two months.

A similar rapid growth rate was found for the Pismo clam, *Tivela stultorum*, in June (Coe, 1947: 10-15) along the California shores near La Jolla in marked individuals planted several months previously. As much as 4 mm was recorded for some clams within a month. The average was 2.6 mm for June, but less than 1.0 mm per month during the winter. The author did not state the size limits of individuals in which these rates occurred. The Pismo clam has a second period of increased growth rate beginning in September near the end of its spawning period which lasts about three months. (The temperature range of the habitat was only about 8° C). This clam is about 42 mm in length at the end of its second year and may reach lengths of about 70 mm during its life-time. In *Mercenaria* Pratt and Campbell (1956) found that more than half the year's growth occurred before mid July.

H. *Predators*

No observations were made that provided a basis for either a qualitative or quantitative account of predators. However, the appearance of considerable amounts of freshly broken adult and juvenile shells with periostracum intact indicated heavy predation by either fishes or crabs or both.

Suttkus *et al.* (1953-54) reported "clams" among the stomach contents of 14 species (representing eight families) of "the 74 different fish forms" found in Lake Pontchartrain. Five of these species were of the Family Sciaenidae and one of these, the Atlantic croaker *Micropogon undulatus*, was one of the three most numerous species found in either trawl or seine catches during the period reported. The authors also reported "clams" among the stomach contents of the blue crab *Callinectes sapidus*, commonly found throughout the period, and among the stomach contents of the white shrimp *Penaeus setiferus* found abundantly in July through November of 1953. Gunter and Shell (1958) reported catfish (*Ictalurus furcatus*) living on *Rangia* and the attached *Congeria*.

I. *Associated Mollusks*

Other mollusks in the two areas were the pelecypods *Polymesoda caroliniana* Bosc, *Macoma mitchelli* Dall, *Congeria leucophaeata* Conrad, and one small gastropod *Littoridina (Texadina) sphinctostoma* Abbott and Ladd. The shells, but no living representatives of the two other species, *Brachidontes recurvus* Rafinesque and *Tagelus plebius* Solander, occasionally were found in both areas and more frequently in the south shore area. The latter two species may have become established temporarily in the lake during preceding years when salinity in the lake was higher or they may have been carried in by fishes that could have passed them through the digestive tract whole. Shells of these species were sent to The Academy of Natural Sciences of Philadelphia where they were identified by Dr. R. Tucker Abbott.

Polymesoda, comparable in size to *Rangia*, was found in relatively small numbers in both areas, and was seemingly more abundant in the north shore area but the largest specimens were found in the south shore area. The differences in shell erosion were comparable to those of *Rangia*, being more extensive in north shore specimens. The other associated species also seemed to be more abundant in the north shore area, although this is based on empirical observations since counts of these species were not made for every collection. The density distributions of size classes (fig. 12) indicate that the peak in the spawning activity of these mollusks may occur simultaneously with that of *Rangia* or at least that their spawning periods are overlapped by the most intense part of the breeding cycle of *Rangia*. Growth rate of north shore mollusks as indicated by shifts to the right of modal peaks seems to be constant regardless of species and size if only individuals under about 9 mm (size class 15) are considered. Maximum size of presumed adults of *Macoma mitchelli* was about 22 mm, and 3 mm for the gastropod *Littoridina*, when measured from the tip of the spire to the base of the aperture.

V. REPRODUCTION

A. *Gonadal Analysis*

Sex ratio and the gametogenic cycle.—The gonad in *Rangia* is similar to that of other pelecypods, not a discrete organ, but a mass of specialized tissue within the mantle enveloping the ramified digestive gland and loops of the intestine. The gonad develops seasonally to greater proportions, swelling the mantle tissues, and effecting more firmness and opacity just before presumed spawning periods. At this time recognizable gametes have suddenly become differentiated and the sex of the individuals can be distinguished.

The percent of individuals in which the sex was determinable or non-determinable for each qualitative collection is represented in Table 3 for each study area. The percent of the total individuals of a collection that were male or female is plotted in Figure 20 for each study area. The difference between 50 percent and the percent of one sex or the other of the total number in which sex was determinable was tested either by a simple test of proportions, when the sample number was above 30, or otherwise by application of the binomial distribution, for each collection. The probabilities ranged between 0.18 and 0.85 for all collections except that of June 12, 1958 from the north shore area in which no determinable males were found (p, approximately 0.03). No indications of hermaphroditism or juvenile sexual phases such as those known in *Mercenaria mercenaria* and *Crassostrea virginica* were found (*cf.*, Coe, 1943: 161).

In other pelecypods whose seasonal gonadal changes have been studied (Loosanoff, 1937; Coe and Turner, 1938; Coe, 1947; Tranter, 1958a, 1958b) the rate of which gametogenesis proceeds is variable depending upon environmental conditions and may not be the same in all individuals of a population. In general, spawning is followed by a gonadal recovery phase in which non-spawned residual gametes are resorbed by autolytic processes and phagocytosis. Mitosis and gametogenic proliferation follow this into the next spawning period. These periods or phases may or may not be clear cut. In *Mya arenaria* (Coe and Turner, 1938: 99) continued intermittent spawning may occur after the first spawning of the season early in June. In *Mercenaria mercenaria* (Loosanoff, 1937: 408-409) at least a few ripe appearing ova and mature spermatozoa can be found at all seasons of the year except for a brief post-spawning period when no mature spermatozoa are likely to be found.

According to Tranter (1958b: 150-152) no distinction can be made between the developing and the declining phases nor can the degree of development or regression be estimated except by microscopic examination of stained gonad sections, at least for *Pinctada albina*. In the latter species the gonad may develop more than once in the same season with overlapping of breeding cycles; spawning frequently may be incomplete in both sexes and there are occasional instances of non-spawning in which cases the entire gametic production is resorbed. Spawning usually continues for 3-4 months and recovery for 2-3 months, but it is not unusual for gametogenesis to continue after the first spawning of the season nor for the resorption of gonad material to commence before spawning is complete.

TABLE 3.
Proportions of sexes and gonadal parasitism.
(ND, non-determinable sex; NS, north shore area; SS, south shore area.)

Date and Location	Females %	% ND	% Males	No. of Specimens	Size Range mm	% Infested by Trematodes	Sizes of Individuals Infected with Trematodes (in mm)
7/13/57 NS	25	55	20	40	21-50	0	
11/ 5/57 NS	13	72	15	39	27-44	5.13	40, 41
2/10/58 NS	0	100	0	49	32-46	6.12	33, 38, 41
4/21/58 NS	27	33	40	67	31-48	6.00	36, 39, 41, 42
5/ 5/58 NS	22	48	30	50	27-48	4.00	42, 47
6/12/58 NS	15	85	0	40	33-51	4.76	38, 45
6/22/58 NS	29	54	17	48	28-41	4.00	39, 40
NS Average	18.7	63.9	17.4	total 333			Mean size infected 40.13 Total inspected for trematodes 337 % infected 4.15
8/26/57 SS	45	0	55	58	34-56	1.72	52
10/13/57 SS	70	0	30	23	33-47	0	
3/ 3/58 SS	26	55	19	58	36-55	3.45	45, 53
3/21/58 SS	45	0	55	51	27-58	0	
4/28/58 SS	56	0	44	52	27-56	0	
6/ 6/58 SS	35	21	44	84	27-56	3.57	49, 50, 51
7/31/58 SS	53	0	47	40	34-48	2.50	47
SS Average	47.1	10.9	42	total –363			Mean size infected – 49.57 Total inspected for trematodes –366 % infected – 1.91

The gametogenic cycle in *Rangia* may be little different from that of other pelecypods except in the timing of spawning and recovery. The percentage distributions of determinable sexes for the study areas appear almost identical in timing but consistently different in proportions of individuals whose sex is determinable (fig. 20). The proportion of determinable sexes evidently depends upon extent of spawning. The mean percent of individuals of non-determinable sex (Table 3) for the north shore collections was considerably greater than for the south shore collections (p, infinitesimal). The highest percentages of individuals of non-determinable sex in the collections from both areas (or lowest percentages of determinable sex, fig. 20), occurred within at least a month of each other. The gonads of clams collected on February 10, 1958 from the north shore area and those collected on March 3, 1958 from the south shore area were firmer, more well filled, and milkier in appearance than those seen in any of the other collections. The condition can undoubtedly be regarded as one of prespawning development and imminent ripeness. Apparently this phase was proceeded by a long recovery phase with some individuals spawning later than others in the fall in view of the large numbers of juveniles represented in the January and February quantitative collections. Artificial fertilization of eggs taken from females collected October 13, 1957 was relatively successful, but difficult with eggs from females of the November 5 collection. Development of fertilized eggs from females collected 24 March and 6 and 12 of June, 1958 appeared normal. The collections of April and May, 1958 showed high proportions of individuals with ripe gametes; also, the corresponding quantitative bottom samples had high proportions of small juveniles. Low percentages of clams with recognizable gametes were evident again in the early June collection but collections later in June and July indicated a rapid increase in gametic production.

That the first maturation of gametes in the spring occurs only after water temperatures begin to rise (figs. 2, 3) is probably significant and indicates that the effect of temperature upon the gametogenic cycle is as important for *Rangia* as for other pelecypods in which temperature has been experimentally raised in laboratory situations to induce spawning (Loosanoff, 1954).

The data suggest that *Rangia* has two incompletely definitive spawning periods per year with post-spawning recovery phases indicated by low percentages of individuals with recognizably mature gametes. A spring spawning period of about three months duration (March, April, May) and a more prolonged but less intense spawning beginning in late summer and lasting at least into November is indicated. Many individuals during the latter period may be undergoing recovery at a more rapid rate than others and some may be spawning more intensely than others. The post-spawning recovery phase apparently occurring in mid-summer is more rapid or intense than that occurring in fall and mid-winter.

In general there was a distinct difference in the gross appearance of the gonadal tissues of the north shore and south shore clams. The north shore specimens were nearly always flaccid and pale in coloration while those of the south shore were generally firm, opaque, and of definite color. This difference in appearance and the differences in perecntages of clams of determinable sex probably indicate that spawning is more complete in the north shore clams.

Gonadal coloration.—Distinctive gonadal coloration is found generally throughout the pelecypods (Coe, 1943: 156; Ricci, 1957: 13; Tranter, 1958a: 136) and depends directly upon the sexual type of the mature gametes, the mass of mature ova being more richly colored than the gonad with mature spermatozoa which is opaque and white, or cream, or some other light shade. The color is seen through the transparent epithelium of the mantle. Even in truly hermaphroditic species such as *Pecten irridians* (Coe, 1943: 156) the male part of the gonad is distinct in color from the part producing ova.

Data concerning the intensity of coloration of gonadal tissues of *Rangia* were recorded for most of the collections at the time of inspection determining sexuality. The percentages of individuals of each sex and of indeterminable sex fitting four categories of color ranging from white to red are represented in Table 4 and their seasonal distributions of color intensity are plotted in Figure 21. Generally, few males were found that could be classified as red, but either white or red females were not uncommon.

TABLE 4.

Gonadal coloration in proportions of the population.
(NS, north shore area; SS, south shore area; R, red; P, pink; Y, yellow or cream; W, white; ND, non-determinable as to sex.)

Date and Location		Females				Non-determinable				Males				No. Animals Inspected			
		R %	P %	Y %	W %	% R	% P	% Y	% W	% R	% P	% Y	% W	female	ND	male	total
24 April 58	NS	0	40	20	40	6	44	17	33	0	27	21	52	15	9	29	62
5 May 58	NS	9	9	73	9	0	0	14	86	7	0	53	40	11	22	15	48
12 June 58	NS	0	17	50	33	0	0	12	88	—	—	—	—	6	34	0	40
22 June 58	NS	13	40	40	7	0	13	48	39	0	16	42	42	15	23	12	50
NS Average		5.5	26.5	45.8	22.3	1.5	14.3	22.8	61.5	2.3	14.3	38.7	44.7				200
26 Aug. 57	SS	43	36	0	21	—	—	—	—	0	23	12	65	14	0	17	31
3 Mar. 58	SS	0	29	0	71	13	30	0	57	0	17	0	83	14	23	12	49
24 Mar. 58	SS	0	35	35	30	—	—	—	—	0	29	25	46	23	0	28	51
28 April 58	SS	45	25	17	10	—	—	—	—	0	0	52	48	29	0	23	52
6 June 58	SS	11	28	29	32	6	0	19	75	3	8	56	33	28	16	36	80
31 July 58	SS	27	55	0	18	—	—	—	—	0	0	6	94	22	0	18	40
SS Average		21.0	35.2	13.5	30.3	9.5	15.0	9.5	66.0	0.5	12.8	25.2	61.5				303

Those of indeterminable sex were more often white or translucent.

The following statements are based on tests of proportions concerning the observed differences (Table 4) in gonadal coloration of clams of the two study areas: (a) the proportion of south shore females that were red or pink was higher than the proportion of north shore females that were red or pink ($p = 0.019$); (b) the proportion of south shore males that were white or yellow was not significantly different from the proportion of north shore males that were white or yellow ($p = 0.28$); (c) the proportion of individuals of indeterminable sex from the north shore did not differ significantly (at the five percent level) from the proportion from the south shore in intensity of red coloration ($p = 0.11$).

The data in Figure 21, when compared to Figure 20, show that the intensity of coloration for each sex is greatest at times of greatest gonadal development, and that periods of least distinctive coloration for the sexes coincide with periods when sex is least distinct, (*i.e.*, presumed post-spawning recovery or prespawning phases). The individuals of indeterminable sex had least coloration at the end of the first, and apparently more intense, spawning period of the season.

The gonadal coloration of clams from the south shore was at all times more intense than in clams from the north shore (fig. 21) and supports the data of Figure 20 in indicating a more extensive release of mature gametes (spawning) among the north shore clams. Presumably the current load of unspawned gametes of the south shore clams is resorbed and proliferation recurs before spawning in the spring.

Gonadal parasitism.—Occasionally individuals were found whose gonads were spotted with distinct orange coloration. The gonadal fluid of these clams contained larvae of trematodes (cercariae, and often sporocysts). Only rarely did such clams have mature gametes. Specimens of the trematode larvae preserved in formalin were sent for identification to Dr. Franklin Sogandares (then, of the Florida State Board of Conservation). They appear to be fellodistomatids, but the adult form is not known and no positive identification could be made without further investigation involving possible secondary hosts. The suggestion was made that pinfishes (*Lagodon rhomboides*) might harbor the adults.

In Table 3 the sizes of parasitized individuals found in both study areas are given together with the extent of parasitism in terms of percent infected in the respective areas. The mean size of those infected appears to be greater than the mean size for the population in the areas concerned. This may mean that the infected clams have had better chances of becoming parasitized because of greater age as indicated by the size, or that they are larger because parasitic castration has allowed them to put more energy into shell growth in lieu of the energy required for gametogenesis as in the gastropod *Peringia ulvae* (Rothschild, 1935). The difference in extent of parasitism between the two areas is conclusive ($p = 0.05$).

B. *Early Embryonic Development*

The eggs of *Rangia cuneata* are about 69 μ in diameter. Immature ova, often seen in gonadal fluid samples are likely to have rather long attachment stems such as those described by Tranter (1958b) for *Pinctada albina*, and do not develop normally, even if penetrated by spermatozoa, when artificial fertilization is attempted. But, a female may contain both mature and immature ova so that some of the eggs may develop normally.

Eggs from females collected in October, March, and June were artificially fertilized and development was observed to a veliger stage from eggs of all three collections. Following is a developmental sequence with descriptions based on the observations of several larvae, hatched from eggs at temperatures between 73 and 80° F:

Hours after fertilization	Description
0.00	Egg or zygote, 69 μ
8.50	First appearance of spyherical ciliated blastula and movement (rotating or rolling along bottom).
26.25	First apperance of pelagic trochophore (acorn-shaped with long stiff flagellum protruding from obtuse end, surrounded by ring of cilia at base, no other cilia present).
34.25	First appearance of veliger, 93 μ (flattened, with thin growth of shell, ciliated velum well developed, flagellum retained, apparent early differentiation of gut; swimming rapid).

C. *Larvae*

The most abundant animal organisms found in the plankton collections were copepods and the nauplius and cypris stages of higher crustaceans. Molluscan larvae in the collections were either absent or non- recognizable. What may or may not have been molluscan larvae appeared only in the January collections. Since all of the collections were taken from near the surface most molluscan larvae present may have been excluded from the collections. According to Thorson (1946: 462) "indications are that newly hatched larvae will either rise to the surface after hatching or react indifferently to light" and old larvae are likely to stay near the bottom and many are photonegative.

Had more extensive collections of plankton been made, the larvae of *Rangia* would likely have appeared but their identification by the investigator may not have been reliable. Pelecypod larvae of identical age and species are known to vary greatly in size and shape with some individuals being more than twice the size of others. Published photographs and descriptions of the larvae of some species do not agree with observations of the larvae grown in the laboratory under controlled but apparently healthy conditions (*cf.*, Loosanoff, 1954: 609, 621).

The sizes of pelecypod larvae are apparently highly variable. Descriptions by Thorson (1946: 287) includes a range of 245 to 400 μ for the veliger of one species and comparable variability for other species. Sizes above 500 μ seem to represent the beginning stages, at least, of post-larval life. Loosanoff (1954: 621) described sizes from 100 to 236 μ for larvae reared in the laboratory.

Since no shells of juvenile *Rangia* were found that were less than 375 μ this may be the minimum size at which settling occurs, or this size may be slightly larger than minimum size at metamorphosis for this species. Duration of larval life and larval size of *Rangia* is probably dependent, as in other species, on temperature and food. Duration of the larval period of some pelecypods is known to be two to four weeks (Thorson, 1946: 453) or seven to sixteen days under laboratory conditions (Loosanoff, 1954: 621).

The trochophores and veligers developed in the laboratory from *in vitro* fertilized eggs proved to be fragile organisms and difficult to transfer with a pipette. The larvae frequently broke up into their constitutent cells, particularly when released from a small pipette onto a cover slip. Occasionally while their swimming movements in a hanging drop were being observed they became entangled in the surface film near the edge of the drop and disintegrated, the constituent cells subsequently agglomerating without organization. This fragility seemed more common in the trochophores than in the veligers. Because of the short duration of this stage before the shell develops the risk of disintegration may not be great under natural conditions, although attempts at collecting with a plankton net may have been destructive for such small (90 μ) veligers. Time spent in the pelagic stage will have to be established by further investigation.

However, speculation to the effect that a pelagic existence for *Rangia* is of short duration seems reasonable in view of what is known of the life history, habitat, and physiology of other members of the Phylum. Of the five classes of mollusks only the two largest (in number of species) have representatives in freshwater. Adaptation to freshwater by the gastropods has apparently come about by evolution through at least two different routes, one involving primary adaptation to the terrestrial habitat with pulmonary specializations and secondary adaptation to freshwater, the other route undoubtedly by way of brackish-water and these are few in comparison to the great numbers of marine and pulmonate species. To the writer's knowledge no freshwater gastropod has a pelagic developmental stage. The advantages during development of a nidamental enclosure or ovoviviparity, common to the fresh-water gastropods and to shallow water coastal marine forms such as *Buccinum, Urosalpinx, Lacuna* (*cf.*, Abbott, 1954: 225, 212, 131; Lankester, 1906: 139), *Littorina* (*cf.*, Lankester, 1906: 139; Abbot. 1954: 133), and *Acteonia* (*Cenio* of Lankester, 1906: 139; Thiele, 1931: 416), apparently have outweighed any potential for adaptation to freshwater by pelagic larvae. The pelecypods have relatively few families represented in feshwater and their adaptation may have depended greatly, if not entirely, upon a modified sequence of development such as that characteristic of the Unionidae, incubation in the parental gills, formation of the glochidium and parasitism upon fishes. The latter modification has been held responsible for their extensive world-wide dispersion within the freshwater habitat (Thiele, 1935: 1149). Incubation in the Sphaeriidae until the young are well developed also may represent fortuitous circumvention of exposing the early developmental stages to the medium of freshwater. Pelecypods inhabiting shallow-water coastal areas, subject to vicissitudes in salinity, commonly have what may be regarded as adaptive modifications benefiting survival of the young. The latter include: nidamentous forms such as *Nucula delphinodonta* and *Milneria kelseyi* (*cf.*, Abbott, 1954: 42, 380); incubatory genera such as *Gemma, Parasterte, Transennella* (*cf.*, Abbott, 1954: 42, 412-19); species with testaceous larvae characteristic of some of the Nuculidae (*cf.*, Lankester, 1906: 248-249; Abbott, 1954: 334-335); and, the incubatory oysters of the genus *Ostrea* (*cf.*, Abbott, 1954: 373-374). Pelecypods inhabiting low salinity brackish waters, without obvious modification of the early developmental stages, seem rare and with little or nothing known of the duration of their pelagic stages nor size attained before settling (or, *e.g.*, affixation as in the case of the Dreissenidae). The problem of buoyancy would seem to be particularly cogent for molluscan larvae in a medium so much less dense than that of a strictly marine environment, and the problem becomes greater with increasing size. One solution might be a shortening of the pelagic stage and an early metamorphosis (perhaps accompanied by adaptive decreased density of the body and cell fluids, *i.e.* osmotic adjustment, of developmental stages and adults). Maintaining a pelagic existence in low salinity waters is also made more difficult by shell growth resulting in increased relative density of the organism.

The lack of observed sizes of *Rangia* between 93 and 375 μ either as pelagic larvae or metamorphosed juveniles calls for a tentative explanation to the effect either that the young, if pelagic during this size, are confined to the bottom (and were missed in the plankton samples, all taken from near the surface), or that they were destroyed or rendered unrecognizable in taking and preserving the plankton samples. On the other hand, smaller sizes (than 375 μ) of juvenile shells of *Rangia* may have been present on the bottom at times of collection and could have been missed in the counting due to breaking up or chemical disintegration during storage of the bottom samples, due to their extreme fragility.

VI. Inclusion of an Undescribed Species of Rangia (Rangianella)

In July, 1960 the existence of a small undescribed species of *Rangia* (*Rangianella*) occurring in Lake Pontchartrain was made known to this writer by the late Mr. Percy Viosca Jr. of the Louisiana Wild Life and Fisheries Commission and Dr. J. P. E. Morrison of the U. S. National Museum. The maximum size of this species was said to be 10 mm. The inclusion of this small species as juveniles of *R. cuneata* in the 1957-58 collections by the present unsuspecting investigator seems certain. An adequate estimate of the error involved in estimates of population density of juveniles of *R. cuneata* 10 mm and under cannot be made because complete quantitative collections were not kept beyond 1959.

Table 5.

Qualitative collections of clams within size range limits of Rangianella sp.

Collection Dates	*Rangianella* sp. in Proportion to Total Number of Small Clams Collected			
	Range (1-12 mm)		Range (1-10 mm)	
	Number	Percent	Number	Percent
16 July 1960	567	4.2	557	4.3
21 Oct. 1960	121	19.8	65	37.0
24 Jan. 1961	56	8.9	43	11.6
4 April 1961	58	6.9	26	7.7

Additional collections were made in 1960 and 1961, however, in an attempt to clarify the relation between the densities of the two species. What the relation was in 1957 and 1958 can only be inferred with reservation from these later findings.

The morphological differences between equal sized individuals of the two species are distinct. The *Rangianella* have the subgeneric distinction of short non-serrated lateral hinge teeth; the pallial sinus is shallow, wide and only slightly evident. Externally they are more triangular in outline, narrower in transverse diameter; the beaks are lower, less divergent and projecting and more likely to be eroded than in the juveniles of *R. cuneata* of corresponding size (from correspondence between Morrison and the editor of *T.S.Z.*, August, 1960).

Qualitative and quantitative collections made in 1960 and 1961 are represented in Tables 5-8 and Figure 22. The qualitative collections were made at north shore station Number 1 (fig. 1). Because the meshes of the dredge retained clams 4 mm and over the critical size range in comparing proportions of the two species would be 4-10 mm. In some collections a few specimens of *Rangianella* were as large as 12 mm. As Dr. Morrison has stated the maximum size to be 10 mm, and this seems to be generally true, comparison was made on the basis of two size ranges (4-10 mm and 4-12 mm).

Data showing the proportion of small clams recognizable as *Rangianella* are presented in Table 5. More than half the July collection of 1960 was sent to Dr. Morrison for identification of the *Rangianella.* Three and six tenths percent of the small clams 10 mm and under were identified as *Rangianella. Rangianella* in the remainder of the collection (as well as the *Rangianella* in the later collections) were identified by me. In the entire July collection 4.3 percent of the clams 4-10 mm in length were *Rangianella* (Table 5). The distributions of sizes are shown diagrammatically for both species in Figure 22. The proportion of *Rangianella* was at its highest in the October collection while the following January and April collections showed a progressive decline in the proportion. This decline was accompanied by an increase in maximum size of *Rangianella:* 7 mm in July, 8 mm in October, 11 mm in January, and 12 mm in April (fig. 22).

Examination of gonadal fluid from specimens of *Rangianella* revealed mature eggs and spermatozoa in individuals as small as 4.75 mm, hence individuals of this size and larger can be considered potentially sexually mature. Only five specimens of the July collection were examined; each contained mature gametes. Specimens from the other collections were examined; the results are presented in Table 8 in comparison with findings from gonadal fluid examinations of *Rangia cuneata* collected on the same dates. Mature eggs of *Rangianella* were 30 μ in diameter (*cf.*, 69 μ for *Rangia cuneata*). In the October and January collections proportionally more *Rangianella* were found with recognizable gametes than *R. cuneata.* In the April collection, however, no significant difference was indicated. This infers that spawning by *Rangianella* may extend later into the fall and winter htan that of *R. cuneata*.

Apparently this small species of *Rangianella* is short lived; some may live as long as one year perhaps, with few adults and a greater number of juveniles surviving the winter to initiate repopulation of the habitat each spring. Mortality due to predation and physical hazards seem to be especially heavy in the fall. Early sexual maturity conveys the impression that with rapid growth in the spring reproductive age may be attained easily within a few weeks after the initial spawning of the season when temperature is rising. By the end of the summer or in mid-autumn several generations may be added to the population, thus explaining the great contrast in the July and October proportions of *Rangianella* to *Rangia cuneata*. The production of several generations rapidly in one year may be one reason why this small clam, having a ratio of egg size to parental biomass many times greater than that of *R. cuneata*, can compete with the latter species which has an advantage in obviously producing greater numbers of young per female early in the spring and summer.

The collections made in 1960 and 1961 indicate that the greatest error caused by inclusion of *Rangianella* in the 1957-58 collections was an over-estimation of juveniles (under about 10 mm, size class 15) in the later summer and fall collections. The two quantitative collections (Table 7, fig. 22) were intended to provide additional information, concerning relative density of the two species, in comparison with the qualitative collections and particularly to provide specimens smaller than 4 mm (because these were not taken by the qualitative dredge). The October quantitative collection was based on eight hauls of the small Elkman dredge "randomly" taken in the north shore

TABLE 6.
Qualitative collections of clams within size range limits of Rangia cuneata.

Collection Dates	*Rangianella* sp. and Juveniles of *R. cuneata* combined (4-24 mm)	Juveniles of *R. cuneata* (4-24 mm)		Adults of *R. cuneata* —24 mm	Adults of *R. cuneata* (25-30 mm incl.)	
		Number	Percent of Total		Number	Percent of Total Adults
16 July 60	575	551	95.8	—	—	—
21 Oct. 60	137	113	82.5	51	3	5.9
24 Jan. 61	92	87	94.6	86	12	14.0
4 April 61	158	151	97.5	81	2	2.4

TABLE 7.
Quantitative estimates of population density (North Shore area, 1960-61).

Collection Dates	Density/sq. ft. 4-24 mm *Rangianella* sp. and Juveniles of *Rangia cuneata*	4-24 mm Juveniles of *Rangia cuneata* Density/sq. ft.	—24 mm Adults of *Rangia cuneata* Density/sq. ft.
21 Oct. 60	165.500	96.500 (58.3%)	.500
24 Jan. 61	7.637	7.637	1.455

TABLE 8.
Results of gonadal inspection of clams collected in 1960 and 1961.

Collection Dates	Species	Number Examined	Females	Males	Sex Undeterminable	Number Parasitized
16 July 60	*Rangia cuneata*	0	—	—	—	—
	Rangianella sp.	5	1	4	0	0
21 Oct. 60	*Rangia cuneata*	33	19 (57.6%)	5 (15.1%)	9 (27.2%)	3 (9.1%)
	Rangianella sp.	23	10 (43.5%)	11 (47.8%)	2 (8.7%)	0
24 Jan. 61	*Rangia cuneata*	32	0	0	32	1 (3.1%)
	Rangianella sp.	5	1	2	2	0
4 April 61	*Rangia cuneata*	30	2	5	23	0
	Rangianella sp.	1	0	1	3	0

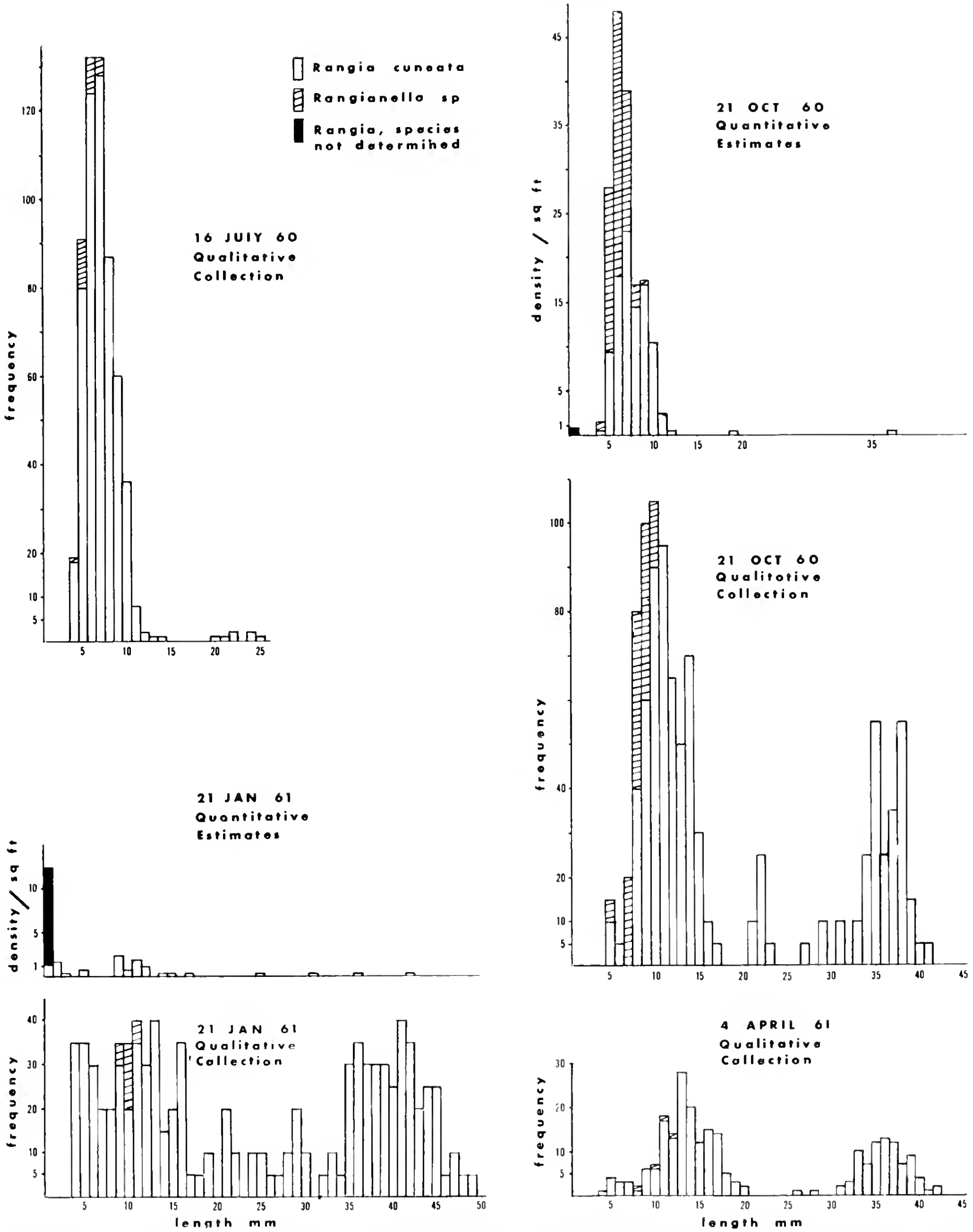


Figure 22. Proportional relations of *Rangia* and *Rangianella* in collections from the north shore area.

area among the several collecting stations. The January collection was based on twelve hauls in the same area. Small specimens of *Rangia* were found in both the October and the January quantitative collections but *Rangianella* smaller than 2 mm were not distinguishable with any certainty from *Rangia cuneata* among these small clams. In January quantitative collections all specimens except those under 2 mm were identified as *R. cuneata* and in the qualitative collection taken in January no specimens of *Rangia-*

nella were found that were less than 9 mm. The large numbers of juveniles less than 2 mm in length may have included *Rangianella* and *Rangia cuneata* as well.

Agreement between the qualitative collections (Table 6) and the quantitative collections (Table 7) of the two species is not exact as would be expected because of both paucity of quantitative samples and the effect of clumping. However, the essential reduction in *Rangianella* is clear in both sets of data.

VII. DISCUSSION

The data present the impression that Lake Pontchartrain is highly productive as indicated by criteria such as the littoral qualities, shallow water and long shore line (when marshland extensions are included), and high concentration of total phorphorus, variable electrolytes, relatively high amounts of organic matter (both in suspension and in bottom deposits), and the presence of large aquatic plants. However, physical factors such as temperature changes, high winds that disturb bottom deposits and increase turbidity thereby interfering with light and consequently phytoplankton growth, connection with waters of contrasting salinity and tidal fluctuation, periodic influxes of fresh water, and dark coloration of the latter, probably tend to reduce biological productivity.

The immoderate nature of these contrasting conditions can only prohibit the establishment of many species and allow a few to dominate. A direct relation between size and salinity of the water has been found for many species of fish and invertebrates (Gunter, 1950: 48-50) in Gulf coastal regions and the significance of this has been considered to be better adaptation to fresh water or low salinity on the part of younger members of species the adults of which are recognized as marine forms. That possibilities of high potential food supply for growth and development, relative to that of the marine environment (and aside from protection afforded from marine predators and parasites) aid in such an adaptation appear not to have been investigated extensively by anyone. Strictly brackish water species of invertebrates in the Louisiana marshlands are apparently few (Gunter and Shell, 1958: 14, 19, 20) but there seems to be little doubt that *Rangia cuneata* could be assigned to any other categorical rank based on salinity, since it is not found in freshwater nor commonly in seawater.

The paucity of other molluscan species in the areas studied and the small adult sizes of those present seems to indicate that *Rangia* has few competitors as a filter feeder and does not suffer greatly from intraspecific competition when the tendency for clumping is taken into account.

The utilization of a wide variety of organic matter by pelecypods has been deduced by authors (*e.g.*, Coe, 1947) on the basis of discoveries of weak cellulases in the crystalline style as well as amylase and glycogenase. Experiments with filtered phagocyte-free stomach juice of *Tridacna* and *Pinctada* supposedly have proved the presence of free proteolytic and lipolytic enzymes as well as those acting on carbohydrates (Mansour, 1946: 482). Yonge (1946: 729), however, maintained that lamellibranchs are specialized herbivores and stated that the proteolytic and lipolytic enzmyes were probably from ruptured phagocytes and that there is no cytological or histochemical evidence for extracellular enzymes of this nature in lamellibranchs. Whatever the case may be, the variety of organic matter in Lake Pontchartrain seems to offer abundant possibilities of food for *Rangia cuneata.*

Pelecypod larvae reared by Loosanoff (1954: 614-615) and his associates could be classified into two general types based on food requirements. The oyster larvae, both Atlantic and Pacific species, apparently were able to utilize only a few species of marine bacteria, while clam and mussel larvae thrived on almost any organism small enough to be ingested. *Rangia* seems to belong to the latter group unless dependency for food upon some particular organisms in its environment can be demonstrated.

The problems of population sampling in ecological investigations are still to be solved, according to Odum (1953: 156-157), before dependable estimates of density can be obtained. One suggestion made by Odum was the selection of as homogeneous an area as possible for sampling and caution was advised concerning the possibility that the organisms to be sampled could be responding to local factors unknown to the investigator. The writer's estimates of 1.62 or 5.45 percent adult *Rangia* added to the population each year, on the basis of certain size class densities observed, appear small assuming a theoretically stable population. If 5 percent of the adult population was added annually, 20 years of general stability would be required for one year class to enter and leave the population. Marked specimens of different sizes allowed to remain in the habitat and recovered after one or two years are needed to establish the growth rate of certain sizes of adults and to better infer the life span of *Rangia*. Assuming that the population fluctuates yearly and in some years greater numbers are added or lost or die would seem logical considering environmental differences from one year to another. Extreme fluctuation in bottom populations from one year to another seems to be associated with possession of a pelagic larvae (*cf*., Moore, 1958: 317). Maintenance of the breeding population undoubtedly depends upon a combination of many factors including number spawned and settled in any one year which in turn depends upon food and temperature, accidental death due to unfavorable physical environment, and predation of both adults and juveniles which probably varies from one year to another. An average life span of eight years, for example, does not preclude the possibility that some adults may live much longer and, in view of the possible large numbers spawned, a large area reasonably could be repopulated in a relatively short time even if the major part of the breeding population were suddenly eliminated.

In this investigation of *Rangia* local factors were expected to influence population density. Since several were possibly involved in the differences found between the two study areas the consideration of some of these factors separately is reasonable.

Among the environmental conditions measured, temperature, although important in a general way to the species, or as a primary factor in controlling both maturation of gametes and spawning, cannot be held responsible for the difference found in *Rangia cuneata* of the two areas. Temperature was not greatly different in the two areas. This is not surprising considering the shallow depth, wind action and response of water temperature to that of the air in both areas.

Salinity was slightly different in the two areas and because of proximity to fresh-water inlets the north shore area may, at times, be greatly different in regard to this factor. If salinity were a factor responsible for the differences (in sizes of adults, shell thickness, population density of adults, incidence of unreleased mature gametes, and extent of parasitism) in *R. cuneata* of the two areas, a gradient extending away from the mouth of Bayou Bonfouca involving some of these characteristics (*e.g.*, size of adults) would be expected. The only such gradient indicated by the collections was that of increasing population density toward the mouth of the bayou (where decaying vegetation in the bottom deposits was noticably plentiful). Specimens taken from near the mouth of Bayou Bonfouca, where salinity was most likely to have been lowest and more variable in the north shore area, were not noticeably different in size or incidence of unreleased gametes from specimens taken two miles further west where there were no major inlets. The extent of any differences seen in *Rangia cuneata* of the north shore area, as compared to south shore specimens, that may be attributable to salinity differences is not readily apparent.

Since animals generally obtain phosphorus secondarily from plants, the population density and/or growth of *Rangia* would necessarily first be limited by lack of living or dead plant matter. Since all total phosphorus values were high, this element cannot be considered limiting either to plants or *Rangia* in the lake. According to Hutchinson (1948: 232) rooted aquatic plants are capable of taking up phosphorus from the water and storing this element until released by decomposition after the plant dies; also bottom sediments release part of their phosphorus content back into the water. In view of the great extent of marshland whose waters are directly connected with Lake Pontchartrain, its sediments of high organic content and its "freedom of expanse" (Steinmayer, 1939) the high total phosphorus values might be explained by regarding the entire lake and its adjacent marshland as a storage area for this element, with possible additions from some inorganic sources by erosion and leaching.

On the basis of the differences in phytoplankton pigment concentration there may be reason to suspect that phytoplankton could be more abundant in the north shore area, particularly if species are involved that may be better adapted to fresh-water. More food might explain greater population density but does not reasonably account for smaller size and the differences in the gonadal condition. On the other hand, the differences in pigment values were not great and may not have been conclusively different. Wind action may effect considerably homogeneity in plankton concentration in the east end of the lake, except perhaps at certain times of the year, or depending upon differences in seasons from one year to another.

The remaining major accountable factor to be considered is organic matter, both in solution and in the bottom deposits. Wind action may be expected to keep the lake water fairly homogeneous part of the time during the year so that organic matter in solution might generally be little different in concentration from one area to the other. However, a considerable difference appeared in the estimates for the two areas in the spring and early summer of 1958. On the basis of empirical observations organic matter in the bottom deposits is unquestionably greater in the north shore area. Steinmayer (1939: 17-19), in describing the sediments from Lake Pontchartrain, stated "In general, high organic content is associated with low texture, and conversely low organic content implies high coarse grain content. . . . The size of the sediment varies from coarse to fine out from the shore in some places and at other places varies in the other direction. A section normal to Little Woods is an example of the former, and a section normal to Bayou Lacombe is an example of the latter." According to this author organic material is chiefly of plant origin and varies in average percentage from 0.528 in bottom sediments classified as "sands" to 6.72 in bottom classified as "clays".

In recent years a few authors have studied a direct correlation between organic matter in bottom deposits and population density of pelecypods of several species. The correlation has apparently been noticed by several investigators through the years but the explanations were that pelecypod larvae settled in regions of high organic matter or mud bottom because those areas were in locations where reductions in current velocity left deposits of silt and mud (organic matter) as well as the settling spat (*cf.* Pratt, 1953: 66-67; Moore, 1958: 317).

Newcombe and Kessler (1936), in a study of growth indices of *Mya arenaria*, compared plots of shell weight on shell length and dry body weight on shell length in specimens from the Bay of Fundy, the Gulf of Maine, the Gulf of St. Lawrence and Chesapeake Bay. The ratios of shell weight per shell length were higher for clams from the Bay of Fundy and the Gulf of Maine (a twofold difference in the larger specimens from the Bay of Fundy). Both areas were similar in salinity and in having a high "mud" content although they differed in temperature. The Gulf of St. Lawrence and Chesapeake Bay were characterized predominantly by "sand" bottom but salinity was considerably lower in Chesapeake Bay. The ratios of shell length to shell weight were nearly identical for the latter two areas. The bottom deposits of these two areas were described as differeing from those of the Bay of Fundy "in that the soil is not nearly as compact." Apparently the differences in salinity had no effect on the ratio of shell length to shell weight. Salinity in the Gulf of St. Lawrence was said to be comparable to that in the Bay of Fundy. The ratio values of dry body weight on shell length were determined for clams from the Bay of Fundy and Chesapeake Bay only. The values of this ratio were considerably lower for clams from the Bay of Fundy.

The study of Newcombe and Kessler suggests that mud or organic content in bottom deposits may have been partly responsible for greater shell weight per unit length and lesser percentage dry body weight (perhaps involving the gonadal condition) although the authors emphasized the correlation of shell weight with temperature, an inverse relation resulting. An opposite trend was found in the case of body weights.

Swan (1952: 530-531) reported a difference in shell weight for comparable lengths in populations of *Mya arenaria* living only a few miles apart. The longer but relatively lighter shells were from clams grown in a bottom type varying from slightly muddy sand to sand and fine gravel mixture. The heavier shorter shells were from clams living in a compact mud-gravel-mixture. In experimentally planted clams in sand and a combination of mud-gravel side by side, the clams grown in sand averaged roughly twice the gain in length of those in the mud-gravel mixture and had shells of appreciably lighter weight and of proportionally smaller width and thickness.

Pratt (1953) studied abundance and

growth of *Mercenaria mercenaria* and *Callocardia morhuana* in relation to bottom sediments. He found that population density was negatively correlated with the particle size of the major bottom constituent; greatest average concentration was in predominantly muddy grounds, less in sandy bottoms and least in rocky areas. *Mercenaria* was most abundant in predominantly fine sediments, but in such sediments the abundance was generally a function of the coarseness of the minor constituents. Both species occurred in greater average numbers in predominantly muddy bottoms than in sandy or rocky areas, and where sand was the major constituent the presence of mud favored both species. In experimental plantings of *Mercenaria* in contiguous frames, one with sand and the other with soil of high organic content, the specimens in sand grew 24 percent faster than those in mud. The difference was "highly significant" and "no observations were made which might have explained the difference in growth". Pratt reasoned that the difference in growth rate must have arisen directly or indirectly from benthonic factors and suggested that a mud bottom, rich in decomposing organic matter might reduce the oxygen content of the water much more than does the sand.

Pratt and Campbell (1956) studied the growth rate of *Mercenaria mercenaria* in Naragansett Bay over a five year period by using retrievable boxes placed on the bottom and containing natural sediments and individually identifiable animals. Growth rates in different parts of the bay showed variations up to nearly three-fold in any given year and were consistently slower in sediments with higher silt-clay content although growth rates were not strictly proportional to this or any other observed property of the sediment. The authors stated that growth was not appreciably influenced by existing differences in the speed of current, dissolved oxygen, or salinity of the bottom water. In discussing the relationship between slower growth rate and mud or silt-clay bottom the authors included the possibility that fine sediments may cause interruptions in feeding and additional expenditure of energy occasioned by the necessity for frequent clearing of the animal's filtering apparatus, also the possibility that mud may produce harmful or inhibitory substances. Experiments by these authors, unfortunately interrupted before completion, involving the pH of mud and sand bottom deposits in aquaria showed a minutely higher value for mud than for sand.

Growth rate of *Mya arenaria* on sandy bottom was over four times greater than in clams less than one-half mile away on silted bottom (Spear and Glude, 1957).

High densities of juvenile clams in the Chesapeake Bay area reported by Manning and Pfitzenmeyer (1958) were associated with bottom deposits of mud over clay.

Bader (1954) studied organic matter of bottom deposits in relation to the distribution and population density of 16 species of pelecypods in the Gulf of Maine. There appeared to be an overall potential toward an increase in pelecypod density as the median diameter of sedimentary particles decreased and approached a range of 0.15 to 0.05 mm, beyond this toward the extremely fine sizes there was a sharp drop in the densities. Salinity in the area varied only 0.2 $_{0}/_{00}$ and temperature only 4° F so there was no relation apparent between the two factors and the pelecypod populations. In consideration of the abrupt decline in population density with decrease in particle size beyond a certain point an investigation was made concerning the state of decomposition of the organic matter. This was done by subjecting samples to chemical analysis and comparing the proportion of lignin which is highly refractory to the non-refractory portion by the coefficient or ratio, L/Rn (L = lignin, Rn = total non-refractory or readily decomposable organic matter) which was taken to indicate a stage of decomposition of the organic matter in the bottom deposits. As the numerical value of the ratio increased an increase in the degree of decomposition was indicated. The plotted relationship of the decomposition coefficient of organic matter in the sediment to pelecypod density showed that the population density was lowered sharply when the coefficient exceeded 1.0. The pelecypod density increased initially with increase in organic content of the sediment, but beyond 3 percent organic content "the products of decomposition and/or decline in available oxygen became limiting variables". No pelecypods were found at 4.5 percent organic content. Bader discussed the possibility that microbiological decomposition of organic matter in sediments can produce aldehydes, hydrogen sulphide, methane, and many other toxic products and that degree of decomposition is correlated with abundance of bacteria which can cause serious drain in available oxygen supply.

Moore (1958: 95-99) discussed possibilities of specific reactions to particular organic compounds in seawater. Collier, *et. al.* (1953) showed a correlation between the activity of oysters and the abundance of an unidentified carbohydrate in the water. Clam beds (*Mercenaria mercenaria*) which have declined in value through failure of spat to settle may be recolonized when soil is spread over the bottom surface or even if the surface is ploughed (Moore, 1958: 309).

According to Loosanoff (1954) clam larvae may be specialized as to food type according to their age and size, smaller specimens requiring smaller food organisms such as bacteria and other small types of nannoplankton. If larger amounts of bacteria are commonly associated with bottom sediments high in organic content this may be an explanation, in part at least, for greater abundance and possibly survival of older juveniles in this type of bottom, if older juveniles (one year of age) also may be somewhat specialized. This could partly account for the apparent greater survival of young *Rangia* in the north shore area, or lack of survival in the south shore area. On the other hand comparatively high density of tiny juveniles in the south shore area may not be a regular occurrence but occasionally may follow temporary high organic content on the surface of the sand in that area.

Publications concerning comparisons of gonadal conditions of clams from bottom types differing in organic content are unknown to this writer. Since the gametogenic cycle appears to be a dominating physiological response to environmental conditions, it could be as profoundly affected by such conditions as shell growth and population density. At least this appears to be a possibility in *Rangia.* Larger size in *Rangia* grown on more sandy bottom such as that of the south shore area may result from more energy being available for growth since the gametes apparently are not spawned out completely but are resorbed. This does not appear to be the case for *Rangia* of all ages, however, because growth rate is already considerably greater in the south shore clams in the first and second year sizes before gonadal development is complete. Whether or not the differences in length/weight relationship hold for young clams of the two areas before reaching sexual maturity would be interesting to know. The differences both in growth rate and gonadal condition appear to be separate direct results of the environment. That the difference in shell weight in comparable sizes is more closely related to growth rate differences seems logical if shell thickness is affected at the expense of shell area. If this is true an explanation is necessary to account for the greater relative weight and smaller size of the north shore shells. Since the pelecypod shell is decalcified or eroded on its inner surfaces when the animal is exposed to increases in CO^2 (Dugal and Irving, 1937), greater shell thickness or weight may be the result of physiological compensation as a protective reaction to carbonic acid or any other acid present. A low pH value might well be suspected for the highly organic subsurface bottom deposits of the north shore area, particularly in view of the greater umbonal erosion of the shells in that area. A smaller size and greater shell thickness might have two advantages in such an environment: less surface area exposed and greater reserve of calcium carbonate per size for buffering.

That the gonadal condition of north shore *Rangia* generally appears to be more "spawned out" than that of the south shore clams may indicate that the full extent of gonadal development comparable to the latter is never or rarely attained. This difference may also mean that spawning continues for equally long periods in both areas but the "spawned out" condition is seen more often in the north shore clams, because these animals might have had fewer gametes to shed and recovery may take longer. The latter view of the differences in gonadal condition allows the possibility that gonadal fullness or ripeness may be positively correlated with growth rate and negatively correlated with shell weight, or at least that the differences in shell weight and gonadal condition are caused by the same factor or factors. On the other hand, possibly more extensive spawning may be caused simply by greater chemical stimulation due to the greater density of clams in the north shore area since the spawning of one individual is known to initiate spawning in others in many pelecypods (Loosanoff, 1954). Certainly the concentration of the substance eliciting spawning would be greater in the north shore area if population density there is as much greater as the quantitative bottom samples indicate.

The bearing that this question, of causal factors in differential spawning in pelecypods, may have upon the commercial problem of "watery" oysters produced each summer in Gulf coastal waters may be important in indicating need for greater attention to control of bottom conditions (*e.g.*, selection of bottom for "seeding", or for seasonal exploitation). This is of particular interest if high growth rate and incomplete spawning in oysters are ecologically linked and determined largely by bottom type. Retention of gametes seems certain to make for better quality in the oyster as a commercial product, while high growth rate has obvious economic advantages.

Evidence presented by investigators (*e.g.*, Orton, 1928; Coe, 1947) supporting the conclusion that growth rate of adults (sexually mature individuals) is modified by the gametogenic cycle seems sufficient to warrant the possibility that the growth rate of the north shore adult *Rangia*, presumably at the height of sexual maturity, is greatly curtailed by increased gametogenic activity and spawning over and above that from the south shore clams. The shape of the curve of size distribution from the north shore clams leads one to suspect that the majority nearly cease growing at a certain size since a greater percentage of the entire population of adults represented falls within a narrow range of size limits about the mean. The comparative gonadal condition can only support the assumption that greater spawning activity slows the growth rate of these clams. The relatively few individuals achieving larger sizes in the area may be less active in spawning and have higher growth rates. The small modal peak on the left in the distribution of south shore sizes (fig. 9) may indicate something of the same phenomena in the south shore clams shortly after achieving sexual maturity, namely slowed growth rate affected by slightly greater spawning activity which does not continue, as indicated by the plateau to the right in the distribution curve. That the shape of the size distribution curves of the larger sizes (larger 10 percent of the adult population) in both areas is similar and that the length weight ratio is similar for this portion of the population may indicate that a differential reaction to the respective environments is non-functional after a certain age has been reached. This would affect the north shore clams more than the south shore clams because the former hypothetically would have been restrained from expressing full growth rate potential. The size or age at which this differential reaction ceases to function is represented in the length weight distributions where the differences in the ratio values become non-significant with increasing size. The irregularity in the north shore distribution clearly indicates a greater comparative increase in rate of linear increment, "overshoot" or possibly over-compensation and recovery with further increase in size or age.

That the larger north shore clams were grown in sandy places in that area, and were large because of this, is improbable since no clams were found in that area equaling the largest sizes of the south shore area. The possibility that smaller size of the north shore *Rangia* is due exclusively to crowding seems untenable because, on an empirical basis, adults of maximal size (for the north shore area) were more commonly found where population density was highest in that area; *i.e.*, there were no indications that within the general area a negative correlation existed between maximal size and population density. However, an investigation producing conclusive results concerning this question is certainly in order.

Local environmental conditions other than salinity or temperature are known to affect the growth rate, size, and shape of nonburrowing pelecypods such as *Mytilus* (Lubinsky, 1958) and *Crassostrea* (Butler, 1954). The effects of mud on oysters are fairly well known but are generally believed to result from the direct inhibitory effects of particles in suspension and crowding in such environments. The extent of the differences, seen in pelecypods living on muddy bottoms, directly referable to chemical and physical phenomena would be difficult to separate from other influential factors abounding in these habitats, *e.g.*, inter- and intra-specific competition, predation, and parasitism. The significantly higher percentage of *Rangia* infected with trematodes in the north shore area and the empirically observed greater densities of other mollusks and annelids and the probability of high density of unobserved microorganisms in this area as well as the possibility of great fluctuation in the physical environment suggest a gradation in an estuarine ecotone as described by Odum (1953: 283).

VIII. SUMMARY AND CONCLUSIONS

Between February 10, 1957 and July 30, 1958 the habitat of *Rangia cuneata* in Lake Pontchartrain varied in temperature between 47 and 90° F. Monthly mean lake temperatures varied between 48.2 and 85.1 in close conformity with monthly mean air temperatures which varied between 48.1 and 84.2° F.

Salinity varied between 0.5 ‰ and 5.7 ‰ during the period but is known to vary between 1.5 and 9.78 ‰ within a year. Salinity is influenced chiefly by runoff into the lake and tide level and partly by wind direction and velocity.

Total phosphorus values representing the two study areas ranged between 0.0035 and 0.0113 μg at/ml, a range considerably higher than that for seawater generally, and indicative of potentially high productivity. Phosphorus cannot be considered a limiting element in the environment. Total phosphorus varied directly with salinity during the period.

Phytoplankton pigment values were highly variable; highest values occurred in the early summer of 1958.

Estimates of oxidizable organic matter in solution were higher in the early summers of both 1957 and 1958, with the highest estimates representing the north shore area in the early summer of 1958. All values were generally higher than average values recorded for certain other coastal waters.

With the exception of organic matter in solution the physical and biological environmental factors that were quantitatively measured or estimated did not differ greatly between the two study areas. With reference to the north shore area the greatest differences in the two environments were: (1) empirically determined higher organic content of the bottom deposits; (2) greater general variability in (a) salinity, (b) organic matter in solution, and possibly (c) phytoplankton concentration.

The north shore area has a greater population density of adult (sexually mature) *Rangia* than the south shore area. The adults of the north shore area are smaller and less variable in length than those of the south shore area. A majority (90 percent) of the smaller of the north shore adults have heavier shells than adults of comparable size in the south shore area. The shells of the north shore clams are generally darker in color and more extensively eroded than those of the south shore area.

Sex is more frequently distinguishable and the gonad firmer in the south shore clams; also coloration of the gonadal tissues is more distinctive in the south shore clams. Sex was least distinguishable in the clams of both areas in early March and in June coinciding with times of least gonadal color distinction. Gonadal parasitism is more extensive in clams of the north shore.

The growth rate of *Rangia* of all sizes is highest in early summer. Growth rate of all sizes, except approximately the larger 10 percent of adults in each area, is consistently higher in the south shore area.

Evidence was presented suggesting that the observed differences in *Rangia cuneata* of the two areas investigated were attributable chiefly to differences in organic content of bottom deposits and organic matter in solution.

IX. REFERENCES CITED

ABBOTT, R. TUCKER 1956. *American Seashells.* Van Nostrand, Princeton, 560 pp.

ALLEE, W. C., ALFRED E. EMERSON, ORLANDO PARK, THOMAS PARK and KARL P. SCHMIDT 1949. *Principles of Animal Ecology.* W. B. Saunders Company, Philadelphia and London. 729 pp.

AMERICAN PUBLIC HEALTH ASSOCIATION 1936. *Standard Methods for the Examination of Water and Sewage.* 8th ed., 288 pp.

AWATI, P. R. and H. S. RAI 1931. The Bombay oyster, *Ostrea cucullata. Indian Zool. Mem.* 3: 1-107.

AYERS, JOHN C. 1956. Population dynamics of the marine clam, *Mya arenaria. Limnol. & Oceanography* 1(1): 26-34.

BADER, R. G. 1954. The role of organic matter in determining the distribution of pelecypods in marine sediments. *Jour. Marine Res.*, 13: 32-47.

BEHRE, E. H. 1950. Annotated list of the fauna of the Grand Isle region 1928-46. *Occ. Pap. Marine Lab., L. S. U.* 6: 1-66.

BUTLER, PHILIP A. 1954. Summary of our knowledge of the oyster in the Gulf of Mexico. *U. S. Fishery Bull.* 89, 55: 479-489.

COE, W. R. 1943. Sexual differentiation in mollusks. *Quart. Rev. Biol.* 18: 154-164, also 19: 85-97.

———— 1947. Nutrition, growth and sexuality of the Pismo clam (*Tivela stultorum*). *Jour. Exp. Zool.* 104(1): 1-24.

———— and Harry J. Turner 1938. Development of the gonads and gametes in the soft shelled clam (*Mya arenaria*). *Jour. Morph.* 62: 91-111.

Collier, Albert, S. M. Ray, A. W. Magnitzky, and Joe E. Bell 1953. Effect of dissolved organic substances on oysters. *U. S. Fishery Bull.* 84, 54: 166-185.

Creitz, B. I. and F. A. Richards 1955. The estimation and characterization of plankton populations by pigment analyses. III. A note on the use of "millepore" membrane filters in the estimation of plankton pigments. *Jour. Marine Res.* 14: 211-216.

Curl, Herbert J. 1959. The origin and distribution of phosphorus in western Lake Erie. *Limnol. & Oceanography* 4(1): 66-75.

Deming, Horace G. 1944. *General Chemistry.* 5th Ed., John Wiley & Sons, N. Y. 692 pp.

Dall, Wm. H. 1894. Monograph of the genus *Gnathodon* Gray (*Rangia* Desmoulins). *Proc. U. S. Nat. Mus.* 17: 89-106.

Dugal, Louis and Laurence Irving 1937. The increase of CO_2 and decalcification in certain pelecypods. (Abstract) *Biol. Bull.* 73: 379.

Gunter, Gordon 1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. *Publ. Inst. Marine Sci.* 1(2): 7-51.

———— 1952. Historical changes in the Mississippi River and the adjacent marine environment. *Ibid.* 2(3): 119-139.

———— and Wm. E. Shell, Jr. 1958. A study of an estuarine area with water level control in the Louisiana marsh. *Proc. La. Acad. Sci.* 21: 5-33.

Hansen, A. L. and R. J. Robinson 1953. The determination of organic phosphorus in seawater with perchloric acid oxidation. *Jour. Marine Res.* 7: 17-21.

Harris, G. D. 1902. The geology of the Mississippi embayment with special reference to the state of Louisiana. *Special Report No. I. Part VI. Geology and Agriculture.* (A report on the geology of Louisiana) Baton Rouge, Louisiana 39 pp.

Harris, R. A. 1902. The tides in the Rigolets. *Ibid.* (A report on the geology of Louisiana) Baton Rouge, Louisiana, pp. 256-260.

Harvey, H. W. 1928. *Biological Chemistry and Physics of Sea Water.* Cambridge Univ. Press, 188 pp.

———— 1948. The estimation of phosphates and total phosphorus in seawater. *Jour. Marine Biol. Assoc. U. K.* 27(2): 337-359.

———— 1955. *The Chemistry and Fertility of Sea Waters.* Cambridge Univ. Press, 218 pp.

Haskin, Harold H. 1954. Age determination in mollusks. *Trans. N. Y. Acad. Sci., Ser. II,* 16(6): 300-305.

Hedgpeth, Joel W. 1950. Notes on the marine invertebrate fauna of salt flat areas in Aransas National Wildlife Refuge, Texas. *Publ. Inst. Marine Sci.* 1(2): 103-119.

———— 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. *Ibid.* 3(1): 111-224.

Hutchinson, G. E. 1948. Teleological mechanisms: circular causal systems in ecology. *Ann. New York Acad. Sci.* 50: 221-246.

———— 1957. *A Treatise on Limnology.* Vol. I, John Wiley & Sons, N. Y.

Johnson, Charles W. 1934. List of the marine mollusca of the Atlantic coast from Labrador to Texas. *Proc. Boston Soc. Nat. Hist.* 40(1): 1-204.

Korringa, P. 1956. Oyster culture in South Africa (Hydrographical, biological and ostreological observations in the Knysna Lagoon, with notes on conditions in other South African waters). *Investig. Rept. No. 20, Dept. Commerce and Industries. Commerce and Industry* 14(7): 287-370.

Kozminski, Z. 1938. Amount and distribution of the chlorophyll in some lakes of northeastern Wisconsin. *Trans. Wisc. Acad. Sci., Arts & Lett.* 31: 411-438.

Ladd, Harry S. 1951. Brackish-water and marine assemblages of the Texas coast, with special reference to mollusks. *Publ. Inst. Marine Sci.* 2(1): 125-165.

Lankester, E. Ray (Ed.) 1906. *A Treatise on Zoology. Part V. Mollusca,* Adam & Charles Black, London, 346 pp.

Loosanoff, Victor L. 1937. Seasonal gonadal changes of adult clams, *Venus mercenaria* L. *Biol Bull.* 72(3): 406-417.

———— 1954. New advances in the study of bivalve larvae. *Amer. Sci.* 42(4): 607-623.

Lubinsky, I. 1958. Studies on *Mytilus edulis* L. of the "Calanus" expeditions to Hudson Bay and Ungava Bay. "Calanus" Series No. 16. *Canadian Jour. Zool.* 36(6): 869-879.

Manning, W. M. and K. E. Juday 1941. The chlorophyl content and productivity of some lakes in northeastern Wisconsin. *Trans. Wisc. Acad. Sci., Arts & Lett.* 33: 363-393.

Manning, J. H. and H. T. Pfitzenmeyer 1958. Exploratory survey of tidewater bottoms, Sommerset County, Maryland. (A preliminary report) *Resources Study Report No. 12. Maryland Dept. Res. and Educ., Chesapeake Biol. Lab., Solomons, Md.,* 6 pp.

Mansour, K. 1946. Food and the digestive processes of the lamellibranchs. *Nature* 157: 482.

Marmer, H. A. 1954. Tides and sea level in the Gulf of Mexico. *U. S. Fishery Bull.* 89, 55: 101-118.

Maury, C. J. 1920-22. Recent mollusks of the Gulf of Mexico and Pleistocene and Pliocene species from the Gulf states. *Bull. Amer. Palaeontol.* 8(34): 1-115; 9(38): 34-142.

Moore, Hilary B. 1958. *Marine Ecology.* New York, John Wiley & Sons 455 pp.

Moore, Donald R. 1961. The marine and brackish water Mollusca of the state of Mississippi. *Gulf Research Repts.*, 1(1): 1-58.

Newcombe, Curtis L. and Herman Kessler 1936. Variations in growth indices of *Mya arenaria* L. on the Atlantic coast of North America. *Ecology* 17(3): 429-443.

Odum, Eugene P. 1953. *Fundamentals of Ecology.* W. B. Saunders Co. Philadelphia, 351 pp.

Orton, J. H. 1928. On rhythmic periods of shell growth in *Ostrea edulis* with a note on fattening. *Jour. Marine Biol. Assoc. U. K.* 15: 365.

Pratt, David M. 1953. Abundance and growth of *Venus mercenaria* and *Callocardia morrhuana* in relation to the character of bottom sediments. *Jour. Marine Res.* 12(1): 60-74.

——— and D. A. Campbell 1956. Environmental factors affecting growth in *Venus mercenaria. Limnol. & Oceanography* 1: 2-17.

Pulley, T. E. 1952. An illustrated check list of marine mollusks of Texas. *Texas Jour. Sci.* 4(2): 167-199.

Redfield, Alfred C., Homer P. Smith, and Bostwick Ketchum 1937. The cycle of organic phosphorus in the Gulf of Maine. *Biol. Bull.* 73: 421-443.

Richards, Horace G. 1939. Marine Pleistocene of the Gulf coastal plain: Alabama, Mississippi and Louisiana. *Bull. Geol. Soc. Amer.* 50(2): 297-316.

Ricci, Edmond 1957. Contribution a la biometrie a la biologie et la physicochimie de la moule commune (*Mytilus galloprovincialis* Lmk.). Station *Oceanograph. de Salambo, Annales* No. 11, 147 pp.

Rothschild, M. 1935. Gigantism and variation in *Peringia ulvae* Penn caused by infection with larval trematodes. *Jour. Marine Biol. Assoc. U. K.* 20: 537-546.

Ruttner, Franz 1953. *Fundamentals of Limnology.* Univ. Toronto Press, 217 pp.

Spear, Harlan S. and John B. Glude 1957. Effects of environment and heredity on growth of the soft clam (*Mya arenaria*). *U. S. Fishery Bull.* 114, 57: 279-292.

Steinmayer, R. A. 1939. Botton sediments of Lake Pontchartrain, Louisiana. *Bull. Amer. Assoc. Petrol. Geol.* 23(1): 1-23.

Stephenson, William 1949. Certain effects of agitation upon the release of phosphate from mud. *Jour. Marine Biol. Assoc. U. K.* 28: 371-379.

Strecker, John Kern 1935. Notes on the marine shells of the Texas coast. *Baylor Bull.* 38(3): 48-60.

Suttkus, Royal D., Rezneat M. Darnell, and Jeanne H. Darnell 1953-54. Biological study of Lake Pontchartrain. (Annual Report 1953-54) Zoology Dept. Tulane Univ. 59 pp.

Sverdrup, H. U., Martin W. Johnson, and Richard Fleming 1942. *The Oceans, their Physics, Chemistry and General Biology.* Prentice Hall, New York.

Swan, E. F. 1952. The growth of the clam, *Mya arenaria*, as affected by the substratum. *Ecology* 33: 530-534.

Thiele, Johannes 1931. *Handbuch der Systematischen Weischtierkunde.* Bd. I, Abb. 783, 742 ss., Gustav Fisher, Jena.

——— 1935. *Ibid.*, Bd. II, Abb. 114, ss. 779-1153.

Thorson, Gunnar 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (oresund). *Meddel. Komm. Danmarks Fiskeri-og Havundersogelser, Serie Plankton.* Bind 4, Nr. 1, 484 pp.

Tranter, D. J. 1958a. Reproduction in Australian pearl oysters (Lamellibranchia) I. *Pinctada albina* (Lamarck): primary gonad development. *Austral. Jour. Marine & Freshwater Res.* 9(1): 135-143.

——— 1958b. Reproduction in Australian pearl oysters (Lamellibranchia) II. *Pinctada albina* (Lamarck): gametogenesis. *Ibid.* 9(1): 144-158.

U. S. Department of Commerce 1956. Coast and Geodetic Survey. Chart 1269, Lakes Pontchartrain and Maurepas.

——— 1957-58. Coast and Geodetic Survey. Tide tables (high and low water predications) 1957 and 1958 for East Coast North and South America including Greenland.

——— 1958. U. S. Weather Bureau. Climatological data (Louisiana). Annual Summary 1957. 57(13): 169.

——— 1958. U. S. Weather Bureau. Climatological data (Louisiana). 58(1-7): 3, 16, 31, 43, 55, 67, 83.

——— 1959. U. S. Weather Bureau. Current records. Post Office Bldg., New Orleans.

U. S. Department of War 1936. Corps of Engineers. (Map) Chef Menteur, La.

——— 1939. Corps of Engineers U. S. Army, (Map) Slidell, La.

Welch, Paul S. 1948. *Limnological Methods.* Blakiston Co., Philadelphia, 370 pp.

——— 1952. *Limnology.* McGraw-Hill Book Co., N. Y., 442 pp.

Yonge, C. M. 1946. Digestion of animals by lamellibranchs. *Nature.* 157: 729.

Abstract

Rangia cuneata, a pelecypod mollusk commonly inhabiting brackish water coastal areas of the northern Gulf of Mexico, is known from Neocene fossiliferous deposits of the Mississippi embayment and is abundantly represented into the Recent epoch. References to

this species in the literature are generally limited to mention in faunistic and geological surveys and species checklists. An investigation was made to determine pertinent physical and biological factors in the habitat of *R. cuneata* concerning population density, sizes of individuals, and the reproductive cycle. Two areas, approximately ten miles apart in Lake Pontchartrain, Louisiana were selected for the investigation carried out from February, 1957 to September, 1958. Temperature, salinity, total phosphorus, phytoplankton pigment concentration, and oxidizable organic matter in solution were measured and/or estimated. Population densities by size classes of adult clams and juveniles greater than 0.375 mm in length were estimated for the two areas from quantitative bottom samples collected throughout the period. Non-quantitative samples of adults were collected routinely for gonadal analysis to elucidate the reproductive cycle and estimate the extent of gonadal parasitism. Growth rates of clams under three years of age were estimated from analyses of the quantitative bottom samples and lines of growth interruption in the shells of adults.

Water temperature varied between 47° and 90° F. Salinity ranged between 0.5 and 5.77 o/oo. Total phosphorus ranged between 0.0035 and 0.0113 μg at/ml, values considerably higher than average for seawater indicating potentially high productivity. Total phosphorus varied directly with salinity (lowest in the summer of 1958) during the period. Phytoplankton pigment values were highly variable with the highest values representing the early summer of 1958. Estimates of oxidizable organic matter in solution were higher in the early summers of both 1957 and 1958. The environments of the two study areas differed chiefly in textural type and concentration of organic matter in the bottom deposits, and organic matter in solution.

Greater density (estimated 2.88 per sq. ft.) of adults occurred in the area having higher concentrations of organic matter. Also, in the area having higher organic matter mean size of adults and growth rate of clams under three years of age were less, and shell weights of comparable sizes were greater in the smaller 90 percent of adults (size frequency distribution). Survival of juveniles and spawning by the adults were indicated to be greater in the area of higher concentration of organic material. Sex was more frequently distinguishable and the gonadal tissue firmer and more distinctly colored among clams of the area having a sandy bottom with less organic matter.

Density of juvenile clams was not significantly different in the two areas.

Spawning of *Rangia* may occur at any time but is more extensive in late spring and early summer and least during mid-summer.

PROXIMAL RETINAL PIGMENT RESPONSES AND THEIR RELATIONSHIP TO TOTAL PHOTOMECHANICAL ADAPTATION IN THE DWARF CRAYFISH, *CAMBARELLUS SHUFELDTI*[1]

MILTON FINGERMAN
and
R. NAGABHUSHANAM,
Department of Zoology, Newcomb College, Tulane University, New Orleans, Louisiana

The compound eye of crustaceans has three retinal pigments, distal, proximal, and reflecting, that are used for photomechanical adaptation in response to changes in intensity of illumination. An appreciable amount of information exists concerning the physiology of the distal retinal pigment, but a relatively small amount of data is available for the other pigments. The most recent review of the literature concerned with these pigments is that of Kleinholz (1961).

In the few species of crayfishes whose eyes have been studied in detail, the distal and proximal pigments migrated in response to illumination changes but the position of the reflecting pigment was fixed (Welsh, 1939; Kleinholz, 1949, 1961). Migration of the distal pigment is under endocrine control, but crayfishes show diversity in the mechanism of regulation of the proximal pigment.

Welsh (1939) and Kleinholz (1949) appear to be the only investigators to have studied the controlling mechanisms for the proximal pigment in crayfishes. Welsh reported that eyestalk extracts caused light-adaptation of the proximal as well as the distal pigment in *Cambarus bartoni*. However, a higher concentration of eyestalk extract was required to activate the proximal pigment than the distal pigment. This observation was interesting in view of the earlier report of Kleinholz (1936) that the distal and reflecting pigments of the prawn *Palaemonetes vulgaris* migrated toward the light-adapted positions after injection of eyestalk extract, but that the proximal pigment was unaffected. In another crayfish, *Pacifastacus trowbridgi*, the proximal pigment seems to be an independent effector (Kleinholz, 1949). This hypothesis was based on the observation that the proximal pigment of isolated eyestalks maintained in moist chambers continued to respond to light and darkness by appropriate migrations.

The distal retinal pigment of the dwarf crayfish, *Cambarellus shufeldti*, the animal used in this investigation, was first studied by Fingerman (1957). He showed that the eyestalks and supraesophageal ganglia contain the distal retinal pigment light-adapting hormone. Fingerman also determined (1) the rate of migration of the distal pigment and (2) the relationship between the position of this pigment and intensity of illumination. In 1959, Fingerman, Mobberly, and Sundararaj showed the existence of a distal retinal pigment dark-adapting hormone in the optic ganglia of the eyestalks and other central nervous organs of *Cambarellus*.

In view of the small amount of information available concerning the proximal and reflecting pigments of crustaceans in general and crayfishes in particular, the present study was undertaken with the dwarf crayfish. Among the experiments was a determination of the migration rate of the proximal pigment to provide a basis of comparison with the distal pigment. This rate has never been accurately determined for the proximal pigment in any crayfish. An attempt was also made to understand the mechanism controlling migration of the proximal pigment in *Cambarellus*, in view of the strikingly different mechanims postulated for *Cambarus* and *Pacifastacus*.

MATERIALS AND METHODS

Specimens of the dwarf crayfish, *Cambarellus shufeldti*, found in roadside ditches at Hickory, Louisiana, were used in these experiments. In the laboratory the crayfish were kept in aerated tap water at 72-75° F.

The positions of the retinal pigments were determined by observation of sectioned eyestalks. To fix the retinal pigments in position, the crayfish were killed rapidly by immersion in boiling water for at least 15 seconds. Both eyestalks were then removed

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

and place in Bouin's solution. After the eyestalks were dehydrated and embedded in paraffin, sections 20 μ thick were prepared. The compound microscope was arranged so that both transmitted and reflected light shone on the eyestalk sections. In this manner, the three pigments could be distinguished readily from one another. To express the positions of the pigments in quantitative terms, four measurements were made with the aid of an ocular micrometer. The technique of measurement was similar to that employed by de Bruin and Crisp (1957) for use with eyes of marine crustaceans. The measurements were: (A) distance from outer corneal surface to the distal edge of the proximal pigment, (B) distance from outer corneal surface to the distal edge of the reflecting pigment, (C) distance from the outer corneal surface to the basement membrane whose position is fixed, and (D) width of the band of distal pigment. The ratios A C and B C were called the proximal and reflecting pigment indexes respectively. Use of ratios minimized the effects on the measurements of size differences among the eyestalks. At the magnification used to observe the pigments, 100X, each unit of the ocular micrometer represented 10.9 μ.

EXPERIMENTS AND RESULTS

Relationship between time in light and dark and the positions of the proximal and reflecting pigments.—The objectives of this group of experiments were (1) to learn whether the proximal and reflecting retinal pigments of *Cambarellus* migrate, and if so (2) to determine the times required for migration between the maximally light-adapted and maximally dark-adapted positions. For use in the first experiment five white pans each containing at least seven crayfish were placed in a darkroom for two hours. At the end of this period the animals in one pan were killed. The remaining four pans were placed under an illumination of 120 ft. c. Light intensities were measured with a General Electric photometer calibrated at the Department of Physics, Newcomb College. The animals in one of the four pans were sacrificed after exposure to illumination for five minutes. Successive groups were killed after exposures of 10, 15, and 30 minutes. In this manner the time required for light-adaptation of the pigments was determined. To learn the time necessary for dark-adaptation, the reciprocal experiment was performed with five groups of crayfish that had been exposed to an illumination of 120 ft. c. for two hours. Then the crayfish in one of the white pans were killed while the remaining four groups were placed in the darkroom. Successive groups were sacrificed 15, 30, 60, and 90 minutes after having been put in the darkroom. The eyes were sectioned and the positions of the pigments observed. Both experiments were performed twice.

In a dark-adapted eye (fig. 1) the distal pigment lies just below the cornea and surrounds the crystalline cone; the proximal pigment migrates proximally exposing the distal portions of the retinula cells. The reflecting pigment cells lie against the basement membrane, the row of light dots near the middle of the black band at the base of the eye, and extend distally. This pigment appears black by transmitted light. The distal portion of the black band at the base of the eye is reflecting pigment; the proximal portion, proximal pigment. In a light-adapted eye (fig. 2) the distal pigment migrates proximally and the proximal pigment moves distally. The proximal pigment lies within the retinula cells and migrates to fill the distal portion of these cells; some proximal pigment, however, always remains proximal to the basement membrane. The distal pigment in a light-adapted eye forms a sleeve completely enveloping the crystalline cone stalk. As the distal pigment migrates proximally, the band of pigment becomes progressively wider.

In a maximally dark-adapted eye the proximal pigment index was 1.0; in a maximally light-adapted eye approximately 0.65 (fig. 3). Light-adaptation required 10 minutes (fig. 3A); dark-adaptation 60 minutes (fig. 3B). Each point in Figure 3A represents the mean index of 12 eyestalks, each from a different crayfish; in Figure 3B, eyestalks from 13 different crayfish. The average distance from the outer corneal surface to the basement membrane in 41 eyestalks, each from a different individual, was 345 μ. The mean maximum distance the proximal pigment migrated above the basement membrane in 40 fully light-adapted eyes was 107 μ. Comparison of the position of the distal pigment in 20 light-adapted eyes with the position in a like number of

Figures 1-2. **1**. Sagittal section of a dark-adapted eyestalk of *Cambarellus*, X180. **2**. Saggital section of a light-adapted eyestalk of *Cambarellus*, X110. See text for descriptions.

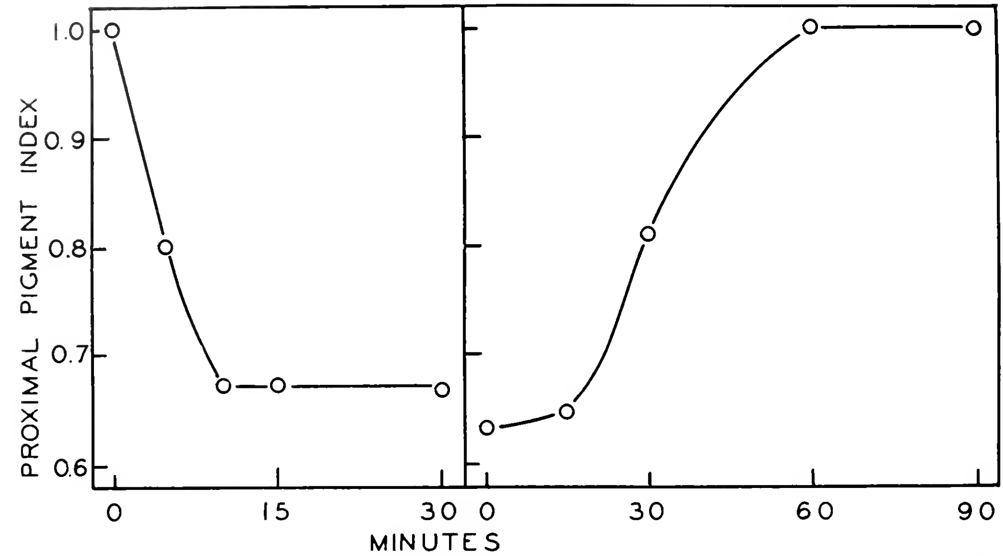

Figure 3. Relationships between proximal pigment index and time; **A** (left) in light, **B** (right) in darkness.

dark-adapted eyes revealed that the distal edge of the distal pigment migrated a mean distance of 92 μ between these two states.

The mean reflecting pigment indexes of the same eyestalks from which the proximal pigment indexes of Figure 3 were obtained are presented in Table 1. Inspection of the data in this table reveals that the reflecting pigment does not migrate. The mean width of the band of reflecting pigment in 32 eyestalks was 49 μ.

TABLE 1.

Reflecting pigment indexes (R. P. I.) of dwarf crayfish kept in light (120 ft. c.) or darkness for different periods of time.

In light		In darkness	
Minutes	R. P. I.	Minutes	R. P. I.
0	0.85	0	0.86
5	0.85	15	0.87
10	0.86	30	0.87
15	0.86	60	0.85
30	0.87	90	0.87

Relationship between proximal pigment index and light intensity.—The object of this experiment was to determine the light intensity at which the proximal pigment became maximally light-adapted. White pans containing dwarf crayfish were exposed to incident illuminations of 17, 29, 75, and 120 ft. c. for two hours. An additional pan of crayfish was placed in the darkroom for two hours. Thirteen proximal pigment indexes, each representing one eyestalk from a different crayfish, were determined for each intensity. The means of the indexes were used in the preparation of Figure 4. Maximal light-adaptation of the proximal pigment required an illumination of approximately 75 ft. c.

Effect of extracts of eyestalks and supraesophageal ganglia with the circumesophageal connectives attached upon the position of the proximal retinal pigment.—Extracts having a concentration of 100 eyestalks per ml of Van Harreveld's solution (Van Harreveld, 1936) were prepared. The dose per crayfish was 0.02 ml. The assay animals were maintained for two hours in black containers under an illumination of 29 ft. c. prior to injection of the extract. A preliminary experiment had revealed that under these conditions the proximal pigment would be close to midway between the maximally light-adapted and maximally dark-adapted positions. Each crayfish in a control group received 0.02 ml Van Harreveld's solution. The animals were killed 45-60 minutes after injection of the eyestalk extract or saline. As anticipated, the distal pigment of the crayfish injected with eyestalk extract showed a light-adaptational response. However, the proximal pigment showed a dark-adaptational response; this

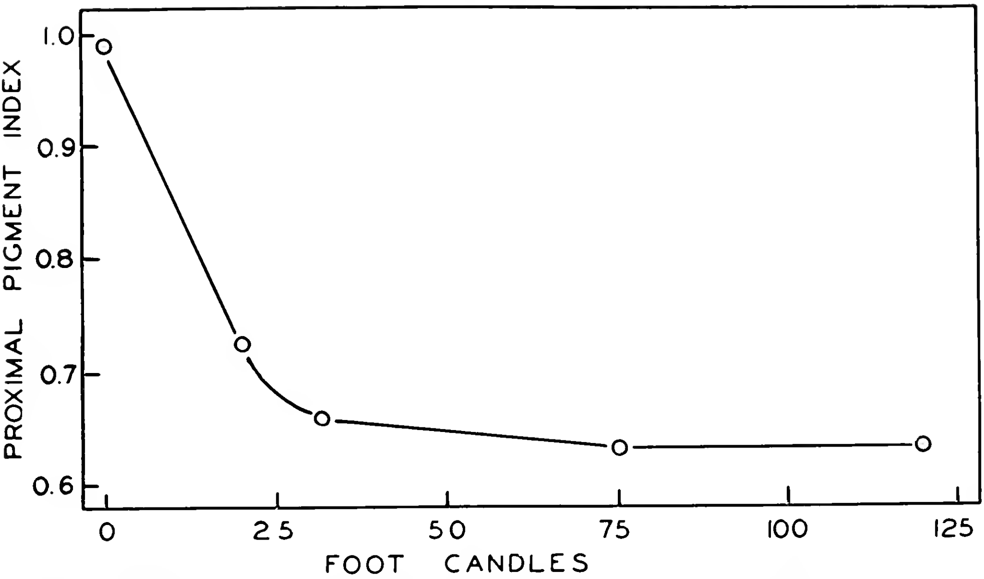

Figure 4. Relationship between proximal pigment index and incident light intensity.

pigment had migrated proximally. The experiment was done three times with the same results. The proximal pigment indexes of the crayfish used in the three experiments are shown in Figure 5. The mean proximal pigment index of the controls was 0.73; that of the experimentals was 0.88. Student's *t* test revealed that the difference between the means was highly significant ($p < 0.001$). The eyestalk extracts had caused the proximal pigment to migrate 56 percent of the mean distance between the position of the pigment at the start of the experiment and the fully dark-adapted position. Eyestalk extracts injected into dark-adapted crayfish had no effect on the proximal pigment, but, as expected, light-adapted the distal pigment. In two experiments extracts of supraesophageal ganglia with the circumesophageal connectives attached, 50 organs per ml, were injected into dwarf crayfish maintained under the same conditions as those that received eyestalk extract. Here also, a dark-adaptational response of the proximal pigment was observed. Thirteen animals received extract and a like number served as controls. The mean proximal pigment indexes for the experimentals and controls were 0.86 and 0.74 respectively. The response was not as large as observed with eyestalk extracts. However, Student's *t* test revealed that the difference between the means was highly significant ($p < 0.001$).

Discussion

Light-adaptation of the proximal retinal pigment of *Cambarellus* required 10 minutes and dark-adaptation 60 minutes. Comparison of these values with previously determined times (Fingerman, 1957) for light-adaptation (30 minutes) and dark-adaptation (90 minutes) of the distal pigment in the same crayfish, reveals that both processes are slower for the distal pigment than the proximal pigment. Furthermore, with both pigments, dark-adaptation is slower than light-adaptation. The rates of migration of these pigments have not been determined in any other crayfish. However, de Bruin and Crisp (1957) determined the times required for light-adaptation of the distal and proximal pigments in the prawns *Palaemon serratus* and *Pandalus montagui*, and the mysid *Praunus flexosus*. The times required by the proximal pigment in these three crustaceans were 4, 4-6, and 4 minutes respectively. Corresponding times for the distal pigment were 90, 40, and 20 minutes. Just as observed herein with *Cambarellus* the distal pigment migrated slower than the proximal pigment in the three species. The times required for dark-adaptation were not deter-

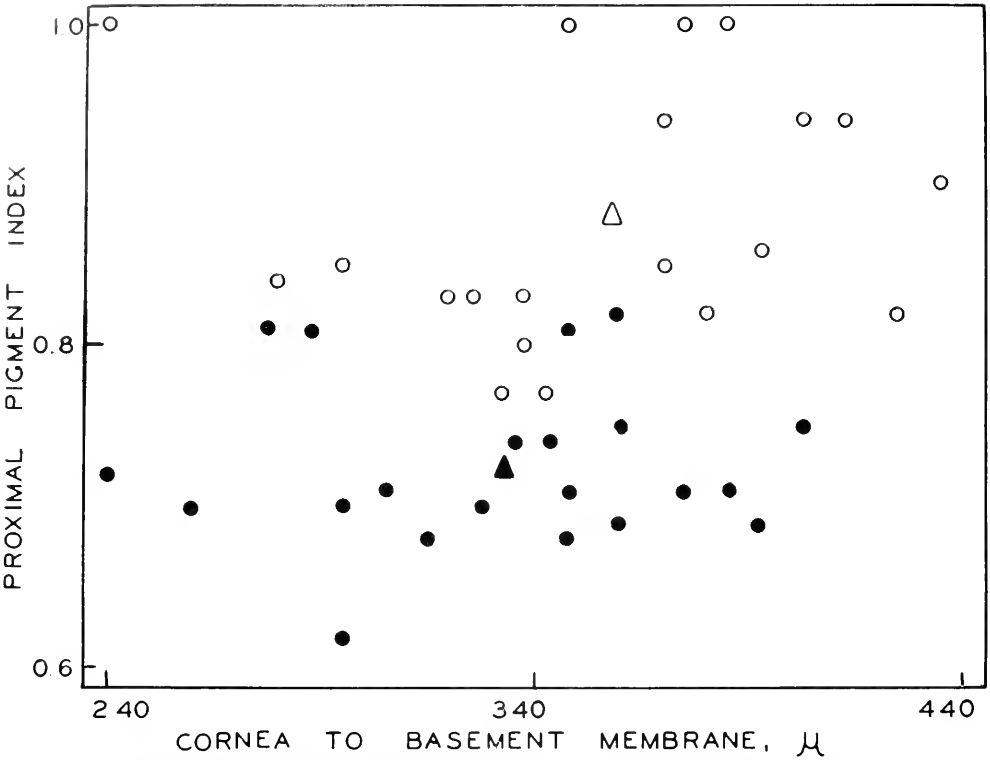

Figure 5. Relationship between proximal pigment index and distance from outer corneal surface to basement membrane. Circles = eyes of crayfish that had received eyestalk extract; dots = eyes of control specimens; triangles = means of the two sets of data.

mined by de Bruin and Crisp who obtained complete light-adaptation of both pigments with an illumination of 1.1 ft. c., a very low value compared with what has been found for other crustaceans. For example, with *Cambarellus*, an illumination of approximately 75 ft. c. was required for complete light-adaptation of the proximal pigment (fig. 4) and about 3500 ft. c. for the distal pigment (Fingerman, 1957). Sandeen and Brown (1952) found that 50 ft. c. was required for complete light-adaptation of the distal pigment of the prawn *Palaemonetes vulgaris*.

Bernhards (1916), apparently the first investigator of retinal pigment migration in a crayfish, found that the distal pigment of a dark-adapted European crayfish, *Astacus astacus*, resided in the region of the crystalline cone of each ommatidium, just as in *Cambarellus*. However, in a light-adapted eye the distal pigment still abutted against the cornea but extended proximally beyond the middle of the crystalline cone stalk, forming a broader band than in the dark-adapted condition. In contrast, in *Cambarus bartoni*, reported by Welsh (1939), and in *Cambarellus* (fig. 2) the distal pigment migrated proximally in light with the result that the portions of the distal pigment cells among the crystalline cones were devoid of pigment. In these three crayfishes all of the proximal pigment lay proximal to the basement membrane in the dark-adapted condition. However, in *C. bartoni* all of the proximal pigment migrated distal to the basement membrane in light, whereas in light-adapted *Cambarellus* and *Astacus astacus* some of the proximal pigment always remained proximal to the basement membrane. The position of the reflecting pigment cells, however, was the same in the three crayfishes.

Welsh (1930) noted that the band of distal pigment in the prawn *Palaemonetes vulgaris* is wider in the dark-adapted condition than in the light-adapted one, but in crayfishes the opposite situation is found.

For example, the mean width of the distal pigment in 15 light-adapted eyes of *Cambarellus* was 99 μ, but only 61 μ in 15 dark-adapted eyes, whereas in *Palaemonetes* the values presented by Welsh (1930) were 70 μ in darkness and 35 μ in light. This difference may depend upon the manner in which the distal pigment migrates. Welsh (1930) believed that migration of the distal pigment in *Palaemonetes* is accomplished by shortening of contractile fibrils whereas in crayfishes protoplasmic streaming may be responsible (Kleinholz, 1961).

The mean proximal pigment index for *Cambarellus* in a white pan at 29 ft. c. was 0.66 (fig. 4). At the same light intensity, the mean proximal pigment index of crayfish in a black pan was 0.73 (fig. 5), *i.e.* the pigment was closer to the dark-adapted position in specimens in black pans than in white ones. A similar situation was observed with the distal pigments of *Palaemonetes* by Sandeen and Brown (1952) and of *Cambarellus* by Fingerman (1957). The difference between the positions of the distal pigments was due to the fact that a black background decreased the brightness of the visual field and was not a true background or albedo response. Further investigation is required, however, before one can say with certainty that this explanation also applies to the proximal pigment of *Cambarellus.*

Evidence was presented herein for a principle in the eyestalk and supraesophageal ganglia with the circumesophageal connectives attached that dark-adapted the proximal pigment of *Cambarellus.* As mentioned above, Kleinholz (1936) noted that eyestalk extracts did not cause migration of the proximal pigment in *Palaemonetes.* Welsh (1939), on the other hand, observed that eyestalk extracts of *Cambarus bartoni* light-adapted the proximal pigment.

The immediate responses to the eyestalk extracts were light-adaptation of the distal pigment but dark-adaptation of the proximal pigment. When extracts of the optic ganglia from eyestalks of *Cambarellus* were assayed on the distal pigment, the dark-adapting hormone expressed itself only after the light-adapting principle had run its course (Fingerman, Mobberly, and Sundararaj, 1959). Herein, because of the apparent absence of a light-adapting principle for the proximal pigment, the dark-adapting substance for the latter pigment was able to operate immediately.

SUMMARY AND CONCLUSIONS

1. The distal and proximal retinal pigments of the dwarf crayfish, *Cambarellus shufeldti,* migrate in response to changes in intensity of illumination. The position of the reflecting pigment is fixed.

2. The width of the distal pigment layer is greater in light-adapted eyes than in dark-adapted ones.

3. The times required for maximal light-adaptation and maximal dark-adaptation of the proximal pigment were determined. Maximal light-adaptation occurs faster than maximal dark-adaptation.

4. The relationship between the position of the proximal pigment and light intensity was determined.

5. Evidence is presented for a principle that causes dark-adaptation of the proximal retinal pigment.

6. The data are discussed in relation to the findings of other investigators.

REFERENCES CITED

BERNHARDS, H. 1916. Der Bau des Komplexauges von *Astacus fluviatilis* (*Potamobius astacus* L.). Ein Beitrag zur Morphologie der Decapoden. *Zeit. wissen. Zool.* 116: 649-707.

DE BRUIN, G. H. P. and D. J. CRISP 1957. The influence of pigment migration on vision of higher Crustacea. *Jour. Exper. Biol.* 34: 447-463.

FINGERMAN, M. 1957. Regulation of the distal retinal pigment of the dwarf crawfish, *Cambarellus shufeldti. Jour. Cell. and Comp. Physiol.* 50: 357-370.

, W. C. MOBBERLY, JR. and B. I. SUNDARARJ 1959. Hormonal regulation of the distal retinal pigment of crayfishes, and the effects of long exposure to light and darkness. *Amer. Midl. Nat.* 62: 429-439.

KLEINHOLZ, L. H. 1936. Crustacean eyestalk hormone and retinal pigment migration. *Biol. Bull.* 70: 159-184.

1949. Responses of the proximal retinal pigment of the isolated crustacean eyestalk to light and to darkness. *Proc. Nat. Acad. Sci. Wash.* 35: 215-218.

1961. Pigmentary effectors. *In The Physiology of Crustacea, Vol. II, Sense Organs, Integration, and Behavior.* T. H. Waterman, ed. Academic Press, Inc., New York.

SANDEEN, M. I. and F. A. BROWN, JR. 1952. Responses of the distal retinal pigment of *Palaemonetes* to illumination. *Physiol. Zool.* 25: 222-230.

VAN HARREVELD, A. 1936. A physiological solution for fresh water crustaceans. *Proc. Soc. Exper. Biol. and Med.* 34: 428-432.

WELSH, J. H. 1930. The mechanics of migration of the distal pigment cells in the eyes of *Palaemonetes*. *Jour. Exper. Zool.* 56: 459-494.

——— 1939. The action of eyestalk extracts on retinal pigment migration in the crayfish. *Cambarus bartoni*. *Biol. Bull.* 77: 119-125.

ABSTRACT

Photomechanical adaptation of the compound eye of the dwarf crayfish, *Cambarellus shufeldti*, in response to changes in intensity of illumination is described. The reflecting pigment does not migrate, whereas the distal and proximal pigments show considerable movement. Evidence is presented for a proximal pigment dark-adapting hormone in the eyestalk and supraesophageal ganglia with the circumesophageal connectives attached. Maximal light-adaptation of the proximal pigment requires 10 minutes; 60 minutes are necessary for maximal dark-adaptation. The relationship between the position of the proximal pigment and incident light intensity is also described. An illumination of approximately 75 ft. c. is necessary for complete light-adaptation of the proximal pigment. The width of the distal pigment band is greater in light-adapted than in dark-adapted eyes. These observations are discussed in relation to the data of other investigators.

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

J. F. FITZPATRICK, JR.,
Department of Biology, University of Virginia, Charlottesville, Virginia

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

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

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

HISTORICAL STATEMENT

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

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

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

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

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

MATERIALS AND METHODS

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

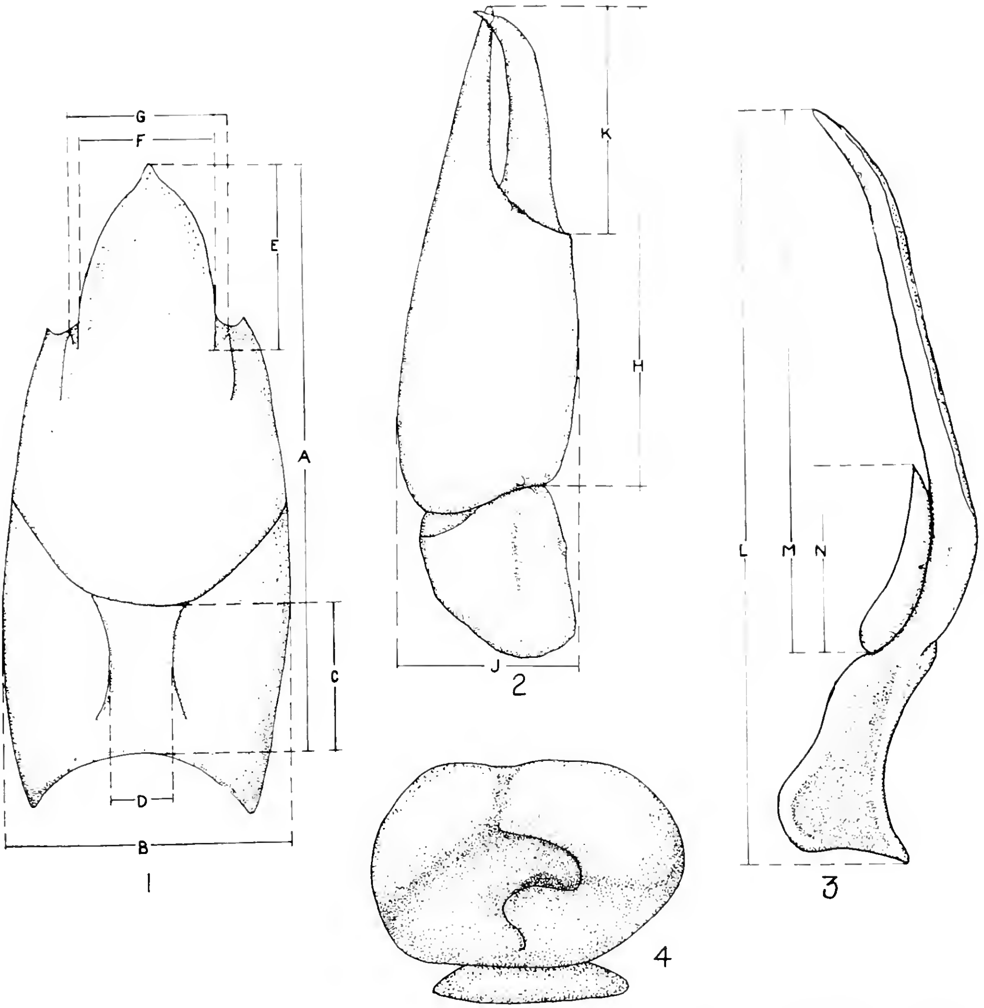
Measurements.—The standard measurements of only inflexible parts common to crawfish taxonomy were used. Females and form II males of less than 10.4 mm cephalothorax length were not used because of Black's (*loc. cit.*) observation that pleopod and growth increments were not correlated below this size.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

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

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

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

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



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

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

Statistical Procedures.—After measurement each population was assigned to an appropriate river drainage for further grouping. The grouping of *F. clypeata* by river drainage is totally artificial, and by no means should be interpreted as anything other than convenience in analyzing data. Form I males, form II males, and females of each river drainage were analyzed separately, but where analysis showed no significant difference for a character in all drainages, the males were grouped as a unit for reporting. Analyses are presented in graph form following a modification of the method of Hubbs and Hubbs (1953) with the exception of meristic and qualitative characters which are best expressed in other ways. Appropriate mathematical procedures were performed on an IBM Digital Computer, Model 650, through the courtesy of the Tulane University Computer Center. Significant differences between any two samples for any character were calculated by Student's *t* test.

The Subgenus *FAXONELLA*, Creaser, 1933.

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

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

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

Key to the Genera of the Subfamily Cambarinae[2]

(Including the species of *Faxonella*)

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

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

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

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

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

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

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

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

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

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

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

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

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

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

TABLE 1.

Cephalothorax size ranges of Faxonella clypeata.

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

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

GENUS *FAXONELLA*,

Creaser, 1933: 21

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

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

FAXONELLA CLYPEATA (Hay, 1899)

Cambarus clypeatus Hay, 1899.

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

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

Orconectes clypeatus (Hay), Hobbs, 1942a.

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

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

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

Type locality, Bay St. Louis, Mississippi.

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

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

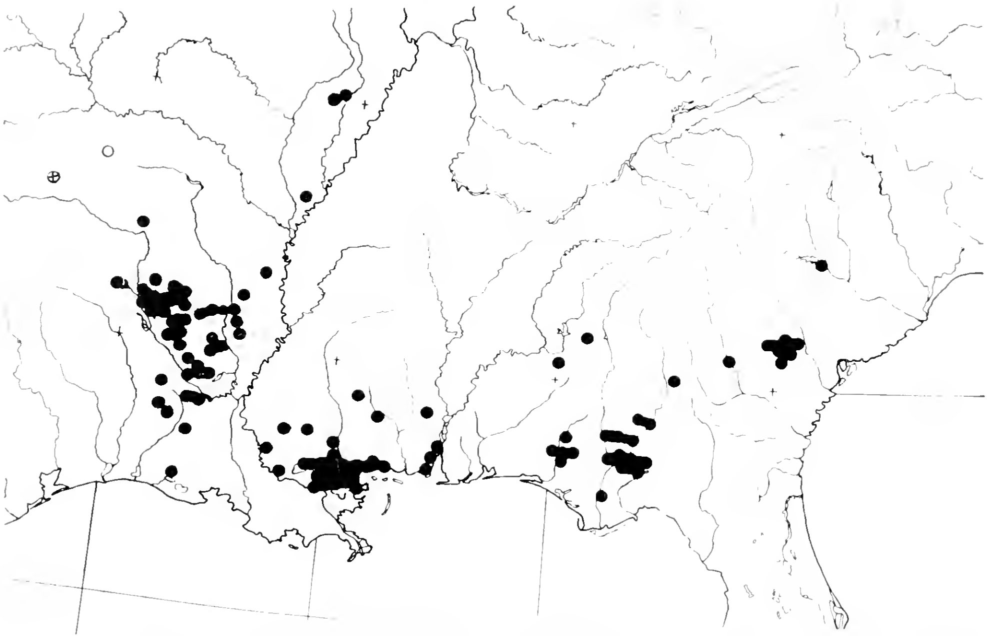


Figure 5. Localities studied. Dots = material examined; circle = report of Creaser and Ortenburger (1933); crossed circle = U.S.N.M. collection referred to in the text.

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

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

FAXONELLA BEYERI (Penn, 1950)

Orconectes (Faxonella) beyeri Penn, 1950.

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

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

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

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

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

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

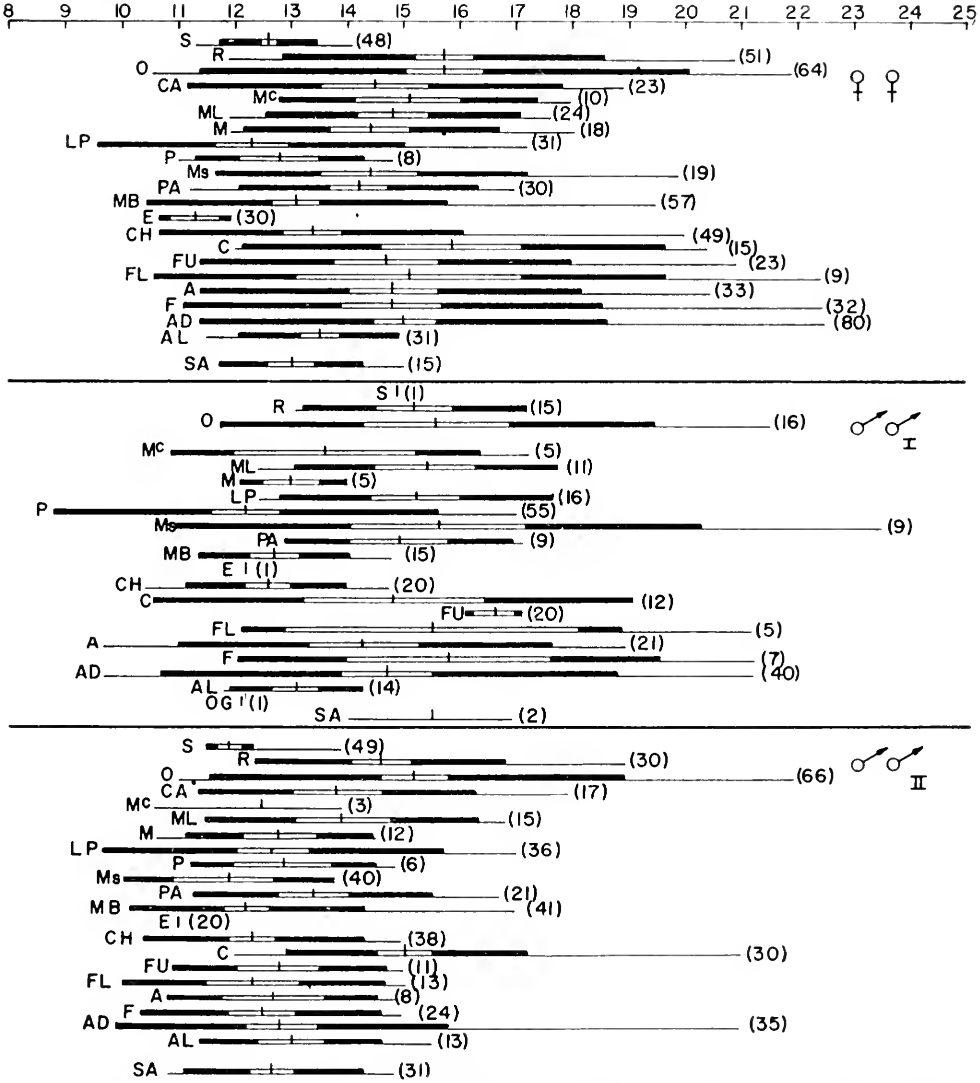


Figure 6. Length of cephalothorax. Numbers in parentheses at right of each bar represent the number of specimens used. Key to symbols at left of bar: S = Sabine River; R = Red River; O = Ouachita River; CA = Calcasieu River; MC = central Mississippi River; ML = lower Mississippi River; M = Mississippi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

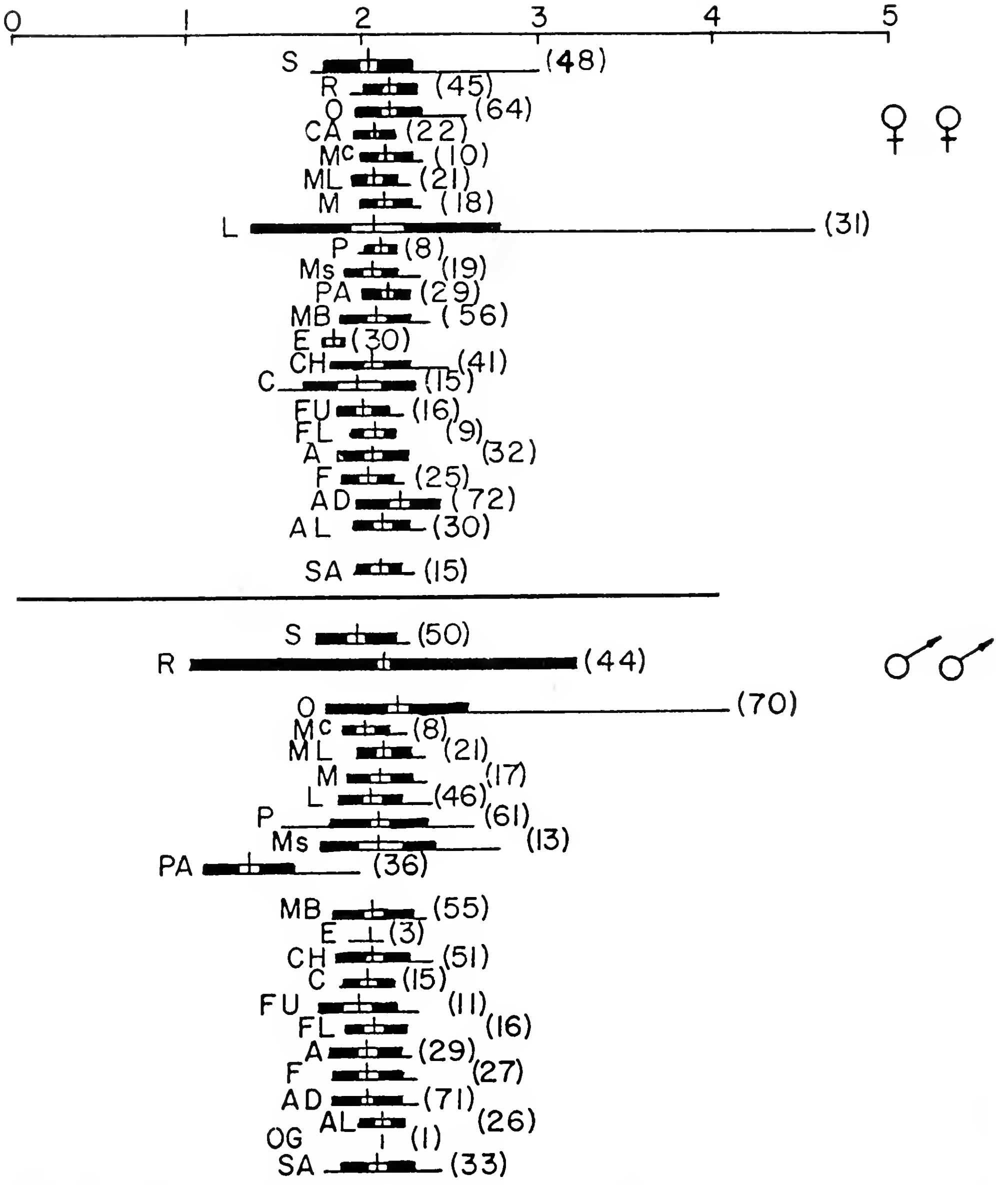
with palm inflated and somewhat depressed, surface of palm covered with small tubercles, dactyl subequal in length to inner margin of palm. First pleopod of male with mesial process less than 50 per cent length of central projection, central projection flattened and somewhat sickle-shaped. Annulus ventralis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

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

GEOGRAPHIC VARIATION IN *F. CLYPEATA*

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

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



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

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

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

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

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

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

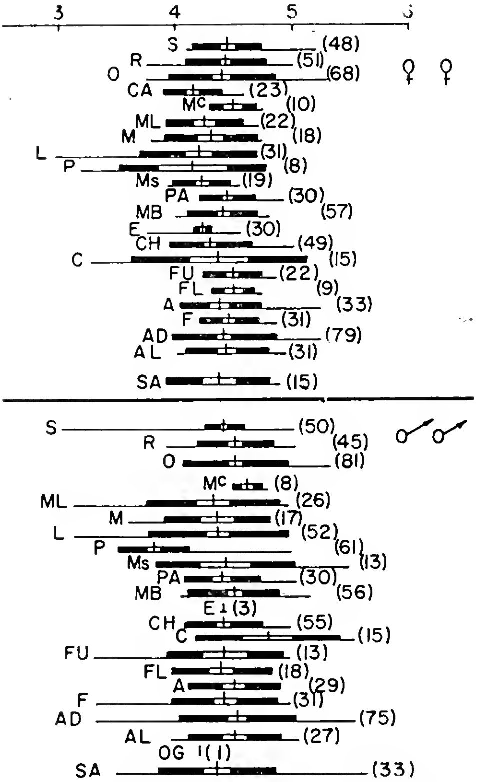


Figure 8. Distance between postorbital spines. Symbols same as fig. 6.

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

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

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

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

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

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

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

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

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

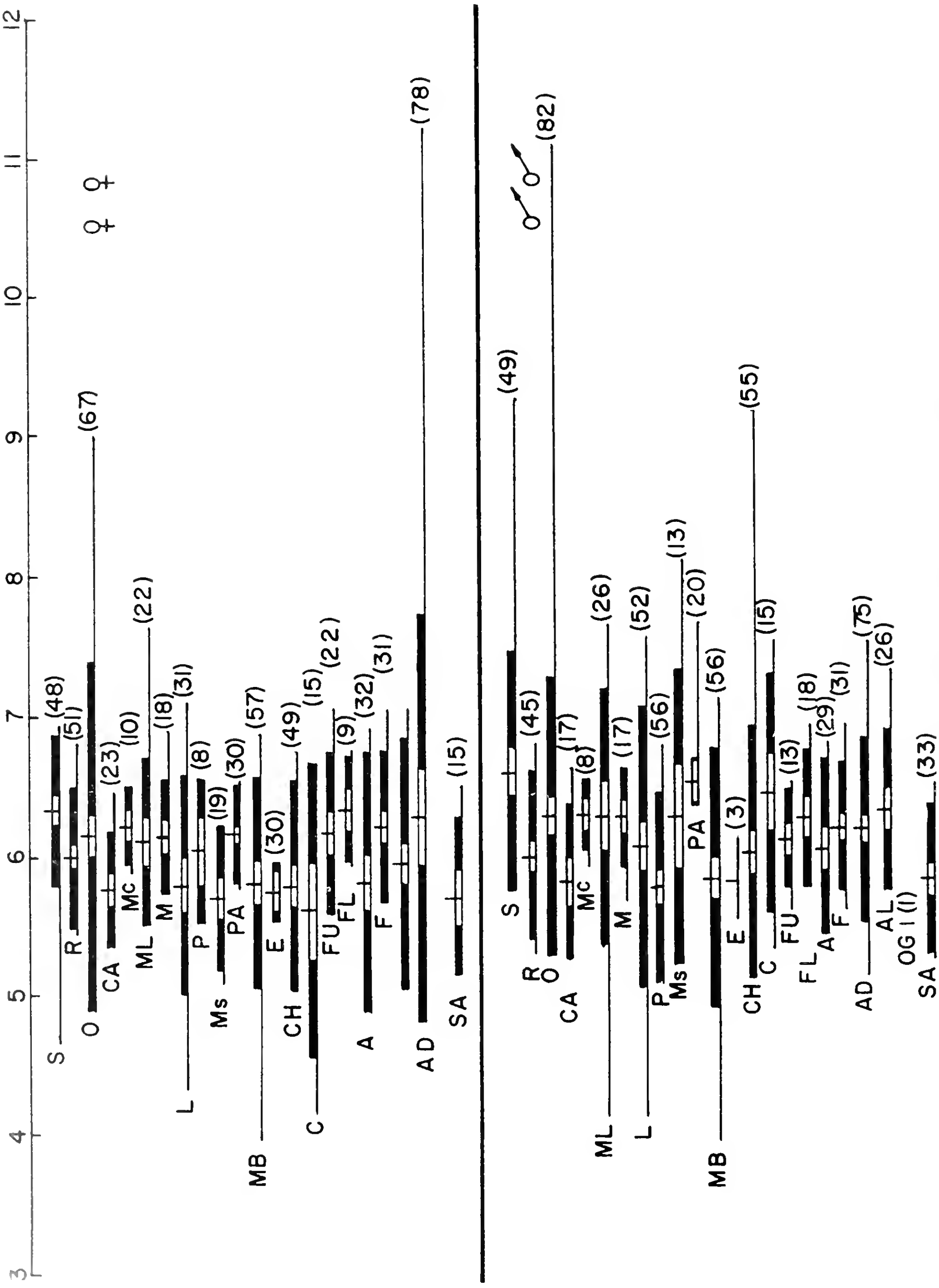


Figure 9. Rostrum length. Symbols same as fig. 6.

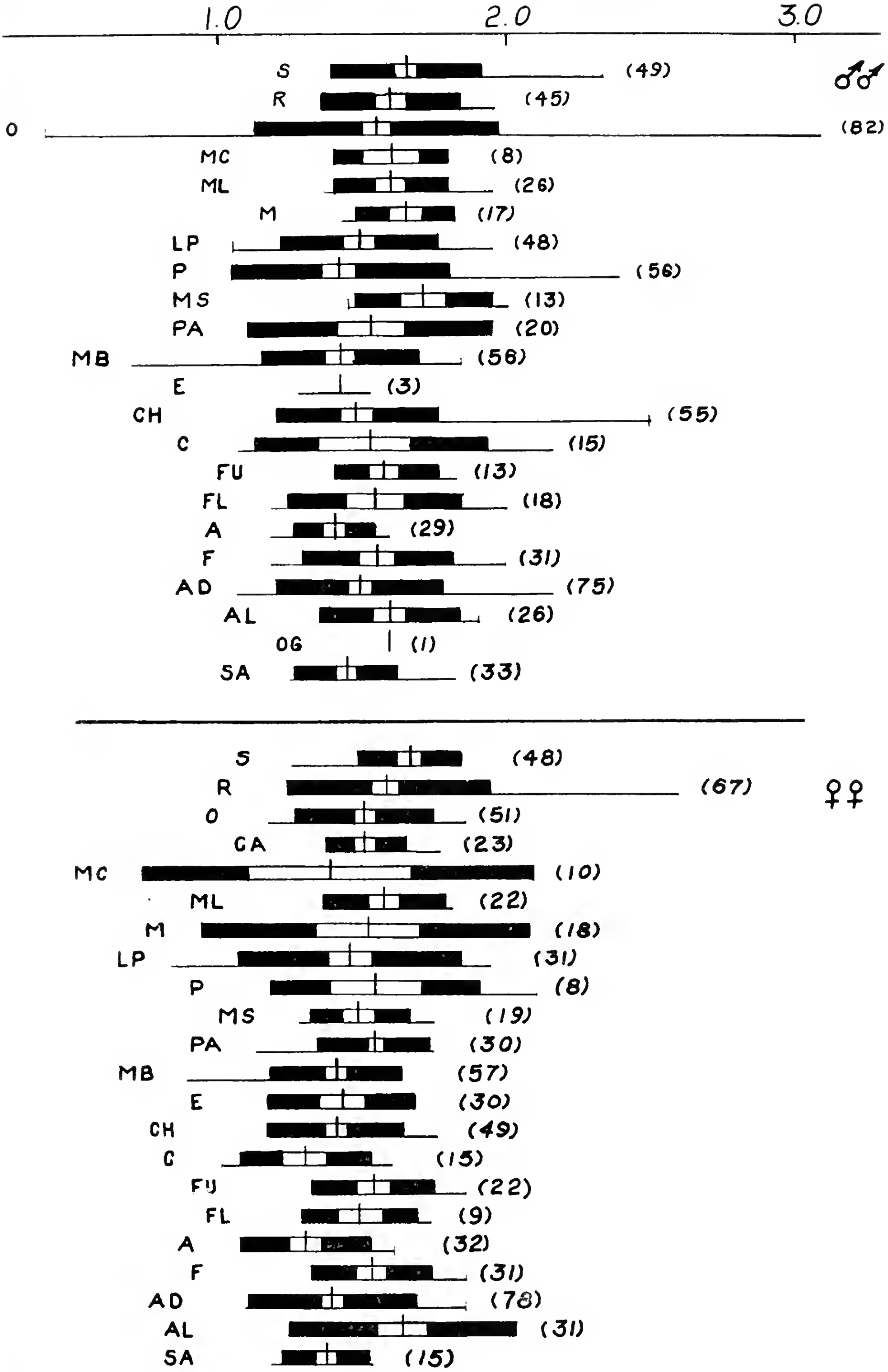


Figure 10. Rostrum width. Symbols same as fig. 6.

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

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

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

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

There was no evidence of clinal variation

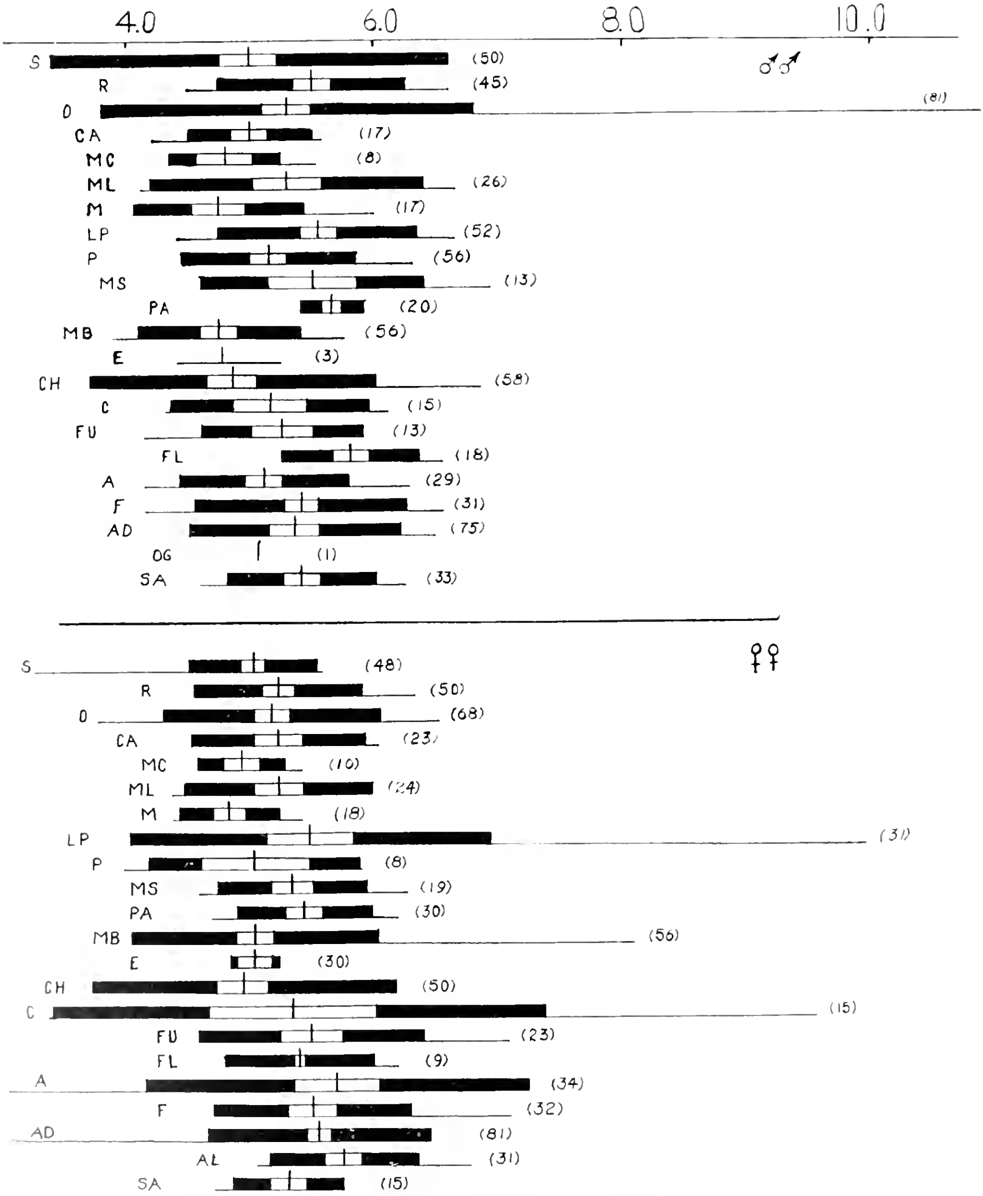


Figure 11. Antennal scale length. Symbols same as fig. 6.

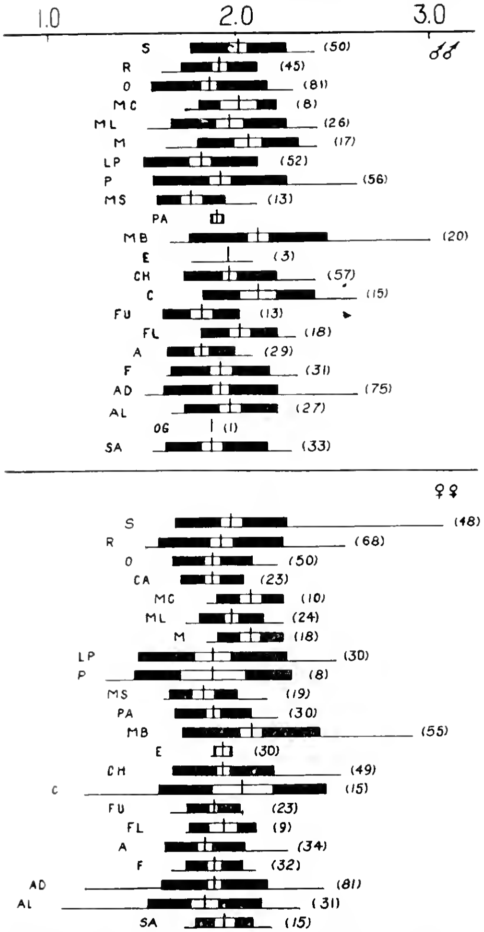


Figure 12. Antennal scale width. Symbols same as fig. 6.

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

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

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

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

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

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

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

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

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

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

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

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

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

LIFE HISTORY

Smith (1953) made a thorough study of the life history of *clypeata.* Basing her study on populations of the west bank of the southern Pearl River drainage, she determined that seasonal breeding of this crawfish occurs from May until September with erratic post-seasonal spawning from November until December. The height of seasonal spawning is in September. Because of the burrowing habit of ovigerous females, free-water collections of *F. clypeata* showed a marked decrease in the relative numbers of females present during the spawning season. At other times the sex ratio of females:males was 1.07. During the seasonal spawning period the percentage of form I males increased. These phenomena were utilized to

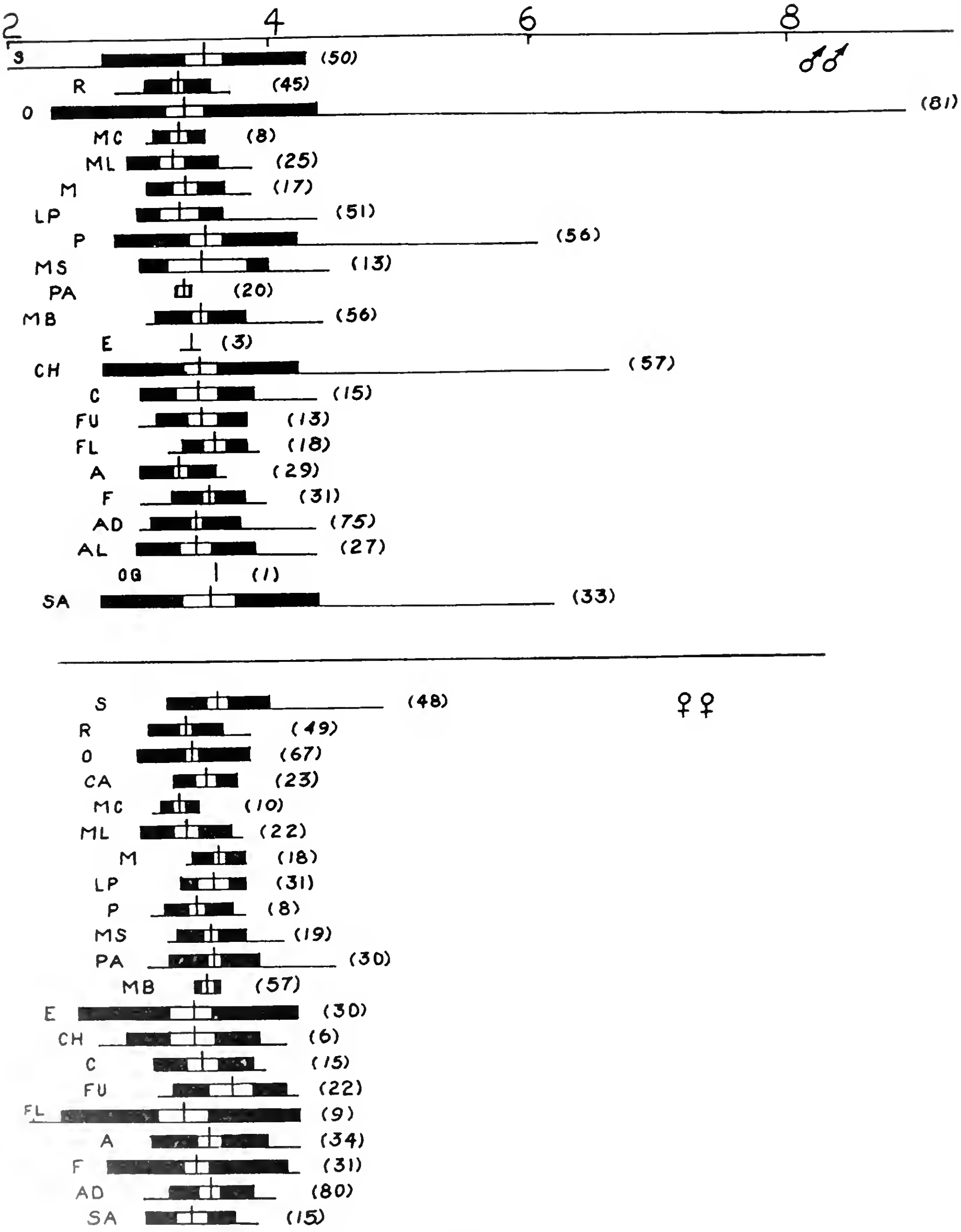


Figure 13. Areola length. Symbols same as fig. 6.

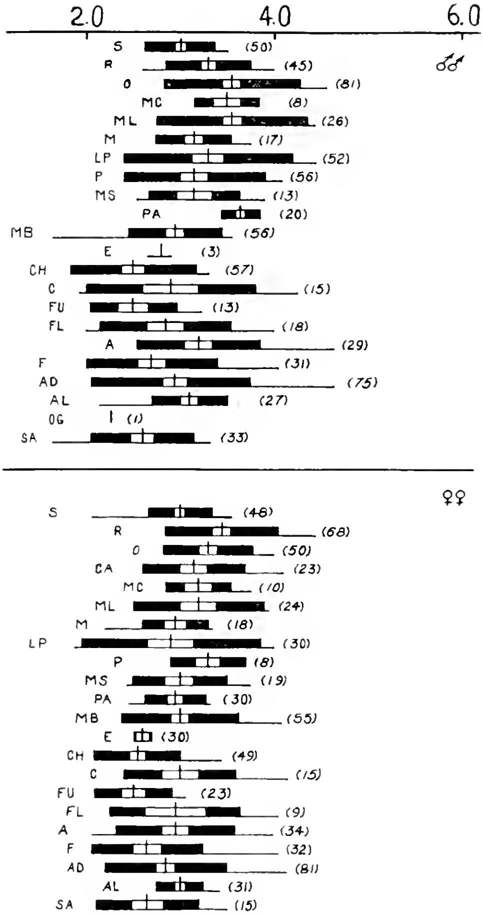


Figure 14. Areola width. Symbols same as fig. 6.

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

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

State	Month	♂♂ II	♂♂ I	% ♂♂ I	♀♀	% ♀♀
La.	Jan.	191	51	4.3	643	54.3
	Feb.	405	73	7.5	489	50.6
	Mar.	99	22	8.2	145	54.5
	Apr.	358	68	8.0	421	49.9
	May	169	33	8.3	196	49.2
	June	310	42	6.4	308	46.7
	July	173	61	13.6	216	48.0
	Aug.	13	19	28.4	35	52.2
	Sep.	57	144	55.2	60	23.0
	Oct.	90	34	23.4	21	14.5
	Dec.	179	16	4.1	197	50.3
Tex.	Aug.	0	1	—	1	—
Ark.	June	23	9	15.5	26	44.8
	July	3	5	33.3	7	46.7
Miss.	Feb.	2	2	20.0	6	60.0
	Mar.	7	5	22.7	10	45.5
	Apr.	19	16	21.9	38	52.1
	June	26	20	22.7	42	47.7
Ala.	Feb.	8	1	6.3	7	43.8
	Apr.	2	0	—	2	—
	June	36	14	13.7	52	50.1
Fla.	Mar.	0	2	—	1	—
	Apr.	41	35	25.9	59	43.7
	Sep.	1	2	—	1	—
Ga.	Feb.	0	1	—	2	—
	Mar.	6	2	15.4	5	38.5
	Apr.	64	7	5.8	49	40.8
	May	0	1	—	0	—
	June	2	1	—	3	—
	Aug.	3	10	37.0	14	51.9
	Sep.	0	3	—	0	—
	Dec.	0	0	—	1	—
S. C.	Sep.	1	0	—	0	—

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

DISCUSSION

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

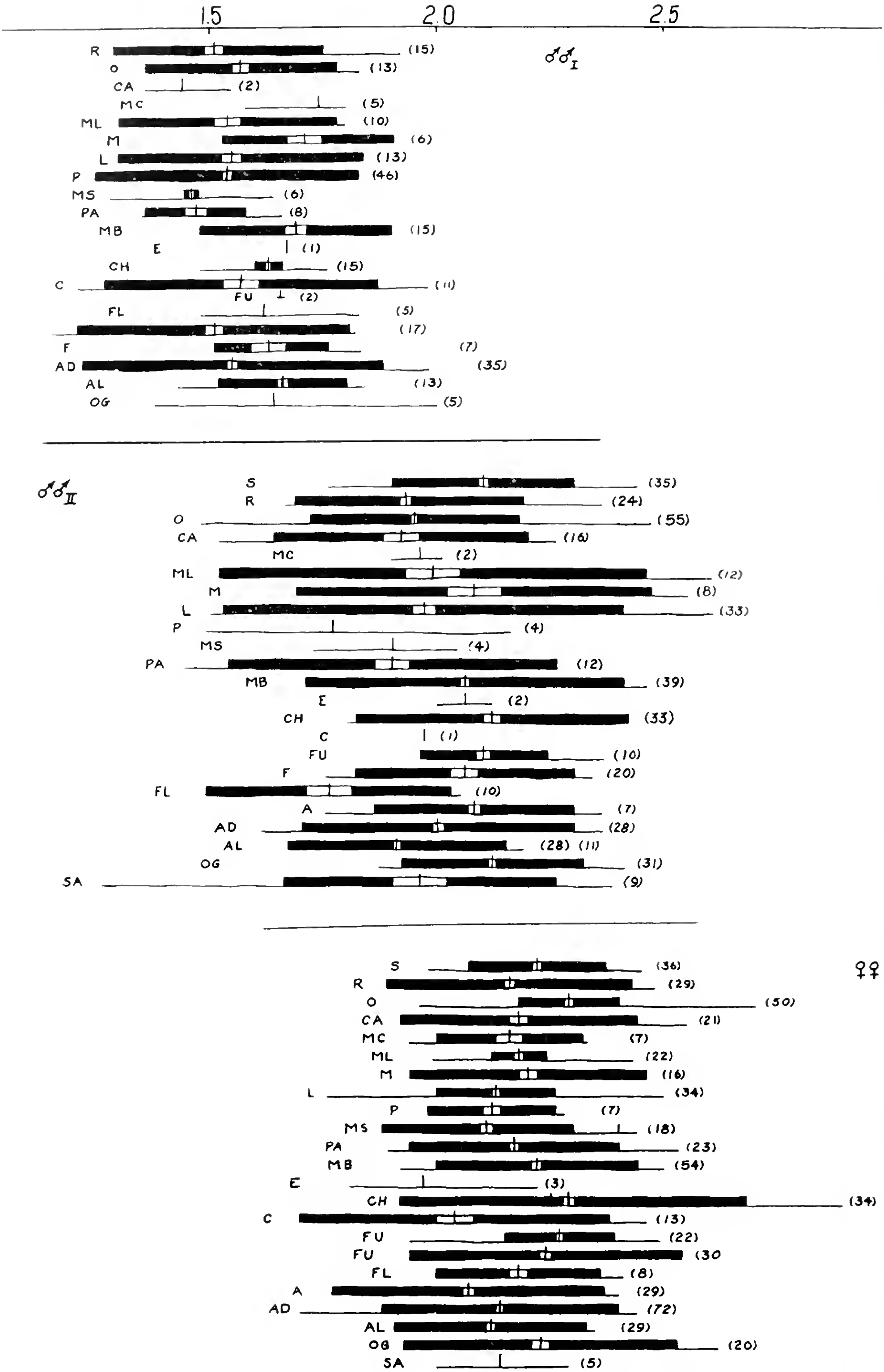


Figure 15. Chela length. Symbols same as fig. 6.

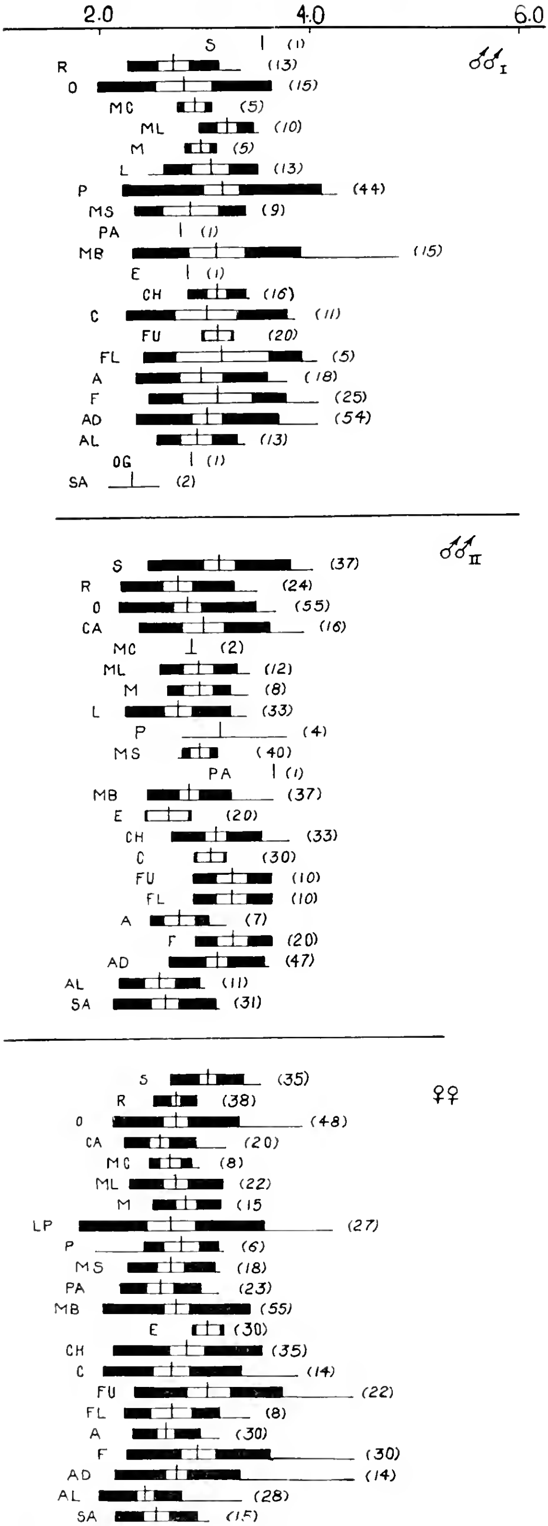


Figure 16. Palm width. Symbols same as fig. 6.

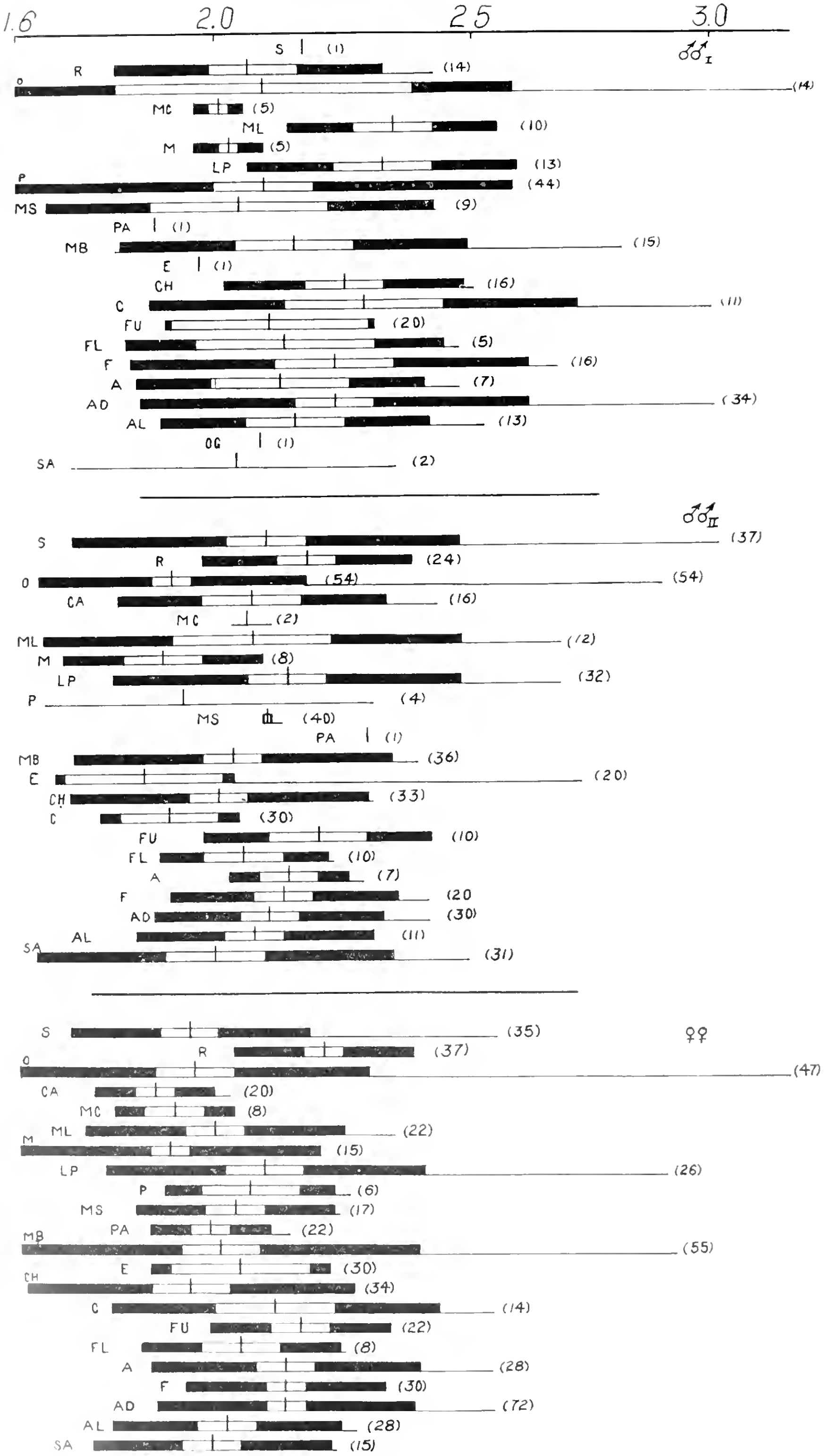


Figure 17. Dactyl length. Symbols same as fig. 6.

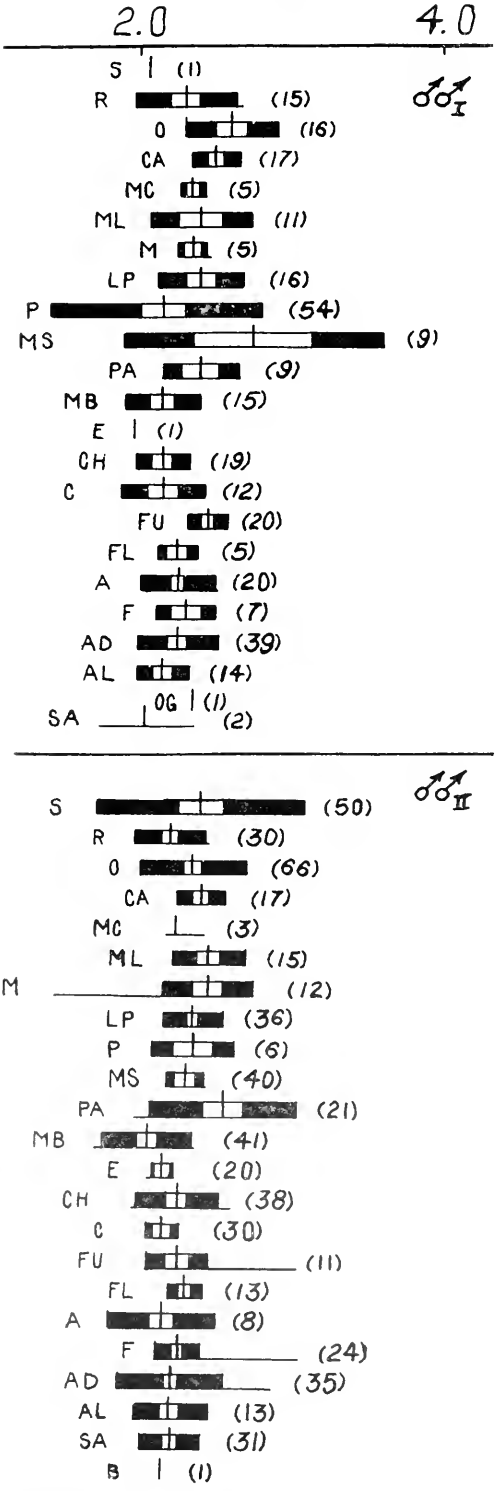


Figure 18. Pleopod length. Symbols same as fig. 6.

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

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

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

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

Size ranges for each sex category are presented in Table 1. The maximum sizes are recorded here, but one should keep in mind that other areas of the range produced specimens closely approximating the ones recorded. Only one form I male—the one reported (Table 1)—was below 10.4 mm cephalothorax length; therefore, this specimen was probably precocious. Fortunately two females with young were present in the Tulane University collections. Because of the difficulty in obtaining such specimens, the cephalothorax measurements of each are included here (12.9 mm, 13.0 mm). Other measurements were typical for the population. Both of these females were included in the statistical analyses. Both are from Pearl River, Louisiana.

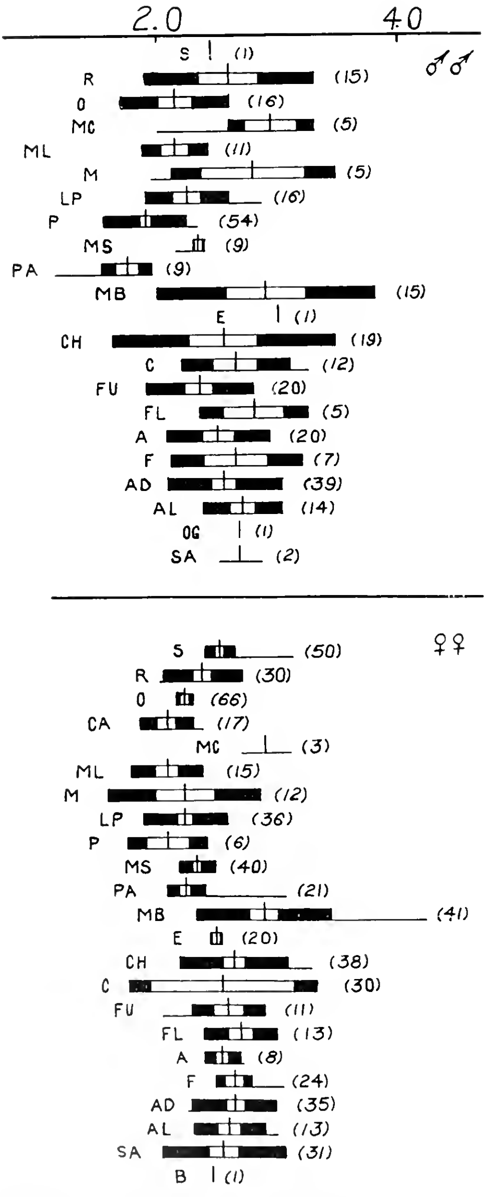


Figure 21. Ratio of length of central projection to length of mesial process. Symbols same as fig. 6.

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

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

SUMMARY

1. The subgenus *Faxonella* Creaser, 1933: 21 is accorded full generic status; the genus was defined and defended.
2. The crawfish *Faxonella clypeata* (Hay) was examined taxonomically.
3. Life history data for *F. clypeata* were accumulated.
4. East-west clines were discovered in three characters: width of rostrum, width of areola, and length of mesial process. None was pronounced.
5. Sexual dimorphism was found in length of chela and width of palm.
6. Differences existed between first and second form males in length of central projection, length of mesial process, and ratio of length of central projection to length of mesial process.
7. Range limits were discussed.
8. No subspecies of *F. clypeata* exist.

ACKNOWLEDGEMENTS

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

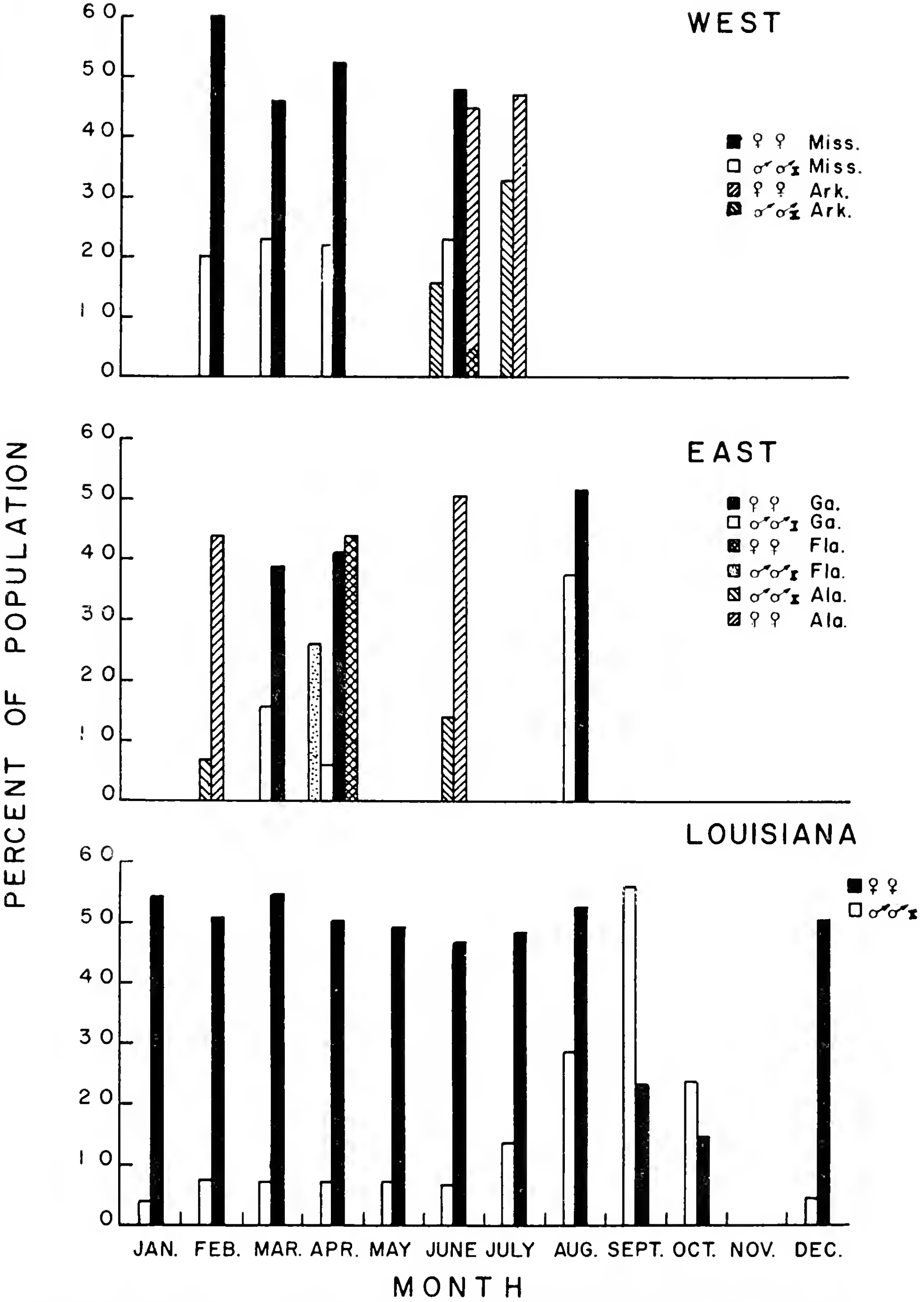


Figure 22. Geographic variation in the life history of *Faxonella clypeata* (Hay).

REFERENCES CITED

BLACK, J. B. 1958. Ontogeny of the first and second pleopods of the male crawfish *Orconectes clypeatus* (Hay). *Tulane Stud. Zool.*, 6(4): 190-203.

COPE, E. D. 1872. On the Wyandotte Cave and its fauna. *Amer. Nat.*, 6: 406-422.

CREASER, E. P. 1933. Descriptions of some new and poorly known species of North American crayfishes. *Occ. Pap. Mus. Zool., Univ. Michigan*, No. 275: 1-21.

———— 1962. Notes on homologies and genetic relationships in the Cambarinae crayfishes. Publ. by the author. 1-7.

———— and A. I. ORTENBURGER 1933. The decapod crustaceans of Oklahoma. *Publ. Univ. Okla., Biol. Surv.*, 5(2): 14-47.

FAXON, W. 1914. Notes on the crayfishes in the United States National Museum and the Museum of Comparative Zoology with descriptions of new species and subspecies to which is appended a catalogue of known species and subspecies. *Mem. Mus. Comp. Zool., Harvard Coll.*, 40(8): 347-427.

FINGERMAN, M. and C. OGURO 1962. Alternation in the number of neurosecretory cells in the eyestalk of the crayfish, *Orconectes clypeatus*, maintained in darkness. *Amer. Zool.*, 2(3): 408. Abstract.

FITZPATRICK, J. F., JR. 1962. Geographic variation in the crawfish *Orconectes* (*Faxonella*) *clypeatus* (Hay). *Virginia Jour. Sci.*, 13(4): 246-247. Abstract.

HARRIS, J. A. 1903. An ecological catalogue of the crayfishes belonging to the genus *Cambarus*. *Univ. Kansas Sci. Bull.*, 2(3): 51-187.

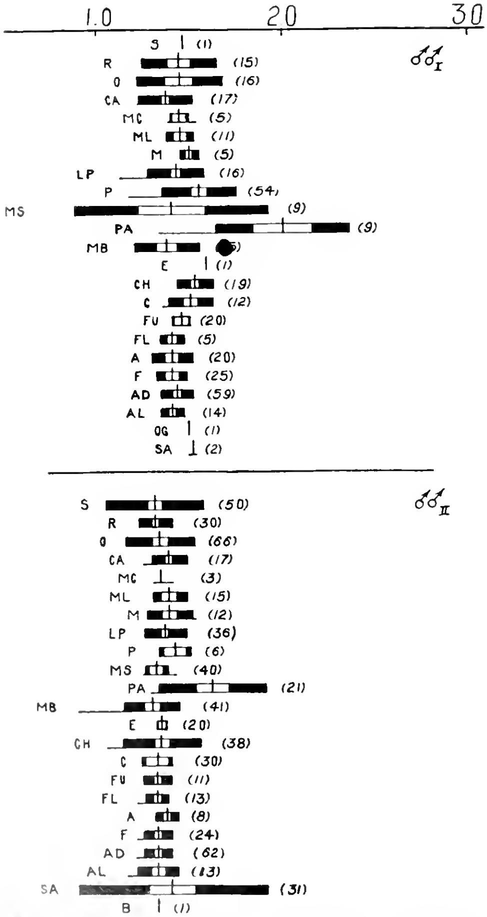


Figure 19. Length of central projection. Symbols same as fig. 6.

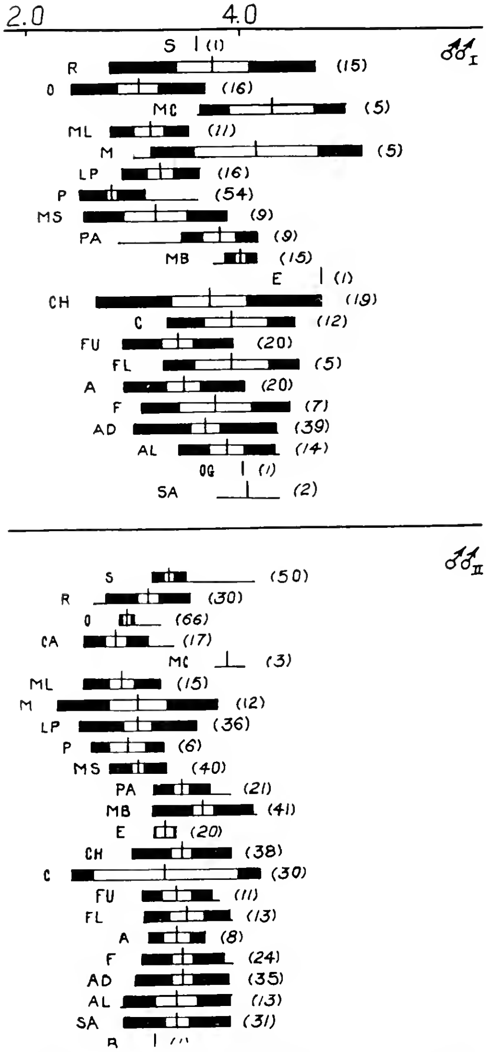


Figure 20. Length of mesial process. Symbols same as fig. 6.

HART, C. W. 1953. Serial homologies among three pairs of abdominal appendages of certain male crayfishes. *Jour. Morph.*, 93(2): 285-299.

——— 1956. The postembryonic development of the first pleopod of *Cambarus longulus longulus* Girard. *Virginia Jour. Sci.*, 7(1): 9-13.

HAY, W. P. 1899. Description of two new species of crayfish. *Proc. U. S. Nat. Mus.*, 22: 121-123.

HOBBS, H. H., JR. 1940. On the first pleopod of male *Cambari*. *Proc. Florida Acad. Sci.*, 5: 55-61.

——— 1942a. A generic revision of the crayfishes of the subfamily Cambarinae (Decapoda, Astacidae) with the description of a new genus and species. *Amer. Midl. Nat.*, 28(2): 334-357.

——— 1942b. The crayfishes of Florida. *Univ. Fla. Publ., Biol. Sci. Ser.* 3(2): pp. 1-179; 24 pl.

——— and C. W. HART 1959. The fresh water decapod crustaceans of the Apalachicola drainage system in Florida, southern Alabama, and Georgia. *Bull. Fla. State Mus.*, 4(5): 145-191.

HUBBS, CARL L. and CLARK HUBBS 1953. An improved graphical analysis and comparison of samples. *Systematic Zool.* 2(2): 49-57.

ORTMANN, A. E. 1902. The geographical distribution of fresh water decapods and its bearing upon ancient geography. *Proc. Amer. Phil. Soc.*, 41(171): 267-400.

PENN, G. H. 1950. A new crawfish of the genus *Orconectes* from Louisiana. *Jour. Wash. Acad. Sci.*, 40(5): 166-169.

——— 1952. The genus *Orconectes* in Louisiana. *Amer. Midl. Nat.*, 47(3): 743-748.

——— 1959. An illustrated key to the crawfishes of Louisiana with a summary of their distribution within the state. *Tulane Stud. Zool.*, 7(1): 3-20.

——— and H. H. HOBBS, JR. 1958. A contribution toward a knowledge of the crawfishes of Texas. *Texas Jour. Sci.*, 10(4): 452-483.

SMITH, E. W. 1953. The life history of the crawfish *Orconectes* (*Faxonella*) *clypeatus* (Hay). *Tulane Stud. Zool.*, 1(7): 77-96.

VILLALOBOS, A. 1955. Cambarinos de la fauna Mexicana. *Tesis, Facultad de Ciencias. Univ. Nal. A. De Mexico*, pp. 1-290.

WILLIAMS, A. B. 1954. Speciation and distribution of the crayfishes of the Ozark Plateaus and Ouachita Provinces. *Univ. Kansas Sci. Bull.*, 36, Pt. II: 803-918.

ABSTRACT

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

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GYRODACTYLUS SHORTI, A NEW SPECIES OF MONOGENETIC TREMATODE FROM THE BROOD POUCH OF THE SOUTHERN PIPEFISH, *SYNGNATHUS SCOVELLI* (EVERMANN AND KENDALL)

RHODES B. HOLLIMAN,
DEPARTMENT OF BIOLOGY, VIRGINIA POLYTECHNIC INSTITUTE, BLACKSBURG, VIRGINIA

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FRANCIS L. ROSE,
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GYRODACTYLUS SHORTI, A NEW SPECIES OF MONOGENETIC TREMATODE FROM THE BROOD POUCH OF THE SOUTHERN PIPEFISH, *SYNGNATHUS SCOVELLI* (EVERMANN AND KENDALL)[1]

RHODES B. HOLLIMAN,
Department of Biology, Virginia Polytechnic Institute,
Blacksburg, Virginia

More than 60 species of *Gyrodactylus* are known from 18 families of fishes encompassing 10 orders. Many of these hosts are euryhaline. Members of this genus are known also from amphibians (tadpoles of the genus *Rana*) as reported by Sproston (1946).

The most valuable and comprehensive studies on the Gyrodactylidae are found in the works of Johnston and Tiegs (1922), Price (1937a, 1937), Mizelle (1938), Sproston (1946), Hargis (1955), and Bychowsky (1957).

Members of the family Gyrodactylidae are viviparous and have an unusual type of life cycle. According to Bychowsky (1957), *Gyrodactylus sp.* from the stickleback produces 4 embryos, one inside the other, from each egg. The first born individual has 3 embryos inside the uterus, the second born has 2 embryos, the third has 1 embryo and the fourth has none. Within this fourth individual, a new egg enters the uterus and the process is repeated. Likewise, as each embryo is born, the remaining mother indivdual produces a new egg which enters the uterus and 4 more embryos subsequently develop. Bychowsky reports that the number of births from one mother individual is probably not less than 3 or 4, and the period of development of the embryo from egg to time of birth is about 4 to 5 days. Therefore, the life span of the individual *Gyrodactylus* is 12 to 15 days, or possibly longer.

Since gyrodactylids do not have a larval form which may serve to infect new hosts, transfer of the mature parasites may occur when the hosts are close together. Little is known of this phenomenon and further experimental evidence will be necessary for confirmation. These worms are difficult to study due to their minute size and the displacement of internal organs by uterine embryos.

The new species here reported was discovered a considerable length of time after the host had been preserved in 10 percent formalin. Numerous worms were found attached to the lining of the brood pouch, many being distorted and poorly fixed. Only those specimens having a normal extended appearance were selected for study, and stained whole mounts were prepared using Semichon's Acetocarmine and Harris's hematoxylin. All drawings were made with the aid of a camera lucida. Measurements are in millimeters and ranges are followed by averages in parentheses.

This writer wishes to express his appreciation to Dr. E. B. Joseph, who collected the host from Tampa Bay and donated the specimen to the Division of Zoology, Department of Biological Sciences, Florida State University.

GYRODACTYLUS **SHORTI**, sp. nov.[2]

Description.—Body oval to weakly fusiform, 0.176-0.360 (0.256) long, 0.062-0.106 (0.084) wide. Cuticle thin and smooth. Prohaptor a pair of anterior papillate head organs connected by ducts to lateral glands located at level of anterior margin of pharynx. Opisthaptor irregularly oval, 0.044-0.068 (0.053) long, 0.037-0.054 (0.046) wide, armed with 2 anchors, 1 bar and 16 marginal hooklets. Anchors 0.034-0.037 (0.036) long, 0.005 wide, 0.008 deep, with short, diverging, knob-like roots, ventro-mesial knobs and strongly recurved tips. Ventral bar indistinct, trapezoidal in ventral outline, 0.012-0.015 (0.014) long, 0.007-0.009 (0.008) wide, with ends articulating with ventro-mesial knobs on anchors. Dorsal bar absent. Haptoral hooks 0.023-0.026 (0.024) long, with long, thin shafts and small, sickle-shaped tips. Pharynx

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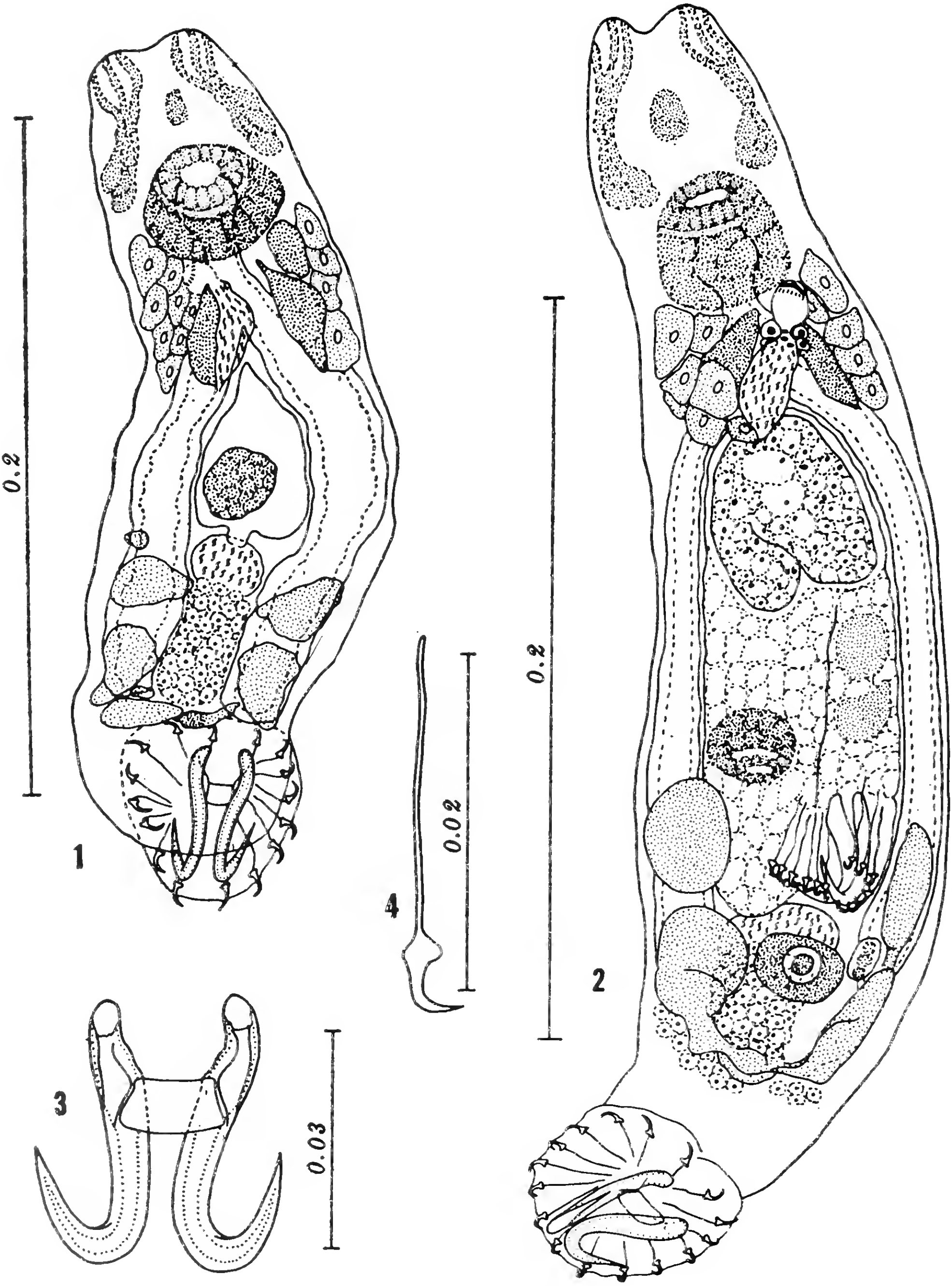
[1] This investigation was supported in part by a grant (AI-05177-02) from the U. S. Department of Health, Education and Welfare, Public Health Service.

[2] This species is named in honor of Dr. Robert B. Short.



Figures 1-4. **1.** *Gyrodactylus shorti*, sp. nov., dorsal view, with uterine embryo in early stage of development. **2.** Same, ventral view, showing large uterine embryo containing third generation embryo; drawn from holotype. **3.** Anchor complex, ventral view. **4.** Haptorial hook.

0.025-0.042 (0.032) long, 0.031-0.052 (0.042) wide, muscular, darkly staining; esophagus short; gut bifurcate with nonconfluent, thick-walled caeca extending to level of ovary. Testis indistinct, 0.018 in diameter, situated dorsal to anterior margin of ovary and generally obscured by other organs. Cirrus globular, 0.008-0.014 (0.01), located on left submedian ventral surface at posterior margin of pharynx; armed with a single large spine or plate 0.01 long, and a row of minute spines. Seminal vesicle posterior to cirrus with darkly staining prostate cells (?) surrounding junction of organs. Granular cells of two types situated in region between posterior margin of pharynx and anterior margin of uterus. Ovary irregular, averaging 0.027 long, 0.024 wide, located between terminal extensions of caeca. Large, ovum-like object, often referred to as the "ootype", situated ventral to anterior margin of ovary in many specimens. Vitellaria consisting of two irregular, lateral groups of darkly staining bodies ventral to ends of intestinal caeca and joining at posterior margin of ovary. Embryo *in utero* filling most of region between intestinal caeca; smallest measured 0.024 long, 0.020 wide; largest measured 0.137 long, 0.053 wide; average 0.084 long, 0.044 wide. Several specimens contained three embryos, one lying inside the other.

Host.—*Syngnathus scovelli* (Evermann and Kendall) southern pipefish.

Location.—Brood pouch of one male specimen.

Locality.—Tampa Bay, Florida.

Number studied and measured.—25.

Holotype.—U.S.N.M. Helm. Coll. No. 59597.

Discussion.—*Gyrodactylus shorti* resembles *G. funduli* Hargis (1955) but differs from that species in lacking a dorsal bar in the opisthaptor armament, shape of the ventral bar, shape of the ovary, relative positions of the ovary, testis, and ovum-like object ("ootype"), and host.

Finding this new species on a syngnathid fish serves to elaborate the lack of host specificity shown by members of the genus *Gyrodactylus*, and brings the total of orders of fishes on which this genus is found to 11. The present work also constitutes the first report of a monogenetic trematode from any member of the Syngnathiformes.

REFERENCES CITED

BYCHOWSKY, B. E. 1957 Monogenetic trematodes. *Their Systematics and Phylogeny (translation from Russian).* Graphic Arts Press, Inc., Washington. 627 p.

HARGIS, W. J. JR. 1955 Monogenetic trematodes of Gulf of Mexico fishes. Part I. The superfamily Gyrodactyloidea. *Biol. Bull.* 108(2): 125-137.

JOHNSTON, T. H. and O. W. TIEGS 1922 New gyrodactyloidid trematodes from Australian fishes, together with a reclassification of the superfamily Gyrodactyloidea. *Proc. Linn. Soc. New South Wales* 47: 83-131.

MIZELLE, J. D. 1938 Comparative studies of trematodes (Gyrodactyloidea) from the gills of North American fresh-water fishes. *Ill. Biol. Monogr.* 17: 1-81.

PRICE, E. W. 1937a North American monogenetic trematodes. I. The superfamily Gyrodactyloidea. *Jour. Wash. Acad. Sci.* 27: 114-130.

———— 1937b North American monogenetic trematodes. I. The superfamily Gyrodactyloidea (cont.) *Ibid.* 27: 146-164.

SPROSTON, N. G. 1946 A synopsis of the monogenetic trematodes. *Trans. Zool. Soc. London* 25: 185-600.

ABSTRACT

Gyrodactylus shorti, sp. nov. is described from the brood pouch of a male *Syngnathus scovelli* (Evermann and Kendall), the southern pipefish. This minute, viviparous trematode was found on one host from Tampa Bay, Florida. Finding this worm on a member of the Syngnathiformes constitutes the first record of a monogenetic trematode on that order of fishes, and brings the total of orders on which species of *Gyrodactylus* are found to eleven.

NOTE: A CHANGE OF NAMES

In a recent paper (Holliman, 1961), 24 new species of marine cercariae were described and named. However, since the publication date, four of the names proposed were found preoccupied by names of fresh water cercariae. The marine cercariae involved do not belong in the same genera with the fresh water cercariae having nomenclatorial priority. Nevertheless, if the "collective group" name of *Cercaria* is to be treated as a single genus, and since these "collective groups" are governed by the Law of Homonymy (Article 57, *International Code of Zoological Nomenclature*), nomenclatorial accuracy must take preference over zoological and taxonomic considerations.

Therefore, to avoid confusion in the literature, the following changes in names are proposed:

Cercaria fimbriata Holliman, 1961, to *Cercaria stupulosa*, nomen novum, from the Latin *stupulosus*, meaning "covered with fine, short hairs"; *Cercaria pusilla* Holliman, 1961, to *Cercaria glareosa*, nomen novum, from the Latin *glareosus*, meaning "full of gravel"; *Cercaria opaca* Holliman, 1961, to *Cercaria munita*, nomen novum, from the Latin *munitus*, meaning "armed"; *Cercaria paradoxa* Holliman, 1961, to *Cercaria protensa*, nomen novum, from the Latin *protensus*, meaning "extended".

REFERENCE

HOLLIMAN, RHODES B. 1961 Larval trematodes from Apalachee Bay area, Florida, with a checklist of known marine cercariae arranged in a key to their superfamilies. *Tulane Stud. Zool.* 9(1): 2-74.

A COLLECTION OF THE BAT *LONCHOPHYLLA ROBUSTA* MILLER FROM COSTA RICA

DAN W. WALTON,

Department of Biology, University of New Mexico,
Albuquerque, New Mexico

Bats of the genus *Lonchophylla* Thomas, 1903 are known only from Recent specimens (Simpson, 1945). They have been reported from the Central and South American parts of the Brazilian Subregion of the Neotropical Region (Hershkovitz, 1958), from Bahía in Brazil to Costa Rica (Bourliere, 1955). Cabrera (1957) and Hall and Kelson (1959) recognized five species in this genus (type localities in parentheses): *Lonchophylla mordax* Thomas 1903 (Lamarão, State of Bahía, Brazil); *L. hesperia* G. M. Allen 1908 (Zorritos, Perú); *L. thomasi* J. A. Allen 1904 (Ciúdad Bolivar, Venezuela); *L. robusta* Miller 1912 (cave on Río Chilibrillo, Panamá); and *L. concava* Goldman 1914 (Cana, 2000 ft. eastern Panamá). *Lonchophylla robusta* is restricted to Colombia and Panamá (Cabrera, 1957). *Lonchophylla concava* is known only from its type locality (Hall and Kelson, 1959). Goodwin (1946) included both species in his list of Costarrican mammals although none of the specimens he listed was from Costa Rica. Hall and Kelson (1959) did not include all of Panamá in the range map of *L. robusta* but showed the range ending slightly north of the Canal Zone. No specimens of *Lonchophylla* have been recorded from Costa Rica.

Tulane University field crews and Dr. John L. DeAbate (University of Costa Rica) collected the first known specimens of the genus *Lonchophylla* from Costa Rica in 1956 and 1957. These collections represent an extension of the known geographic distribution of the genus and a new record for Costa Rica.

Materials and Methods.—Comparison of the specimens from Costa Rica to those from Panamá revealed considerable size variation in this little known species. Sixteen measurements were taken of each specimen (Table 1). Range, arithmetic mean, standard deviation, and standard error of the mean for each measurement was calculated. All measurements made follow those of Cockrum (1955) or are those given in the original description of *Lonchophylla robusta* (Miller, 1912). Statistical methods employed, including comparison of the means by Student's t test, follow Simpson *et al* (1960). All measurements are expressed in millimeters.

The two samples dealt with in this study include 27 specimens from Panamá and ten from Costa Rica. Each sample included adults of both sexes. Complete epiphyseal closure in the humerus indicates that all animals used were adults. The Costarrican sample contained four males and six females collected from an unnamed cave approximately four kilometers southwest of Hacienda de Moravia, State of Cartago, Costa Rica. The sample from Panamá contained nine females and 18 males. Specimens of *L. robusta* examined, the specimen number and institution are: Tulane University, TU 605, 606, 607, 608, 609, 610, 611, 612, 613, 614; University of Kansas, KU 45074*, 45075*; University of California, UC 114388*, 114390*, 114389*, 114391*; Museum of Comparative Zoology, MCZ 26467, 26468, 33444, 33445, 33446, 33447, 33448, 33449, 33450, 33451, 33452, 33453, 33454, 33455, 33456, 33457, 33458, 33459, 33460, 34243*, 34244*. All Panamanian specimens of *L. robusta* are topotypes except two (MCZ 34243 and MCZ 34244), collected at Rio Pequeni, Salamanca Hydrographic Office, Canal Zone.

Other specimens examined are: 1 *Lonchophylla mordax*, MCZ 33216*, Cidada da Barra, Río San Francisco, Bahía, Brazil; and 1 *Lonchophylla thomasi*, AMNH 97272*, Mocajuba, Río Tocantins, Brazil. Those specimens prepared as study skins are indicated by an asterisk.

COMPARISON

External characters.—Three external characters (height of the ear from notch, total length, and length of the hindfoot) differ significantly at the 5 percent level (fig. 1). In each instance, the Costarrican animals are smaller than those of the Panamanian sample.

TABLE 1.

Ranges of measurements, means, standard deviation, standard error, and levels of significance on all measurements made. Figures in parentheses indicate number of specimens.

	Panamanian Specimens					Costarrican Specimens			
	Range of Measurements	Mean	SD	SE	Level of Significance	Range of Measurements	Mean	SD	SE
Total Length	(8) 76.0-82.0	79.4	2.2	0.77	0.1%	(8) 66.0-75.0	70.6	2.9	1.0
Tail Length	(8) 8.0-10.0	9.3	0.88	0.31	not sig.	(10) 7.7-10.0	8.7	0.73	0.23
Hindfoot Length	(27) 11.0-15.0	12.0	1.0	0.20	1%	(10) 9.0-11.0	10.3	0.81	0.25
Height of Ear	(27) 14.0-18.0	15.7	0.90	0.17	0.1%	(9) 13.0-15.0	13.7	0.66	0.07
Length of Forearm	(25) 39.7-44.0	41.9	1.1	0.22	not sig.	(10) 41.6-45.0	42.7	1.0	0.34
Length of Tibia	(27) 15.3-18.4	17.3	0.82	0.16	not sig.	(10) 15.4-20.7	18.0	1.6	0.50
Length of Thumb	(27) 11.0-13.3	12.0	0.49	0.09	not sig.	(10) 11.5-13.2	12.0	0.55	0.17
Skull Length	(9) 25.0-26.7	26.1	0.50	0.17	5%	(10) 24.7-26.3	25.6	0.52	0.16
Skull Width	(9) 10.5-11.4	10.9	0.28	0.03	0.1%	(9) 10.0-10.5	10.3	0.21	0.07
Interorbital Width	(10) 4.9- 5.3	5.0	0.18	0.06	5%	(10) 4.6- 5.0	4.9	0.13	0.04
Width of Rostrum Over Canines	(11) 4.0- 4.4	4.1	0.12	0.04	1%	(9) 3.5- 4.1	3.8	0.25	0.08
Depth of Brain Case	(10) 7.1- 7.7	7.5	0.20	0.06	not sig.	(10) 7.2- 7.6	7.4	0.17	0.05
Length of Maxillary Tooth Row	(11) 9.3-10.1	9.8	0.25	0.08	not sig.	(10) 9.1-10.0	9.6	0.26	0.08
Mandible Length	(10) 17.4-19.1	18.5	0.55	0.17	not sig.	(10) 18.0-19.1	18.5	0.39	0.12
Length of Mandibular Tooth Row	(10) 9.8-10.5	10.2	0.23	0.07	not sig.	(10) 9.5-10.3	10.0	0.32	0.10
Condylo-basal Length	(9) 22.9-24.7	24.0	0.62	0.21	not sig.	(9) 23.0-24.0	23.5	0.30	0.10

Cranial characters.—Four of the cranial measurements (length of the skull, width of the skull across the brain case, inter-orbital width, and width of the rostrum over the canines) differ at the 5 percent level (fig. 2). The Costarrican specimens have a shorter skull, are narrower across the brain case, at the inter-orbital constriction, and above the canines. The two measurements made on the mandible showed no significant difference.

Sexual differences.—No sexual dimorphism in color or size was noted.

DISCUSSION

Although the means of skull length of the two samples differed significantly, this accounts for a very small part of the difference exhibited in total length. Tail length did not differ significantly. The Costarrican animals differ from those from Panamá mainly in the length of the region between the base of the skull and the first caudal vertebra. Ear height of the Costarrican sample seems to distinguish this group from the longer eared Panamanian specimens. Since the hind foot measurements of the Pana-

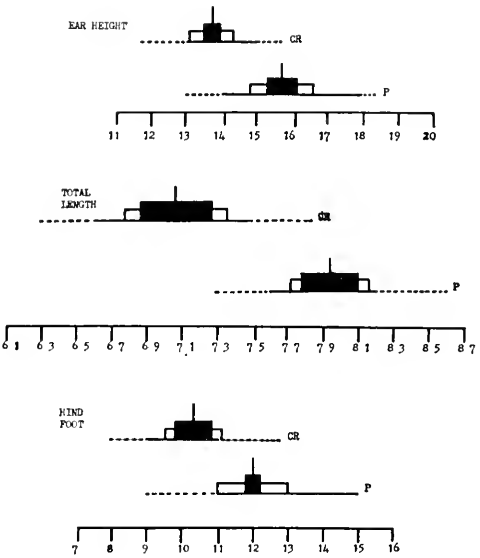


Figure 1. Distribution frequency of external measurements that differ significantly. The solid horizontal line represents range and the dotted extensions represent computed range. The vertical bar represents the mean, the hollow rectangle ± 1 standard deviation, and the solid rectangle twice the standard error on either side of the mean. CR = Costarrican sample, P = Panamanian sample.

manian sample were obtained largely from alcoholic specimens, the degree of difference shown may not be true.

Possibly, the animals from Costa Rica and those from Panamá might be regarded as subspecifically distinct. However, due to lack of material from the intervening area and the small sample from Costa Rica, such a course seems premature.

Table 1 shows all the measurements made on both samples, the ranges, means, standard deviations, and standard errors of the means for each character measured in each sample, and the level of significance of the differences between the means.

ACKNOWLEDGEMENTS

The writer expresses his gratitude to the following individuals: Drs. Norman C. Negus and Andrew A. Arata, and Mr. James L. Dobie of Tulane University, Dr. Charles O. Handley, Jr. of the United States National Museum, and Dr. John L. DeAbate of the University of Costa Rica.

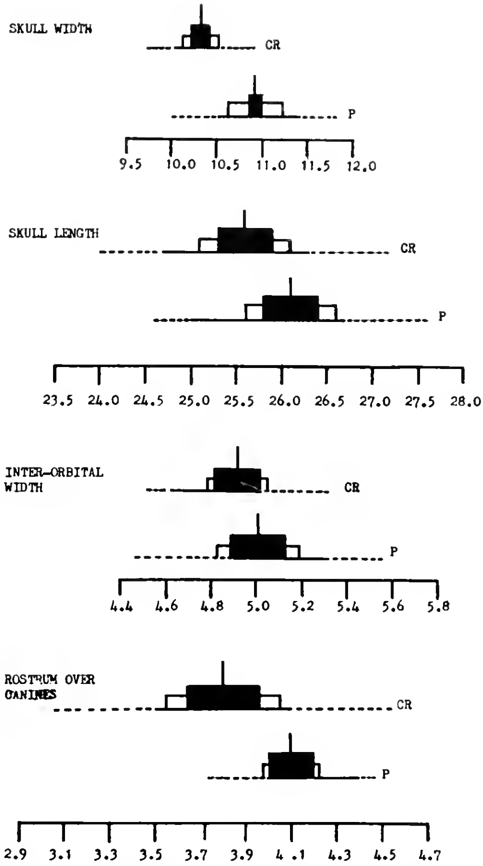


Figure 2. Distribution frequency of skull measurements that differ significantly. Explanation same as Figure 1.

REFERENCES CITED

BOURLIERE, F. 1955 Systematique, p. 1806-1844. *In* Pierre-P. Grassé (Ed.), *Traité de Zoologie*, Tome XVII, Sec. Fasc. Masson et Cie, Paris.

CABRERA, ANGEL 1957 Catalogo delos mamiferos de America del Sur. *Rev. Mus. Argent. Cienc. Nat. Bernardino Rivadaria, Cienc. Zool.* 4: 1-308.

COCKRUM, E. LENDELL 1955 *Laboratory Manual of Mammalogy.* Burgess Publ. Co., Minneapolis.

GOODWIN, G. G. 1946 Mammals of Costa Rica. *Bull. Amer. Mus. Nat. Hist.* 87: 271-474.

HALL, E. R. and KEITH R. KELSON 1959 *The Mammals of North America* Ronald Press, N. Y. 2 vols.

HERSHKOVITZ, PHILIP 1958 A geographic classification of neotropical mammals. *Fieldiana (Zool.)* 36: 581-620.

MILLER, GERRIT S., JR. 1912 A small collection of bats from Panama. *Proc. U. S. Nat. Mus.* 46: 23.

SIMPSON, G. G. 1945 The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.* 85: 1-350.

SIMPSON, G. G., ANNE ROE, and RICHARD C. LEWONTIN 1960 *Quantitative Zoology.* Harcourt, Brace & Co., N. Y.

THOMAS, OLDFIELD 1903 Notes on South American monkeys, bats, carnivores, and rodents, with descriptions of new species. *Ann. Mag. Nat. Hist.*, ser. 7, 12: 458.

ABSTRACT

Ten *Lonchophylla robusta* were collected from an unnamed cave approximately four kilometers southwest of Hacienda de Moravia, State of Cartago, Costa Rica on 12 September 1956 (eight specimens) and 2 July 1957 (two specimens). These represent the first published record of *Lonchophylla* from Costa Rica. The specimens from Costa Rica are smaller than Panamanian representatives, differing significantly in seven of sixteen characters. Possibly the animals from Costa Rica should be regarded as subspecifically distinct, but until more material becomes available from the intervening area formal recognition as a distinct taxon seems premature.

STUDIES ON THE POSTEMBRYONIC DEVELOPMENT OF THE FAIRY SHRIMP *STREPTOCEPHALUS SEALI* RYDER

IZHAR U. BAQAI,
Department of Biology, Dillard University,
New Orleans, Louisiana

CONTENTS

I. INTRODUCTION

The subclass Branchiopoda is one of the most remarkable among freshwater crustaceans. They not only have an unusual morphology and life history, but exhibit some primitive and some advanced characters.

Claus (1873, 1886) described the morphology and a few developmental stages of *Branchipus stagnalis.* Spangenberg (1875) described the adult morphology of *Branchipus stagnalis* and development of the egg up to hatching. Packard (1883) gave a detailed description of the adult fairyshrimp, with brief notes on the developmental stages of several species of fairyshrimps; Sars (1896) worked mainly on the adult morphology of *Branchinecta paludosa* but described an incomplete series of larval stages. Shantz (1905) gave a brief description of the telson, cercopod, and the antenna of the male of *Branchinecta coloradensis.* Oehmichen (1921) provided a rather complete description of the external morphology of the head appendages of *Branchipus grubei,* but gave no information concerning their internal morphology. Heath (1924) gave a brief account of almost all the larval stages from nauplius to adult of *Artemia salina* and *Branchinecta occidentalis,* but with no description of the internal structures. Furthermore his studies were based mainly on random field collections. Cannon and Leak (1933) and Lowndes (1933) briefly discussed postembryonic development of the internal systems of *Chirocephalus diaphanus* and gave a good account of the external morphology of mouthparts and their use in feeding. Hsü (1933) worked mainly on the structure of adult *Chirocephalus nankinensis,* but also gave a brief morphological description of the larval stages. Linder (1941), besides giving a good account of the taxonomy of fairy shrimps discussed briefly a few morphological and developmental points. Dexter and Ferguson (1943) on *Eubranchipus serratus,* and Coopey (1950) on *Eubranchipus oregonus* published brief descriptions of morphology and life history. Preuss (1957) provided a fairly good description of the musculature of the thoracic appendages of *Chirocephalus grubei.* Nourisson (1958) published a brief description of the postembryonic development of the thoracic appendages of *Chirocephalus stagnalis.* Pai (1958) published a brief comparative description of the postembryonic development of three representatives of the subclass Branchiopoda.

II. MATERIALS AND METHODS

Adult *Streptocephalus seali* were collected at Alton, Louisiana, on U.S. hwy. 11 about 4 miles north of Slidell. Most of the collections were made from two ditches located in the pine forest about 400 yards apart. The specimens were brought into the laboratory and 20 mature pairs were kept, one pair per dish in culture dishes having a diameter of four inches and containing pond water. They were fed with two drops of yeast suspension every other day. After three to four days eggs were laid at the bottom of the dishes. The eggs were removed and stored in small glass vials with a few drops of pond water for four to eight weeks. Hatching took place in distilled water; but, after hatching, pond water of the same volume as the distilled water was added to the dish.

The larval stages hatched in the laboratory were preserved at regular intervals in Zenker's fluid. Dissections were made in pure glycerine. Sections of the thoracic region and the abdomen were cut at 10 to 12 microns and stained with modified Van Geison's stain. The figures were made with the help of a camera lucida and drawn with black India ink.

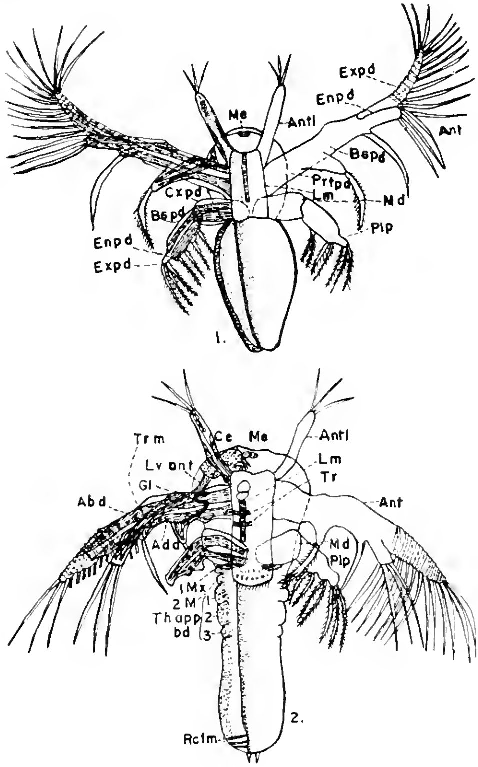
III. POSTEMBRYONIC DEVELOPMENT

A. General Features

Heath (1924) described larval stages on the basis of the number of ecdyses. In the present study, after several attempts, the exact number of ecdyses could not be determined accurately. Following Weisz (1947) my descriptions of the various stages were based on the number of body segments with reference to the length of the body.

The egg and its hatching process.—The spherical egg varied from 0.20 to 0.31 mm in diameter (average 0.26 mm). They were yellowish-brown in color, with numerous ridges and furrows on the external surface.

During the hatching process, the nauplius of *Streptocephalus seali* made its way out of the egg shell in a way similar to that described by Myint (1956) for *Artemia salina.* A few hours before hatching the shell cracked and the nauplius, enclosed in two very thin transparent membranes, bulged out. During emergence the posterior part of the nauplius showed jerky movements and the appendages moved vigorously over a limited range at regular intervals. Due to these movements the larva became free from the shell at the head end and released itself from the shell. The fully emerged larva was still enclosed within the inner membrane that was twisted and remained attached to the hind end of the outer membrane on one side and the inside of the shell on the other side. Due to twitching movements of the trunk and jerking of the appendages, the outer membrane broke open at the anterior end. This caused the inner membrane, with the nauplius enclosed, to move out and shifted the outer membrane posteriorly. The function of the two membranes may be as explained by Myint (1956). The out membrane (called emergence membrane) when burst helped move the larva for emergence, and gave a leverage point for the larva to pull out from the inner membrane. At the same time the larva was still inclosed within the inner membrane (called hatching membrane) which helped the larva to become free.



Figures 1-2. **1.** Ventral view of nauplius; right side showing musculature; left side showing external features. **2.** Ventral view of second larval stage; right side showing musculature; left side showing external features.

First larval stage or nauplius (fig. 1).—The free-swimming larvae hatched after 20 hours in the culture dish. Nineteen nauplii ranged from 0.24 to 0.46 mm (average 0.38 mm). The body was divided into two distinct regions, head and trunk. The head possessed three paired appendages: uniramous antennules, biramous antennae, and biramous mandibles. The head was larger than the trunk region and was covered dorsally with a round, plate-like structure, the dorsal (nuchal) organ. This covered the whole dorsal area of the head and continued posteriorly up to the bases of the antennae. The anterior part of the head bore a single pigmented median eye. At this time there was no indication of the paired compound eyes. On the ventral side and between the bases of the antennules and the antennae, a large labrum was directed from the head towards the trunk. It was elongated with a round distal margin and covered the mouthparts and a part of the postcephalic region.

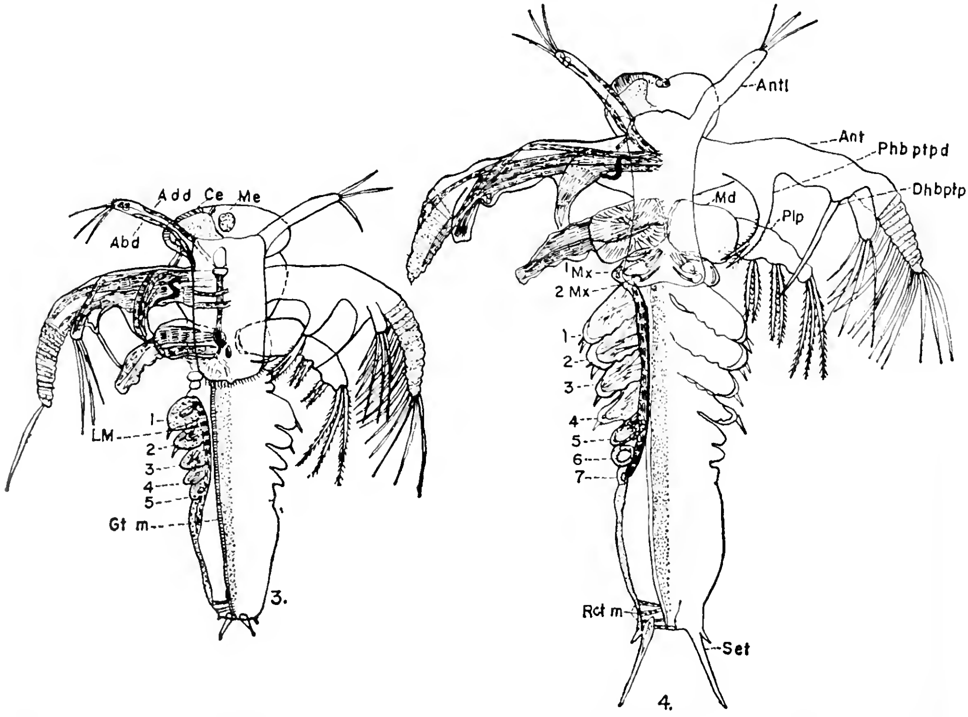
The trunk (postcephalic part) was oval and elongated and had no segmentation or appendages. At its posterior end an anal invagination was noted. On either side of the anal opening there was one lobe consisting of the anlagen of the setae, but there was no external indication of the setae.

Second larval stage or metanauplius (fig. 2).—After the growth of the nauplius for 19 hours (or, after 39 hours from the time of immersion of the eggs) five segments were added posterior to the mandibular segment including two maxillary segments in the five added segments. Sixteen specimens ranged from 0.49 to 0.60 mm (average 0.55 mm) in length. The antennules and the antennae were more elongate than in the previous stage. The anlage of the paired compound eyes appeared on the antero-lateral part of the head. The posteriorly directed labrum was reduced in length to the extent of just covering the mandibles, leaving the anlage of both maxillae uncovered. The first three thoracic segments were distinguishable. Heath (1924) in *Branchinecta occidentalis* observed eight thoracic segments in the second instar, but I observed only three segments with a minute seta on the anterior end of each of the first two. The caudal setae developed one on either side of the anus.

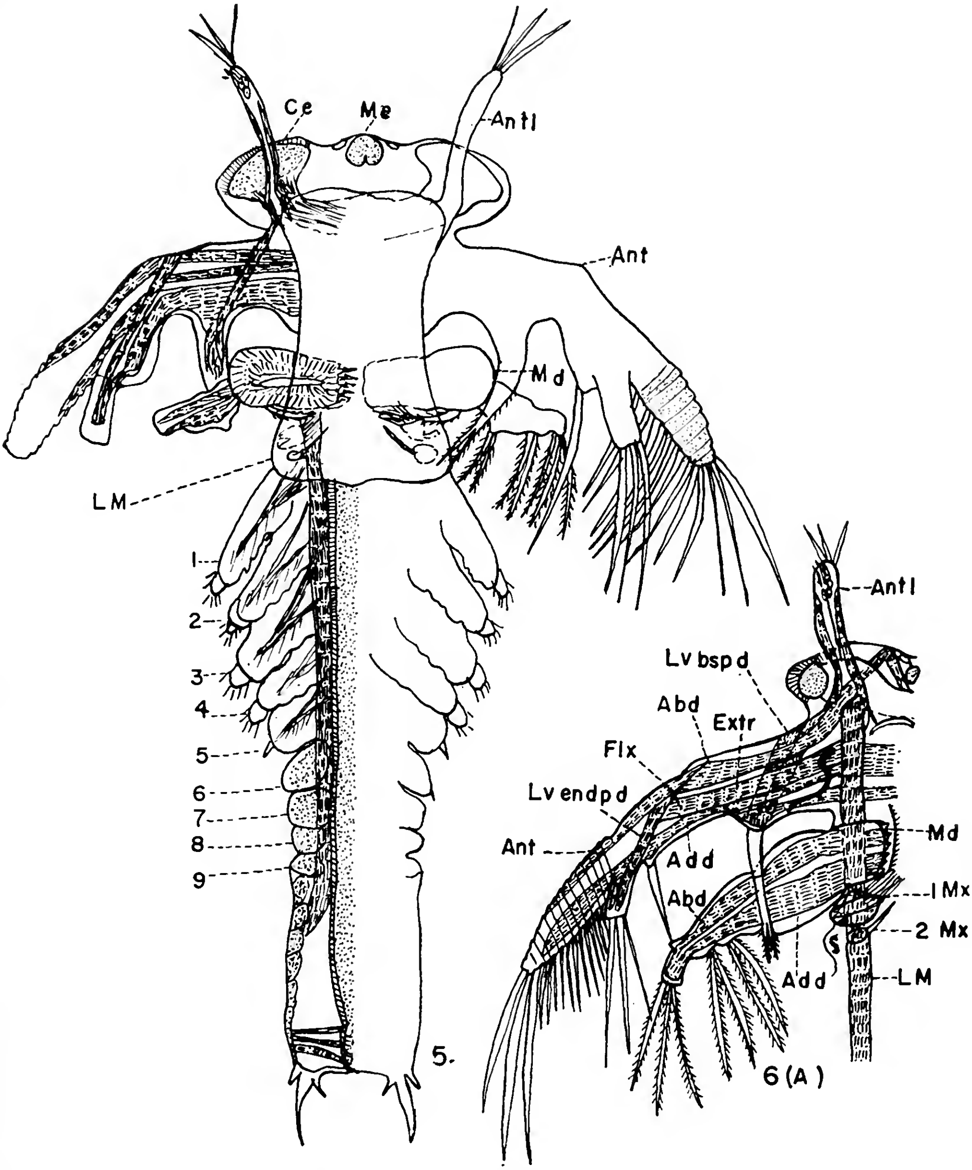
Third larval stage (fig. 3).—Seven hours after the previous stage (or, 46 hours from the time of immersion of the eggs) eight specimens ranged from 0.67 to 0.83 mm (average 0.74 mm) in length. In the head region the paired compound eyes became more prominent and pigmented. The maxillae developed into conical structure, but both pairs were still devoid of setae. The first six thoracic segments with anlagen of the appendages appeared; five had one seta each on the distal end (future flabella). The abdominal segments were not yet differentiated. The caudal setae became longer and stouter. In other structures of this stage, no apparent change was observed.

Fourth larval stage (fig. 4).—Nine specimens of the 56-hour stage, from the time of immersion of the eggs, ranged from 0.81 to 0.90 mm (average 0.86 mm) in length. In the head region the paired compound eyes showed rudimentary development of the eyestalks and became more pigmented. There was no apparent change in the first three head appendages. Both pairs of maxillae became more adult-like but were still without setae. The first seven thoracic segments were clearly differentiated. Six showed the development of appendages in a rudimentary stage with setae on the rudimentary flabella. The appendages also showed distinct endopodites and exopodites. Two caudal setae showed further development in length, and two additional setae were formed on either side of the cercopods.

Fifth larval stage (fig. 5).—Eight specimens of the 70-hour stage ranged from 1.00 to 1.20 mm (average 1.10 mm). The changes in the head region were slight except that the paired compound eyes became more prominent and more pigmented. The coxopodite of the mandibles became stouter, while the palps were slightly reduced. Both maxillae were developed into a spatulate form at the free extremities, but were still devoid of setae. The first five thoracic segments had well developed appendages; of these the anterior three had six endites. The development of the flabellum and other parts of the appendage will be discussed later. The remaining six thoracic segments were visi-



Figures 3-4. **3.** Ventral view of third larval stage. **4.** Ventral view of fourth larval stage.



Figures 5-6A. **5**. Ventral view of fifth larval stage. **6A**. Ventral view of right half of head region of sixth larval stage showing head appendages and their musculature.

ble but the last two (10th and 11th) were in a rudimentary stage. One more pair of caudal setae was added—making a total of three on each side.

Sixth larval stage (fig. 6: A, B).—Six specimens of the 91-hour stage ranged from 1.46 to 1.96 mm (average 1.78 mm). In the head region no change in the antennules or antennae was observed. The palp of the mandible was slightly reduced. First and second maxillae had attained their normal adult form but had few setae. In the thoracic region eleven segments were differentiated: The first nine segments had well developed appendages, and now the tenth and eleventh rudimentary appendages contained a seta on each rudimentary flabellum. Posterior to the eleventh thoracic segment the first two abdominal segments were also differentiated; these were the anlagen of the external genitalia. Two more caudal setae (a total of four pairs) were added and setules were present on each seta. The rudiments of the cercopods also were formed as protuberances on either side of the anus.

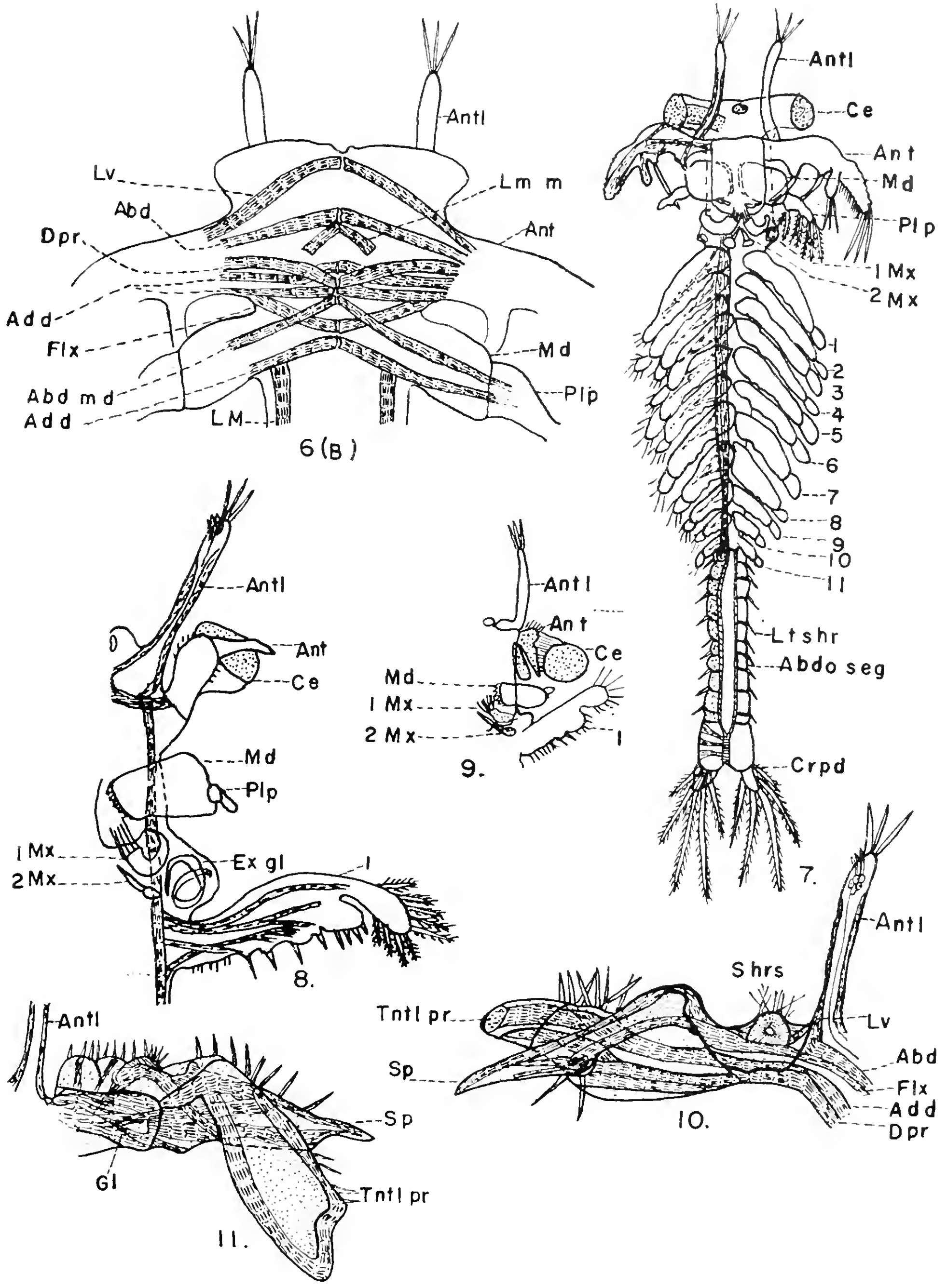
Seventh larval stage (fig. 7).—Six specimens of the 115-hour stage ranged from 2.26 to 2.34 mm (average 2.30 mm). In the head region the eyestalks were further elongated. The first ten thoracic appendages were fully developed, each bearing a flabellum. Seven more abdominal segments posterior to the first two abdominal (genital segments) segments were differentiated. Each genital and abdominal segment had a pair of sensory hairs attached on the posterolateral side near each segmental joint. Five well developed setae with setules were present on each developing cercopod.

Eighth larval stage (figs. 20, 30, 32, 36, 43, 54).—Six specimens of the 132-hour stage ranged from 2.65 to 3.00 mm (average length of males: 2.67 mm; females: 2.87 mm). In the head region the eyestalks were well differentiated. The palp of the mandible was further reduced. All evelen thoracic appendages were well developed and had flabella. The first eight thoracic appendages were differentiated, each with six endites. The twelfth and thirteenth trunk segments showed the development of two lobe-like protuberances which later gave rise to the external genitalia. For the first time the sexes could be distinguished by the structure of the antennae. In the male antenna the setae on the exopodite and on the first antennal segment were degenerated or reduced. The endopodite of the male antenna was completely degenerated. At the distal end of the basal joint of the male antenna, a tentacle-like process protruded. But in the female antenna the reduced endopodite was retained and the setae on the exopodite persisted. One pair of minute sensory hairs near each genital and segmental joint (posterolaterally) distinguished nine abdominal segments. Eight setae with setules were observed on each developing cercopod.

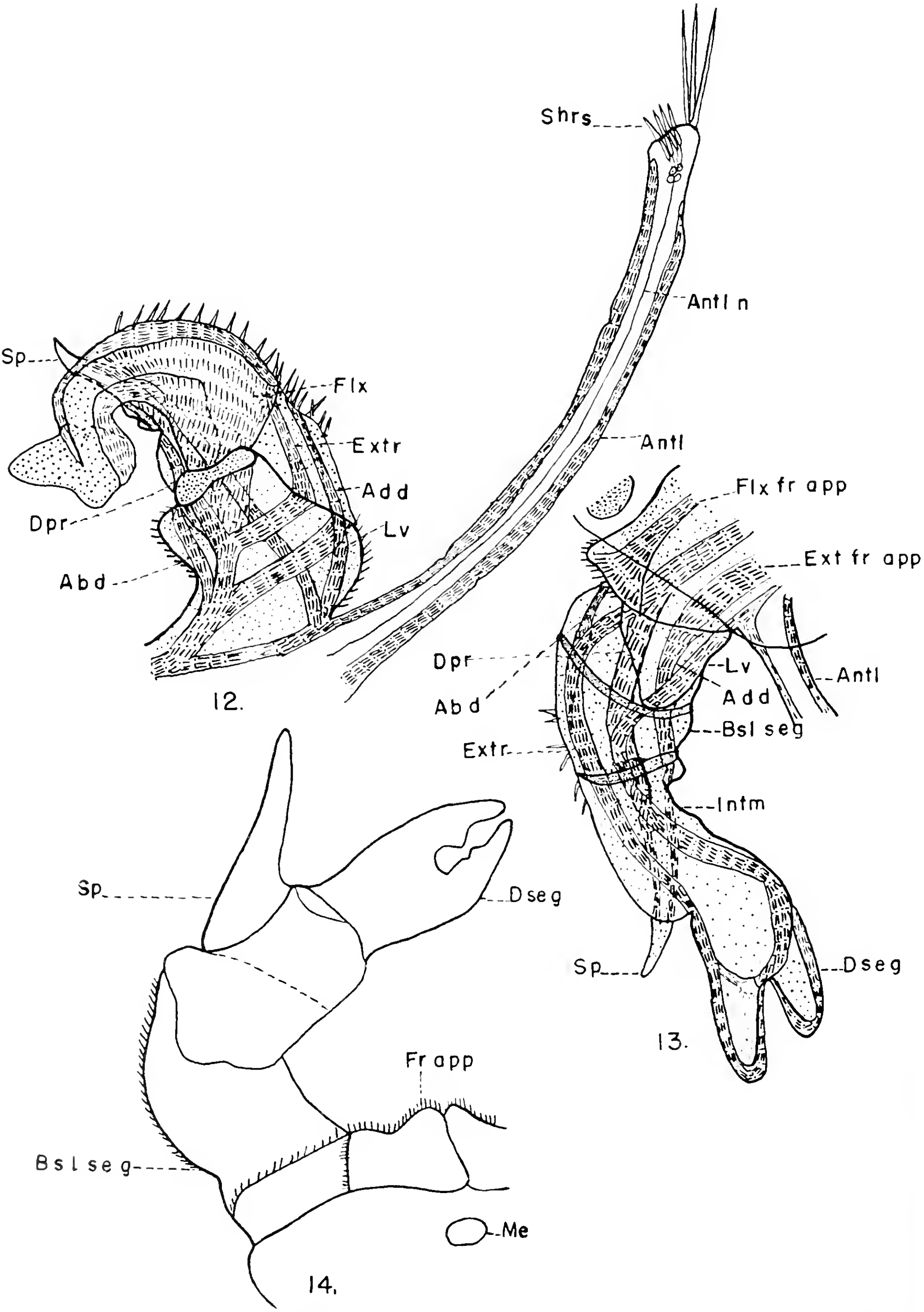
Ninth larval stage (figs. 8, 21, 22, 33, 49, 55) —Seven specimens of the 160-hour stage ranged from 3.35 to 4.00 mm (average length of males: 3.49 mm; females: 3.91 mm). In the head region the female antenna still retained setae, but they were shorter and stouter, with a vestigial endopodite. In the male antenna the tentacle-like process became elongated, and the antennae moved slightly toward the anterior side of the head. All the thoracic appendages now had six endites, and the exites were each differentiated into a praeepipodite, epipodite and flabellum. In the female the two genital segments were fused and grown out laterally to form the rudiment of the egg pouch (fig. 49). In the male the anlagen of the male gentialia consisted of two small tube-like protuberances projecting on the ventral side of the two fused genital segments. The seven abdominal segments were now differentiated with a pair of lateral sensory hairs persisting near each segmental joint. Eight setae with setules were observed on each further elongated cercopod.

Tenth larval stage (figs. 10, 23, 45, 46, 56).—Six specimens of the 178-hour stage ranged from 4.23 to 4.68 mm (average length of males: 4.23; females: 4.68 mm). in the head region the antennae of the male and female were further moved to the anterofrontal part of the head. The male antennae showed further growth of the tentacle-like process, and the length of the hook (the remnant of the exopodite) remained the same as in the previous stage. On the female antenna all setae were degenerated, and the basal segment was flattened including the greatly reduced exopodite on its distal margin. In both sexes the mandibular palps and the sensory spines on the ventral side of the coxopodite of the mandibles were degenerated with their setae. The thoracic appendages were now completely developed. The male genitalia were further elongated and extended up to the whole length of the 14th body segment. The egg pouch in the female also was elongated. The abdominal segments also showed growth in length. The cercopods were further elongated and had twenty setae with setules on each.

Eleventh larval stage (figs. 11, 24, 34, 46, 50, 57).—Five specimens of the 210-hour stage ranged from 4.72 to 5.27 mm (average length of males: 4.72; females: 5.25 mm) The antenna of the male was elongated and the tentacle-like process was further developed. In the female antenna the exopodite showed further degeneration and the protopodite (or, basal segment) was broader with sensory hairs developed on its anterior mar-



Figures 6B-11. **6B**. Dorsal view of head of sixth larval stage showing attachments of antennae and mandibular muscles (diagrammatic). **7**. Ventral view of seventh larval stage showing external and internal structures. **8**. Ventral view of head region of male ninth larval stage. **9**. Ventral view of tenth larval stage. **10**. Ventral view of antennule and antenna of male tenth larval stage showing musculature and external morphology. **11**. Ventral view of male antenna of eleventh larval stage.



Figures 12-14. **12**. Anterior view of male antennule and antenna of twelfth larval stage. 13. Anterior view of male antenna and frontal appendage of thirteenth larval stage. 14. Anterior view of male antenna and frontal appendage of fourteenth larval stage.

gin. The genitalia in both the sexes were more differentiated. The cercopods were further elongated and there were twenty-six setae with setules on each of them.

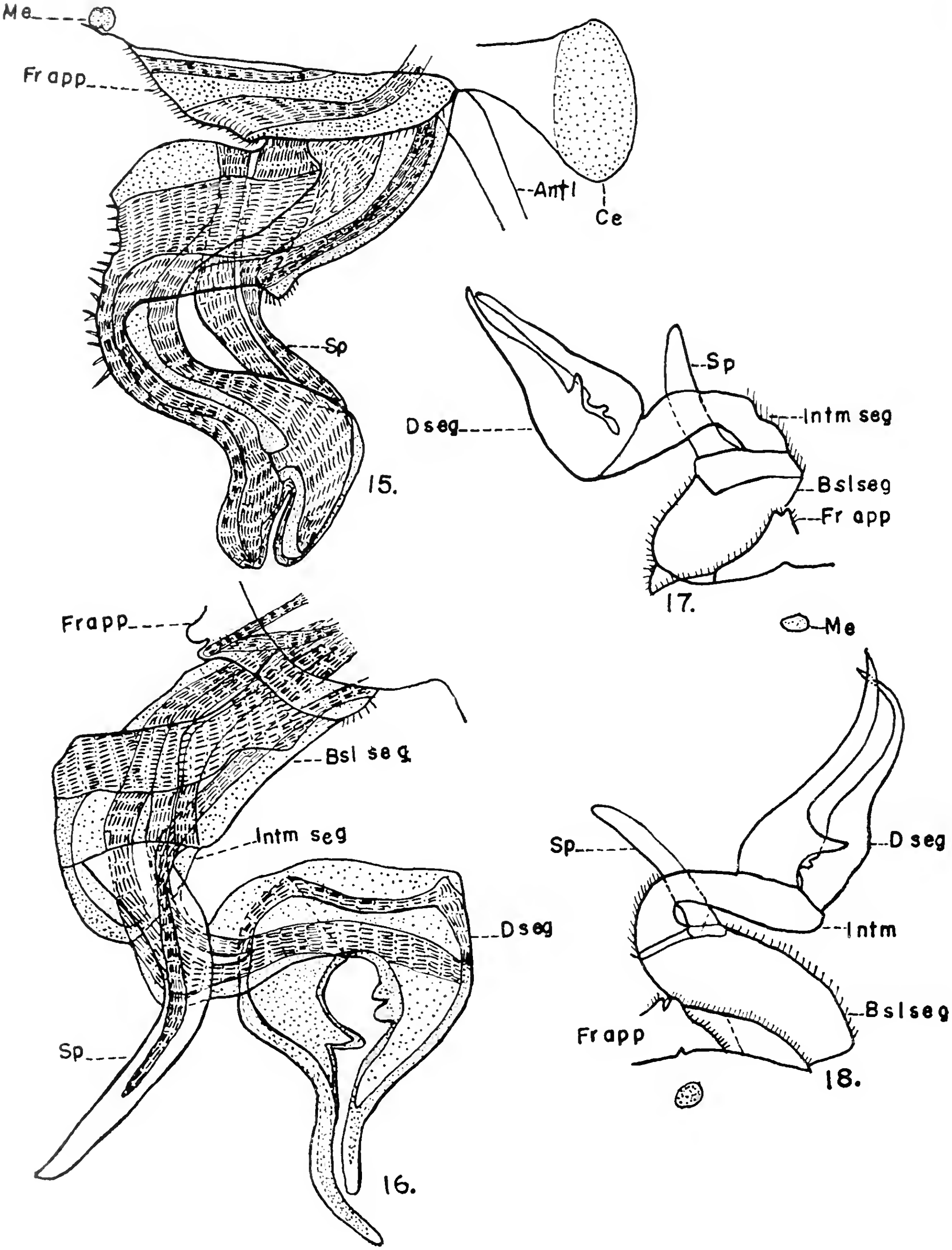
Twelfth larval stage (figs. 12, 25, 51).—Five specimens of the 245-hour stage ranged from 5.40 to 6.17 mm (average length of males: 5.80 mm; females: 6.17 mm). The antennules showed increase in length. The male antennae were further differentiated; a third segment originated from the second segment which had been the tentacle-like process of the earlier stages. This was the anlage of the terminal hand of the adult fairy shrimp. The three antennal segments were distinct in this stage. From the lateral side of the first antennal segment a protuberance developed; this was the anlage of the frontal appendage of the adult. The antennae of the female showed further expansion of the protopodites and the reduction of the exopodites to spine-like projections arising from the anterior apices; also, the anterior margins showed the numerous sensory hairs. The palps and the spines of the mandibles were completely degenerated. The number of setae with setules on the maxillae was adult-like. The compound eyes with their eyestalks were completely developed. The excretory gland was completely differentiated and was enclosed in the body on either side and located between the second maxilla and the first thoracic appendage. The thoracic appendages increased serially in length from first to fifth and then decreased from sixth to eleventh. The eleventh appendage was the smallest and nearly equal to the first. The genitalia of both sexes showed little development from the previous stage except for further elongation of the body and distinction of the internal structures. Lateral sensory hairs of the abdominal segments had degenerated. Each cercopod had fifty setae with setules.

Thirteenth larval stage (figs. 13, 61).—Five specimens of the 300-hour stage ranged from 6.50 to 7.60 mm (average for males: 6.50; females: 7.60 mm). Antennae of males and females now had completely moved to the anterior portion of the head. The male antennae were longer and the segments were more distinct. The distal end of the terminal segment was developed into a bifurcated claw-like structure, which was the anlage of the chitinous hooks of adult fairy shrimp. The lateral proturberances on the basal segment of the male antennae had moved between the antennae to form the future median frontal appendage. The female antennae showed no change from the previous stage. The genitalia were further differentiated into adult-like form. The cercopods were further elongated and had sixty setae with setules on each.

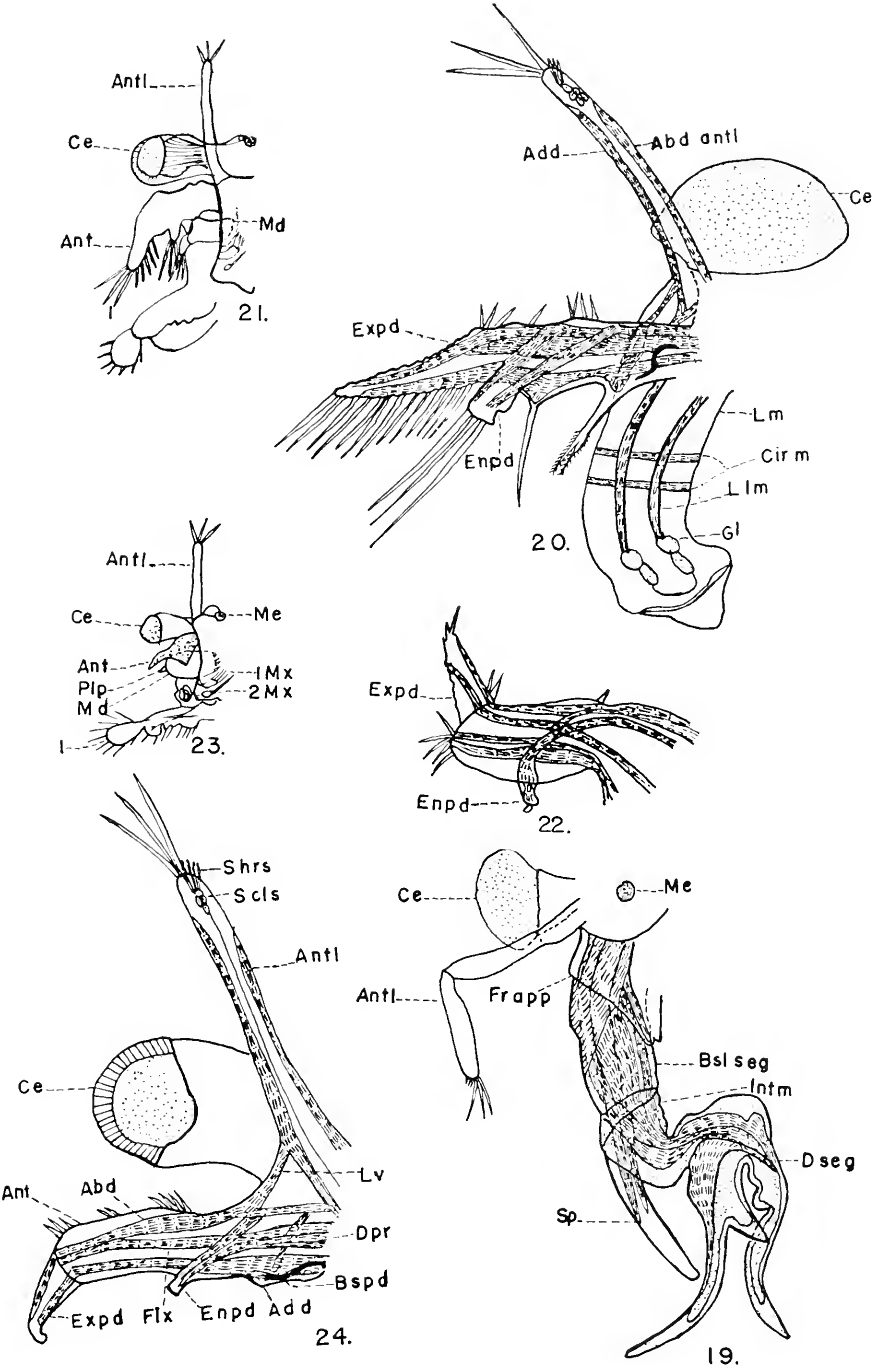
Fourteenth larval stage (figs. 14, 28, 52, 58).—Five specimens of the 336-hour stage ranged from 7.65 to 8.75 mm (average for males: 7.70; females: 8.42 mm). The hand (third segment) of the male antenna differentiated on its inner edges into chitinous projections on the left hook and two blunt protuberances on the right hook. The lobes on the basal segment of the male antennae moved into a median position and fused basally. The male genitalia showed little modification from the previous stage, but the egg pouch of the female was more elongated and the upper and lower lips of the egg pouch were now clearly distinct. Each cercopod had seventy setae with setules.

Fifteenth larval stage (figs. 15, 47).—Six specimens of the 385-hour stage ranged from 9.00 to 10.30 mm (average for males: 9.00 mm; females: 10.10 mm). The antennae of the male had become coiled and there was further elongation of the third segment and more differentiation of the hand. The frontal appendage became more inclined toward the median position. The antennae of the female showed no apparent change. The genitalia in both sexes differentiated into adult-like structures. The number of setae with setules increased to eighty on each cercopod.

Sixteenth larval stage (figs. 16, 26, 53).—Five specimens of the 475-hour stage ranged from 10.50 to 12.50 mm (average for males: 10:50; females: 11.75 mm). The antennae of the male showed further coiling of the third segment; the hook originated from the first (or, basal) segment, and also was longer than in the previous stage. The hand of the third antennal segment of the male had developed chitinous hook-like claspers and had assumed the adult form except for the protuberances on its inner side. The frontal lobes of both antennae were fused except at the anterior tip, which had the form of the adult frontal appendage. The male genitalia had developed the basal lobe, a chitinous spur with four minute setae on its ventral side, and the membranous eversible part of the penes had had developed minute spines



Figures 15-18. **15.** Anterior view of male antenna and frontal appendage of fifteenth larval stage. **16.** Anterior view of male antenna and frontal appendage of sixteenth larval stage. **17.** Anterior view of male antenna and frontal appendage of seventeenth larval stage. **18.** Anterior view of male antenna and frontal appendage of eighteenth larval stage.



Figures 19-24. **19.** Anterior view of male antenna and other structures of fully grown fairy shrimp. **20.** Lateral view of antennule, antenna, and labrum of female eighth larval stage. **21.** Ventral view of head region of female larval stage. **22.** Ventral view of female antenna in ninth larval stage. **23.** Ventral view of female head region of tenth larval stage. **24.** Ventral view of antennule and antenna of female in eleventh larval stage.

on the inner side as in the adult. The egg pouch of the female also assumed the adult shape. There was no increase in the number of setae on the cercopods.

Seventeenth larval stage (figs. 17, 27).—Five specimens of the 576-hour stage ranged from 13.00 to 14.79 mm (average for males: 13.60 mm; females: 14.70 mm). The antenna of the male showed some minor changes from the previous stage: the second segment was narrower, the distal part of the third segment had increased in length, and the chitinous projections on both hooks of the hand were further differentiated. No apparent change in the female antennae was noticed. The genitalia of both sexes also showed no change. The number of setae with setules on the cercopods remained the same in both sexes.

Eighteenth stage (figs. 18, 59).—Twelve specimens of the 696-hour stage ranged from 14.85 to 20.00 mm (average for males: 16.00 mm; females: 17.50 mm). The fairy shrimp now had acquired all the adult features except that the third segment of the male antenna showed further elognation and coiling of the hooks of the hand. The egg pouch of the female contained matured eggs though no copulation had been observed. On the female, setae with setules increased to eighty-six on each cercopod, but on the male the number was reduced to seventy-five on each cercopod. Spines had developed at the bases of some degenerated setae on the male cercopods.

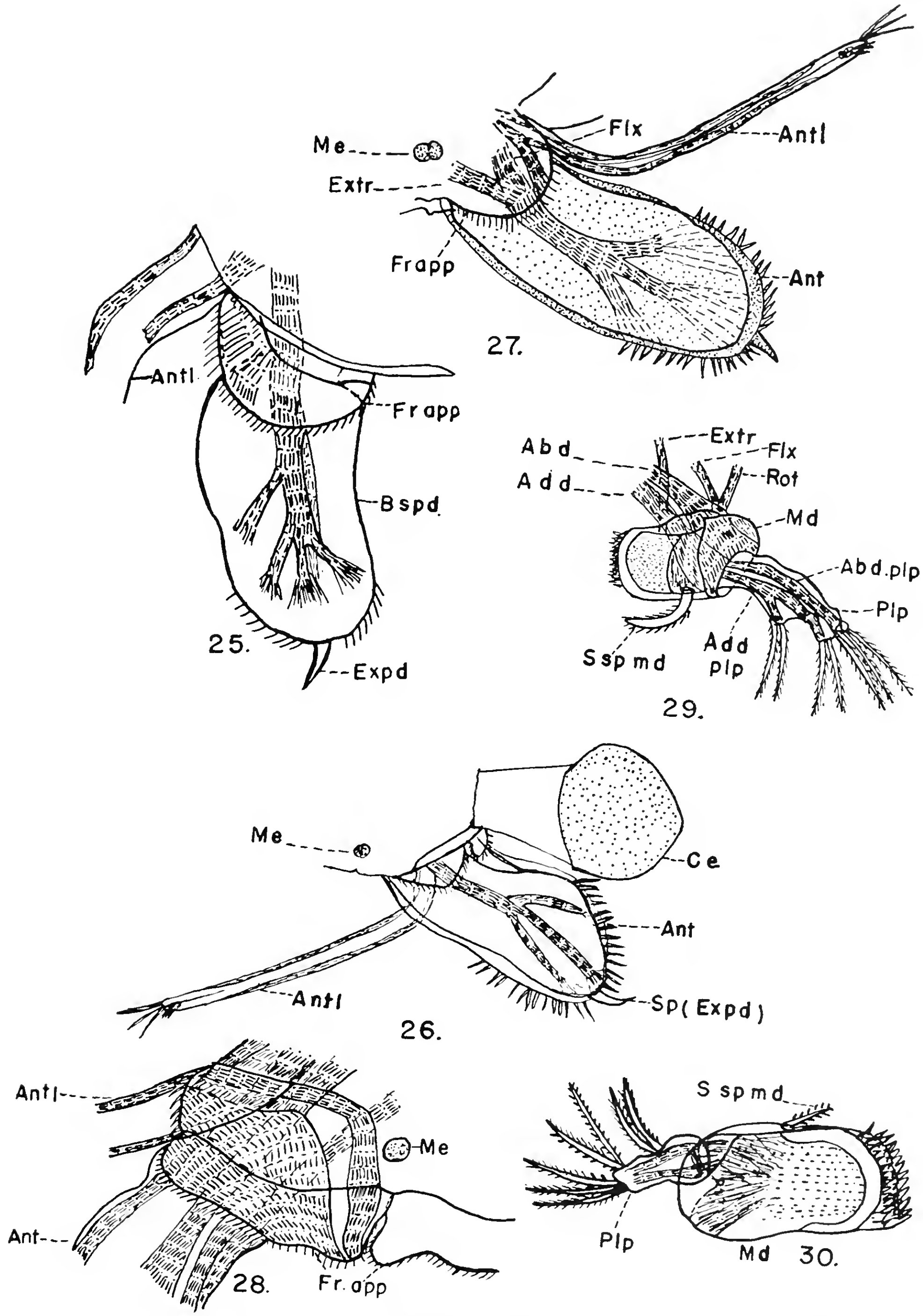
Fully grown fairy shrimp (figs. 19, 31, 37(9), 60, 62).—Ten specimens of more than the 30-day stage had increased in body length, but showed little difference from the structures of the eighteenth stage. The third segment of the male antennae showed further elongation of the claspers of the hand. The chitinous projection on the median hook of the hand was well developed; also the two tooth-like structures had formed on the inner side of the lateral hook of the hand. The frontal appendage was completely fused except at the distal end which had a bifid tip. The cercopods of the male now consisted of fifty-two setae with setules and eighteen spines on each cercopod. This indicated the reduction in the number of the setae and spines from seventy-five to seventy from the eighteenth stage. The cercopods were now completely fused with a single telson which was fused with the preceding abdominal segment. In the cercopods of the female there was no development of the spines on the distal end of the cercopods, but the setae retained the bristle-like structure that was present in the earlier larval stages.

B. Head Appendages and Their Musculature

Antennules (figs. 1-8, 10, 12, 19, 20, 24).—In the nauplius stage, the antennules were short finger-like rods, projecting anteriorly from the anterolateral head region. The length at the time of hatching was 0.09 mm. They were uniramous, non-segmented, and their distal ends each had three setae and five minute sensory setae, which were connected with the nerve fibers. In the second larval stage the antennules had increased to 0.12 mm in length. In the third stage the rudiments of the nerve fibers and two muscle fibers extended into the cavity of the antennules. In later stages there was not much change in structure, except for an increase in length and more differentiation of the nerve and muscle fibers. In the eight stage the length reached 0.32 mm. In the seventeenth stage the length of the antennules was 1.67 mm in females, and 1.31 mm in males. In the adult stage the length in the female was 2.18 mm and in the male was 1.84 mm.

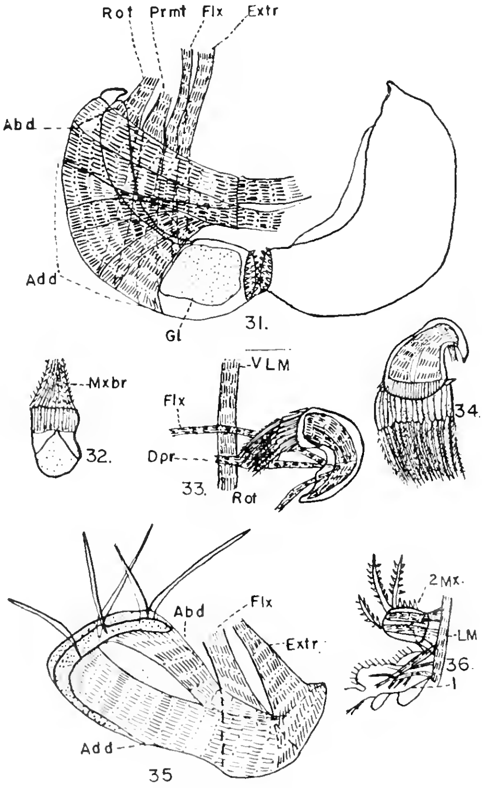
The musculature of the antennules consisted of two muscle fibers, which originated from the head and ran along the inner walls of the antennules. These muscles are used for lowering and raising the antennules; they may be called depressors (Dpr) and levators (Lv) of the antennules.

Antennae (figs. 1-7; *male,* figs. 9-19; *females,* figs. 8, 20-27).—In the first larval stage the antennae were biramous and had a length of 0.23 mm. The antennae were swimming appendages and were attached ventrolaterally on the head. Each antenna consisted of a protopodite, endopodite, and exopodite as found in a typical crustacean birmaous appendage. The protopodite was composed of basipodite and coxopodite (Oehmichen, 1921). The coxopodite had a process on the posterior side which was terminated into a single seta with setules, but in later stages this seta was bifurcated at the distal end. The basipodite also was a single process with a long seta having setules. At the distal



Figures 25-30. **25.** Anterior view of female antennule and antenna of twelfth larval stage. **26.** Anterior view of female antennule and antenna of sixteenth larval stage. **27.** Anterior view of female antennule and antenna of seventeenth larval stage. **28.** Anterior view of male frontal appendage of fourteenth larval stage. **29.** Ventroposterior view of mandible with musculature of sixth larval stage. **30.** Right mandible of eighth larval stage.

end of the basipodite there was an endopodite with one short and three long setae bearing setules on its distal end. The basipodite also had an exopodite with thirteen setae and setules on its posterior side. At the base of the antenna the anlagen of the antennal gland was present. In later stages (up to 7th stage) the antennae in both sexes increased in length and moved slightly to the anterolateral side of the head. After the seventh stage the antennae had slow rate of growth in length and began to show male and female characteristics. The differentiation became apparent in the eighth larval stage when the length was 2.69 mm. In the female the endopodiate and the exopodite were reduced successively in the later stages, while the protopodite expanded and became sac-like. In the adult stage of the female the endopodite completely degenerated and the setae on the protopodite and the exopodite were lost. In the twelfth larval stage the exopodite appeared as a spine-like structure at the distal end of the expanded protopodite. Numerous sensory hairs also were developed on the distal margin of the protopodite. The basal part of the protopodite had a reduced lobe which could be compared to the well developed frontal appendage of the male antennae. The basal lobe of the female antenna had sensory hairs around its margin and served as a sensory organ. The female antenna in the eighth stage showed an indication of migration anteriorly from the sides of the head; migration was completed in the twelfth stage.

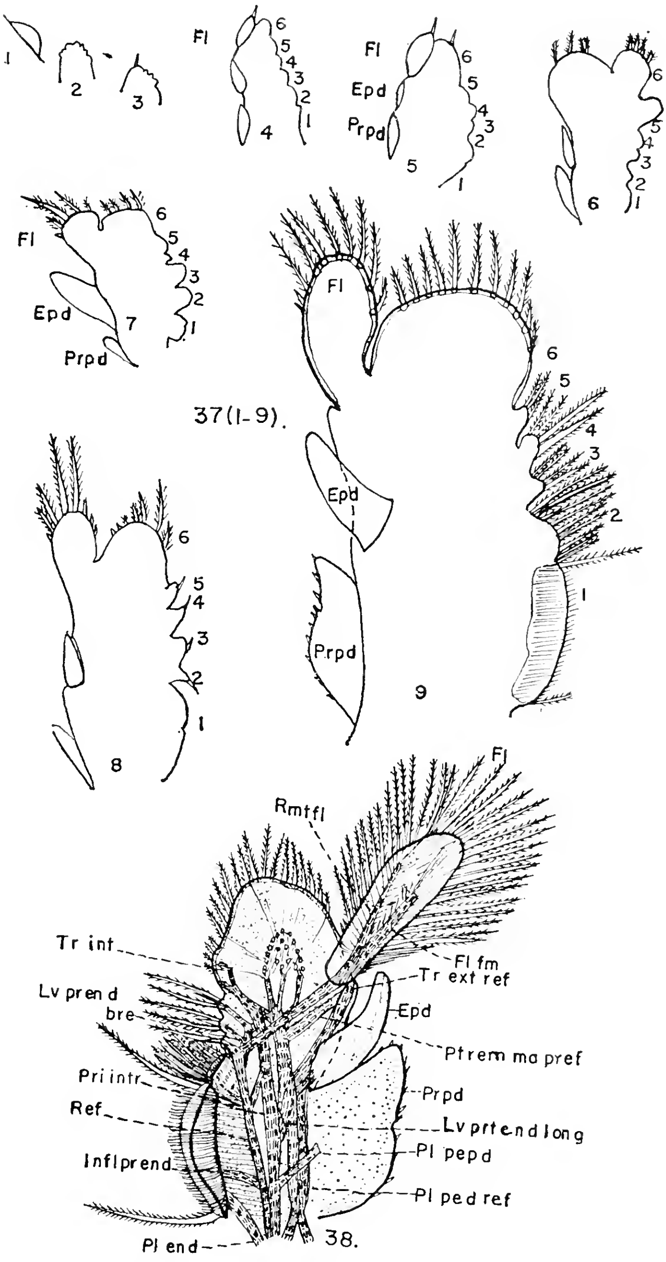


Figures 31-36. **31**. Mandibles of adult with musculature of right mandible. **32**. Ventroposterior view of first maxilla of eighth larval stage. **33**. Ventral view of first maxilla with musculature of ninth larval stage. **34**. Dorsal view of first maxilla, with some muscles, of ninth larval stage. **35**. Ventroposterior view of second maxilla with musculature of sixth larval stage. **36**. Ventral view of second maxilla with musculature of eighth larval stage.

In the male, antennae, development of the complicated clasping organs was completed progressively starting with the seventh stage, even though the male fairy shrimp was sexually mature at the 16th stage, development of the antennae continued through four or five later stages.

Modification of the male antenna started in the advanced seventh larval stage. At the anteroventral region of the protopodite a fold-like protuberance developed, and at the same time the two segments of the protopodite fused. The exopodite with its setae and the endopodite started to reduce in the eighth stage, and were completely degenerated in the ninth stage. At the same time the male antennae started to move towards the anteromedian side of the head. The fold-like protuberance increased in length and developed into two triangular plates at the ends of the antennae (fig. 13, D *seg*) as seen in the thirteenth stage. From the fourteenth stage to the adult, the third antennal segment was developed from the curved second segment and its distal end acquired the hand-like structure. The hand included one chitinous projection on the inner side of the median hook and two blunt chitinous, tooth-like projections on the inner side of the lateral hook (fig. 19). The antenna of the first stage was 0.23 mm long; and in the adult was 4.39 mm. Thus in the female the antennae reduced in size proportionately in subsequent stages, while in the male the antennae showed increase in length proportionately from the eighth stage to the adult.

Internally the muscle cells were differ-



Figures 37-38. **37.** Development of thoracic appendage: 1. anlage of thoracic appendage; 2. second stage of developing appendage; 3. third stage; 4. fourth stage; 5. fifth stage; 6. sixth stage; 7. seventh stage; 8. eighth stage; 9. ninth stage (completely developed). **38.** Ventroposterior view of third thoracic appendage with musculature of the adult.

entiated into muscle fibers in the sixth stage, and attained their elaborate form. A dorsal set of the muscles composed of five pairs of indivdual strands originated in the dorsal organ (fig. 6(B), *Lv, Abd, Dpr, Add, Flx*). Three additional pairs of muscles originated ventromedially beneath the anterior portion of the intestine and also just posterior to the esophageal connection (fig. 6(B), *Lm m, Abd md, Add*). These muscles were so arranged that they formed a continuous horizontal, contractile band, running between the antennae and the mandibles. Both dorsal and ventral muscles were inserted along the inner side of the antennal wall. According to the function of each muscle strand the following terminology is suggested; the anterior muscle strand whch raises the antennae is called levator of the antennae (*Lv*). It originates from the anterior portion of the dorsal (nuchal organ) and insertes on the inner anterior surface of the antennal wall. The second strand which moves the antennae away from the body is called abductor of the antennae (*Abd*). The third muscle strand which moves the antennae back is called depressor of the antennae (*Dpr*). Adjacent to the depressor muscle, two muscles originate anteroventrally and posteroventrally, and are inserted in the exopodite region of the antenna. These pull the antennae toward the body and are called adductors of the antennae (*Add*). Another muscle band, which originates ventrally, adjacent to the mandibular tendon, and is inserted at the posterior part of the exopodite flexes the antennae towards the body; these are called the flexors of the antennae (*Flx*).

The musculature of the adult male antenna showed little difference from that of the early larval stage as described above. The transverse muscle (*tr m*) of the endopodite after the degeneration of the endopodite became attached to the spur of the antenna of the adult which was located at the distal end of the protopodite.

The musculature in the female antenna of the adult degenerated. Instead of the five muscle strands as in the sixth larval stage, there were now only two muscle bundles arranged as two overlapping bands of the muscles in a dorsoventral position. Minute muscle fibers that originated from these bundles were inserted into the anterior margin of the protopodite and spine-like exopodite. This stage of the musculature and the antenna was reached in the twelfth stage of the female. This stage was almost adult-like except that the antenna was shorter than in the adult.

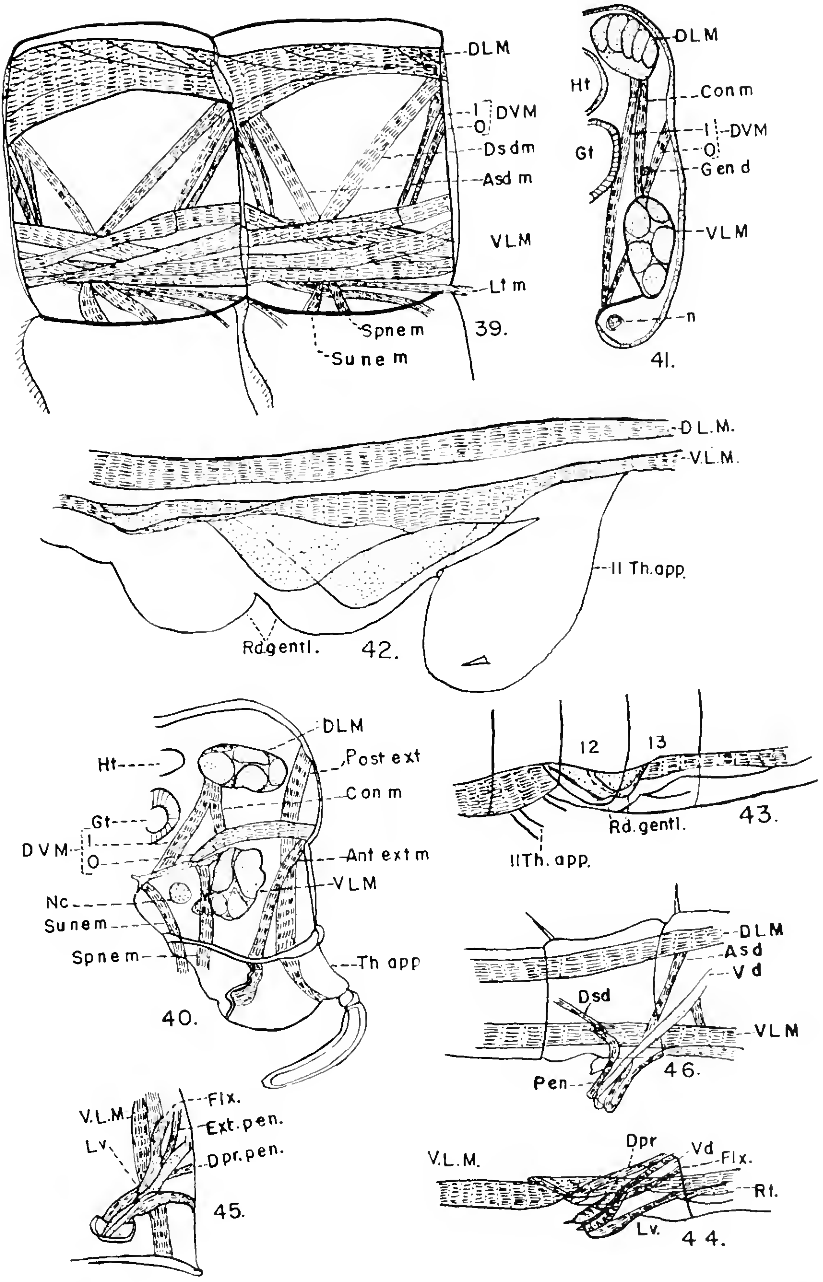
Frontal appendage (figs. 11-19, 28).—The development of the frontal appendage was worked out by Claus (1886) on *Streptocephalus torticornis,* Health (1924) on *Branchinecta occidentalis,* and by Hsű (1933) on *Chirocephalus nankinensis.* In *Streptocephalus seali* development of the frontal appendage started from the eleventh stage when the larva was 4.70 mm long. In that stage a small outgrowth developed from the dorsolateral side of the basal joint of the male antenna, which had sensory hairs around its margin (fig. 11). In subsequent larval stages this outgrowth of the male antenna moved into the anteromedian position at the base of the antenna and then migrated from the antenna to the head. In the fourteenth stage the two lobe-like structures of the antennae came closer and ultimately coalesced at their bases forming a common anterior union of the head and antennae. In the adult stage the fusion was almost complete except at the tip which remained bifid indicating the fusion of two basal lobes of the antennae. A similar type of frontal appendage development was observed by Claus (1886), and Linder (1941) in other species of the genus *Streptocephalus.*

The musculature included flexor muscles (*Flx*) of the two basal lobes of the antennae, coalesced to form a single strand, which was inserted in the anterior end of the dorsal or nuchal organ and functioned to raise as well as bend the frontal appendage of the adult. The extensor muscle (*Extr*) remained separate inside the frontal appendage. They originated from the anterolateral side of the dorsal or nuchal organ and functioned to straighten the frontal appendage (fig. 28).

In the female similar outgrowths at the base of the antennae were observed. Each developed into a lobe at the base of the antenna, but the two were separated from each other and each had sensory hairs around the margin.

The musculature was not as well developed in the adult female as in the male; two minute muscle strands originated from the head and inserted in each basal lobe of the antennae.

Mandible (figs. 1-9, 21, 23, 29-31).—The mandibles in the first larval stage were swim-



Figures 39-46. **39**. Lateral view of thoracic region of adult showing musculature. **40**. Transverse section of thoracic region of adult showing musculature. **41**. Transverse section of abdominal region of adult. **42**. Lateral view of anlage of genital apparatus of seventh larval stage. **43**. Lateral view of male genitalia of eighth larval stage. **44**. Lateral view of male genitalia of tenth larval stage. **45**. Anterior view of the same (*i.e.,* fig. 44). **46**. Lateral view of male genitalia of eleventh larval stage.

ming appendages. They were articulated on the dorsal plate of the mandibular segment which was quite distinct between the head plate and nuchal plate. They were biramous and consisted (Oehmichen, 1921) of a protopodite having a chitinous coxopodite and the basipodite. The coxopodite consisted of a rudimentary jaw and a sensory spine with setules located at the lateral side of the coxopodite and at the base of the palp. The basal segment of the palp (the basipodite) had two backwardly directed setae with setules. On the distal end of the basipodite there were two small processes, the exopodite and the endopodite. The exopodite had two setae with setules, while the endopodite had three setae with setules. In the later larval satges the development of the mandible involved degeneration of the palp and the sensory spine. Each chitinous jaw was differentiated on the distal edge of the coxopodite during the development of the later stages. The degeneration of the mandibular palp and the sensory spine was completed in the twelfth stage in both sexes, when the male was 5.80 mm long and the female was 6.17 mm. After the twelfth stage the mandibles attained adult form.

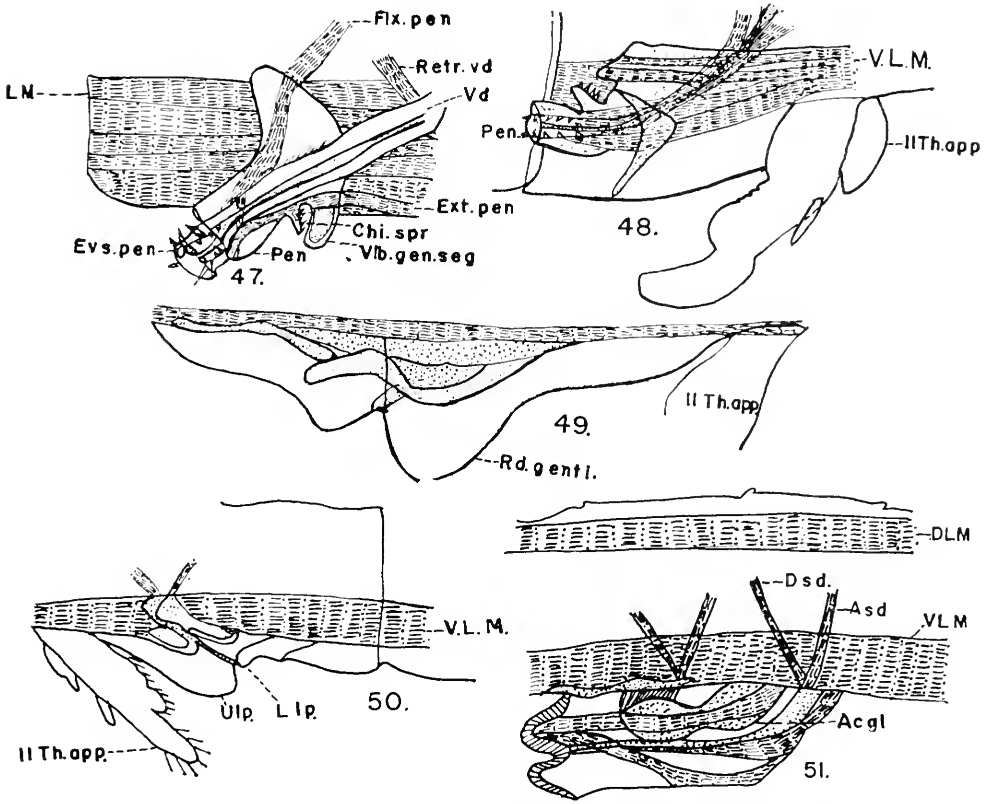
The development of the musculature involved formation of the transverse and horizontal muscle bands laid down in the first larval stage; these were fully differentiated in the third stage. These muscles were attached to the lateral wall of the coxopodite, converged to a point in the median plane, and were ventral to the intestine (fig. 6B). Two longitudinal muscles (*L M*) originated at the posterior tendinous points of the dorsal or nuchal organ, and were inserted in the distal part of the protopodite and the mandibular palp respectively. The muscles of the mandibular palp degenerated in later stages.

The terminology of the mandibular muscles given by Snodgrass (1950) is partially followed for the mandibular muscles of *S. seali* (fig. 31). The ventral muscle of the mandible consisted of two well developed strands called *adductor* (*Add*) and abductor (*Abd*) respectively, which functioned to close or open the jaws. In the median part of the nuchal organ two pairs of suspensory ligamentous muscles originated. They were inserted in the tendinous part of the ventral muscles; flexor (*Flx*) and extensor (*Extr*), to pull the jaw inward and to straighten it. There were also two longitudinal muscle strands called anterior dorsal remotor (*Rot*) and posterior dorsal promotor (*Prmt*) muscles respectively. Their contractions, apart from moving the palp in the early larval stages, pulled the mandibles outward and slightly forward, a movement opposite to that produced by the transverse ventral muscles.

Maxillae (first and second), (figs. 2-6, 32-36).—In the first larval stage the anlage of both pairs of maxillae consisted of layers of cells on either side and surrounded by the ventral ectodermal cells of the head. In the second stage the bud of the first maxilla was developed and resembled a short sac-like outgrowth. In the following stages the first maxilla enlarged and assumed a stubby finger-like shape. In the first four stages the first maxilla appeared as an elevation without setae at the distal end. In the seventh stage, when the larva was 2.15 mm long, the first maxilla consisted of two segments; one proximal, the protopodite, and one distal, the exopodite. The latter became the maxilla proper of the adult. The distal segment of the first maxilla terminated in nine setae with interlocking setules. In subsequent stages there was an increase in the number of the serae. In the eleventh stage the first maxilla was adult-like. Finally in the adult stage the number of the setae had increased to thirty-one.

The second maxilla appeared as an elevation without setae in the second larval stage. The second maxillae were located at the base of the first pair of developing thoracic appendages. The anlage of the second maxilla developed subsequently into a very short, minute round appendage, located on either side and posteromedial to the first pair of maxillae.

The musculature of the maxillae differentiated in the fifth larval stage. At this stage the fibers of some of the muscles at their points of attachment had lost the striations characteristic of muscle tissue; thus, they were considered as non-contractile and tendinous in function. The muscles of the first maxilla consisted of a ventral transverse bundle which originated on the nuchal organ and formed a connection between the maxillae. Three dorsal longitudinal muscles (*DLM*) were also present: one originated from the median mandibular tendon bridge; the other two originated from the lateral



Figures 47-51. **47.** Lateral view of male genitalia of fifteenth larval stage. **48.** Lateral view of male genitalia of fully grown fairy shrimp. **49.** Lateral view of female genitalia of ninth larval stage. **50.** Lateral view of female genitalia eleventh larval stage. **51.** Lateral view of female genitalia of twelfth larval stage.

side of the mandibular and antennal tendon bridges. These three muscle bands called flexor (*Flx*), retractor (*Retr*) and rotator (*Rot*), respectively, were used for moving and rotating the first maxilla in upward and downward directions. These movements were used for filtering food with the setae before it reached the mandibles for chewing.

In the second maxilla the muscles developed in a way similar to that of the first maxilla, but the muscles were not well developed and apparently nonfunctional. The chief function of the second maxillae seemed to be sensory due to the presence of five minute setae in the sixth larval stage; these were reduced to three in the eighth stage. In the adult the second maxilla became membranous with a basal lobe and two long, thick setae with setules. No movement was observed, which explained the reduction of the musculature and indicated the sensory function.

Labrum (figs 1-5, 9, 20-23).—In the nauplius stage a labrum on the ventromedian side of the head was directed backward and covered the mouth region. It was elongate with a round distal margin and extended to the trunk region. In the sixth stage the labrum was reduced in size and reached only to the mandibles. In subsequent stages the labrum showed no external changes and retained the same structure to the adult form. Functionally the labrum represented the most anterior portion of the food grooves leading to the mouth; the posterior part was formed by the first endites of the thoracic appendages. The most distinct components of the labral cavity were numerous storage cells, which were fully developed by the third larval stage.

A muscle strand on each side attached to the wall of the labrum (fig. 20, *L lm*) was differentiated in the second larval stage. These longitudinal muscles ran laterally to the intestine and originated from the anteriormost tendon of the nuchal organ. Contraction of these muscles raised the labrum towards the ventral head surface. Two transverse or circular muscles (fig. 2, *Tr*) also differentiated in the third larval stage; they were used for the transverse contraction of the labrum.

C. Median and Compound Eyes

The anlage of the median eye was present in the first larval stage (fig. 1, *Me*); at that time it was pigmented and light sensitive. In later stages the median eye increased steadily in size and pigmentation (figs. 2-10).

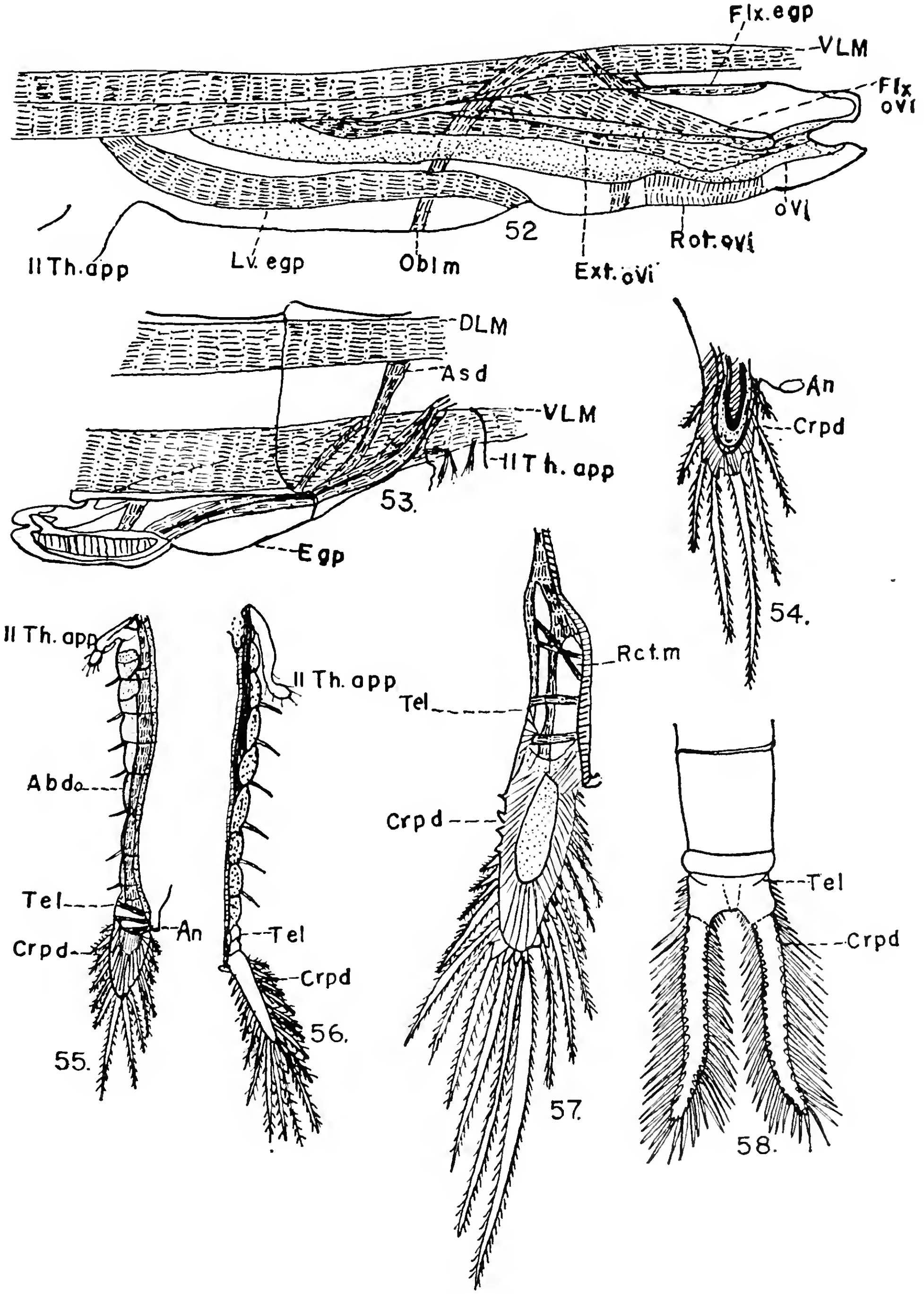
In the first larval stage there was no indication of paired eyes. In the second stage rudiments of compound eyes occurred as slight lateral ectodermal proliferations just behind the bases of the antennules. In the fourth stage the ectodermal proliferations were converted into ommatidia. Then up to the tenth stage the eyes bulged laterally from the head surface and became more prominent. Development of eyestalks was completed between the seventh and tenth stage. After that developments of the eyes involved elongation of the eyestalks and increase in the size of the pigmented portion; this was complete in the eighteenth stage.

Movement of the eyes was controlled by two oblique muscles and one transverse muscle (not shown in my figure) as described by Claus (1886) for *Branchipus stagnalis*. The two oblique muscles originated from the median tendon of the head, one from the anterior tendon of the head (used for raising the eye in the forward position); the second set originated from the posterior tendon, crossed the oblique muscles at the base of the eyestalk, and were inserted at the distal end of the eyestalk. It functioned to move the eyestalk anteroposteriorly. The transverse muscle originated from the median tendon and was inserted near the posterior base of the retinal nerve cells; it was used to move the eye posterolaterally and ventrodorsally.

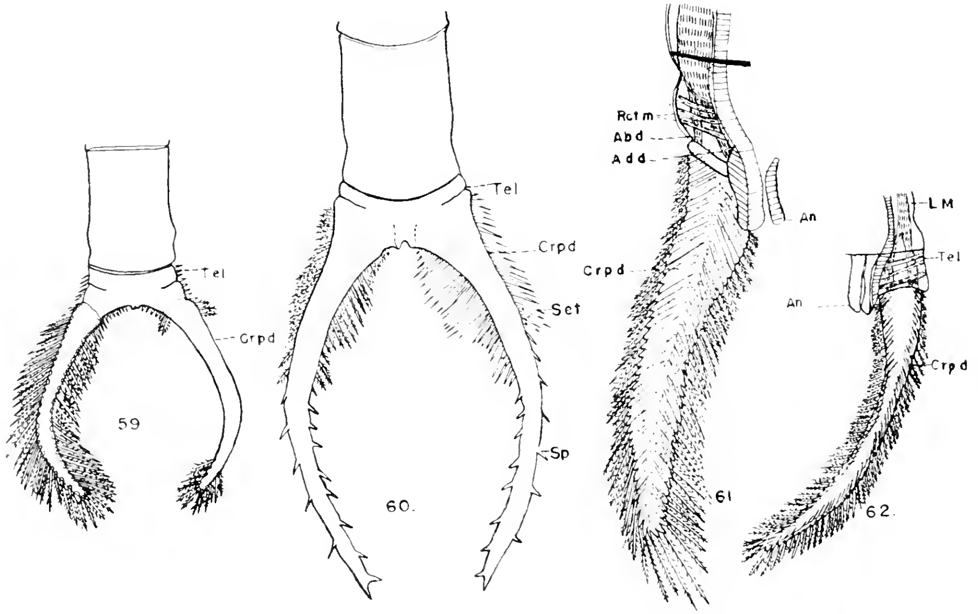
D. Thoracic Appendages and Their Musculature

Rudiments of the thoracic appendages appeared in the second larval stage (fig. 2, *Th app bd*). They developed progressively from the anterior end of the postcephalic region; therefore several stages of appendage development were represented in each larval stage. In the second stage each of the three thoracic segments had a group of cells branching out laterally from the ventrolateral ectoderm. In subsequent stages (figs. 3-5, 7) the appendages expanded to fuse loosely with the anterior haemocoelomic cavity. During subsequent stages (figs. 37, 38) several lobes were added to the ventral side of the appendage bud to form the exopodite (*Fl*), two lobes to the anterior side to form one distal epipodite (*Epd*), and one praeepipodite (*prpd*) with a notch on its outer margin. The setae produced on the distal end of the exopodite and the endopodite (1-6) were at first very few in number. Subsequently they increased in number and contained setules in the adult.

In the third stage five rudimentary appendage buds had developed. A seta was present on the first four. In the fourth stage there were seven thoracic appendicular buds; in the fifth stage, nine buds; and in the sixth stage eleven thoracic appendages in various stages of development had differentiated. In this stage two genital segments (1st and 2nd abdominal) had also developed. All thoracic appendages had setae with setules on their distal ends. The number of setae on the sixth endites and the flabella increased progressively from the first stage to the adult. In the sixth stage, the eleventh thoracic appendage had one seta each on the flabellum and the sixth endite. That number increased to 45 and 26 respectively in a fully grown fairy shrimp. From the seventh stage, the larvae were differentiated by the number of setae on the flabella and the sixth endites of the eleventh thoracic appendage as suggested by Heath (1924) for *Branchinecta occidentalis*. In the ninth stage the structures of the thoracic appendages were adult-like except for the number of setae on the flabellum and the sixth endite (fig. 37). The endopodite consisted of six endites; the sixth endite had a row of 19 setae. The exopodite had a flabellum at the distal end with a row of 39 setae with setules. The exopodite included one epipo-



Figures 52-58. **52**. Lateral view of female genitalia of fourteenth larval stage. **53**. Lateral view of female genitalia of sixteenth larval stage. **54**. Ventral view of cercopod of eighth larval stage. **55**. Ventral view of abdomen and cercopods of ninth larval stage. **56**. Ventral view of abdomen and cercopods of tenth larval stage. **57**. Ventral view of right cercopod of eleventh larval stage. **58**. Ventral view of last abdominal segment and cercopods of fourteenth larval stage of the male.



Figures 59-62. **59**. Ventral view of last abdominal segment and cercopods of eighteenth larval stage of the male. **60**. Ventral view of last abdominal segment and cercopods of fully grown male. **61**. Ventral view of left cercopod of thirteenth larval stage of female. **62**. Ventral view of left cercopod of adult female.

dite on the posterolateral side of the flabellum, and one praeepipodite posterior to the epipodite. The last two were membranous and had no setae. The praeepipodite had serrations around its margin with a notch on its middle.

The musculature of the thoracic appendage is complicated. Interpretation of thoracic musculature is presented according to Preuss (1957) (fig. 38). In the seventh stage the muscle pattern was clearly established. In each appendage there were four main dorsal muscle strands spread into a fan-like shape in an anteroposterior sequence. These muscles originated along the dorsolateral body wall and were inserted along the inner side of the wall of the appendage. Similarly a series of ventral muscle strands originated on the ventral body wall near the base of the appendage and were inserted along the appendage wall. Two sets of axial and longitudinal muscles were developed in each segment; one set of these three individual strands ran laterally (fig. 39, *Lt m*) to the nerve trunk along the base of the appendage. There was also a set of several dorsal and lateral muscle strands located between the epidermis and the intestine. Each axial muscle (*Sp ne m, Su ne m*) extended a little posteriorly into the next segment, where it overlapped with its corresponding muscle. When these muscles were contracted unilaterally the axial muscles caused the thorax to flex in any direction, and on simultaneous contraction the entire thorax was shortened while the segments were telescoped into one another. The ultimate differentiation of the musculature in the subsequent stages involved only the appearance of striations and increase in size.

The muscles of the trunk region of adult fairy shrimp are shown in Figures 39 and 40 in the longitudinal and the transverse sections through the thoracic region. The terminology for the muscles of the trunk follows the description given by Cannon (1926) for *Chirocephalus diaphanus.*

E. Genital Ogans and Their Musculature

The anlagen of the external genital organs in both sexes appeared in the sixth stage, but could not be distinguished from the thoracic segmental anlagen. The primordia of the two genital segments were formed posterior to the eleventh thoracic appendage (fig. 42, *Rd gentl*) and developed into male and female genitalia respectively by the fusion of these two segments in the subsequent stages. The segmental rudiments were developed from the ventral ectoderm in a way similar to that of the thoracic segments. In the eighth stage the fused genital segments had shown growth only in length in the axial direction. In the tenth and eleventh stages the genitalia became distinctly male and female externally. The genital segments attained adult form in the fifteenth stage (fig 47) in both sexes. The gonads developed in the eleventh stage on either side of the intestine and extended back into the abdomen.

In the male the posterior portion of the first genital segment ultimately developed into a pair of ventrolateral, finger-like outgrowths called penes (figs. 44-48), each consisting of a chitinous fixed part and an eversible membranous tube with spines on its inner side. These both developed from the ectodermal part of the two genital segments. At the distal end of the protruded penis the vas deferens opened to the exterior.

In the development of the female genitalia (figs. 49-53), the mid-ventral parts of the genital segments and the primordia of the oviducts were fused. At the point of fusion a continuity was established with the distal end of the oviduct. The uterus was developed medially from the rudiment of the second genital segment. At the distal end of the developing egg pouch a large opening connected the developing uterine cavity with the outside. In subsequent stages the yolk and shell glands were developed. In the seventeenth stage of the female the yolk and the shell glands filled most of the empty space in the egg pouch and the ventral portion of the fused genital segments. The eggs in various stages of development were also observed in this stage.

The muscles of the genital segments are homologous to the muscles of the thoracic segments except for the absence of the appendicular muscles. In the male the penis was supplied with three powerful posterior muscles called the retractors (fig. 44, *Retr*) of the penis, and the other two muscle strands called the anterior and posterior extensor muscles (*Extr pen*). These five muscle strands were inserted on the vas deferens and were used for its constriction (fig. 47, *Retro vd*). Two well developed segmental muscles were also inserted on the penis, originating from the inner dorsal wall of the genital segments (transverse and oblique descending muscles), and were used for the retraction of the genitalia.

In the female the segmental muscles (transverse and oblique descending (fig. 52, *obl m*) were attached to the egg pouch at the anterior and posterior positions. The uterus, shell and yolk glands, and oviductal portion in the egg pouch were supplied with several muscle bands (fig. 52, *extra ovi, Rot ovi, Flx ovi*) used for the etxension, retraction, and rotation of these organs.

F. Abdominal Segments and Their Musculature

In the first five larval stages there was no distinction of the abdominal segments. The abdomen was present in these early stages as a cylindrical, unsegmented trunk located between the developing thoracic segments and the anal opening. The external rudiments of the first two true abdominal segments (14th and 15th body segments) appeared in the sixth stage when the body length was 1.78 mm. In the ninth stage the 16th, 17th, 18th, and 19th trunk segments (fig. 55, *Abdo*) were differentiated. On the lateral side of each segmental joint a pair of minute hairs was developed. Their sensory function was indicated by the attachment of the nerve fiber at their bases. These sensory hairs persisted to the fifteenth stage; they degenerated in subsequent stages. The adult form of the abdominal segments was attained in the ninth stage (fig. 55) when the body length was 3.67 mm. During the subsequent gradual development of the abdominal segments there was only an increase in size.

The rudiment of the musculature was formed soon after the anlagen of the abdominal segments appeared. In the fully developed segment there were two sets of longitudinal muscles, dorsal and ventral bundles on each side (fig. 41). The gonads were developed between the dorsolongitudinal and ventrolongitudinal muscles. The abdominal nerve trunks were developed medial to the ventral strands.

The musculature of the abdomen in the adult fairy shrimp consisted of segmental muscles as observed in the thoracic and genital segments; appendicular muscles were lacking (fig. 41). The muscles of the abdomen consisted of a set of dorsal and ventral longitudinal bands (*DLM, VLM*) running throughout the abdominal segments. There was also a pair of muscles joining dorsal and ventral longitudinal muscle bands. Two pairs of inner and outer dorsoventral muscles (*I dvm, O dvm*) were developed, which originated from the inner dorsal and lateral body wall, and were inserted into the tendinous fiber at the ventral side of the ventrolongitudinal muscle bands, likewise located dorsal to the abdominal nerve. The abdominal muscles functioned to push the eggs or sperm from the gonads to the genitalia, and also help to steer the body during swimming.

G. Telson, Cercopods and Their Musculature

In the first larval stage there were no seta around the anus. In the second stage, at the posterior end of the unsegmented part of the postcephalic region, a pair of setae projected on each side of the anus. In the third stage another pair of setae developed on the lateral to the previous pair of setae. In the fifth stage one more pair of setae projected posteriorly on the inner side of the previous two pairs of setae which had become longer. In the seventh stage the cercopods first appeared (fig. 7, *Crpd*). According to Hsü (1933) the last abdominal segment, which was smaller than the others was the telson, and the two rami with setae on either side developed into the cercopods. In this stage each ramus or developing cercopod had five setae with setules. In the eighth stage (fig. 54) of both sexes each developing cercopod had eight setae with setules; then in the ninth stage (fig. 55) the number increased to fourteen on each cercopod. Following this there were twenty setae in the tenth stage (fig. 26), twenty-six in the eleventh stage (fig. 57), fifty in the twelfth stage, sixty in the thirteenth stage (fig. 61), and seventy in the seventeenth stage in both sexes. In the adult female (fig. 62) the number of setae with setules increased to eighty-five and that number was retained throughout life. In the male the increase in the number of the setae was not so rapid after the seventeenth larval stage. In the eighteenth stage the male had seventy to seventy-five setae on each cercopod, and some of these were degenerated at their distal ends with their bases showing development of the chitinous spines of the mature adult (fig. 60). In the fully grown male each cercopod had about sixteen spines distally and fifty-six setae with setules proximally. During this stage there was a gradual increase in the length of each cercopod and the number of setae with setules. In the fully grown male each cercopod was fused with the telson and had only a faint line indicating the fusion.

The telson contained four transverse muscle strands originating on the lateral walls and inserted on sides of the rectum (fig. 57, *Rct m*). These muscles were used for dilation of the rectum.

There were two muscles attached to each cercopod; they originated from the posterior end of the ventrolongitudinal muscle bands and were inserted on the proximal and distal ends of the cercopods. The outer muscle (fig. 61, *Abd*) of each cercopod was used to pull the cercopod away from the body, while the inner one (fig. 61, *Add*) pulled the cercopod towards the body. The bases of the setae projected internally and were attached to minute muscle fibers. The latter were continuations of the abductor and the adductor muscles of the cercopods. These minute muscle fibers were used to move the setae in an upward and downward direction.

H. Growth Rate

Observations made on the growth rate of the different parts of the body were more or less similar to those of *Artemia salina* as described by Weisz (1946). In the development of the thoracic segments, when a new segment was differentiated, the preceding segment increased in length and width. The longer thoracic appendages were located anteriorly. As the eleventh thoracic segment appeared in a rudimentary stage, the fifth segment and its appendages were completely developed, and at the same time the rudiment of the nineteenth trunk (6th abdominal) segment appeared. At the advanced sixth stage the segments of the abdomen, which had retained constant length during the development of the thoracic segments and their appendages, started to grow rapidly in length. The genital segments (12th and 13th) developed in equal length and remained equal throughout their later development. The genital segments were longer than the eleventh thoracic segment but became progressively shorter in relation to the fourteenth and other abdominal segments. When the nineteenth abdominal segment

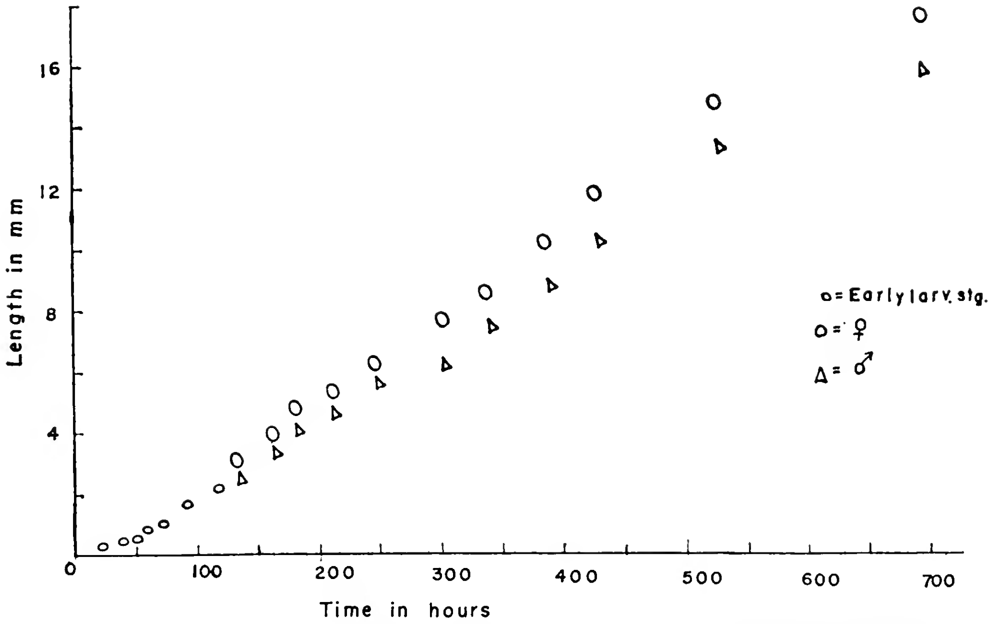


Figure 63. Growth rate of male and female larval stages of *Streptocephalus seali.*

appeared as a rudiment, the eleventh thoracic segment reached the mature stage.

As the graph shows (fig. 63), the growth rate was rapid up to the seventh stage at which time there was no distinction in sex. From the eighth stage the sex of the larvae was differentiated and rate of growth of the females were more rapid. In comparison to the female, growth of male larvae was slower between the tenth and eleventh stages; then there was a slight increase, but growth rate decreased again between the twelfth and thirteenth stages. In subsequent stages up to the adult and even after the adult stage the rate of growth in the males and females was nearly constant.

I. Abbreviations Used in Figures

Abd—Abductor muscle
Abdo—Abdomen
Abdo seg—Abdominal segment
Acl gl—Accessory gland
Add—Adductor muscle
An—Anus
Ant—Antenna
Ant ext—Anterior extensor muscle
Antl—Antennule
Asd m—Ascending muscle
Bsl seg—Basal segment of the antenna
Bspd—Basipodite
Ce—Compound eye
Chi spr—Chitinous spur
Cir m—Circular muscle
Con m—Connective muscle
Crpd—Cercopod
Dhb ptpd—Distal hook bristle of the protopodite
DLM—Dorsal longitudinal muscle
Dpr—Depressor muscle
Dsd m—Descending muscle
D seg—Distal segment of the antenna
Egp—Egg pouch
Endp—Endopodite
Epd—Epipodite
Evs pen—Eversible penis
Ex gl—Excretory gland
Expd—Exopodite
Extr—Extensor muscle
Fl—Flabellum
Fl fm—Flabelliformis muscle
Flx—Flexor muscle
Fr app—Frontal appendage
Gen d—Genital duct
Gl—Gland
Gt—Gut
Gt m—Gut muscle
Ht—Heart
Infl pr end—Inflexor of protenditis
I dvm—Inner dorsoventral muscle
Intm—Intermediate segment of the antenna
Larv stg—Larval stage
L lp—Lower lip of the egg pouch
L lm—Longitudinal muscle of the labrum
Lm—Labrum
LM—Longitudinal muscle
Lm M—Labral muscle
Lt m—Lateral muscle
Lt shr—Lateral sensory hairs
Lv—Levator muscle
Lv prend brc—Levator protenditis brevis
Lv prend long—Levator protenditis longus

Md—Mandible
Me—Median eye
Mx 1—First maxilla
Mx 2—Second maxilla
Mx br—Maxillary brush
N—Nerve
Nc—Nerve cord
Obl m—Oblique muscle
Ovi—Oviduct
O drm—Outer dorsoventral muscle
Pen—Penis
Phb Ptpd—Proximal hook bristle of the Protopodite
Pl end—Pleuro-endopoditis
Plp—Palp
Pl pepd—Pleuro-Praaeepoditicus
Pl ped ref—Pleuro-pedalis refigens
Post ext—Posterior extensor muscle
Pri intri—Prior internus
Prmt—Promotor muscle
Prpd—Praeepipodite
Prtpd—Protopodite
Pt ram ma pref—Post ramus major praefigens
Rct m—Rectal muscle
Rd gentl—Rudimentary genitalia
Ref—Refigens muscle
Retr vd—Retractor muscle of the vas deferens
Rmt fl—Remotor of flabellum
Scl—Sensory cells
Set—Seta
Shrs—Sensory hairs
Sp—Spine
Sp ne m—Supra-neural muscle
S sp md—Sensory spine of the mandible
Sn ne m—Sub-neural muscle
Tel—Telson
Th app bd—Thoracic appendage bud
Tntl pr—Tentacular process
Tr ext ref—Transverse externus refigens
Tr int—Transverse internus muscle
U lp—Upper lip of the egg pouch
V lb—Ventral lobe of the genital segment
VLM—Ventral longitudinal muscle
Vd—Vas deferens
1-11—Thoracic appendages
12-13—Genital segment

IV. Discussion

Studies were made on the postembryonic larval stages of the fairy shrimp *Streptocephalus seali* Ryder to determine the number of larval stages, and when the development of individual structures and their musculture took place.

Distinctions of the larval stages were made according to the method of Weisz (1947). The number of stages was determined by the number of body segments and the body length. The total length of any one larval stage was nearly the same regardless of the number of ecdyses (mean ± 2). The constant conditions in the laboratory and the above-mentioned method of identification minimized the influence of external factors such as variance in salinity, temperature, pH, etc. Thus, I agree with Weisz (1947) that his method of identification of larval stages was more reliable than identifying them by molting cycles as employed by Heath (1924).

For the complete development of *Streptocephalus seali,* eighteen larval stages were involved. After the eighteenth stage there was only an increase in the body length, and in the apical segment (hand) of the male antenna. The distinction in sex was observed from the eighth larval stage. The basis for that distinction was the rudiment of the developing projection from the protopedite of the male antenna, which later developed into the apical segment or the hand. From the eighth stage the development was gradual, faster in the females than in the males. In the tenth stage the setae on the antennal exopodite of the male and female degenerated and the antennae moved gradually toward the anterofrontal side of the head.

The first few larval stages of *S. seali* had structures, especially antennae, more or less similar to those described by Packard (1883) for *Streptocephalus texanus,* and for *Branchipus stagnalis;* and by Oehmichen (1921) for *Branchipus grubei.* The similarities were the development of the saber-shaped hook bristle on the inner and ventral side of the protopodite or first basal segment of the second antennae. This hook bristle (figs. 1-7, 20) at first was naked, then became beset with two rows of fine setules in the first larval stage; later, in the second stage it split into two flat branches possessing setules at the distal end of each branch. The second segment of the second antenna also had a long, flat and curved inward hook bristle which though first naked had setules in the advanced first larval stage. At the distal end of the antennae there were two branches each of which had three long setae; but, *S. texanus,* according to Packard (1883) had five setae on the exopodite of the antenna. In the ninth stage, the antennal setae were completely degenerated; the same was described by Packard (op. cit.) for *S. texanus.* Similarly the antennal exopodite had thirteen long setae in *S. seali,* but in *S. texanus* had fifteen.

Considerable controversy had existed regarding the number of segments in the male antenna. Baird (1852), Claus (1873, 1886), Cissler (1883), and Daday (1910) explained that the antennae of the male have three segments with joints; namely, basal segment, intermediate curved segment, and apical segment (or hand). Barnard (1929) and Linder (1941) favored the idea that the male antennae of *Streptocephalus* species have only two segments as in other families of the fairy shrimp. From my observations on the development of the male antenna, I concluded that the male antenna consisted of three segments. This conclusion was based on observation of the development of the apical lobe of the antenna of the male from the eighth stage to the adult. The apical lobe or the tentacle-like process (fig. 10) became the intermediate segment; from its distal end in the eleventh stage the third segment (or hand) developed with distinct demarcations of the joints. The spur or the hook (remnant of the earlier exopodite) was just the continuation of a process from the basal segment of the antenna.

The development of the frontal appendage has been described by several authors. Grube (1853) traced the development of the frontal appendage from the basal segment of the male antenna in *Streptocephalus proboscideus.* Daday (1910) stated that the frontal appendage in *S. purcelli* arose from the head. Evans (1915) in *S. texanus* traced its origin from the union of the basal parts of the antennae which had separated from the antennae and fused with the head. In *Chirocephalus grubei* Oehmichen (1921) showed that the rudiment of the frontal appendage arose from the distal part of the protopodite although in the adult its position was rather proximal; a similar origin was described by Heath (1924) in *Branchinecta occidentalis* and by Hsű (1933) in *C. nankinensis.* Claus (1886) described the origin of the frontal appendage in the Streptocephalidae and stated that during larval development the paired rudiments of the frontal appendage migrated from the male antennae to the head where they coalesced and formed a common structure. The twofold origin of the frontal appendage was disclosed by a notched tip at the distal end. I found that in *S. seali* the origin of the frontal appendage was similar to that described for the family Strepotocephalidae by Evans (1915) and Linder (1941).

During the development of the larval stages, there was a gradual degeneration of the mandibular palp with its setae. The sensory spine originated on the posterior side of the coxopodite of the jaw, and curved towards the mouth. This spine also degenerated completely in the later stages. Nothing has been mentioned in the literature about this sensory spine of the mandible except by Spangenberg (1875) and Oehmichen (1921) who stated that in the adult this spine was a remnant of the mandibular palp. But, in the early larval stages I found that this sensory spine originated independently and separately from the palp. Also, no description had been given in the literature concerning the function of this spine, except that Oehmichen (1921) gave it the name "sensory spine". I presumed that when the palp was a swimming appendage in early larval stage, this spine with setules was a sensory organ, but later both degenerated and the sensory function was taken over by the second maxillae. The complete degeneration of the palp and the sensory spine of the mandible was accomplished in the twelfth stage of *S. seali.* Heath (1924) maintained that the remnant of the palps was present in adult *B. occidentalis,* while Hsű (1933) observed that the palps had completely degenerated in *C. nankinensis* when the larva was 3.6 mm long.

Development of the first and second maxillae was followed in detail up to the fifth larval stage. Beyond that stage the changes in both pairs of maxillae were comparatively slight and limited mainly to an increase in size and addition of more setae possessing setules on the first maxillae.

Formation of the different parts of each thoracic appendage was gradual and each part was differentiated from a rudimentary stage to the adult form during development. Considerable confusion has existed in the literature regarding the interpretation of the appendicular components. Proximally near the epipodite a lamelliform lobe-like structure developed; this was called the praeepipodite by Linder (1941) while other authors such as Daday (1910) referred to it as a bract. The terminology used by Linder seemed to be more convincing, thus, I have followed it in the present description of all parts of the appendage. During the development of the appendage the rudiment of the praeepipodite originated as a single lobe and was envaginated from the anlage of the appendage. In the adult the margin of the praeepipodite was serrated and had a notch on the mediolateral side. According to Linder (1941) and others, the notch represented the fusion point of two praeepipodites to the adult stage, but during the whole developmental course I did not find any indication of the division of the praeepipodite, except a minute notch in the adult.

A confusion in the naming and the interpretation of the number of the endites exists in the literature. Packard (1883), Calman (1909), Linder (1941), and Nourisson (1958) identified six endites considering the gnathobase or first endite to consist of only one endite, while the last or sixth endite was considered to be adjacent to the flabellum. Cannon and Leak (1933), Lowndes (1933), and Borradaile (1959), on the other hand, counted seven endites, considering the first to be composed of two fused endites; thus the endite adjacent to the flabellum was considered the seventh endite. Claus (1873) and Hsű (1933) labelled the first endite as the foot lobe or gnathobase, the second endite as the first foot lobe or endite and the endite adjacent to the flabellum called fifth endite. Claus labelled the flabellum as sixth endite, but Hsű called it an exite. My observations on the development of the thoracic appendage indicated there were only six endites, one flabellum which was a part of the exopodite, one epipodite, and one praeepipodite. The gnathobase or first endite consisted of only one endite and not two as implied by others. Claus' (1873) interpretation of the flabellum as the sixth endite seemed to be wrong. From the external as well as the internal structure of the appendage and also from a description of other authors, I think that the flabellum is the exopodite.

Two interpretations regarding the origin of the genital segments have been published. Nitsche (1875), Packard (1883), Claus (1886), Sars (1896), Hsű (1933), and Linder (1941) hypothesized that the genital segments were the modified first two abdominal segments, and from their ventral side the external genitalia were developed. Borradaile (1959) stated that the genital segments included a twelfth thoracic and the first abdominal segment. My observations indicate that the genital segments should be regarded as the first two abdominal segments. The basis for this contention is that the development of the genital segments was more or less similar to the development of the abdominal segments. The sensory hairs on posterolateral side near the abdominal and genital segmental joints were present up to the 15th larval stage, and degenerated together after that stage. In addition to that the musculature of the genital and abdominal segments showed more similarity to each other than to the musculature of the thoracic segments. Though the genital segments contained more muscles than other abdominal segments, the segmental muscle pattern was the same in both.

Spangenberg (1875) observed that the genitalia developed as two independent outgrowths from the ventral side of the twelfth and thirteenth trunk segments in *Branchipus stagnalis.* I observed a similar origin of the genitalia in *S. seali.*

V. SUMMARY AND CONCLUSIONS

1. A review of the literature on the biology of fairy shrimp was made.

2. Eighteen larval stages occurred in 29 days; their distinction was based on the increase in the number of the segments and the body length.

3. Studies were made on the external development, the musculature of the head, the thoracic segments, and their appendages, genitalia, abdominal segments, and cercopods.

4. The origin and the development of the frontal appendages and the male antenna were traced. The conclusion was reached that the frontal appendage originated from the basal segment of the male antenna, which then coalesced with the head and fused medially; also, that the male antenna was composed of three segments.

5. The conclusion was reached that the sensory spine of the mandible of the early stages was not the remnant of the palp but a separate structure and both degenerated in preadult stage. Also, the thoracic appendage was composed of six endites and one praeepipodite besides other structures of the appendage. The genital segments were modified from the first two abdominal segments.

6. A brief study was made to observe the rate of growth of the larval stages and their structures at various periods. The rate of growth in the female larva was faster than in the male.

VI. ACKNOWLEDGEMENTS

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VII. REFERENCES CITED

BAIRD, W. 1852 Monograph of the family Branchipodidae etc. *Proc. Zool. Soc. London.*, Part 20.

BARNARD, K. H. 1929 Contributions to the crustacean fauna of South Africa. No. 10. A revision of South African Branchipoda (Phyllopoda). *Ann. So. Afr. Mus.* 29.

BORRADAILE, L. A. 1926 Notes on crustacean limbs. *Ann. Mag. Nat. Hist., Ser.* 9, 17: 193-213.

———— and others 1959 *The Invertebrata.* Cambridge University Press, 795 pages.

CALMAN, W. T. 1909 Appendiculata, Crustacea. *IN* R. Lankester *A Treatise on Zoology*, Fasc. 3, Part 7: 29-55.

CANNON, H. G. 1926 On the postembryonic development of the fairy shrimp *(Chirocephalus diaphanus). Jour. Linn. Soc. London* 36: 401-416.

———— and F. M. C. LEAK 1933 On the feeding mechanism of the Branchiopoda, with appendix on the mouth parts of the Branchiopoda. *Phil. Trans. Roy. Soc. London.* B, 222: 267-352.

CLAUS, C. 1873 Zur Kenntniss des Baues und der Entwicklung von *Branchipus stagnalis* und *Apus cancriformis. Abh. Kgl. Ges. d. Wiss. Z. Gottingen* 18: 93-140.

———— 1886 Untersuchungen über die Organisation und Entwicklung von *Branchipus und Artemia. Arbeiten aus dem Zool. Inst.* 6: 1-104.

COOPEY, R. W. 1950 The life history of the fairy shrimp *Eubranchipus oregonus. Trans. Amer. Micros. Soc.* 69: 125-132.

DADAY, D. DEÈS E. 1910 Monographie systématique des Phyllopodes Anostracés. *Ann. Sci. Nat. Zool.*, Ser. 4, 11: 91-492.

DEXTER, R. W. and M. S. FERGUSON 1943 Life history and distributional studies on *Eubranchipus serratus* Forbes. *Amer. Midl. Nat.* 29: 210-222.

EVANS, A. T. 1915 The morphology of the frontal appendage of the male in the phyllopod crustacean *Thamnocephalus platyurus* Packard. *Jour. Morph.* 26: 703-717.

GISSLER, C. F. 1883. Miscellaneous notes on the productive habits of Branchipodidae, *I. Eubranchipus vernalis* Verril. *U. S. Geol. and Geogr. Surv., Ann. Rept.* 12: 420-424.

GRUBE, A. E. 1853 Bemerkungen über die Phyllopoden, nebst einer übersicht ihrer Gattungen und Arten. *Arch. f. Naturgesch*, 19: 71-172.

HEATH, H. 1924 The external development of certain phyllopods. *Jour. Morph.* 38: 453-483.

HSŬ, F. 1933 Studies on the anatomy and development of the fresh water phyllopod *Chirocephalus nankinensis* (Shen). *Contrib. Biol. Lab. Sci. Soc. China, Zool. Ser.* 9: 119-163.

LINDER, F. 1941 Contributions to the morphology and the taxonomy of the Branchiopoda Anostraca. *Zool. Bid. från Upsala* 20: 103-302.

LOWNES, A. G. 1933 The feeding mechanism of *Chirocephalus diaphanus* Prevost, the fairy shrimp. *Proc. Zool. Soc. London* 1933 (B): 1093-1118.

MOORE, W. G. 1957 Studies on the laboratory culture of Anostraca. *Trans. Amer. Micros. Soc.* 78: 159-173.

MYINT, T. 1956 New details of excystment of *Artemia salina* Leach. *Proc. La. Acad. Sci.* 19: 24-28.

NITSCHE, H. 1875 Uber die Geschlechtsorgane von *Branchipus grubei* (von Dybowsky). *Zeit. f. Wiss. Zool.* 25 (Suppl.): 281-296.

NOURISSON, M. 1959 Quelques donneés relatives au dévelopement postembryonnaire du *Chirocephalus stagnalis* Shaw. *La Terre et la Vie*, 106: 174-182.

OEHMICHEN, A. 1921 Die Entwicklung der äusseren Form des *Branchipus grubei* Dyb. *Zool. Anz.* 53: 241-253.

PACKARD, A. S. 1883 A monograph of the phyllopod Crustacea of North America with remarks on the order Phyllocarida. *Ann. Rept. U. S. Geol. Geogr. Surv. Terr.* 12, Sect. 2: 295-592.

PAI, P. G. 1958 On the postembryonic stages of phyllopod crustaceans *Triops (Apus), Streptocephalus* and *Estheria. Proc. Ind. Acad. Sci.* 48: 229-250.

PREUSS, G. 1957 Die Muskulatur der Gliedmassen von Phyllopoden und Anostraken. *Mitt. Zool. Mus. Berlin* 33: 221-257.

SARS, G. O. 1896 *Fauna Norvegiae.* Vol. 1, Phyllocarida og Phylloda: vii-140, 20 plates, Christiana.

SHANTZ, H. C. 1905 Notes on North American species of *Branchinecta. Biol. Bull.* 9: 249-264.

SNODGRASS, R. E. 1950 Comparative studies on the jaws of mandibulate arthropods.

Smithson. Inst. Publ., Misc. Coll. 116: 1-85.

―――――――― 1956 Crustacean metamorphosis. *Ibid.* 131: 1-78.

SPANGENBERG, F. 1875 Zur Kenntniss von *Branchipus stagnalis, Zeit. f. Wiss. Zool.* 25 (Suppl.): 1-64.

WEISZ, P. B. 1946 The space time pattern of segment formation in *Artemia salina. Biol. Bull.* 91: 119-140.

―――――――― 1947 The histological pattern of metameric development in *Artemia salina. Jour. Morph.* 81: 45-89.

ABSTRACT

The postembryonic larval stages of the fairy shrimp *Streptocephalus seali* Ryder were studied. Eighteen larval stages completed in 29 days are described from the first stage to adult. The development of the head appendages, thoracic appendages, genitalia, abdominal segments, and cercopods are described. The development of the male antenna and frontal appendage with their musculature is detailed especially due to their importance in the taxonomic studies of fairy shrimps. The various parts of the head appendages, thoracic appendages, and the genital segments are described and interpreted.

Conclusions were reached that male antenna have three segments; the frontal appendage originated from the basal segments of the male antennae; the sensory spine of the mandible was not the remnant of the mandibular palp; and, the two genital segments were the modified first two abdominal segments. The development of the musculature of the various structures of the fairy shrimps was described.

The growth rate of the early male and female larval stages was described. The female larval stages showed a faster growth rate than those of males.

To elaborate the development of the postembryonic larval stages and various developing structures, sixty-three figures are included.

A NEW SPECIES OF *EURYCEA* (AMPHIBIA: CAUDATA) FROM THE SOUTHEASTERN UNITED STATES

FRANCIS L. ROSE,
Department of Zoology, Tulane University,
New Orleans, Louisiana

FRANCIS M. BUSH,
Department of Biology, Howard College,
Birmingham, Alabama

Morphologically, the plethodontid genera *Eurycea* and *Pseudotriton* are related closely (Dunn, 1926). *Eurycea* typically has unfused nasal processes of the premaxilla, discontinuous prevomerine and parasphenoid teeth, nasals in contact with the maxillae, no prootic-squamosal crests, a slender body, and long tail. *Pseudotriton* is considered less specialized, and has fused nasal processes of the premaxilla, prootic-squamosal crests, nasals separated from the maxillae by the prefrontals, and continuous prevomerine and parasphenoid teeth. In addition, *Pseudotriton* is stocky-bodied, short-tailed, and exhibits no sexual dimorphism.

Within the genus *Eurycea* there are three natural assemblages: group 1 includes the brook salamanders, *E. bislineata* and *E. multiplicata*, species that usually reside near the edges of streams beneath rocks and leaves; group 2 contains the long-tailed salamanders, *E. longicauda* and *E. lucifuga,* species essentially terrestrial but also found close to water; group 3 includes the neotenic forms, *E. nana, E. neotenes, E. troglodytes,* and *E. tynerensis,* species that retain larval characters throughout life. Thus, each group occupies a somewhat different habitat (with overlap), either metamorphoses and leaves the water, or remains in the water as a breeding larva.

The new *Eurycea* described herein apparently is aquatic and yet undergoes normal metamorphosis. Many of its cranial features are shared with salamanders of the genus *Pseudotriton.* For this new salamander we propose the name:

EURYCEA **AQUATICA**, sp. nov.

Holotype.—USNM No. 147138, collected October 6, 1962, by Francis L. Rose, Francis M. Bush, and James Jackson.

Type locality.—Small springs and permanent streams two miles west of Bessemer, Jefferson County, Alabama, along county highway 20

Paratypes.—All paratypes have the same collection data as the holotype. USNM 147139-147141; UMMZ M123349, M123350; CNHM 134998, 134999; AMNH A69032, A69033; CM 38647, 38648; UF 14907-14909; TU 18765 (65 specimens).

Diagnosis.—A moderate-sized stocky *Eurycea* (fig. 1) with a brownish dorsum, dusky-black sides and lightly stippled to immaculate venter. A dorsal light band extends to the tip of the tail and is bordered by the black edge of the lateral ground color. The legs are short but well developed, there are 13 costal grooves, from two to four costal grooves between adpressed limbs, and a tail usually shorter than the snout-vent length. The new species resembles *E. bislineata* but differs from that species in coloration, in being much stockier, in having a shorter tail, fewer prevomerine teeth, high percentage of adults with continuous prevomerine and parasphenoid teeth, fused nasal processes of the premaxilla, and prominent prootic-squamosal crests. In addition, *E. aquatica* produces more eggs per individual and sexual maturity is attained near transformation.

The characteristic pattern and short tail distinguish *E. aquatica* from *E. longicauda* and *E. lucifuga.* The lower number of costal grooves makes it discernible from *E. multiplicata* and the ability to undergo normal transformation separates it from the neotenic species.

Description of holotype.—An adult male with the following characters: total length, 85.5 mm; snout-vent length, 44.8 mm (tip of snout to anterior angle of vent); tail compressed and short, relative tail length, 0.91; head length, 9.9 mm (tip of snout to midventral edge of gular fold); head width at angles of jaws, 6.4 mm; gular width, 8.0 mm; 13 costal grooves; 4 costal grooves between adpressed limbs; fingers $3<2<4<1$ and toes, $3<4<2<5<1$; prevomerine teeth on left side, 7; prevomerine teeth on right

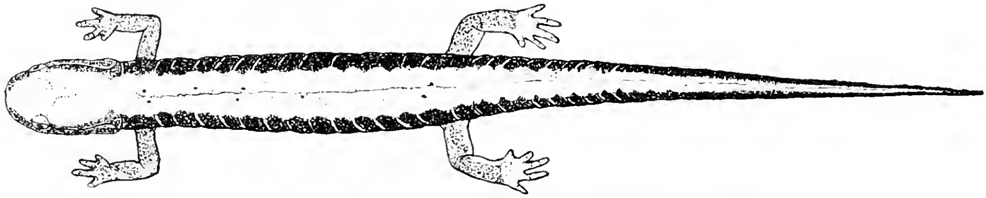

Figure 1. Dorsal view of adult female *Eurycea aquatica*, sp. nov.

side, 8; dorsal light band, in life, Brussel's Brown (Ridgway, 1912); lateral ground color, black. There are short cirri and numerous dark specks within the dorsal light band. The digits of the right forelimb and left hindlimb are slightly deformed.

Variation.—Size: The longest specimen, a male, is 48 mm (snout-vent lengths are given throughout this report unless otherwise stated and were measured from the tip of the snout to the anterior angle of the vent), four millimeters longer than the next longest specimen (fig. 2). The shortest transformed male is 28 mm; the shortest female, 29 mm. The longest larva, a female, is 36 mm. Seven larval males longer than 28 mm have large black testes and black, coiled vasa deferentia; these are considered sexually mature. Six larval males longer than 28 mm have small white testes and are considered immature. Twenty larval females longer than 28 mm have enlarged ova with small yolk deposits, ten others show no egg development. All larvae showing signs of gonadal development have an adult pattern. One transformed male (28 mm) is im-

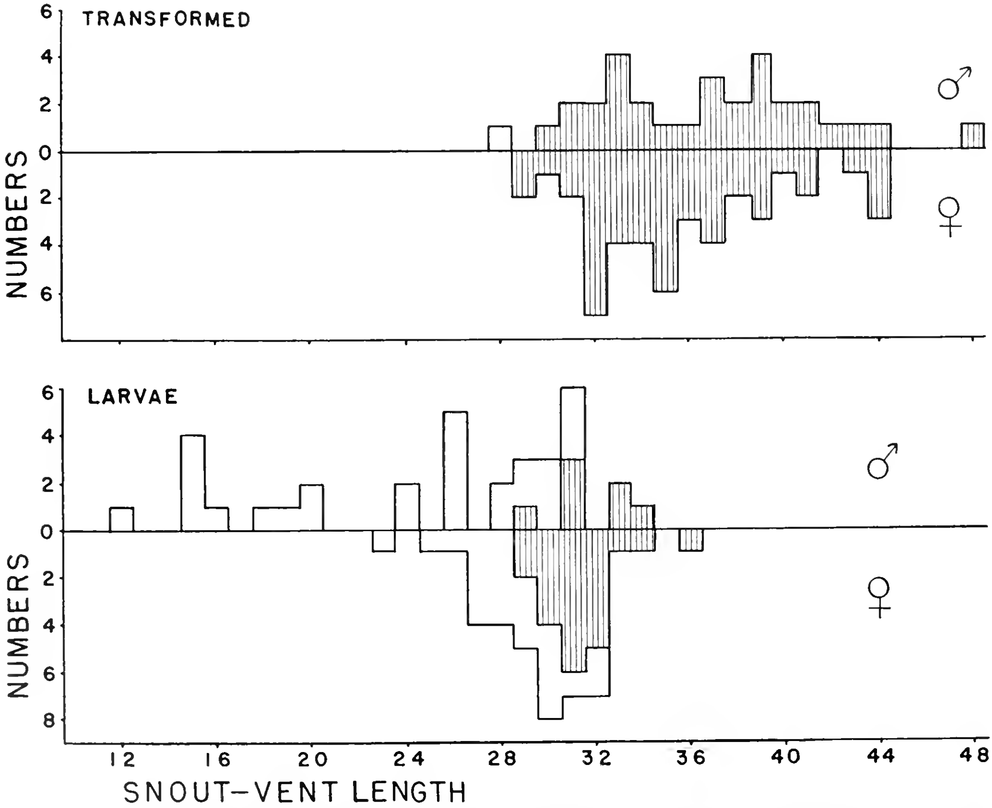

Figure 2. Distribution of snout-vent lengths in larval and adult *E. aquatica*. Vertical lines indicate animals showing gonadal activity. Measurements in millimeters.

mature, but has an adult pattern. These data are indicative of precocious reproductive development and not true neoteny.

Relative tail length: The relative tail length (fig. 3) is the difference between the total length and snout-vent length, divided by the snout-vent length. Relative tail lengths of 38 adults average 0.94 (0.80-1.14). Only 11 specimens have a tail longer than the snout-vent length. Thus, *E. aquatica* is the shortest-tailed *Eurycea* that undergoes normal transformation. The average relative tail length of 30 adult *E. bislineata* from Alabama is 1.34 (1.11-1.57).

Color: Colors are based on Ridgway's color standards. The dorsum varies from Buckthorn Brown to Raw Umber and Brussel's Brown. In most specimens, the dorsal base of the tail appears Lime Green, Olive Yellow, or Empire Yellow. The sides of the body and tail are black and, in most specimens, the sides of the tail are darker than the sides of the body. Usually there is a row of light spots along the sides of the body and tail. Most specimens are uniformly brown on the dorsum of the limbs. The venter may be clear, Wax Yellow or Strontian Yellow; the chin is mottled with black, intensely so in old males.

In preservative the bright colors fade quickly. The dorsum becomes various shades of dull brown and the lateral black ground color lightens.

Skull: The skull of *E. aquatica* is distinctive. The most significant difference from other *Eurycea* is the fused nasal processes of the premaxilla (fig. 4). In 11 of 12 large mature individuals, the processes are fused solidly. In three transforming specimens they are separate, and in two others they are slightly fused. All larvae have unfused processes, suggesting that fusion is associated with transformation. The premaxillary fontanelle is well developed and there is a "V" shaped notch in the posterior projection of the fused processes.

Wilder (1924) reported four per cent of *E. bislineata* from Massachusetts had fused nasal processes of the premaxilla but the degree of fusion was not associated with a particular developmental stage. Six adult *E. bislineata* from Alabama, two from northeastern Mississippi, and three from southern Louisiana, have unfused processes. One adult from Butler County, Alabama, has fused processes. Seven *E. longicauda* and five *E. lucifuga* lack fused processes.

A significant feature of *E. aquatica* is the

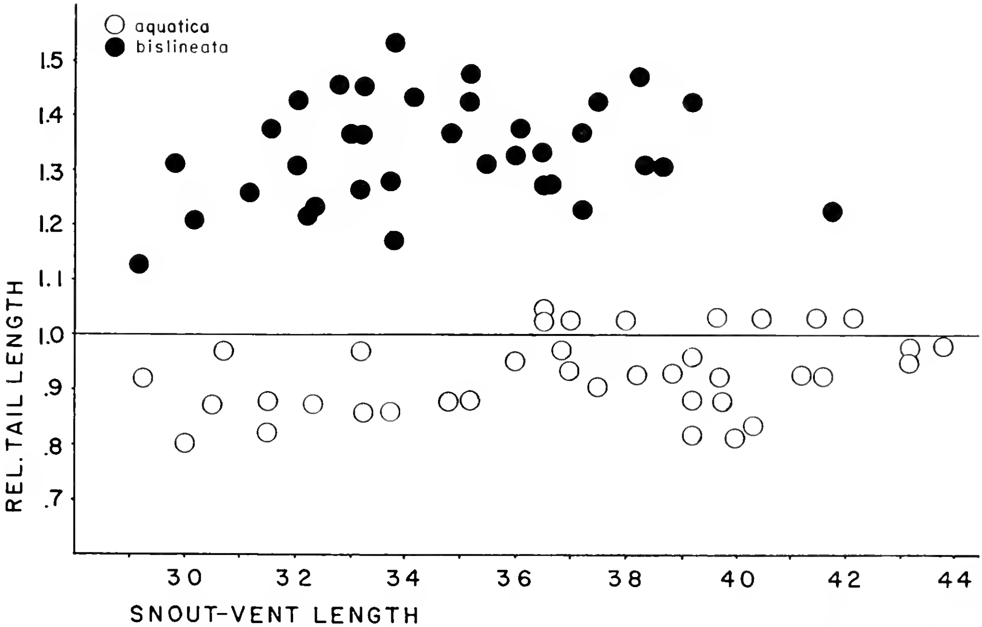

Figure 3. The relationship of snout-vent length to relative tail length in *E. aquatica* and *E. bislineata*. A large male *E. aquatica* (48 mm) with a relative tail length of 1.14 is not represented.

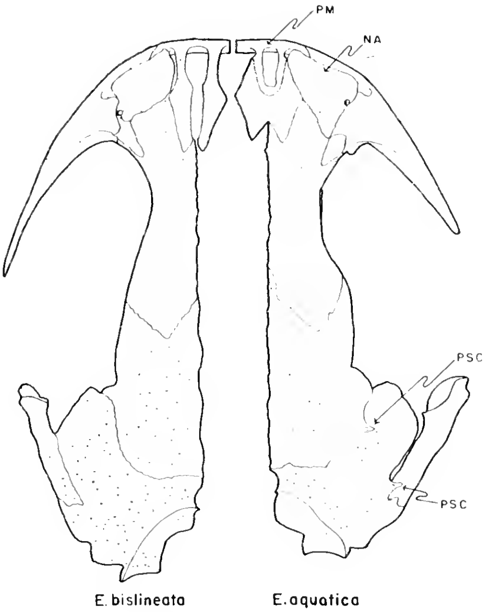

Figure 4. Dorsal view of the skulls of *E. bislineata* and *E. aquatica*. Only one-half of each skull is represented. Differences in the nasals are due to individual variation. The septomaxillae have been omitted. (PM = premaxilla, N = nasal, PSC = prootic-squamosal crests)

presence of prominent prootic-squamosal crests. These occur on ten of the 12 adults stained and cleared. *Pseudotriton, Gyrinophilus,* and *Aneides* are the only North American plethodontids previously known to have these crests (Dunn, 1926).

A third distinctive feature is the short, thick maxilla. Four *E. aquatica* and four *E. bislineata* with the same snout-vent lengths were measured to determine the extent of lengthening of these elements. This feature is best measured along a line from the tip of the snout to a line drawn across the tips of the maxillae. The maxillae of *E. aquatica* are approximately 17 per cent shorter than those of *E. bislineata.*

Teeth: The prevomerine and parasphenoid teeth of *Gyrinophilus* and *Pseudotriton* are continuous. They are also continuous in *Eurycea* shortly after transformation. This continuity results from the posterior growth of the prevomers along the roof of the mouth with subsequent incorporation of the parasphenoid. The connection is transitory and, "soon after transformation the slender rod of bone which connects the growing parasphenoid tooth patches with the body of the vomer undergoes atrophy" (Wilder, 1925). The subsequent separation into two distinct series was considered a derived character by Dunn (1926).

The number of prevomerine teeth of ten adult male *E. aquatica* average 11.0 (8-15); 13 females, 10.6 (6-13). Nineteen adults (45.2 per cent) have continuous prevomerine and parasphenoid teeth; however, the connecting teeth are relatively small. In accordance with Wilder's observations one would expect the shortest animals to have the continuous series; this is not the case. Animals with continuous series are represented in all size groups, from 32.0 to 44.0 mm. In contrast, only the shortest transformed *E. bislineata* (below 32.0 mm) have continuous series.

The number of prevomerine teeth in 16 adult male *E. bislineata* from Alabama and Louisiana average 16.2 (11-19); 18 females, 17.1 (15-20). Although there is an overlap between some specimens of *E. aquatica* and *E. bislineata* in this character, *E. aquatica* has about 35 per cent fewer teeth.

Fecundity.—The reproductive potential of *E. aquatica* is high (Table 1). The average number of eggs, in corpora, for seven females is 80 (60-96). In contrast, the average number of eggs for seven *E. bislineata* from Alabama and Louisiana is 52 (40-59). The latter data are in partial agreement with those of Wood and Duellman (1951) for *E. bislineata* from Ohio. They found the number of large ova per female ranged from 22 to 95 and there was a correlation between snout-vent length and the number of large ova ($r = +0.462$). The average number of eggs for Ohio specimens between 30 and 35 mm (tip of snout to

TABLE 1.

The relationship between number of enlarged ova and snout-vent length in E. aquatica and E. bislineata from Alabama. Measurements in millimeters.

aquatica		bislineata	
Snout-vent	No. large ova	Snout-vent	No. large ova
36.1	80	35.2	40
38.4	60	38.0	59
39.2	73	38.1	50
41.0	81	42.5	57
42.5	80	43.2	52
43.1	96	44.0	46
43.3	90	45.1	58

posterior angle of vent) was 35; for animals above 45 mm, 57 ova. When the ontogenetic increase of egg number is considered, *E. aquatica* has considerably more eggs per female than either northern or southern *E. bislineata.*

Habitat and habits.—The type locality is a series of small, natural springs that converge to form a stream. The water is clear, has an average yearly temperature of less than 60°F, and attains a velocity of 3.5 ft./sec. in the swiftest part of the stream. The spring and stream beds are mostly gravel and sand, but silt accumulates in several sections. Near the middle of the stream there is a heavy growth of water cress, *Nasturium officinale;* most of the adult *E. aquatica* were collected here. They remained hidden among the entangled roots below the surface. Larvae resided near or on the gravel or sandy bottom. A few adults and many larvae were collected along the shallow edges where sand had accumulated; here the dominant plant was wild spearmint, *Mentha spicata.* Individuals seem to avoid the silted areas almost entirely, and none was found along the stream bank.

Other amphibians found along the stream or in its vicinity were *Pseudotriton ruber, Gyrinophilus porphyriticus,* and *Desmognathus fuscus.* Two *Ambystoma tigrinum* and one *Gastrophryne carolinensis* were collected near the spring source.

Inasmuch as the new species somewhat resembles *E. bislineata,* attempts were made to collect the latter, at or near the type-locality. Two adults were collected only eight miles east of the type locality and two others examined from the University of Alabama collections (48-492, 48-493) were collected from Jefferson County, Alabama. All have well developed dorsolateral stripes bordered by yellow; in two the tails are long (average relative tail length, 1.29), and two have broken tails. Numerous larvae were collected throughout Jefferson County.

Description of larvae.—Larval coloration and pattern are variable. The small larvae are black with a clear venter. As ontogeny proceeds the dorsal coloration lightens, becoming brownish; the sides remain dark. The adult dorsal pattern and coloration become evident as transformation and sexual maturity near. Thus, larval coloration varies from black to brownish and dorsal pattern from indistinct to the condition found in adults.

There is a dark, irregular stripe posterior to the eye, and a row of tiny spots dorsal to the limbs. The lower row of small spots found on most *E. bislineata* larvae is absent. A few larvae have the two rows of dorsal spots as in *E. bislineata,* but the majority do not. The tail fin, although well developed, is not as high as in *E. bislineata* larvae (fig. 5).

The larval pattern of *E. aquatica* is darker and less reticulate laterally than that of *E. bislineata.* Examination of larval *E. bislineata* from the Piedmont of Georgia, showed that transformation may occur at a large size; however, none was observed with an adult pattern.

Phylogenetic considerations.—The status of the premaxilla as a phylogenetic indicator among plethodontids is not clear.

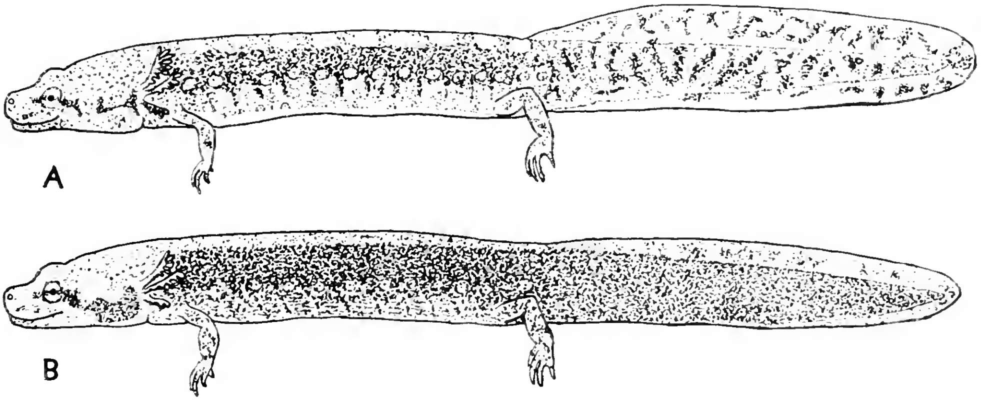

Figure 5. Lateral view of larval (A) *E. bislineata* and (B) *E. aquatica* from Jefferson County, Alabama. Larvae are approximately 24 mm.

Wilder (1924) stated the element was too variable to indicate relationships. Among plethodontids, however, three patterns are evident; maintenance of the presumed primitive condition, fusion of parts, and separation of parts (fig. 6).

Plethodontids have premaxillae that form as single elements (Martof and Rose, 1962). At formation the element is shaped like the Greek letter pi (π). This type of premaxilla is probably the primitive plethodontid premaxilla (Grobman, 1959), not the paired structure as Dunn (1926) thought. Among the eastern boletoid-tongued plethodontids, *Eurycea* and *Manculus* retain this primitive pattern. In *Gyrinophilus,* the dentigerous corpus of the premaxilla separates early and the nasal processes remain unfused. *Pseudotriton* retains the solid corpus and the nasal processes fuse solidly. Thus, fusion or separation of parts of the premaxilla would be advanced features. *Eurycea,* although advanced in most characters, has maintained the primitive premaxilla, except for *E. aquatica,* which shares other features with salamanders of the supposedly less specialized *Pseudotriton.*

Ensatina, Hydromantes, Plethodon, Hemidactylium, and *Gyrinophilus* are the North American plethodontids that have paired premaxillae as adults. Obviously, this condition has evolved independently several times. *Hydromantes* is the only North American boletoid-tongued genus that we have not considered here. Probably it is related closely to *Gyrinophilus* (Dunn, 1926), but its relationships to eastern genera are not clear.

The dorsal pigment patterns of plethodontids are complex and caution should be exercised in their interpretation. However, this should not impede efforts to better understand pattern relationships where conclusions are justifiable. *Pseudotriton* and *Gyrinophilus,* probably the least specialized plethodontids, have uniform colors with dark speckles. This may be considered a basic pattern as their larvae also have indistinct patterns. *Eurycea* larvae have six rows of spots; four lateral and two dorsal. In *E. aquatica,* the lower rows appear absent. The light dorsal band and dark sides of *E. aquatica* may be a basic *Eurycea* pattern derived from the spotted condition. All of the previously described species of *Eurycea* that undergo normal transformation, except *E. lucifuga,* exhibit modifications of the *E. aquatica* pattern. Many *E. bislineata* pass through a stage immediately after transformation when they have dark sides and a light dorsal band.

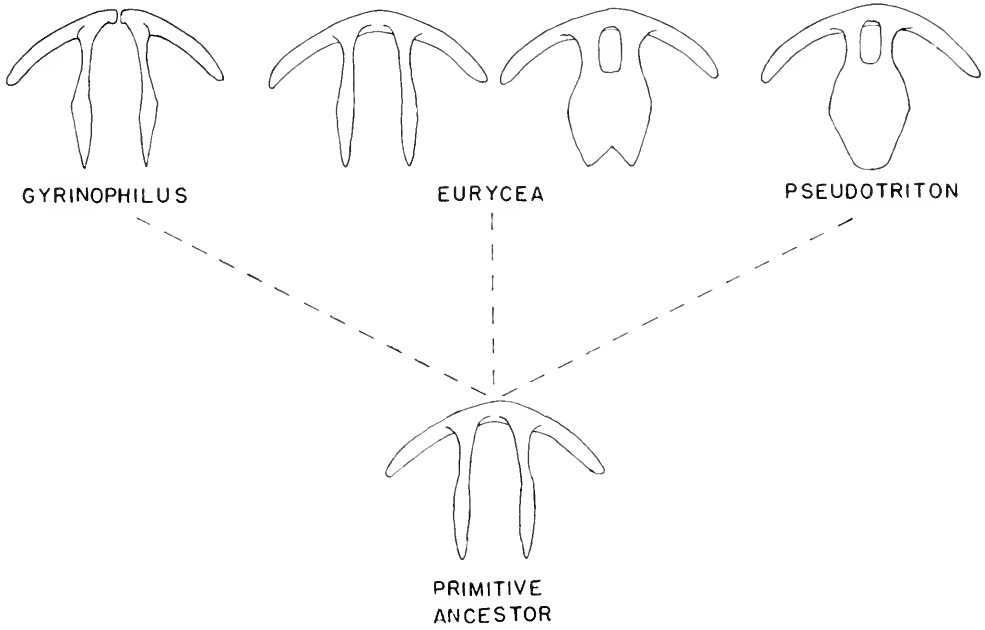

Figure 6. Divergence of the premaxilla as seen in three genera of plethodontids.

However, they soon develop the two dark stripes by pigment intensification along the edges of the dorsal light area and the ventrolateral loss of dark pigment.

Eurycea aquatica could be the product of neotenic evolution. The dorsal pattern, short tail, and continuous prevomerine and parasphenoid teeth in a high percentage of individuals may be larval characters. In addition, the animals exhibit precocious gonadal development. The well ossified skull and fused nasal processes of the premaxilla are not neotenic features. Within a group that characteristically has separate nasal processes of the premaxilla, one would expect a neotenic member also to retain unfused processes; this *E. aquatica* does not do.

Superficially, *E. aquatica* appears to be a morphologically unspecialized *Eurycea,* being somewhat more advanced than *Pseudotriton,* and yet, not as advanced as other *Eurycea.* The premaxilla of *E. aquatica,* however, is not primitive; neither is that of *Pseudotriton.* Obviously, unspecialized forms do not necessarily remain unspecialized in all characters. The similarity of characters between the new species and *Pseudotriton* is due probably to the close relationship among the eastern boletoid-tongued plethodontids, but is not indicative of lines of descent within the group.

Whether *E. aquatica* is unspecialized or has evolved through neoteny cannot be answered. Possibly after other aspects of its life history are known, and a more thorough study of plethodontid osteology is completed, we will be better able to understand the phylogeny of the group.

Distribution.—The range of *E. aquatica* is unknown. The type locality is within the Ridge and Valley Province near the edge of the Cumberland Plateau. To the north, there are numerous springs of the same type found at Bessemer; however, there is no reason to assume the species is restricted to this type of habitat. A series of larvae collected by Dr. Royal D. Suttkus in Chattooga County, Georgia, may be this species, but they are greatly faded. The habitat there is a fast flowing stream containing much aquatic vegetation. Dr. Richard Johnson of the Tennessee Polytechnic Institute informed us he has collected the animals in the Cumberland Plateau region of Tennessee. These observations indicate *E. aquatica* may occur in northwest Georgia, southwest Tennessee, northeast Mississippi (especially Tishimingo County), and northern Alabama.

Methods.—Specimens were killed in chloretone, hardened in ten per cent formalin, and stored in seven per cent formalin. Measurements were made with vernier calipers. At least two weeks elapsed between hardening the specimens and making the measurements to avoid bias by different degrees of shrinkage. The prevomerine teeth were counted with the aid of a binocular microscope after the fluid and mucous within the buccal cavity were blown-out with compressed air. Skeletal preparations were made by clearing, then staining with alizarin red S.

Museum abbreviations are as follows: AMNH = American Museum of Natural History; CM = Carnegie Museum; CNHM = Chicago Natural History Museum; TU = Tulane University; UF = University of Florida; UMMZ = University of Michigan Museum of Zoology; USNM = United States National Museum.

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We would like to express our sincere gratitude to professors Harold A. Dundee, Robert E. Gordon, Bernard S. Martof, Ronald A. Brandon, Fred R. Cagle, Royal D. Suttkus, and George H. Penn for reading the manuscript and making constructive criticisms; Ronald Brandon, Bernard Martof, Royal D. Suttkus, and Harold A. Dundee kindly loaned us specimens in their care; James Jackson aided in much of the field work and M. Philip Kahl helped with the photography. Harold A. Dundee deserves especial thanks for his constant encouragement and advice.

REFERENCES CITED

DUNN, E. R. 1926 *The Salamanders of the Family Plethodontidae.* Smith College, Northampton, Mass. xi + 441 pp.

GROBMAN, A. B. 1959 The anterior cranial elements of the salamanders *Pseudotriton* and *Gyrinophilus. Copeia* 1959:60-63.

MARTOF, B. S. and F. L. ROSE 1962 The comparative osteology of the anterior cranial elements of the salamanders *Gyrinophilus* and *Pseudotriton. Copeia* 1962: 727-732.

RIDGWAY, R. 1912 *Color Standards and Color Nomenclature.* Washington, D. C. liii col. pl.

WILDER, I. W. 1924 Variation in the premaxillae of *Eurycea bislineata. Amer. Nat.* 58:538-543.

——— 1925 *The Morphology of Amphibian Metamorphosis.* Smith College, Northampton, Mass. 161 pp.

WOOD, J. T. and W. E. DUELLMAN 1951 Ovarian egg complements in the salamander *Eurycea bislineata rivicola* Mittleman. *Copeia* 1951:181.

ABSTRACT

Eurycea aquatica, sp. nov., occurs in the Ridge and Valley Province in Alabama. The new species is superficially similar to *E. bislineata* but differs from the latter by having a shorter tail, stockier body, duller coloration, fused nasal processes of the premaxilla, prootic-squamosal crests, shorter maxillae, and continuous prevomerine and parasphenoid teeth in a large percentage of the adults. The new species apparently is aquatic and specimens mature just prior to transformation. Many cranial features are shared with salamanders of the genus *Pseudotriton*, *e.g.*, the type of premaxilla. The premaxilla probably is not a good indicator of phylogeny, but, among plethodontids three premaxillary patterns are evident; maintenance of the supposedly primitive condition, separation of parts, and fusion of parts.

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Volume 10, No. 3 June 29, 1963

GEORGE HENRY PENN MEMORIAL NUMBER

GEORGE HENRY PENN—FOUNDING EDITOR OF TULANE STUDIES IN ZOOLOGY

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DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY
NEW ORLEANS.

THE FOSSIL SNAKES OF FLORIDA

WALTER AUFFENBERG,
BIOLOGICAL SCIENCES CURRICULUM STUDY,
UNIVERSITY OF COLORADO,
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TULANE UNIVERSITY
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George E. Gunning, *Associate Editor*
Department of Zoology,
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New Orleans, U. S. A.

Royal D. Suttkus, *Director*
Meade Natural History Library,
Tulane University,
New Orleans, U. S. A.

Francis L. Rose,
Assistant to the Editors

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THE FOSSIL SNAKES OF FLORIDA

GEORGE HENRY PENN
FOUNDING EDITOR OF TULANE STUDIES IN ZOOLOGY

The passing on May 10, 1963 of George Henry Penn, Professor of Zoology at Tulane University and Editor and founder of Tulane Studies in Zoology, ended a ten year reign of conscientious and scholarly guidance of the development of Tulane Studies in Zoology to its present prestige. From the release of the first number on June 1, 1953 Dr. Penn devoted much of his time to the management and direction of the journal and simultaneously conducted a highly successful and productive career as a teacher and researcher.

Dr. Penn was born in New Orleans, Louisiana on November 20, 1918. His early education was received in New Orleans; he attended Tulane University earning the B.S. and M.S. degrees in zoology in 1939 and 1941 respectively. His studies were interrupted by World War II in which he served as a commissioned officer in a U. S. Navy malaria control unit in the Southwest Pacific. During his service tour he accumulated considerable material on the mosquitoes of the area and after his separation from the navy he developed this information into a doctoral dissertation, "The Pupae of the Mosquitoes of New Guinea", at Cornell University where he earned the Ph.D. in 1947 in medical entomology under the direction of Dr. Robert Matheson.

Professor Penn's interest in zoology was an early one cultivated by his tutor and beloved friend, a notable Louisiana naturalist, the late Percy Viosca, Jr. On many occasions he reminisced of his early days as Percy's assistant; the influence of the varied experiences working with Viosca is reflected in the diversified topics reported in literature by Dr. Penn.

Following his graduation from Cornell University Dr. Penn was appointed Assistant Professor of Zoology at Tulane University. He rose to Associate Professor in 1952 and to Professor in 1957. At the time of his death he was Assistant Head of the Department of Zoology at Tulane and served as Acting Head during 1958-1959. His campus activities were wide and varied: he served on many important University committees. At the beginning of each academic year he and his wife were the gracious hosts to graduate students in the Department of Zoology, for he felt strongly about making personal social contact with all students in the department. Students were always welcome to discuss their problems with Dr. Penn.

Professor Penn was never one to publicize himself and many of his efforts might easily have gone unnoticed. He authored at least 70 papers on parasites, molluscs, branchiobdellids, crustaceans, porocephalids, mosquitoes, reptiles, and birds. He was a world authority on crayfishes. There is an unconfirmed rumor that he and his colleague and friend, Dr. Horton H. Hobbs, Jr., Head Curator of the Department of Zoology of the U. S. National Museum, had divided the United States between them for purposes of studying crayfishes! At the time of his death he was compiling a crayfish omnibus and was engaged in a study of competition and behavior of the dwarf crayfishes *(Cambarellus)*. In spite of his interest in crayfishes, Professor Penn liked to regard himself as a general biologist rather than a specialist. He was a serious teacher who led scores of undergraduates into useful and productive careers in biology and medicine. His graduate students are many, and their theses are primarily on invertebrate animals.

At the time of his death Professor Penn was a member of 11 learned societies: Louisiana Academy of Sciences, Tennessee Academy of Sciences, Entomological Society of America, American Society of Limnology and Oceanography, Society of Systematic Zoology, American Institute of Biological Sciences, Association of Southeastern Biologists, American Society of Zoologists, Ecological Society of America, Society of the Sigma Xi, Biological Society of Washington, and the American Association for the Advancement of Science. He is listed in *American Men of Science*, *Who's Who in the South and Southwest*, and *Leaders in American Sciences*. In 1962 he was elected a Fellow in the AAAS.

As editor of Tulane Studies in Zoology Dr. Penn exerted every effort to prevent the journal from becoming a captive one publishing only local manuscripts. Over half the manuscripts came from authors elsewhere in the world. Editor Penn actively sought the advice and criticisms of experts on each manuscript submitted: this approach plus his meticulous attention to the preparation of copy and format has given us a journal of which we are proud.

The memory of George Henry Penn will long be held by those associated with him at Tulane and by the present and future generations of biologists whose studies focus on crayfishes.

HAROLD A. DUNDEE
Department of Zoology
Tulane University
New Orleans, Louisiana

GEORGE HENRY PENN—1918-1963

THE FOSSIL SNAKES OF FLORIDA

WALTER AUFFENBERG,
Biological Sciences Curriculum Study,
University of Colorado,
Boulder, Colorado

I. Introduction

For many years Florida, among the eastern states, has been recognized as an important source of Cenozoic fossils, both invertebrate and vertebrate. The material collected in this state since the middle of the 19th century has contributed materially to our knowledge of past faunas of eastern United States. However, as in other areas, the earlier studies in Florida dealt almost entirely with larger vertebrates, and comparatively little was known of the smaller forms that inhabited this region. The vertebrate paleontologist of that period considered the smaller Tertiary and Pleistocene species somewhat rare as fossils, and concerned himself chiefly with the study of the larger extinct animals.

New techniques of exploration and excavation opened up a new field in paleontology—that of microvertebrate paleontology. The considerable effort spent on collecting and studying small fossils during the last few years has greatly extended our knowledge of the evolutionary history of certain groups of animals. Snakes, formerly thought to be rather uncommon as fossils, have been found quite plentiful. Detailed studies on the past herpetofauna of North America constitute a new phase in paleontology. They are contributing concrete information on the evolution of a group of which virtually nothing was known a few years ago.

The excavations conducted at Vero, Melbourne, and Seminole Field, Florida during the early part of the 20th century provided most of the fossil snakes known heretofore from the eastern United States. However, these collections are composed mainly of the larger species. The new material accumulated during this study includes many species of smaller snakes previously unknown as fossils, and adds a number of new localities for other fossil forms.

Various systematic studies on modern animals have indicated that peninsular Florida played an important role in the evolution and dispersion of many forms inhabiting the southeastern Coastal Plain. The shape, position, and geological history of the peninsula have undoubtedly influenced former patterns of gene flow and the dispersal of organisms. Its present fauna suggests it to have been both a haven for relict populations and a focal point of speciation. Thus further study of the rich fossil deposits in this region may contribute materially to our knowledge not only of the extinct forms, but of the derivation of our present Coastal Plain fauna.

II. Materials and Methods

This study is based on many hundreds of fragmentary and complete elements of fossil snakes, most of them in the collections of the University of Florida. The fossil snake material in other collections was also examined. At least 36 species have been found as fossils in the State, ranging in age from Lower Miocene to Upper Pleistocene. As might be expected, Pleistocene fossils are much more numerous than those from the preceding epochs.

Vertebrae and ribs are by far the most common elements, although various cranial and mandibular elements are also represented in the collections. For the most part this study is based on the vertebrae. So far no one has found ribs to be diagnostic on even a generic level.

In peninsular Florida terrestrial vertebrate fossils are practically always found disarticulated in a soft matrix. The techniques most useful in extracting small fossils from such matrices follow, essentially, those outlined by Hibbard (1949a).

Many fossils were obtained from the bottom of stream beds with diving apparatus. Some of these were found in water-filled caverns as much as 80 feet below the surface. Many fossil elements were also found on the surface of the ground in several isolated localities. Material from stream bottoms, as well as from isolated finds, is of limited value as a basis for stratigraphic conclusions. These fossils are used here merely as substantiating evidence for conclusions based on material of known derivation.

The Florida fossil snake material is identified largely by comparing it with skeletons of modern species. For this purpose it was necessary to assemble a large number of snake skeletons, representing a wide variety of species. Skeletons of over 300 species of snakes, most of them New World forms, were prepared, though in many cases only a representative portion of the vertebral column was cleaned. All of the North American genera are represented in this material, as well as representative genera from the rest of the Americas and from the Old World. For some genera all the known species were examined. Skeletons of different subspecies were studied to obtain some idea of geographic variation, and in many of the common species individuals of different sizes were examined for ontogenetic differences.

The following abbreviations have been used in referring to specimens in collections: *AMNH*, American Museum of Natural History; *CNHM*, Chicago Natural History Museum; *FGS*, Florida Geological Survey; *MCZ*, Museum of Comparative Zoology; *UF*, University of Florida Collections; *UMMP*, University of Michigan Museum of Paleontology.

III. Fossil Snake Localities of Florida

Among the eastern states, Florida is exceptionally rich in fossil remains of Tertiary and Quarternary land vertebrates. Fossil land vertebrates of this area are known from three epochs, all of which contain snake remains: the oldest are from the Lower Miocene, some occur in the Middle Pliocene, and finally, most abundant and widespread of all, are the remains from the Upper Pleistocene.

Chief among the features making Florida so rich in fossil material is that a soft, easily soluble limestone underlies a large part of the peninsula. Where these beds come close to the surface deep sinkholes and caverns are numerous. Such openings in the bed rock served as traps for land animals whenever the peninsula rose above the sea and sinkholes began to form. In addition, innumerable ponds and small lakes formed in the shallower sinks, each containing a rich fauna that became, in part, preserved in the bottom sediments.

There is another group of vertebrate-bearing deposits in the peninsula that have little, or no relation to the underlying limestone. These are the Pleistocene deposits formed close to the sea, either in old stream beds or in low coastal marshlands.

The classic localities of Florida represent both major types of deposits. As the fossil-bearing zones are relatively superficial, rivers and streams have cut through them and thoroughly mixed the faunas from different epochs in some localities. Earlier paleontological studies, based at least in part on such mixed deposits, have led to considerable confusion.

Not a few authors have mentioned the difficulty encountered in deciphering the past Florida faunas, especially in the central part of the peninsula. The reasons are found in the geologic history of the region and the nature of the sediments. None of the splendid sections which display faunal sequences so clearly in the West occur here. Solution of the underlying limestone has been highly active since at least Miocene time. The resulting sinkholes and caves have accumulated animal remains as small isolated deposits ever since. The deposits of any small geographic area may represent a considerable part of the Late Tertiary, so that a small sink containing Miocene vertebrates may be only a few feet from another sink containing Pliocene or Pleistocene remains. Thus, in Florida, vertebrate paleontology must, of necessity, be conducted on a detailed scale. Each sinkhole is a unit in itself, containing a fauna which may or may not be related to that in the next sinkhole. Unfortunately, this point has been emphasized too infrequently in the literature and has resulted in considerable confusion.

Because many of the localities from which fossil snakes have been collected have not been adequately described, or because they are new and have never been described, a short account of each deposit containing snake fossils is given. I hope that these remarks may somehow contribute to future correlation between the various localities in Florida. Most of the elevations in the following descriptions have been taken from Gunter, *et al.* (1948).

A. *Miocene Deposits*

The only Miocene locality from which snake remains have been taken is the Thomas Farm in Gilchrist County (R15E, T7S, Sec. 20). This deposit is usually considered Lower Miocene (Zone B), Arikareean (White, 1942a; Wood, *et al.*, 1941; Cooke, 1945; Romer, 1948; *et al.*). Several vertebrate groups from this deposit have been studied in some detail.[1] The most important paper that relates to the present study is that by White (1942a), in which the geology and paleoecology of the deposit are discussed in some detail. White postulates, on the basis of both faunal and stratigraphic evidence, the presence of an island in this part of Florida during the time of deposition. The marked similarity between the Garvin Gulley fauna of Texas and the Thomas Farm suggests that the isolation of Florida at this time, if it did occur, must have been short-lived. From the stratigraphic standpoint the evidence is not altogether conclusive. More detailed geologic studies are needed in the area between this and the Georgia-Florida boundary to determine the Lower Miocene geography of Florida accurately.

White believes the Thomas Farm deposit represents an old stream channel. This he bases mainly on the nature and disposition of smooth, rounded limestone boulders which, in a large part of the pit, seem to form a bar-like deposit. Similar rounded boulders are now known to form by solution in many of the sinkholes in Florida. Many of the boulders at the Thomas Farm are rather large. A stream of sufficient velocity to carry such loads requires a considerable gradient. Realizing this, White postulates fairly high elevations for this part of Florida during the period of deposition. Though really good evidence is lacking, most geologists refute such elevations during the Lower Miocene.

The presence of the genus *Siren* in the deposit (Goin and Auffenberg, 1955) suggests slow-moving or still water. Only one fish vertebra has been found in the deposit so far, whereas in known fossil stream deposits such elements are very common. On the other hand, they are frequently rare or absent in sinkhole, fissure, and cave deposits. More recent evidence (Bader, 1956) indicates that the fossil-bearing beds are much more steeply inclined than would be expected in a stream deposit. However, steeply dipping beds are to be expected in a sink, fissure, or cave deposit. The surrounding area is well marked with ancient sinkholes, and Cooke (1945) advocates sink deposition. Bader (1956) apparently favors this interpretation.

A point not previously sufficiently emphasized is the fact that remains of small rodents and bats are quite numerous, especially in the boulder bed. Accounting for the abundance of these small animals in a stream deposit is difficult, particularly in view of the fact that such remains occur commonly only in caves and fissures in a number of karst areas throughout the world. At present these animals commonly live in caves, fissures, and in the crumbling walls of steep sinkholes. Therefore from both a faunal and stratigraphic standpoint the writer interprets the locality as representing a linear fissure in the Ocala Limestone which became filled with clayey sediments during a relatively short period in the Lower Miocene.

The absence of any noticable depression at the surface of the present site has been used to argue against sink deposition, but there is no reason to suppose that the present land surface reflects such minor details as might have been present during the Miocene. Considerable exploratory drilling throughout the peninsula has shown many irregularities on the surface of the Ocala Limestone underlying the relatively flat Recent surface.

The writer presumes that if seas encroached on the peninsula they had a planing effect, smoothing much of the limestone bedrock by wave action. This is well illustrated along the upper edges of many limestone quarries where the projecting peaks of a typically developed karst topography have been evenly truncated. Marine erosion in the relatively low-lying Thomas Farm area easily could have removed much of the upper portion of what was perhaps at one time a deep and steeply walled sink or joint fissure. As the supposed Hawthorne Clay overlies the eastern part of the deposit, seas of Hawthorne time may well have truncated the projecting peaks. On the other hand, practically any of the high seas during Pleistocene time could have been responsible.

The Lower Miocene age of the deposit is based partially on correlation with vertebrates from western localities, partly on the nature of residual material and, to a lesser

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[1] *Mammals:* White, 1940, 1941, 1942a, 1947; Romer, 1948; Simpson, 1932; Wood, 1932, 1947; Lawrence, 1943; Bader, 1956. *Reptiles:* Vanzolini, 1952; White, 1942b; Williams, 1953. *Amphibians:* Tihen, 1951; Goin and Auffenberg, 1955; Auffenberg, 1956. *Birds:* Wetmore, 1943; Brodkorb, 1954a.

extent, on the overlap of a deposit believed to represent the Hawthorne formation of Middle and Upper Miocene. The vertebrate fauna of the Thomas Farm is not identical to the well known Arikareean. This might be expected on geographical grounds alone (Romer, 1948), or may be due to a slightly different time period being represented (Wilson, 1959). The residual materials point to post-Suwanee time. The eastern end of the deposit is overlain with a clay referred to the Hawthorne, though the clays of Florida, and especially those of the Late Tertiary, are difficult to define on general lithology alone. These clays are in turn truncated by a sandy clay, presumably Pleistocene in age.

The fossil snakes now known from this deposit include the following forms: *Pseudoepicrates stanolseni* new genus, *Ogmophis pauperrimus, Calamagras floridanus* new species, *Anilioides minuatus* new genus and species, *Pseudocemophora antiqua* new genus and species, *Paraoxybelis floridanus* new genus and species.

The material from this locality provides our first glimpse of anything representing a rich snake fauna during the Miocene of North America. This period marks the first occurrence of the Colubridae in the New World, and also marks the last appearance of the large boids in both North America and Europe.

B. *Pliocene Deposits*

Fossil snake remains are known from two localities which seem to represent the Pliocene. These are:

Haile VI

Locality A.—(R 17 E, T 9 S, NW¼ and SW¼, Sec. 24): 0.2 miles east of Route 235, near the town of Haile, Alachua County; elevation approximately 84 feet. The stratigraphy of this deposit is as follows:

3. Recent sod and a thin black to gray sandy soil 3 in
2. A yellowish clay, weathering to red, containing lenses of a white to grayish clay; very smooth eroded Ocala Limestone boulders in the basal portion, with many small phosphatic grains which may or may not be cemented together to form rounded smooth boulders as much as 6″ in diameter 3-4 ft
1. Ocala Limestone (very irregular).

Fauna.—Bed 2 contains remains of the following snakes: *Heterodon brevis* new species; *Diadophis elinorae* new species; *Stilosoma vetustum* new species; Elapidae ? genus; Crotalidae ? genus.

Several members of the family Sirenidae have been reported by Goin and Auffenberg (1955), a glass lizard by Auffenberg (1955), and the anurans by Auffenberg (1957). The mammalian fossils have not yet been studied. Remains of fossil birds apparently are rare. The fossil fishes have been reported on by Caldwell (1956).

Correlation.—On the basis of the presence of *Hipparion, Serridentineus* and ? *Machairodus*, the deposit is here considered Pliocene. *Pseudemys caelata*, abundant at this locality, is known from only one other locality, Mixson's Bone Bed, which is considered by most workers as Pliocene. The snake fauna is different from those existing in either known Pleistocene or Miocene deposits from the peninsula.

On the basis of lithology, stratigraphy, and fauna, these beds seem to represent the Alachua formation, a non-marine series of beds sometimes considered contemporaneous (in part) with the Bone Valley Gravel formation. The present locality is in or very near that usually indicated as the Alachua Clay member of the Alachua formation (Dall, 1887, 1903; Sellards, 1910, 1914; Simpson, 1930a; Cooke, 1939, 1945; Cooke and Mossom, 1929; Parker and Cooke, 1944; Vernon, 1951, *et al.*). Cooke (1945) and Vernon (1951) correctly indicated that the Alachua formation represents at least portions of the Miocene, Pliocene and Pleistocene Epochs. However, Simpson (1930a) showed that the fossils in this formation are not always thoroughly mixed, as is sometimes contended, but are frequently found as discreet faunas in unmixed portions of many of the sinkholes. The present locality shows no indications of mixing, with the exception of a few worn shark teeth, apparently derived from the Hawthorne formation. Considerably more mixture is found in a Pliocene locality one-half mile west, where the upper bed of a fossiliferous deposit contains both Pliocene and Pleistocene faunal elements.

Both *Hipparion* and *Pseudemys caelata* currently are considered Middle Pliocene forms in Florida. However, the only well known terrestrial Pliocene fauna occurs at the Mixson locality (excluding the possible Pliocene forms in the marine-deposited Bone Valley Gravel formation). Other occurrences are scattered and the deposits contain no real *fauna*. The present locality may be an exception, but until the deposits are explored more fully and the mammals are examined in some detail it seems best to refer the locality to the Middle Pliocene; that is, perhaps equivalent to Mixson's Bone Bed (Simpson, 1929a).

Paleoecology.—The nature of the deposit and the fauna leaves little doubt that the locality represents an ancient stream deposit, perhaps close to the sea (Caldwell, 1956). The contained fauna shows no evidence of climatic conditions different from those now existing in the area. Knowlton (1927) and Berry (1916) suggest that climate in Florida during the Pliocene was similar to that at the present time. Extinct species of plants described from various Florida deposits are apparently ancestral to Recent forms (Berry, 1916).

Lithia Springs

Fossils have been found in the spring run, close to its head near the Alafia River, Hillsborough County (R 21E, T 30S, Sec. 16). The stratigraphic origin of the remains is unknown. The stream flows across the limestone facies of the Hawthorne formation, which forms the bedrock in this entire general area (Cooke and Mossom, 1929). The stream bed contains many phosphatic pebbles, apparently derived from the limestone, as well as fragments of Miocene marine vertebrates. The conditions of deposition are similar to those in the Peace River a few miles east.

Fauna.—Similar to that of the Peace River beds, in that Miocene, Pliocene, Pleistocene, and Recent elements are present.

Correlation.—The Peace River beds in the past have been considered Middle Pliocene in age (Dall, 1892). However, as Sellards (1915) pointed out, the streams in this area cut through Pliocene and Pleistocene mammal-bearing deposits. The fossils found on the bottoms of these streams are derived from older beds. Simpson (1929a) emphasized that fossils from such beds do not constitute a fauna. The fossils can be interpreted only by checking them against test faunas derived from localities where admixture has not occurred.

Only one snake vertebra was obtained from the bottom of the stream formed by Lithia Spring. Yet this element is different from those found in known Miocene or Pleistocene beds and represents a new genus (*Paleofarancia*), which is described below. It is much more heavily mineralized than most Pleistocene vertebrae. No Miocene land vertebrates are known from this part of the State. As this genus is not present in any of the Pleistocene deposits, and since many streams in this region frequently carry Pliocene fossils, the specimen is tentatively referred to that period.

C. *Pleistocene Deposits*[2]

For the Pleistocene deposits of Florida the difficulties in deciphering faunal succession are even greater than for the earlier epochs. The fossils are frequently isolated, are often mixed with older or with younger faunas, are seldom found in place and in many instances in the early explorations the exact location and horizon were unknown. To avoid confusion, data on fossil snakes are used only when the specimens were found in place, or of surely known derivation in a single locality with a considerable number of other species that are known to be contemporaneous.

In virtually all the papers describing various Pleistocene localities throughout the state, the standard section on which most correlations within the state rest is that at Vero, where three distinct horizons are manifest. The lowest, Stratum 1 of Sellards and

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[2] Pleistocene time as used here includes that period from the beginnings of the Nebraskan ice movement to the recession of the Mankato sheet (about 11,000 years ago, *fide* Libby, 1951). The suggestion by Flint (1942) to include all post-Pliocene time in the Pleistocene has not been followed. The term postglacial is too local and has no meaning in a nonglaciated area (Flint, 1942). For the same reason the "zero" varve of DeGeer (6839 BC) is too local. Distinct climatic changes in Europe (7912 BP), *fide* Zeuner (1950), seem to agree with the beginnings of the North American postglacial phase. There is little reason to believe that the extreme climatic changes experienced by more northern states occurred in Florida during the Pleistocene, although changes of lesser magnitude may be indicated by the fauna of several localities. However, these faunas have not yet been correlated positively with marine terraces or even with definite glacial or interglacial periods.

subsequent authors, is the Anastasia formation, a marine deposit. Above this is Stratum 2, a complex deposit clearly of Pleistocene age and containing a large land fauna. This horizon has been termed the Melbourne Bone bed (Cooke and Mosson, 1929), and is probably of Wisconsin or Post-Wisconsin age.[3] Above this bed is a stratum, more recent in age, which apparently represents at least some admixture of Pleistocene and Recent faunal elements and is known as Stratum 3. In this paper it is considered Recent in age.

To facilitate correlation of the Florida Pleistocene localities Simpson (1929a) set up a number of test faunas which contain many species of presumably contemporaneous mammals. These include Sabertooth Cave (Lecanto or Allen Cave), Citrus County; Seminole Field, Pinellas County; Melbourne Golf Course Locality, Brevard County; and Vero Beach, St. Lucie County. Only the faunas from Stratum 2 of the last three localities are considered as test faunas.

A surprising feature of the Florida Pleistocene vertebrate deposits is the marked similarity of the mammalian faunas from one locality to the next. This is well shown in Simpson's test faunas, where he assumes contemporaneity on the basis of faunal similarity. A number of new fossil localities have been discovered since Simpson's paper was published, and the faunas from each agree surprisingly well with Simpson's test faunas. Thus, the test faunas have not yet served to separate the Pleistocene deposits on their faunas alone. A possible explanation may be that the Pleistocene fauna in Florida, unlike that in other parts of North America, was relatively static and only slightly affected by minor climatic shifts. Faunal differences between deposits representing different periods in the Pleistocene may be much more subtle than those presented in periglacial zones. The mere absence of a faunal element can be due so easily to chance preservation or varying ecological conditions that it cannot be considered seriously unless it occurs over and over again. This has not been the case so far. Correlation of these deposits may be based much better on a study of the degree of morphological differentiation perhaps in the rodents of the various localities.

All the Florida Pleistocene localities so far known contain a surprising number of species of vertebrates indistinguishable from those inhabiting the same region today. This has been a major point in assigning these deposits to the Late Pleistocene. In well-known periglacial zones the Early Pleistocene apparently is distinguished by the fact that many of the smaller animals and most of the larger ones are extinct forms (Simpson, 1929a). Furthermore there is no evidence to support any concept involving greatly fluctuating climates for Florida on the basis of the known Pleistocene localities. All the Florida Pleistocene localities known so far possess fair numbers of large land tortoises, as well as other more southerly ranging reptiles, suggesting a warm climate for the periods represented by these deposits. An equitable Pleistocene climate in Florida is expected as the peninsula lies at a considerable distance from the periglacial zones. Davis (1946) reported spruce pollen from a peat bed in Leon County, but provided no information on its abundance. Isolated pollen grains can be expected in deposits far from their origin (Cain, 1926), and if Odum's (1952) postulate of high winds in southeastern United States during the Pleistocene is correct, even more caution is needed in interpretating pollen analyses in this area.

Pleistocene deposits of South Carolina contain remains of moose, walrus, elk, and seals. Although the walrus has been shown to be a warm water form, peat beds in the Carolinas contain considerable spruce and fir pollen, as well as twigs and branches of these trees (Berry, 1907, 1909, 1925; Buell, 1939, 1945; Frey, 1951, *et al.*). If taiga or boreal communities were common in South Carolina during glacial periods one would reasonably expect some sort of climatic changes in Florida, which should be noticable in the vertebrate faunas of at least some

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[3] Hay (1923) correlated these deposits on the basis of simultaneous extinction of related species widely separated geographically, and assigns Stratum 2 to the earliest Pleistocene (Aftonian and Nebraskan stages). There is no evidence to indicate that the periods of extinction of certain vertebrate groups in Florida coincides with those for related species in the periglacial zones (Simpson, 1929a). While the reference of this deposit to a substage of the Wisconsin is far from fully substantiated, it seems at present a reasonable assignment (Weigel, 1958).

of the Florida deposits.[4] Only a few northern vertebrates have been recorded from the Florida Pleistocene. However, Simpson (1929b) pointed out that the range of most superspecific taxonomic units was probably less restricted in the Pleistocene than at present. He also suggested the possibility that the native Florida animal population could not escape to the south, and thus its very presence would hamper the entrance of more northern types.

Another interesting feature of the Pleistocene deposits of Florida is that no genus or species is definitely known to have evolved into a new form during the time represented by the known deposits. The modern Florida fauna is simply a reduced Pleistocene fauna.

None of these deposits is over 100 feet in elevation and all seem to be located below the Pleistocene marine terrace level termed the Wicomico (Cooke, 1939; MacNeill, 1950). This indicates that no vertebrate fossil in Florida so far represents the maximum stage of the earlier interglacial stages. The known fossil fauna as a whole seems to reflect one somewhat characteristic of a climate essentially similar to that of the present, or possibly even one which could have extended into more southern climes (Simpson, 1929a). The known deposits probably represent Middle and/or Late Pleistocene time. Stratum 2 at many coastal localities may represent a substage of the Wisconsin, or even Post-Wisconsin time. This is substantiated by geologic evidence, though not conclusively (Cooke, 1945, *et al.*). Various fissure and sinkhole deposits in central Florida may be Illinoian in age (Brodkorb, 1957), as the fossiliferous zones lie below the presumed Wicomico terrace sands and clays, which some consider Sagamon in age. There are, however, some problems encountered in this interpretation: *i.e.*, the Wicomico terrace sands, presumably marine in origin, contain surprisingly few, if any, marine fossils; the Wicomico terrace level has not definitely correlated with Sangamon Interglacial deposits, which raises the question, are all Pleistocene fossiliferous beds below these terrace sands necessarily contemporaneous?

The simple fact that workers are not in agreement as to the number of terraces, their elevation, or even their mode of development, indicates our nearly complete ignorance in these matters.

Regarding correlation of the deposits, surprisingly few facts are known which bear on the problem. Some of the more important of these are as follows. (1) Up to the present time, no vertebrate fossil beds have been found at an elevation greater than 100 feet. (2) Fossiliferous vertebrate beds have been found at least 18 feet below sea level. (3) Adjacent sinks, caves and fissures may represent different ages. (4) There is no conclusive evidence that cold conditions occurred in Florida during any part of the Pleistocene. On the other hand, conditions warmer than those at present are suggested by the presence of large reptiles, such as *Geochelone*, which have been found in almost all localities. (5) Minor differences in faunal composition between many of the deposits are suggested in all three terrestrial classes. These differences could have their bases in ecology. (6) The modern fauna is largely a reduced Pleistocene one with many of the genera and species of Pleistocene mammals and birds now extinct. (7) Most genera (of at least mammals) in the Florida Pleistocene are typically found in the Pleistocene of other areas. (8) Some genera or species now found only to the north of Florida are present in the Pleistocene deposits of the State. (9) A number of fossil forms are larger than the same forms living in the peninsula at the present time. (10) On the other hand, many Recent species are morphologically identical with their Pleistocene ancestors. (11) Certain immigrant South American groups are present in most of the localities. (12) Some of the extinct genera or species are most closely related to forms now living in southwestern United States. (13) There has been some replacement on a specific, or subspecific level from Pleistocene to Recent.

Some features of the Pleistocene of Florida are frequently taken as fact, but in reality are only tentative points of departure in the absence of conclusive data. (1) Pleistocene climate was not greatly different from the present. The climate during glacial

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[4] Knowlton (1927) pointed out that the glaciers did not affect the vegetation of the periglacial zones greatly. In addition Flint (1942) and Bryon (1928) suggested that the periglacial zones in North America were probably much narrower than those in Europe, where glacial climatic effects are seen far southward.

stages may have been wetter than at present, and probably not much cooler. The interglacial climates were probably warmer and drier than that at present. (2) The terraces in Florida were formed basically during changes in sea level, though (3) upwarping in the peninsula during the Pleistocene may have modified terrace formation. (4) The Pamlico Terrace was formed during a stage of the Wisconsin, and the Wicomico during a stage of the Sangamon Interglacial. (5) All of the glacial and interglacial periods will eventually, on some basis or another, be recognized in Florida. (6) The ecological variation throughout the peninsula was as great during any one stage of the Pleistocene as it is today. (7) Similar populations of the same species, or the same genus, have had similar modes of existence during and since the Pleistocene. (8) Changing ecology brought about at least minor changes in the biota that can be recognized on analysis of the fossil record. (9) Most of the Pleistocene is represented by the deposits already known from Florida, though (10) the known deposits probably represent a greater number of Late than Early Pleistocene localities on chance alone. (11) The peninsula acted as a refugium, and as a center of speciation with island formation during interglacial periods.

There are a number of important problems which must be solved before workers will realize the full potential from these interesting series of Quaternary beds. (1) What were the extremes of temperature witnessed in Florida during the Pleistocene? (2) What is the total time represented by all of the Pleistocene deposits; of each deposit? (3) What is the exact extent of fluctuations in sea level, and when did these fluctuations occur? (4) What is the exact paleoecology of all of the major deposits in the area? (5) What is the extent of faunal admixture in each case?

Until more work is conducted in Florida on a detailed scale no one can assign positive ages to the known Pleistocene deposits of the area. A tentative correlation recently was attempted (Auffenberg, 1958a), but needs considerable verification before it will be of any use. Better correlation with terrace levels (marine, pluvial, or otherwise) is sorely needed. Further work being undertaken at the present time by a number of interested workers in Florida should shed considerable light on the interesting remaining problems concerned with correlation of these highly fossiliferous beds.

Fossil snake remains are now known from a number of Pleistocene localities throughout the peninsula. A description of each of these localities follows.

Arredondo, Pit I

A limestone quarry 4.2 miles west-southwest of Gainesville, Alachua County, just north of U. S. Highway 24 (R 19 E, T 10 S, sec. 22); elevation about 85 feet. Terrestrial vertebrate remains have been found on the northern and western sides of this quarry in clay-filled sinkholes, solution channels and fissures.

Locality A.—This is a vertical fissure 2 to 3 feet wide, extending from the surface of the Ocala limestone to an unknown depth below the bottom of the quarry. The fossils occur in a brownish to bluish clay, frequently with lenses of yellowish clay, weathering to reddish brown. For the stratigraphy and mammalian fauna of this locality see Bader (1957).

Fauna.—The snakes from this deposit include the following forms: *Carphophis amoenus, Heterodon platyrhinos, Drymarchon corais, Coluber constrictor, Masticophis flagellum, Opheodrys aestivus, Elaphe guttata, Elaphe obsoleta, Lampropeltis getulus, Tantilla coronata, Natrix sipedon, Thamnophis sirtalis, Storeria dekayi, Micrurus fulvius, Crotalus adamanteus.*

Correlation.—The mammalian fauna found in this locality suggests a Middle or Late Pleistocene period of deposition resembling closely that from Stratum 2 of various east and west coast localities in the state. Stratigraphic evidence at the present time suggests that the deposit may be Illinoian in age, but this is not definitely established.

Paleoecology.—The locality must have been located very close to a fresh water pond or stream on the basis of the fauna (*Tapirus, Neofiber, Siren, Pseudobranchus, Alligator,* etc.). On the other hand, such forms as *Geomys, Drymarchon,* etc. suggest open, dry forest conditions. *Pitymys,* which is known from the locality, usually inhabits dry forests or even scrub. The paleoecological conditions as interpreted on the basis of the known fauna differs little from that found in the area at the present.

Locality B.—A brownish sandy clay filling a diagonal fissure a few feet east of Locality A, and which may have been connected with it at one time, approximately 12 feet below the surface.

Fauna.—The only known snake is *Drymarchon corais.* Bader (1957) described the stratigraphy and mammalian fauna.

Correlation.—Middle or Late Pleistocene (Illinoian?).

Paleoecology.—Essentially the same as that of Locality A.

Locality D.—A brownish sandy deposit with large boulders of Ocala limestone, broken and eroded, filling a vertical fissure above Locality A, and possibly grading into it. Bedded sediments are evident in the lower 1-2 feet of the deposit. Above these beds is a reddish, homogenous sandy clay, which may be equivalent to Locality B. The fossils are well-mineralized, but sometimes somewhat chalky.

Fauna.—The following snakes are known from this locality: *Drymarchon corais* and *Elaphe guttata.*

Correlation.—Middle or Late Pleistocene (Illinoian?).

Paleoecology.—The entire fauna from this deposit suggests dry, open forested conditions, possibly similar to those existing in the same area today.

Locality H.—This deposit, located in the same quarry, but northwest of the area containing the deposits described above, is a horizontal fissure in the limestone. The fissure is approximately 3 feet thick, and about 18 feet from the surface. It is filled with a rather homogeneous buff-colored sand, containing small lumps of grayish clay.

Fauna.—The only fossil snake known from this locality is *Crotalus adamanteus.*

Correlation.—Middle or Late Pleistocene.

Paleoecology.—Too little is known of the fauna of this locality at the present time to warrant any serious ecological considerations.

Arredondo, Pit II

A limestone quarry 4.3 miles west-southwest of Gainesville, Alachua County, just south of U. S. Highway 24 (R 19 E, T 10 S, Sec. 22); elevation 85 feet. Terrestrial vertebrate remains have been found in place in a fissure on the west side of the quarry. For a list of the mammals collected there see Bader (1957). Remains of fossil snakes were collected from the spoil dumps, so that their exact origin is unknown, though they were undoubtedly associated with the extinct Pleistocene mammals.

Fauna.—The snakes known from this locality include the following forms: *Heterodon platyrhinos, Coluber constrictor, Opheodrys aestivus, Elaphe guttata, Cemophora coccinea, Stilosoma extenuatum, Thamnophis sirtalis.*

Correlation.—Middle or Late Pleistocene (Illinoian?).

Paleoecology.—The vertebrate fauna known from this locality suggests dry, open forested conditions very similar to those existing in the area at the present time.

Kanapaha I

A limestone quarry 4.8 miles west, southwest of Gainesville, Alachua County, just south of U. S. Highway 24 (R 19 E, T 10 S, SW¼ of SW¼ of Sec. 22); elevation about 85 feet. The vast bulk of the vertebrate fossils collected at this locality came from spoil dumps which originally filled a few solution channels and fissures in the Ocala Limestone on the southern side of the quarry. For this reason specific localities are not given.

Fauna.—The snakes known from this quarry include the following forms: *Drymarchon corais, Opheodrys aestivus, Pituophis melanoleucus, Elaphe obsoleta.*

Correlation.—Apparently Middle or Late Pleistocene.

Paleoecology.—The somewhat restricted fauna definitely points to a dry, open wooded area, similar to that in the area at the present time.

Haile, Pit I

A limestone quarry near Haile, Alachua County (R 17 E, T 9 S, SE¼ of SW¼ of Sec. 24); elevation about 84 feet. This is one of a series of limestone quarries located in the immediate area. The present pit is 0.4 miles east of State Highway 235.

Locality A.—This is a large opening in the Ocala Limestone on the west face of the quarry, and filled with bedded and steeply dipping laminae of clays, sands and fresh water marls. The stratigraphy of the deposit has been given by Brodkorb (1953).

Fauna.—The fossil snakes known from this deposit include the following: *Drymarchon corais, Masticophis flagellum,* *Elaphe guttata, Lampropeltis getulus, Natrix sipedon, Natrix cyclopion, Natrix* cf. *erythrogaster, Thamnophis sirtalis, Agkistrodon piscivorus.*

Brodkorb (1953, 1954b) listed the birds from this deposit. *Rana grylio* was reported from the locality by Tihen (1952).

Correlation.—Middle or Late Pleistocene (Pamlico?).

Paleoecology.—This locality evidently reprepresents an ancient fresh water spring head. This conclusion is based on both the stratigraphy and the vertebrate and invertebrate fossils. The beds are well sorted and the entire deposit is located in a funnel-shaped opening in the Ocala Limestone. In some parts of the deposit the sorted materials are definitely cross-bedded. On the other hand, the presence of dark laminated organic clays between lenses of sorted marls and sands seem to suggest still or slowly moving water. Faunal elements representing both stream and pond forms are common. Mixture of these units apparently has occurred so they do not reflect the alternating conditions indicated by the stratigraphy.

A reconstruction of the locality as it probably existed during the latter part of the Pleistocene would thus seem to call for an aquatic situation fluctuating between a flowing spring and a sinkhole pond. Sinks are common in the surrounding area, though water levels are so low that very few contain permanent ponds. Flowing springs are not found in the area at the present time.

Vernon (1951) discussed the possibility of the presence of a large Pleistocene river in this general area. It presumably flowed southward across central Gilchrist County, from the present Sante Fe to the Waccassasa rivers, and apparently occupied the Pleistocene valley of the Waccassasa River. He correlated this stream with Pamlico time, when sea level was thought to be approximately twenty-five feet higher than at present. The water table in large caverns in the immediate area varies depending on local rainfall, but is generally twenty-five to thirty feet below the surface. The river, perhaps larger than the Suwanee, was probably captured by underground drainage at the close of the Pleistocene.

The Pleistocene spring deposit at Haile I A probably represents the head of a stream that flowed westward into the larger Pamlico river described by Vernon. The rise of water table during this period allowed the spring to flow, whereas lowered water tables near the end of the Pleistocene caused the flow to cease altogether. Judging on the laminated nature of the deposit the spring probably flowed slowly for long periods of time, and may even have become ponded at different periods. Edwards (1949) reported an abandoned stream valley and spring head near the present Sante Fe River which may also date from this period. Aerial photographs of the area show no indications of any ancient stream bed.

Haile II

This is a limestone quarry 0.3 miles east of State Highway 235, near Haile, Alachua County (R 17 E, T 9 S, SW1/4 of SW1/4 Sec. 24); elevation about 84 feet.

Locality B.—The locality is represented by a horizontal fissure on the north face of the quarry, about twenty feet below the surface of the Ocala Limestone. The entire fissure varies from 1 to 4 feet thick, and extends back into the limestone for an unknown distance. Two beds make up the deposit. The uppermost is composed of a reddish sandy clay containing few fossils. Separating this from the lower bed is a thin band of limonitic clay, yellowish-brown to red in color, and which is found separating the same beds in many other sinkholes and fissures of the entire area. The lower bed contains considerable remains of rather small vertebrates, and is composed of a dark brownish, somewhat consolidated sand.

Fauna.—The snakes known from this locality include the following: *Carphophis amoenus, Opheodrys aestivus, Elaphe guttata.*

Correlation.—Presumably Middle or Late Pleistocene on the basis of the mammalian fauna (equivalent to Reddick I B?).

Paleoecology.—This deposit, because of the fairly large number of bat remains, probably represents a Pleistocene cave or fissure. The opening to the surface was presumably small, since larger bones are uncommon. The presence of *Ophisaurus compressus* (Auffenberg, 1955a, 1956b) suggests that an area of scrub vegetation existed nearby. However, the large bulk of the fauna indicates a more mesic, forested condition.

Haile IV

Locality B.—This deposit is located on the north side of a limestone quarry near

Haile, Alachua County, 0.1 miles west of State Highway 235 (R 17 E, T 9 S, SE¼ of NE¼ of Sec. 23); elevation about 84 feet.

The locality is a horizontal fissure in the Ocala Limestone, about one foot thick, but extending for a considerable distance around the quarry. It is located about thirty feet below the surface of the limestone. The only fossils found in the fissure so far are some limb elements of *Bufo* sp. and one vertebra of *Drymarchon corais*, all from just above the limonitic clay layer described under Haile II B.

Haile VII

A large limestone quarry near Haile, Alachua County, about 0.8 miles east of State Highway 235 (R 18 E, T 9 S, NE¼ of SE¼ of Sec. 24); elevation about 84 feet.

Locality A.—This locality is located on the northern end of the quarry. It is a large sinkhole depression from which the superficial layers have been removed during mining operations. The stratigraphy is as follows:

4.	Reddish-brown sandy clay (?Wicomico Terrace sands)	3-4 ft
3.	A stratum composed of many intergrading lenses of white sands, brownish to yellow sandy clays with numerous bits of eroded Ocala Limestone, etc.	3-4 ft
2.	Bluish to bluish-gray clay, definitely bedded and found only in the lower parts of the deposit	3-11 ft
1.	Ocala Limestone.	

Fauna.—The locality has an extensive mammalian fauna which has not been completely studied. The fossil snakes known from the locality include the following species, all from Bed 3: *Drymarchon corais, Coluber constrictor, Elaphe obsoleta, Masticophis flagellum, Heterodon platyrhinos, Heterodon simus, Lampropeltis getulus, Natrix sipedon, Thamnophis* cf. *sirtalis, Micrurus fulvius, Sistrurus miliarius, Crotalus adamanteus.*

Correlation.—Presumably equivalent to Arredondo I and Reddick I.

Paleoecology.—The nature of the beds and the associated fauna seem to indicate that this was a sinkhole pond. Bed 3 may represent the fluctuating borders of this pond.

Wall Company Pit I

This is a limestone quarry approximately 7.2 miles west of Gainesville, Alachua County, and 0.6 miles north of U. S. Highway 26 (R 18 E, T 9 S, Sec. 35). At present one fossil deposit is known, and this of rather limited extent. It is situated in a vertical fissure on the east side of the quarry, approximately 2 to 4 feet wide, running from the surface of the limestone downward for about 12 feet. The fissure is filled with a very dark reddish-brown sandy clay. Only one species of snake has been found here: *Crotalus adamanteus.*

Correlation.—I assume this small locality is somewhat equivalent to those at Kanapaha, Arredondo and Reddick I.

Paleoecology.—Unknown.

Reddick I

A limestone quarry approximately one mile south of Reddick, Marion County (R 21 E, T 13 S, SW¼ of NW¼ of Sec. 14), east of U. S. Highway 441; elevation approximately 95 feet. At least two well defined deposits containing vertebrate fossils can be distinguished.

Locality A.—A reddish sandy clay is found in the northern parts of the quarry and fills various fissures and sinkholes. In some places this deposit is fairly consolidated, while in others it is loose. In thickness it varies from 2 to 18 feet, and is overlain by a reddish brown, yellowish brown, or gray sand (Wicomico Terrace sands=(?) Sangamon interglacial (Brodkorb, 1957)). The upper portion of certain parts of this deposit clearly seems to have been truncated, perhaps by an encroaching Pleistocene sea (Sangamon ?). Several fossil turtles were found whose shells were definitely and smoothly sheared off at their junction with the overlying Wicomico Terrace sands. This seems to substantiate the sequential events important in the development of these beds as outlined by Brodkorb (1957). In some places this fossil-bearing bed is clearly shown to rest upon that bed composing the major part of locality B. It thus appears to be younger than that from which the majority of bird and rodent fossils have been taken.

Fauna.—The mammalian fauna from this locality is fairly extensive. Fossil birds are much less numerous than at Locality B. The only species of snakes found in the deposit are: *Elaphe obsoleta* and *Drymarchon corais.*

Paleoecology.—A deposit presumably representing terrestrial conditions; most likely open, dry forest, and possibly similar to that found in the immediate area at the present time.

Correlation.—Presumably younger than Reddick I B.

Locality B.—These beds are best described as the "rodent beds" since these small mammals are remarkably abundant. The deposits collected under this heading show definite bedding planes, and are composed of pinkish, buff, yellow to dark brown sands and clayey sands (Bed 2 of Brodkorb, 1957). One of the most diagnostic features of the deposit is the vast number of fossil vertebrates found. Details of stratigraphy are given by Brodkorb (1957).

Fauna.—This deposit has produced one of the largest Pleistocene faunas yet known from Florida. The list of mammals from this series of beds includes a large number of species, of which approximately 50 percent are extinct. The birds were studied in detail by Brodkorb (1952, 1954b, 1957). Of the reptile and amphibian fossils taken from this deposit there are but a few species missing from a list comprising the known herpetofauna of the central part of the peninsula at the present time. In addition, certain species, such as *Carphophis amoenus* and *Eumeces fasciatus* are at present known only from areas to the north of the fossil locality. The snake fauna includes the following species: *Carphophis amoenus, Diadophis punctatus, Farancia* and/or *Abastor, Rhadinea flavilata, Heterodon platyrhinos, Heterodon simus, Opheodrys aestivus, Coluber constrictor, Masticophis flagellum, Drymarchon corais, Lampropeltis getulus, Elaphe guttuta, Elaphe obsoleta, Pituophis melanoleucus, Tantilla coronata, Storeria* cf. *dekayi, Thamnophis sirtalis, Micrurus fulvius, Sistrurus miliarius, Crotalus adamanteus.*

Correlation.—There is fairly good evidence (Brodkorb, 1957) that this fauna is at least partly equivalent to the deposits at Haile VII, Haile II, and Arredondo I. It is presumed to be Illinoian. Such evidence is found, not only in the similar stratigraphy, but in the identity of certain mammalian, avian and amphibian faunas as well.

Paleoecology.—The large number of bat remains, bones of three cathartid vultures, barn owls, and a swallow, as well as the stratigraphy clearly indicate that this deposit represents a Pleistocene cave. Most important is that several of these birds are represented by bones of individuals too young to fly, as well as by adults (Brodkorb, 1957). The large number of rodents and snakes is attributed to pellets cast by the barn owls.

The smaller vertebrates from this locality represent a wide range in habitat; perhaps a reflection of the wide area covered by the owls in their search for prey. The primary reptilian faunal elements suggest a dry, open forest, but not necessarily scrub. Such conditions exist in the area at the present time. The absence of such aquatic genera as *Natrix* or *Farancia* suggests that there were no ponds close by. Pond dwelling reptiles, such as *Alligator* and *Pseudemys*, though found at Locality B, are uncommon. On the basis of the bird fauna, Brodkorb (1957) suggests that the ecology was that of a wet grassland, or fresh water marsh community. He points out that the fauna indicates that no sizeable body of open water was near, and that the grassland probably was not fed by a permanent stream. These two somewhat divergent views of the paleoecology of the area, both based on a large number of fossils, indicates that considerable additional work must be done before we can hope to obtain a fairly accurate picture of the paleoecology of even one of the best fossil localities in Florida. It should be pointed out, however, that the vast bulk of the bird fossils were obtained from the main bone bed, while most of the snakes were collected from a second locality approximately 260 feet southwest of this area. Possibly the two localities are not contemporaneous, and may represent different ecological conditions. This again points to the need for detailed paleontological research in the complex fissure deposits of the Ocala Limestone.

Williston III

This locality, near Williston, Levy County, was discussed in some detail by Holman (1959).

The snakes reported from the locality include the following forms (after Holman): *Rhadinea flavilata, Diadophis punctatus, Heterodon platyrhinos, Heterodon simus, Coluber constrictor, Masticophis flagellum, Drymarchon corais, Elaphe* sp., *Pituophis melanoleucus, Thamnophis* cf. *sirtalis, Mi-*

crurus fulvius, Agkistrodon piscivorus, Sistrurus miliarius, Crotalus adamanteus.

Eichelberger Cave

A cave west of Belleview, Marion County (R 22 E, T 16 S, Sec. 35); elevation about 90 feet. Fossil vertebrates are known from two localities within the cave.

Locality A.—This deposit is located in the upper level of the cavern. Here the cave earth is redish-brown. The fossils are buff-colored and chalky. There is reason to believe that the northeastern end of this level was open to the surface during the Pleistocene. This is based on some of the fossils themselves, which represent species much too large to pass through the present narrow passageway, and also on the fact that the northeastern end of the upper level apparently is sealed with a mass of limestone boulders and rubble. Here the cavern is close to the surface, and was probably the site of the opening through which the animals passed into the cave.

Fauna.—The only snake known from this deposit is *Coluber constrictor*. Brodkorb (1955) listed the birds from this, and the following locality. *Dasypus bellus*, *Equus* sp. and *Geochelone* attest to the Pleistocene age of the deposit.

Correlation.—Late Pleistocene ?

Locality B.—This deposit, now fully excavated, was located in a small room near the entrance to the cavern on the lower level. The fossiliferous bed is composed of grayish sands, somewhat cemented together in places. The fossils are buff to dark reddish-brown, and chalky.

Fauna.—The extinct mammalian forms from this deposit point to Late Pleistocene time. The snakes now known from the locality include the following species: *Masticophis flagellum, Elaphe guttata, Pituophis melanoleucus, Heterodon platyrhinos, Crotalus adamanteus, Crotalus giganteus.*

Correlation.—Presumably Late Pleistocene.

Paleoecology.—Both the localities within Eichelberger Cave apparently were laid down under water flowing into the cave from the outside. The fauna suggests a dry, open forested area, similar to but probably more open than that existing in the present area today.

Mefford Cave I, A

A rather extensive cave in the Ocala limestone approximately 1½ miles south of Reddick, Marion County, Florida (R 12 E, T 13 S, S½ Sec. 16), just west of U. S. Highway 441; elevation about 100 feet. As far as is known, Pleistocene fossils occur in only the farthest reaches of the cave, particularly the fissures leading southeastward. Fairly complete extinct animals have been found in a bedded dark brownish sand. Occurring as isolated elements are numerous vertebrae of snakes. The fossils are light buff in color, slightly chalky, little mineralized, and quite fragile.

Fauna.—Besides several extinct mammals and some isolated fragments of birds, the following snakes are known from the deposit: *Carphophis amoenus, Heterodon simus, Heterodon platyrhinos, Diadophis punctatus, Elaphe guttata, Thamnophis sirtalis, Crotalus adamanteus.*

Correlation.—The presence of *Carphophis* in this deposit suggests that it may be contemporaneous with Reddick I B and Arredondo I (Illinoian?).

Paleoecology.—On the basis of the known fauna there is little reason to postulate climatic conditions very different from those existing in the area at the present time, although the presence of *Carphophis* suggests slightly cooler, and perhaps more mesic conditions (Auffenberg, 1958a).

Bradenton Field

Locality A.—This locality was mentioned by Simpson (1930b) as being an important one for fossil mammals. It is located one mile south of the business district of Bradenton, Manatee County, approximately 100 yards east of the Tamiami Trail, in the north bank of a drainage canal (for a stratigraphic section see Simpson, 1930b). The elevation is approximately 27 feet. The fossil reptiles and amphibians collected at the site were obtained from a series of thin laminae of blackish to dark gray-colored sand, containing small balls of grayish clay, with bits of broken shells. The laminae were located in white beach sands, approximately four feet below the surface. The delicacy of preservation is remarkable, for even fish scales are faithfully preserved.

Fauna.—Simpson (1930b) reported on the mammals from this locality. The snakes include: *Natrix sipedon, Natrix cyclopion, Thamnophis sirtalis.*

Correlation.—Wisconsin or Post-Wisconsin?

This deposit most certainly represents a series of thin beds formed very close to the mouth of a creek as it flowed across the Pamlico beach. That this deposit is probably younger than Haile VII, A, or the Arredondo and Reddick localities is suggested by the fact that the *Pseudobranchus* is *striatus*, the form found in peninsular Florida today; and not the extinct species *robustus*, which is known from several Pleistocene localities in Alachua County. It seems unlikely that this deposit is equivalent to Stratum 3 of various coastal localities, since there is no evidence of admixture with more recent faunas. It may, however, be intermediate in age between Stratum 2 and Stratum 3.

Paleoecology.—The preponderance of fresh water forms (mammalian, reptilian, and amphibian) and the beach sands stained with tannic acid are certainly indicative of a stream or pond close to the beach. The small clay balls might be interpreted as the effects of marine erosion on an older Pleistocene deposit, except that it is then difficult to account for the finely preserved, and very fragile fish scales. The most likely answer seems that the deposit represents a small, probably slowly moving stream that flowed over the Pamlico beach. At the present time such streams are common on the Gulf Coast of Florida.

Allen Cave, Lecanto Cave, or Saber Tooth Cave

Approximately one mile northwest of Lecanto, Citrus County; elevation about 100 feet. According to Simpson (1928) the floor and pockets within the cave were filled with a reddish sandy clay from which the fossils were taken by Mr. Walter W. Holmes in 1928 for the American Museum of Natural History. As in most cave deposits, the fossils were chalky.

Fauna.—Simpson (*loc. cit.*) gave an excellent review of the fossils obtained from this cavern. The fossil snakes now known from this locality include (after Holman, 1958, unless indicated) the following forms: *Carphophis amoenus, Heterodon platyrhinos, Coluber constrictor, Masticophis flagellum, Drymarchon corais, Elaphe* sp., *Lampropeltis getulus* (Brattstrom 1953a), *Natrix sipedon, Micrurus fulvius, Agkistrodon piscivorus, Crotalus adamanteus* (Brattstrom, 1954a; Holman, 1958), *Crotalus giganteus* (Brattstrom, 1954a), *Rhadinea flavilata.*

Correlation.—Simpson (1929a, 1929b) suggested that this deposit is, at least in part, contemporaneous with Stratum 2 of Seminole Field. On the other hand, it bears just as many resemblances to Arredondo I (Illinoian?).

Paleoecology (after Simpson, 1928).—The general impression is that the fauna is of a rather limited ecological scope, indicating a wet lowland, with swamps, drier wooded areas, and a few open glades. The fauna does not suggest a spelean habitat. There is no suggestion that the climate differed from that of the same region at the present time. Many of the mammals indicate warm and moist conditions. The snake fauna suggests a similar ecology.

Payne's Prairie

Locality B.—Vertebrate fossils were first collected on the prairie in 1930 while a causeway was being constructed over the low-lying area. The new locality (B) is on the Camp Ranch, at the eastern end of the prairie, approximately 4½ miles south of Gainesville, Alachua County, on the north side of a drainage canal, about 1½ miles east of Highway No. 441 (R 20 E, T 10 S, Sec. 36); elevation about 73 feet. The fossils collected at this site were obtained from spoil along the north bank of the canal.

Fauna.—Aside from the typical Pleistocene assemblage of mammals the collections contain the following snakes: *Drymarchon corais, Elaphe guttata, Coluber constrictor, Natrix cyclopion, Thamnophis sirtalis.*

Correlation.—Late Pleistocene?

Paleoecology.—The fauna from this deposit, with the exception of the extinct mammals, may be expected in the immediate area at the present time; namely, inhabitants of shallow ponds and marshes.

Seminole Field, Stratum 2

Only the fossils derived from one bone bed overlying the marine Pleistocene Anastasia formation (Pamlico time) at several localities in the vincity of Seminole, west of St. Petersburg, Pinellas County, are included in this section. Fossils from Stratum 3 are briefly discussed under "Pleistocene and/or Recent Deposits". Simpson (1929a, 1929b, 1930b) listed the fauna of this deposit. Both Simpson (1929a) and Cooke (1926) gave stratigraphic sections of these deposits. Attention should be drawn to the fact that the Seminole beds are complex, and there is every reason to believe that many of these represent recent reworking of the older beds, which may be Wisconsin, or Post-Wisconsin in age.[5] This has been mentioned by Bullen and Winters (1953), and is the view held by most workers in this area. The elevation is from 20-30 feet.

The snake fauna includes (after Gilmore, 1938 and Brattstrom, 1953a): *Drymarchon corais, Lampropeltis getulus, Lampropeltis doliata, Coluber constrictor, Elaphe obsoleta, Pituophis melanoleucus, Natrix* sp., *Thamnophis* sp., *Farancia abacura* (?), *Agkistrodon piscivorus, Crotalus adamanteus.*

Melbourne Golf Course, Stratum 2

A locality 3 miles west of the center of Melbourne, Brevard County. Gidley (1927), Loomis and Gidley (1926) and Gidley, in Hay (1932) gave the stratigraphy of this deposit. These workers, as well as Simpson (1929a) gave a complete faunal list.

The snakes (after Gilmore, 1938 and Brattstrom, 1953a) include the following species: *Drymarchon corais, Crotalus adamanteus, Coluber constrictor, Lampropeltis getulus.*

As mentioned under Seminole Field, care should be exercised in assigning forms from these deposits to the Pleistocene, since at least Stratum 3 suggests considerable admixture with much more recent faunas.

Vero Beach, Stratum 2

There is very extensive literature on this deposit. The more important papers are by Sellards (1916, 1919, 1937), Simpson (1929a), Cooke (1928, 1941, 1945), Hay (1926, 1923), Gidley (1929a, 1929b) and Weigel (1958). The deposit is located near Vero, St. Lucie County; elevation about 21 feet. Only Statum 2 is included in this section. Stratum 3 is discussed later under "Pleistocene and or Recent Deposits".

The only snake known from Stratum 2 is *Natrix* sp.

Florida Lime Company, Pit 2

A limestone quarry approximately two miles south of Ocala, Marion County, Florida (R 22 E, T 15 S, Sec. 28); elevation about 84 feet. The known snake fauna consists of *Crotalus adamanteus,* as originally reported by Gilmore (1938).

Winter Beach

This locality is located in a marl pit near Winter Beach, St. Lucie County, (R39E., T32S., S½ of NE¼ Sec. 3), approximately 5.6 miles north of the original Vero locality; elevation about 3 feet. The stratigraphy of the deposit is as follows (after Winters, personal communication):

6.	Muck, arenaceous, probably containing mainly mangrove refuse	4 in-1 ft
5.	Banded limestone, quartzose and argillaceous sand	3 in-6 in
4.	Marl, of fresh water and perhaps in part of brackish origin	5 ft
3.	Coquina, much quartz silt and fine sand near the top, becoming relatively quartz-free one foot down	2 ft
2.	Marine shell bed	2½ ft
1.	Oolitic-looking quartz sand	?

Fauna.—Bed 4, near the top of the marl contains the following invertebrates: *Helisoma, Menetus, Polygyra, Deroceras.* Near the base of Bed 4 the following invertebrates are found: *Euglandina,* and *Anadera.* In addition, the following reptiles (exclusive of the snakes) and amphibians are known from the same zone: *Bufo* sp., *Rana* sp., *Siren lacertina, Anolis carolinensis, Ophisaurus ventralis, Kinosternon* sp. The snakes include: *Coluber constrictor, Farancia* or *Abastor, Natrix sipedon, Liodytes alleni, Thamnophis sirtalis.*

Bed 3 contains the following forms: *Helisoma, Polygyra, Gastrocopta, Helicodiscus, Strobilops, Donax,* Gomphotheriidae, *Megatherium.*

The dominant elements of Bed 2, a marine stratum, are: *Donax* and *Mulinia.* Many other marine forms are also found in this stratum.

In addition to the above, the following mammals were taken from the spoil banks, and probably originated from near the contact between beds 3 and 4: *Megatherium, Equus, Holmsina, Boreostracon* (?), *Procyon*

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[5] The radiocarbon date of 82 BC ± 90 (Bullen, 1958) is obviously too young for the entire faunal assemblage of the Seminole Field localities, though it points out the fact that mixing has occurred.

lotor, Tapirus veroensis, Tanupolama and *Odocoileus.*

Correlation.—Winters suggested that the sediments and fossils are part of the Silver Bluff Terrace and that the "Pleistocene" mammals persisted in Florida until near the end of Silver Bluff time, perhaps as recently as 4,000 years ago. There are, however, some arguments contrary to this. The fauna is practically identical to that known from definite Pleistocene deposits, and there is no evidence of admixture of faunas, other than the possible Gomphotherid. Winters hypothesis suggests a rather recent period of deposition, and this may be correct. However, until more evidence becomes available it seems best to refer the locality to the Pleistocene on the basis of its contained fauna.

Paleoecology.—The stratigraphy of the deposit apparently suggests a retreating sea, with fresh water, or slightly brackish ponds near the beach and/or mangrove-covered shores. Bed 4 is of much more importance in the present study, since only from this bed have fossil snakes been obtained. The presence of *Deroceras* certainly suggests that at least during certain periods, this pond was entirely fresh water. The fresh water turtles and salamanders point to the same interpretation. The large number of *Anolis carolinensis* suggests a hammock, or at least heavily wooded areas nearby. Similar ecological conditions can be found in a number of areas along both the east and west coasts of Florida, both behind the dunes and behind the mangrove swamps.

D. *Pleistocene and/or Recent Deposits*

Under this heading are gathered all of those deposits for which field data are inadequate, or localities which seem to indicate admixture of fossils of different ages. In no cases are the fossils from these deposits used as the basis for interpretations of faunistic changes, but only to substantiate such interpretations wherever possible. Many of these localities are considered here as at least partly equivalent to Stratum 3 of Vero, Melbourne, Seminole Field and other similar deposits. In all probability this stratum represents recent re-deposition of Pleistocene fossils, along with more recent remains of man and other animals. The conditions for its formation, as well as the somewhat complex stratigraphy of the deposits, makes for uncertainty that a given fossil specimen was not derived from older beds. Where the three strata are found along the coasts, it is frequently impossible to tell from which particular stratum a given fossil originates, since the contact between Stratum 2 and Stratum 3 is sometimes irregular. Unless Stratum 3 is found where Stratum 2 does not occur it will always be extremely difficult to exclude admixture of the faunas. To my knowledge, no such deposit has yet been located in Florida. Stratum 3 seems to occur only if Stratum 2 is present. Stratum 3 is always found along historically old, or Recent stream courses. The problem was admirably discussed by Cooke and Mossom (1929), Cooke (1945), and Simpson (1929a). Bullen and Winters (1953) discussed the age of this stratum at the Seminole Field locality, pointing out the difficulty encountered in complex beds of this type, and suggested the possibility of admixture. Radio carbon dating of material from Seminole Field (82 BC ± 90, Bullen, 1958) indictates that the interpretation of Recent age for Stratum 3 is, in all likelihood, correct. Weigel (1958) discussed the same stratum at Vero in some detail.

A large number of reptiles, birds, and mammals have been termed Pleistocene in the literature that actually came from Stratum 3 of several localities in peninsular Florida. In the present paper reptiles and amphibians reported from this bed have been excluded from the list of the Pleistocene herpetofauna of the state. In certain cases these records will be discussed under particular fossil species.

Snakes reported from Stratum 3 (after Brattstrom) or without precise data as to horizon include (after Hay, 1917; Gilmore, 1938; Brattstrom, 1953a): *Farancia abacura, Coluber constrictor, Drymarchon corais, Lampropeltis getulus, Pituophis melanoleucus, Natrix* sp., *Crotalus adamanteus.*

In addition to Stratum 3 of the Vero, Seminole and Melbourne localities, certain other deposits in Florida must be classified as Pleistocene and/or Recent.

Crystal Springs, Pasco County

A large freshwater spring located in southern Pasco County (R 21 E, T 26 S, Sec. 35); elevation about 70 feet. Fossil vertebrates have been taken from the bed of this spring under conditions similar to those to be described for Itchatucknee Springs.

The only snake reported from this deposit is *Agkistrodon piscivorus* (Brattstrom, 1953a).

Wakulla Springs, Wakulla County

A large freshwater spring located about 4.5 miles west of Wakulla County (R1W, T2S, Sec. 7, unsurv.); elevation approximately 20 feet. A number of fossil vertebrates have been found along the run of this spring in the past, including one, or possible two proboscidian skeletons (Sellards, 1916; Hay, 1923; Simpson, 1929a). Apparently these remains were taken from the reddish clay over which the spring run flows. The snakes reported from this locality are: *Natrix* sp. and *Thamnophis* sp. (Brattstrom, 1953a).

Hornsby Springs, Alachua County

A large freshwater spring located 1.8 miles north of High Springs, and 0.9 miles east of U. S. Highway No. 25 (R 17 E, T 7 S, SW¼ Sec. 27); elevation about 62 feet. Vertebrate fossils have been found both on the bottom of the stream just down from the head spring, and from the cavernous opening of the spring itself. Some of these fossils were obtained from depths greater than 50 feet. The fossils are dark mahogany to black in color and not well mineralized.

The following snakes are known from this locality: *Farancia abacura* (or *Abastor erythrogrammus*), *Natrix sipedon, Natrix taxispilota, Thamnophis sirtalis, Crotalus giganteus.*

From the nature of the fossils and the mode of deposition, likely the fossils were laid down under conditions similar to those existing at the site today. However, the smaller fossils have been shifted around considerably, so that mixing of Pleistocene and Recent faunas has certainly occurred.

Rock Springs, Orange County

This is a spring about 4 miles south of Mt. Plymouth (R 28 E, T 20 S, Sec. 11); elevation about 35 feet. Fossil remains of Pleistocene vertebrates have been taken from the bed of the stream about 100 yards below the head. The stream flows over the limestone facies of the Hawthorne formation and the deposit contains Miocene, Pleistocene, and Recent vertebrates. The list of mammals from this deposit is rather extensive and the material is being studied by Mr. James Gut. Preservation is good. The fossils are buff to light brown in color, rather than black or dark reddish brown as in most fossils collected from stream beds in Florida.

Fossil snakes from this deposit include *Drymarchon corais* and *Crotalus giganteus.* In washing the bottom deposits numerous light gray non-mineralized elements of *Rana* sp. were found. These are probably Recent. The *Drymarchon* and *Crotalus* vertebrae exhibited the same color and degree of mineralization as the extinct mammals.

Wekiwa Springs, Levy County

A large freshwater spring approximately 12 miles southwest of Williston, Levy County (R 17 E, T 13 S, Sec. 33); elevation about 32 feet.

The known vertebrates from this locality include several extinct Pleistocene forms. Only one snake vertebra has been collected from the stream bed. It apparently represents either *Farancia abacura* or *Abastor erythogrammus.* Obvious Pleistocene-Recent admixture has occurred along the stream bottom.

Itchtuckanee Springs, Columbia County

A series of large springs approximately 5 miles northwest of Fort White (R 16 E, T 6 S, W½ Sec. 7); elevation about 70 feet. The fossil snakes taken at this locality have been washed out of the banks and the bed of the Itchtuckanee River and its tributaries which flow in a southerly direction to empty into the Santa Fe River. Although extinct Pleistocene mammals have been found along almost the entire course of the Itchtuckanee River, and along its springfed tributaries, the vast bulk of the fossil snake material has come from four small areas along the upper reaches of the river.

The river and its tributaries provide an excellent opportunity to study the degree and nature of the admixture of Pleistocene and Recent fossils in a stream bed. There are ample undisturbed Pleistocene beds along the banks of the stream, constantly being eroded by the swift current. The present stream is inhabited by many animals and their bones may be seen scattered along almost the entire bed. The water is clear and studies on rate of mineralization and color change could be carried out easily.

Locality A.—This is a small tributary running into the pool of the head spring of Jug, or Blue Spring, which continues to the Itchtuckanee River, a few hundred feet downstream. The smaller tributary heads in a spring depression approximately one-half mile north of Jug Spring. A section along the tributary is given below.

4. A black, highly organic soil	6 in - 1 ft
3. A white to gray, soft and loose clay near the water level (this stratum is more or less localized, since it has not been found in exploratory trenches a few hundred yards north)	1-2 ft
2. A soft, loose grayish clay containing considerable mineralized remains of vertebrates, as well as leaves, twigs, barks, etc., which in places may be peat-like. There are numerous small cross-bedded lenses of white sand and broken shells	2-3 ft
1. Ocala limestone	?

A section a few hundred feet down the small tributary and along the west bank of the stream formed by Jug Spring is as follows:

5. A black, highly organic soil at water level	1 ft
4. A white to gray, loose and soft clay without fossils	1 ft
3. A bedded layer of sand, grayish clay, bits of bark, twigs, etc., and containing some fossils and a vast quantity of broken and eroded *Goniobasis* shells	1-1½ ft
2. A fairly homogeneous layer of grayish clay containing many fossils, some *Goniobasis* shells and small pieces of vegetable matter	3-8 ft
1. Ocala limestone	?

Highly mineralized, black-colored remains of snakes are abundant along the bottom of the tributary and along the stream formed by Jug Springs before it enters the Itchtuckanee River. They have been found in place in Bed 2 of the first section given above, and in beds 2 and 3 in the second section.

A third locality, also containing numerous remains of snakes, is found in the cavernous opening of Jug Spring, from depths of 35 to approximately 60 feet below the surface. Here the vertebrae occasionally are found in place in a freshwater marl at a depth of about 35 feet. The marl bed, approximately one foot thick, overlies a soft orange to reddish clay. Fossil remains are found in both the marl and the clay. The bones are heavily mineralized, and reddish-brown in color; not black, as those found on the bed of the stream near the surface. The remains in this cavern evidently have not been moved too much, since fairly complete turtles and alligators are found imbedded in the marl.

Remains of Recent animals undoubtedly have been washed into the large opening of Jug Spring, but whether they could be carried into the deeper parts of the grotto is unknown. Many limbs and twigs of trees, large, practically pure masses of loose *Goniobasis* shells, and large numbers of mineralized bones of various species of animals, both brown and black in color, are found directly under the shaft-like opening at a depth of 35 feet. In addition, two flint projectile points, some bottles, and a steel gig also were found in this same place. That mixture has occurred, at least directly below the opening, is obvious.

Locality B.—This area, called the "flats" by the local inhabitants, is a place where the Itchtuckanee River broadens considerably, forming a wide, marshy tract, but with deeper channels through which the river flows with considerable current. Some snake vertebrae have been found in this area, as well as remains of many extinct larger vertebrates. A section through the bank of the largest and deepest channel is as follows:

3. A soft brownish, oozy clay silt, at, and slightly above water level, which is apparently Recent in age. This stratum contains bones in varying degrees of mineralization, which display colors ranging from gray to black	1-2 ft
2. A fairly loose grayish clay that becomes more compact downwards, containing a considerable number of fossils which are black to reddish-brown in color. Farther down the stream this same bed contained an articulated half of a *Sternotherus* shell, gray in color and showing no indications of mineralization. Just a few inches from this same shell, and also deeply buried in the same matrix was the worn molar tooth of a *Mastodon americanus*	7-10 ft

1. A sandy clay to pure sand, grayish to white in color, in which the sand grains have a definite tendency to become cemented together. This bed contains remains of *Mastodon* and *Equus*, etc. The sand is frequently tightly cemented arcund the bone, and is usually stained a rusty color where it touches it. The fossils from this zone are usually dark gray, brown, or buff in color, and at times may even approach a lavender hue 3 ft

The flood plain along the upper reaches of the river is well developed, being level, and a few feet above the surface of the water. On either side of this plain the Ocala limestone is exposed at higher elevations, so that apparently the river may have been much broader at one time. This period of increased flow may, or may not, be correlated with the rise of sea level in Pamlico time. Abandoned stream valleys are sometimes found in the northern part of the peninsula (Edwards, 1949). The soil of the flood plain is highly organic. Under this is found a peat layer, or a loose grayish clay. Both contain twigs and many pieces of mineralized black to dark mahogany-colored bones. These seem to represent re-worked beds, containing fossils derived from older deposits (Bed 1 of the last section given?), as well as containing the remains of animals living in and around the stream at the time of re-deposition. This stratum is Bed 2 of the first, second, and third sections given above. It is intermediate in age between the very recent deposits and the Pleistocene beds exposed in the flats on the bottoms of the deepest holes (Bed 1 of Locality B). Bed 2 contains numerous remains of *Odocoileus*, which are less common in the lower, probably Pleistocene stratum.

Thus, the situation in the Itchtuckanee River is similar to that in many of the coastal localities, where Stratum 3 contains the remains of leaves, twigs, etc., and the remains of Pleistocene vertebrates, and more recent forms, including man. This same stratum also contains remains of deer, and is sometimes termed the "deer zone". Bed 2 of the Itchtuckanee River is probably equivalent to, or nearly contemporaneous with, Stratum 3 of Vero and Seminole Field. Bed 1 of Locality B may be equivalent to Stratum 2 of the coastal localities, which is generally considered to represent a substage of the Wisconsin. As in the coastal deposits the upper fossil-bearing bed contains fossils from the lower bed, as well as a fauna of its own. Unfortunately they cannot be completely separated.

The Itchtuckanee River area and the Vero and Seminole sites are also similar in that modern streams are flowing over the older Pleistocene bed, re-working and re-depositing these fossils. Above this is a Recent soil.

Further work conducted at Itchtuckanee River in a detailed scale, preferably with the mammals, would probably increase our knowledge of the fauna at the close of the Pleistocene considerably.

Fauna.—Simpson (1929a, 1930b) provided a list of the mammals of the Itchtuckanee River complex. In addition, there is a very large avian and herpetological fauna represented in the deposits. Unfortunately, most of the material collected to date was taken from Bed 2. The earlier collections described by Simpson (1939b) were taken from the grayish muck (Bed 2). Lately the majority of the fossils have been found by diving and washing the bottom deposits. The fossil birds from this series of localities are being studied by Mr. John McCoy, Jacksonville University. The snakes now known from this complex series of beds and localities include the following: *Coluber constrictor, Drymarchon corais, Pituophis melanoleucus, Elaphe guttata, Elaphe obsoleta, Lampropeltis getulus, Heterodon platyrhinos, Farancia abacura* (or *Abastor erythrogrammus*), *Natrix sipedon, Natrix cyclopion, Natrix taxispilota, Liodytes alleni, Thamnophis sirtalis, Crotalus adamanteus.*

Paleoecology.—Clearly, much of the material from the river and the various springs represents the fauna of a former stream, probably similar to the present one. However, certain faunal elements strongly suggest a still water environment. This would indicate that perhaps large portions of the stream formed flat, marshy areas, as are now present at the "flats"; or, may indicate that at one time, or several times, the river became ponded, or with flowage reduced to a bare minimum. A thin bed of marsh peat has been found just below the surface in the flood plain of the small stream flowing into the head pool of Jug Spring. It is underlain with a bed representing an old stream channel deposit from which a few fossil bones have been taken. The peat bed may be the stratum from which remains of the pond forms originate.

Haile I

Locality B.—This deposit is located in a lateral fissure 12 feet below the original ground level, at the bottom of a steeply-walled sinkhole, approximately 250 feet north of Locality A. Both deposits are near the edges of an abandoned limestone quarry near the town of Haile, Alachua County (R 17 E, T 9 S, SE¼ of SW¼ Sec. 24); elevation about 84 feet.

The fossil-bearing zone is composed of a thinly bedded gray to reddish-brown sand, containing many small eroded pieces of Ocala limestone. The bones collected from the fissures are buff to grayish in color and not heavily mineralized. Preservation is very delicate.

Fauna.—No extinct vertebrates have been found in this deposit. The snake remains collected from the fossiliferous zone represent the following species: *Coluber constrictor, Drymarchon corais, Thamnophis sirtalis, Sistrurus miliarius, Crotalus adamanteus.*

Correlation.—The relative lack of mineralization and the absence of extinct forms suggests that the locality represents post-Pleistocene time. Both *Sylvilagus floridanus* and *S. palustris* are known from this deposit. The latter is more common than the former. As far as is known, *S. palustris* does not occur in the immediate area today. The species is an inhabitant of marshes and swales. The present conditions in the area of the deposit are almost the opposite; freshwater ponds or lakes being restricted to very small, usually steeply-walled sinkholes. Surface streams are at present absent.

Paleoecology.—Since so few remains are as yet available from this deposit little can be said concerning the conditions during sedimentation. Most of the vertebrates that have been collected from the fossil beds live in the same area today. However, the large numbers of *S. palustris* present in the deposit suggest conditions considerably more moist than those at present.

IV. SKELETAL ELEMENTS AS DIAGNOSTIC MATERIAL IN THE IDENTIFICATION OF FOSSIL SNAKES

Practically all the various elements comprising the skeletons of snakes have been found as fossils. Cranial and mandibular elements, though found only occasionally, are considered by most workers as the most important, though little is known concerning the extent and nature of variation in these elements in modern species. That the skull has been used by many workers in classification, at least of the major categories, is well known. Studies based on comparative morphology of the teeth, cranium, mandible, and even various aspects of the head musculature all assist in identifying fossil snake crania.

Vertebrae and ribs are the commonest remains of fossil snakes. Yet, few studies have dealt with the diagnostic value of these elements as a tool in paleontology. The increasing interest in fossil snakes makes such studies imperative. The only detailed study was that by Johnson (1955), who examined the degree of inter- and intracolumnar variability of vertebrae. Of considerable importance is that he found no correlation between vertebral shape and "modes of existence". Snakes that are related have similar vertebrae, while unrelated types with similar modes of existence have dissimilar vertebrae.

One could argue that the modes of existence assigned to certain species by Johnson are over-simplified. However, the fact remains that interspecific differences in snake vertebrae appear to reflect phyletic relationships.[6] This fact, assumed by earlier workers, was never demonstrated as fully as in Johnson's study. However, as useful as Johnson's paper may be, it does not aid in the identification of vertebrae; it simply suggests that these elements can be used in the identification of snakes, even on the basis of isolated elements.

Individual snake vertebrae are notoriously difficult to identify. This is partly because the degree of individual variability and specific differences have never been investigated thoroughly. Still, these elements have been used in identification of fossil snakes

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[6] Vertebrae of unrelated species may resemble one another, though these similarities are usually superficial, and the basic type is generally easily discernible.

in studies as early as those by de Rochebrunne (1880, 1881) and Owen (1839, 1841, 1849) (notwithstanding Cuvier's remark in 1824 that all non-boids are so similar that they cannot be identified on vertebrae alone). Most of the earlier studies on fossil snakes dealt with these remains on a generic level, though specific names were frequently used. This is evident when one examines the lists of the comparative material available to these workers. Even Johnson's study dealt with variation on a generic level.

Data on ontogenetic, geographic and individual variation in vertebrae of snakes have never been published. In the present paper variational data are given only when they are useful in the identification of species found as fossils in Florida. Until considerably more skeletal material becomes available than is now found in collections, an analysis of vertebral variation, even in only the New World Colubridae, must be deferred.

The study of snake vertebrae has become specialized with a descriptive technique and terminology somewhat different from other branches of paleontology. Unfortunately, usage of some of the terms is variable. Simpson (1933) attempted to standardize this terminology. In some instances subsequent authors misinterpreted certain terms and some useful characters have never been described from a comparative standpoint and deserve names.

The meaning of terms used in this paper is given below. The list has been adapted mainly from Owen (1849, 1852), de Rochebrunne (1881) and Simpson (1933). Emendations are made wherever necessary. Authorities are given only when there is some question regarding the interpretations given by different workers.

Accessory Process: A spine-like process which, if present, projects laterally from just below the prezygapophysial articular facets, and is more or less continuous with the buttress of the prezygapophysial process. It is a term restricted to the snakes, and not to be confused with the *processus accessorius* of Soemmetring (1726), which is synonymous with the mammalian anapophysis of Owen (1852). The term mammillary process is to be restricted to a special low, rounded boss found only in mammalian vertebrae (Gadow, 1933).

Centrum: The actual body of the vertebrae, below the neural canal and between the condyle and the cotyle.

Condyle (or, condylus): The approximately hemispherical posterior articular surface of the centrum.

Cotyle (or, cotylus): The anterior concavity of the centrum, for the reception of the condyle of the preceding vertebra. This is the glenoid cavity of many other authors, a term which should be avoided, unless used in connection with the shoulder girdle.

Diapophysis: A term restricted to the upper member of a pair of rib articulations found on either side of the centrum (see paradiapophysis).

Epizygapophysial Spine: A new term to be restricted to a small spur, present in only some colubrid and crotalid genera, located on the posterior edge of the neural arch, just above the postzygapophysial articular surfaces (= the "spur-like process" of Gilmore, 1938).

Interzygapophysial Ridge: The more-or-less horizontal ridge connecting the pre- and postzygapophysial buttresses (= the "ridge", lateral ridge, or zygapophysial ridge of other authors).

Hypapophysis: A median ventral process (double in the Paleophidae), either spine-like, or sigmoid-shaped, compressed, or bulbous. It is found in the anterior vertebrae of all snakes. In typhlopids, aniliids, boids, xenopeltids, and most colubrids it becomes reduced to a haemal keel of variable shape in the middle and posterior vertebrae. It may be present in a weakly developed condition along the posterior portion of the precaudal vertebral column. The haemal keel may be secondarily well developed in certain colubrid and boid genera, so that it becomes deep and plate-like, as in *Hypsirrhinchus* and perhaps even in the Xenoderminae. A well-developed spine is found throughout the column in some colubrids (Xenoderminae, Natricinae, Acrochordinae and Sibynophiinae), the Elapidae, Hydrophiidae and Crotalidae. The matter is obviously far more complex than one in which the structure can be said to be either present or absent, since in some cases it is surely secondarily derived. Such secondarily derived structures must, however, still be termed a hypapophysis. It is important that in the future authors describe the shape of these structures if they are present, and not simply state that they are, or are not present.

Laminae (= *lames* of de Rochebrunne, 1881; *tectum* of Hoffstetter, 1939): The upper portion of the neural arch, above the interzygapophysial ridges.

Lymphapophyses: Laterally paired ventral processes occurring only in the caudal region.

Neural Arch: The two plates arising from the top of the centrum, surrounding the neural canal, and meeting at the midline. The two dorsal halves of the plates above the interzygapophysial ridges are the laminae, and the two plates below the ridges and in contact with the centrum are the pedicles.

Neural Canal: The canal for the spinal cord.

Neural Spine (= *apopyse épineuse* of de Rochebrunne, 1881, and the *neurapophysis*, at least in part, of many authors): A dorsal process, either present or absent, spine-like or plate-like, arising at the midline of the neural arch.

Paradiapophysis (= *diapophysis* in the broad sense of Owen, 1849, 1852; Simpson, 1933; Gilmore, 1938; *diapophysis* plus *parapophysis* of Hoffstetter, 1939; *tubercles costaux* of de Rochebrunne, 1881; *transverse process* of many authors, and the *synapophysis* of Remane, 1936): A paired process of the sides of the centrum, below the prezygapophysis and near the lip of the cotyle. On the precaudal vertebrae they bear ribs, and on the caudal vertebrae they are variously produced. As pointed out by Remane (1936) and others the term diapophysis is incorrectly used when applied to this structure, since it is obviously composed of two elements; the upper diapophysis, and the lower parapophysis. The term paradiapophysis is more descriptive than Remane's term, synapophysis.

Parapophysis: The lower articular facet, and its body, of each paired rib articulation (paradiapophysis) on both sides of the centrum.

Parapophysial Process (= *parapophysis*, in part, of Hoffstetter, 1939; *apophysis transversus inferieures* of de Rochebrunne, 1881, "projection of diapophysis" of several authors): A small process, present or absent. If present variously developed, extending downwards and forwards from the anteroventral portion of the main body of the parapophysis.

Pedicular Foramen (= nutritive foramen, in part, of other authors): A foramen in the pedicle of each neural arch, variable in position and size.

Postzygapophysis: One of a pair of posterior processes bearing articular facets facing downward for the articulation with the prezygapophysis of the following vertebra.

Prezygapophysis: One of a pair of anterior processes arising from near the junction of the neural arch and the centrum on each side, bearing articular facets facing upward.

Prezygapophysial Buttress: The thickened, ridge-like strengthening structure on the antero-lateral portion of the prezygapophysial process.

Pterapophysis Abel, 1919 (= *flügelfortsätze* of Janensch, 1906; *aliform process* of Simpson, 1933; Gilmore, 1938 and Hoffstetter, 1939): Restricted to the high, wing-like, or spine-like process found at the posterior portion of the neural arch in the members of the family Paleophidae.

Subcentral Foramen (= nutritive foramen, in part, of previous authors): Paired foramina located on the ventral surface of the centrum on either side of the haemal keel or spine, of variable shape and size.

Subcentral Ridges Gilmore, 1938 (= *lateral ridges* of Hoffstetter, 1939, the "rounded ridge" or "buttress" of Simpson, and the central ridges of other authors): A pair of ridges on the ventro-lateral surface of the centrum, converging posteriorly, running from the diapophysial portion of the paradiapophysis posteriorly toward the condyle.

Subneural Process (= *epapophysis* of Gilmore, 1938, a term which should be restricted to the lateral rib articulations on the inner ridge of the horizontal septum in fishes, according to Remane, 1936): A median ridge, or horizontal spine-like process on the floor of the neural canal.

Zygantrum: A mortise-like depression on the posterior part of the neural arch above the neural canal, articulating with the zygosphene of the following vertebra.

Zygantral Foramen: One of a pair of foramina of variable shape and size, located within the zygantrum, somewhat dorsal and lateral to the zygantral articular surfaces.

Zygosphene: A somewhat wedge-shaped median anterior process from the union of the neural arch above the neural canal, bearing two articular facets facing outward and downward for articulation with the zygantrum of the preceding vertebra.

Of prime importance in the identification of fossil vertebrae is a cognizance of the relative constancy of certain of the vertebral characters, at least in certain parts of the column. Johnson (1955) showed that such constancy definitely occurs. The characters which have been used in this study are listed below, with abbreviations used throughout this publication.

Accessory Processes (ap) — Their shape, extent, direction from above and from the front.

Centrum (c) — Its shape, ridges, processes, length (cl) and width (cw, = naw).

Condylus (co) — Whether it is on a neck or not, oblique or not, its length (col).

Cotyle (ct) — Its shape, height (cth), width (ctw).

Haemal Keel (h) — Its shape, length, position and absence or presence.

Hypapophysis (h) — Its general shape, how far back it projects, and how far forward it can be traced.

Interzygapophysial Ridges — Their general shape and degree of development.

Neural Arch (na) — Its height (nah) its width (naw) and whether or not it is provided with either pterapophyses or epizygapophysial spines.

Neural Canal (nc) — Its general shape, its anterior height (nch) and its greatest width (ncw).

Neural Spine (n) — Its general shape, whether it overhangs posteriorly or anteriorly, or both; whether it is flattened or sharp on its dorsal edge; whether or not it is ornamented on its dorsal edge, and how; its height at the anterior edge (nh), its length along the dorsal edge (nlu) and its shortest length (nls).

Paradiapophysis — Whether or not there are one or two articular facets, their shape and position, whether the paradiapophysial process extends below the centrum, and its shape.

Postzygapophyses (po) — Their general shape, their width (pow), length (pol), the width between the outer edges of the articular facets (po-po), the length from the posterior edge of the postzygapophysis to the anterior edge of the prezygapophysis (po-pr).

Prezygapophyses (pr) — Their general shape, their width from the outer edges of one articular surface to the outer edges of the opposite surface (pr-pr); the shape, length and direction of the accessory processes.

Zygosphene (z) — Its shape from above, from the front, its width (zw), angles of the articular surfaces from the front (z°) and its thickness dorsoventrally (zt).

Figure 1 illustrates the observed variability in the shape of many of the vertebral processes and structures, and gives the descriptive terminology used throughout this paper in referring to particular shapes.

Many ratios have been found of considerable importance in identifying fossil snake vertebrae. The most important of these are

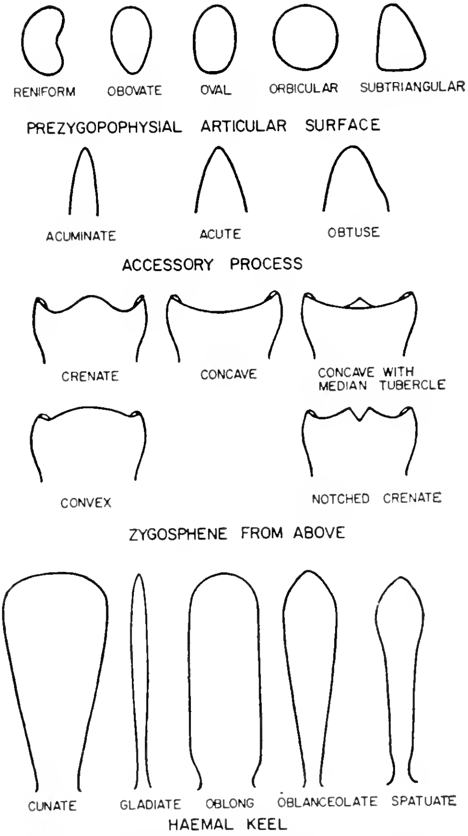


Figure 1. Range of variability in shape of some of the vertebral structures, with the descriptive terms used throughout this paper in referring to shape.

listed below. Others will be found in the diagnoses of certain genera and species.

cl/naw
nlu/nls
naw/po-po
cl/col
nlu/nh
cl/zt
ctw/cth
cl/nlu
zw/naw
nlu/cl
pr-pr/pr-po
zw/cl
cl/zw
pr-pr/naw

Some of the characteristics used in this study to identify fossil vertebrae are constant throughout large numbers of species, distinguishing families and genera; whereas others are confined to particular species. Though there are no well defined vertebral characters to distinguish some genera at the present time, certain species within these closely related genera are sometimes identified easily. This is particularly true in such genera as *Coluber* and *Mastigophis*, *Lampropeltis* and *Elaphe*, *Natrix* and *Thamnophis*, etc. Subgeneric categories are frequently recognizable. Subfamilial levels may or may not be evident; and this is sometimes extended even to the family level.[7] In some cases it is possible to distinguish some well differentiated subspecies where these possess definable vertebral types. These and other points will be more fully discussed under the generic and species descriptions.

The foregoing discussion suggests the possibility of utilizing vertebral characters in studying the relationships of the modern species. Such a study is greatly needed, especially with a view towards the determination of higher systematic groupings, at least within the large family Colubridae.

Of all the vertebrae on the column the middle precaudal series (thoracic of some authors) are the most constant in their structure, and are thus best for purposes of identification. However, the isolated nature of most fossil snake vertebrae, and the similarity between middle and posterior precaudal elements introduces a problem which is not always as adequately solved as might be wished. I have based the identification of middle precaudal vertebrae mainly on the relative size of the neural canal. For this reason the middle precaudal vertebrae are discussed at greater length than any others in the descriptions to follow. Unless stated otherwise, all diagnoses, descriptions or tabu-

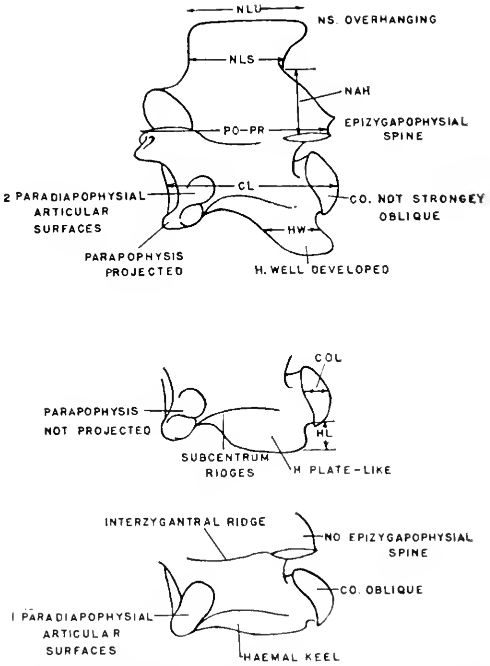
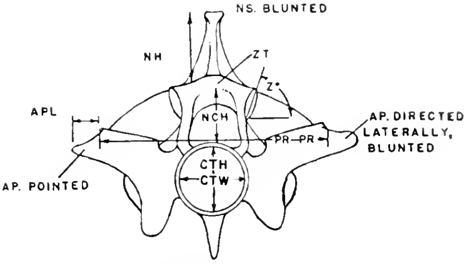
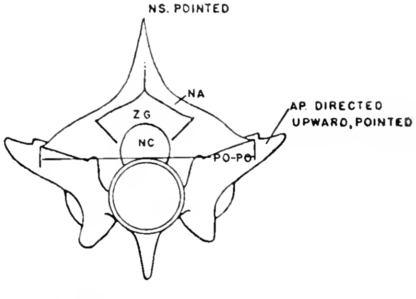


Figure 2. Measurements and terminology used in describing certain vertebral structures, lateral view.



ANTERIOR VIEW



POSTERIOR VIEW

Figure 3. Measurements and terminology used in describing certain vertebral structures, anterior and posterior views.

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[7] Such as the inability to separate the Elapidae and Hydrophiidae, or the anterior vertebrae of certain colubrid and elapid genera.

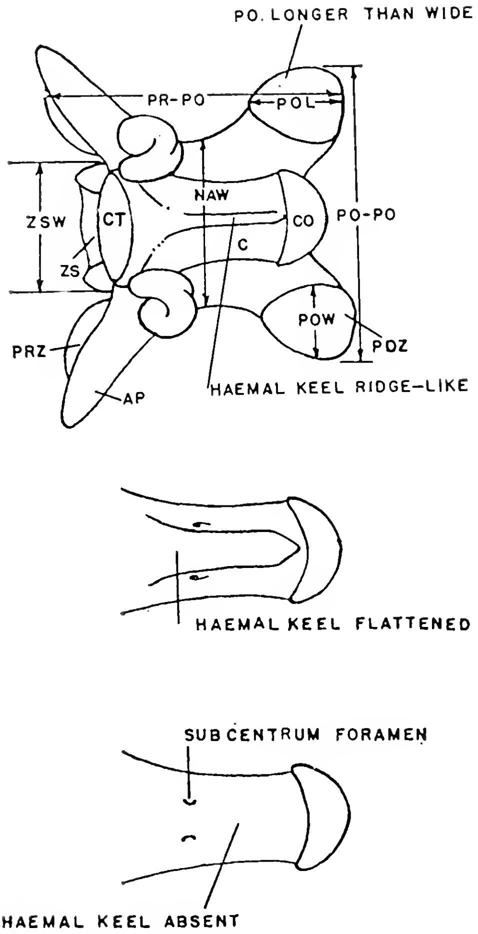

Figure 4. Measurements and terminology used in describing certain vertebral structures, ventral view.

lar data are based on these elements in adult specimens.

Certain measurements were made on both modern and fossil vertebrae so that detailed, objective comparisons could be made. All measurements were taken from single, isolated vertebrae with a micrometer with an altered anvil. In very small vertebrae the measurements were made with an ocular micrometer. Figures 2 to 4 show the various measurements found of some importance in identifying fossil snakes, or in comparing individual vertebrae of extant species of snakes.

V. TAXONOMIC DESCRIPTIONS AND DISCUSSIONS

When identification is based on a specialized knowledge, as is required in the present study, it is desirable to include a key to facilitate identification for those less familiar with the characteristics and variability of the organisms involved. The fact that the degree of variability in snake vertebrae is not too well known lessens the value of such a key. Furthermore, there is every reason to believe that additional undescribed species will be found in the Mio-Pliocene of Florida. Inter- and intracolumnar variation is known to be considerable. Vertebral differences between many genera and species are minor. Such factors tend to complicate any key which is produced. Nevertheless, several keys are included below, since I feel the time saved the worker identifying the material justifies whatever faults the keys may be found to contain with further study. The keys are relatively simple and definitive. They should enable the worker to identify all of the described fossil snakes of Florida from Miocene and Pliocene deposits. A key to the Pleistocene snakes is not given, because I feel that the Pleistocene snake fauna of Florida eventually will be found to contain all of the Recent species found in the area, as well as some extra-limital forms. The large number of species which would have to be included and their variability makes such a key unwieldly. At present a key is being devised which will identify any Pleistocene or Recent snake of southeastern United States to generic level. Beyond this the worker will have to turn to Recent comparative material. The following keys are presumably based on middle precaudal vertebrae.

A. KEY TO THE KNOWN MIOCENE SNAKES OF FLORIDA

1. Neural spine higher than long; centrum length to 8 mm. *Pseudoepicrates stanolseni* (fig. 8, p. 160)

   Neural spine as long as, or longer than high; centrum length to 4 mm. 2.

2. Centrum long, narrow (cl/naw 1.86 - 1.99); hypapophysial spine extending posteriorly to, or beyond the base of the condylus *Paraoxybelis floridanus* (fig. 39, p. 189)

Centrum shorter, wider (cl/naw 0.82-1.25); hypapophysial spine not extending to, or beyond base of condylus, but shorter .... 3.

3. Neural spine not extending posteriorly to the posterior edge of the laminae of the neural arch; small, centrum length about 2 mm. ..*Anilioides minuatus* (fig. 12, p. 164)

Neural spine extending posteriorly to the posterior edge of the laminae of the neural arch; small to medium, centrum length to 4 mm. .... 4.

4. Neural spine thickened in cross section and along dorsal edge; small, centrum length about 2 mm. .... *Calamagrus floridanus* (fig. 11, p. 162)

Neural spine thin, plate-like, not obviously thickened in cross section, or along dorsal edge; medium in size, centrum length to about 4 mm. .... 5.

5. No accessory processes, zygosphene straight to concave from the front; cotyle distinctly oval (ctw/cth 1.15-1.36); haemal keel without a notch anteriorly; centrum wider (cl/cw 0.82-0.98) .... *Ogmophis pauperrimus* (fig. 10, p. 160)

Accessory processes well developed; zygosphene convex from the front; cotyle more rounded (ctw/cth 1.04-1.11); haemal keel with a notch anteriorly; centrum narrower (cl/cw 1.25-1.36) .... *Pseudocemophora antiqua* (fig. 36, p. 187)

B. KEY TO THE KNOWN PLIOCENE SNAKES OF FLORIDA

1. Vertebrae very small, centrum length about 1.5 mm; zygosphene markedly crenate from above .... *Diadophis elinorae* (fig. 18, p. 170)

Vertebrae larger, centrum to 5 mm; zygosphene straight to concave from above .... 2.

2. Vertebrae relatively small, centrum length about 2.5 mm; neural arch short, wide; prezygapophyses small, oval; neural spine presumably low, long; zygosphene very slightly concave from above and from the front .... *Stilosoma vetustum* (fig. 35, p. 186)

Vertebrae larger, centrum length to 5 mm; neural arch longer, narrower; prezygapophyses larger, oval to subtriangular; neural spine almost as high as long; zygosphene strongly concave from above and either convex or concave from the front .... 3.

3. Zygosphene concave from the front; prezygapophysial articular surfaces subtriangular; neural arch and spine longer; subcentral ridges moderately developed .... *Heterodon brevis* (fig. 22, p. 174)

Zygosphene convex from the front; prezygapophysial articular surfaces oval or subrectangular; neural arch and spine shorter; subcentral ridges well developed .... *Paleofarancia brevispinosus* (fig. 16, p. 169)

C. *Family Boidae*

1. *Subfamily Boinae*

Description.—Middle vertebrae usually without marked compression or aberrant development of processes; usually with oval cotyle, but frequently rounded; neural spine variable, but usually higher than long, always with a straight anterior edge, frequently thickened, sometimes thinner and plate-like; one paradiapophysial articular surface, sometimes faintly indented medially, hypapophyses present anteriorly, absent posteriorly;[8] haemal keel usually gladiate to oblanceolate, rarely greatly flattened, sometimes almost absent.

This family consists of about 20 extant genera with a wide distribution through the tropical and subtropical parts of the world. However, during parts of the Cenozoic the range of this family embraced portions of even Canada and Patagonia. Their known history extends to at least the Eocene in both the New and Old Worlds.

A large number of Tertiary fossil snakes have been placed in this family. Perhaps some do not belong here. According to Gilmore (1938), "the term Boidae as used paleontologically is much broader and more inclusive than as used by modern herpetologists." There is, however, little reason why this should be true when complete vertebrae

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[8] Except in the genera *Tropidophis* and *Trachyboa* (placed in the subfamily Tropidophiinae by Brongersma (1951), and *Bolyeria* and *Caesarea* (placed in the subfamily Bolyerinae by Hoffstetter (1946), where the middle and posterior vertebrae are provided with hypapophyses. Romer (1956) incorrectly states that *Sanzinia* possesses hypapophyses throughout the column.

are available. The vertebrae of snakes are different from one group to another, and the familial relationships based on individual vertebrae usually are easily demonstrated, at least in modern snakes. However, in fossil vertebrae processes are usually eroded or broken so that the shape of important characters cannot be determined always.

A further difficulty experienced in the case of even the modern members of the family Boidae is that vertebral characters which will hold for all of the genera are difficult to define. This is mainly due to the fact that, based on vertebral elements alone, the family is composed of several groups; reflecting only in part, the current subfamilial distinctions within the family.

A classification of the family Boidae based on vertebral characters is obviously beyond the scope of this paper, though a more detailed study of these characters probably will show that such a classification is possible. The Eryciinae and Bolyerinae are in fact based on vertebral characters.

The fossil boids of Florida obviously represent at least two distinct groups, and perhaps three. *Pseudoepicrates*, a new genus from the Miocene of Florida, apparently is representative of a group including the modern genera *Boa, Constrictor, Epicrates, Eunectes, Sanzinia* and related forms. *Boavus*, a fossil North American Eocene genus, apparently belongs to this group. *Paraepicrates* of the same period is definitely closely related. The vertebrae in all of these genera are relatively short, rarely longer than wide. The cotyle is large, usually oval (at least in all juveniles and in the anterior vertebrae of larger specimens). The condylus is strongly oblique. The neural spine is always short, usually high, and rounded or oval in cross section. The second group represented in fossils from Florida possess vertebrae which are longer (occasionally longer than wide). The cotyle is usually rounded and directed more posteriorly. The neural spine is generally lower, longer, and frequently platelike in cross section. The paradiapophysial articular facets usually are more indented medially, and more projected ventro-anteriorly, but not below the level of the centrum. Both *Calamagras* and *Ogmophis* belong to this group, though the latter possesses some rather distinctive characters. The modern genera *Lichanura* and *Charina* may belong here.

Two genera of boids previously were reported from the Miocene of Florida. These are *Ogmophis* and *Neurodromicus* (Vanzolini, 1952). To these should be added *Calamagras*. In the case of *Neurodromicus* additional comment is necessary.

"*Neurodromicus*"

Cope (1873) described *Neurodromicus dorsalis*, the type species, on the basis of one anterior vertebra from the Oligocene *Oreodon* beds of northeastern Colorado. This genus generally has been placed close to the vipers; Hay (1902) placed it in the Crotalidae, Williston (1925) in the Viperidae, and Gilmore (1938) in the Crotalidae provisionally, awaiting additional material. Vanzolini (1952) placed the genus in the family Boidae on the basis of fossil material from Thomas Farm, Florida. Hoffstetter (1953) stated he thought the type vertebra of *N. dorsalis* represented an anterior thoracic vertebra of a colubrid, possibly even Recent because of its slight mineralization in a deposit where mineralization is usually markedly noticeable. After examining the type I am inclined to agree with Hoffstetter that the specimen is not a fossil, but a Recent vertebra that became mixed with material from the fossiliferous bed.

The type (AMNH 1599) has always been considered an anterior vertebra. This is indicated by the very large neural canal, the high neural arch, the weak accessory processes, the shape of the zygapophysial articular surfaces and the relatively short centrum. The important question is its family relationships.

The cotyle of young boids is oval in shape. With growth this structure becomes more rounded (cth ctw in a very young *Constrictor constrictor* 24 inches long, mean 0.73; in an adult 7½ feet long, mean 0.96). According to Vanzolini the anterior vertebrae of definite boids from Thomas Farm are similar to those of the type of *Neurodromicus*. The most anterior vertebra from this deposit seems to represent a snake about 4 feet long, and the cotyle is decidedly oval. In the type of *Neurodromicus* the cavity is round, yet it represents a smaller specimen. This relationship should be reversed if the type of *Neurodromicus* is a boid.

The anterior vertebrae of elapids, most colubrids, as well as *Sistrurus* and *Agkistro-*

don among the crotalids, have a rounded, rather than an oval cavity.

The type specimen of *Neurodromicus* seems to represent a snake about 3 feet long. Many genera of Colubridae are excluded as possibilities on size alone.

A complete tabulation of the data comparing all the possible snake genera to which *Neurodromicus* might be assigned is of no practical value. It is sufficient to point out that the neural spine length along its base and its height, as well as the ratio of the centrum length divided by neural arch width, exclude all possibilities among the colubrids now inhabiting northeastern Colorado. Comparison of measurements and the resulting ratios of the anterior vertebrae of an adult *Sistrurus catenatus* with those obtained from the type show the closest possible agreement with the 39th vertebra (Table 1). The shape of this element and that of the type are identical. The species has not yet been reported in the immediate area at the present time, though this is apparently very close to the western limits of its range. For those reasons *Neurodromicus dorsalis* is tentatively referred to the synonymy of *Sistrurus catenatus*.

TABLE 1.

Comparison of certain measurements (in mm) and ratios between the type of Neurodromicus dorsalis and the 39th vertebra of an adult Sistrurus catenatus

Measurements and Ratios	*N. dorsalis*	*S. catenatus*
Centrum length (cl)	3.81	3.80
Centrum width (naw)	3.12	3.18
cl/naw	1.22	1.20
Cotyle width (ctw)	1.98	2.16
Cotyle height (cth)	2.01	2.03
ctw/cth	1.00	1.06
Zygosphene width (zw)	2.69	2.74
cl/zw	1.41	1.39
naw/zw	1.16	1.16

However, Vanzolini correctly assigned the fossil remains from the Thomas Farm to the family Boidae. As boids, these snakes cannot be assigned to the genus *Neurodromicus*.

Since no name is available for these boids, the name *Pseudoepicrates* is proposed. In vertebral shape they are approached most closely among Recent boid genera by *Epicrates*, and among fossil genera by *Paraepicrates*.

PSEUDOEPICRATES, *gen. nov.*

Diagnosis.—A Miocene snake representing the subfamily Boinae on the basis of the absence of hypapophyses in the posterior dorsal vertebrae, and the presence of zygosphene-zygantral articulations in the caudal vertebrae. It differs from most members of this subfamily in being smaller and in possessing a longer centrum. From the modern genus *Epicrates* it differs mainly in possessing a higher neural spine. *Eunectes*, *Boa*, and *Constrictor* have precaudal vertebrae in which the centrum is decidedly shorter. It is distinguished from *Loxocemus* in having a longer centrum, a high neural spine, and a smaller zygosphene. From the modern genera *Charina* and *Lichanura* it differs chiefly in being much larger and in having vertebrae which are shorter in proportion to their length. In addition, the neural spine is shorter and higher in proportion.

From the fossil North American boid, *Boavus*, it is distinguished by its longer centrum and more pronounced subcentral ridges. The fossil genera *Calamagras* and *Ogmophis* are smaller and possess vertebrae with lower, longer neural spines. It differs from *Paleryx* in possessing a longer centrum, and from *Paleopython* and *Gigantophis* in being smaller and in having a longer neural spine along its base. It differs from *Paraepicrates* in having a shorter neural spine along its base.

Genotype. — *Pseudoepicrates stanolseni* (Vanzolini).

Vanzolini (1952) described two species of *Neurodromicus* (*Pseudoepicrates*) from the Thomas Farm Miocene, Gilchrist County, Florida. These are *stanolseni* and *barbouri*. Of the former he had seven available specimens, and of the latter five. Later collections at the same deposit have brought 34 additional specimens to light. Comparison of all of the material now available indicates that only one species is involved. On the basis of page priority *stanolseni* becomes the valid specific name.

Vanzolini distinguished the two species by the following characters: the small tubercle on the lip of the zygosphene, the angle formed by the buttress of the prezygapophyses and the paradiapophyses, the width of the neural arch, the length of the neural spine and the thickness of the zygosphene. Furthermore, the size of the two species is different, *stanolseni* being the smaller. All of these differences are demonstrated easily in the proportional changes associated with ontogeny.

A character given considerable weight in the original description is the shape of the articular surfaces of the prezygapophyses. In *barbouri* these surfaces are more triangular, and have their anterior edges perpendicular to the axis of the centrum. In *stanolseni* the surfaces are more rounded and the anterior edge is not straight and perpendicular to the axis of the centrum. This character is a function of the age of the individual. Older specimens of many species of snakes attain relatively larger and more angular prezygapophysial articular facets than are found in the young. This is particularly true of the boids in general, and is well illustrated in figure 5.

The zygosphene of *barbouri* is thicker than that of *stanolseni*. This is a character that also shows considerable ontogenetic change. Young boids have relatively thin zygosphenes, while adults have these structures very heavily developed. The ontogenetic change in this character in a modern boid is shown in figure 5, and in the available specimens of *P. stanolseni* in figure 6.

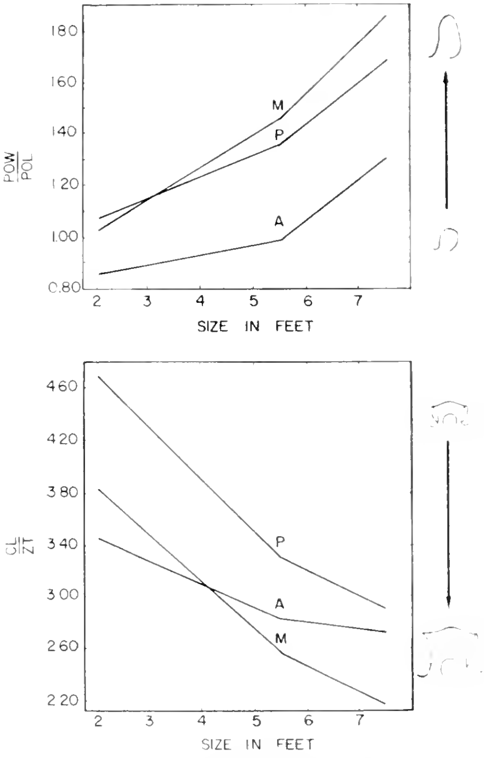

Figure 5. Top: Ontogenetic change in the thickness of the zygosphene. Bottom: Ontogenetic change in the shape of the prezygapophysial articular surface. All data from *Constrictor constrictor*. A = anterior, M = middle, P = posterior precaudal vertebrae.

Young specimens of *Constrictor constrictor* have a neural spine which is very short, while in adults this process becomes relatively longer for its height. The anterior edge of the zygosphene is never provided with a tubercle in young specimens, whereas this structure frequently becomes quite evident in many species with increasing size. Vanzolini stated that the angle formed by the prezygapophysis and the paradiapophysis differs in the two species (p. 456) and referred to his figures 1 and 2. However, such differences are to be expected when comparing vertebrae from the anterior and middle precaudal regions in any snake, even within the same column. The accessory process is usually shorter and directed downward in anterior precaudal vertebrae, whereas it is usually more well-developed, and projected laterally in more posterior vertebrae. He also stated that the height of the neural arch differs in the two species and referred to his figures 8 and 3. Again, such differences are to be expected between anterior and middle precaudal vertebrae.

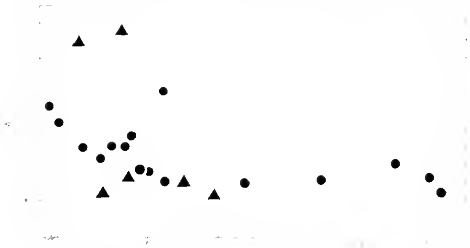

Figure 6. Ontogenetic change in the thickness of the zygosphene of *Pseudoepicrates stanolseni*. Triangles represent vertebrae with hypapophyses, dots represent vertebrae without hypapophyses.

Of the many measurements and ratios which have been gathered from the available specimens of *Pseudoepicrates* from the Thomas Farm, no differences are found which are not easily explained on the basis of ontogenetic change or vertebral position. Furthermore, identical differences can be demonstrated in several species of modern boids when comparisons are made between the ratios of the vertebral characters in different-sized individuals of the same species. Accordingly, *stanolseni* and *barbouri* are here considered conspecific.

Pseudoepicrates stanolseni (Vanzolini)

Diagnosis.—Since this genus, as now known, is monotypic, the specific characters remain those of the genus.

Holotype.—MCZ 1977, an anterior precaudal vertebra.

Type Locality and Horizon.—Thomas Farm, Gilchrist County, Florida, Lower Miocene, Arikareean, Hawthorne formation.

TABLE 2.

Some measurements (in mm) and ratios obtained from the available vertebrae (N = 23) of Pseudoepicrates stanolseni, gen. nov.

el	2.59-8.66
naw	3.61-10.72
el/naw	0.68-1.00
pow	1.22-3.51
pol	1.04-4.27
nlu/nh (middle)	0.99-1.32
eth	1.83-5.23
etw	2.16-5.92
etw/eth	0.99-1.35
zw	2.08-5.61
nh	1.55-3.79
zw/el	0.57-0.88
nlu/nh	0.70-1.32
po-pr	4.50-12.19
pr-pr	5.54-15.77
pr-pr/po-pr	1.22-1.29
nlu	1.63-5.26
nls	1.60-4.70
nlu/nh (ant.)	0.70-1.07

It is known only from the type locality, where it is apparently most numerous in the Boulder Bar deposit.

Table 2 shows the variation in certain of the vertebral ratios of this species. Figure 7 shows the intra-columnar variation in vertebral shape based on individual vertebrae which are assumed to come either from one individual, or from a series of specimens of comparable size. Figure 8 illustrates a typical middle precaudal vertebra.

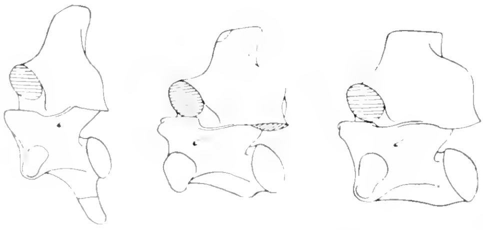

Figure 7. Intracolumnar variation in the vertebrae of *Pseudoepicrates stanolseni*.

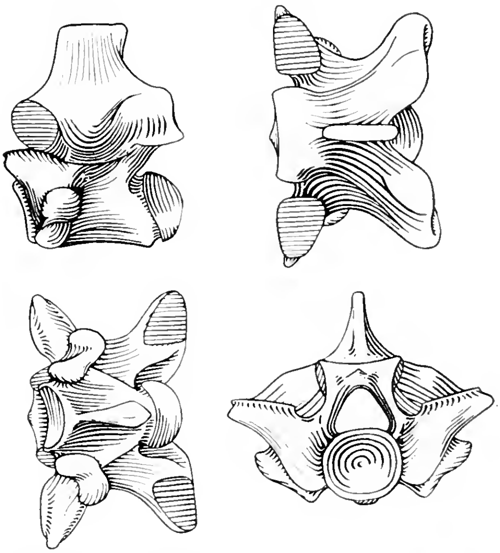

Figure 8. A precaudal vertebra of *Pseudoepicrates stanolseni*.

Ogmophis Cope

Of considerable interest is the fact that Vanzolini described a new species of an apparently semi-fossorial snake, *Ogmophis*, from the Florida Miocene. This genus formerly was known from the Lower Oligocene to Upper Miocene of western United States. A number of additional vertebrae are now available, permitting the original species description by Vanzolini to be supplemented considerably.

Ogmophis pauperrimus Vanzolini

Holotype.—MCZ 1976; a precaudal vertebra.

Type Locality and Horizon.—Thomas Farm, Gilchrist County, Florida, Lower Miocene, Arikareean, Hawthorne formation.

Description (largely after Vanzolini).—Centrum short to moderately long, tapering little, with a distinct pair of subcentral ridges; neural arch flattened, distinctly emarginated between the pre- and postzygapophyses; neural spine low, occupying three-quarters of the length of the neural arch (in middle precaudal vertebrae), reaching a little beyond its posterior margin; zygosphene flat, a little wider than the cotyle, with or without a small tubercle on the anterior surface of the lip, convex to crenate from above, convex from the front; neural canal relatively broad and high, subneural process distinct; prezygapophyses markedly oblique to the midline; zygantrum wide and low; cotyle oval; paradiapophyses auriculiform; condylus slightly oblique with a distinct neck; hypapophyses of middle precaudal vertebrae reduced to a low haemal keel, usually gladiate to oblanceolate, well developed into a ventral spine anteriorly. A typical mid-precaudal vertebra is shown in figure 9.

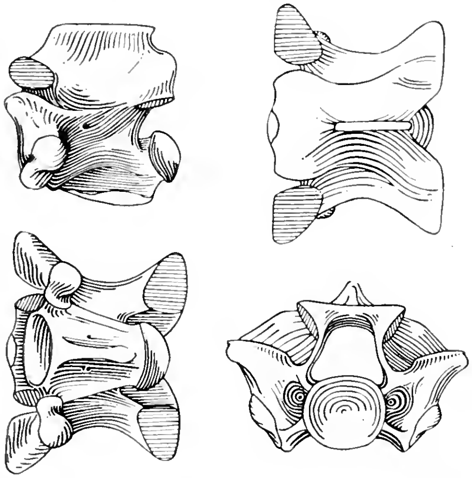

Figure 9. A precaudal vertebra of *Ogmophis pauperrimus* (UF 5131).

In addition to the holotype, 16 vertebrae are now available in the collections of the Museum of Comparative Zoology and the University of Florida. A series of 8 vertebrae from juvenile specimens in the University of Florida collections are also placed in this species. All of the additional material was collected from the Boulder Bar at the type locality.

The additional material allows some comparison of different portions of the vertebral column. These variations are shown in figure 10. Ratios of vertebral measurements are given in Table 3.

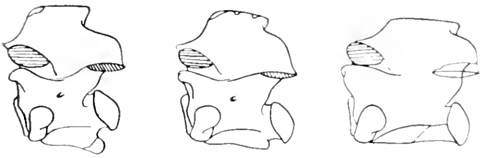

Figure 10. Intracolumnar variation in the vertebrae of *Ogmophis pauperrimus*. From left to right: an anterior precaudal (UF 5137), anterior-middle precaudal (UF 5139), middle precaudal (UF 6312).

TABLE 3.
Measurements (in mm) and ratios obtained from the available specimens (N = 13) of Ogmophis pauperrimus

cl	2.11-3.48
naw	2.13-4.22
cl/naw	0.82-0.98
pow	1.02-1.37
pol	0.89-1.37
pow/pol	0.94-1.20
ctw	1.25-2.69
cth	0.94-2.31
ctw/cth	1.15-1.36
zw	1.80-3.07
zw/cl	0.76-0.91
po-pr	2.36-4.70
pr-pr	4.42-6.45
pr-pr/po-pr	1.38-1.80
nlu	1.09-2.06
nh	4.57-1.05
nlu/nh	1.45-2.52

Remarks.—The genus *Ogmophis* generally has been placed close to *Calamagras*. As originally described by Cope (1873) the two genera are presumably separated by the presence or absence of subcentral ridges extending posteriorly from the diapophyses. However, as Gilmore (1938) pointed out, this character does not separate the two genera satisfactorily.

The type of *Ogmophis* (*oregonensis*) is lost. According to Cope's figure, it is, in many characters, distinct from other species placed in the same genus. Thus the neural spine, which leans forwards and is as high as long, the strong interzygapophysial ridges, etc., separate *O. oregonensis* from *O. arenarum*, *O. compactus* and *O. pauperrimus*. Such differences are of generic level in modern snake vertebrae. Thus there is some doubt that *Ogmophis*, as now recognized, forms a natural group. The presence of one paradiapophysial articular facet, at least in those specimens where it has not been eroded, suggests boid affinities. The type species, *oregonensis*, and *arenarum* definitely have only one articular surface. The surfaces are somewhat eroded in the available specimens of *compactus*, and in most of those of *pauperrimus*. Where they are present, they are somewhat intermediate between a condition which is usually described as either one or two surfaces. Obviously the character is variable in the group currently recognized as the Colubridae; the intermediate condition being uncommon, but certainly present in some genera. *Ogmophis pauperrimus* is similar to *compactus* in possessing two well-defined ridges running from the lateral edges of the glenoid cavity, outward and downward to the paradiapophyses. Such well developed ridges are practically non-existent in the known fossil boids. As far as is known they are absent in all modern members of this family.

The neural spine is broken off in the only available specimen of *compactus*, but a fairly long spine is suggested by the length of the break itself. In *pauperrimus* the neural spine is longer and lower than in any other boid, with the possible exception of *Epicrates inornatus*. The neural spine in *pauperrimus* is rather thin, not flattened dorsally, and thick as in most boids, including *Epicrates inornatus*. Some of the characters of *O. pauperrimus* are rarely found in the Colubridae, and may even be somewhat characteristic of the anilids. Whether or not *pauperrimus* and *compactus* actually belong in the genus *Ogmophis*, or even among the Boidae is a point which will have to await more complete, and preferably articulated material. It is more probable that they have been placed in the correct family than that they have been placed in the correct genus. The Florida species *pauperrimus* is left in *Ogmophis* for the present.

2. *Subfamily Erycinae*

Calamagras Cope

The genus *Calamagras* appears close to the modern boid genera *Charina* and *Lichanura* (a view apparently shared with Hoffstetter, 1955; Brattstrom, 1958, and Hecht, 1959). This seems indicated by its small size, the tendency for a more elongate centrum, a lower neural spine (generally), a rounded rather than oval cotylus, etc. The vertebrae of *Lichanura roseofusca* show agreement with those of *Calamagras angulatus* in many regards (as has already been indicated by Brattstrom, 1958).

According to Gilmore (1938), the genus *Calamagras* is composed of three species: *murivorus*, *angulatus*, and *talpivorus*. The types of *murivorus* and *talpivorus* were examined during the course of this study.

Calamagras truxalis Cope (1873) was referred to *C. murivorus* Cope (1873) by Cope (1884). Gilmore (1938) followed this arrangement. However, examination of the zygosphene from the front in the types of both species indicates considerable differences; *murivorus* is characterized by a concave zygosphene, while in *truxalis* it is convex. In modern forms differences of this magnitude are generally characteristic of species. Until a fossil column is found in which both conditions are present it seems best to retain *truxalis* as a valid species.

Gilmore (1938) suggested also the possibility that the vertebrae assigned to *C. talpivorus* may really represent more posterior vertebrae of *C. murivorus*. This seems reasonable, since the slight differences which are supposedly characteristic of the two species are demonstrated easily along the vertebral column of almost any modern snake. However, it seems best to retain *talpivorus* as a distinct form until intermediate vertebrae are actually found.

Gilmore (1938) suggested also that *C. angulatus* may represent a different section of the column from which the type of *murivorus* originated, and the former thus may be synonymous with the latter. However, *angulatus* is well distinguished on the basis of a number of characters. *Calamagras primus*, a distinctive species, was described from the Eocene of Wyoming (Hecht, 1959).

In addition to the species mentioned above, known from western United States, two vertebrae have been found at the Thomas Farm which are tentatively placed in this genus. The two specimens are distinct. The first may be known as:

CALAMAGRAS **FLORIDANUS**, *sp. nov.*

Diagnosis.—A small Miocene boid, possessing a short, thick, truncated neural spine, similar to *C. angulatus* in the shape and angle of the interzygapophysial ridge, but differing from that species in the shorter neural spine (nlu/cl—0.56 in *angulatus*) and the sharper hypapophysial, or haemal keel. The short neural spine is found also in *C. talpivorus* (nlu/cl—3.93), but the shape of this structure in the two species is quite different.

Holotype.—UF 6150, collected by Walter Auffenberg, 1954; a middle precaudal vertebra.

Type Locality and Horizon.—Boulder Bar, Thomas Farm, Gilchrist County, Florida; Lower Miocene, Arikareean, Hawthorne formation.

Type Description.—(fig. 11). A somewhat fragmentary precaudal vertebra with the zygosphene missing, and a part of the left postzygapophyses broken. Centrum short, triangular from below, with a median haemal keel, which is gladiate-shaped, not well-defined anteriorly, but extending from the cotyla to the base of the condylus, which is directed posteriorly. The right paradiapophysis is not abraded, possessing one articular facet, parapophysial process faintly projected anteriorly and downward; subcentral ridges present, but not sharply developed, extending from the diapophysis toward the condylus, but not reaching it. Neural arch low, without epizygapophysial spines; postzygapophysis triangular, much wider than long; prezygapophysial processes not projected as an accessory process; neural spine low, short, thick, truncated and thicker on the upper edge; interzygapophysial ridges not parallel to the axis of the centrum, but higher posteriorly, as in *C. angulatus*.

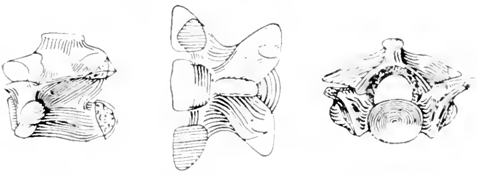

Figure 11. The type vertebra (UF 6150) of *Calamagras floridanus*, sp. nov., Thomas Farm, Gilchrist County. Hawthorne fm., Lower Miocene (Arikareean).

Only one vertebra can be referred clearly to this species. Table 4 gives some of the measurements and ratios obtained from the type specimen.

Figure 13 illustrates the hypothetical relationships of *Calamagras*, *Ogmophis*, *Charina*, *Anilioides*, and *Lichanura*. Brattstrom (1958, pl. 3) suggested a slightly different arrangement. Brattstrom's suggestion that *Cheilophis* is ancestral to this entire group is obviously incorrect in view of the presence of *Calamagras primus* in the Eocene. Furthermore, his view that *Cheilophis* is "questionable" seems unwarranted. The genus seems distinctive. This view apparently is held also by Hecht (1959).

TABLE 4.
Measurements (in mm) and ratios obtained from the type vertebra of Calamagras floridanus

cl	2.49
naw	2.97
cl/naw	0.84
nlu	1.40
nh	0.71
nlu/cl	0.56
nlu/nh	1.96
ctw	2.49
cth	1.35
ctw/cth	1.85

D. *Family Aniliidae*

Description.—Dorsal vertebrae without marked compression or aberrant development of processes; cotyle rounded to oval; neural spine long and low to absent; one or two paradiapophysial articular facets; hypapophyses present anteriorly, absent posteriorly; haemal keel usually greatly flattened, wide, sometimes absent.

The family consists of about 12 genera, though the relationships of most of these are not at all clear, and the family as currently defined (Romer, 1956) may be polyphyletic. Although the vertebral columns of all of the various genera now included in the family have not been studied there is some evidence that three vertebral types are represented in this group. (1) *Loxocemus*, (2) *Xenopeltis*, and (3) *Anilius-Cylindrophis-Uropeltis*. *Loxocemus* and *Xenopeltis* presently are placed in monotypic subfamilies. Their vertebrae are quite different. Without going into great detail, suffice it to say that *Loxocemus* possesses vertebrae similar to certain genera placed in the Boidae. *Xenopeltis* is transitional between more primitive types and the Colubridae, perhaps through parallel evolution. *Anilius* and *Cylindrophis* possess vertebrae which are basically similar. The neural spine is better developed in the former. *Anilius* is placed in a separate subfamily. *Cylindrophis* and *Uropeltis* are both referred to the Uropeltinae. *Uropeltis* possesses a much longer vertebra. The paradiapophysial articular surface is single, whereas it is double in all of the other genera mentioned above. It is suggested on the basis of vertebral form alone that the Uropeltinae may be polyphyletic. If the familial assignment is retained it may be best to exclude *Cylindrophis* and its close relatives from the Uropeltinae. Either another subfamily should be erected for *Cylindrophis*, etc., or it should be placed with *Anilius*. Before such changes are made the entire group should be restudied and vertebral characters should be considered as well as skull, pelvic and soft anatomy.

ANILIOIDES, *gen. nov.*

Diagnosis.—A small species of Miocene anilid, distinguished from all fossil and Recent members of the family by the presence of a keel on the dorsal surface of the zygosphene, being a continuation of the very short, presumably low, neural spine. In addition, the articular surfaces of the zygosphene project noticeably above the dorsal surface of that element. It differs from *Calamagras floridanus* in the same deposit mainly in not having the interzygapophysial ridge at an angle to the axis of the centrum when viewed from the side, and the neural spine does not extend posteriorly to the edge of the laminae of the neural arch.

Genotype.—*Anilioides minuatus*. sp. nov.

ANILIOIDES MINUATUS, *sp. nov.*

Diagnosis.—Sole known member of the genus.

Holotype.—UF 6151, a precaudal vertebra, collected by Walter Auffenberg, 1954.

Type Locality and Horizon.—Boulder Bar, Thomas Farm, Gilchrist County, Florida; Lower Miocene, Arikareean, Hawthorne formation.

Type Description.—(fig. 12, table 5). A middle, or possibly posterior, precaudal vertebra. Centrum short, somewhat triangular; subcentral ridges sharp, but diminishing posteriorly, not straight when seen from the side extending from the edge of the cotyle to the base of the condylus; paradiapophyses broken, but apparently with a short, parapophysial projection forwards and downwards; one (?) articular facet. Cotyle rounded; condylus directed upwards. Neural arch short, low, without epizygapophysial spines, with raised portions above the outer edges of the articular surfaces of the zygantrum; with part of the postzygapophyses broken off of both sides. The interzygapophysial ridges are sharp and well-developed. Prezygapophysial articular surfaces oval, the right one broken; zygosphene entire, straight to concave from the front, convex from above with the upper edge of the articular surfaces projected above the level of the lip of the zygosphene. Neural spine broken, but presumably low, definitely long, reaching from the base of the zygosphene to the posterior end of the neural arch, with a slight, but evident keel extending forward to the anterior edge of the zygosphene. A large pedicular foramen, moderate in diameter, is located just above the pedicular-central articulation.

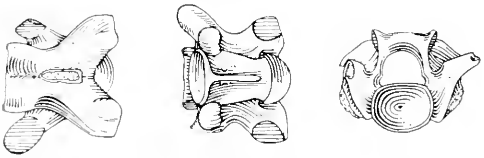

Figure 12. The type vertebra (UF 6151) of *Anilioides minuatus*, sp. nov., Thomas Farm, Gilchrist County. Hawthorne fm., Lower Miocene (Arikareean).

TABLE 5.

Measurements (in mm) and ratios obtained from the type vertebra of Anilioides minuatus

cl	1.96
naw	2.03
cl/naw	1.04
ns along base	1.37
zw	1.37
cl/zw	1.44
ctw	1.27
cth	1.14
ctw/cth	1.11
ns along base/zw	1.00

In addition to the type, a more fragmentary, smaller vertebra (UF 5895) is available from the same locality and horizon. The hypapophysial ridge, or haemal keel, is much more developed. The subcentral ridges stand out boldly from the ventral surface of the centrum. The zygosphene is more rounded from the front, and the dorsal keel of the zygosphene is much less evident. In addition, the pedicular foramen is much smaller. The element most certainly represents a posterior precaudal vertebra. Whether it represents this species, or another undescribed form, is unknown at the present time.

Although both of these specimens are small, they do not represent juvenile specimens. This is evident from the proportional size of the neural canal. In juvenile specimens of *Ogmophis pauperrimus* from the same locality the vertebrae themselves are not only longer, but they have proportionately larger neural canals. This is true of all of the juvenile specimens of modern skeletons examined to date. That *Anilioides minuatus* represents an adult specimen, or nearly so, is indicated also by the raised portions of the posterior edge of the neural arch, allowing the zygosphene of the following vertebra to fit into the rather highly placed zygantrum. On the basis of modern comparative skeletons these raised areas occur most often in adults, rarely in juveniles.

The presence of a low neural spine frequently is, though certainly not always, associated with fossorial habits. Presumably *Anilioides, Calamagras,* and at least *Ogmophis pauperrimus*, were semi-fossorial or at least highly secretive forms, as *Charina* and *Lichanura* are at the present time.

E. *Family Colubridae*

Anterior vertebrae always with simple hypapophyses though sometimes modified. Middle and posterior vertebrae either with simple hypapophyses, or the latter reduced to a haemal keel. Accessory processes evident, but of varying lengths. Zygosphene thin, of variable shape. Neural spine always thin, plate-like, never oval in cross section. Cotyle usually round, rarely distinctly oval. Condylus from nearly straight to oblique. Paradiapophyses usually well developed with two articulating surfaces.

If the vertebrae of the Boidae are difficult to identify as fossils, then individual vertebrae of the Colubridae are even more so. Fully three-quarters of the known modern snake genera of the world currently are recognized as belonging to this family. Many forms have become highly specialized and their vertebral form is divergent from one group to the next. Still, vertebral characters are conservative enough so that identification is sometimes difficult, or even impossible in certain cases. This is especially true in species or genera that are close externally.

The vertebrae of a large number of genera and species of modern colubrid snakes have been examined (118 genera, 190 species). Much of the variation in this family pertinent to the identification of the fossils from Florida is discussed under the appropriate form.

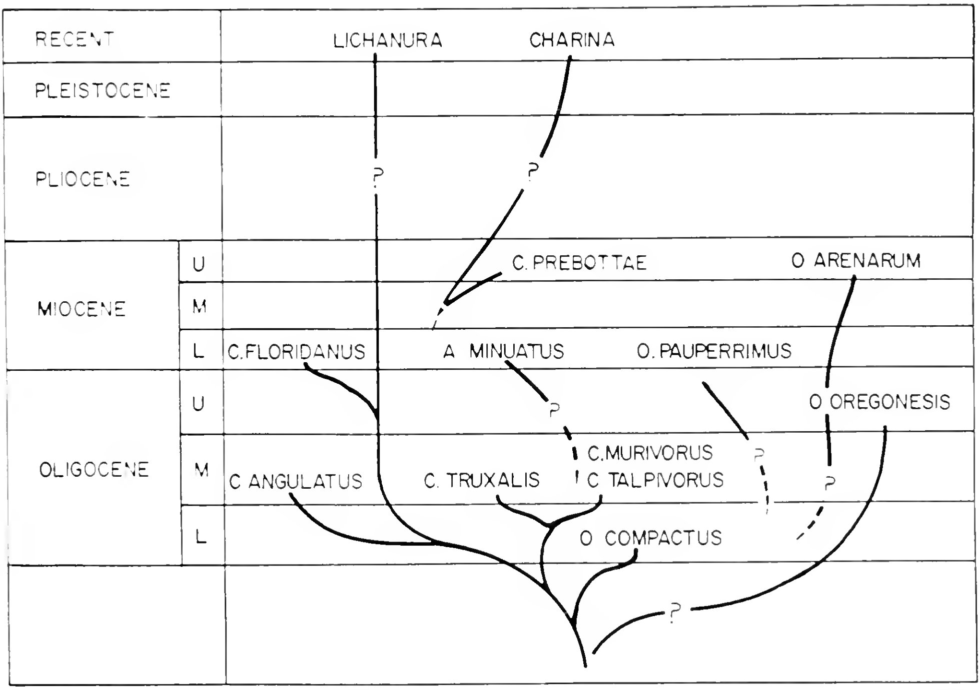

Figure 13. The hypothetical relationships of boids currently placed in the genera *Calamagras* and *Ogmophis*, and *Anilioides*, as well as the possible positions of the Recent genera, *Lichanura* and *Charina*.

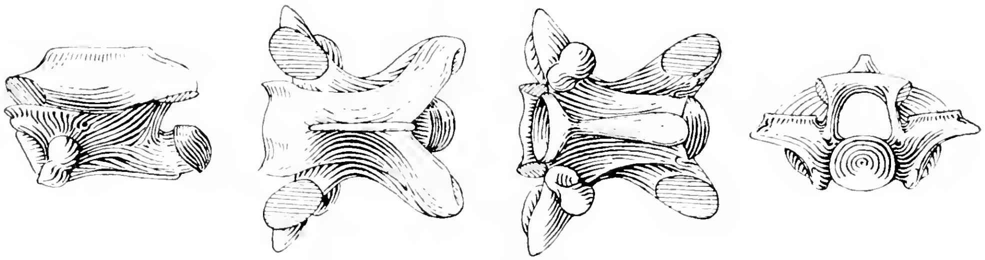

Figure 14. A precaudal vertebra of *Carphophis amoenus* (UF 6141) Reddick I B, Pleistocene (Illinoian ?).

1. *Subfamily Colubrinae*

Hypapophyses reduced to a low haemal keel.[9]

Carphophis amoenus Say

Description.—Typical colubrid vertebrae in which the anterior members are provided with a well developed hypapophysis. Those of the middle and posterior precaudal region are reduced to a low, broad, subspatulate, oblanceolate or cunate-shaped haemal keel, extending from just behind the cotyle to just before the condylus. The centrum is long and narrow, somewhat cylindrical, with fairly well developed subcentrum ridges, extending from the diapophyses at least half way to the condylus, and usually farther. Paradiapophyses with two well defined articular facets, not projecting strongly below and anteriorly. Condylus on a moderately long neck, moderately oblique, slightly to strongly oval. Neural arch long, low, without epizygapophysial spines. Neural spine low, long, occasionally flattened on its dorsal edge, extending forward slightly beyond the base of the zygosphene. Zygosphene crenate from above, convex the front. Prezygapophysial articular surface oval to obovate; accessory process short, acute, flattened dorso-ventrally, directed laterally from above.

The vast majority of the very small vertebrae from the Reddick I deposit can be assigned to this genus. Many vertebrae are provisionally placed here, exhibiting characters very slightly different from those of the modern comparative series. Well over 200 vertebrae are available from the Pleistocene of Florida. That these vertebrae do not represent younger and smaller specimens of larger species is indicated by the neural canal, which is not noticeably enlarged (fig. 14).

A number of modern genera of snakes have been examined and are similar to the fossil form. Genera which have been examined and which may be confused with *Carphophis* when only vertebrae are available are: *Diadophis* (*punctatus*, 4 skeletons examined; *amabilis*, 1 specimen examined), *Sonora* (*episcopa* 1), *Tantilla* (*coronata* 2, *nigriceps* 1, *eiseni* 1), *Enulius* (*flavitorquatus* 1), *Toluca* (*lineatus* 1), *Atractus* (*trilineatus* 1) and *Rhadinea* (*flavilata* 1). Three modern skeletons of *Carphophis amoenus* were examined for intra-columnar variation.

The fossil middle precaudal vertebrae are distinguishable from those of *Diadophis* mainly in having a lower and longer neural spine (nlu nh fossil form, 6.6-8.80; *Diadophis*, 2.2-5.0). In addition, the haemal keel is usually spatulate to cunate in the fossil vertebrae, depending on the amount of flattening, and gladiate to oblanceolate (but keeled) in the latter. From *Tantilla*, *Carphophis* is distinguished by having much stronger subcentral ridges and a much broader haemal keel, which is gladiate to slightly oblanceolate in the former. From *Toluca* it is distinguished, among other characters, by the convex zygosphene as seen from the top, and by the shorter neural spine, which does not project anteriorly beyond the base of the zygosphene. Differing from *Atractus* by a much wider and more rounded haemal keel. The fossil vertebrae differ from *Rhadinea* by the absence of such well defined subcentral ridges as are found in that genus, by a wider and more rounded haemal keel and by a thicker, shorter and more flattened prezygapophysial accessory process.

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[9] With the exception of certain forms, such as *Ninia* and possibly *Xenophis*, etc. in which these structures appear to have been secondarily developed.

The fossil vertebrae are even more similar to those of *Enulius* and *Sonora*. The fact that the fossil vertebrae obviously belong to a form not present in Florida today is of considerable interest. *Enulius*, *Sonora* and *Carphophis*, though similar in vertebral structure, reflect entirely different ecological conditions, and thus the determination of the fossil vertebrae takes on additional importance. Of the three genera, *Carphophis* seems the best choice on both ecological and zoogeographical grounds. The vertebrae of these three genera are, however, separable on structural bases, though the differences may be considered slight. *Sonora* differs from the fossils and *Carphophis* in having a shorter centrum (cl/zw 1.00-1.32 in *Sonora*, 1.54-1.88 in the fossil form). However, there are a number of species of *Sonora* which were not available for study, and perhaps some of these have longer centra. *Enulius* apparently differs from the fossils in having a longer neural spine in relation to the width of the zygosphene (nlu/zw 0.89-1.02 in *Enulius*, 1.54-1.88 in the fossil form). In size, and practically all the ratios, the fossil form is similar to the available specimens of *Carphophis amoenus*. There is, however, one character (pr-pr/po-pr) in which a fair proportion of the fossil specimens surpass the lower limits exhibited in the three modern skeletons available for study. The fossil material most certainly represents a much larger number of specimens than were available as modern specimens. The range of variation in this character is somewhat low in the comparative material, yet not exceedingly high in the fossils. The fossil vertebrae are thus assigned to *Carphophis amoenus*: some specimens provisionally until the degree of variability of the pr-pr/po-pr character is fully evaluated. Table 6 compares the ratios obtained from modern and Pleistocene vertebrae.

TABLE 6.
Comparative vertebral ratios in Pleistocene and Recent specimens of Carphophis amoenus

Ratios	Pleistocene (N=51)	Recent (N=38)
cl/naw	1.54-1.88	1.50-1.89
ctw/cth	1.04-1.39	1.08-1.32
pr-pr/po-pr	0.88-1.12	0.96-1.15
po-pr/cl	1.12-1.33	1.15-1.32
nlu/zw	1.20-1.36	1.21-1.46
nlu/nh	6.00-8.80	5.52-7.83
cl/col	4.86-5.82	4.24-5.50
naw/cw	0.88-1.18	0.97-1.17
cl/zw	1.80-2.10	1.86-2.20
pol/pow	1.80-1.92	1.75-2.01

The genus is now known from five Pleistocene localities in Florida: Arredondo I, A (UF 6260, one vertebra), Reddick 1, B (UF 5044, 5046, 6141, 6464, 6461, representing many vertebrae), Mefford Cave (UF 2556), and Haile II, B (UF 5778). Holman (1958) reported the genus from Sabertooth, or Lecanto Cave, Florida.

Farancia abacura Holbrook and/or *Abastor erythrogramus* Latreille

The vertebrae of these two genera are difficult, if not impossible to separate, so that the fossil elements from Florida cannot be assigned to one genus or the other with a degree of certainty. On paleoecological evidence there is every reason to believe that both are represented among the fossil vertebrae. The diagnosis given below will apply equally well to both *Farancia* and *Abastor*.

Description.—Anterior vertebrae provided with well developed hypapophyses, which are reduced to a haemal keel in the middle and posterior series. In the middle precaudal vertebrae the haemal keel is oblanceolate to spatulate, whereas it is usually cunate in posterior members. The centrum is subtriangular from below, moderate in length, and provided with strong subcentral ridges from the diapophyses to the condylus. Paradiapophyses well developed, with two articular facets, the diapophysial facet larger and more rounded than the parapophysial member. The parapophysial process is not projected downward or anteriorly. The condylus is fairly large, on a short neck, slightly oblique. The cotyle is rounded, not oval. Neural arch long, low, without epizygapophysial spines. Interzygapophysial ridges prominent, sharp. Neural spine overhanging anteriorly as well as posteriorly, its greatest length equal to, or greater than its height at the anterior edge. Zygosphene concave to straight from above, the same from the front. Prezygapophysial articular surfaces obovate, oval, or subtriangular. Accessory processes directed laterally to slightly downward from the front, laterally from above, obtuse, truncated, and usually flattened.

These genera are similar to some specimens of *Lampropeltis*, especially large adults of the latter. From this genus the former are separable by their more truncated accessory processes, the lower neural arch, which has a thinner zygantral roof and the somewhat lower neural spine.

Hay (1917) reported *Farancia* from Stratum 3 of Vero on the basis of a surangular. Gilmore (1938) questioned the authenticity of Hay's reference of the single element, then no longer available, to *Farancia.* Brattstrom (1953a) reported the presence of this genus in the Seminole Field based on five vertebrae in the American Museum of Natural History (AMNH 7177). I have seen the specimens and agree fully with the determination. Both of these localities are considered here Pleistocene and/or Recent.

A large number of vertebrae, as well as some cranial elements, are now available from additional localities in Florida. These include specimens from the Winter Beach locality (UF 5620) and Reddick I, B (UF 5811). From Itchtuckanee Springs about 40 vertebrae are available from Locality A, most of these coming from the tributary deposit. These are located in the University of Florida Collections. In addition, an occiput (UF 4288) is also available from the same locality. There are two vertebrae (UF 5909, 6263) available from Hornsby Springs. One specimen (UF 9883) was washed out of the cranial cavity of a skull of *Holmesina* from the bottom of Hornsby Springs. A small series of specimens is also available from Jug Springs (UF 5853, 5859, 5886, 5707).

Figure 15 illustrates a middle precaudal vertebrae. Table 7 compares the measurements and ratios of the vertebrae of *Abastor*, *Farancia* and the fossil series from Itchtuckanee Springs.

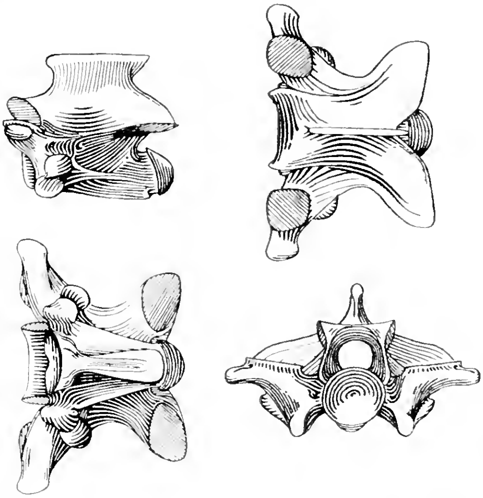
Figure 15. A precaudal vertebra referred to *Farancia* (or *Abastor*) (UF 5359) Itchtuckanee Springs, Pleistocene and/or Recent.

In addition to the remains referred to *Farancia* and/or *Abastor* a single vertebra from Lithia Springs seems close to these two genera, but is provided with characteristics distinct enough to warrant the erection of a new genus.

PALEOFARANCIA, *gen. nov.*

Diagnosis.—A Pliocene (?) colubrid which is apparently related to *Farancia* and *Abastor*, but differing from both in having a higher neural spine, which is less overhanging posteriorly.

Genotype.— *Paleofarancia brevispinosus*, sp. nov.

TABLE 7.

Comparison of vertebral measurements (in mm) and ratios in Farancia abacura, Abastor erythrogramus and the fossil specimens

Measurements and Ratios	*Farancia* (N = 61)	*Abastor* (N = 33)	*Fossils* (N = 138)
cl	5.66- 7.98	5.08-5.33	5.54- 7.75
naw	4.85- 7.80	4.19-4.65	5.11- 7.14
cl/naw	0.91- 1.14	1.01-1.22	1.08- 1.23
pr-pr	8.26-13.72	7.62-7.93	7.75-11.74
po-pr	6.50-10.03	6.17-6.86	6.93- 9.65
pr-pr/po-pr	1.09- 1.29	1.15-1.23	1.12- 1.26
zw	3.43- 5.59	3.35-3.71	3.63- 5.08
cl/zw	1.20- 1.71	1.41-1.58	1.38- 1.63
nlu	2.72- 5.99	3.58-3.96	3.94- 5.11
nls	2.62- 4.42	3.38-3.61	3.25- 4.19
nlu/nls	1.03- 1.42	1.00-1.22	1.05- 1.36
nh	1.55- 4.42	1.52-1.91	1.83- 3.89
nlu/nh	1.75- 2.28	1.78-2.30	2.02- 2.26

PALEOFARANCIA **BREVISPINOSUS**, *sp. nov.*

Diagnosis.—The specific characters remain unknown since the genus is monotypic.

Holotype.—A single precaudal vertebra collected by Samuel Telford, 1952. UF 5566.

Type Locality and Horizon.—The stream formed by Lithia Springs, Hillsborough County, Florida (R21E, T30S, Sec. 16). Alachua formation (as defined by Sellards, 1914), Middle Pliocene (?), Hemphillian.

Type Description.—A middle precaudal vertebra of a colubrid snake, in which the centrum is subtriangular when seen from below, possessing a well-defined haemal keel, which is thin, high, and somewhat spatulate-shaped. The centrum is moderate in length and provided with strong and well developed subcentral ridges, extending from behind the diapophyses to the base of the condyle, bending inward slightly near the condylus. The paradiapophyses are well developed, not projected, presumably with two articular surfaces, but which have been badly eroded. The condylus is moderate in size, directed posteriorly. The cotyle is round, not oval. The neural arch is moderate in length, without epizygapophysial spines. The interzygapophysial ridges are prominent, but not overly developed. The neural spine overhangs both anteriorly and posteriorly, its greatest length (nlu) slightly greater than its height at the anterior edge. Zygosphene convex from both the front and from above, prezygapophysial articular facets oval in shape. Accessory process broken on the right side, moderately developed on the left, not nearly so truncated as in *Farancia* or *Abastor*. directed slightly downward from the front, laterally from the top. Figure 16 illustrates the type specimen. Table 8 gives the more important measurements and vertebral ratios exhibited in the type.

TABLE 8.
Measurements (in mm) and ratios of the type vertebra of Paleofarancia brevispinosus, gen. nov., sp. nov.

cl	4.13
zw	3.30
pr-pr	7.96
nlu	2.44
naw	4.90
cl/zw	1.25
po-pr	5.53
nh	1.89
cl/naw	0.85
naw/zw	1.48
pr-pr/po-pr	1.44
nlu/nh	1.28

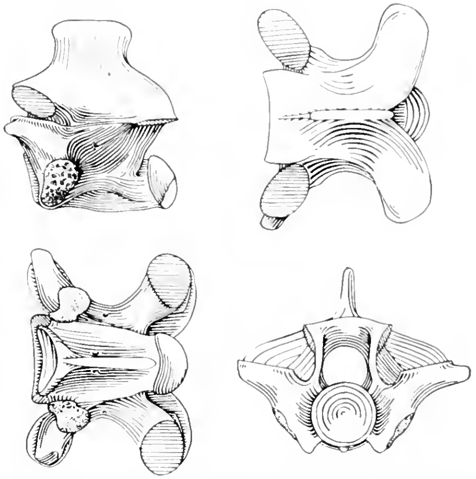

Figure 16. The type vertebra of *Paleofarancia brevispinosus* (UF 5566), gen. nov. et sp., Lithia Springs, Hillsborough County, Middle Pliocene ?.

The relationship of *Paleofarancia brevispinosus* is not clear, though it certainly seems close to both *Farancia* and *Abastor*. No vertebra definitely referrable to either of the modern genera is known from the Pliocene, so possibly *Paleofarancia brevispinosus* is ancestral to one, or both of them.

Diadophis Baird and Girard

Description.—Anterior precaudal vertebrae provided with well developed hypapophyses, which are reduced posteriorly to somewhat rounded haemal carinae, oblanceolate to subspatulate in shape, extending from the cotylus posteriorly to immediately in front of the condylus, ending in an acute point. Centrum subcylindrical to subtriangular, with rounded, usually rather faintly developed subcentral ridges, extending from the diapophyses posteriorly to near the condylus, sometimes less. Parapophyses somewhat projected, paradiapophyses with two articular facets. Condylus moderate in size, directed backward to slightly upward. Cotyle round to slightly oval. Neural arch moderate in length and height, without epizygapophysial spines. Interzygapophysial ridges evident, but not strongly developed. Neural spine long, overhanging posteriorly, and usually anteriorly as well, its greatest length much greater than its height along the anterior edge. Zy-

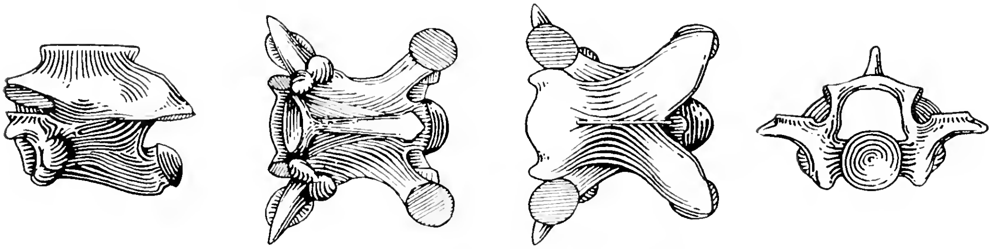

Figure 17. A precaudal vertebra of *Diadophis* cf. *punctatus* (UF 6131) Reddick I B, Pleistocene (Illinoian ?).

gosphene convex from the front, crenate from above (fig. 17).

Skeletons of *Diadophis p. punctatus* (3), *D. p. edwardsi* (1) and *D. amabilis similis* (1) exhibit no constant differences which serve to separate them from one another. Pleistocene remains of this genus from Florida are provisionally referred to *Diadophis punctatus* on zoogeographic grounds. The genus has never before been reported as a fossil.

Diadophis cf. *D. punctatus* Linnaeus

A number of vertebrae provisionally referred to this species are available from Reddick I, B (UF 6131), and Mefford Cave I (UF 2559). They agree in all particulars with those of modern skeletons. Table 9 illustrates the similarity of the ratios of Pleistocene and modern vertebral ratios of

TABLE 9.
Comparative ratios of Pleistocene and Recent specimens of Diapophis punctatus

Ratios	Pleistocene (N=31)	Recent (N=42)
cl/naw	1.31-1.57	1.23-1.62
ctw/cth	1.11-1.28	1.05-1.38
pr-pr/po-pr	0.96-1.12	0.98-1.16
po-pr/cl	1.15-1.32	1.02-1.44
nlu/nh	3.01-4.86	2.10-5.00
cl/col	4.50-6.09	4.77-6.70
naw/zw	0.90-1.08	0.87-1.11
pol/pow	0.91-1.38	0.08-1.50

Diadophis punctatus. Holman (1959) reported this species from Williston, Florida (FGS V-5797).

In addition to the Pleistocene vertebrae mentioned above, at least two vertebrae are available from a Pliocene locality which are referrable to this genus, and appear to represent a new species. The new form may be known as:

DIADOPHIS **ELINORAE**, *sp. nov.*

Holotype.—UF 6413, a middle precaudal vertebra, collected by Walter Auffenberg.

Type Locality and Horizon.—Haile VI, A, Alachua formation, Middle Pliocene, Hemphillian.

Diagnosis.—A snake whose vertebrae are similar to those of the extant species of *Diadophis*, but which differ from them in having a shorter centrum, in having a straight anterior edge on the neural spine, instead of overhanging anteriorly; in having stronger subcentral ridges; a higher neural spine, and a haemal keel which is less spatulate-shaped.

Type Description.—A middle precaudal vertebra, moderate in length and height, centrum somewhat subtriangular from below. The haemal keel is well developed, slightly rounded, spatulate-shaped, and flattened at the posterior tip where it ends in an acute point, extending from the edge of the cotyle to just in front of the condyle. Subcentral ridges present, but not overly developed, somewhat rounded, extending from the diapophyses posteriorly to little over half way to the condylus, where it disappears. Parapophyses slightly projected downward and forward, the facet of which is smaller than the diapophysial facet. Condylus moderate in size, directed more posteriorly than upwards. Cotyle round, not distinctly oval. Neural arch moderate in length, somewhat compressed dorso-ventrally, but not excessively, without epizygapophysial spines. Interzygapophysial ridges moderate. Neural spine low, straight anteriorly, overhanging posteriorly, longer than high. Zygosphene crenate from above, convex from the front. Prezygapophysial facets oval. Postzygapophysial facets orbicular.

In some respects *Diadophis elinorae* may be confused with *Lampropeltis doliata*, but the neural canal is too small for the centrum length, since it is considerably larger in specimens of *L. doliata* of equal size. From *Chionactis* it differs in that the haemal keel is much narrower, the cotyle is more rounded, and the zygosphene is not as crenate-shaped from above. *Enulius, Sonora, Atractus, Liophis, Toluca,* and *Coronella* also are somewhat similar, but can be separated from the fossil form by a combination of characters involving the shape of the neural spine, the zygosphene, and the width and shape of the haemal keel. For a separation of these and other similar genera, see the section on *Carphophis.*

In addition to the type, two other vertebrae from the same deposit are provisionally placed with it. UF 6153, an anterior vertebra with hypapophysis, and UF 6412, a smaller, somewhat narrower vertebra, is here interpreted as a more posterior element. Figure 18 illustrates the type vertebra as well as one of the referred specimens. Table 10 gives the measurements and ratios obtained from the type.

TABLE 10.
Certain measurements (in mm) and ratios obtained from the type vertebra of Diadophis elinorae, sp. nov.

cl	1.45
naw	1.30
cl/naw	1.12
nlu	1.09
nh	0.25
nlu/nh	4.30
zw	1.24
cl/zw	1.16
ctw	0.79
cth	0.73
ctw/cth	1.07

Rhadinea flavilata Cope

Description.—Centrum long, somewhat cylindrical to subtriangular from below, with well developed hypapophyses anteriorly, reduced to a haemal keel in the middle and posterior vertebrae. Haemal keel low, extending from the cotyle to just in front of the condylus, rounded at its anterior end, flattened posteriorly, compressed laterally near the middle of the length of the keel, oblanceolate to spatulate in shape. Subcentral ridges developed, but not strongly, extending to the condylus. Parapophyses well developed, but not projected. Paradiapophyses with two articular facets, the diapophysial member being larger and more spherical. Condylus on a short neck, moderate in size, slightly oblique, cotyle rounded, not distinctly oval. Neural arch long, moderately low, without epizygapophysial spines. Neural spine long, low, much longer than high at its anterior edge, extending anteriorly beyond the base of the zygosphene. Zygosphene crenate from above, convex from the front. Prezygapophysial articular surface obovate to oval. Accessory processes well developed, acute, directed laterally from the top, laterally to slightly downward from the front, somewhat compressed dorso-ventrally.

Rhadinea flavilata is known from only

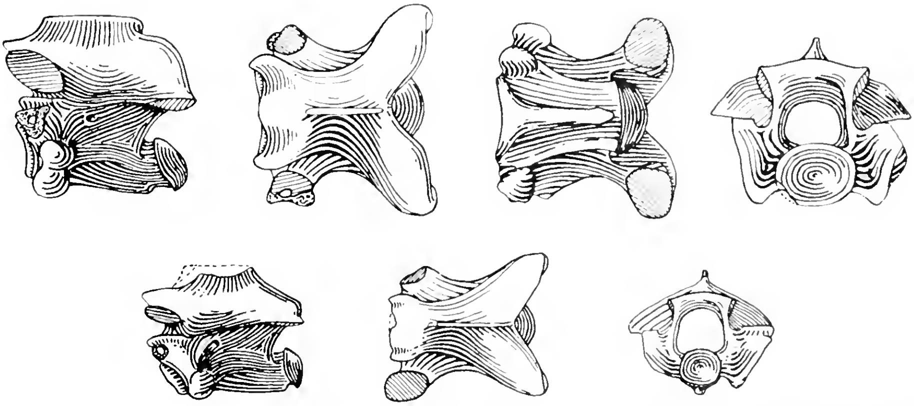

Figure 18. Upper: The type vertebra of *Diadophis elinorae*, sp. nov., (UF 6413), Haile VI A, Alachua fm. (restricted) Middle Pliocene (Hemphillian). Lower: A more posterior vertebra (UF 6412) referred to this species from the same locality.

three localities in Florida: a number of precaudal vertebrae (UF 6134) are available from Reddick I, B. Holman reports it from Sabertooth Cave (1958) and Williston (1959).

In the Reddick deposit this species is most easily confused with *Diadophis* and *Carphophis*. From both it is fairly well distinguished by its stronger subcentral ridges. From the latter it may be separated by its narrower and more ridge-like haemal keel (*cf.* figs. 14, 19). For the characters separating this genus from other similar North American genera, see the section on *Carphophis*. Table 11 compares the ratios of fossil and modern vertebrae of *Rhadinea flavilata.*

Heterodon Latreille

The anterior portion of the column possesses well developed hypapophyses, but they are absent in the middle and posterior series. The haemal keel is somewhat variable, from ridge-like to flattened, gladiate to cunate, extending from just behind the cotyle posteriorly to the edge of the condylus. The centrum is moderate in length and width, somewhat depressed, with subcentral ridges which may be either well developed or weak; if present, extending from the diapophyses posteriorly to near the condylus. Paradiapophyses with two well developed facets. Parapophyses not strongly projected. Condylus on a short neck, moderately oblique. Cotyle round. Neural arch low, depressed, without epizygapophysial spines. Neural spine slightly longer than, or equal to, its height, usually overhanging on the anterior and posterior edges. Zygosphene crenate to convex from above, convex from the front. Accessory process well developed, usually thin and broad, acute to obtuse, usually directed upwards, at least slightly so. Prezygapophysial facets oval to obovate.

On the basis of 8 skeletons of *Heterodon platyrhinos*, 2 *H. simus* and 1 *H. nasicus,* apparently the vertebrae may be separated into two groups: one representing *platyrhinos*, the other the two remaining species. These two groups may be distinguished fairly readily on the basis of the following characters:

(1) Vertebral ratios: pr-po naw (*platyrhinos* about 2.0, *nasicus* and *simus* about 1.5). The centrum is usually longer in relation to the width in *platyrhinos,* though there is considerable overlap (cl naw; *platyrhinos* 1.3-1.6 in adults, 1.1-1.2 in hatchlings; *nasicus* and *simus* 0.9-1.4 in adults, no juveniles available).

(2) In *simus* and *nasicus* the ventral keel is flattened to such an extent that it is just about as wide as the ventral portion of the centrum itself. In *platyrhinos* the keel is ridge-like, and not nearly as greatly flattened, except in juveniles.

(3) The vertebrae of *platyrhinos* are generally larger, though this admittedly serves as a character which can be utilized only in certain instances.

Other characters, such as the ratio pr-pr/nah, though they show significant differences in their mean ratios, are considerably more variable, and not suitable for purposes of identification.

TABLE 11.
Comparative ratios of Pleistocene and Recent specimens of Rhadinea flavilata

Ratios	Pleistocene (N=18)	Recent (N=38)
cl/naw	1.42-1.64	1.38-1.54
naw/zw	0.88-1.09	0.97-1.00
cl/zw	1.46-1.65	1.52-1.63
nlu/nh	3.12-4.06	3.14-4.04
pr-pr/po-pr	0.98-1.06	1.00-1.07
po-pr/cl	1.70-2.00	1.73-2.03
cl/col	1.50-1.81	1.57-1.72
pol/pow	0.96-1.16	0.94-1.20

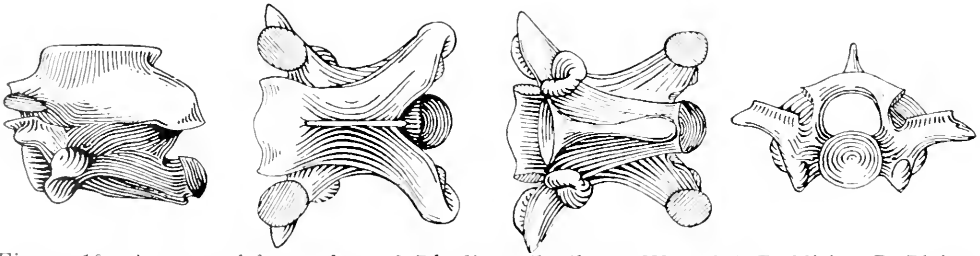

Figure 19. A precaudal vertebra of *Rhadinea flavilata* (UF 6134) Reddick I B, Pleistocene (Illinoian ?).

Heterodon platyrhinos Latreille

This species is now known from the following Pleistocene or Pleistocene and or Recent localities in Florida: Reddick I, B. UF 6134, 6126, 6099, 6046, 6126, 6132, 6049, 6109, 6102, 6107, 6106, 6123, all single dorsal vertebrae; UF 5695, 6 vertebrae, UF 6254, 4 vertebrae, and UF 4312, 3 vertebrae, probably from the same individual. CNHM PR 373. Mefford Cave I. UF 2553, several vertebrae. Haile VII, A. UF 5904, 6330, 5164, 6327, 6323, all single precaudal. Sabertooth Cave, FGS V-5723 (Holman, 1958). Arredondo I, A. UF 6128, one vertebra. Arredondo II, A. UF 2071, 2075, several vertebrae. Eichelberger Cave, B. UF 3331, one precaudal vertebra. Williston, FGS V-5798 (Holman, 1959). Itchtuckanee Springs, A. UF 4390, a complete parietal element, identical in every regard to that of Recent specimens of *H. platyrhinos*.

Figure 20 illustrates a middle precaudal vertebra of this species. Table 12 gives the vertebral ratios of the available fossil and Recent specimens.

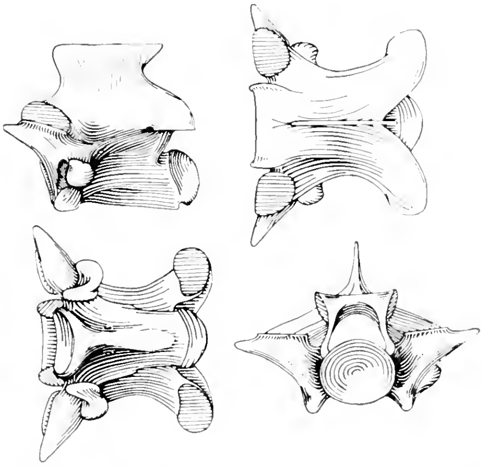

Figure 20. A precaudal vertebra of *Heterodon platyrhinos* (UF 6125) Reddick I B, Pleistocene (Illinoian ?).

Heterodon simus Linnaeus

Heterodon simus has been collected from the following Pleistocene localities: Mefford Cave I. UF 2554, 2 vertebrae. Reddick I, B. UF 5692, 1 vertebra, 5696, 4 vertebrae. Haile VII, A. UF 6213, 1 vertebra. Haile II, A. UF 6032, 1 vertebra. Williston. FGS V-5799 (Holman, 1959).

Figure 21 illustrates a middle precaudal vertebra of this species. Table 12 gives the vertebral ratios of both fossil and Recent specimens of this species.

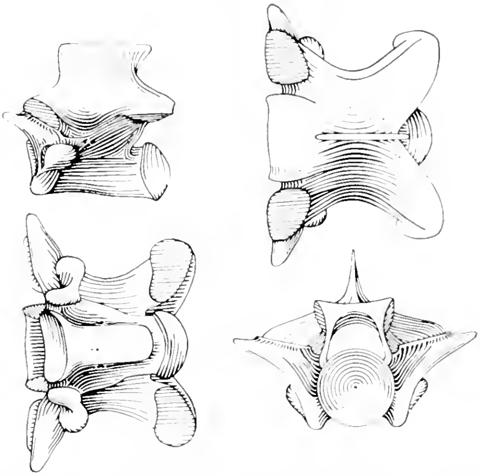

Figure 21. A precaudal vertebra of *Heterodon simus* (UF 5696) Reddick I B, Pleistocene (Illinoian ?).

In addition to the specimens listed above, vertebrae referrable to this genus have been collected from the Pliocene locality of Haile VI. However, these vertebrae are different from either *simus*, *nasicus*, or *platyrhinos*. The species they represent may be called:

TABLE 12.
A comparison of the vertebral ratios of Recent and fossil Heterodon platyrhinos, H. simus and H. brevis, sp. nov.

	Pleistocene		Recent		Pliocene
Ratios	*platyrhinos* (N = 33)	*simus* (N = 41)	*platyrhinos* (N = 43)	*simus* (N = 40)	*brevis*
cl/naw	1.12-1.58	0.92-1.06	1.09-1.62	0.88-1.05	1.19
cth/ctw	0.83-1.00	0.80-0.98	0.81-1.03	0.83-1.00	1.04
pr-pr/po-pr	0.98-1.11	1.08-1.21	0.95-1.18	1.03-1.28	?
zw/naw	0.75-0.87	0.81-0.89	0.73-0.86	0.82-0.92	?
nsl/nah	1.08-1.37	1.06-1.51	1.04-1.41	1.04-1.67	?

HETERODON **BREVIS**, *sp. nov.*

Holotype.—UF 6153, a middle precaudal vertebra collected by Walter Auffenberg.

Type Locality and Horizon.—Haile VI, A, near Haile, Alachua County, Florida. Middle Pliocene, Hemphillian, Alachua formation.

Diagnosis.—A Pliocene species of the genus *Heterodon* in which the middle precaudal vertebrae are similar to those of *H. platyrhinos* in the degree of flattening of the neural arch, with a longer centrum than in *simus* or *nasicus* (cl naw 1.19), subcentral ridges evident, haemal keel obvious, not as flattened nor as broad as in *simus* or *nasicus*, constricted near the middle. From *platyrhinos* it differs chiefly in possessing a shorter neural spine at its base (cl nsb 2.07 in the type, 1.32-1.82 in *platyrhinos*). In addition, the prezygapophyses are directed slightly more anteriorly in *brevis*, and the diapophysial facets are proportionately smaller.

Description of Type.—A medium-sized *Heterodon* vertebra from the middle of the column, somewhat fragmentary. The upper portion of the neural spine is broken off. In addition, the right half of the zygosphene and the prezygapophyses on the same side are missing. The condylus is also broken. The zygosphene is slightly concave from above and from the front. There are two articular facets on the paradiapophyses. The zygapophyses are oval. The centrum is provided with two grooves, one on either side of a prominent haemal keel, compressed in the middle, and running from the cotyle, where it is wide, to the condylus, where it is again wide. The keel is not provided with sharp edges, but is somewhat rounded in cross section, not obviously flattened. The cotyle is rounded, slightly higher than wide. The neural canal is somewhat square in outline from the front.

Referred Material.—UF 6466, a fragmental vertebra from the same locality and horizon is provisionally placed in the species. It differs but slightly from the type.

The only other fossil *Heterodon* previously reported is *plionasicus* Peters (1953), a rather large species from the Upper Pliocene of Kansas (Rexroad fm.) (Hibbard 1944, 1949b). This extinct species is most closely related to *H. nasicus*, and is probably ancestral to it. *H. brevis*, on the other hand, is closest to *platyrhinos* and direct phyletic relationship is hardly questionable. Table 12 gives the vertebral ratios of the type. Figure 22 illustrates the type specimen.

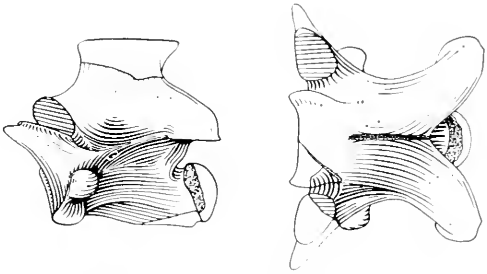

Figure 22. The type vertebra (UF 6153) of *Heterodon brevis*, sp. nov., Haile VI A, Alachua County, Florida. Alachua formation (restricted), Middle Pliocene (Hemphillian).

Opheodrys Fitzinger

Description.—Centrum long, subcylindrical to subtriangular from below, with well developed subcentral ridges, extending from the diapophyses to near the base of the condylus. Condylus on a moderate to long neck, directed more posteriorly than upwards. Haemal keel gladiate to slightly oblanceolate, not spatulate, extending from the lower lip of the cotyle to near the condylus, where it usually ends in an acute point. Paradiapophyses rather small, with two articular facets. Parapophysis not projected ventrally or anteriorly. Neural canal moderate to large. Neural arch without, or with very weakly developed epizygapophysial spines. Zygosphene thin, crenate from above, convex from the front. Neural spine moderate to long, slightly overhanging to straight at the anterior end, overhanging posteriorly.

Opheodrys can be separated from *Coluber* and *Masticophis* on the basis of the height of the neural spine and the width of the zygosphene (nlu nh: *Opheodrys* 1.39-1.45; *Coluber* 1.77-3.18; *Masticophis* 1.72-2.97; cl zw: *Opheodrys* 1.20-1.26; *Coluber* 1.41-1.67; *Masticophis* 1.32-1.67). In addition, the haemal keel is not as spatulate in *Opheodrys* as in *Coluber*, but more gladiate-shaped, and usually narrower. The epizygapophysial spines are much less developed than in either *Masticophis* or *Coluber*, and the vertebrae are never as large as in these two genera.

On the other hand, *Opheodrys* is similar to *Salvadora* in vertebral structure. The two genera apparently are separable on the basis of the proportions of the neural spine (nle/nh: *Opheodrys* 1.39-1.45; *Salvadora* 1.54-1.58). In addition, the ratio pr-pr po-pr will separate many individual vertebrae, but not all of them (*Opheodrys* 0.94-1.01; *Salvadora* 1.00-1.05).

As comparative material of *Salvadora* and *Opheodrys* the following specimens were available: *Opheodrys aestivus* (4), *Opheodrys vernalis* (2), *Salvadora lineata* (1), *Salvadora hexalepis* (1) and *Salvadora mexicanus* (1).

Opheodrys aestivus may be separated from *O. vernalis* by a shorter centrum (cl naw: *O. aestivus* 1.04-1.07; *O. vernalis* 1.19-1.24), and a longer neural arch (po-pr pr-pr: 1.07-1.11 in *O. aestivus*, 0.99-1.06 in *O. vernalis*). The remaining ratios and measurements of the two species are practically identical. Both species possess faint, or no epizygapophysial spines. The fossil vertebrae from Florida are clearly referred to *aestivus* on the basis of the two ratios mentioned above.

Opheodrys aestivus Linnaeus

The genus *Opheodrys* has never before been reported as a fossil. Only seven vertebrae are definitely referrable to *O. aestivus*. Two vertebrae (UF 5016 and 6247) are from Reddick I, B. The others are from Arredondo I, A. (UF 6124), Kanapah I. (UF 6184), Haile II, B. (UF 5040 and 5683) and Arredondo II, A. (UF 2072). One of the fossil elements is illustrated in figure 23. Table 13 gives the more important vertebral ratios of the two Recent species, as well as those of the fossil vertebrae.

Coluber Linnaeus

Description.—Middle precaudal vertebrae without well developed hypapophyses; centrum somewhat conical to subtriangular from below, with well developed subcentral ridges. The haemal keel is rounded to somewhat flattened, extending from the lip of the cotyle posteriorly to near the condyle, where it ends in an acute to obtuse point which is usually flattened and broadened, forming a spatulate-shaped haemal keel. The paradiapophyses are provided with two well developed articular facets, with a fairly well developed parapophysial process extending downwards and forwards. The cotyle is suboval to round. The condyle is on a short neck, directed posteriorly. The neural canal is round to subtriangular from the front. The neural arch is moderately long, with well developed epizygapophysial spines. The neural spine is as long, to slightly longer than high, overhanging both anteriorly and posteriorly. The zygosphene is slightly convex from above and from the front. The prezygapophyses are oval to subtriangular, or obovate. The accessory processes are well developed, acuminate, long and directed laterally or slightly downward from the front, and somewhat anteriorly from the top.

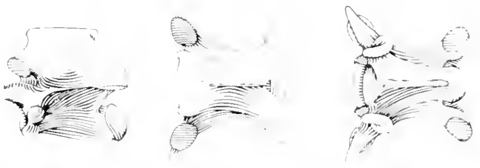

Figure 23. A precaudal vertebra of *Opheodrys aestivus* (UF 6247) Reddick I B, Pleistocene (Illinoian ?).

The vertebrae of *Coluber* differ from most other elongate colubrids possessing well developed epizygapophysial spines. However, this character seems to have been developed independently several times in both the Colubridae and Viperidae. In the latter they are faintly evident in *Sistrurus* and most specimens of *Agkistrodon*. They are well developed in at least some species of *Vipera*, but are absent in *Crotalus*, *Bothrops*, *Azemiops*, *Bitis*, and *Trimeresurus*. In the New World colubrids they appear to be absent in all of the endemic South and Central American genera which I have seen.

TABLE 13.
Comparison of the vertebral ratios of Opheodrys aestivus, both Pleistocene and Recent, and Opheodrys vernalis

Ratios	*O. aestivus* (N = 25)	*O. vernalis* (N = 16)	*fossils* (N = 32)
cl/naw	1.04-1.07	1.19-1.24	1.04-1.12
nlu/nh	1.39-1.44	1.40-1.45	1.43-1.44
ctw/cth	1.05-1.10	1.06-1.12	1.06-1.08
pr-po/pr-pr	0.99-1.06	1.07-1.11	1.07-1.09
cl/zw	1.20-1.23	1.23-1.26	1.22-1.24

They are weakly developed in *Elaphe,* more strongly in *Pituophis.* They are strongly developed in *Coluber, Masticophis, Drymarchon,* and most of the Natricinae. They are absent, or practically so, in *Opheodrys* and *Salvadora,* two genera sometimes placed close to *Coluber.*

Middle and posterior vertebrae of *Drymarchon* can be separated from both *Coluber* and *Masticophis* by the proportionately shorter centrum, the longer maximum size, the beveled anterior edge of the neural spine and the shape of the haemal keel.

Opheodrys, besides possessing very weak epizygapophysial spines, can also be separated on the basis of other characters from both *Coluber* and *Masticophis.* In *Ophedrys* the neural spine is lower, and the zygosphene is proportionately wider (nlu nh: *Opheodrys* 1.39-1.45; *Coluber* 1.77-3.18; *Masticophis* 1.72-2.97; cl zw; *Opheodrys* 1.20-1.26; *Coluber* 1.41-1.67; *Masticophis* 1.32-1.67). *Salvadora* can be separated from *Coluber* and *Masticophis* by the lower neural spine (nlu nh 1.54-1.58). *Salvadora* usually lacks on epizygapophysial spine.

Other ratios between the four genera are practically identical, or overlap sufficiently so that determination of a single vertebra becomes difficult, if not impossible, on the basis of these characters alone.

The vertebrae of *Coluber* and *Masticophis* are distinct from most other attenuate snakes, including such forms as *Oxybelis, Dryophis, Lygophis, Psammophis, Leptophis, Chlorophis, Alsophis, Dromicus, Uromacer, Immantodes,* and *Leimadophis.*

On the other hand, the vertebrae of the genera *Coluber* and *Masticophis* are similar, and not all specimens of the latter can be separated from the former with any degree of certainty. Brattstrom (1955a: 151-2) separated them on the basis of the smaller size of *Coluber* plus the fact that ". . . the subcentrum keel is narrow, thin and ends anteriorly at the edge of the centrum cup . . . in *C. contrictor,* not thick, flattened, and ending prior to the cup as in *Masticophis.*"

Smaller size is not a particularly good character to separate species (though it must sometimes be used in the absence of the better ones), since younger specimens of snakes can, and do occur as fossils. More important, in eighteen skeletons of *C. constrictor* and nine of *Masticophis* the character concerning the anterior end of the haemal keel will not satisfactorily separate these genera in more than one-third of the total number of vertebrae at hand.

Coluber constrictor frequently has the posterior end of the haemal keel more flattened, and the entire keel is generally thicker. However, this character will not separate more than one-half of the adult specimens, and less than one-third of the younger specimens.

The similarity of these two genera leads to a study of their characters to determine, objectively, the value of some of their vertebral ratios. The best ratio seems to be that of pr-pr/po-pr. There is some suggestion, though slight, of ontogenetic change in this particular character, at least in *Coluber.* This ratio will clearly separate slightly over 65 percent of the specimens of *Masticophis flagellum* and *Coluber constrictor.* However, it will not separate the latter from at least *M. lateralis,* and perhaps other species of *Masticophis.* Based on this ratio, the fossil material from Florida clearly falls into two groups; one certainly representing *Coluber constrictor* and the other *Masticophis flagellum* (fig. 24). Additional vertebrae may be allocated to one genus or the other utilizing the characters mentioned by Brattstrom. However, many of the vertebrae cannot be clearly referred to either genus.

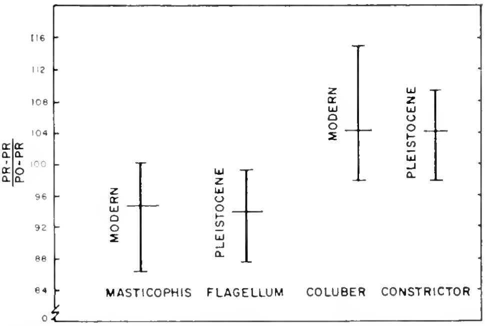

Figure 24. A comparison in the ratio pr-pr/po-pr between Late Pleistocene and Recent specimens of *Coluber constrictor* and *Masticophis flagellum.*

The fact that these two genera are not readily separable on vertebral characters lends another argument in favor of re-uniting the two forms under *Coluber* (Auffenberg, 1956b). All other North American genera known to me are separable on vertebral ratios, with the possible exception of some of the natricines, and some forms of

Elaphe and *Lampropeltis*, and *Farancia* and *Abastor*. There is additional evidence suggesting that the two latter genera should be united.

Comparative material of these two genera available to me for study include: *Coluber c. constrictor* (2), *C. c. stejnegerianus* (1), *C. c. mormon* (1), *C. c. flaviventris* (2), *C. c. priapus* (12), *C. c. paludicolus* (2), *C. c. anthicus* (1), *Masticophis f. flagellum* (6), *M. f. piceus* (1), *M. f. testaceous* (1), *M. lateralis* (1), and *M. taeniatus girardi* (1).

Coluber constrictor Linnaeus

The reader is referred to the generic description of the vertebral character of *Coluber*, since the vertebrae of the two remaining species, *oaxaca* and *spinalis*, are not available for study.

Coluber constrictor is known from a number of Pleistocene and or Recent deposits in North America. From Florida it was reported from Pleistocene and or Recent localities (Hay, 1917; Gilmore, 1938; Brattstrom, 1953a; Holman, 1958, 1959). In addition, it is now known from the following Pleistocene localities in the State: Arredondo I, A. UF 6058. Arredondo II, A. UF 2078. Payne's Prairie B. UF 5750. Sabertooth Cave. FGS V-5730 (Holman, 1958). Williston. FGS V-5800 (Holman, 1959). Reddick I, B. UF 5669, 5665, 5667, 5672-4, 5601, 5670, 5572, 5709-12, 5731, 5733-40, 5742-3, 6019, 6045, 6332, 6371, 6456, 9874. Haile VII, A. UF 5188, 5181, 5200, 6328, 5164, 5172, 5840-2, 6195, 9870, 5151-2, 5846-9, 5187, 5179, 5202, 5191, 9884-6, 5176, 5174, 5184, 6307, 5194, 6391, 5157, 5160. Winter Beach Locality. UF 5840. Eichelberger Cave A. UF 5925. Mefford Cave I, A. UF 3512.

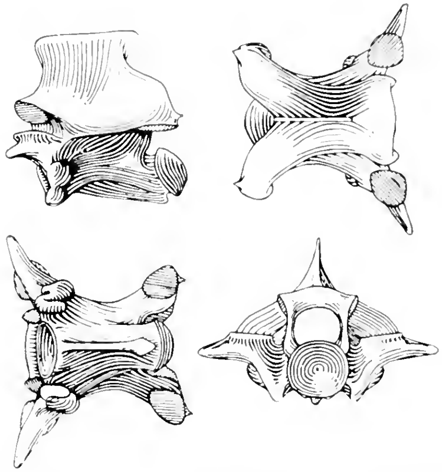

Figure 25. A precaudal vertebra of *Coluber constrictor* (UF 5200) Haile VII A, Pleistocene (Illinoian ?).

A typical precaudal vertebra is illustrated in Figure 25. Table 14 compares the various vertebral ratios of modern and Pleistocene *Coluber constrictor* and *Masticophis flagellum*. Fossil records of *Coluber* from Europe probably should be referred to *Zamenis*, or some closely related genus. The Pliocene specimens referred to this species by Brattstrom (1955a) should be re-examined carefully, since, after examining these vertebrae, I am reasonably certain that not all of them belong to the genus *Coluber*.

Masticophis flagellum Shaw

Description.—Middle precaudal vertebrae without well developed hypapophyses; centrum somewhat conical to subtriangular, with well developed subcentral ridges. The haemal keel is rounded to somewhat flattened, extending from the lip of the glenoid cavity posteriorly to near the condyle, where it ends in an acute point, which is not usually flattened or overly broadened, but gladiate-shaped, and ridge-like. The paradiapophyses are provided with two well developed ar-

TABLE 14.
A comparison of some of the vertebral ratios of Coluber constrictor and Masticophis flagellum, both Pleistocene and Recent

	Coluber		*Masticophis*	
Ratios	Pleistocene (N = 51)	Recent (N = 45)	Pleistocene (N = 36)	Recent (N = 41)
cl/naw	1.32-1.48	1.23-1.53	1.42-1.53	1.34-1.64
ctw/cth	0.96-1.08	0.90-1.16	1.01-1.09	1.00-1.18
pr-pr/po-pr	1.03-1.07	0.98-1.25	0.92-0.98	0.87-1.00
cl/zw	1.33-1.60	1.26-1.67	1.40-1.59	1.38-1.76
zw/naw	0.93-1.05	0.89-1.18	0.97-1.09	0.94-1.16
nlu/nh	2.45-3.18	1.86-3.46	2.20-2.63	1.93-2.97
nlu/nls	1.13-1.21	1.09-1.33	1.11-1.21	1.09-1.28

ticular facets, with a fairly well developed parapophysial process extending downwards and forwards. The cotyle is rounded. The condylus is on a short neck, directed posteriorly. The neural canal is round to subtriangular from the front. The neural arch is long, with well developed epizygapophysial spines. The neural spine is long, to slightly longer than high, overhanging both anteriorly and posteriorly. The zygosphene is slightly convex from above and from the front. The prezygapophyses are oval to obovate. The accessory processes are well developed, acuminate, long, and directed anteriorly from above, laterally from the front.

The vertebrae of *Masticophis* can usually be separated from *Coluber*. These differences are discussed in the section dealing with *Coluber*.

Masticophis flagellum is known from the following Pleistocene localities in the State: Arredondo I, A. UF 6141. Haile I, A. UF 5494. Haile VII, A. UF 6303-4, 6392, 5903. Reddick I, B. UF 5713-5, 5720-5, 5728, 5571, 5574, 5634, 5671, 5678, 6014, 6048, 4068, 6351-2, 6368, 8404, 6408, 6475-6. Sabertooth Cave. FGS V-5727 (Holman, 1958). Eichelberger Cave B. UF 6160. Williston. FGS V-5801 (Holman, 1959).

In addition, it is known from Itchtuckanee Springs (UF 5708, 5368), a locality listed in this paper as representing Pleistocene and or Recent deposits.

A mid-precaudal vertebra of this form is shown in Figure 26. Table 14 compares the various vertebral ratios of modern and Pleistocene vertebrae of *Coluber constrictor* and *Masticophis flagellum*.

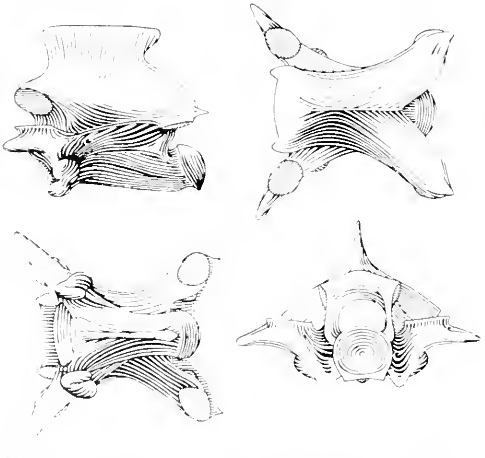

Figure 26. A precaudal vertebra of *Masticophis flagellum* (UF 5722) Reddick I B, Pleistocene (Illinoian ?).

Drymarchon corais Holbrook

Description.—Middle precaudal vertebrae without hypapophyses. Centrum triangular to subtriangular from below, with well developed subcentral ridges, and a rounded or flattened haemal keel, extending from the edge of the cotyle to near the condylus. It ends in an obtuse, or acute, flattened point, directly anterior to the condylus. The haemal keel is frequently thickened laterally near its middle. The cotyle is round, with or without a straight, lower margin, forming two latero-ventral corners. The paradiapophysial articular facets are double, with a parapophysial process extending downward and outward, as well as slightly anteriorly. Although usually present, this process is never overly developed. The condylus is on a short neck, and is directed more posteriorly than dorsally. The neural arch is moderate in length and height, with well developed epizygapophysial spines. The neural canal is rounded to square. The zygapophysial articular facets are oval to obovate in outline. The accessory processes are well developed, acute to broadly obtuse, directed laterally both from the front and from above. The zygosphene is straight above, occasionally notched, or even with a median tubercle in large adults, straight to convex from the front.

The following comparative material of this genus has been examined: *D. corais melanurus* (1), *D. c. erebennus* (2), *D. c. couperi* (6).

The vertebrae of this genus are easily recognized and can be assigned with certainty if they are not broken. In appearance they are typical colubrid vertebrae in which the neural spine is particularly distinctive. It is slightly longer than high, overhanging posteriorly, and with a beveled edge anteriorly. Apparently this is the only genus of snake in the New World with this peculiar anterior edge of the neural spine, with the possible exception of very large specimens of *Drymobius*. From this genus *Drymarchon* may be separated by its lower neural spine (nlu nh: *Drymarchon* 0.93-1.51, *Drymobius* 2.14-2.53), more obviously beveled neural spine in specimens of the same size, and generally less accentuated epizygapophysial spines. Other differences of lesser significance are seen on direct comparison of the vertebrae of the two genera, though the above will serve to separate them.

When the neural spine is broken difficulty is experienced in separating *Drymarchon* vertebrae from large specimens of *Coluber* or *Masticophis*. especially the latter. The centra of the last two genera are narrower and longer (cl naw: *Drymarchon* 0.85-1.30 [M = 1.21], *Masticophis* 1.03-3.59 [M = 2.36] and *Coluber* 1.92-3.50 [M = 2.52]. The accessory processes are heavy, but pointed in *Drymarchon*, whereas they are usually more acute in larger specimens of *Masticophis*, and in some specimens of *Coluber*. Small specimens of the last two genera easily are told from *Drymarchon* in a number of characters. The haemal keel is thinner in *Masticophis* and *Coluber*. The vertebrae of *Spilotes* also are somewhat similar to those of *Drymarchon* and may be distinguished by the width of the zygosphene, which is as wide as the narrowest part of the neural arch in *Spilotes*, and narrower in *Drymarchon*. In addition, the shape of the neural spine is different, the beveled edge being absent in *Spilotes*.

Drymarchon is known in the fossil record only from the Pleistocene of Florida. In addition, it has been reported from a number of localities in the peninsula that are here regarded as Pleistocene and or Recent.

Gilmore (1938: 66) mentioned that the fossil remains of this snake are identical to those of modern specimens with one exception: "The hypapophysial keel in many of the Pleistocene vertebrae has flattened ventral surfaces, whereas it is rounded in the skeleton of the living form . . . [and] (p. 64) the extinct form . . . probably . . . represents a distinct species . . ." The most careful examination of the vertebrae of both modern and Pleistocene specimens shows that the flattened keel is by no means restricted to fossil specimens, but is found in larger modern skeletons as well, and is a result of ontogenetic development.

One excellent fossil specimen of *Drymarchon* was found in the Pleistocene of Florida (UF 5076), including 52 vertebrae from all portions of the body, as well as certain of the cranial elements. When this specimen is compared with a large modern skeleton of this species the closest agreement is found in both the vertebrae and the cranial elements. However, certain vertebral ratios are significantly different in the two forms. These differences have their bases in the ontogenetic development of the vertebral elements, and are not necessarily indicative of a distinct species or subspecies (fig. 27). From all available data this fossil specimen seems to have been about 8-9 feet long, only slightly, if at all, larger than modern specimens. When Pleistocene vertebrae are compared with modern vertebrae of the same centrum length, the ratios are not significantly different. In view of the above, the Pleistocene remains of *Drymarchon* are referred to the Recent species, *corais*.

Because of its large size, this species is one of the most common fossil snakes in collections. Well over 200 vertebrae are known from Florida. However, almost all of these were found in localities here listed as Pleistocene and or Recent. The species is known from the following Pleistocene localities: Arredondo I, A. UF 5009-10, 5076. Arredondo I, E. UF 5901. Reddick I, B. UF 6071-2, 5011, 6011, 5014, 5012, 5575, 6364, 6492, 5805, 6491, 6369, 5263, 5716, 6350, 5915, 6015, 5635, 6142, 5602, 5916, 5107, 6353, 5467, 6036. Haile VII, A. UF 5205, 6208, 6283, 6277, 6292, 6301, 9864, 9868. Haile IV, A. UF 6022. Haile I, A. UF 5463, 5920. Kanapaha I. UF 5746. Winter Beach. UF 9872, 9882. Payne's Prairie B. UF 6488, 5748-9. Williston. FGS V-5823 (Holman, 1959). Eichelberger Cave A. UF 5302.

In addition to those reported by Gilmore (1938) and Brattstrom (1953a), the following are reported from the additional Pleistocene and or Recent localities: Ichtuckanee Springs I. UF 5204, 5206, 5208, 5229, 5302, 5274, Haile I, B. UF 5104.

Figure 27 illustrates the ontogenetic change in the ratio zw cw. Figure 28 illustrates a typical mid-precaudal vertebra of this species.

Elaphe Dumeril and Bibron

Description.—Vertebrae of colubrid type, with well developed hypapophyses anteriorly, centrum triangular, moderate in length, slightly depressed, provided with a well developed haemal keel in the middle and posterior vertebrae. This keel is usually slightly expanded posteriorly, with subcentral ridges extending from the diapophyses to the condylus. The paradiapophyses are below, usually behind the prezygapophyses. with two articular facets, and the parapophysial process is not projected greatly

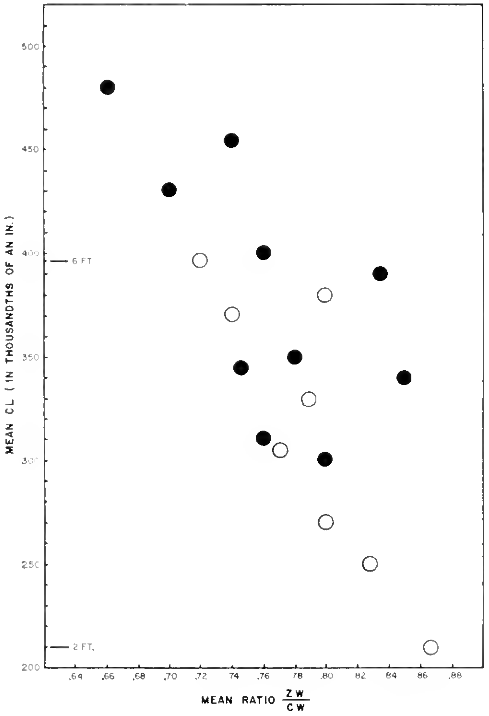

Figure 27. The mean ratio zw/cw plotted against cl to illustrate ontogenetic changes in this ratio in *Drymarchon corais*. Circles = modern specimens, dots = fossil specimens.

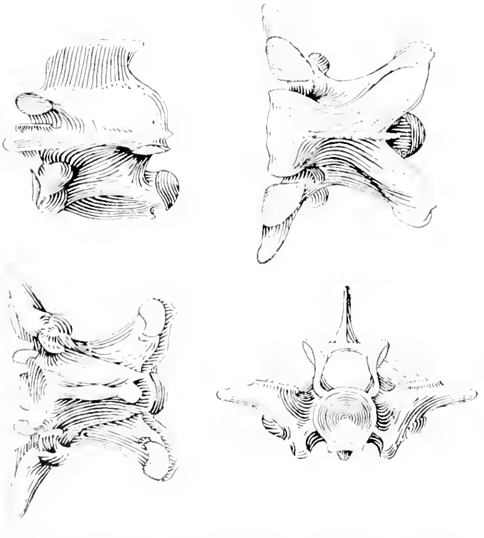

Figure 28. A precaudal vertebra of *Drymarchon corais* (UF 5079) Arredondo I A, Pleistocene (Illinoian ?).

below the centrum. The interzygapophysial ridges are evident. The prezygapophysial articular facets are oval to obovate, with the accessory processes directed downward to laterally from the front, laterally from the top; condylus directed more posteriorly than dorsally. The cotyle is slightly horizontally oval in young specimens, or in the anterior vertebrae of some adults, changing to round, or even vertically oval in the posterior thoracic vertebrae of large specimens. Neural arch moderate in height, not greatly flattened from behind. The zygosphene is about as wide as the narrowest part of the neural arch, being convex, straight or rarely concave from above, with or without a median notch, convex to straight from the front. Epizygapophysial spines usually absent, but sometimes feebly developed in large specimens. Neural spine almost always as high as long, lower in young specimens and in large adults.

The vertebrae of the genus *Elaphe* are sometimes difficult to separate from at least some species of *Lampropeltis*, *Arizona*, and *Pituophis*, among North American snakes. From the former the vertebrae of *Elaphe* may be separated by the presence of subcentral ridges which are straight, not bent from below as they are in most species of *Lampropeltis* (Brattstrom, 1955a). Furthermore, these ridges are more strongly developed in *Lampropeltis*. From *Pituophis*, *Elaphe* is most easily distinguished by the higher neural spine of the former, the more strongly developed epizygapophysial spine of the former, and the shape of the zygosphene, which is practically always concave from above in *Pituophis*, and rarely so in *Elaphe*. However, small specimens of *Pituophis* approach *Elaphe* in all of these characters. Exceptionally large examples of *Elaphe* may approach the vertebral structure more characteristic of *Pituophis*. Identification of individual vertebrae of *Elaphe*, *Lampropeltis* and *Pituophis* is frequently a specific rather than a generic identification. The reason is that the formulation of a series of characters for a generic definition is difficult.

At least representative portions of the vertebral column of the following species of *Elaphe* have been examined: *Elaphe obsoleta* (12, including the subspecies *lindheimeri*, *quadrivittata*, *obsoleta*, and *spiloides*), *E. subocularis* (1), *E. guttata* (6, including the subspecies *guttata* and *laeta*), *E. climacophora* (1), *E. dione* (1), *E. situla* (1), *E. vulpina gloydi* (1), and *E. taeniurus* (1).

E. situla apparently is separable from the species listed above on the basis of the hypapophysial keel, which is more expanded just anterior to the condylus. *E. dione* apparently is characterized by its extremely narrow zygosphene (cl/zw 1.81, varying from 1.09-1.50 in all of the other species), its low neural spine (at least two times longer than high, being higher in other species), which overhangs anteriorly (usually straight in other species). *E. vulpina* apparently is distinguished by possessing a longer centrum in the mid-dorsal vertebrae than in any of the remaining species (cl/naw = 1.09-1.18, and from 0.86-1.11 in the other species; cl/zw = 1.34-1.50, 1.09-1.33 in the other species). *E. taeniurus* and *E. climacophora* are similar to *E. obsoleta* and *E. guttata* as regards their middle dorsal vertebrae. *E. climacophora*, on the basis of one available specimen, may be separated by the ratio of the shortest length of the neural spine (nls), which is practically equal to the width of the zygosphene (zw). In the remaining species it is much less, regardless what part of the column is being considered. *E. taeniurus*, on the other hand, is similar to the two American species examined. No vertebral character was found which will consistently separate it from them. The fossil *Elaphe* from Florida clearly represents one or more of these three species. The remaining Pleistocene genera do not suggest the presence of any species now restricted to the Old World, and there is no reason to suppose that the condition is any different in *Elaphe*.

E. obsoleta and *E. guttata* may be separated readily on the basis of the relative height and width of the neural spine. However, there is considerable overlap in the ratios when they are taken by themselves. These ratios change with growth, and if the ratios are plotted against centrum length, the species are, for the most part, separable (fig. 29).

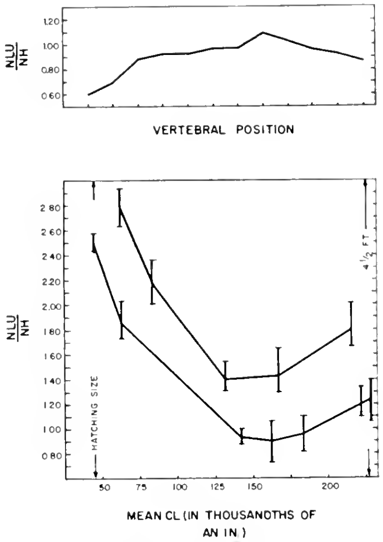

Figure 29. Upper: Intracolumnar variation in the ratio nlu/nh in one Recent, average-sized specimen of *Elaphe obsoleta*. The distance between marks along the horizontal axis is equal to 10 vertebrae. The first two vertebrae on the left are provided with hypapophyses. Lower: The same ratio plotted against mean cl in Recent specimens of *E. obsoleta* and *E. guttata*.

The fossil vertebrae of *Elaphe* fall along one curve or the other, and the vast majority of the specimens thus may be identified with some degree of certainty. The one available specimen of *E. taeniurus* has a different ratio than *E. obsoleta* or *E. guttata*, falling between them. However, since only one specimen is available, and since some variation in this character does exist (at least ontogenetically) the value of this difference as a diagnostic character is questionable. However, the character is constant in any individual specimen of *Elaphe*, disregarding the variation in the anterior portion of the column, where the vertebrae possess well developed hypapophyses. This relative constancy provides a character of considerable merit in distinguishing at least the two American species considered here.

Of considerable interest and importance is a re-evaluation of the Pliocene genus, *Palaeoelaphe* Gilmore (1938: 64). The generic characters, according to Gilmore, concern its larger size, more robust hypapophyses with dilated distal ends which are truncate, and the flattened haemal keel. The latter occurs in almost all middle and posterior vertebrae of larger specimens of *E. obsoleta*. The anterior vertebrae of *E. obsoleta* have hypapophyses which are robust, as well as truncated. They are more elongate, and not as obviously truncated, in *E. guttata*. The shallow notch in the zygosphene of the type vertebra of *Palaeoelaphe* suggests *E. obsoleta*, but is sometimes found in large specimens of *E. guttata*. *Elaphe obsoleta* attains a much larger size than *guttata*. Thus, the majority of the characters of *Palaeoelaphe* fall closer to *obsoleta* than to *guttata*. The shape of the hypapophyses seems to be the most diagnostic character. This structure varies considerably within the genus, sometimes being remarkably adapted for specific feeding habits (Gans and Oshima, 1952; Gans, 1952). There is little evidence to indicate that *Palaeoelaphe* deserves recognition as a distinct genus, and every reason to believe that it should be referred to the synonymy of *Elaphe*. Furthermore, *Elaphe* (*Palaeoelaphe*) *kansensis* is closest to *obsoleta*, and probably is ancestral to it.

Elaphe obsoleta Say

The generic description of the vertebrae suffices since the American species considered in this paper are similar. To separate this species from *E. guttata* reference should be made to Figure 29. A mid-precaudal vertebra of *Elaphe obsoleta* is illustrated in Figure 30. Table 15 compares some of the vertebral ratios of Pleistocene and Recent *Elaphe obsoleta* and *E. guttata*.

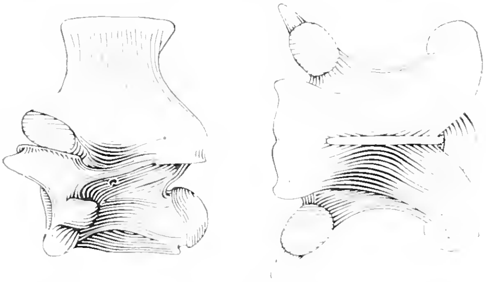

Figure 30. A precaudal vertebra of *Elaphe obsoleta* (UF 5177) Reddick I B, Pleistocene (Illinoian ?).

Elaphe obsoleta was collected from the following *Pleistocene* localities in Florida: Haile VII, A. UF 5177, 6270, 5173. Reddick I, B. UF 6444, 5605, 5177, 5049, 5567, 5694, 6264. Kanapaha I, A. UF 6118.

This species has been collected also from the Pleistocene and/or Recent locality of Itchtuckanee Springs, Locality A. (UF 5260). Brattstrom (1953a) reported it from Seminole Field (AMNH 7176).

Elaphe guttata Linnaeus

Figure 29 illustrates the method by which the vertebrae of this species are separated from those of *E. obsoleta*. Table 15 compares some of the vertebral ratios of Pleistocene and Recent *E. obsoleta* and *E. guttata*. Figure 31 illustrates a middle precaudal vertebra of *E. guttata*. Because of the degree of ontogenetic change in vertebral proportions and its importance as a character used to distinguish between this species and *E. obsoleta*, the ontogenetic changes in vertebral form of a middle precaudal vertebra are shown in Figure 32.

Elaphe guttata was collected from the following Pleistocene localities in Florida: Reddick I, B. UF 4309, (3)—10, 6290 (3), 6116, 6086, 6052, 6288 (2), 6091, 9878, 9890-1, 5480, 4310, 5690, 5808, 6366, 6462, 6163. Arredondo I, E. UF 6024-6. Arredondo II, A. UF 2077. Mefford Cave I, A. UF 2557. Eichelberger Cave B. UF 6161. Haile I, A. UF 5480, 5037. Haile II, B. UF 6031, 5041, 6030, 5683-4, 5633-4, 5679-80, 5681. Payne's Prairie B. UF 5754. Winter Beach. UF 5833, 5839.

Holman (1958, 1959) reported *Elaphe* sp. from both Sabertooth Cave and Williston.

In addition, the species is known from Itchtuckanee Springs A, a locality considered Pleistocene and/or Recent in age (UF 5386, 5405, 5403, 5398).

TABLE 15.

A comparison of certain vertebral ratios in Recent and Pleistocene specimens of Elaphe obsoleta and Elaphe guttata

	E. obsoleta		*E. guttata*	
Ratios	Pleistocene (N=15)	Recent (N=52)	Pleistocene (N=46)	Recent (N=50)
cl/naw	0.93-1.03	0.86-1.11	0.95-1.01	0.96-1.04
pr-pr/po-pr	1.28-1.31	1.23-1.36	1.25-1.27	1.21-1.29
cw/zw	1.10-1.17	1.07-1.25	1.13-1.26	1.08-1.23
cl/zw	1.12-1.16	1.08-1.33	1.09-1.20	1.03-1.36
nlu/nls	1.11-1.14	1.08-1.18	1.14-1.21	1.10-1.23
nlu/nh	1.01-1.05	0.94-1.17	0.92-1.16	0.89-1.21
cl/nlu	1.25-1.31	1.18-1.48	1.20-1.26	1.16-1.31

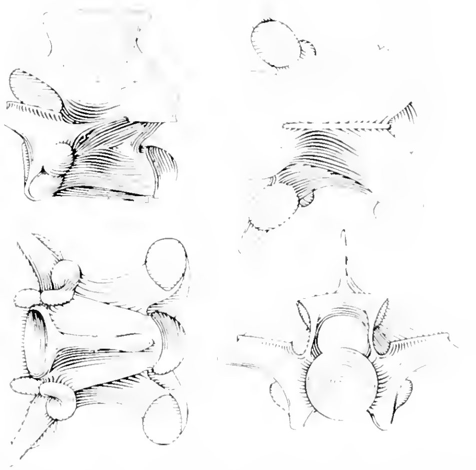

Figure 31. A precaudal vertebra of *Elaphe guttata* (UF 5684) Reddick I B, Pleistocene (Illinoian ?).

Figure 32. Ontogenetic change in the shape of the precaudal vertebrae of *Elaphe guttata*. Left: hatchling. Middle: specimen 2½ feet long. Right: specimen 4½ feet long.

Based solely on the amount of material available from the Pleistocene deposits of Florida, *E. guttata* may have been more widely distributed and more common than *E. obsoleta*. However, paleoecological conditions in the vicinity of the deposits may have been such to favor habitation by *guttata* rather than *obsoleta*.

Pituophis Holbrook

Description.—Centrum moderate in length, subtriangular from below, with strong subcentral ridges, extending from the posterior edge of the diapophyses posteriorly to the condylus. The haemal keel is gladiate to sub-spatulate in shape, extending from the lower lip of the cotyle to near the condylus. Condylus on a short neck, facing posteriorly more than dorsally. Cotyle rounded, but sometimes vertically oval in vertebrae at the posterior part of the body of large specimens. Paradiapophysial facets double, the diapophysial facet more or less above the lower parapophysial facet. The former is also larger and more convex. The neural arch is moderate to high, usually without epizygapophysial spines in smaller specimens, to moderately developed in larger individuals. Zygosphene thin, concave from above, convex from the front, sometimes with a slight median notch. Neural spine as long, or higher than long, sometimes slightly overhanging anteriorly, but usually rather straight, overhanging posteriorly. Prezygapophyses well developed, the articular facets oval. The accessory processes are acutely pointed, moderately long, directed anteriorly from above, laterally to slightly upwards from the front. The postzygapophyses are oval to obovate in shape.

The genus is most easily confused with *Elaphe*. From that genus it can be separated by the concave zygosphene from above (only rarely so in *Elaphe*), the somewhat better developed epizygapophysial spines, and the neural spine, which is usually much higher in *Pituophis*.

The following specimens have been used for comparative purposes: *Pituophis m. melanoleucus* (2), *P. m. mugatus* (4), *P. c. catenifer* (1), *P. c. annectens* (1), *P. c. deserticola* (1) and *P. c. sayi* (3).

On the basis of the available comparative material, *P. catenifer* possesses lower neural spines than does *P. melanoleucus* (nlu nh: *catenifer* 1.14-1.22, *melanoleucus* 0.90-1.16). However, the specimens of *catenifer* available for study were smaller than those of *melanoleucus*, and the character may be associated with growth and or age. The fossil vertebrae from Florida all possess the high neural spines found in the modern skeletons of *melanoleucus*, and they thus are referred to this species.

Pituophis melanoleucus Daudin

The apparent vertebral differences between *catenifer* and *melanoleucus* have been pointed out above. Figure 33 illustrates a typical middle precaudal vertebra of this species. Table 16 compares the vertebral ratios of modern specimens of *P. melanoleucus* and Pleistocene specimens referred to this species.

Pituophis melanoleucus vertebrae are known from the following Pleistocene localities in Florida: Reddick I, B. UF 5000-1, 5003-8, 5102, 6143, 5812. Kanapaha I. UF 6017. Williston. FGS V-5805 (Holman,

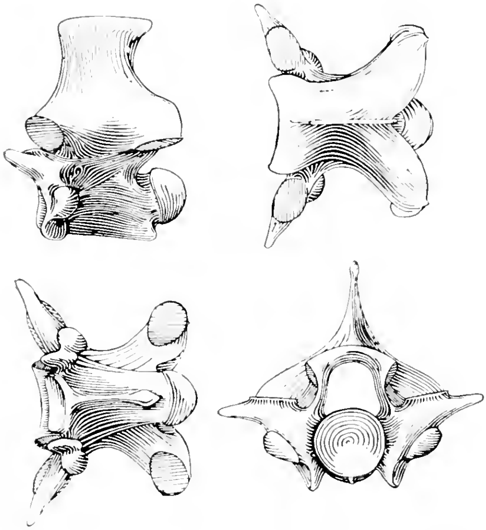

Figure 33. A precaudal vertebra of *Pituophis melanoleucus* (UF 5002) Reddick I B, Pleistocene (Illinoian ?).

1959). Eichelberger Cave B. UF 6180.

In addition, the species is known also from Itchtuckanee Springs, I. (UF 5275-8, 5231), a locality classed as Pleistocene and or Recent. Brattstrom (1935a) reported this species from Vero Beach, Stratum 3, and Seminole Field.

Lampropeltis Fitzinger

Description.—Centrum moderate in length, the anterior series possessing well-developed hypapophyses, which are reduced in the middle and posterior series to a haemal keel. However, within the genus there is considerable variation in the development of the keel. It is low and somewhat broad in some forms, especially the posterior series, whereas it is high and narrow in young specimens, or in *L. doliata*, *L. multicincta*, *L. zonata* and *L. polyzona*, and especially small individuals of these species.

TABLE 16.

A comparison of some vertebral ratios of Recent and Pleistocene specimens of Pituophis melanoleucus

Ratios	Pleistocene (N=38)	Recent (N=45)
cl/naw	0.94-1.07	1.05-1.18
ctw/cth	1.02-1.11	1.00-1.17
pr-pr/pr-po	1.05-1.32	1.13-1.31
zw/naw	0.72-0.89	0.83-0.98
cl/zw	1.11-1.31	1.10-1.28
nlu/nh	0.90-1.12	0.90-1.16
nlu/nls	1.06-1.14	1.10-1.24

The subcentral ridges extend from the posterior portion of the diapophyses posteriorly to near the condylus. The haemal keel is usually gladiate-shaped, with an acute posterior tip. The cotyle is round. The condylus is on a short neck, directed more posteriorly than upwards. The neural arch is strongly depressed in all but the anterior vertebrae. Epizygapophysial spines are absent. The zygosphene is thin, crenate, straight or convex from above, convex from the front. The articular facets are obovate to oval in outline. The neural spine is somewhat variable in shape, being very low and long in the *doliata* group, and higher in *calligaster* and *getulus*. It is always overhanging posteriorly, and either straight or overhanging anteriorly.

Comparative material examined includes the following skeletons: *Lampropeltis z. zonata* (1), *L. z. multicincta* (1), *L. polyzona* (1), *L. g. getulus* (3), *L. g. holbrooki* (1), *L. g. splendidus* (1), *L. g. californiae* (1), *L. c. rhombomaculata* (1), *L. c. calligaster* (1), *L. d. doliata* (3), *L. d. syspila* (1) and *L. d. triangulum* (3).

On the basis of the comparative material apparently within the genus *Lampropeltis* there are at least two groups which may be distinguished on vertebral characters. These are, (1) the somewhat smaller species, composed of *zonata*, *polyzona*, and *doliata* and, (2) the larger forms, composed of *getulus* and *calligaster*.

Other than size (a poor character), these two groups can be distinguished on the basis of the relative height of the neural spine (Table 17). Group 1 may be confused with *Rhadinea*, from which it may be separated by the ratio cl/naw (0.94-1.17 in Group 1 of *Lampropeltis*, 1.42-1.64 in *Rhadinea*). Furthermore, the haemal keel of *Rhadinea* usually is more flattened than it is in *Lampropeltis*, with the exception of *L. d. triangulum*. Some species of *Liophis* and *Leimadophis* have vertebrae similar to those of *Lampropeltis*. Usually they can be separated on the basis of the development of the subcentral ridges, which are weakly developed in *Liophis* and *Leimadophis*, stronger in *Lampropeltis*.

Group 2 is confused easily with *Rhinocheilus* and *Cemophora*. From the former it may be distinguished in that it lacks the

TABLE 17.
Comparison of certain vertebral ratios in Recent skeletons of Lampropeltis

	cl/naw	ctw/cth	pr-pr/po-pr	zw/naw	cl/zw	nlu/nh
calligaster (N=22)	1.00-1.18	1.00-1.08	1.23-1.33	0.95-0.98	1.20-1.30	1.04-1.18
getulus (N=55)	0.85-1.11	0.92-1.10	1.10-1.45	0.67-0.95	1.05-1.50	1.12-1.53
zonata (N=18)	1.00-1.03	1.01-1.04	1.19-1.24	0.94-0.98	1.01-1.06	4.00-4.10
doliata (N=27)	1.04-1.17	1.02-1.09	1.05-1.16	0.85-0.97	1.07-1.38	2.70-4.28
polyzona (N=21)	0.92-1.00	1.05-1.12	1.39-1.54	0.95-0.99	0.95-1.02	2.30-3.20

much thicker neural spine of *Rhinocheilus*. In addition, the upper edge of the spine in *Lampropeltis* is sharp, not flattened as in that genus. From *Cemophora*, *Lampropeltis* may be separated by its more depressed neural arch and in having a much greater overhang on both the anterior and posterior edges of the neural spine. From *Elaphe*, *Pituophis*, *Salvadora*, and *Arizona* it may be separated by its more depressed neural arch and, in general, the better developed subcentral ridges. *Stilosoma* is different in a number of characters; a much shorter neural spine, paradiapophysial articular facets not well separated, a strongly concave zygosphene when seen from above, a neural arch which is much less depressed, and an oval cotyle. On the basis of vertebral form only it is difficult to see how *Stilosoma* can be related to *Lampropeltis*. If any relationship exists between the two genera it will certainly be remote. In fact, among North American colubrid snakes, *Stilosoma* appears unique in vertebral form.

Brattstrom (1955a) illustrated the vertebrae of a number of species of *Lampropeltis*, describing the subcentral ridges and pointing out differences between the various species in this character. After examining the comparative material available to me, I find a somewhat less clear demarcation between the various species than was indicated by Brattstrom. However, there is a general tendency for these ridges to be bent in *getulus*, whereas they are convex, concave, or straight in the other species examined. Both inter- and intracolumnar variation is exhibited in this character. However, if only middle precaudal elements are compared, their utility in a diagnosis is warranted. All the remaining characters given by Brattstrom as diagnostic seem to be valid.

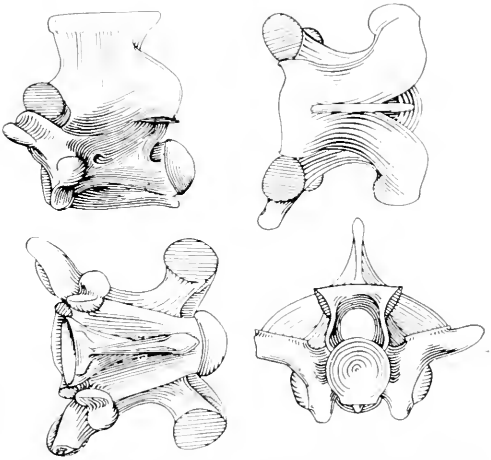

Figure 34. A precaudal vertebra of *Lampropeltis getulus* (UF 5153) Haile VII A, Late Pleistocene (Illinoian ?).

Lampropeltis was reported from the Pliocene of North America (Brattstrom, 1953a, b, c, 1954b). *Lampropeltis doliata* and *L. getulus* were reported from Seminole Field. The latter has, in addition, been reported from Melbourne (Brattstrom, 1953c). These localities are considered Pleistocene and/or Recent. He also reported *L. getulus* from the Pleistocene locality of Allen Cave (AMNH 6772). In addition, the following localities should be added: *Pleistocene:* Reddick I, B. UF 6296. Arredondo I, A. UF 5924, many vertebrae from one individual. Haile VII, A. UF 6308, 6325, 5173, 6270, 5153, 6193, 6396. Haile I, A. UF 5472. *Pleistocene and/or Recent:* Itchtuckanee Springs, A. UF 5448, 5386.

A typical middle precaudal vertebra is illustrated in Figure 34.

Stilosoma Brown

One mid-precaudal vertebra from the Pliocene locality of Haile VI, A, is not only unique, but interesting because it provides some information as to the length of time that *Stilosoma*, an endemic Florida genus, has been present in the peninsula. The basic structure of the single element is similar to that in the modern species, *S. extenuatum*, and the vertebra is provisionally referred to that genus. Additional material should be helpful in determining its exact generic status. *Stilosoma* has never before been reported in the fossil record. The new form may be known as:

STILOSOMA **VETUSTUM**, *sp. nov.*

Diagnosis.—A Pliocene colubrid snake most closely resembling the modern genus *Stilosoma*, but differing from the living species, *extenuatum*, in the narrower and somewhat more ridge-like haemal keel. *Stilosoma* is distinguished from all other modern or fossil New World colubrids I have seen in possessing a very short, wide vertebra, by the small prezygapophyses, by the low, but not excessively long neural spine and a reduction of the division between the two articular surfaces of the paradiapophyses.

Holotype.—UF 6467, a fairly complete vertebra, collected June, 1954, by Walter Auffenberg.

Type Locality and Horizon.—Haile VI, A, near Haile, Alachua County, Florida, Middle Pliocene, Hemphilian, Alachua fm.

Description of the Type.—One vertebra which is similar in size and structure to those found in *Stilosoma extenuatum*, except as mentioned above. The upper portion of the neural spine is broken off, as are the accessory processes on both sides. The centrum is short and wide, triangular from below, possessing moderately strong subcentral ridges, extending from the diapophyses posteriorly to near the condylus. Condylus on a short neck, directed posteriorly. Paradiapophyses well developed, but the separation between the two surfaces not as distinct as in most colubrids. The parapophysial surface is much smaller than the diapophysial one. Parapophysial process not projected downwards or anteriorly beyond the ventral margin of the cotyle. Cotyle somewhat oval horizontally, the edge broken on the right side. Neural arch wide, depressed, without epizygapophysial spines. Neural spine presumably low on the basis of the thin broken edge. Prezygapophysial surfaces oval, broken on the right side, small as in *Stilosoma extenuatum*. Zygosphene worn in the type, but convex from above and from the front on the basis of the remainder of the structure, thin dorso-ventrally. Neural canal moderately large, somewhat oval from the front. Haemel keel broadly gladiate, but not overly flattened.

The type vertebra is compared with a vertebra of a recent specimen of *Stilosoma extenuatum* in Figure 35.

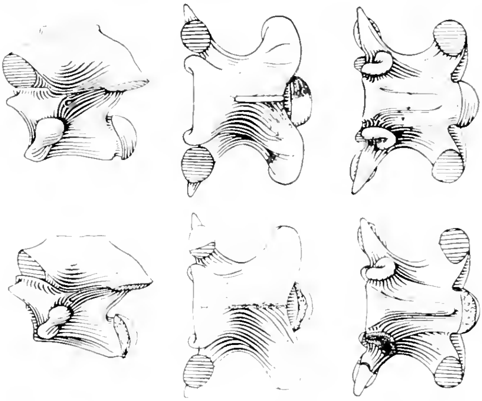

Figure 35. Upper: A precaudal vertebra of *Stilosoma extenuatum*. Lower: The type vertebra (UF 6467) of *Stilosoma vetustum*, sp. nov., Haile VI A, Alachua Co., Florida, Alachua fm. (restricted), Middle Pliocene (Hemphillian).

(?) *Stilosoma extenuatum* Brown

A single vertebra (UF 2076) from the Pleistocene locality of Arredondo II, A may represent the short-tailed snake, *S. extenuatum*. However, the element is somewhat fragmental, and even the generic assignment is tentative until more material becomes available.

The genus *Stilosoma* is usually considered close to *Lampropeltis*. Only one Recent vertebral column is at present available for study. This specimen is rather small, and at least some ontogenetic change is expected in larger individuals. However, a comparison of the vertebrae of this specimen with those from a number of modern species of *Lampropeltis* indicates many differences. The ontogenetic change in the vertebral form of *S. extenuatum* should not be so great that these differences would be nullified. This view is supported by the fossil vertebra from Haile VI, which apparently represents a snake about two feet long (or about the size of an average specimen of *S. extenuatum*), yet it is similar to that of the smaller comparative Recent specimen.

The relict distribution of the genus, as well as its external characteristics, seem to indicate that it has been separated from its closest relatives for a long time. This view is certainly substantiated by the vertebral form of this genus. It is, in fact, so different from all of the available skeletons of New World colubrids that one is tempted to look for possible relatives among the Old World genera; a search that has, as yet, been unsuccessful.

PSEUDOCEMOPHORA, *gen. nov.*

Diagnosis.—A Miocene colubrid, closest to *Lampropeltis* and *Cemophora* in vertebral characters, but differing from these in the following characters: from the former in the shape of the haemal keel when seen from the side, in that it does not extend anteriorly to the lower lip of the cotyle. From *Cemophora* it differs chiefly in the longer vertebrae, the lower neural spine, the subcentral ridges originating lower on the paradiapophyses. In the same deposit it is most easily confused with *Ogmophis*, but separated on the basis of its longer centrum and the better developed diapophysial articular facets.

Genotype.—*Pseudocemophora antiqua*, sp. nov.

PSEUDOCEMOPHORA ANTIQUA,
sp. nov.

Diagnosis.—Sole known species of the genus.

Holotype.—UF 6458, a fairly complete precaudal vertebra, collected March, 1954, by Walter Auffenberg (Fig. 36).

Type Locality and Horizon.—Boulder Bar, Thomas Farm, Gilchrist County, Florida; Lower Miocene (Arikareean), Hawthorne fm.

Referred Material.—UF 5744; four somewhat more fragmentary vertebrae, collected at the same time from the same locality.

Type Description.—A colubrid vertebra with a relatively long centrum, which is provided with a sharp to truncated, haemal keel, extending from the cotyle to near the condylus, with a slight depression in the keel at approximately one third of its length. The subcentral ridges are well developed, extending from the diapophyses to the condylus. There are deep grooves between these ridges and the haemal keel. The paradiapophyses are well developed, with the parapophysial part possessing an articular facet which is well separated from the diapophysial one. The parapophysis is projected downwards and anteriorly to the ventral edge of the centrum. The neural arch is moderately low, long, and without epizygapophysial spines. The neural spine is long, low, overhanging posteriorly, straight anteriorly. Cotyle nearly round, but not distinctly oval. The condylus is on a short neck, projected backwards and slightly upwards. The zygosphene is crenate from above, convex from the front. Prezygapophysial articular surfaces probably obovate, but broken. The accessory processes are broken in the type, but in some of the referred specimens they are long, acute to acuminate, directed slightly anteriorly from above, laterally from the front. Measurements of vertebrae are given in Table 18.

Of particular interest is the relationship of this extinct genus with the modern forms. Along with *Paraoxybelis* (gen. nov.) it shares the distinction of being the earliest known colubrid from North America. Its relationships are apparently with, or close to *Cemophora*, *Rhinocheilus*, or *Lampropeltis*, espe-

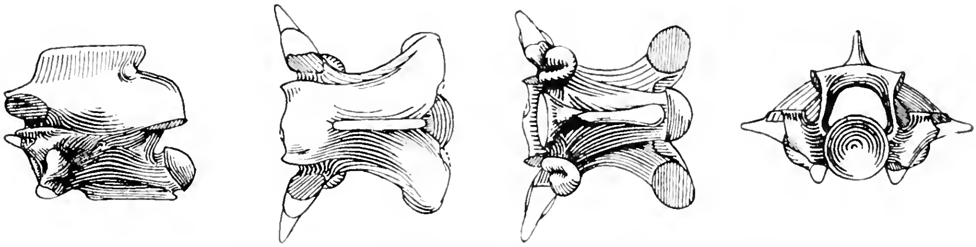

Figure 36. The type vertebra (UF 5744) of *Pseudocemophora antiqua*, gen. nov., et sp., Thomas Farm, Gilchrist County, Hawthorne fm., Lower Miocene (Arikareean).

TABLE 18.
Important measurements (in mm) and ratios of the available vertebrae (5) of Pseudocemophora antiqua

cl	2.52-3.15
naw	1.80-2.08
col	0.43-0.91
naw/cl	0.64-0.75
nlu/nh	2.47
zw	1.65-1.70
nh	0.61-0.81
ctw	0.94-1.07
ctw/cth	1.04-1.11
cl/nh	1.90-2.20
nlu	2.01
pr-pr	3.63
cth	0.86-1.09
cl/zw	1.47-1.54

cially the *doliata* group. Of these three genera, the available fossil vertebrae are closest to *Cemophora.*

In addition to the vertebrae, one small palatine (UF 6144, Fig. 37) is referred to this genus and species. In size, shape, and the number of teeth it seems close to *Lampropeltis* and *Cemophora.*

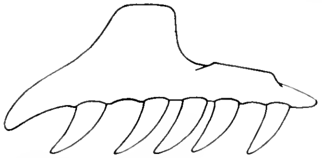

Figure 37. A palatine (UF 6144) from the Lower Miocene Thomas Farm locality, tentatively referred to *Pseudocemophora antiqua.*

The somewhat intermediate nature of the vertebrae and the palatine provisionally placed with them, is not surprising in view of the age of the fossils. *Lampropeltis* is frequently placed close to *Cemophora* by workers studying the Recent forms. However, too little is known of the extinct snake fauna of North America beyond the Pleistocene to draw any conclusions of evolutionary significance from this isolated find of elements apparently representing this group. It is of interest to know that such a form existed in the Lower Miocene, but the more important question of whether or not it is ancestral to either *Lampropeltis* or *Cemophora,* or both, is unknown at the present time.

Tantilla Baird and Girard

Description.—Middle precaudal vertebrae with a long centrum, with the subcentral ridges either weakly developed, or sometimes even absent. The haemal keel is narrow, keel-like, to gladiate in shape; or in some species even flattened, broad, oblanceolate, or cunate. There are two articulating surfaces on the paradiapophyses. The parapophysial process is only slightly projecting. The condyle is directed backwards more than upwards. The cotyle is rounded to very slightly oval. Neural arch long, low, depressed, without epizygapophysial spines. Neural spine long, low, with straight anterior and posterior edges. Zygosphene crenate to convex from above, convex from the front. Prezygapophysial facets oval to obovate. Accessory processes well developed, acuminate to acute, directed slightly anteriorly from above, and slightly downward from the front.

Comparative material includes the following: *Tantilla coronata* (3), *T. eiseni* (2), *T. nigriceps* (1) and *T. melanocephalus* (1). All of these species show the closest agreement in structure and vertebral ratios, and I find them impossible to tell apart. Remains of this genus from the Pleistocene of Florida are tentatively referred to *coronata,* which occurs in the peninsula at the present time. The genus has not been reported as a fossil previously.

Tantilla coronata Baird and Girard

This species is known from two localities in the State, Reddick I, B, from which a number of vertebrae are available (UF 6081, CNHM, PR. 375) and Arredondo I, A (UF 5921). Both of these localities are Middle or Late Pleistocene (Illinoian?).

Table 19 compares the vertebral ratios of Recent and Pleistocene vertebrae of this species. Figure 38 illustrates a middle precaudal vertebra.

PARAOXYBELIS, *gen. nov.*

Diagnosis.—A miocene colubrid snake which differs markedly from other known Miocene snakes in possessing a much longer centrum, a spatulate-shaped, flattened haemal keel, and very large prezygapophysial articular surfaces. In centrum length this form is approached only by *Oxybelis, Leptophis,* and *Uromacer* among New World colubrid snakes.

From *Oxybelis* and *Uromacer* it is distinguished clearly in not possessing the greatly overhanging anterior edge of the neural spine as is found in these two genera. From

TABLE 19.
A comparison of certain vertebral ratios in Pleistocene and modern specimens of Tantilla coronata

Ratios	Recent (N=40)	Pleistocene (N=33)
cl/naw	1.61-1.86	1.57-1.84
naw/zw	0.96-1.00	0.98-1.00
nlu/nh	3.21-7.80	3.68-7.73
pr-po/pr-pr	0.97-1.03	0.98-1.01
ctw/cth	1.00-1.06	0.98-1.03

Leptophis it differs chiefly in its higher neural spine (nlu nh: *Paraoxybelis* 3.24; *Leptophis* 2.48-2.59). In addition, it differs from these three genera in its larger prezygapophysial articular facets and the spatulate-shaped haemal keel, which is broadly gladiate in the three modern genera.

Genotype.—*Paraoxybelis floridanus*, sp. nov.

PARAOXYBELIS **FLORIDANUS**, *sp. nov.*

Diagnosis.—The sole known species of the genus. The generic diagnosis is given above.

Holotype.—UF 5134, a fragmentary precaudal vertebra, collected by Walter Auffenberg, March, 1954.

Type Locality and Horizon.—Boulder Bar, Thomas Farm, Gilchrist County, Florida; Hawthorne fm., Lower Miocene (Arikareean).

Type Description.—Vertebra typically colubrid. Centrum long, slightly depressed. Haemal keel flattened, extending from the lower lip of the cotyle to near the condylus, spatulate-shaped. Anteriorly the keel expands rapidly near the cotyle. Centrum flattened on either side of the keel. Subcentral ridges straight, well developed, extending from the diapophyses posteriorly to the condylus. The condylus is on a neck of moderate length, directed slightly obliquely. Cotyle round, narrower than the zygosphene. Paradiapophyses below, but set just under the base of the prezygapophyses, the two articular surfaces facing outward and downward. The diapophysial articular surface is somewhat oval, while the parapophysial one is more flattened, and pointing downward and slightly to the front, extending moderately below the level of the cotyle. Neural arch somewhat depressed, but not greatly. Epizygapophysial spines apparently missing. Neural spine long, low, not overhanging anteriorly or posteriorly. Zygosphene thin dorso-ventrally, with the facets approximately 45 degrees to the vertical, slightly crenate from above, convex from the front. Prezygapophysial articular facets oval, large, with very small accessory processes. Interzygapophysial ridges well developed. Neural canal nearly as wide as the zygosphene.

Two other vertebrae are tentatively assigned to this species. These are; UF 6007a, a well preserved caudal vertebra, and UF 6007b, a fragmentary precaudal vertebra, composed of only the centrum. In as many details as can be compared these specimens are similar to the type. The caudal vertebra has a proportionately higher neural spine in which both the anterior and posterior upper margins are somewhat overhanging. The smaller prezygapophysial articular facets of this vertebra, when compared with the type, are to be expected in the caudal region.

The specimen represented by a centrum only is logically placed with *P. floridanus*, on the basis of the ratio cl naw if on no other. As in the type, the centrum is long and narrow and the haemal keel is flattened and spatulate.

All of the available fossil vertebrae suggest an attenuate species of snake. When these fossils are compared with *Coluber* and *Masticophis* a considerable number of differences are found, with the exception of a general agreement in the shape of the haemal keel. Thus, the neural spine is different in shape; and the centrum is considerably

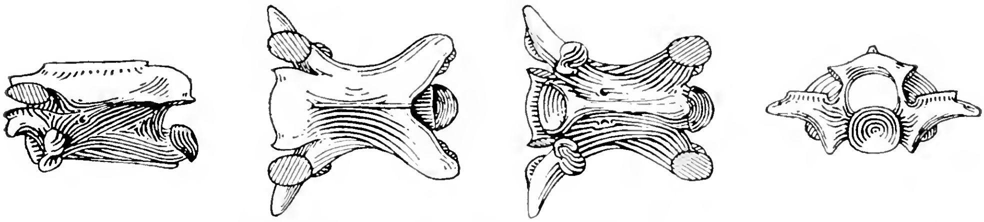

Figure 38. A precaudal vertebra of *Tantilla* cf. *coronata* (UF 6081) Reddick I B, Pleistocene (Illinoian ?).

longer (cl naw: *Coluber* 1.40-1.51; *Masticophis* 1.19-1.64; *Paraoxybelis* 1.86-1.99). On the other hand, the spatulate haemal keel is approached in *Coluber* and *Masticophis*, particularly the former.

The centrum length of *Paraoxybelis* is approached by *Leptophis* (cl naw = 1.73-1.92), *Oxybelis* (cl naw = 1.56-2.11) and even exceeded by *Uromacer* (cl naw = 1.97-2.03). However, all of these genera differ in a number of regards, as has been pointed out above.

Among the Old World colubrid snakes, the vertebrae of *Chlorophis* are slightly shorter (cl naw = 1.57-1.66), and those of *Dryophis* even longer (cl/naw = 2.20-2.28). In addition to the large prezygapophysial articular facets, the shape of the haemal keel, etc., clearly separates *Paraoxybelis* from these genera.

Of all the vertebral ratios which can be compared with those of modern genera, the closest agreement is found in the New World genus *Oxybelis*. However, the spatulate-shaped haemal keel and the large prezygapophysial articular facets are not found in *Oxybelis*. Thus, the relationships of the Miocene snake remain obscure, though it may be closer to *Oxybelis* than to any other Recent New World genus. This possible relationship is interesting in that another new genus of colubrid snake from the Upper Miocene of North America (Auffenberg, 1958) also may be closely related to a Central American snake, *Conophis*.

Figure 39 illustrates the available vertebrae of *Paraoxybelis floridanus*, while Table 20 gives the available vertebral ratios of this species.

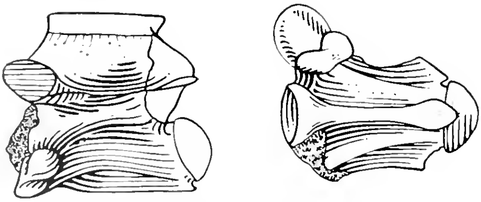

Figure 39. Left: Type vertebra (UF 5143) of *Paraoxybelis floridanus*, gen. nov. et sp., Thomas Farm, Gilchrist County, Hawthorne fm., Lower Miocene (Arikareean). Right: (UF 6007), a fragmental vertebra from the same locality, and referred to the same species.

TABLE 20.
The available vertebral ratios of Paraoxybelis floridanus (N = 2)

cl/naw	1.86-1.99
zw/naw	0.84
cl/nlu	1.47
cl/col	4.00-5.81
nlu/nls	1.19
naw/nah	2.20
cl/zw	1.64-2.20
nlu/nh	3.25
pr-po/col	1.18

2. *Subfamily Natricinae*

Description.—Colubrid vertebrae which possess well developed hypapophyses on all of the vertebrae. Epizygapophysial spines are usually present. The vertebrae are usually long, with well developed, acuminate to acute accessory processes, which are directed mainly laterally from above and from the front. The parapophyses are nearly always projected downwards and anteriorly so that they extend beyond the lower level of the centrum and the margin of the cotyle.

The problems in identifying vertebrae belonging to this subfamily are great. The main reason is simply that all snakes possess hypapophyses in at least the anterior part of the column. It is not always a simple matter to separate middle dorsal vertebrae of a natricine from anterior dorsals of a colubrine although in most cases this is possible. Furthermore, the various natricine genera possess vertebrae similar to one another, so in many cases certain genera and species can not be separated even after one is positive that the vertebrae belong to this subfamily. For the most part, anterior vertebrae are easy to recognize, largely on the basis of the ratio cl naw. In anterior vertebrae the centrum is shorter in proportion to the width than in the middle or posterior series. A comparison of this ratio in the anterior portion of the column in the Colubrinae with the entire column in the Natricinae will usually indicate sufficient differences between the various portions of the column so that middle precaudal members may be recognized by this means alone. As pointed out previously, the middle dorsal vertebrae are, by far, the best vertebrae to use in identifying fossils.

Characters other than the ratio cl naw may be useful in separating anterior and middle dorsal vertebrae. However, in many cases, the determination of middle dorsal vertebrae remains difficult at best, and here identifications are based more on the composition of the entire sample than on individual vertebrae. With the entire sample considered as a unit the middle precaudal elements become evident. In any case, the anterior vertebrae of colubrid snakes must be recognized as such before the middle precaudal vertebrae of the Natricinae can be compared.

Because of the considerable similarity between the vertebrae of various genera of this subfamily, the comparative material is listed below as a unit, rather than listed below each species as had been done in the Colubrinae. Skeletons of the following forms have been examined: *Seminatrix pygaea* (4), *Liodytes alleni* (8), *Haldea striatula* (3), *Haldea valerae* (1), *Storeria dekayi* (5, representing 3 subspecies), *Storeria occipitomaculata* (2, representing 2 subspecies), *Tropidoclonion lineatum* (2, representing 2 subspecies), *Thamnophis elegans hammondi* (1), *Thamnophis sirtalis* (6, representing 3 subspecies), *Thamnophis radix* (2, representing 2 subspecies), *Thamnophis sauritus* (6, representing 3 subspecies), *Thamnophis ordinoides* (1), *Thamnophis cyrtopsis* (1), *Thamnophis marciana* (1), *Thamnophis brachystoma* (1), *Natrix natrix* (2, representing 2 subspecies), *Natrix tesselatus* (1), *Natrix stolata* (1), *Natrix grahami* (1), *Natrix septemvittata* (4), *Natrix harteri* (2), *Natrix rigida* (1), *Natrix rhombifera* (2), *Natrix taxispilota* (6), *Natrix cyclopion* (6, representing 2 subspecies), *Natrix sipedon* (14, representing 6 subspecies), *Natrix erythrogastor* (2).

Various genera of snakes belonging to the family Colubridae possess hypapophyses besides those placed in the Natricinae. These include members of the Colubrinae, Xenoderminae, and Xenodontinae. The Xenoderminae are distinct and present no major problems in identification. On the other hand, certain colubrine and xenodontine genera are difficult to separate from the Natricinae on the basis of the middle precaudal vertebrae. In some of these genera the hypapophyses are found only on the posterior members of the column. These may be extremely difficult, if not impossible, to separate from natricines if only a few vertebrae are available. *Helicops* is such a form. Comparative material of this genus includes two species, *leopardinus* (2 specimens) and *caricaudae* (1 specimen).

Several colubrid genera possess a haemal keel which may become so well developed in individual species, or even specimens, that it must be considered a hypapophysis. Of the material I have examined, *Ninia* is an excellent example of this kind of variation. Comparative material of this genus includes *atrata* (1 specimen) and *sebae* (2 specimens).

Purely for purposes of vertebral identification, the New World natricines may be separated into two groups, based largely on the relative heights of the neural spine. Group I: vertebrae with a long centrum, and a low, long neural spine. The genera are usually rather small in total length. The group includes at least the following genera: *Haldea*, *Tropidoclonion*, *Seminatrix*, and *Storeria*. Group II: vertebrae with a moderate to long centrum, and a much higher neural spine than is found in Group I. The snakes in this group usually attain a greater adult size. It includes at least the following genera: *Natrix*, *Thamnophis*, *Liodytes*, and *Helicops* for those who wish to place this genus in the Natricinae.

Some species of *Natrix* (*septemvittata*, *rigida*, and *grahami*) might be considered intermediate in all of these characters.

Group I is composed of a somewhat varied assemblage of genera. Thus, *Storeria* apparently is characterized by a very long centrum and a high, narrow neural arch. *Haldea*, *Seminatrix*, and *Tropidoclonion*, in that order, approach the characteristics of Group II. The latter can be subdivided further into at least four groups. (a) *Liodytes-Helicops*, a group in which at least many specimens have the neural spine "ground-off" at the upper edge, particularly in the adults. (b) *Natrix rhombifera - taxispilota - cyclopion*, a group characterized by their large adult size, and by their very high neural spine, which is usually overhanging anteriorly in *cyclopion*, less so in *taxispilota* and *rhombifera*, especially in large specimens. (c) *Natrix sipedon-Thamnophis*, a group having a lower neural spine than subgroup (b), approaching *Tropidoclonion*, in *Thamnophis radix* and *T. brachystoma*. *Natrix erythrogastor* may belong to this group, but in this species the neural spine leans anteriorly more than it does in any other species of *Natrix* I have seen. (d) *Natrix septemvittata-rigida-grahami-harteri-natrix-stolata* and *tesselatus*. These species seem to form a group intermediate between those of Groups I and II, possessing long, low neural spines, but having shorter centra than in Group I. They are also intermediate in adult size between the extremes of Groups I and II.

The outline given above is not meant to convey phyletic concepts, but is added to aid in identifying snake vertebrae. There is, however, a suggestion in the groupings that seems to reflect relationship. Perhaps a more comprehensive examination of the vertebral types or skulls in this subfamily may shed considerable additional light on the relationships of the New World Natricinae as they are now defined.

Storeria cf. *S. dekayi* Holbrook

Description.—Centrum long, somewhat cylindrical to subtriangular from below, provided with a typical natricine hypapophysis on the ventral surface of each vertebra. The subcentral ridges are well developed, extending from the diapophyses posteriorly to near the condylus. Condylus on a short neck, oblique. Paradiapophyses with two articular facets. The parapophysial process is projected considerably anteriorly. The cotyle is rounded, but with two small projections at the ventral lip. The neural canal is large. The neural arch is very high, without epizygapophysial spines, or if present, faint. Neural spine longer than high, with overhanging anterior and posterior edges. The zygosphene is crenate from above, somewhat angular from the front. The prezygapophysial articular facets are oval in outline. The accessory processes are short.

Fossils representing this genus are now known from only a few Pleistocene localities in Florida. There are approximately forty vertebrae known from Reddick I, B. (UF 5047-8, 6241, 5045), two from Arredondo I, A. (UF 6223 and 5922) and one (UF 6222) from Mefford Cave. The genus has never been reported before in the fossil record.

The vertebrae of *Seminatrix* and *Haldea* are similar to those of *Storeria*. From the former the fossils differ in possessing a longer centrum. From *Haldea* the fossil vertebrae may be separated by the ratio nlu/zw, in which there is no apparent overlap (at least in the middle precaudal vertebrae) (Table 21). The fossil vertebrae from Reddick possess vertebral ratios practically identical to those found in *Storeria*, and are thus placed in this genus.

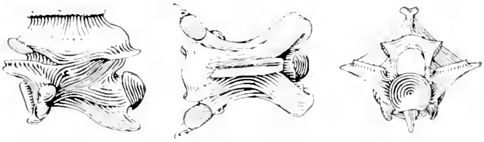

Figure 40. A precaudal vertebra of *Storeria dekayi* (UF 6241) Reddick I B, Pleistocene (Illinoian ?).

Examination of the vertebrae of *Storeria d. dekayi*, *S. d. victa*, *S. d. wrightorum*, *S. o. occipitomaculata* and *S. o. obscura* indicates that vertebrae of these forms apparently are difficult to separate on the basis of present knowledge. However, a comparison of the ratios of only the *middle* precaudal vertebrae of the two modern species and those of the fossils, indicates that the latter are, in all probability, *Storeria dekayi*. However, it should be pointed out that this comparison is only as good as the ability to distinguish middle precaudal vertebrae among the disassociated fossils. If *all* of the vertebrae of both the modern species and the fossils are tabulated a considerable overlap in ratios is found. Of particular importance is that there is then an extensive overlap with *Haldea* as well. Thus, at least *Storeria dekayi* is represented in the fossil sample. The absence of either *Haldea* or *Storeria occipitomaculata* is not assured. Figure 40 illustrates a fossil specimen of *Storeria dekayi* from Reddick, Florida. Table 21 compares the vertebral ratios in the two modern species of *Storeria*, *Haldea* and the fossil vertebrae.

TABLE 21.
A comparison of the vertebral ratios in Storeria, Haldea and the available fossil vertebrae

Ratios	*S. d.** (N=28)	*S. o.** (N=16)	*Storeria* (N=44)	*Haldea* (N=45)	Fossils (N=30)
po-pr/pr-pr	1.11-1.22	1.05-1.10	1.05-1.22	1.00-1.28	1.10-1.15
nlu/zw	1.23-1.36	1.60-1.64	1.23-1.64	1.06-1.20	1.33-1.57
nlu-nh	3.23-3.66	5.00-5.54	3.23-5.54	3.70-5.70	3.44-4.44
cl/naw	1.86-2.10	1.81-1.97	1.81-2.10	1.63-2.12	1.72-2.01

* *S. d.=Storeria dekayi* *S. o.=Storeria occipitomaculata*

Liodytes alleni Garman

Description.—Centrum moderate in length, provided with a well developed hypapophysis. Subcentral ridges strong, extending from the posterior lower edge of the diapophysis posteriorly to the condylus. Condylus on a short neck, very slightly oblique. Paradiapophysial articular facets well separated. The parapophysial process projects noticeably below, and in front of the centrum. The neural arch is moderate in height and width. Epizygapophysial spines are faint to strongly developed. Neural spine nearly as high as long, with the upper edge frequently "ground-off" in adult specimens. Zygosphene thin dorso-ventrally, crenate to convex from above, convex from the front. Prezygapophysial articular facets oval. Accessory processes lateral to slightly anterior from above, acute to somewhat obtuse, laterally directed from above.

The "ground-off" neural spine in some specimens of this species will separate them clearly from all other natricines of similar vertebral type. The presence of such vertebrae in a fossil deposit provides sufficient evidence for stating that this form occurs in the fossiliferous beds. In the xenodontine (?) genus *Helicops*, which has similar vertebrae, the epizygapophysial spines are much reduced compared with those of *Liodytes*. In addition, the neural spine is not as obviously "ground-off." There is some evidence that a neural spine of this type is variable in at least *Storeria dekayi*. The character may be sexually dimorphic in some genera (*Ninia*), ontogenetically variable in all genera in which it occurs, and a pathologic condition in individuals of many species in various families of snakes. Fossil or modern specimens lacking this peculiar neural spine would be readily confused with *Natrix sipedon*. However, the latter attains a much larger size.

Liodytes has not been reported as a fossil previously. Fossil vertebrae from Florida referred to this genus are available from the following localities: Winter Beach Locality, UF 5520, 5536 (2). Itchtuckanee Springs I. UF 5404, 5394, 5381, 5309, 5396, 5318, CMNH, Pr. 366.

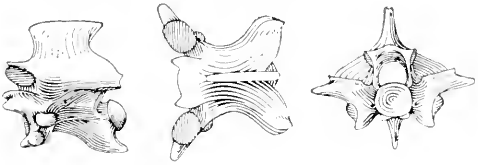

Figure 41. A precaudal vertebra of *Liodytes alleni* (UF 5536) Winter Beach-Luther Locality, Late Pleistocene ?

Figure 41 illustrates a middle dorsal vertebra of this species.

Natrix Laurenti

Description.—Centrum moderate in length, provided with a well developed hypapophysis. Subcentral ridges strong, extending from the posterior, lower edge of the diapophysis to near the condylus. Condylus on a short neck, slightly oblique. Paradiapophysial articular facets well separated. The parapophysial process is projected considerably below and anterior to the lower lip of the cotyle. The neural arch is moderate in height and width. The epizygapophysial spines usually are well developed. The neural spine is variable in height and length, never "ground-off," except in pathological individuals. Zygosphene thin dorso-ventrally, crenate, convex or straight from above, convex to straight from the front. Prezygapophysial articular facets oval to obovate. Accessory processes fairly long, acuminate to acute, directed laterally to slightly anterior from above, laterally from the front.

Numerous moderate to large-sized vertebrae are found in the Pleistocene and the Pleistocene and/or Recent deposits of Florida which are referrable to this genus. Vertebrae of *Thamnophis* apparently can be separated from those of most species of *Natrix* on the basis of the ratio cl/naw (*Natrix* 0.96-1.41, *Thamnophis* 1.36-1.99). The flattened upper edge of the neural spine apparently distinguishes most adult specimens of *Liodytes* from both *Thamnophis* and *Natrix*.

Among the fossils from Florida are a large number of moderate to very large vertebrae which possess relatively higher neural spines than occur in any natricine, with the exception of *Natrix cyclopion*, *N. rhombifera*, and *N. taxispilota*. One of these three species, *cyclopion*, can be separated in the majority of cases by the presence of an overhanging anterior edge on the neural spine. In *taxispilota* and *rhombifera* the anterior edge is generally straight. However, there is at least some variation in this character along the centrum and not all of the vertebrae can be assigned definitely to either spe-

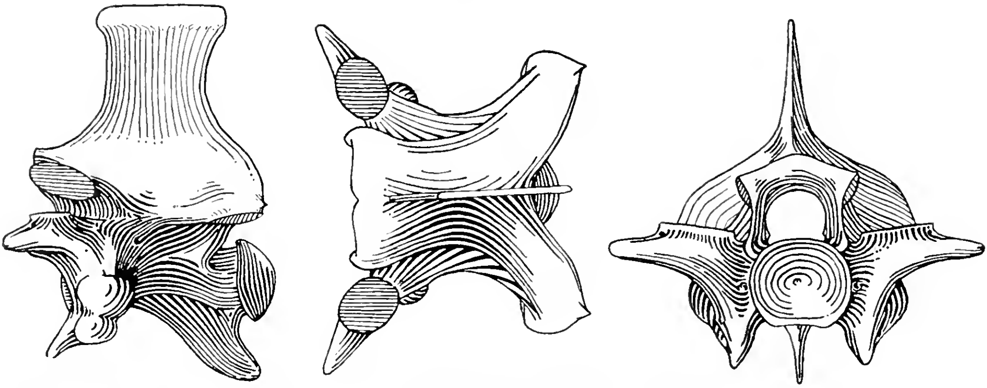

Figure 42. A precaudal vertebra of *Natrix cyclopion* (UF 4292) Itchtuckanee Springs A, Pleistocene and/or Recent.

cies. If only extremes are taken into consideration the presence of these species in a deposit can be determined fairly readily. Both types are now known from deposits in Florida.

Natrix cyclopion Dumeril and Bibron

Description.—Centrum moderate in length, subtriangular when seen from below, provided with well developed subcentral ridges, extending from the diapophyses posteriorly to the condylus. Condylus on a short neck, moderately oblique. Hypapophyses strongly developed, sigmoid-shaped from the side. Paradiapophysial process projected anteriorly well beyond the level of the lower lip of the cotyle; cotyle rounded. Neural arch moderate in height and width, wider in larger specimens. Epizygapophysial spines usually well developed. Neural spine high, short, with overhanging posterior and anterior edges. Zygosphene thin dorso-ventrally, crenate to convex from above, convex from the front. Prezygapophysial articular facets oval to obovate. Accessory process well developed, long, acuminate to acute, directed laterally from above, laterally from the front.

This species has not been reported as a fossil previously. Fossil specimens are known from the following Pleistocene localities: Haile I, A. UF 5471, 5814. Bradenton Field A. UF 5910.

In addition, a number of specimens are known from several deposits at Itchtuckanee Springs, a Pleistocene and or Recent locality: Locality A. UF 4281-6, 4292, 5926, 5354, 5286, 5255, all vertebrae. One maxillary (UF 4287) from the same locality is tentatively assigned to this species. Jug Springs Locality. UF 5850, 5854, 5862, 5867, 5884, 5887, all vertebrae.

One vertebra of this species is illustrated in Figure 42. Table 22 compares the vertebral ratios of modern and Pleistocene specimens of this species with modern and Pleistocene vertebrae of *Natrix taxispilota.*

Natrix taxispilota Holbrook

Description.—Centrum moderate in length, subtriangular when seen from below, pro-

TABLE 22.
A comparison of certain vertebral ratios in modern and fossil vertebrae of Natrix cyclopion and Natrix taxispilota

	Natrix cyclopion		*Natrix taxispilota*	
Ratios	Recent (N=45)	Pleistocene (N=50)	Recent (N=40)	Pleistocene (N=43)
cl naw	1.01-1.21	1.05-1.15	0.93-1.17	1.00-1.19
naw pr-po	1.18-1.34	1.23-1.30	1.08-1.27	1.10-1.23
nlu nls	1.28-1.43	1.25-1.33	1.38-1.44	1.32-1.41
nlu nh	0.85-1.12	0.92-1.08	0.75-1.09	0.86-1.10
naw nah	1.42-1.55	1.46-1.50	1.38-1.71	1.42-1.63
pr-pr po-pr	1.08-1.23	1.11-1.24	1.00-1.17	1.04-1.21
naw zw	1.00-1.09	1.05-1.09	1.00-1.11	1.02-1.09
cl zw	1.08-1.36	1.11-1.27	1.12-1.36	1.06-1.30

vided with well developed subcentral ridges extending from the diapophyses posteriorly to the condylus. Condylus on a short neck, moderately oblique to very slightly oblique. Hypapophyses strongly developed, sigmoid-shaped from the side. Paradiapophysial articular surfaces well separated. The parapophysial process is projected strongly below and anterior to the lower lip of the cotyle. Cotyle rounded. Neural spine high, short, with a straight anterior edge, overhanging posteriorly. In small specimens of *N. cyclopion* the anterior edge of the neural spine may be straight, as in most specimens of *taxispilota.* Zygosphene thin dorsoventrally, crenate to convex from above, convex from the front. Prezygapophysial articular facets oval to obovate. Accessory processes well developed, long, acuminate to acute, directed laterally from above and from the front.

This species has not been reported as a fossil. Fossil specimens are known from the following Pleistocene localities: Haile I, A. UF 5474, 5483, 5510, 6324, 5493, 5556, 6164, 5811, 5816.

In addition a number of specimens are known from the Itchtuckanee River area, as follows: Locality A. UF 5344, 5221, 5216, 6191, 4305, 5379, 4295, 5391, 6495, 5444, 5254, 5228, 5390, 5283, 5250, 4298, CNHM, PR. 363.

A single middle precaudal vertebra is illustrated in Figure 43. Table 22 compares the vertebral ratios of modern and Pleistocene specimens of this species with modern and Pleistocene vertebrae of *Natrix cyclopion.*

In addition to the specimens listed above under *N. taxispilota* and *N. cyclopion,* the following specimens represent one or the other species, but they are too fragmentary for exact determination: Pleistocene: Haile I, A. UF 5504, 5522. Pleistocene and/or Recent: Itchtuckanee Springs, Locality A. UF 5272, 5343, 5413, 5249, 5257, 5393, 5365, 5330, 5288, 5253. Jug Springs Locality. UF 5888, 5892.

Natrix erythrogaster Forster

Description.—Centrum moderate in length, subtriangular when seen from below, provided with well developed subcentral ridges, extending from the diapophyses posteriorly to near the condylus. Condylus on a short neck, moderately oblique. Hypapophyses strongly developed, sigmoid-shaped from the side. Paradiapophysial articular facets well separated. The parapophysial process is projected strongly below and anterior to the lower lip of the cotyle. Cotyle round. Neural arch moderate in height and width, wider in large specimens. Epizygapophysial spines usually well developed. Neural spine high, short, with a straight anterior edge (rarely overhanging), leaning anteriorly, slightly higher than long, overhanging posteriorly. Zygosphene thin dorsoventrally, crenate to convex from above, convex from the front. Prezygapophysial facets oval to obovate. Accessory processes well developed, long, acuminate to acute, directed laterally from above and from the front.

On the basis of the available comparative specimens the vertebral ratios of *N. erythrogaster* and *N. sipedon* are practically identical. However, in the former the neural spine usually leans anteriorly, whereas it is perpendicular to the main axis of the cen-

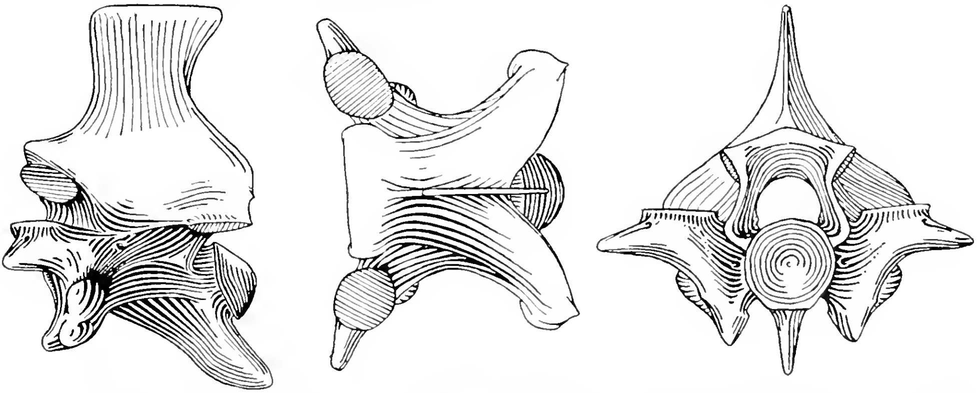

Figure 43. A precaudal vertebra of *Natrix taxispilota* (UF 5391) Itchtuckanee Springs A, Pleistocene and/or Recent.

trum in *N. sipedon.* Not every individual vertebra can be assigned with certainty to one or the other species, since considerable variation occurs throughout the column, and from one individual to the next. However, by taking the extremes the presence or absence of either species usually can be demonstrated for each fossil sample.

Only a few isolated vertebrae have been found in Florida which are referrable to this species. These specimens all come from the same locality, Haile I, A. (UF 5559, 5038). The species has not been reported as a fossil previously.

Figure 44 illustrates one of the fossil vertebrae of this species.

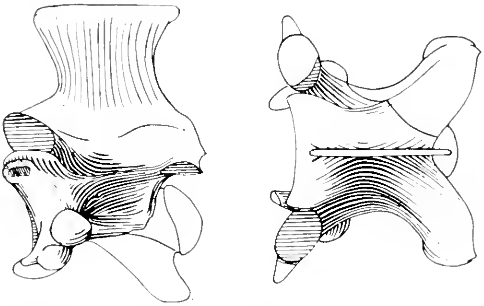

Figure 44. A precaudal vertebra referred to *Natrix* cf. *erythrogaster* (UF 5038) Haile I A, Pleistocene.

Natrix sipedon Linnaeus

Description.—Centrum moderate in length, subtriangular when seen from below, provided with well developed subcentral ridges, extending from the diapophysis posteriorly to near the condylus. Condylus on a short neck, moderately oblique. Hypapophyses strongly developed, sigmoid-shaped from the side. Paradiapophysial articular facets well separated. The parapophysial process projected strongly below and anterior to the lower lip of the cotyle. Cotyle round. Neural arch moderate, wider in larger specimens. Epizygapophysial spines usually well developed. Neural spine approximately as high as long, more or less perpendicular to the main axis of the centrum, overhanging posteriorly, rarely anteriorly. Zygosphene thin dorso-ventrally, crenate to convex from above, convex from the front. Prezygapophysial facets oval to obovate. Accessory process well developed, long, acuminate to acute, directed laterally from both above and from the front.

This species is most easily confused with *Natrix erythrogaster.* Most vertebrae can be separated on the basis of the shape of the neural spine. In *sipedon* the spine is directed upwards, rarely anteriorly. In *erythrogaster* the spine is directed anteriorly, that is, it appears to lean forward. A fossil vertebra of *erythrogaster* is illustrated in Figure 44. An isolated vertebra of *N. sipedon* is illustrated in Figure 45. Table 23 compares the vertebral ratios of modern and fossil vertebrae of *Natrix sipedon.*

TABLE 23.
A comparison of certain vertebral ratios of Recent and Pleistocene vertebrae of Natrix sipedon

Ratios	Recent (N=60)	Pleistocene (N=21)
cl/naw	1.21-1.49	1.26-1.33
nlu/nls	1.09-1.36	1.28-1.32
pr-pr/po-pr	1.18-1.34	1.28-1.31
naw/zw	1.03-1.09	1.06-1.10
cl/zw	1.18-1.41	1.23-1.36
nlu/nh	1.29-1.62	1.37-1.53
naw/po-pr	1.05-1.18	1.12-1.19
naw/nah	1.28-1.40	1.32-1.38

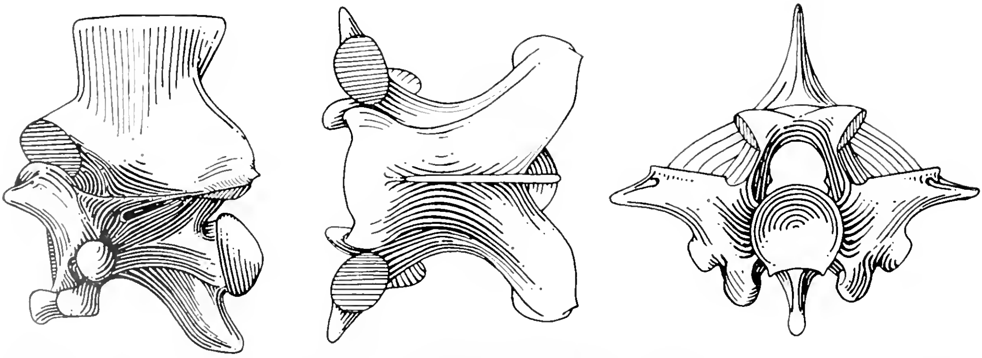

Figure 45. A precaudal vertebra of *Natrix sipedon* (UF 9867) Haile VII A, Pleistocene (Illinoian ?).

Isolated vertebrae of this species are known from the following localities: Pleistocene: Haile I, A. UF 5033, 5468, 5478, 5491, 5550, 5541, 5815, 6318. Arredondo I, A. UF 6060-1. Haile VII, A. UF 9867. Saber Tooth Cave. FGS V-5717 (Holman, 1958).

In addition, a number of vertebrae assigned to this species are known from the various localities at Itchtuckanee Springs, a Pleistocene and or Recent series of deposits: Locality A. UF 4297, 4304, 4299, 4296, 4306, 5363, 5430, 5373, 5296, 5292, 5352, 5327, 5387, 5243, 6252. Jug Springs Locality. UF 5857, 5855.

A small series of specimens (UF 6453) is known also from Hornsby Springs.

Thamnophis Fitzinger

Description.—Centrum long, subtriangular from below, provided with well developed subcentral ridges, extending from the diapophyses posteriorly to near the condylus. Condylus on a short neck, slightly oblique. Hypapophyses strongly developed, and sigmoid-shaped from the side. Paradiapophysial articular facets well separated. The parapophysial process is projected strongly below and anterior to the lower lip of the cotyle. Cotyle rounded. Neural arch moderate to low. Epizygapophysial spine usually well developed. Neural spine longer than high, to as long as high, overhanging anteriorly or not, always overhanging posteriorly. Prezygapophysial articular facets oval to obovate. Accessory processes well developed, long, acuminate to obtuse, directed laterally to slightly downward from the front.

Unfortunately, not only is there a general lack of comparative material of the species composing this genus, but from the available material, obviously many species cannot be separated on vertebral characters alone. However, the fossil elements from Florida can be separated from the *radix* group in having a neural spine which is higher than in that group. From *Thamnophis sauritus* they can be separated on the basis of the ratio cl naw (*sauritus* 1.20-1.33; fossils 1.62-1.81). *Thamnophis cyrtopsis* also possesses a shorter centrum than do the fossils from Florida (cl naw = 1.13-1.23 in *T. cyrtopsis*). The fossil vertebrae cannot be separated from *T. sirtalis*. On the other hand, *T. sirtalis* does not seem to be separable on vertebral characters alone from the remaining species in the genus not mentioned above. The fossil vertebrae from Florida are referred to *sirtalis* on zoogeographic grounds.

Thamnophis cf. *T. sirtalis* Linnaeus

Because of the similarity of the vertebrae of species in this genus a separate description of the vertebrae of *T. sirtalis* is not given. Reference should be made to the generic description.

A large number of isolated vertebrae are known from two localities within the state that are referred to this species. One of these localities is Pleistocene, and the other Pleistocene and or Recent. Isolated vertebrae occur in a number of localities in the state. Pleistocene: Reddick I, B. Approximately 50 vertebrae, UF 6040-1, 6115, 6110, 5802, 6402, 5106, 6039, 5166, 6042, 6138, 5167, 6258, 6095, 6312, 6073, 6016, 6345. Payne's Prairie B. UF 5755. Mefford Cave I. UF 2555. Arredondo I, A. UF 4294. Arredondo II, A. UF 2074. Winter Beach. UF 5834. Haile VII, A. UF 5182, 5199, 5147, 6089. Bradenton A. UF 5913. Williston, FGS V-5806 (Holman, 1959). Pleistocene and/or Recent: Itchtuckanee Springs A. UF 6493, CNHM, P.R. 370. Hornsby Springs, UF 6268.

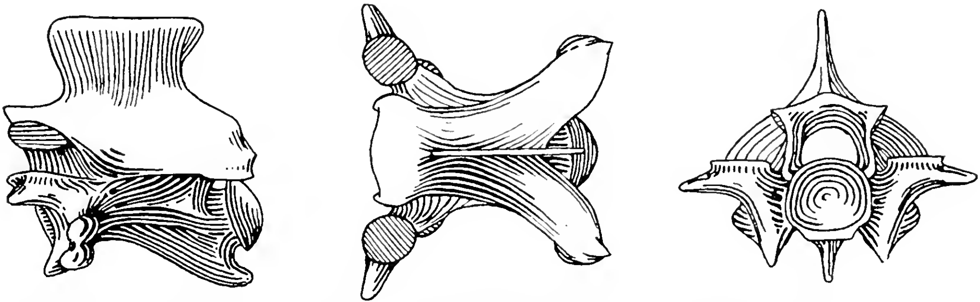

Figure 46. A precaudal vertebra of *Thamnophis sirtalis* (UF 6402) Reddick I B, Pleistocene (Illinoian ?).

A middle precaudal vertebrae is illustrated in Figure 46. Table 24 compares both fossil and modern vertebrae of *Thamnophis sirtalis.*

TABLE 24.
A comparison of certain vertebral ratios in Recent and Pleistocene vertebrae of Thamnophis sirtalis

Ratios	Recent (N=52)	Pleistocene (N=29)
cl/naw	1.60-1.80	1.62-1.81
pr-pr/po-pr	1.00-1.05	1.01-1.06
zw/naw	1.03-1.11	1.03-1.12
cl/zw	1.47-1.66	1.50-1.62
nlu/nh	1.52-1.83	1.47-1.78

Many hundreds of vertebrae, obviously representing various genera of the Natricinae are represented in the collections. However, to list these would serve no real purpose, since in no case is more than a generic identification possible. Undoubtedly, with further study, especially of vertebrae from the Reddick I, B. locality, *Haldea,* and perhaps some of the smaller species of *Natrix* will be found. There are, as yet, no vertebrae which indicate definitely the presence of species other than those described above.

F. *Family Elapidae*

Description.—Hypapophyses well developed throughout the vertebral column, straight, not as sigmoid-shaped as in the Natricinae, strongly compressed, pointed, directed posteriorly. Centrum long, with subcentral ridges well developed. Condylus on a short to moderate neck, moderately oblique. Cotyle rounded to oval. Paradiapophyses well developed, with the articular surfaces well separated, with the parapophysial process projected downwards and forwards, well beyond the lower lip of the cotyle. Neural arch usually depressed, without epizygapophysial spines. Neural spine low, long, to as high as long. Anterior edge overhanging or straight. Posterior edge always overhanging, except in a few burrowing forms. Zygosphene thin dorso-ventrally, crenate, straight or convex from above, convex to straight from the front. Maxillary poison teeth fixed in position, grooved or hollow, with or without additional posterior maxillary teeth, which are not specialized to conduct poison.

Vertebrae of the following genera have been examined: *Micrurus, Naja, Bungarus, Dendroaspis, Notechis, Haemachatus, Denisonia,* and *Ophiophagus.* In addition, the vertebrae of three genera of Hydrophidae have been examined: *Hydrophis, Laticauda,* and *Pelamis.* The vertebrae of the hydrophid snakes, though generally shorter and higher than most elapids, are similar to the latter, and if occurring as fossils probably would be placed in the family Elapidae.

Most elapid snakes possess vertebrae that vary slightly from the general description given above. However, *Bungarus* deserves special mention. In this genus the vertebrae are somewhat unusual in that the accessory processes have developed laterally into broad, flattened structures. As far as I am aware this is absent in genera belonging to other snake families, with the exception of certain xenodermines among the Colubridae.

Fossil elapids from Florida are represented by vertebrae and various portions of the skull and mandible. These constitute the first record of the Elapidae as fossils in the New World. The long, low, narrow centrum, low haemal spine and small size of these fossils all suggest a reference to genera such as *Micruroides* or *Micrurus.* The absence of any non-conducting teeth behind the enlarged fang on the maxillary suggests that at least the Pleistocene fossils represent the genus *Micrurus,* rather than the other American elapids, *Micruoides* and *Leptomicrurus.* In addition to the Pleistocene remains, one fragmentary vertebra from the Pliocene locality of Haile VI, A is tentatively referred to the genus *Micrurus.*

Micrurus Linnaeus

Description.—Each maxillary with one, or rarely two functional poison fangs, with no auxiliary teeth behind the fang, which is erect and fixed.

Middle precaudal vertebrae of typical small elapid type, with very slightly compressed, fairly straight, pointed hypapophyses, extending the entire length of the centrum. Centrum long, low, narrow, somewhat cylindrical, with strong subcentral ridges; cotyle rounded, with or without emarginated lower edge, Condyle directed more posteriorly than dorsally. Paradiapophyses well developed, parapophysial articular facets are oval to obovate. The accessory processes are acute, moderately long, directed laterally from above and from the front. Neural arch low, long, without epizygapophysial spines. Neural spine very low, long, usually with a straight anterior edge; posterior edge overhanging, at least slightly. Zygosphene convex from above, and from the front.

The vertebral columns of the following species of *Micrurus* were examined: *M. circinnalis* (1), *M. frontalis* (1), *M. corralinus* (1), *M. fulvius* (12), and *M. n. nigrocinctus* (1). Comparison of the actual vertebrae and the vertebral ratios of the several forms listed above show a close similarity among the species.

Micrurus sp.

One fragmentary vertebra (UF 9676) from the Pliocene locality of Haile VI, A is tentatively assigned to this genus. The hypapophysis, though broken, is provided with a long base and directed posteriorly as in the Recent genus. In addition, the centrum is long and the neural spine long and low. The latter is, however, higher than in most vertebrae of Pleistocene or Recent specimens of *Micrurus fulvius*. Although seemingly distinctive in this feature, description of this form as a new species is delayed until more complete material becomes available.

Micrurus cf. *M. fulvius* Linnaeus

The fossil *Micrurus* from the Florida Pleistocene cannot be assigned to any particular species with any degree of certainty, since all of the species of the genus are so similar. However, on zoogeographical grounds, as well as the composition of the remaining Pleistocene snake fauna of Florida, a tentative assignment to *fulvius* seems warranted.

Vertebrae of fossil coral snakes are known from the following localities in the state, all Pleistocene: Haile VIII, A. UF 6211, 6303 (4). Saber Tooth Cave U-5727 (Holman, 1958). Arredondo I, A. UF 6059, 6062. Williston FGS V-5808 (Holman, 1959). Reddick I, B. UF 6135 (64), 6136 (3), 6336, 6082 (80), 6178 (6), 4312, 5215 (20 vertebrae, all from the same specimen), 5311 (6 vertebrae, all from the same specimen), 6181-2, 5917 (1 complete maxillary with poison fang in place, and 1 complete surangular, from the same specimen), 5918 (the posterior portion of a cranium), MCZ 7608 (a few vertebrae and CHNM, P.R. No. 372 (a few vertebra).

About 200 vertebrae of this genus are now available from Florida Pleistocene deposits. A typical middle precaudal vertebra is illustrated in figure 47. Table 25 compares the range of variation in certain ratios obtained from six Recent specimens of *Micrurus fulvius fulvius* with the same ratios in 63 vertebrae from the Reddick Locality. The mandibular and cranial elements are identical to those found in *M f. fulvius.*

TABLE 25.
Comparison of vertebral ratios in modern and Pleistocene vertebrae of Micrurus fulvius

Ratios	Recent (N=53)	Pleistocene (N=60)
cl/naw	1.48-1.81	1.31-6.60
cl/col	5.46-6.29	4.24-6.60
ctw/cth	0.98-1.04	0.96-1.12
pr-pr/po-pr	1.01-1.07	0.95-1.08
naw/zw	0.92-1.16	0.94-1.22
cl/zw	1.49-1.74	1.45-1.93
nlu/nh	3.41-4.04	3.06-3.78

G. *Family Viperidae*

Description.—Centrum short, with well developed subcentral ridges, extending from the diapophyses posteriorly to near the condylus. Condylus large, on a short neck, directed posteriorly. Paradiapophysial articular

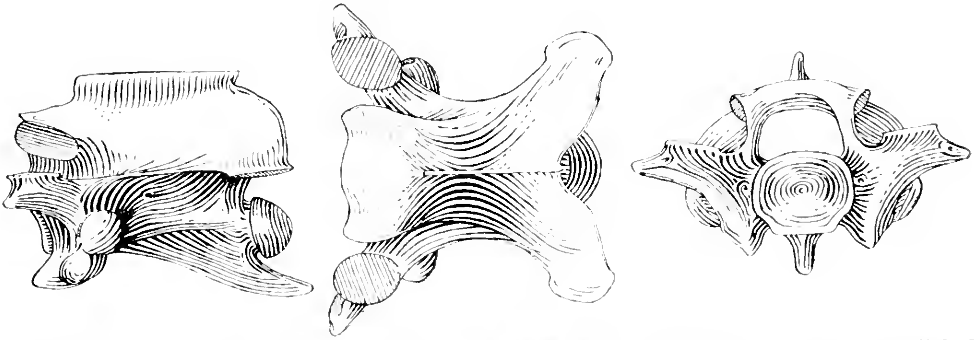

Figure 47. A precaudal vertebra referred to *Micrurus* cf. *fulvius* (UF 6135) Reddick I B, Pleistocene (Illinoian ?).

facets well separated, the parapophysial process projected anteriorly and ventrally, well beyond the lower lip of the cotyle. Hypapophyses long, not compressed laterally, straight, on all of the vertebrae, sometimes thickened distally. Cotyle obviously oval to round, depending on age and/or position in the column. Neural arch wide, short, depressed, sometimes with epizygapophysial spines. Neural spine from slightly longer than high to much higher than long, either straight at the anterior edge or overhanging, usually overhanging posteriorly. Zygosphene thin to somewhat thickened dorsoventrally, crenate or angular from the front. Prezygapophysial articular surfaces oval, obovate or subtriangular. Accessory processes not well developed, hardly projecting beyond the outer margins of the prezygapophysial articular facets.

Vertebrae of the following genera were examined: *Azemiops, Agkistrodon, Bitis, Bothrops, Causus, Crotalus, Sistrurus, Trimeresurus,* and *Vipera.*

Among the viperines, the genus *Vipera* seems most distinctive. The vertebrae are longer than in the other genera examined. The neural spine is lower than in most, and epizygapophysial spines are fairly well developed. These characters are somewhat approached by *Causus.* There is a tendency in the Viperinae for the hypapophysis to be proportionately shorter than it is in the Crotalinae. However, *Bitis arietans* approaches the condition found in the Crotalinae, since the hypapophyses in this genus are fairly long.

The fossil viperid vertebrae from Florida most certainly represent the Crotalinae rather than the Viperinae. Comparative material of Recent forms in the Crotalinae includes the following: *Agkistrodon halys* (1), *A. contortrix* (4), *A. piscivorus* (8), *A. bilineatus* (1), *Bothrops atrox* (3), *B. jararacussu* (1), *B. schlegelii* (2), *B. neuweidii* (3), *B. alternata* (1), *Crotalus adamanteus* (8), *C. horridus* (4), *C. ruber* (1), *C. atrox* (2), *C. mitchelli* (1), *C. tigris* (1), *C. durrissus* (2), *C. molossus* (1), *Sistrurus miliarius* (6), *S. catenatus* (3), and *Trimeresurus viridisoma* (1).

A variety of vertebral types are found in this subfamily. The genus *Bothrops,* for example, is made up of at least two groups on the basis of vertebral form. In *Bothrops schlegelii* the vertebrae are much longer in proportion to their width than in any of the other species examined. The vertebrae of *B. atrox* and *B. neuweidii* are somewhat intermediate. The remaining species examined have much wider vertebrae in proportion to their length. *Bothrops schlegelii* approaches the condition found in *Trimeresurus, Agkistrodon,* and *Sistrurus;* genera in which the vertebrae are usually somewhat lengthened. In *Agkistrodon, A. contortrix* possesses a longer vertebra than *A. piscivorus* and *A. bilineatus,* the latter being somewhat intermediate between the two other species. The genus *Crotalus* seems to be composed of species all of which possess short centra. However, the more primitive species, *triseriatus* and related forms, have not been examined, and perhaps they too possess the longer vertebrae observed in other genera in this subfamily.

Among the Pleistocene fossil viperid remains from Florida, there are a large number of vertebrae which have a rather long centrum, a proportionately low neural spine, and all of moderate size, which certainly seem to represent the genus *Sistrurus.* They can be separated from vertebrae of *Bothrops schlegelii* in centrum length and in that they possess higher neural spines; from *Trimeresurus* by the much more projected lower diapophysial process; from *Agkistrodon* and *Crotalus,* as well as the remaining species of *Bothrops,* by their longer centrum.

Sistrurus Garman

Description.—Vertebrae of typical basic viperid type; *i.e.,* with long, straight hypapophyses, directed downward more than backward. Subcentral ridges strongly developed, extending from the diapophyses to the condylus. Parapophysial process strongly developed, greatly projected anteriorly and downward, beyond the lower lip of the cotyle. Paradiapophyses with well developed articular surfaces, separated, the diapophysial member much more obviously rounded. Cotyle almost always round. Condylus on a short neck, only slightly oblique. Neural arch moderately depressed, long, with or without faint epizygapophysial spines. Neural spine moderately high, approximately as high as long. Zygosphene thin dorsoventrally, convex, crenate, straight or sometimes concave from above, convex or angular from the front, sometimes with a small median tubercle, or with a small dorsally-directed process at the base of the zygosphene, just anterior to the neural spine. A keel may or may not be present on the dorsal surface of the zygosphene. Zygosphene wider than the cotyle. Prezygapophysial articular facets oval to obovate, sometimes subrectangular.

The rounded cotyle, virtual absence of epizygapophysial spines, wide zygosphene, small size, longer and narrower centrum will usually suffice to separate it from practically all other viperid snakes. In most small specimens of *Crotalus* the cotyle is oval in shape when the zygosphene is convex. In *Sistrurus* the zygosphene is convex from the front, but the cotyle is always much more rounded than oval. However, not every vertebra can be identified with certainty, especially as fossils, since correct identification depends on a perfectly preserved specimen.

The two species of *Sistrurus* available as comparative material, *catenatus* and *miliarius* have similar vertebrae. On the basis of the available skeletons, they are most easily separated by the ratios zw/cl, ctw/cth, and cl/naw. In the latter two ratios there is considerable overlap, but extremes can be identified. In the case of the former only a slight overlap appears to exist. On the basis of these three ratios the fossil vertebrae from Florida seem closer to *miliarius*, and they are assigned to this species.

Some of the fossil vertebrae exceed the size of those of Recent specimens with the possible exceptions of individuals from southern Florida. In this area, *Sistrurus miliarius* attains a greater size than in any other part of its range. This is also the population which Gloyd (1940) chose as probably representing the most primitive one of the species. The fossil vertebrae, collected mainly from central Florida, may be interpreted as supporting this general hypothesis; *i.e.*, that the Florida population of *S. miliarius* is more primitive than those to the north and west of this area. However, other factors may be responsible for the presence of somewhat larger vertebrae of this species in the Pleistocene of Florida than are found in the general area at the present time. Climate has been thought to be important in bringing about larger size in other Pleistocene snakes (Brattstrom, 1953b).

Sistrurus miliarius Linnaeus

Specimens representing this species are now known from the following localities, all Late Pleistocene: Haile VII, A. UF 6425 (3), 6427 (3), 6426 (3), 5614 (1), 6435 (27), 5189 (1). Williston, FGS V-5809 (Holman, 1959). Reddick I, B. UF 5637 (1), 5604 (1), 6416-18 (7), 6442 (1), 6311 (1), 6441 (1), 6443 (1), 5108 (1), 6066 (1), 6051 (1), 5640 (1), CNHM, P.R. 371 (5).

Figure 48 illustrates a middle precaudal vertebra. Table 26 compares the vertebral measurements and ratios of the fossil vertebrae with those of *S. catenatus* and *S. miliarius.*

The remaining viperid vertebrae from Florida apparently belong to both *Agkistrodon* and *Crotalus.* These two genera are not always separable on vertebrae alone. However, both genera seem to be represented in the Pleistocene deposits of the state.

Agkistrodon Beauvois

The vertebrae of large specimens of both *Agkistrodon piscivorus* and *Crotalus* are sometimes difficult to separate. In *Agkistrodon piscivorus* there is a tendency for the neural spine to be lower, thinner, and without a thickening on the upper anterior edge. The hypapophysis is, in general, shorter. The parapophysis is more projected, the projections being more parallel from below; not shorter and usually more diverging as in *Crotalus.* The area between the lateral edge of the cotyle and the buttressed base of the prezygapophysis is more deeply indented in *Agkistrodon piscivorus.* The prezygapophysial articular surfaces are usually more

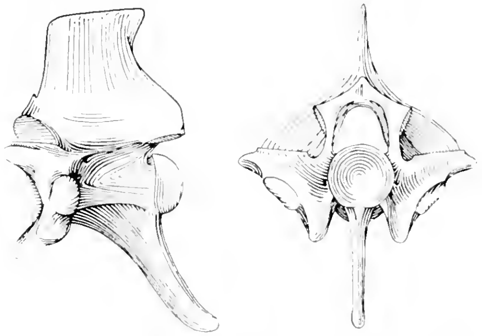

Figure 48. A precaudal vertebra of *Sistrurus miliarius* (UF 6417) Reddick I B, Pleistocene (Illinoian ?).

TABLE 26.

Comparison of vertebral measurements (in mm) and ratios in Recent specimens of Sistrurus miliarius, S. catenatus and Pleistocene vertebrae from Florida

Ratios	*Sistrurus miliarius* (N=52)	*Sistrurus catenatus* (N=25)	*Fossils* (N=20)
cl	3.28-4.19	3.28-4.14	3.35-4.70
naw	2.34-3.12	2.34-3.05	2.79-3.91
cl/naw	1.04-1.42	0.98-1.23	1.06-1.37
ctw	1.42-2.06	1.52-2.92	1.60-2.21
cth	1.40-2.03	1.45-2.87	1.78-2.29
ctw/cth	0.93-0.99	1.00-1.12	0.95-1.06
zw	2.36-3.12	2.62-4.37	2.46-2.95
zw/cl	0.67-0.76	0.78-0.94	0.59-0.79
nh	2.18-2.74	2.54-3.79	1.60-3.48
nlu	2.36-3.20	2.69-4.24	2.59-3.18
nlu/nh	1.00-1.20	1.00-1.38	0.98-1.30
pr-pr	4.78-5.40	4.50-8.84	5.44-7.72
po-pr	4.24-5.28	4.14-6.68	4.39-5.94
pr-pr/po-pr	1.10-1.24	1.09-1.35	1.11-1.21
zw/ctw	1.30-1.67	1.41-1.71	1.20-1.39

horizontally directed in *Agkistrodon* than in *Crotalus*.

I have not been able to assign, with certainty, all the fossil Florida crotaline vertebrae to either *Crotalus* or *Agkistrodon*. However, I am sure that at least a few of the vertebrae definitely represent the latter. The remaining specimens cannot be assigned, or are referred to the genus *Crotalus*. The large size of the fossils assigned to *Agkistrodon*, the shorter centrum length and the high neural spines suggest *A. piscivorus*, and not *A. contortrix*. The latter is most easily confused with *Sistrurus*, from which it can be separated most readily by its somewhat shorter centrum and the shape of the zygosphene.

Agkistrodon piscivorus Lacepede

Description.—Centrum length moderate to short, provided with strong subcentral ridges, extending from the base of the diapophyses posteriorly to near the base of the condyle. Condylus large, on a short neck, moderately oblique. Paradiapophyses well-developed, with two articular facets, occasionally with what appears to be a third directly anterior to the dorsal one. Parapophysial process strongly projected downwards and forwards, somewhat flattened, looking outwards and upwards, more or less parallel when seen from below. Cotyle slightly oval to round. Neural arch moderate in width, becoming much wider in larger specimens. Epizygapophysial spines usually faint, if present at all. Neural arch depressed. Interzygantral ridges moderate to strongly developed, strongly emarginated. Zygosphene straight, convex or with a median notch from above, rarely concave from above; straight, convex from the front. Prezygapophysial articular facets oval to subtriangular. Neural spine high, short, very thin at its anterior edge, usually leaning posteriorly, over-hanging slightly posteriorly.

This species was reported by Brattstrom (1954a) from the following localities in Florida: Seminole and Bradenton Fields and Crystal Springs, all Pleistocene and/or Recent in age. In addition, vertebrae referred to this species are now available from the following localities, all Pleistocene in age: Haile VII, A. UF 6394, 9865, 6284, 5620. Saber Tooth Cave. FGS V-5728 (Holman, 1958). Williston. FGS V-5810 (Holman, 1959). Haile I, A. UF 5499, 5508, 5466, 6323. Payne's Prairie B. UF 5753.

Figure 49 illustrates a middle precaudal vertebra of this species.

Crotalus Linnaeus

The problems involved in distinguishing the various species of *Crotalus* on the basis

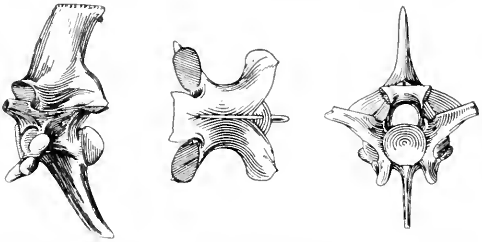

Figure 49. A precaudal vertebra of *Agkistrodon piscivorus* (UF 5733) Payne's Prairie B, Late Pleistocene.

of only their vertebrae have been more difficult for me than those encountered in separating *Agkistrodon* from *Crotalus*.[10] On the basis of the available comparative material, *C. tigris* is certainly distinctive. It is distinguished from other species in the same genus by a longer centrum and a lower neural spine. *C. mitchelli, horridus, durissus,* and *molossus* all possess precaudal vertebrae which seem shorter, broader and with lower neural spines than are found in *ruber, atrox,* and *adamanteus*, though the differences are not striking, and there is considerable overlap. *C. adamanteus* possesses very high neural spines, especially in large individuals. The parapophysial processes are frequently more strongly developed than in the remaining forms. Some of the fossil vertebrae from Florida are certainly referrable to this species, but there is no certainty that *horridus* is not also represented in the available fossil material.

Gilmore (1938) stated that except for larger size, *C. adamanteus* cannot be separated from other species on vertebral characters alone. For this reason he refers most of the fossil crotaline vertebrae from Florida to *C. adamanteus* on size alone. Hay (1917, *et al.*) assigned vertebrae to separate species, without stating on what bases the distinctions were made. One is left with the impression that most of the identifications were based on the ranges of the modern species. Brattstrom (1954a) referred the available fossil rattlesnake vertebrae to several modern species, but gave no hint of the means by which they were separated other than a reference to the ratio of log-differences of a series of analogous measurements. However, I believe this statistic is not applicable readily in distinguishing between two samples in which variation (ontogenetic, non-determinant growth, and intracolumnar) is so great. However, its use in snake vertebrae may have considerable value if the samples are known to have originated from specimens of equal size and/or age. Using the same statistic, greater differences can be demonstrated between hatchling and adult specimens of *C. adamanteus* than between adults of *adamanteus* and *horridus*.

Young rattlesnakes definitely are represented in the Florida Pleistocene, frequently to the exclusion of adults in the same deposit. Statistically validated size differences between two samples of fossil vertebrae do not indicate necessarily the presence of two or more species, but simply suggest that the samples differ in size. On the basis of the log-difference statistic Brattstrom described two new fossil rattlesnakes from Florida, *C. adamanteus pleistofloridensis* and *C. giganteus*.

According to Brattstrom (p. 35), *C. a. pleistofloridensis* differs from *C. a. adamanteus* ". . . in having a higher neural spine, a longer hypapophysis, the parapophysis longer and bent laterally, and the process of the prezygapophysis wider than the process of the postzygapophyses . . . (p. 36) . . . but especially in its larger size."

As far as I can determine, the characters which are given as diagnostic are all somehow related to total size; that is, they all seem to exhibit ontogenetic variation.

The length of the neural spine and the hypapophysis depends, in part, on the position within the vertebral column, shortest posteriorly. According to Brattstrom's figure 1, the hypapophysis of *pleistofloridensis* is not significantly longer than in *adamanteus*. Furthermore, the fossil vertebrae referred to *pleistofloridensis* by Brattstrom and measured by myself (AMNH 6776, AMNH 6778, MCZ 2101, MCZ 2112-3, USNM 11333) are not significantly larger than those from a six and a half foot living specimen from Astor Park, Lake County, Florida. Gilmore (1938: 74) stated that some of the fossil vertebrae "rival" and "are nearly as large" as those of a recent specimen in the United States National Museum that was seven feet in length. In fact, many of the vertebrae placed in *pleistofloridensis* are much smaller than those of the largest modern specimens available. The parapophysial process in a young *C. adamanteus* from Daytona Beach, Florida is pointed, proportionately short and directed upwards, not outwards. In a three and a half foot specimen from High Springs, Florida the process is longer, not as pointed, but with a rounded anterior edge, and facing outwards slightly, as well as being proportionately wider. This

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[10] According to Brattstrom (pers. comm.) some of his studies suggest that characters are now available which are not only useful in separating the precaudal vertebrae of various species of crotalids, but will position the elements within the vertebral column as well. This publication will do much to clarify what is at best described as a difficult problem at present.

trend is continued in larger specimens and becomes exaggerated in the overly large species, *C. giganteus.*

The prezygapophysis is wider than the postzygapophysis in very young rattlesnakes (po pr 0.91), becoming equal in average-sized specimens (po pr 1.00), and thence becoming wider again in very large specimens (po pr 0.92).

The largest specimen of *C. adamanteus* recorded measured eight feet, nine inches (Gilmore, 1938). However, apparently this is based on Stejneger's specimen, which has since been lost, so that there is no means by which the length can be checked. There is every reason for believing that *C. a. pleistofloridensis* attained lengths of from seven to eight feet. The largest Recent specimen of *C. adamanteus* for which reliable data are available is seven feet, four inches in total length; larger than the Recent comparative material available to Gilmore and to myself. It is larger than most specimens of *pleistofloridensis.*

Larger rattlesnakes are becoming more unusual with continuing human development of the southeastern states. Large specimens of *C. adamenteus* apparently were more common during the past than at the present time. Man is certainly an important factor in reducing the number of the larger specimens found in any one area. Vertebrae collected from Indian mounds in Florida indicate that unusually large specimens were more common during that period than at the present time. Many of the specimens equal, or even exceed, the size of *C. a. pleistofloridensis.*

Based on the above, *Crotalus adamanteus pleistofloridensis* is referred to the synonymy of *Crotalus adamanteus.*

The problems involved in determining the validity of *Crotalus giganteus* are somewhat greater. This species differs from *adamanteus* in its larger size and, according to Brattstrom (1954a: 36) ". . . in having the hypapophysis widest (antero-posteriorly) at its tip and not at its base". This species may have been as long as twelve feet, considerably larger than the largest Recent *C. adamanteus.*

The hypapophysial character loses some importance when one realizes that there is at least some intra- and intervertebral variation in this character (in the anterior vertebrae the tips of the hypapophyses are generally narrower than at their bases, in the posterior vertebrae the tips may be somewhat wider). A much more important character is the ratio cl naw. In Recent specimens examined this ratio varies from 0.79-1.08. In the type of *C. giganteus* (AMNH 6772), two very large vertebrae from Hornsby Springs (UF 6269 and UF 6281), and a series from Eichelberger Cave B (UF 6376) the ratio varies from 0.67-0.78. This difference cannot be explained easily on an ontogenetic basis, at least with the comparative material available. Therefore, for the present I think *C. giganteus* should be retained as a valid species. Figure 50 illustrates the ontogenetic change and variation of the ratio cl naw in Recent and Pleistocene *Crotalus adamanteus* and *C. giganteus.* This ratio may also provide a means of distinguishing juvenile specimens of *giganteus* from *adamanteus,* something which was not possible before. So far, none of the smaller vertebrae referrable to *Crotalus* can be assigned clearly to *giganteus.* However, the sample of *C. giganteus* from Eichleberger Cave B contains specimens no larger than the largest specimens previously referred to *C. a. pleistofloridensis.* There is no overlap in the ratio when plotted against centrum length.

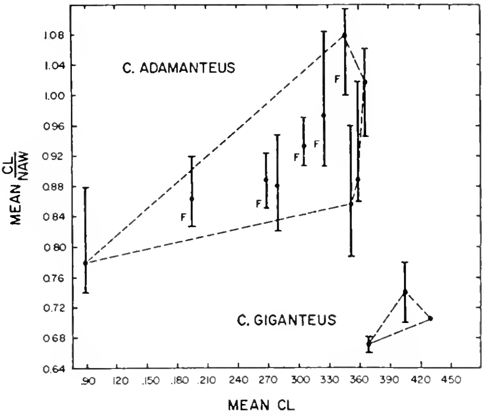

Figure 50. Ontogenetic change and comparison of the ratio cl/cw in Recent and Pleistocene *Crotalus adamanteus* and *C. giganteus*, plotted against the mean cl. Vertical bars represent the actual variation for each Recent specimen, or for each series of fossil vertebrae from one locality. The letter "F" indicates a fossil sample. The dot in the distribution of *C. giganteus* represents the holotype (AMNH 6772).

? *Crotalus*

One very fragmentary vertebra from the Pliocene locality of Haile, VI, A is tentatively referred to this genus. That the specimen represents a crotalid snake is indicated by the long, somewhat rod-like hypapophysis with parallel anterior and posterior sides, directed almost vertically, and with very short accessory processes. The snake was presumably the same size as an average specimen of *Agkistrodon piscivorus*. The vertebra is important in that it represents the earliest record of the family in eastern United States.

Crotalus adamanteus Beauvois

Description.—Centrum length moderate to short, provided with strong subcentral ridges, extending from the base of the diapophysis posteriorly to near the base of the condylus. Condyle very large, on a short neck, moderately oblique to facing directly posteriorly. Paradiapophysis well developed, with two distinct articular facets, occasionally with what appear to be a third surface directly anterior to the dorsal one. Parapophysial process strongly projected downwards and forwards, somewhat flattened, looking upwards, to upwards and outwards, diverging to just about parallel from below. Cotyle strongly oval to round. Neural arch moderate in width, wider in larger specimens, depressed. Epizygapophysial spines absent or weakly developed. Interzygapophysial ridges moderate to strongly developed, emarginated. Zygosphene straight, concave from above, sometimes with a median notch, straight or convex from the front, thin to very thickened dorso-ventrally. Prezygapophysial articular surfaces oval to decidedly rectangular. Neural spine high, narrow, usually with a tubercle on the anterior, upper edge, especially in the more anterior vertebrae, higher and narrow in the anterior vertebrae, to slightly longer than high in the posterior members.

This species was reported from a number of localities in Florida by Hay (1917, 1923), Gilmore (1938), Brattstrom (1953a, 1954a), and Holman (1958, 1959). These included the following localities: Pleistocene: Pit No. 2, Florida Lime Co. FGS V-2987. Allen Cave. AMNH 6778. Saber Tooth Cave. FGS V-5717. Williston, FGS V-5811. Pleistocene and/or Recent: Vero Beach. USNM 11333, FGS V-2414, 2411, 2399, 2412, 1702, 191, 1765, MCZ 2112-3. Seminole Field. AMNH 6776, UMMP 1009-10. Melbourne Field. USNM 13678, 13679, 13677, 11220, 11856, MCZ 2101.

To these should be added the following localities: Pleistocene: Mefford Cave. I, A. UF 2558. Eichelberger Cave B. UF 6477-9. Reddick I, B. UF 5015, 6038, 4314, 5801, 6012, 6366, 6111, 4315, 4313, 6372, 5806, 6008, 5636, 6034, 5638, 6043, 4303, 5718-9. Wall Co. Pit. UF 5717. Haile VII, A. UF 6274, 5614, 6440, 6028, 6395, 5628, 5613, 5618, 5631, 5615, 5632, 5631, 5146, 5608, 5630, 5609, 5607, 5610, 5625, 5616, 5627, 5158, 5629, 6200, 5619, 5621, 5612, 5622, 6270, 6305, 6423, 6282, 5905, 6286, 6399, 5611, 5617, 6278, 6285, 9866, 6302. Kanapaha I, A. UF 6005, 6055, 5761. Haile I, A. 5293, 5339, 5455. Haile I, B. UF 5039.

In addition, vertebrae are also available from the following new Pleistocene and/or Recent deposits: Itchtuckanee Springs: UF 5293, 5339, 5455. Haile I, B. UF 5039.

Various available cranial elements are placed in this species. They are identical to those of the Recent species in Florida. These include the following specimens: UF 6249, a replacement fang, Kanapaha I, A; UF 6342, two replacement fangs, Itchtuckanee Springs; UF 6035, a fragmental surangular, Reddick I, B; a fragmentary maxillary, Haile VII, A; UF 5207, a fragmentary maxillary, Haile I, B; UF 5120, a functional fang, Reddick I, B; UF 5125, a replacement fang, Reddick I, B.

Table 27 compares the vertebral ratios of *Crotalus adamanteus*, both Pleistocene and Recent, with *Crotalus giganteus*. Because of the similarity of these two species, except in size and centrum width, only the latter is illustrated (Fig. 51).

Crotalus giganteus Brattstrom

Description.—A large rattlesnake, characterized, besides size, by its very wide vertebrae. Centrum short, wide, with well developed subcentral ridges, extending from the diapophysis posteriorly to near the condylus. Condylus large, on a very short neck, directed posteriorly. Parapophysial processes strongly projected anteriorly and downwards, facing more laterally than dorsally, rounded at the end. Two articular facets on the paradiapophyses, with a smaller surface immediately in front of the diapophysial surface. Cotyle somewhat oval to round. Neural arch depressed, without epizygapophysial spines.

TABLE 27.
Comparison of some vertebral ratios in Crotalus adamanteus, both Pleistocene and Recent, with Crotalus giganteus

Ratios	*C. adamanteus* Pleistocene (N=60)	Recent (N=78)	*C. giganteus* (N=8)
cl/naw	0.99-1.05	0.79-1.08	0.67-0.78
zw/cl	0.96-1.01	0.90-1.03	0.95-0.97
nlu/nh	0.68-1.15	0.63-1.10	0.54-0.81
pr-pr/po-pr	1.58-1.86	1.61-1.92	1.75-1.98
nh/cl	0.77-1.22	0.63-1.31	0.87-1.41
ctw/cth	1.00-1.17	0.98-1.21	1.00-1.04

Zygosphene thick dorso-ventrally, concave to straight from above, straight to convex from the front. Neural spine much higher than long, slightly overhanging posteriorly. Hypapophysis long, straight, with or without the tip wider than the base.

This species was described originally by Brattstrom on the basis of the two very large vertebrae from Allen Cave (AMNH 6772, 7171). As pointed out above, it differs from *C. adamanteus* in its larger size and in the wider vertebrae (Fig. 51). However, further study of larger comparative specimens of Recent *Crotalus adamanteus* and additional fossil material may show that this species should be referred to *C. adamanteus*. Vertebrae are now known from a few additional localities in Florida, as follows: Pleistocene: Haile VII, A. UF 9863. Eichelberger Cave B. UF 6376. Pleistocene and/or Recent: Hornsby Springs. UF 6269, 6281, two very fine vertebrae of this species. Rock Springs. UMMP 11013.

Figure 51 illustrates a perfect vertebra assigned to this species. Table 27 compares the vertebral ratios of this species with those of *C. adamanteus*, both fossil and Recent.

In addition to the fossil elements described and/or discussed throughout this paper, several hundred elements, mostly Pleistocene, have not been assigned to species because of their fragmentary nature. Thus, many vertebrae, not listed above, may be assigned to *Elaphe* sp., or *Natrix* sp., etc. However, these specimens have not been considered if other vertebrae from the same deposits could be correctly assigned to a certain species. Many vertebrae are so fragmentary that they can-

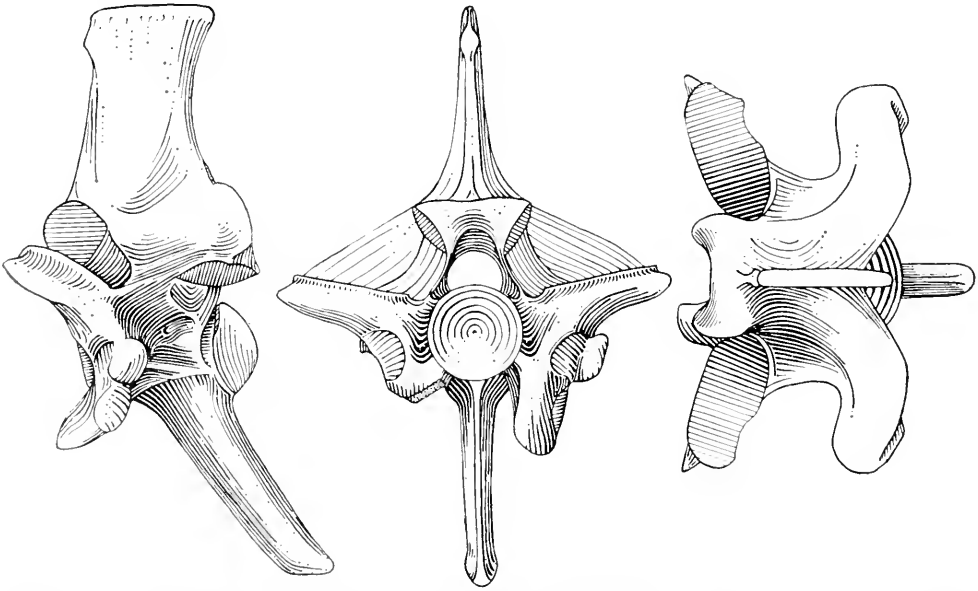

Figure 51. A precaudal vertebra of *Crotalus giganteus* (UF 6281) Hornsby Springs, Pleistocene and/or Recent.

not be assigned to even a particular genus, some not even to a particular family. For the most part, I feel that these un-assigned elements would not add greatly to either faunal or distributional patterns as now understood. Of particular interest, however, are three fragmental vertebrae (UF 6469, 6473, 6411) from the Pliocene locality of Haile VI, A. These elements undoubtedly represent a new species of colubrid snake, perhaps belonging to the genus *Elaphe*, but which, because of their fragmental nature, have not been described.

Table 28 summarizes the data on the known geological range of the families, genera and species of snakes found as fossils in Florida.

VI. DISCUSSION

The material on which this study is based contains a fair proportion of the Late Tertiary and Quaternary snake fossils of the New World, particularly in number of species. For the first time it is possible to describe from the Miocene to the present the changing snake fauna of a somewhat restricted area in reasonable detail. The record from all but the Late Pleistocene is too meager to permit evaluation of the classification of modern snakes in the light of their fossil history. This remains for the future.

In the New World the terrestrial Lower Miocene beds of Florida provide the earliest members of the Colubridae. In the Old World the earliest colubrids are also known from the Miocene (Gilmore, 1938, *et al.*). Miller (1955) placed the North American Eocene snake, *Cheilophis*, in the Colubridae, but this seems unwarranted on the basis of our present knowledge.

The family Colubridae is represented in the Lower Miocene of Florida by at least two genera, *Paraoxybelis* and *Pseudocemophora*. *Paraoxybelis* seems unrelated to any modern North American genus, but may be close to one of several Central and South American forms, particularly *Oxybelis*. If true, then the presence of this group in North America during the Miocene supports Dunn's view (1928) that *Oxybelis* belongs in the Colubrinae rather than the Xenodontinae. The re-establishment of the connection between the two continents during the Pliocene would have allowed *Oxybelis* and related forms to spread into South America at that time.

The remaining Miocene colubrid from Florida, *Pseudocemophora*, seems close to the modern genera *Lampropeltis* and *Cemophora*, and may be ancestral to one or both of them, thus tending to support Blanchard's hypothesis (1921) that *Lampropeltis* was derived during the Miocene.

The only other Miocene colubrid known from North America is *Dryinoides* from the upper portion of the Madison Valley formation of Wyoming (Auffenberg, 1958b). It seems close to *Conophis*, a genus which Dunn (1928) places in the Xenodontinae.

The first known fossil of the family Aniliidae is from the Cretaceous of North America (Hecht, 1959). Two species are known from the Eocene of Wyoming (Hecht, 1959). It is now known from the Florida Miocene as well. Conceivably certain other fossil snakes described from other formations in various parts of the world, placed in the Boidae at present, belong here. Unfortunately the generic relationships of the Florida fossil anilid, *Anilioides minuatus*, are unknown.

The remaining Miocene snakes of Florida are members of the family Boidae. The largest of these is *Pseudoepicrates*, a form similar to *Epicrates* and *Constrictor*. Like the former, *Pseudoepicrates* was probably equally adjusted to both an arboreal and a terrestrial existence. It may also have frequented caves and fissures in search of bats.

The end of the Miocene marks the last appearance of the larger terrestrial and arboreal boas in temperate areas of both North America and Europe (Kuhn, 1939), ending a nearly unbroken record from the Lower Eocene to the Lower Miocene on both continents.

The two remaining genera of Miocene boids found in Florida, *Calamagras* and *Ogmophis* (the latter at least in part), may be related to the Recent North American genera *Charina* and *Lichanura*. On the other hand, the suggested relationships may be the results of parallel development, in which case the relationships of the fossil forms remain obscure. In any event, the general nature of the vertebrae (small size, low neural spines, etc.) seems to suggest fossorial or semifossorial habits. On the basis of the presumed paleoecological conditions at the Thomas Farm there is doubt that the fossil

TABLE 28.
The fossil snakes of Florida and their geologic distribution

Taxa	Cret.	Paleo.	Eoc.	Olig.	Mio.	Plio.	Pleist.	Recent
Aniliidae	X		X		F			X
Anilioides minuatus +					F			
Boidae	?	X	X	X	F		X	X
Erycinae		X	X	X	F			X
Calamagras +			X	X	F			
C. floridanus +					F			
Ogmophis +				X	F			
O. pauperrimus +					F			
Boinae			X	X	F		X	X
Pseudoepicrates stanolseni +					F			
Colubridae					FX	FX	FX	FX
Colubrinae					FX	FX	FX	FX
Carphophis amoenus							FX	FX
Farancia abacura or *Abastor erythrogramus*							F	FX
Paleofarancia brevispinosus +						F		
Diadophis						F	FX	FX
D. elinorae +						F		
D. punctatus							FX	FX
Heterodon						FX	FX	FX
H. platyrhinos							FX	FX
H. simus							FX	FX
H. brevis +						F		
Opheodrys aestivus							F	FX
Coluber						X	FX	FX
C. constrictor						X	FX	FX
Masticophis							FX	FX
M. flagellum							FX	FX
Drymarchon corais							FX	FX
Elaphe						X	FX	FX
E. obsoleta							FX	FX
E. guttata							F	FX
Pituophis melanoleucus							FX	FX
Lampropeltis						X	FX	FX
L. getulus							F	FX
L. doliata							FX	FX
Stilosoma						F	F	F
S. vetustum +						F		
S. extenuatum							F (?)	F
Pseudocemophora antiqua +					F			
Tantilla coronata							F	FX
Rhadinea flavilata							F	FX
Paraoxybelis floridanus +					F			
Natricinae					X	X	FX	FX
Storeria dekayi							F	FX
Liodytes alleni							F	F
Natrix						X	FX	FX
N. cyclopion							F	FX
N. taxispilota							F	FX
N. erythrogaster							F	FX
N. sipedon							F	FX
Thamnophis						X	FX	FX
T. sirtalis							FX	FX
Elapidae					X	F	FX	FX
Micrurus fulvius							F	FX
Micrurus sp.						F		
Viperidae				X	X	FX	FX	FX
Sistrurus miliarius							F	FX
Agkistrodon						X	FX	FX
A. piscivorus							F	FX
Crotalus						FX	FX	FX
C. adamanteus							F	FX
C. giganteus +							F	
C. sp.						F		

F = Florida X = Other than Florida + = extinct taxons boids from this deposit were true leaf burrowers. Like the modern boid genus *Eryx*, *Ogmophis* and *Calamagras* probably burrowed in loose, dry soil.

According to Chaney (1940), climate was equable all through the Miocene, and the fossil snakes of Thomas Farm seem to suggest semi-arid tropical to subtropical conditions in a karst type topography with open shrubby vegetational community types, perhaps slightly more lush near permanent or even temporary shallow ponds, sink holes, etc.

There is every reason to believe that the modern families of snakes have a longer history than the available fossils seem to indicate. Although the relationships of some of the earlier fossil snakes have not been established definitely, the Boidae certainly extend back to the Paleocene. The fossil boids from Florida merely represent the culmination of several North American lines. The Miocene also seems to mark the last appearance of the Aniliidae in North America. The present disjunct range of the family is a phenomenon associated with the general pre-Pliocene modernization of the snake fauna of the world. The Colubridae known from the Lower Miocene of Florida indicate that this family also extends at least to the Oligocene, and probably the Eocene. The Florida Miocene species seem to represent, at least to some extent, the first stages in the deployment of higher forms represented by the Recent fauna of North America.

No terrestrial deposits of Middle or Late Miocene age are known from Florida as yet. During this period the peninsula was presumably almost completely covered by a shallow sea (Pirkle, 1957). During this time the Boidae, Aniliidae and certain members of the Colubridae apparently disappeared from eastern North America, their ranges approximating that of the tropical and subtropical parts of the New World at the present time.

Following the extinction of certain snake genera in the Miocene, the Pliocene marks, with few exceptions, the first occurrence of Recent genera found in North America. This period thus represents a time in which snake faunas were becoming modern in their general aspect. Zoogeographical distribution of snakes on the generic level was probably similar to that of the present time. In North America the Viperidae made their appearance in the (?) Lower Pliocene of Driftwood Creek, Nebraska (Brattstrom, 1954a), and are found in the Middle Pliocene of Florida. *Lampropeltis* and *Heterodon* are present in the Pliocene of Central and Western United States and Mexico (Brattstrom, 1955a, 1955b; and Peters, 1953). *Heterodon, Stilosoma, Diadophis*, a crotalid (*Crotalus?*), and an elapid (*Micrurus?*) also occur in the Middle Pliocene of Florida.

However, all the Pliocene snakes reported represent species distinct from the Recent generic representatives (with the exception of *Agkistrodon contortrix*), and apparently are ancestral to at least some of the Recent forms.

Only two extinct North American Pliocene genera have been recognized nomenclatorialy: *Paleoelaphe* Gilmore (which is very close to *Elaphe*, and should be synonymized with it) and *Paleofarancia* (which is *probably* Pliocene in age, and may be ancestral to either *Farancia* or *Abastor*, or both).

On the basis of data obtained from the amphibians of the Florida Middle Pliocene locality of Haile VI (Auffenberg, 1956b) there is every reason to believe that it was between Lower Miocene and Middle Pliocene that Florida felt the effects of a western herpetofaunal immigration. This is also suggested by the presence of certain genera of snakes in the Middle Pliocene which are thought to have their ancestral home in southwestern North America (*Crotalus, Micrurus*, etc.).

There is no evidence that either of the Floridian endemic genera of snakes (*Liodytes, Stilosoma*) evolved in Florida. *Liodytes* is, perhaps, a form that evolved in southeastern United States, but its extreme similarity to *Helicops* makes one wonder whether these two genera simply represent relict populations of a formerly much more extensive stock. The Florida worm lizard, *Rhinura*, is today found exclusively in the Florida peninsula, though as a fossil it is known from several widely scattered Oligocene localities in western, north-central United States. *Stilosoma* is reported from the Pliocene of Florida, a time when it is believed that immigrations from more western parts of North America were being felt in the peninsula. *Rhinura* and *Stilosoma* (as well as *Neoseps?*) probably entered Florida at this time.

Paleofarancia, from the Pliocene of Florida, is here considered as a possible ancestor of *Farancia* and or *Abastor,* two Recent genera more or less restricted to southeastern United States. However, *Paleofarancia* is provided with vertebrae which, although more similar to *Farancia* and *Abastor* than to any other Recent North American snake, are distinctive. It may represent the culmination of a line which became extinct near the beginning of the Pleistocene, ancestral to no modern forms.

The Pleistocene deposits of Florida present a complex series of beds, deposited locally and of a remarkably uniform faunal composition. Many of these bear indications of admixture with more recent faunas. A large percentage of the fossil forms, mammalian and otherwise, are identical to Recent animals existing in the same area at the present time.

Hay (1923) believed that some of these deposits represented Nebraskan time, but the modern concensus places them in Middle Pleistocene, Late Pleistocene, and Pleistocene and/or Recent. Thus, no Early Pleistocene deposits are recognized in the state at present.

Though remarkably uniform in faunal composition on the whole, certain forms, now found to the north of peninsular Florida are present in some of these deposits. Thus, the bog lemming (*Synaptomys*), now found as far south as northern North Carolina, is present in some of the deposits. Similarly, the porcupine (*Erethizon*), the beaver (*Castor*) and the red fox (*Vulpes*) are all found north of Florida at the present time, though they have been reported from various Pleistocene, or Pleistocene and or Recent localities in the state. Among the birds the ruffed grouse, found as far south as Virginia in historic times, is found in at least one Pleistocene deposit. In the reptiles *Pseudemys scripta* and *Macroclemmys* are found as Pleistocene forms far to the south of their present ranges. *Carphophis amoenus* is found in at least three localities south of where it exists today. *Natrix erythogaster* is also reported from a Pleistocene deposit somewhat south of its present range. The Pleistocene *Pseudobranchus* from Florida, *robustus*, is closest to *striatus*, which at present is restricted to coastal Georgia. *Eumeces fasciatus* is found in a Pleistocene deposit in central Florida, whereas at the present time apparently it is limited in its southward extent to extreme northern Florida.

All of these records suggest Pleistocene glacial climates which were somewhat cooler than those occurring in the area today. Certain forms have been taken as indicative of very cool climates. This is particularly true of some of the mammals. On the other hand, the climatic shift necessary to bring the Georgia-Carolinian herpetofauna into central Florida is not great. Much more important, remains of many of these more northern faunal elements are almost always found with vertebrates generally associated with warmer climates; *Geochelone*, several armadillos, tapirs, capybaras, etc. The presence of the former is particularly important in climatic interpretations. It has not been found to be absent in any of the better known Pleistocene fossil localities of Florida, suggesting that some factor other than temperature may have been responsible for the presumed southward shift of ranges of some more northern types. Greater precipitation during glacial periods may represent one of several such factors. Obviously the problem deserves considerable additional study.

A recent suggestion (Auffenberg, 1958a; Weigel, 1958) was that during the time represented by Stratum 2 at Vero (and deposits at other localities) Florida felt the effects of a migration of certain paludicolous animals. These forms probably migrated eastward along a coastal circumferential Gulf of Mexico route.

At the present time there is at least some evidence to indicate that forms usually taken as indicators of Pleistocene time may have existed until fairly recently in Florida. This has been demonstrated in several other areas in North America. Thus, the mastodon is now thought to have become extinct during, or slightly before Altithermal, or Thermal Maximum time. Winters (personal communication) indicated that the "Pleistocene" forms have not yet been found in definite association with very early indian shell midden material in Florida, other than a few pieces which are presumed to have been collected in a fossil state from some other locality by the inhabitants. Some of the deposits containing extinct vertebrates in Florida are most certainly Post-Pleistocene. Admixture from more recent deposits may or may not be a factor in such occurrences.

Only through further study of the problem of correlation and dating of these deposits can we hope to realize the value of the excellent Quaternary deposits in Florida. It is much too early to speculate intelligently on the age of most of the Pleistocene fossiliferous deposits in the state. Future correlations may alter many of our concepts involving the past history of certain groups, including the snakes.

The most striking fact concerning the Late Pleistocene snake fauna of Florida is its similarity to the modern one. The great degree of extinction witnessed among the mammals and birds in Pleistocene and Post-Pleistocene time apparently is not present in the reptiles. Evidently only one Pleistocene Florida species of snake has become extinct, *Crotalus giganteus*.

As was mentioned above, at least some minor faunal shifting is evident in the Pleistocene mammals of Florida. A similar, though less spectacular change is apparent in the reptiles and amphibians. The exact nature, correlation, and dating of these climatic and faunistic shifts remains uncertain. Brodkorb (1957) suggested that the deposits at Reddick and several other localities represent Illinoian time. A more extensive, but tentative correlation of several Pleistocene localities recently was attempted (Auffenberg, 1958a).

Many students working with Pleistocene glacial phenomena have been struck with the unusual fact that, according to present concepts, each succeeding interglacial period produced marine terrace levels successively lower than the previous interglacial period. Various reasons have been suggested for this, none of them really satisfactory. The simplest hypothesis would call for increasing cooler interglacial periods. Thus the present conditions would be cooler than any of the interglacial periods. Furthermore, in examining the history of Pleistocene marine terrace study one is impressed with the feeling that we are choosing our terraces to fit the known glacial and interglacial history. At least in Florida many of the terraces are difficult to distinguish, and marine fossils are missing in many of them. Conditions similar to those which produced the Miocene shell-bearing clays and marls certainly should have been present in Florida. If so, the contained fossils would not have been leached out, since they had not done so in the much earlier deposits.

Much of the correlation of the Pleistocene fossil deposits of Florida will rest on the final determination of the mode and time of development of the terraces found above, or immediately below, most of these localities. Quinn (1957) recently published a study of the coastal terraces of Texas in which he ascribes these land forms to alternating climates during the Pleistocene, rather than marine erosion and deposition. Whether or not he is completely, or even partly correct is unknown at present, but it is stimulating to see a new approach to the problem of terrace levels in the circumferential Gulf area.

Most of the mammals which became extinct in Pleistocene or Post-Pleistocene represent large forms. Man has been suggested as being the most important factor in this selective extinction. Also he may have been responsible for the extinction of the only three extinct Pleistocene reptiles in Florida, *Geochelone*, *Terrapene c. putnami* and *Crotalus giganteus*: all giant forms when compared to modern related genera or species. Primitive North American peoples are known to have eaten box turtles and rattlesnakes. There is little doubt but that even more ancient inhabitants of Florida also ate them. However, it is difficult to see how men could bring about extinction of animals such as box turtles and rattlesnakes, regardless of size. The giant land turtles are, however, a different proposition. Large turtles related to the genus *Geochelone* are eaten the world over by people of all races. Man has, in fact, brought about the extinction of several species of this turtle during historic times. Pieces of *Geochelone* shell have been found in at least one shell midden, although it is not certain whether or not the remains pertain to an animal alive at that time. Presumably the fragments were picked up elsewhere and carried to the midden as a curio (Bullen, 1956). It is much more likely that the extinction of all of these Pleistocene reptiles was brought about by some changing climatic factor. If the Pleistocene was indeed a period of fluctuating, but increasingly colder stages possibly the cold tolerance of these reptiles was surpassed only during the Wisconsin, and they lived in Florida continuously throughout the earlier part of the Pleistocene. On the basis of present and Pleistocene distributions of some of the reptiles and amphibians in Florida, apparently there is a group composed of a number of genera and species which at present are found only in northern Florida, but which during the Pleistocene extended much farther southward. Among the snakes this includes only *Carphophis* and *Natrix erythrogaster.* By inference, through coincidence of distributional patterns, *Crotalus horridus, Natrix rigida, Natrix septemvittata, Storeria occipitomaculata* (?). *Haldea striatula,* and *Agkistrodon contortrix* should be included in this group. All of these are more northern forms, apparently reaching their southern extent in northern Florida. They may be re-entering Florida since their maximum northward extension in Thermal Maximum, or Altithermal time. Finer techniques of collecting and identification of fossil snake vertebrae probably would show at least some of them present in the Pleistocene of central Florida, as in the case of the distinctive species, *Carphophis amoenus* and *Natrix erythrogaster.*

From the standpoint of vertebrate fossils, the most important contributions yet to be made to our known history of the faunal changes of the Post Pliocene in Florida are concerned with the Early Pleistocene and Post Pleistocene. The latter seems unimportant as regards the fossil reptiles of Florida (disregarding the extinction of a few forms). The early Pleistocene of Florida, however, would be extremely interesting from a paleoherpetological viewpoint, as apparently before this period most of the modern species became established. It is hoped that further prospecting or some reliable method of dating applicable to these deposits will disclose localities representing this period.

VII. SUMMARY

Fossil snakes are now known from three geological epochs in Florida: Miocene, Pliocene, and Pleistocene.

Miocene snakes have been found at only one locality in Florida: Thomas Farm, Gilchrist County. The snake fauna from this deposit includes aniliid, boid and colubrid genera. This is the first record of fossil Aniliidae from eastern North America. A new genus and species is described: *Anilioides minuatus.* The Miocene colubrid genera represent the earliest occurrence of this family in the New World. Two new genera and species are described. *Pseudocemophora antiqua* and *Paraoxybelis floridanus.* The former possibly is related to the modern genera *Cemophora* and/or *Lampropeltis;* the latter seems to be close to the Central American *Oxybelis.* The family Boidae is represented by *Pseudoepicrates* (gen. nov.) *stanolseni, Ogmophis pauperrimus,* and *Calamagras floridanus* (sp. nov.). The genus *Neurodromicus* Cope is considered a synonym of the crotalid genus *Sistrurus;* the fossil boid *Neurodromicus barbouri* Vanzolini a synonym of *Pseudoepicrates stanolseni* (Vanzolini).

Pliocene fossil snakes are known from only two localities in Florida, Haile VI A, Alachua County, and Lithia Springs, Hillsborough County. They are all referred to the family Colubridae. One new genus and species, *Paleofarancia brevispinosus,* may be ancestral to *Farancia* and/or *Abastor.* Three additional new species are described: *Heterodon brevis, Diadophis elinorae,* and *Stilosoma vestustum.* Specifically unidentifiable crotalid and elapid vertebrae are known also from this epoch in Florida.

Pleistocene snakes are now known from about 23 localities in Florida. The species identified from these deposits include the following colubrids: *Carphophis amoenus, Farancia abacura* (and/or *Abastor erythrogrammus*), *Diadophis punctatus, Rhadinea flavilata, Heterodon simus, Heterodon platyrhinos, Opheodrys aestivus, Coluber constrictor, Masticophis flagellum, Drymarchon corais, Elaphe guttata, Elaphe obsoleta, Pituophis melanoleucus, Lampropeltis doliata, Lampropeltis getulus, Tantilla coronata, Storeria dekayi, Natrix sipedon, Natrix cyclopion, Natrix erythrogaster, Natrix taxispilota, Liodytes alleni,* and *Thamnophis sirtalis.* The family Elapidae is represented by *Micrurus fulvius.* Crotalid snakes include *Agkistrodon piscivorus, Sistrurus miliarius, Crotalus adamanteus,* and *Crotalus giganteus.*

The fossil species *Crotalus pleistofloridensis* Brattstrom is referred to the synonymy of *Crotalus adamanteus. Crotalus horridus* may be present in several deposits, but the fragmentary and isolated vertebrae available cannot be separated with certainty from *C. adamanteus. Crotalus giganteus* represents the only Pleistocene species of snake in Florida known to be extinct.

The fossil snake material from Florida suggests some faunistic shifting in the peninsula during the Pleistocene. These are assumed to be correlated with shifting climatic zones during the same period. Two species of snakes, *Carphophis amoenus* and *Natrix* *erythrogaster,* are known from fossil localities in Florida which are located south of their present ranges.

VIII. References Cited

Abel, O. 1919 *Die Stämme de Wirbeltiere.* xviii-914, 669 figs. Berlin and Leipzig.

Auffenberg, W. 1954 Additional specimens of *Gavialosuchus americanus* (Sellards) from a new locality in Florida. *Quart. Jour. Fla. Acad. Sci.* 17: 185-209.

———— 1955a Glass lizards *(Ophisaurus)* from the Pleistocene and Pliocene of Florida. *Herpetologica* 2: 133-136.

———— 1955b A reconsideration of the racer, *Coluber constrictor,* in eastern United States. *Tulane Stud. Zool.* 2: 88-155.

———— 1956a Remarks on some Miocene anurans from Florida, with a description of a new species of *Hyla. Breviora* No. 52: 1-11.

———— 1956b Additional records of Pleistocene lizards from Florida. *Quart. Jour. Fla. Acad. Sci.* 19: 157-167.

———— 1957 A note on an unusually complete specimen of *Dasypus bellus* (Simpson) from Florida. *Ibid.* 20: 233-237.

———— 1958a Fossil turtles of the genus *Terrapene* in Florida. *Bull. Fla. State Mus.* 3: 53-92.

———— 1958b A new genus of colubrid snake from the Upper Miocene of North America. *Amer. Mus. Nov.* No. 1874: 1-16.

Bader, R. S. 1956 A quantitative study of the Equidae of the Thomas Farm Miocene. *Bull. Mus. Comp. Zool.* 115: 49-78.

———— 1957 Two Pleistocene mammalian faunas from Alachua County, Florida. *Bull. Fla. State Mus.* 2: 53-75.

Berry, E. W. 1907 Contributions to the Pleistocene flora of North Carolina. *Jour. Geol.* 15: 338-349.

———— 1909 Additions to the Pleistocene flora of North Carolina. *Torreya* 9: 71-73.

———— 1916 The flora of the Citronelle formation. *U. S. Geol. Surv., Prof. Pap.* No. 98: 193-204.

———— 1925 Pleistocene plants from North Carolina. *Ibid.* No. 140: 203-256.

Blanchard, F. N. 1921 A revision of the king snakes, genus *Lampropeltis. Bull. U. S. Nat. Mus.* No. 114: 1-260.

Brattstrom, B. H. 1953a Records of Pleistocene reptiles and amphibians from Florida. *Quart. Jour. Fla. Acad. Sci.* 16: 243-248.

———— 1953b Records of Pleistocene reptiles from California. *Copeia* 1953: 173-179.

———— 1953c The amphibians and reptiles from Rancho La Brea. *Trans. San Diego Soc. Nat. Hist.* 11: 365-392.

———— 1954a The fossil pit vipers (Reptilia: Crotalidae) of North America. *Ibid.* 12: 31-46.

———— 1954b Amphibians and reptiles from Gypsum Cave, Nevada. *Bull. So. Cal. Acad. Sci.* 53: 8-12.

———— 1955a Pliocene and Pleistocene amphibians and reptiles from south-eastern Arizona. *Jour. Paleo.* 29: 150-154.

———— 1955b Records of some Pliocene and Pleistocene reptiles and amphibians from Mexico. *Bull. So. Cal. Acad. Sci.* 54: 1-4.

———— 1958 New records of Cenozoic amphibians and reptiles from California. *Ibid.* 57: 5-12.

Brodkorb, P. 1952 A new rail from the Pleistocene of Florida. *Wilson Bull.* 64: 80-82.

———— 1953 Pleistocene birds from Haile, Florida. *Ibid.* 65: 49-50.

———— 1954a A chachalaca from the Miocene of Florida. *Ibid.* 66: 180-183.

———— 1954b Another new rail from the Pleistocene of Florida. *Condor* 56: 103-104.

———— 1957 New passerine birds from the Pleistocene of Reddick, Florida. *Jour. Paleo.* 31: 129-138.

———— 1959 The Pleistocene avifauna of Arredondo, Florida. *Bull. Fla. State Mus.* 4: 269-291.

Brongersma, L. D. 1951 Some notes upon the anatomy of *Tropidophis* and *Trachyboa. Rijksmus. Leiden. Nat. Hist.* 56: 15-21.

Bryon, E. 1928 Glacial climate in non-glaciated regions. *Amer. Jour. Sci.,* 2nd ser. 16: 162-164.

Buell, M. F. 1939 Peat formation in the Carolina Bays. *Bull. Torreya Bot. Club* 66: 483-487.

———— 1945 Late Pleistocene forests of southeastern North Carolina. *Torreya* 45: 117-118.

Bullen, R. P. 1958 More Florida radiocarbon dates and their significance. *Fla. Anthropol.* 11: 176.

———— and H. Winters 1953 [Stemmed archaic flint spear point in direct contact with fragmentary bones of a Pleistocene fauna at Seminole]. *Amer. Antiq. Notes and News, Southeast* 19: 105.

Cain, S. A. 1926 Pollen analysis as a paleoecological research method. Chapter 10 in *Foundations of Plant Geography,* New York: Harper Bros., xxiv-453 pp.

Caldwell, D. K. 1957 The biology and systematics of the pin fish *Lagodon rhomboides* (Linnaeus). *Bull. Fla. State Mus., Biol. Sci.* 2: 77-173.

———— 1958 Fossil fish teeth of the family Sparidae from Florida. *Quart. Jour. Fla. Acad. Sci.* 21: 113-116.

Chaney, R. W. 1940 Tertiary forests and

continental history. *Bull. Geol. Soc. Amer.* 51: 469-488.

Cooke, C. W. 1926 Fossil man and Pleistocene vertebrates in Florida. *Amer. Jour. Sci.*, 5th Ser. 12: 441-452.

——— 1928 The stratigraphy and age of the Pleistocene deposits in Florida from which human remains have been reported. *Jour. Wash. Acad. Sci.* 18: 420.

——— 1939 Scenery of Florida. *Fla. Geol. Surv., Bull.* No. 17: 1-118.

——— 1941 Pleistocene man in Florida [abstract]. *Bull. Geol. Soc. Amer.* 52: 1997-1998.

——— 1945 Geology of Florida. *Fla. Geol. Surv., Bull.* No. 29: 1-339.

——— and S. Mossom 1929 Geology of Florida. *Ann. Rept. Fla. Geol. Surv.* 20: 29-228.

Cope, E. D. 1873 *Synopsis of New Vertebrata from the Tertiary of Colorado Obtained During the Summer of 1873.* Wash., Govt. Printing Office, 1873, pp. 16-19.

——— 1884 The Vertebrata of the Tertiary formations of the west. *Rept. U. S. Geol. Surv. Terr.* 3: 770-781.

Cuvier, B. G. 1824 *Recherches sur les Ossemens Fossiles.* Paris: F. G. Levrault, 5: xx-526.

Dall, W. H. 1887 Notes on the geology of Florida. *Amer. Jour. Sci.*, 3rd ser., 34: 161-170.

——— 1892 Correlation papers: Miocene. *U. S. Geol. Surv. Bull.* 84: 1-349.

——— 1903 Tertiary fauna of Florida. *Trans. Wagner Free Inst. Sci.* 3: 1554.

Davis, J. H. Jr. 1946 The peat deposits of Florida. *Fla. Geol. Surv. Bull.* 30: ix-247.

DeGreer, G. 1940 Geochronologia suecica principles. *Kon Svenska Vetensk. Handl.*, 3rd ser., 18: 1-256.

DeRochebrune, A. T. 1880 Revision des ophidiens fossiles du Museum d'Histoire Naturelle. *Nouvelle Archiv. Mus. Hist. Nat.*, 2nd ser., 3: 1-265.

——— 1881 Memoire sur les vertebres des ophidiens. *Jour. Anat. Paris* 17: 185-229.

Dunn, E. R. 1928 A tentative key and arrangement of the American genera of Colubridae. *Bull. Antiv. Inst. Amer.* 2: 18-24.

Edwards, R. A. 1949 An abandoned valley near High Springs, Florida. *Quart. Jour. Fla. Acad. Sci.* 11: 125-132.

Flint, R. E. 1942 *Glacial Geology and the Pleistocene Epoch.* London: John Wiley and Sons, viii-589 pp.

Frey, D. G. 1951 Pollen succession in the sediments of Singletary Lake, North Carolina. *Ecology* 32: 518-533.

Gadow, R. F. 1933 *The Evolution of the Vertebral Column.* London: Cambridge Univ. Press, xxi-356 pp.

Gans, C. 1952 The functional morphology of the egg eating adaptations in the snake *Dasypeltis. Zoologica* 37: 209-244.

——— and M. Oshima 1952 Adaptation for egg eating in the snake *Elaphe climacophora* (Boie). *Amer. Mus. Nov.* No. 1571: 1-16.

Gidley, J. W. 1927 Preliminary list of species of Pleistocene vertebrates at Melborne, Florida. *Publ. Carn. Inst. Wash.* 3228: 274.

——— 1929a Ancient man in Florida; further investigations. *Bull. Geol. Soc. Amer.* 40: 491-501.

——— 1929b Further study of the problem of early man in Florida. *Smith. Inst. Exploration and Fieldwork in 1928*, pp. 13-20.

Gilmore, C. W. 1938 Fossil snakes of North America. *Geol. Soc. Amer., Spec. Pap.* 9: 1-96.

Gloyd, H. K. 1940 The rattlesnakes, genera *Sistrurus* and *Crotalus*. *Chicago Acad. Sci., Spec. Publ.* No. 4: 1-266.

Goin, C. J. and W. Auffenberg 1955 The fossil salamanders of the family Sirenidae. *Bull. Mus. Comp. Zool.* 113: 497-514.

Gunter, H., *et al.* 1948 Elevations in Florida. *Fla. Geol. Surv. Bull.* 32: 1-1158.

Gut, H. J. 1939 Additions to the recorded Pleistocene mammals from Ocala, Florida. *Quart. Jour. Fla. Acad. Sci.* 3: 54-55.

——— 1950 A Pleistocene microvertebrate fauna from Marion County, Florida. (Personal communication, March 1954).

Hay, O. P. 1902 Bibliography and catalog of fossil vertebrates of North America. *U. S. Geol. Surv. Bull.* 179: 1-449.

——— 1917 Vertebrata mostly from Stratum No. 3 at Vero, Florida; together with descriptions of a new species. *Ann. Rept. Fla. Geol. Surv.* 9: 43-68.

——— 1923 The Pleistocene of North America and its vertebrated animals from the states east of the Mississippi River and from the Canadian province east of longitude 95. *Publ. Carn. Inst. Wash.* 322: 1-532.

——— 1926 On the geological age of Pleistocene vertebrates found at Vero and Melbourne, Florida. *Jour. Wash. Acad. Sci.* 16: 387-392.

Hecht, M. K. 1959 Amphibians and reptiles, *in* The geology and paleontology of the Elk Mountains and Tabernacle Butte area, Wyoming. *Bull. Amer. Mus. Nat. Hist.* 117: 130-146.

Hibbard, C. W. 1944 Stratigraphy and vertebrate paleontology of Pleistocene deposits of southwestern Kansas. *Bull. Geol. Soc. Amer.* 55: 707-854.

——— 1949a Techniques of collecting microvertebrate fossils. *Contrib. Mus. Paleon., Univ. Mich.* 8: 7-19.

——— 1949b Pleistocene stratigraphy and paleontology of Meade County, Kansas. *Ibid.* 7: 63-90.

Hoffstetter, R. 1939 Contribution à l'etude des Elapidae actuals et fossiles et de l'ostéologie des ophidiens. *Archiv. Mus. Hist. Nat. Lyon* 12: 1-78.

——— 1946 Remarques sur la classification des ophidiens et particulièrement des Boidae des Mascareignes. *Bull. Mus. Hist. Nat. Paris* 18: 132-135.

——— 1953 Apropos de *Neurodromicus*, un pretendu Crotalidae de d'Oligocene nord-american. *Soc. Geol. France, Compt. Rend. Sci.* 8: 122-124.

——— 1955 Sur les Boides fossiles de la Sous-famille des Erycines. *Compt. Rend. Acad. Sci.* 240: 644-645.

Holman, J. A. 1958 The Pleistocene herpetofauna of Saber-tooth Cave, Citrus County, Florida. *Copeia* 1958: 276-280.

——— 1959a A Pleistocene herpetofauna near Orange Lake, Florida. *Herpetologica* 15: 121-125.

——— 1959b Amphibians and reptiles from the Pleistocene (Illinoian) of Williston, Florida. *Copeia* 1959: 96-102.

Janesch, W. 1906 *Pterosphenus schweinfurthi* Andrews und die Entwicklung der Palaeophiden. *Archiv. Biontologie* 1: 313-350.

Johnson, R. G. 1955 The adaptive and phylogenetic significance of vertebral form in snakes. *Evolution* 9: 367-388.

Knowlton, F. H. 1927 *Plants of the Past.* Princeton: Princeton Univ. Press, xxi-275 pp.

Kuhn, O. 1939 Die Schlangen (Boidae) aus dem Mittleozan des Geiseltales. *Geologische-Paleontologie, Inst. Univ. Halle,* pp. 119-133.

Lawrence, B. 1943 Miocene bat remains from Florida, with notes on the generic characters of the humerus of bats. *Jour. Mammal.* 24: 356-359.

Libby, W. F. 1952 *Radiocarbon Dating.* Chicago: Univ. Chicago Press, x-124 pp.

Loomis, C. and J. W. Gidley 1926 Fossil man in Florida. *Amer. Jour. Sci.* 5: 254-264.

MacNeill, S. 1950 Pleistocene shorelines in Florida and Georgia. *U. S. Geol. Surv., Prof. Pap.* 221:95-107.

McConkey, H. H. 1954 A systematic study of the North American lizards of the genus *Ophisaurus. Amer. Midl. Nat.* 51: 133-174.

Miller, H. W. 1955 A checklist of the Cretaceous and Tertiary vertebrates of New Jersey. *Jour. Paleo.* 29: 903-914.

Odum, H. T. 1952 The Carolina Bays and a Pleistocene weather map. *Amer. Jour. Sci.* 250: 263-270.

Owen, R. 1839 Description of some ophidiolites *(Palaeophis toliapicus)* from the London Clay, indicative of an extinct species of serpent. *Trans. Geol. Soc. London,* 2nd ser. 6: 209.

——— 1841 Report on British fossil reptiles. *Rept. Brit. Assoc. Adv. Sci.* 1841: 1-31.

——— 1849 *A History of British Fossil Reptiles.* London: Cassell and Co. Limited, vol. 1, pp. 1-657.

——— 1852 Preliminary observations on the exogenous processes of vertebrae. *Philos. Trans.* 1: 719-764.

Parker, G. G. and C. W. Cooke 1944 Late Cenozoic geology of southern Florida with a discussion of the ground water. *Fla. Geol. Surv. Bull.* 27: 1-119.

Peters, J. H. 1953 A fossil snake of the genus *Heterodon* from the Pliocene of Kansas. *Jour. Paleo.* 27: 328-331.

Pirkle, E. C. 1956 The Hawthorne and Alachua formations of Alachua County, Florida. *Quart. Jour. Fla. Acad. Sci.* 19: 197-240.

——— 1957 Hawthorne exposures southeast of Gainesville, Florida. *Ibid.* 20: 137-142.

——— and H. K. Brooks 1959 Origin and hydrology of Orange Lake, Sante Fe Lake, and Levy's Prairie Lakes of North-central peninsular Florida. *Jour. Geol.* 67: 302-317.

Remane, A. 1936 Wirbelsaule und ihre Abkommlinge, *in Handbuch der Vergleichenden Anatomie der Wirbeltiere.* Berlin: Urban and Schwarzenburg, 4: 1-1031.

Romer, A. S. 1948 The fossil mammals of the Thomas Farm, Gilchrist County, Florida. *Quart. Jour. Fla. Acad. Sci.* 10: 1-11.

——— 1956 *The Osteology of the Reptiles.* Chicago: Chicago University Press: xxi-772.

Ray, C. E. 1957 A list, bibliography, and index of the fossil vertebrates of Florida. *Fla. Geol. Surv. Spec. Pub.* No. 3: 1-175.

Sellards, E. H. 1910 A preliminary paper on the Florida phosphate deposits. *Ann. Rept. Fla. Geol. Surv.* 3: 17-41.

——— 1914 The relation between the Dunnellon formation and the Alachua Clays of Florida. *Ibid.* 6: 161-162.

——— 1915 The pebble phosphates of Florida. *Ibid.* 7: 25-116.

——— 1916 Human remains and associated fossils from the Pleistocene of Florida. *Ibid.* 8: 1-78.

——— 1919 Literature relating to human remains and artifacts at Vero, Florida. *Ibid.* 12: 1-4.

——— 1937 The Vero finds in the light in present knowledge, *in* McCurdy, G. C., *Early Man.* New York: Doubleday, xiv-322.

Simpson, G. G. 1928 Pleistocene mammals from a cave in Citrus County, Florida, *Amer. Mus. Nov.*, No. 328: 1-32.

——— 1929a The extinct land mammals of Florida. *Ann. Rept. Fla. Geol. Surv.* 20: 229-279.

——— 1929b Pleistocene mammalian fauna of the Seminole Field, Pinellas County, Florida. *Bull. Amer. Mus. Nat. Hist.* 56: 561-599.

——— 1930a Tertiary land mammals of Florida. *Ibid.* 59: 149-211.

——— 1930b Additions to the

Pleistocene of Florida. *Amer. Mus. Nov.* No. 406: 1-14.

——— 1932 Miocene land vertebrates from Florida. *Fla. Geol. Surv. Bull.* 10: 7-41.

——— 1933 A new fossil snake from the *Notostylops* beds of Patagonia. *Bull. Amer. Mus. Nat. Hist.* 67: 1-22.

SOEMMETRING, H. 1726 *The Anatomie of the Human Bones.* London, pp. 1-302.

TIHEN, J. A. 1951 Anuran remains from the Miocene of Florida, with the description of a new species of *Bufo. Copeia,* 1951: 230-235.

——— 1952 *Rana grylio* from the Pleistocene of Florida. *Herpetologica,* 8: 107.

VANZOLINI, P. R. 1952 Fossil snakes and lizards from the lower Miocene of Florida. *Jour. Paleo.* 26: 452-457.

VERNON, R. C. 1951 Geology of Citrus and Levy Counties, Florida. *Fla. Geol. Surv. Bull.* 33: 1-186.

WEIGEL, R. D. 1958 Fossil vertebrates of Vero, Florida. (*Unpublished Thesis, Univ. Fla.*, 1-87).

WETMORE, A. 1943 Fossil birds from the Tertiary deposits of Florida. *Proc. New England Zool. Club* 22: 59-68.

WHITE, T. E. 1940 New Miocene vertebrates from Florida. *Ibid.* 18: 31-36.

——— 1941 Additions to the Miocene fauna of Florida. *Ibid.* 18: 91-98.

——— 1942a The Lower Miocene fauna of Florida. *Bull. Mus. Comp. Zool.* 92: 1-49.

——— 1942b A new alligator from the Miocene of Florida. *Copeia* 1942: 3-7.

——— 1947 Additions to the Miocene fauna of North Florida. *Bull. Mus. Comp. Zool.* 99: 497-515.

WILLIAMS, E. E. 1953 A new fossil tortoise from the Thomas Farm Miocene of Florida. *Ibid.* 107: 537-554.

WILLISTON, S. W. 1925 *The Osteology of the Reptiles.* Cambridge: Harvard University Press, pp. 1-300.

WILSON, J. A. 1959 Stratigraphic concepts in vertebrate paleontology. *Amer. Jour. Sci.* 257: 770-777.

WOOD, A. E. 1932 New heteromyid rodents from the Miocene of Florida. *Fla. Geol. Surv. Bull.* 10:45-51.

——— 1947 Miocene rodents from Florida. *Bull. Mus. Comp. Zool.* 99: 489-494.

WOOD, H. E. *et al.* 1941 Nomenclature and correlation of the North American continental Tertiary. *Bull. Geol. Soc. Amer.* 52: 1-48.

ZEUNER, F. E. 1950 *Dating the Past.* London: Methune and Co., iii-474.

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