# TULANE STUDIES IN ZOOLOGY

VOLUME 13
1966-1967

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 receiving the entire series.

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# TULANE STUDIES IN ZOOLOGY
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(New taxonomic entities in boldface)

# TULANE STUDIES IN ZOOLOGY

Volume 13, Number 1 March 17, 1966

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TULANE STUDIES IN ZOOLOGY

Volume 13, Number 1 March 17, 1966

# POPULATION CHANGES IN RHESUS MONKEYS: CAYO SANTIAGO, 1960-1964

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## ABSTRACT

A population of introduced rhesus monkeys increased 16% annually during a five year period. Ultimately it consisted of six bands, five of which were formed by subdivision of one of the two original large bands. Divisions occurred during the fall mating season, apparently due to factors other than band size. Of the males at least three years of age about a third changed bands annually. This tendency to shift bore no constant relation to the size or the sex composition of the bands. Nearly all births occurred January to June each year. Mortality rates were greatest in animals less than two years and over six years of age, and in post puberal' males. In the adult population the females outnumber males by two to one.

Detailed long term studies of the numerical and social relataions in animal populations are feasible only when the individuals are marked and their movements somewhat restricted. Such a population is the colony of rhesus monkeys *(Macaca mulatta)* on Cayo Santiago, a wooded 40-acre islet situated off the east coast of Puerto Rico. All the animals are descendants of monkeys released there in 1938, and though most of their food has been provided by man, the animals are essentially wild. There were about 350 monkeys in 1940 when Carpenter (1942) studied their sexual behavior. Because of subsequent mortality and occasional heavy removals, there were only about 150 left in 1956 when Altmann (1962) commenced a 2-year study of monkey sociobiology. Largely because he tattooed the majority, I was able to account for every individual by the end of 1959, a year after I commenced work (Koford, 1963); at that time there were 277 monkeys. Since 1959 the population has grown about 16% per year, though this natural increase has been partly offset by the removal of 84 animals, mostly young males.

## BAND COMPOSITION

The current (mid-1964) population comprises 482 monkeys. Four are solitary males and the rest live in six bands of 167, 142, 56, 53, 39, and 21 members. The largest band, *A*, has been an entity since early 1956 or before (Fig. 1). The other five bands, *C, E, F, H,* and *I,* were formed by the subdivision of a single band, *B,* in three stages which occurred about one year apart. Although two bands, *A* and *C,* are now larger than any which split, there have been no divisions in the past 4 years. Contrary to

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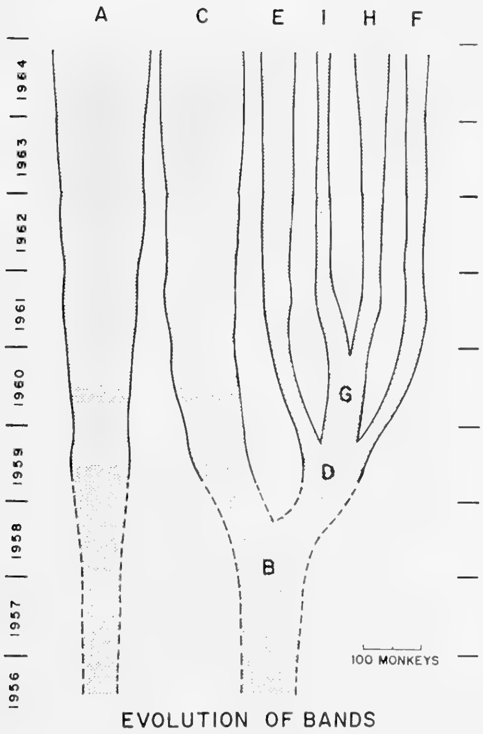

Fgure 1. Changes in the number and size of bands during the period 1956 to 1964. Capital letters are designations of bands. Horizontal widths indicate numbers of animals. Broken outline indicates early period of incomplete data.

expectation, it was not always the largest band which split. At the time when band *G* divided, in 1960. it was a third smaller than band *A* or *C*. Notably at least two of the divisions occurred in fall, when mating and social tensions were highest.

## REPRODUCTION

No monkeys have been added to the colony; numbers have increased only through births. The birth dates of nearly all born from 1960 to 1964 (454) are known within one day. These births occurred from late December to late July, within a span of 210 days. But in any one year a period of 130 days included practically all births (at least 94%). In spite of the increase in numbers born each year from 70 in 1960 to 119 in 1964, there has been no increase in the length of the birth season. In fact, the season with the most births was the shortest, only 126 days (Fig. 2).

From year to year the time of the birth season has varied moderately. For the 5-year period, the range of the initial birth date has been 46 days (December 29 to February 13), and of the median date 34 days (March 2 to April 5), while the final birth date, sometimes more than a month after the others, has ranged 65 days (latest, July 26). The interval from the last birth of one year to the first of the next year has varied from 165 to 224 days. Apparently some of the annual variations in birth season were caused by differences in weather and its influence on the nutritional quality of plant foods, because delay in the start of heavy rains in spring has been accompanied by delay in the onset of mating in summer (Koford, 1965).

In any one year, the distribution of births was also influenced by the survival of infants born the previous year, because multiparous females that failed to reproduce, or which lost their infants before the mating season, tended to come into estrus and conceive earlier than others. In adults the difference was probably caused by the fact that lactation delays the onset of reproductive cycles (Hartman, 1932). Nevertheless, monkeys conceiving for the first time (normally at 3½ years of age) give birth at about the

Figure 2. Distribution of all (119) birth dates during 1964. Ordinate is number of births per one-third-month period.

same time as lactating adults. For the 5 year period, the peak month of births to non-lactating adults occurred in February, a month earlier than the peak for other females (Fig. 3). Therefore, when reproduction is poor and early infant mortality is high, the following birth season tends to be early. There are exceptions and a few non-lactating adult females breed late (Fig. 4).

The overall birth pattern also differed among the bands (Fig. 4). In 1964, the spread of initial births among the six bands was 28 days, and of the median birth dates, 24 days. That birth season was unusually compact; in other years, the respective spreads have been as much as 67 and 33 days. Even between the two largest bands, in a single year (1960) the initial dates (for 21 and 25 births) differed by 32 days. Considerable variations are to be expected, of course, in view of individual differences in the virility of males, irregularities in the frequency, intensity, and duration of estrus in females, and the complex social interactions within the breeding population during the mating season (Conaway and Koford, 1964).

Population growth is influenced by fertility, which varies from year to year and among bands. Over a period of 5 years the reproductive rate, or ratio of births to the number of mature females, has ranged from 78% (1960) to 86% (1964), with an apparent tendency to increase. For newly mature females, 4 years old, the mean reproductive rate has been the same as for older ones (81% of 89 vs. 82% of 460). On rare occasions (7 in 6 years) a 3-year-old female has given birth. So far, there has been no obvious relation between the size of bands and high reproductive rate; the band with the highest mean rate (93%) was the third largest.

### MORTALITY

Births tended to increase numbers about 25% annually, but deaths partly offset this increment. Considering mortality rate to be the number dying during the year as a percentage of the number alive at the start of the year, the mean mortality rate for the years 1960-1963, excluding infants, was 6.7% (N=1235), with little year to year variation (5.9% of 320 in 1961, to 7.3% of 372 in 1963). Mortality tended to be high in the old and young; for yearlings the mean rate was 9.8% (N=235) and for animals

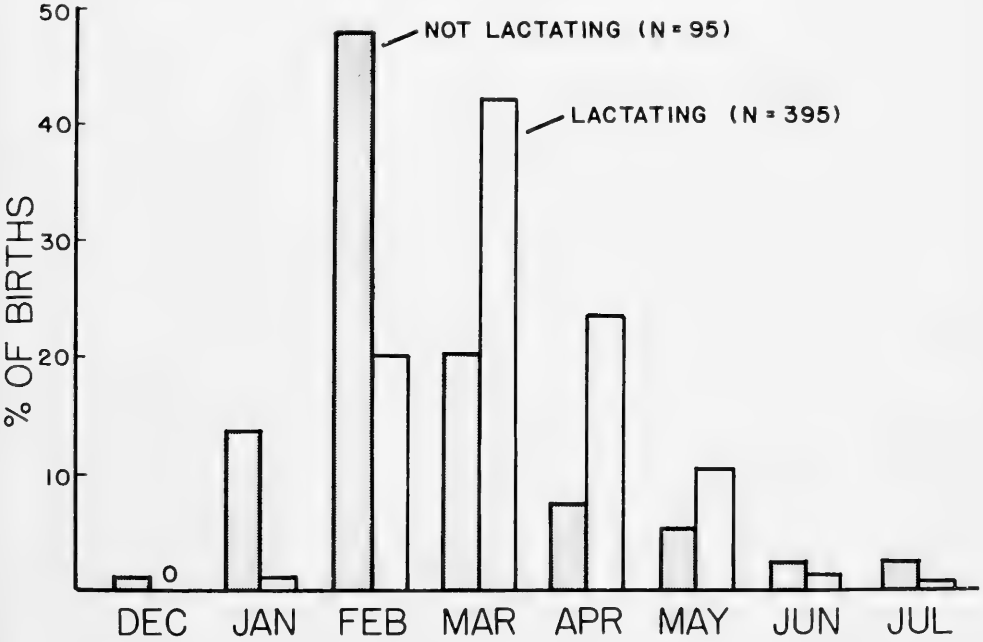

Figure 3. Distribution of births to adults that were not lactating during the mating season (shaded bars, N = 95) and to other females, lactating or primiparous (open bars, N = 359), 1960-1964.

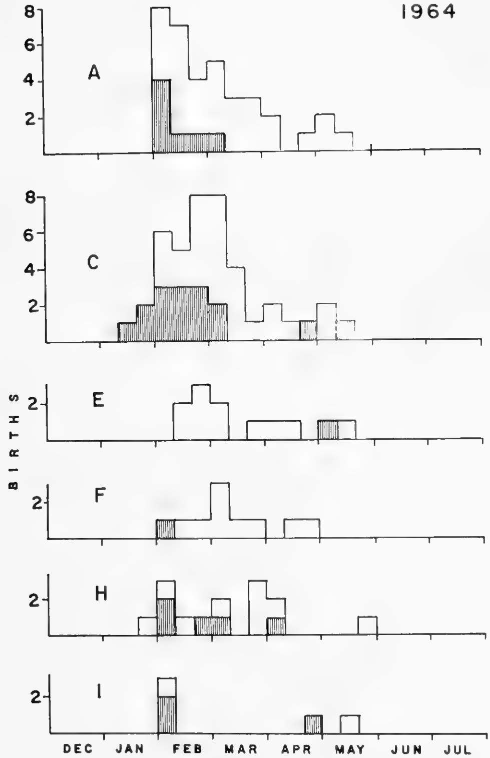

Figure 4. Distribution of birth dates by bands, 1964. Shaded squares indicate births to adults that were not lactating during the preceding mating season. Ordinate as in Fig. 2.

at least 7 years old, 8.4% (N=309), while for those from 2 to 5 years old it was about half as great, only 4.5% (N=575). Over the years the sexes have been born in nearly equal numbers (49% of 518 born were males), and early in life they have died at roughly similar rates. But commencing at four years of age, shortly after puberty, males suffered higher mortality than females. (Fig. 5). For animals at least 4 years old, the comparative rates were 8.8% (N=249) and 5.1% (N=414). This differential mortality largely accounts for the fact that less than half of the mature animals are males. The high mortality of older males is presumably caused by fighting and the debilitating effects of constant strong social tension.

### THEORETICAL POPULATION

The actual composition of the island population is somewhat artificial because some are removed and a few die of handling injuries. Trends in potential numbers and composition can be judged, nevertheless, by using the rates derived for the unaffected animals, as in Fig. 6. This diagram is based on the assumptions that: (1) initially there were 100 monkeys, 55 of them immatures (1 to 3 years old) in a 1:1 sex ratio, and 45 matures; (2) of the matures, 60% (27) were females, of which 85% gave birth at

Figure 5. Mean mortality rates by sex and age class, 1960-1963. For infants, the period involved is from birth to the end of the calendar year, not a full year.

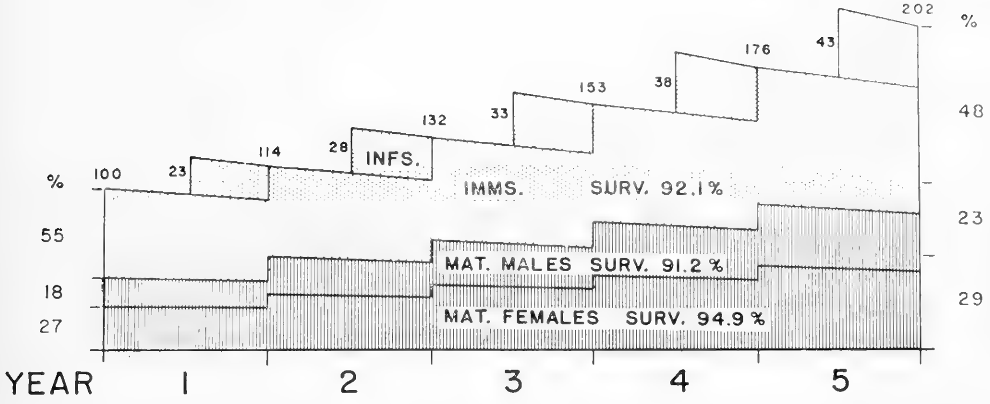

Figure 6. Theoretical growth and composition of a monkey population with reproductive rate of 85% and mean survival rates as computed for the Cayo Santiago population 1960-1963. Numbers above figure indicate population at start of each year and numbers of infants born at midyear.

midyear. The mean survival rates (100% minus mortality rate) derived from data for the period 1960-1963 were 92.1% for infants and immatures pooled, 91.2% for mature males, and 94.9% for mature females. Under these conditions, births would increase numbers about 25% at midyear, but mortality reduces the annual population growth to about 16%. Further, over a period of 5 years the proportion of immatures decreases somewhat, the proportion of females in the mature population decreases slightly, and total numbers approximately double. Assuming that year 1 in Fig. 6 represents 1960, which started with 277 animals, by the end of 1964 there would be 560. This figure is about 85 more than the actual number living on the island, and approximates the number removed.

## INTERCHANGE AMONG BANDS

Population composition is affected not only by reproduction and mortality, but also by the joining and departure of animals. For the whole colony the only such movements have been artificial removals. Among the bands, however, there has been much interchange of animals. Considering only changes persisting at least one month, during the period 1960-1963 there were 151 interchanges among bands or between band and solitary status, 91% of them by males. Infants and yearlings never, and 2-year-olds rarely (3 instances), changed bands unless their mothers did. But of all males at least 3 years old, a mean of 34% (N=301) departed from their initial band each year (Fig. 7). These shifts involved 78 males, about a fourth of which shifted in more than one year. A similar proportion shifted more than once in a single year, and two animals spent a month or more in four different bands over a period of three or four years. Males changed bands in all months, but most frequently during the mating season (Fig. 8). Of 126 male departures from bands, only 14 (11%) occurred from March to June, where 83 (66%) occurred from

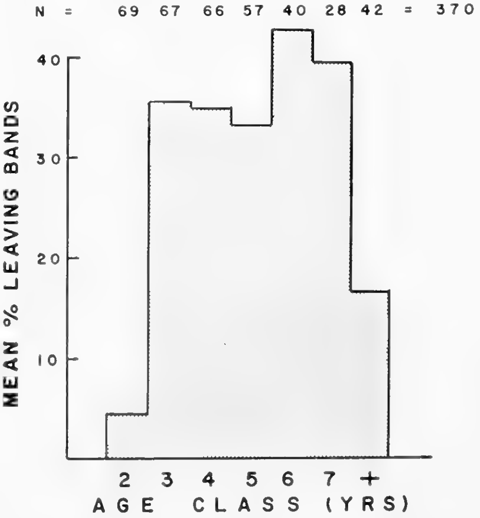

Figure 7. Mean proportion of each male age class departing from bands each year, 1960-1963. N is pooled number of males in each class at the start of the year.

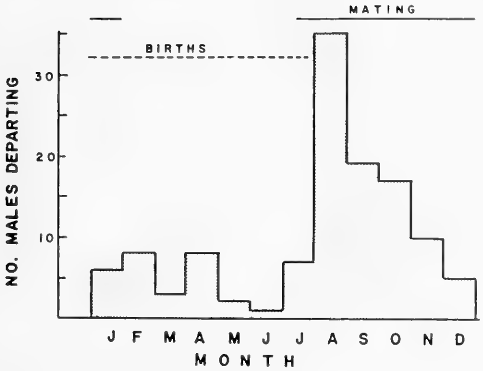

Figure 8. Month of male departures (126) from bands, 1960-1963. Males becoming solitary are included.

August to November. The restlessness of males during the mating season was also indicated by frequent fighting.

The interchange of males among bands was complex, even in single years (Fig. 9). Size, sex ratio, or identity of bands did not affect interchanges; the frequency of departures seemed to depend on social tensions among certain individuals, and in part on the readiness of other bands to accept the aliens. Over the four-year period, the number of males departing from each band constituted from 10% (band *A*. N=263) to 21% (band *H*, N=72) of the sexually mature animals (both sexes, at least 3 years old), except for the smallest band in which the loss was 42% (band *I*, N=46). As to losses versus gains, these were about equal in the four largest bands *(A, C, E,* and *F)* but losses were about twice gains in the two smallest bands *(H, I)*. Lastly, in terms of the sexually mature population of the island, the proportion leaving bands each year has varied from 10% to 15%, with no regular increase in spite of a 45% increase in numbers.

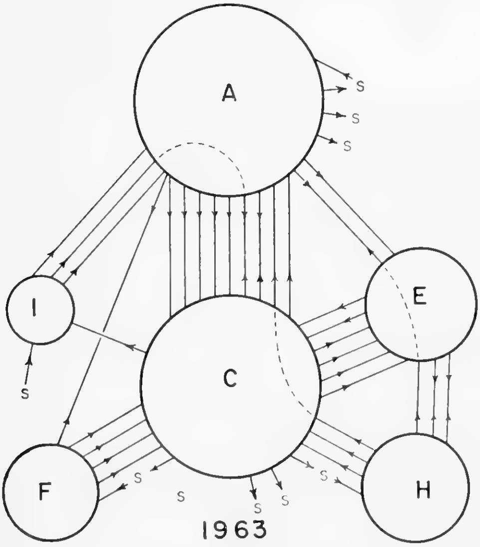

Figure 9. Movements of 49 males among bands, or between band and solitary status (S), during 1963. Only changes persisting at least one month are shown. Areas of circles are proportional to the number of sexually mature animals (at least 3 years old) in each band at midyear. One male remained solitary throughout the year.

Of the male departures from bands, 17% (N=126) were to solitary status, and of the 18 monkeys involved, all save two adults were 4 to 7 years old. Apparently the tendency of a young male to depart from his band is inhibited by the presence of his mother, for of the 2- and 3-year-old males having a mother in the same band only 13% (N=111) departed, whereas for orphans of the same age, 42% (N=24) departed. For older males, the presence of the mother had no apparent influence on the rate of departure.

Females did not become solitary, even temporarily, and less than 3% of the females changed bands. Evidently the social forces causing females to shift bands are different from those affecting males, because most (10 to 14) changes occurred in the birth season, from January to May, rather than in the mating season. These movements involved eight females, at least 3 years old, none of which became a member of more than two bands. Three females changed bands about one month before giving birth, and five were accompanied by infants.

## SUMMARY

Over a period of five years the number of free-ranging monkeys in a provisioned island population increased 16% annually, and in mid-1964 there were 482 animals in six bands. Five of these formed by subdivision of a single large band, whereas a second large band did not divide. Divisions occurred during the fall mating season and apparently depended on social factors other than band size. Nearly all births occurred from January to June, and in spite of a 70% increase in numbers born the length of the

birth season did not increase. Among years the initial birth dates varied 46 days and the median dates 34 days. These variations were presumably caused by annual differences in weather and vegetation, and in the proportion of non-lactating parous females, which tended to breed early. Social factors also probably influenced the time of mating, for the spread of birth dates among bands in some single years was as great as for the entire population in different years. The ratio of births to the number of mature females ranged from 78% to 86%, with an apparent tendency to increase.

Excluding infants, mortality reduced numbers at a mean rate of 6.7%. Animals less than 2 years and over 6 years of age suffered the highest mortality. Commencing about puberty, females survived better than males, so that in the adult population females outnumber males more than two to one. Of the monkeys at least three years old, each year about a third of the males changed bands, principally in the mating season. This tendency to shift bore no constant relation to either the size nor the sex composition of the band, but among immatures orphans shifted more readily than other males.

These data suggest that under natural conditions it is chiefly the adolescent and adult males which tend to disperse and distribute genetic material among all bands in a region. Verification of the theoretical implications of these and other characteristics of the island colony will require similar information for wild populations of rhesus and other primates.

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# TWO NEW SPECIES OF THE GENUS *CAMBARUS* FROM ARKANSAS (DECAPODA, ASTACIDAE)

ROLLIN DEWAYNE REIMER,
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*Fayetteville, Arkansas*[1]

## ABSTRACT

Two new species of the genus *Cambarus* from Arkansas are described. *Cambarus* **causeyi** from northern Arkansas seems to have its closest affinities with members of the Asperimanus Group. *Cambarus* **strawni** from the southern slope of the Ouachita Mountains appears to be closely related to members of the Diogenes Section.

The first specimens of two undescribed species were collected in 1963, during a survey of the crawfishes of Arkansas (Reimer, MS). I had hoped to obtain more individuals before publishing my findings, but since I have not been able to return to the areas it seems best to proceed with the description of these two new species.

My appreciation is extended to Dr. Horton H. Hobbs, Jr., United States National Museum, for the verification of these two species, and to Dr. Kirk Strawn and Dr. David Causey, both of the University of Arkansas, for their assistance while collecting in Arkansas. I am pleased to name these species in honor of Drs. Causey and Strawn.

## *Cambarus* **causeyi**, new species

*Diagnosis.*—Body pigmented; eyes normal. Rostrum short, excavate, lacking lateral spines; acumen indistinctly delimited at base, with dorsally projecting knob at tip: areola open but narrow, approximately 28 times longer than wide: lateral branchiostegal spines absent; suborbital angle absent; antennal scale widest distal to midlength; chela slightly depressed; hooks on ischiopodites of third pereiopod of male only; first pleopod of Form I male terminating in two distinct processes bent at more than 90 degree angle to main shaft; annulus ventralis as figured (Fig. 2); prominent setiferous punctations over most of carapace and pereiopods.

*Holotypic male, Form I.*—Body subovate. Abdomen narrower than thorax (7 & 9 mm, respectively), shorter than carapace. Cephalic section of telson with one spine on each side. Width of cephalothorax less than depth in region of caudodorsal margin of cervical groove (8.5 & 9 mm, respectively). Areola open but narrow; 28.0 times longer than wide. Cephalic section of cephalothorax 1.4 times longer than areola.

Rostrum (Fig. 6) excavate dorsally; acumen indistinct but with upturned corneous tip; marginal spines absent; tip extending cephalic to penultimate segment of peduncle of antennule. Postorbital ridges well developed, with prominent groove extending almost its full length. Subrostral ridges moderately developed. Suborbital angle, branchiostegal spine, and lateral spines absent. Surface of carapace densely punctate and moderately setiferous.

Epistome (Fig. 7) equal in length and breadth, with indistinct cephalomedial projection; cephalolateral edges elevated ventrally.

Eyes normal. Antennules of usual form. Antennae of usual form and only slightly longer than carapace. Antennal scale (Fig. 4) reaching to distal end of penultimate segment of antennule; widest distal to mid-

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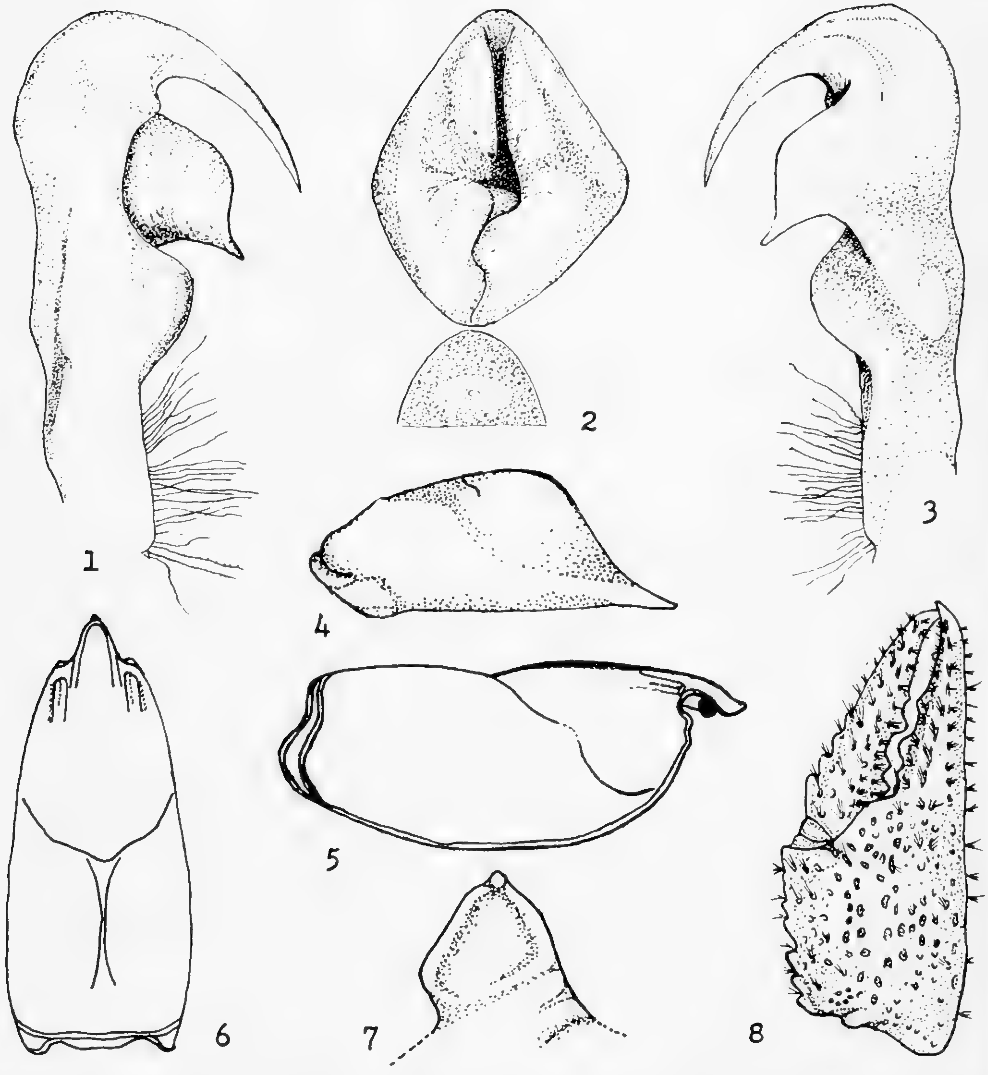


Figures 1-8. *Cambarus causeyi*, new species: **1.** lateral view of first pleopod of holotypic male; **2.** annulus ventralis; **3.** mesial view of first pleopod of holotypic male; **4.** antennal scale of holotypic male; **5.** lateral view of carapace of holotypic male; **6.** dorsal view of carapace of holotypic male; **7.** epistome of holotypic male; **8.** upper surface of chela of holotypic male.

length (approximately 2.3 times longer than wide).

Right chela (Fig. 8) slightly depressed and with palm only slightly inflated. Inner margin of palm with one row of six tubercles. Tubercles on lower surface of palm indistinct. All surfaces of chela bearing setiferous punctations, with setae of various lengths within same punctation. Fingers slightly curved ventrally from their bases, gaping along proximal two-thirds of their length. Inner margin of immovable finger with five distinct tubercles: proximal four noncorneous and placed on mesial border, first much smaller than distal three; tubercle at base of distal third of finger, corneous (like tip of fingers), placed laterally. Lower surface of immovable finger without tubercles but with single row of setiferous punctations. Opposable margin of movable finger with four tubercles; third from base largest.

Upper surface of movable finger with four tubercles near base.

Carpus longer than wide (6.6 & 4.7 mm, respectively) with well defined longitudinal furrow above; two prominent spines located distally (dorsal distal edge-mesial distal edge), remainder of surface lacking tubercles; all surface with setiferous punctations. Merus with two rows of tubercles along ventral margin, converging proximally, six in mesial row, three in lateral row, becoming larger distally; tubercles absent from dorsal surface; setiferous punctations on dorsal and ventral surfaces, diminishing laterally. Hooks present on ischiopodites of third pereiopods only.

First pleopod (Figs. 1, 3) reaching base of third pereiopod and terminating in two distinct parts. Central projection corneous, blade-like, strongly curved caudomesiad at more than a right angle to main shaft. Mesial process noncorneous, bulbiform with small nipple-like apical projection, curving caudolaterally at about same angle as central projection.

*Allotypic female.*—Differs from holotypic male in the following respects: Rostrum longer, with lateral edges upturned dorsally to give deeper excavation. Inner margin of palm with five tubercles. Two rows of tubercles along ventral margins of merus, three in mesial row, seven in lateral row. Cephalic section of telson with three spines on each side.

Annulus ventralis (Fig. 2) situated at caudal end of a deep, narrow V-shaped sternum. Sternum partially hidden by numerous long setae. Annulus ventralis longer than wide with centrally located fossa; sinus extending cephalically and caudally from fossa.

*Male, Form II.*—Unknown.

*Measurements (in millimeters).*—

| | | Holotype | Allotype |
|---|---|---|---|
| Carapace | Height | 9.0 | 12.9 |
| | Width | 8.5 | 12.5 |
| | Length | 20.4 | 31.2 |
| Areola | Width | 0.3 | 0.2 |
| | Length | 8.4 | 12.8 |
| Rostrum | Width | 2.5 | 3.6 |
| | Length | 2.8 | 4.8 |
| Chela (Right) | Length inner margin of palm | 5.7 | 9.7 |
| | Width of palm | 6.0 | 10.4 |
| | Length outer margin of palm | 15.5 | 23.5 |
| | Length of dactyl | 9.1 | 14.4 |

Caudal sinus normal, i.e., lateral surfaces slope away from sinus region. Cephalic sinus with lateral surfaces folding mesially as if to close over top of sinus.

*Type locality and ecological notes.*—Type locality is four miles west of Sandgap, Pope Co., Arkansas, on State Highway 124; from a spring and natural pond. The spring is located on the western side of a gently sloping hill and drains into a small shallow pond about 200 feet away. The hillside and pasture were dotted with several large rocks, under which could almost always be found a burrow. Unconcealed openings to burrows were scattered over the area. No chimneys were observed.

Most burrows had several openings leading to a common tunnel which descended almost vertically. None of the burrows was dug to the bottom. The holotype was taken from a burrow (top capped by a rock) on the hillside. The allotype and paratype, the latter an immature female, were taken from burrows near the natural pond. The pond was clear and contained a large number of frog and toad eggs but lacked crayfish.

*Disposition of types.*—The holotypic form I male and the allotypic female are deposited in the U. S. National Museum, numbers 116678 and 116679, respectively. A juvenile paratypic female also is deposited in the U. S. National Museum.

*Relationships.*—*Cambarus causeyi* seems to have its closest affinities with *Cambarus setosus* Faxon, 1889, and *Cambarus zophonastes* Hobbs and Bedinger, 1964, members of the Asperimanus Group in the Ozark Region. Similarities include the narrow areola, setiferous punctations, single row of tubercles on inner margin of palm, and shape of the chela. *Cambarus causeyi* can be distinguished by normal coloration, normal eyes, and absence of lateral spines on the rostrum and sides of carapace. In addition the mesial process of the first pleopod of the Form I male is bulbiform. The shape of the epistome and annulus ventralis is quite different from either *C. setosus* or *C. zophonastes*.

### *Cambarus* **strawni**, new species

*Diagnosis.*—Rostrum excavate, lacking marginal spines, with indistinct acumen; areola obliterated; spines absent along surface of carapace; suborbital angle absent; antennal scale widest at (or slightly distal to) midlength; chela strongly depressed; carapace and chela lacking conspicuous setiferous punctations; hook on ischiopodites of third pereiopods only, of male; first pleopod of Form I male terminating in three distinct processes bent at approximately a 90 degree angle to main shaft; annulus ventralis as figured (Fig. 17).

*Holotypic male, Form I.*—Body ovate. Abdomen narrower than thorax (8.7 & 13.4 mm, respectively) and shorter than carapace. Cephalic section of telson without spines. Width of cephalothorax equal to depth in region of caudodorsal margin of cervical groove. Areola obliterated in middle; cephalic section of cephalothorax 1.5 times as long as areola.

Rostrum depressed; upper surface excavate; margins converging from base; acumen only slightly delinated basally by small tubercle; marginal spines absent; tip extending cephalically to base of penultimate segment of peduncle of antennule. Subrostral and postorbital ridges moderately developed with postorbital ridges terminating cephalically without spine. Suborbital angle, branchiostegal spines, lateral spines absent. Punctations on dorsal surface of carapace few, increasing in number laterally.

Epistome (Fig. 11) wider than long and terminating cephalically in small cephalomedian projection; cephalolateral margins slightly rounded.

Eyes normal. Antennules of usual form. Antennae broken (see allotypic female). Antennal scale small, reaching slightly beyond tip of rostrum; widest at midlength; approximately three times longer than wide (2.8 & 0.8 mm, respectively).

Right chela (Fig. 18) depressed, palm slightly inflated. Inner margin of palm with two rows of tubercles; inner row of eight much more prominent than outer of five. Tubercles on lower surface of palm indistinct. Palm moderately punctate. Fingers curved ventrally from bases, gaping along entire length; both slightly punctate. Inner margin of immovable finger with three tubercles; first from base being largest. Opposable margin of movable finger with four tubercles; second from base largest, terminating arch originating at base of finger. Upper surface of movable finger with single row of seven indistinct tubercles.

Carpus longer than wide (9.6 & 6.7 mm, respectively) with well defined longitudinal furrow above; dorsal crest with row of four indistinct tubercles; mesial surface with series of 13 irregularly placed spines, largest being near distal dorsal margin; punctations sparsely scattered over all surfaces. Merus with two rows of tubercles along ventral surface converging proximally (8 in lateral row—12 in mesial row); one row of 15 tubercles on dorsal margin becoming indistinct proximally. Punctations few on dorsal and ventral surfaces.

First pleopod (Figs. 9, 13) reaching to base of third pereiopod, terminating in three distinct parts. Central projection corneous, blade-like; curving caudomesiad at slightly more than right angle to main shaft. Mesial process slightly more than right angle to main shaft of pleopod. Third distinct process lying between and mesial to mesial process and central projection; thin, slightly corneous, half as long as central projection and mesial process. According to its position, third process is probably homologous to the cephalic process in *Procambarus* (Hobbs, personal communication).

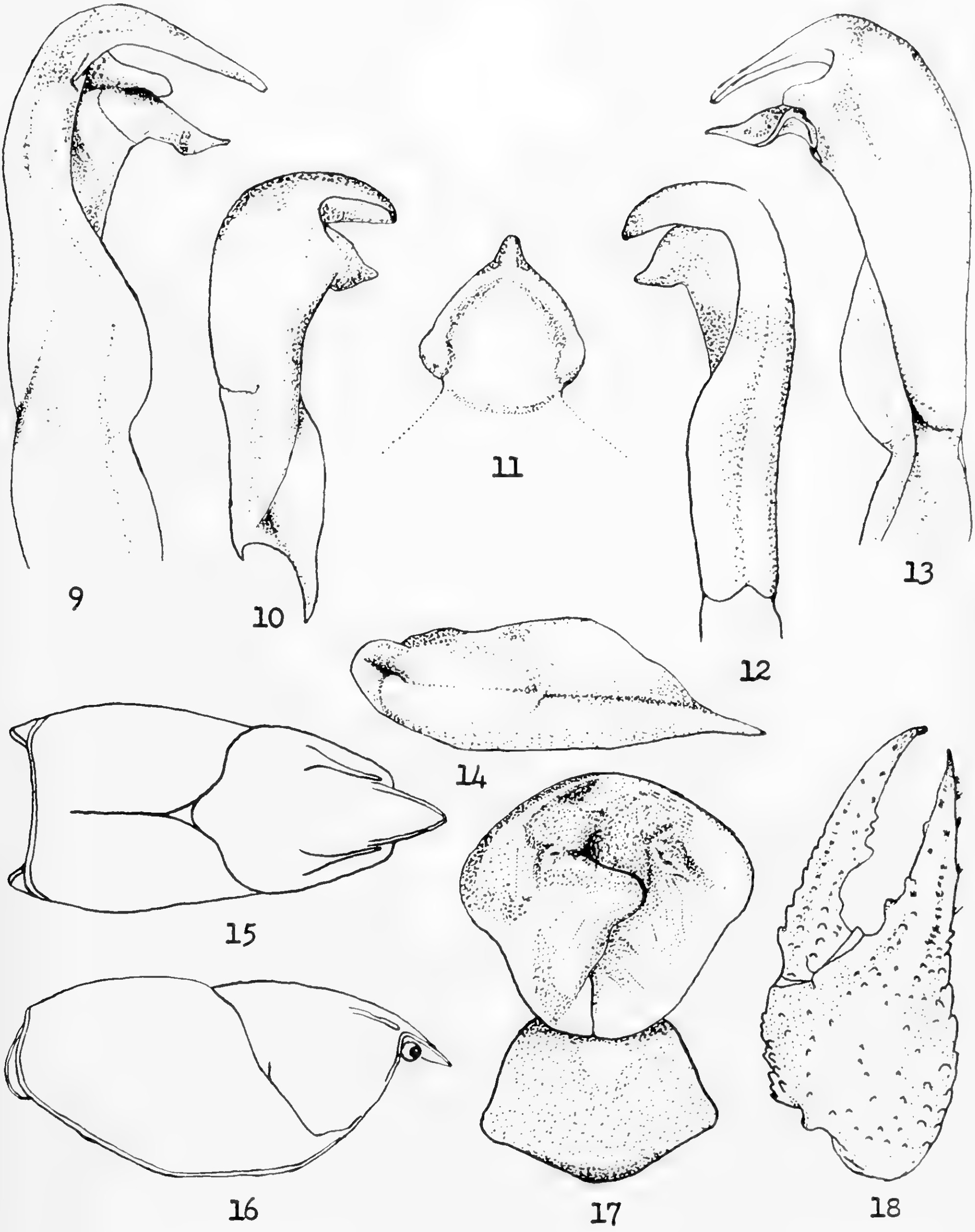
*Allotypic female.*—Allotypic female differs from the holotypic male in the following respects; tubercles on movable finger not as well defined, antennae approximately equal to length of carapace (one broken), slight variation in size and arrangement of tubercles on carpus and merus.

Annulus ventralis (Fig. 17) situated at caudal end of deep V-shaped sternum and divided into right and left sides by prominent sinus leading caudally from cephalomesial fossa.

*Morphotypic male, Form II.*—Morpho-

*Measurements (in millimeters).*—

| | | Holotype | Allotype | Morphotype |
|---|---|---|---|---|
| Carapace | Height | 12.4 | 12.7 | 9.2 |
| | Width | 12.4 | 12.5 | 9.4 |
| | Length | 28.6 | 28.7 | 21.7 |
| Areola | Length | 11.2 | 11.2 | 8.4 |
| Rostrum | Width | 4.3 | 4.3 | 3.0 |
| | Length | 4.8 | 4.9 | 3.6 |
| Chela (Right) | Length inner margin of palm | 6.5 | 5.5 | 3.4 |
| | Width of palm | 5.1 | 4.5 | 2.8 |
| | Length outer margin of palm | 19.5 | 16.3 | 9.8 |
| | Length of dactyl | 12.5 | 10.2 | 6.9 |



Figures 9-18. *Cambarus strawni*, new species: **9.** lateral view of first pleopod of holotypic male; **10.** mesial view of first pleopod of morphotypic male; **11.** epistome of holotypic male; **12.** lateral view of first pleopod of morphotypic male; **13.** mesial view of first pleopod of holotypic male; **14.** antennal scale of holotypic male; **15.** dorsal view of carapace of holotypic male; **16.** lateral view of carapace of holotypic male; **17.** annulus ventralis; **18.** upper surface of chela of holotypic male.

type differs from holotype in following respects; two rows of tubercles on inner margin of palm of right chela with ratio of 6:5 (5 in inner row), third and fourth tubercles on movable finger indistinct, slight variation in size and arrangement of tubercles on carpus and merus, hooks on ischiopodites of third pereiopods greatly reduced in size, first pleopod (Figs. 10, 12) with only two terminal elements (distal half of right pleopod broken).

*Variations.*—Few variations observed. The more obvious are: second tubercle lacking on immovable finger of one specimen, third and fourth tubercles lacking on movable finger of two others. Tubercle number on dorsolateral crest of carpus varies from four to seven, and on one, tubercles not in definite row. Mesial surface of carpus of one small female with 10 tubercles. Epistome shorter and with rounder cephalolateral borders in some specimens. Annulus ventralis on small female (probably immature) swollen and not resembling that of allotype. First pleopods of both second form males lacking third terminal process. In one male Form II, mesial process twice as long as central projection. One paratypic female with spine on left side of cephalic section of telson.

*Type locality and ecological notes.*—The type locality is 2.7 miles north of Dierks, Howard County, Arkansas, on State Highway 4; a small marshy area in the Saline River drainage. All specimens were taken from burrows. The burrows were in a low area adjacent to a small permanent creek. During the wet period of the year this area is quite boggy and standing water is common in places. During the dryer parts of the year the surface water is absent and the area loses its boggy nature. The soil is a sandy clay. The stream nearby is shallow, clear, fast running, and paved with a rocky bottom. *Procambarus simulans simulans* (Faxon), 1884, *Procambarus blandingii acutus* (Girard), 1852, and *Orconectes palmeri longimanus* (Faxon), 1898, were taken from the stream.

The holotypic male, allotypic female, and one paratypic female were taken on June 22, 1963. Another collection at the type locality on February 17, 1965 yielded the morphotypic male and two paratypes (male Form II, female).

Two female paratypes were also taken on June 22, 1963 from the headwaters of the Cossotat River about four miles west of Umpire, Howard County, Arkansas, on State Highway 4.

*Color.*—The carapace is primarily olive tan with the abdomen being slightly lighter. Ventral surfaces are cream colored. Dactyl, suborbital ridge, lateral borders of the rostrum, and articulating areas of the pereiopods grade from a deep olive green to black. The colors are more vivid in the older or larger individuals.

*Burrows.*—Two types of burrow construction have been observed. The burrows at the type locality consisted of a maze of interconnecting tunnels with the primary tunnel proceeding almost vertically. The burrows west of Umpire, Arkansas lacked the maze and the primary tunnel went down in a spiral manner. Some openings at both locations were capped with chimneys.

*Disposition of types.*—The holotypic form I male, allotypic female, and morphotypic form II male are deposited in the United States National Museum, numbers 116675, 116676, 116677, respectively. The five paratypes (four females and a form II male) have been retained in my personal collection.

*Relationships.*—With the exception of having three terminal projections on the first pleopod of the Form I male, *Cambarus strawni* appears to be most closely related to members of the Diogenes Section. *Cambarus diogenes diogenes* Girard (1852), *Cambarus diogenes ludovicianus* Faxon (1884), and *Cambarus hedgpethi* Hobbs (1948) are members of the Diogenes Section which occur in the same area. *Cambarus strawni* can be distinguished from these three species by the three terminal projections on the first pleopod of the Form I male, shape of the antennal scale, shape of the annulus ventralis of the female, tubercle arrangement on the fingers of the chelae, and in the case of *Cambarus diogenes diogenes* and *Cambarus diogenes ludovicianus,* by the absence of suborbital angles.

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March 17, 1966

# *SPEOCIROLANA THERMYDRONIS*, A NEW SPECIES OF CIROLANID ISOPOD CRUSTACEAN FROM CENTRAL COAHUILA, MÉXICO

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ABSTRACT

*Speocirolana* **thermydronis** is described from a single specimen taken in thermal waters of an isolated bolson in northern Mexico. The type locality is high in the Sierra Madre Oriental, suggesting that the genus *Speocirolana* may be of pre-Tertiary origin. The species occurs in an area of high endemism where special habitats afforded by springs permit an ancient fauna to persist.

Extensive spring-fed marshes, lakes and streams occur in the intermontane basin surrounding the town of Cuatro Cíenegas in central Coahuila, México. This bolson, located in the structural axis of the Sierra Madre Oriental, has long been isolated, and evidence exists for a number of faunal invasions, resulting in marked endemism in aquatic, and to a lesser extent in terrestrial, organisms (Webb, *et al.*, 1963; Hubbs and Miller, 1965). In April 1964, a field party from the University of Colorado Museum visited the area. Their collections included a single cirolanid isopod, which is here described as a new species.

We are prompted to describe this form on the basis of a single specimen for a number of reasons. First, extensive field work in the basin since 1958, including three expeditions since 1964 with unsuccessful searching for additional isopod material, indicates the rarity (or difficulty in finding) more specimens of this species. Second, the area of original discovery has been severely modified and may soon be destroyed. Third, description of the isopod may stimulate additional work in the largely-unexplored bolson region of northern México. And, fourth, its description further emphasizes the unique, endemic nature of the biota of that region.

## *Speocirolana* **thermydronis,** n. sp.

Figs. 1-21

The new species is assigned to *Speocirolana* Bolivar (1950), a name originally proposed as a subgenus of *Cirolana* Leach, but elevated to generic rank by Bowman (1964). Generic characters of the new species agree with those given by Bolivar, with minor exceptions. The major character of the genus is the first three pairs of pereopods prehensile and pereopods 4-7 ambulatory. These features are otherwise unknown in North American troglobitic cirolanids, except in the poorly-known *Conilera stygia* Packard (1900) from near Monterrey, Nuevo Leon, México. The last form, when rediscovered, may prove to be a species of *Speocirolana.*

*Type Material and Etymology.*—The type material of *Speocirolana thermydronis* consists of a single female specimen, measuring 15 mm from the tip of the head to the end of the telson. It was collected on 12 April 1964, in the complex habitat associated with Pozos de la Becerra, a large warm spring with its source lying 9.8 miles (13.7 km) south-southwest of Cuatro Cíenegas. The specimen was collected by Mary L. Allesio of the University of Colorado, and was referred to us for study by Clarence J. McCoy, now of the Carnegie Museum. The specimen now is housed in the United

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States National Museum, catalog number 113054.

The name is derived from the Greek *"thermydron,"* a warm spring, and alludes to the habitat of the animal in thermal waters of the Cuatro Cíenegas basin.

*Diagnosis.*—Characters that separate *Speocirolana thermydronis* from S. pelaezi (Bolivar) and from *S. bolivari* (Rioja) are as follows: clypeus of head with posterior ends rounded, shaped in gentle bow, and without deep notch anteriorly; labrum with mandibular margin almost straight; first antennal flagellum with 14 articles, with length of peduncle divided by length of flagellum 0.9; second antenna with 35 flagellar articles, extending posteriorly to seventh pereon segment when deflected; palp relatively short; lacinia of maxilliped paddle-shaped, bearing 12 plumose setae; pleopods with all endopods lacking terminal setae; inner surfaces of endopods of uropods spineless; and, telson shaped as a broad shield, terminating in acute point.

*Description and Comparisons.*—Our comparisons of *Speocirolana thermydronis* with *S. pelaezi* and *S. bolivari* are based on illustrations and data given by Bolivar (1950) and by Rioja (1953); some additional data were graciously provided by Thomas E. Bowman. All three forms are eyeless and unpigmented except for brown masticatory surfaces on the mandibles and darkened tips on the claws of the pereopods. The ratio of body length to greatest body width is 3.5 for *thermydronis* and near 2.7 for the other two species. The head of *thermydronis* is sub-pentagonal in shape, rounded anteriorly (Fig. 1); *bolivari* has a similar head, while that of *pelaezi* is broader and shorter. The inferior frontal lamina of the head of *thermydronis* is similar to that of *pelaezi* in projecting forward between the antennal bases to a rounded terminus (Fig. 3). The lamina of *bolivari* is long and pointed. The clypeus and the labrum of *thermydronis* are distinctive (Fig. 3). The former is bow-shaped, gently rounded to its smooth posterior terminations, and the latter has an almost-straight mandibular margin.

The first pereonite lacks epimera in all three forms. Epimera also appears absent from the second and third pereonite of *thermydronis* (Fig. 1); they probably were lost in preservation or in preparation of the specimen for study, are not visible from dorsal view, or are fused to the segments. Epimera on pereonites 4-7 are well developed in all three species, with strong, acute, postero-lateral angles.

Five segments are visible in the pleon of all three species anterior to the pleotelson. The first two segments are sub-equal in length and twice as long as the third segment. The fourth and fifth visible segments are abruptly shorter and narrower than the first three. Pleon segments 1-3 have acute postero-lateral angles.

The telson of *thermydronis* is slightly longer than broad and ends in an acute posterior tip (Figs. 1, 7). In *pelaezi* the telson is broadly rounded and that of *bolivari* is truncate.

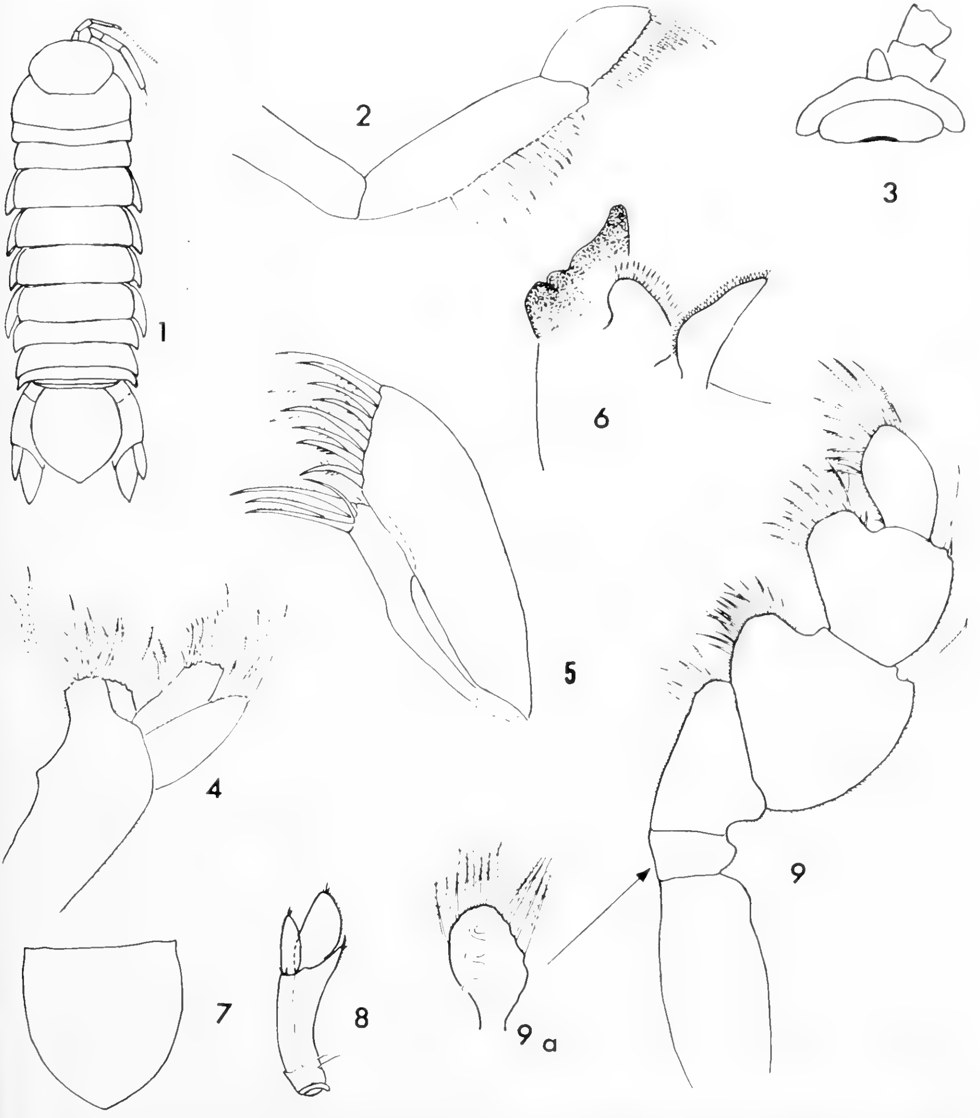
The first antenna is about the length of the peduncle of the second antenna in *thermydronis* (Figs. 1, 14) and in *pelaezi;* it appears shorter than that of *bolivari.* The first antenna has three peduncular joints in all three species, but in *thermydronis* it has 14 flagellar articles (Fig. 14) as opposed to about 20 articles in *pelaezi* and 22-28 in *bolivari.* The ratio of length of the antennal peduncle to length of the flagellum is about 0.9 in *thermydronis.* In *pelaezi* and *bolivari* this ratio is nearly 1.3. *S. thermydronis* resembles *pelaezi* in having the terminal setae of the first antenna relatively uniform in length; *bolivari* bears a number of short setae on the terminal flagellar article and a single elongate seta. The distal flagellar articles of all three species are invested with aesthetases.

The second antenna of *thermydronis* is elongate, reaching back to the seventh pereonite when deflected (Fig. 1). This condition prevails also in *bolivari,* but the second antenna of *pelaezi* reaches only to the fifth peronite. There are 35 articles in the flagellum of *thermydronis*, 48-52 in *bolivari,* and 30 in *pelaezi.* The terminal articles of the flagellum in *thermydronis* (Fig. 10) and *bolivari* are elongate, whereas those of *pelaezi* are shortened. The antennal peduncle of *thermydronis* comprises five clearly delimited joints.

In *S. thermydronis* the mandibles (Fig. 6) are asymmetrcial, with the right incisive process overlapping the left ventrally. The lacinia mobilis of the mandible is subtriangular, bearing on its margin about 34 short, cone-shaped teeth. The second segment of the mandibular palp in *thermydronis* is invested with setae on its distal two-thirds (Fig. 2); in the other two species setae occur on the distal half to two-fifths of this segment.

The first and second maxillae are similar in all three species. The outer lamina of the first maxilla bears 10 toothed distal spines (Fig. 5). The inner lamina has three sparsely-plumose spines and two setae (one long, one short). The second maxilla (Fig. 4) has three conspicuous endites. The outer two are provided with large, incurved spines on their distal margins. The inner endite has numerous setae of differing sizes, some of which are plumose.

The maxilliped of *thermydronis* (Fig. 9) differs from that of *bolivari* and *pelaezi.* The four distal articles of the palp are armed on their inner surfaces with strong setae.



Figures 1-9. *Speocircolana* **thermydronis,** female holotype. **1.** dorsal aspect; **2.** mandibular palp; **3.** inferior frontal lamina, labrum, clypeus; **4.** second maxilla; **5.** first maxilla; **6.** mandible, lacina mobilis, pars molaris; **7.** telson; **8.** left uropod, ventral aspect; **9.** maxilliped; **9a.** lacinia of maxilliped.

There are stout spines on the distal outer corners of the second and third articles of the palp segments, but only fine, hair-like setae occur on the lateral margins of all but the terminal article (which is naked). The outer surface of the fourth joint of the palp in *bolivari* and *pelaezi* is setose. The lacinia (Fig. 9a) is ovoid, with 12 plumose setae and three coupling hooks.

The pereopods (Figs. 11-13, 15, 16) are dimorphic in all three species. The first three pairs are prehensile and sub-cheliform, perhaps more so in *thermydronis* than in the others. The last four pairs are ambulatory, without obvious morphological specialization. Pereopods 1-3 in *thermydronis* have the palmar margins of the propodus armed with two, three, and four stout spines, respectively; however, this character seems variable, in *pelaezi* at least, and may be of little worth. Pereopods 4-7 become progressively longer from front to back in all three forms.

The first pleopod of *thermydronis* is narrower than the succeeding ones (Fig. 17). The expodites of all the pleopods have distal, plumose setae (Figs. 17-21); these are sparsely developed on the fourth. The third exopod has an incomplete transverse suture, and the fourth and fifth exopods have complete sutures. All endopodites lack distal setae; thus Bowman (1964) may have erred in implying that setose first and second pleopodal endopods and the lack of setation on the remainder characterizes the genus *Speocirolana.* In females of *bolivari,* at least the endopods of the first pleopods lack setae (*fide,* Rioja, 1953: lam. 3, Fig. 31). Rioja's illustration (lam. 3, Fig. 30) of the first pleopod of a male of *bolivari* shows profuse setation on the endopod. Bolivar (1950: Fig. 9), on the other hand, shows setation on the endopod of the first pleopod of a female of *pelaezi.* The character needs further study.

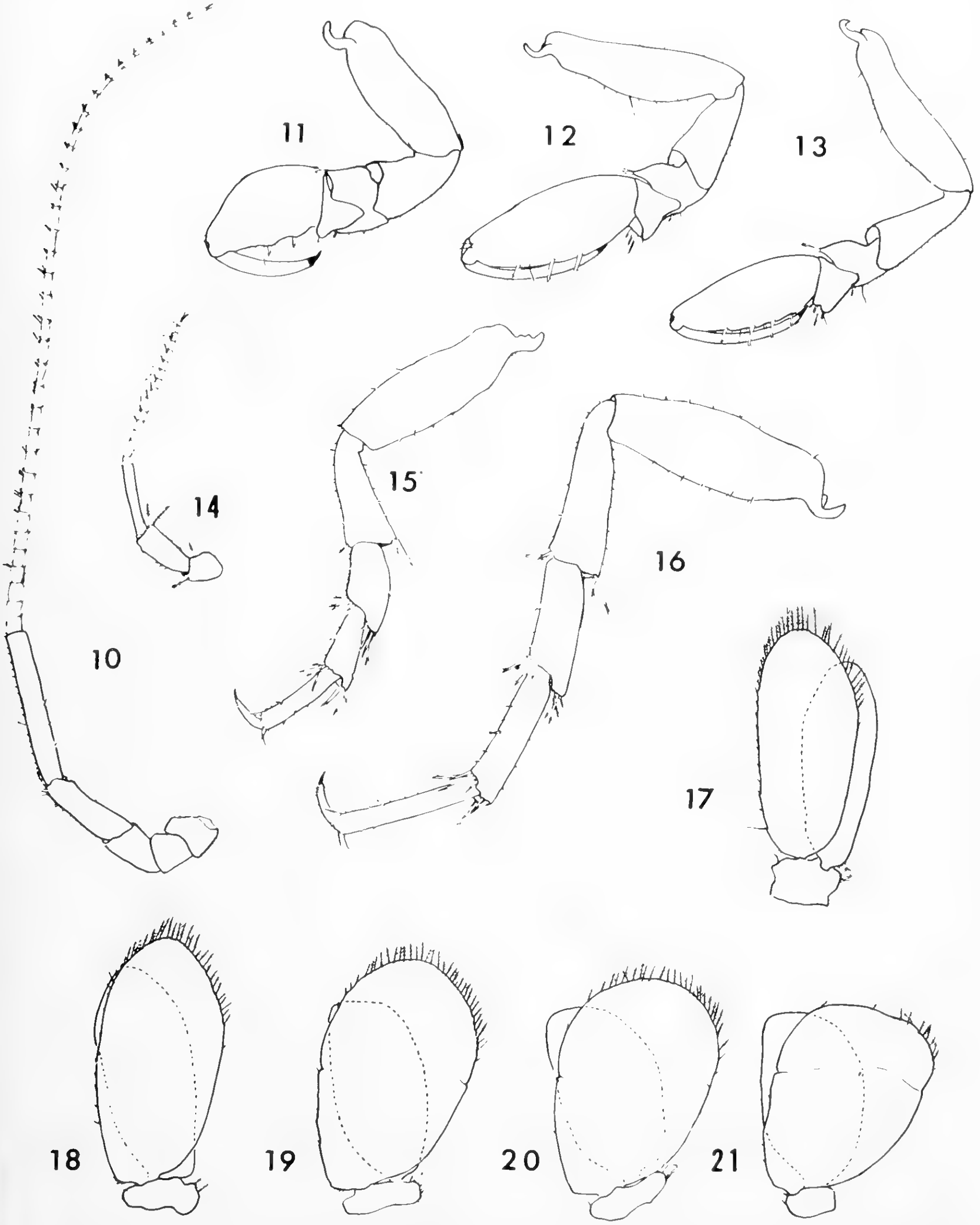
The uropodal base of *thermydronis* has setae on its inner, proximal margin (Fig. 8). The distal part of the inner margin is prolonged, and bears an apical spine that reaches to the middle of the endopod and almost to the end of the telson. In *pelaezi* this spine etxends past the end of the telson. In *bolivari,* it extends only about half the length of that structure. The inner surface of the endopodite of *thermydronis* bears a few scattered, short setae; in *pelaezi* there are three stout spines on this surface and *bolivari* has five such spines. The uropodal exopods and endopods of all three forms have their apices armed with short terminal setae.

*Type Locality.*—Prior to December 1964, Pozos de la Becerra was one of the largest and most complex aquatic habitats in the Cuatro Cíenegas basin. The laguna was elongate and irregular in shape, with depths ranging to more than 10 m at the largest spring inflows. In areas of inflow the bottoms were of gravel and rubble. Other areas had bottoms of deep calcareous silt; most silt bottoms were covered by dense beds of waterlily *(Nymphaea).* The laguna originally measured about 25 m in width at its narrowest place, ranging to more than 150 m wide, and was perhaps two km long. Water was always extremely clear. Temperatures taken in the sources on seven different occasions ranged from 29.4 to 32.2° C. Water levels did not change perceptibly in the period 1960-64, and one estimate of discharge was about 1.34 $m^3$/second at the outlet channel.

The laguna suffered some modification in 1961 through construction of a bathing facility. In 1964, however, the laguna was drastically modified by construction of a canal, and the water level fell 46 cm in about two days. In April 1965, the downcutting of the uncontrolled canal outlet had apparently stabilized, with the laguna surface lowered more than a meter. This resulted in drainage of extensive marshes that were associated with the spring, and reduced the over-all surface area of water and marsh from perhaps 10 $km^2$ to less than 0.2 $km^2$. Swimmers had muddied the laguna in April 1965, and the silty bottoms had been greatly disturbed. Many formerly gravel bottoms were silted and most of the *Nymphaea* beds were dried or uprooted. Only the inflows of the largest springs remained clear of silt.

*Origin of Speocirolana thermydronis.*—The troglobitic cirolanid isopods of the Western Hemisphere, with the exception of *Antrolana lira* Bowman (1964), occur in an arc surrounding the Gulf of México (Rioja, 1953; Bowman, 1964). *A. lira* lives in the Appalachian Valley of Virginia and does not enter directly into the problem of origin for *S. thermydronis.* The distribution of the species of *Speocirolana* in Cuatro Cíenegas and in the Valles-Mante area of San

Luis Potosí and Tamaulipas, and the poorly-known *Conilera stygia* (also with the first three pairs of pleopods prehensile), from Monterrey, Nuevo Leon, form a compact triangle in the northeast of México. These, and *Cirolanides texensis* Benedict from the San Marcos area of Texas, all are in the area inundated by the sea that filled the mid-Cretaceous Mexican Geosyncline (Maldondo-Koerdell, 1964). *S. bolivari, S. pelaezi,* and *C. stygia* all occur near the edge of the Gulf Coastal Plain, slightly inland from areas of



Figures 10-21. *Speocirolana* **thermydronis**, female holotype. **10.** second antenna; **11.** first pereopod; **12.** second pereopod; **13.** third pereopod; **14.** first antenna; **15.** fourth periopod; **16.** seventh pereopod; **17.** first pleopod; **18.** second pleopod; **19.** third pleopod; **20.** fourth pleopod; **21.** fifth pleopod.

mid-Tertiary inundations (West, 1964). The transgressions by the sea in Oligocene may have affected the last three species, but undoubtedly excluded the Sierra Madre Oriental Axis in which *S. thermydronis* occurs.

The Cuatro Cíenegas basin, in addition to a number of endemic vertebrates (Hubbs and Miller, 1965), holds a unique molluscan fauna. This includes a number of genera and species, yet to be described, that show few relationships to other living forms of México, or elsewhere (Dwight W. Taylor, *pers. comm.*), and therefore indicate a great age for aquatic habitats of the area. Cirolanid isopods in freshwater cave habitats are generally thought to be derived from populations of marine forms that are relicted by marine regressions (Bowman, 1964). The discovery of *S. thermydronis* high in the Sierra Madre Oriental may indicate a pre-Tertiary origin of the genus; as part of an ancient plateau fauna it has been able to persist in the special habitats afforded by the springs.

It seems doubtful that distributions of epigean animals, such as fishes, will shed much light on the origins of *S. thermydronis.* However, it is worth noting that Miller and Minckley (1963) found the endemic platyfish of the Cuatro Cíenegas basin (*Xiphophorus gordoni* Miller and Minckley) sharing many characters with *X. variatus xiphidium* (Gordon) of the Río Soto la Marina system. They suggested that an overland dispersal of the aquatic animals might have occurred, utilizing stream captures, from southeast, to the Cuatro Cíenegas area. This is substantiated by the presence of *Gambusia marshi* Minckley and Craddock in the Río Salado system (the stream that now drains the Cuatro Cíenegas basin), a species whose closest relatives also are in the Río Soto la Marina-Río Panuco complex (Minckley, 1962).

The presence of a new cirolanid in the Cuatro Cíenegas basin, a specialized, cavernicolous catfish (*Priatella phreatophila* Carranza, 1954) at Muzquiz, Coahuila, north of Cuatro Cíenegas, and the relative wealth of cavernicolous animals in the limestone Edward's Plateau Region of Texas, points out a need for further exploration in that area for troglobitic organisms. Until extensive surveys are made and additional collections are obtained little can be done in synthesis of the over-all fauna of the region. We defer speculation on the intra-generic relationships of *S. thermydronis* until additional material can be obtained.

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# SOCIAL ORGANIZATION OF THE SOUTH AMERICAN MONKEY, *CALLICEBUS MOLOCH:* A PRELIMINARY REPORT

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## ABSTRACT

*Callicebus moloch ornatus,* a small diurnal South American monkey, was the subject of an 11-month field study. Groups usually consist of an adult pair and one or more young, and each group occupies a definite and fixed territory. Adjacent groups often meet, usually in the early morning, in specific locations at the boundaries of their territories. As opposing pairs approach, each animal draws closer to its mate. Male and female then sit with sides touching, facing the opposing pair a few meters away. There follows an elaborate vocal exchange in which all animals participate. Calling is accompanied by tail-lashing, arching, piloerection, and short rushes which may develop into a chase. One animal rarely overtakes another during a chase and even when this occurs, fighting is not severe. Mateships appear to be stable, although animals will occasionally copulate with members of adjacent groups, especially during the seasonal peak of sexual activity. Arrival of young had no obvious effect on the pair bond. In one group in which reliable identification of sexes was possible, the male carried the infant at virtually all times, except when it was being nursed.

## I. INTRODUCTION

Few New World primates have been studied intensively from a naturalistic point of view and little systematic information is available on the forms and varieties of social organization in these monkeys. Of the more than 15* genera of platyrrhine monkeys, only one, the howler monkey *(Alouatta)* has been the subject of a major field investigation (Carpenter, 1934). Groups of howler monkeys on Barro Colorado Island in Panama averaged about 18 animals, with an upper limit of 35. Observations of red spider monkeys *(Ateles),* indicate that they are frequently found in small subgroups, but join with others in larger groupings of as many as 40 individuals (Carpenter, 1935). More limited observations on *Cebus, Lagothrix,* and *Saimiri* suggest a similar tendency in these primates toward the formation of large groups (Bates, 1944; Fooden, 1963; Kuhlhorn, 1939).

All New World monkeys, however, do not conform to this pattern. Moynihan (1964), for example, notes that Panamanian night monkeys *(Aotus trivirgatus)* are most often found in pairs or in small family units, and the same characteristic is suggested for marmosets (Hampton, 1964; Stellar, 1960). However, there have been no systematic field studies of any South American primate which displays a tendency toward a small, "family unit" type of social organization. Such a tendency was strongly evident in *Callicebus moloch,* the subject of the present report, and was a major consideration in the selection of this species for study in the field.

## II. RANGE AND PHYSICAL APPEARANCE

The range of Amazonian and Orinocoan species of *Callicebus* extends north from the upper Rio Paraguay basin in Mato Grosso, Brazil and Paraguay into Colombia, Venezuela, and extreme northwestern Brazil; and it extends west from Rio Tocantins in the state of Pará, Brazil into parts of Bolivia, Peru, Ecuador, and to the base of the Andes in Colombia (Hershkovitz, 1963).

*Callicebus* is a small monkey, comparable

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* Authorities differ somewhat in number of genera assigned to platyrrhine monkeys.

in size to *Aotus*, the night monkey, but strongly diurnal in habit. A Colombian form, *Callicebus moloch ornatus* (Hershkovitz, 1963) is the subject of this report. This subspecies is distinguished by deep auburn fur covering the throat, chest and forearms, and by a striking white band across the forehead which contrasts sharply with the dark face and chestnut red crown. The appealing and colorful aspect of these animals is enhanced in some individuals by white gloves and ear tufts. Males and females are similar in size and coloration and it is only after close association with specific groups that reliable identification of sexes is sometimes possible.

## III. STUDY SITE

The study site was in the llanos or plains area of eastern Colombia, near the town of San Martin. The region consists of natural grassland and additional thousands of acres of artificial pastures which have been cleared in recent years. In spite of this, a substantial number of forested areas remain as narrow galleries along the rivers and in the form of groves surrounded by savannah. Many of these tracts contain stable populations of *Callicebus* and other monkeys *(Alouatta, Aotus, Cebus, Saimiri)*.

Three groves, ranging in size from approximately 3 to 17 acres, were selected for study. At one time all were part of the same large tract, but they were isolated from each other around 1950 when large sections of the forest were cleared. The study areas were left as a water conservation measure, and the monkey population had apparently been undisturbed for more than 14 years. The largest of the three forests, Socay, was studied intensively from May 1964 through March 1965. The only resident monkeys in this forest were *Callicebus*. The present report is a preliminary description of the social organization and behavior of these monkeys.

## IV. POPULATION CHARACTERISTICS

The first census of Socay Forest, completed on August 2, 1964, indicated that there were 28 monkeys living in nine small groups of from two to four animals each. In the three- and four-animal groups it was clear in most cases that only two of the animals were fully mature. In December 1964 the first birth was noted and five additional animals were born in the next three months. However, owing to the presumed death of one infant and the disappearance of two subadult animals, the total population had increased to only 31 by March 1965. No new groups were formed, but as the result of births, mean group size rose from 3.1 to 3.4. The results of the first census and the final census are presented in Table 1.

## V. GROUP ACTIVITIES AND INTERGROUP RELATIONS

Throughout the study period each group occupied a definite and fixed area which

TABLE I

*Population and Group Composition, Socay Forest*

| | | May-August 1964 | | March 1965 | |
|---|---|---|---|---|---|
| Group | First Count | Composition | Total | Composition | Total |
| 1 | 5/23/64 | 2A,**J**,(I$_2$)* | 3 | 2A,I | 3 |
| 2 | 5/27/64 | 2A,J,I$_2$ | 4 | 2A,2J | 4 |
| 3 | 5/25/64 | 2A,I$_2$ | 3 | 2A,J | 3 |
| 4 | 6/25/64 | 2A,J | 3 | 2A,J (I*) | 3 |
| 5 | 7/ 3/64 | 2A,J | 3 | 2A,J,I | 4 |
| 6 | 6/25/64 | 2A | 2 | 2A,I | 3 |
| 7 | 8/ 2/64 | 2A,1J?,1**J**? | 4 | 2A,J,I | 4 |
| 8 | 5/25/64 | 2A,I$_2$ | 3 | 2A,J | 3 |
| 9 | 6/27/64 | 2A,I$_2$ | 3 | 2A,J,I | 4 |
| | | | 28 | | 31 |
| | | mean/grp | 3.1 | | 3.4 |

A = adult
J = juvenile or subadult
I$_2$ = late infant, no longer carried, considered J in March census
* = died or presumed dead
**J** = presumed to have left forest
? = age class uncertain

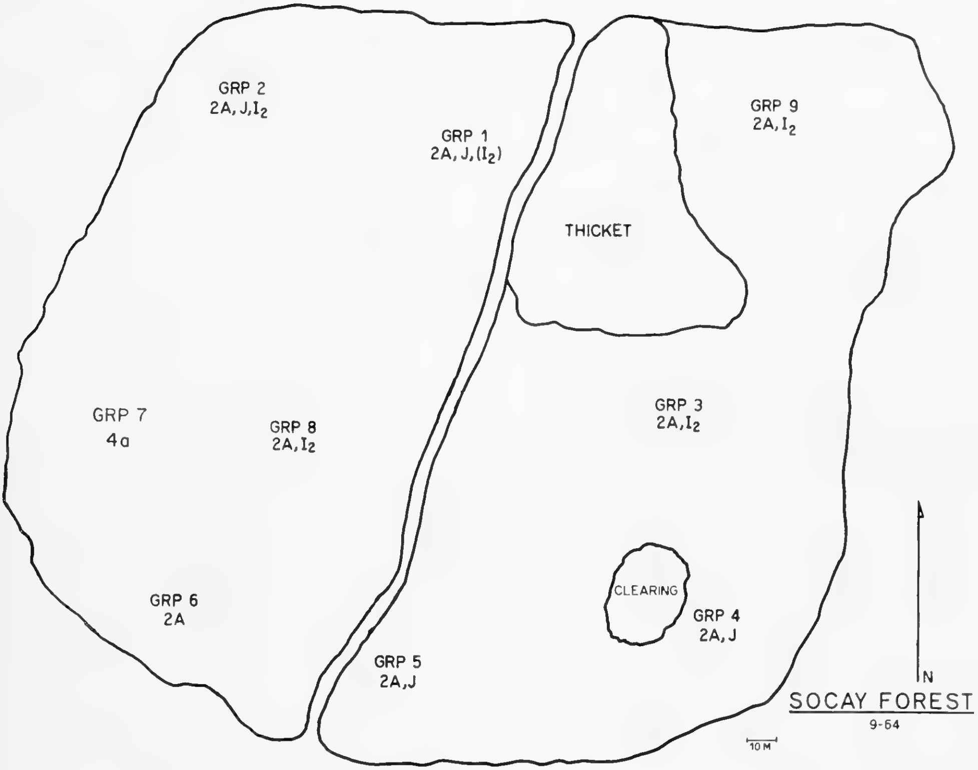

Figure 1. Location of groups in Socay Forest. Group composition at completion of first census, August 2, 1964. A = adult, J = juvenile or subadult, $I_2$ = late infant, no longer carried. Age class of animals in group 7 was uncertain.

contained its food and lodge trees. The approximate location of groups is shown in Figure 1. The nine groups making up the population of Socay Forest constitute a community in which each group has frequent contact with its immediate neighbors. Furthermore, even those groups which are seldom if ever in visual contact may communicate directly by means of the elaborate vocalizations which play such a prominent part in the social life of *Callicebus*. The most interesting social relations, however, are the face-to-face encounters between neighboring groups.

Activity begins at the first hint of dawn. Usually, the initial signs of life are faint stirrings in the lodge tree, the sounds of urination and defecation, followed by one or two moaning vocalizations. Frequently, these lead into a longer series of calls in which both adult and immature animals may participate. The call is elaborate and the arrangement of its several components varies from one occasion to the next (Moynihan, in press). Calling often begins with a series of moaning u-ah notes which increase rapidly in tempo and intensity. At the end of each note there is a sharp chuck or squeal. This form of calling may continue for a minute or more and is often terminated by a series of rather slow, emphatic O-O-O-O sounds. All vocalizations may cease at that point or the entire sequence may be repeated. In anywhere from a few minutes to half an hour after the first call, the group leaves the lodge tree and begins to feed on fruits and berries, which form the bulk of the *Callicebus* diet.

Groups from neighboring areas frequently meet as they move toward food trees. These are not chance encounters, nor do they seem to be merely the result of attraction to a common food source. The animals actively converge toward each other and usually meet in the same areas at the boundaries of their territories day after day. As the opposing pairs approach, each animal draws closer to its mate. Characteristically, male and female sit with sides touching and face the opposing pair in an adjacent tree. One of the animals (male?) begins to make the same low-pitched moans that were heard as the day began. As he vocalizes he presses against his mate and often looks toward her or touches her lightly with his hand; she, together with the members of the opposing pair, may join with him in a sustained call. During vocalization both animals stand and face the opposing pair. Often they seem to swell to half again their normal size as the result of arching their backs, stiffening or bowing of the arms, and piloerection. The animals shake vigorously with the effort of calling and the impression of tension and agitation is enhanced by the rhythmic tail-lashing that often accompanies the call.

The vocal interchange may continue without pause for five minutes or longer. At times only one monkey or one pair will call; often, however, all animals call in concert. The volume of sound is unexpected in view of the relatively small size of the animals; on a quiet day one can hear the sounds from a mile away.

While they call, the opposing pairs often edge closer together; individual animals leap forward or up a few feet, then suddenly, with no apparent forewarning, one monkey dashes toward the opposing pair. It may withdraw at once whether there is a counter-rush or not, or the rush may develop into an extended chase in which the males are probably most often involved. During a chase the customary pathways are abandoned and the monkeys race across the tops of the trees, make perilous crossings, descend to a few feet from the ground, and sometimes fall or leap to the forest floor where pursuit continues until the fleeing animal scampers up a vine or slender tree. Rarely is an animal caught, and even when this happens the consequences are not severe. There is no extended fight; the pursuer pushes and slaps at its victim, may bite him once or twice, there are a few squeals and it is over. The chase is not an invariable climax to the meeting between groups. At times one or more of the participants seem to lose interest and begin to feed, or simply sit quietly. Sometimes both members of a pair sit side by side with their tails twined. This pattern is more often seen, however, during rest periods and is especially common in the evening when the animals settle down for the night.

Another response which is sometimes associated with the interchanges between groups is chest rubbing. *Callicebus* has a small patch of glandular tissue over the chest which is probably implicated in this response. The animal grasps a branch with its hands and draws or pushes itself slowly forward dragging the chest along the surface. Often it pauses at the end of a stroke and sniffs or mouths the area it has just rubbed. Frequently, the chest is rubbed with the hands alternately in slow, downward strokes. Inasmuch as chest rubbing seems to occur most frequently after an encounter between groups, it might be assumed to constitute a form of territorial marking. The response does not always occur in boundary areas, however, and no animal has been observed to react to a limb rubbed by another.

The entire episode from the first meeting of the groups until they resume feeding may occupy less than five minutes to as much as half an hour or more. After the early-morning face-to-face encounters have ended and the animals have returned to their respective areas, there sometimes occurs a remarkable vocal pattern. This is a short call, sounding from a distance very much like the gobbling of a turkey. Its most interesting feature, however, is not its sound quality, but the fact that it is given almost simultaneously by several groups. Typically, one animal or a single group begins the call and within a fraction of a second it is taken up by other groups and passes rapidly through the forest as a kind of chain reaction. Each burst of calling ends abruptly in less than 10 seconds, but the call is usually repeated at frequent intervals for five minutes or more. Preceding and following each call there is a series of brief, high frequency, whistling notes.

The early-morning encounters and vocal chain reactions are similar to the territorial disputes that have been so carefully described for birds. But factors other than the defense or maintenance of territory are definitely involved, and this is particularly evident when the female is sexually receptive. Under these circumstances instead of fleeing from the onrush of the opposing male, as she usually does, she may sit quietly as he approaches, or even approach him. Mutual genital inspection may follow or they may copulate without preliminaries—or at least attempt to do so before her mate countercharges and interrupts the act. At the same time that the female is showing obvious interest in neighboring males she may be indifferent to the sexual advances of her own mate. During a long episode I observed, the male repeatedly solicited the female. He reached toward and manipulated her genitals, sniffed or licked them, and frequently attempted to mount. In spite of his persistence, the female did not accept him. She fled twice, but each time was overtaken before she had joined the male of a neighboring group. On this and other occasions the male was observed to place himself between his mate and the intruding male, or to restrain her as she attempted to move away from him.

Although it is possible that a female may remain with a neighboring male indefinitely, it seems more likely that such associations are brief. In one instance a female stayed with the male of a neighboring group for several hours before returning to her mate. This was the longest liaison of this type I observed. More often, extra-pair associations last only a few minutes, as in the following episode: A male and female of neighboring pairs approached each other near the boundaries of their territories, copulated, then separated, the male moving off while the female returned to her customary partner. Although her mate had twice rushed the pair during copulation, he showed no unusual reaction to the female upon her return. On other occasions, however, mild aggression has been observed.

## VI. THE PAIR BOND

In spite of the sexual attraction of both male and female to opposite-sexed members of neighboring groups, there are many indications that the bond between mates is strong and enduring. Although most animals could not be identified individually, for those pairs in which it was possible, partners remained together from the first contacts until observations terminated as much as 10 months later. Ordinarily, the members of a pair follow each other closely and the animals are usually found within a few meters of each other during feeding, travelling, and resting periods. Generally speaking, the attraction is mutual. Either sex may follow the other and leadership changes frequently throughout the day. Often when one animal has finished feeding it will sit at the edge of the food tree and wait until its mate approaches before moving on. Grooming, nuzzling, gentle grasping, and sitting for long periods of time with sides pressed together and tails twined, provide further evidence of the breadth of social ties. When the animals become separated and lose contact there are various signs of distress, particularly whining vocalizations which, if ineffective, may lead to more elaborate calls.

The arrival of infants has provided additional information on the relationship between mates. In a single pair which I was able to observe intensively and at close range it was clear that the male almost always carried the infant except when it was being cleaned or nursed by the mother. At times the transfer seemed to be accomplished by the infant while the adults sat in contact. On many occasions, however, I saw the mother remove the infant from the male's shoulders, lick its genitals (which stimulates urination), and place it on her ventral surface. When nursing was completed the infant climbed to the mother's shoulders from which it moved to the male or was removed by him. In groups of three and four monkeys, I suspect that immature animals also carry the infant occasionally, but the burden probably devolves chiefly upon the adult male.

## VII. FACTORS REGULATING GROUP SIZE

Socay Forest is a relatively small area and most of the available space is utilized by the present occupants. One might ask how this spatial limitation will affect social organization as the population becomes more numerous. One possibility is that group size will increase. This may have occurred in the two smaller forests which were included in the study. One of these contained five *Callicebus* monkeys and a single male *Saimiri;* the other contained at least five and possibly six *Callicebus* monkeys. In both forests the animals were organized into a single group. Animals were sometimes scattered throughout the forest during feeding, but moved together on some occasions and appeared to occupy the same lodge tree at night. It seems likely, however, that five or six animals is approaching the upper limit for *Callicebus* groups, even though the factors that determine this limit are imperfectly understood. Pressure by mature adult on subadult and young adult animals probably is important. In at least three groups in Socay Forest there were definite indications that young adult or near-adult animals were the occasional targets of adult aggression. In one of these groups (Group 1) a young male disappeared from the parental group several months before the end of the study period and was not seen again. This occurred well in advance of the birth of an infant into the group. In another case (Group 7) a young adult remained with its group, which included a sibling, until the birth of an infant, then disappeared. In a third group of four animals (Group 2) a young adult was the object of sporadic adult aggression extending over a period of several months, but was still closely associated with the group when the study ended. These observations suggest that there is no single factor, such as the arrival of infants, which plays a critical part in forcing young adults from the natal group, but rather that the process of separation occurs slowly, over a period of several months.

There is no indication of what has become of the animals in Socay Forest which have left the natal group. It seems unlikely that they could have remained in the forest undetected. One possibility is that these animals have moved across the savannah to other, less crowded, forests. Although there is no direct evidence for this hypothesis, I have on several occasions seen *Callicebus* for brief periods on the forest floor and local residents claim that migration of individual animals across the savannah does occur.

## VIII. ACKNOWLEDGMENTS

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# A COMPARATIVE BIOSYSTEMATIC STUDY OF *FUNDULUS NOTATUS* AND *FUNDULUS OLIVACEUS* (PISCES: CYPRINODONTIDAE)

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## Abstract

Western populations of *Fundulus notatus* (Guadalupe, Colorado, Brazos, San Jacinto, Trinity, Neches and Sabine rivers) tend to have more dorsal (average 9.9) and anal (average 12.8) rays. Eastern populations (Mississippi Valley, Lake Pontchartrain drainage, Pearl River and Tombigbee River) tend to have fewer dorsal and anal rays (average 9.2 and 12.1 respectively). Trends in caudal ray number are roughly parallel. Lateral-scale number is generally 34 or 35. Northern fish tend to have broader heads and shorter snouts than southern fish. Dorsolateral spots, if present, are irregular, or diffuse, or both.

The westernmost population of *Fundulus olivaceus* (Navasota River, Texas) has fewer dorsal and anal rays (9.4 and 12.0 respectively). Populations from the Trinity River east to the Mississippi Gulf drainage average 9.8 dorsal rays. Dorsal ray number decreases clinally to the east to a low average of 8.9 for Choctawhatchee Bay drainage samples. Trinity and Neches river populations average 12.5 anal rays. Anal ray number decreases clinally to the east to a low average of 11.2 for Choctawhatchee Bay drainage samples. Caudal ray number tends to be high from the Alabama River west, and low to the east. But average lateral-scale number is greatest (35.7) for the Chattahoochee sample. Northern fish tend to be more robust than southern fish. Dorsolateral spots are the best character to separate *F. notatus* from *F. olivaceus*. With rare exceptions, *F. olivaceus* has discrete, regular, black dorsolateral spots.

Reproductive isolation is primarily ecological and is reinforced by homospecific mating preference. The two species are interfertile and produce fertile and distinctive hybrids in the laboratory. Only two natural hybrids are known. The two species have broadly overlapping ranges but are seldom syntopic. Syntopic associations are unstable and character displacement is not demonstrated. Ecological preferences are not uniform throughout the ranges of *F. olivaceus* and *F. notatus*, but *F. notatus* seldom occurs in "blackwater".

## Introduction

*Fundulus notatus* (Rafinesque) and *F. olivaceus* (Storer) are two of the most widely distributed species of the North American cyprinodontid genus *Fundulus* (Fig. 1). Both sexes of these two species have a single black, more or less solid, lateral stripe originating at the tip of the snout and terminating at the distal end of the caudal peduncle or on the caudal fin. This character separates them from all other presently recognized species of *Fundulus*.

Both *F. notatus* (personal communication, Clark Hubbs) and *F. olivaceus* (Miller, 1955) have been reported from brackish water near the Gulf of Mexico, but they ordinarily swim at the surface of the water near the margins of freshwater lakes, rivers, ponds and streams. Both species occur in many different types of environment and both are quite variable. Almost all characters that have been used to separate them have considerable overlap and are unreliable over large parts of their sympatric range.

Most early workers considered them to be conspecific (Garman, 1895; Jordan and Evermann, 1896; Forbes and Richardson, 1920; Hubbs and Ortenburger, 1929).

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Figure 1. Known ranges of *Fundulus notatus* and *Fundulus olivaceus* and distribution of material examined. The dashed line outlines the range of *F. notatus* and the dotted line outlines the range of *F. olivaceus.* Solid circles are *F. olivaceus* localities and open circles are *F. notatus* localities. Solid triangles are *F. olivaceus* localities and open triangles are *F. notatus* localities plotted from data given by Brown (1956).

Kuhne (1939) used *F. n. notatus* and *F. n. olivaceus* as subspecific names in his study of the fishes of Tennessee.

Moore and Paden (1950) considered *F. notatus* and *F. olivaceus* as separate species and presented evidence that they can occur together without interbreeding in the Illinois River of Oklahoma and Arkansas. Jurgens and Hubbs (1953) and Knapp (1953) recognized both species in Texas. Brown (1956) compared specimens from several areas and concluded that both species are valid. Braasch and Smith (1965) reached the same conclusion from their study of the two forms in the upper Mississippi Valley. Their paper includes a synonomy for both species.

This study was undertaken in an attempt to answer the following questions: How do various systematic characters vary from population to population? Do populations in the area of sympatry exhibit character displacement (Brown and Wilson, 1956)? Are *F. notatus* and *F. olivaceus* capable of hybridizing? Do they hybridize in nature? If the two forms are in fact valid species, what isolating mechanisms keep them separate? The results of this study indicate that *F. notatus* and *F. olivaceus,* though completely interfertile, are valid species separated in nature primarily by different ecological requirements and secondarily by behavioral reproductive isolation.

## RANGE

### *Fundulus notatus*

The westernmost Gulf drainage inhabited by *F. notatus* is the Guadalupe River system in southern central Texas. Hubbs, Kuehne, and Ball (1953) considered Landa Park Lake in Comal County as closely defining the upstream limit of the species in the Guadalupe River. It is abundant in the mainstream of the Colorado River at Austin in Travis County and is known from tributaries from Colorado County (Clark Hubbs, personal communication) upstream to Llano County (TU uncatalogued). *Fundulus notatus* is distributed generally throughout the Brazos (upstream to Palo Pinto and Eastland counties), San Jacinto, Trinity, and Neches rivers (Clark Hubbs, personal communication). It also occurs in isolated bayous and creeks draining into the Gulf between the Brazos and Sabine rivers. I have no records of *F. notatus* from any of the rivers between the Sabine River and the various eastern tributaries of the Mississippi River. This area is hereafter referred to as "western Louisiana drainage".

The southernmost record of *F. notatus* in the Mississippi Valley is approximately 20 miles west of New Orleans, Louisiana (TU 387). The species ranges north to southeastern Wisconsin, southern Michigan, northeastern Iowa, and western and central Ohio; west to eastern Oklahoma and Kansas (Brown, 1956); and east to Jackson County, Tennessee (UMMZ 125113).

A few specimens have been taken from the Lake Pontchartrain tributaries: Amite (TU 35697), Natalbany (UMMZ 182345), and Tangipahoa (UMMZ 182344) rivers. *Fundulus notatus* has been collected from the Pearl River from the vicinity of Jackson, Mississippi (UMMZ 170728) and downstream.

The species has not been recorded from

any of the small drainages between the Pearl River and the Tombigbee River (hereafter called Mississippi Gulf drainage), but is known from the Tombigbee drainage of the Alabama system (Brown, 1956). I have no record of *F. notatus* from the Alabama River.

### *Fundulus olivaceus*

The range of *F. olivaceus* overlaps the range of *F. notatus* in large part but is displaced to the east (Fig. 1). The westernmost population known is from the Navasota River, Texas (see *Material Examined*), an eastern tributary of the Brazos River. No records are available from the rest of the Brazos system. The species is abundant along the Gulf Coast eastward to the Choctawhatchee Bay drainage of western Florida and Alabama. In the Apalachicola (Chattahoochee) drainage *F. olivaceus* occurs in a limited area south of the fall line in Alabama and Georgia. This distribution is strikingly similar to that given by Suttkus (1955) for *Notropis euryzonus.* Fowler (1945) recorded *F. notatus* (=*F. olivaceus?*) from the Okefenokee Swamp. Since I have been unable to verify this record or obtain additional records of *F. olivaceus* east of the Apalachicola drainage, I doubt that the species occurs east of that drainage. In the Mississippi Valley, *F. olivaceus* ranges north to southern Missouri and Illinois, west to eastern Oklahoma, and east to western Kentucky (Brown, 1956) and to Anderson County, Tennessee (Cornell University 19148 cited by Brown, 1956).

## GEOGRAPHIC VARIATION

### *Methods*

Dorsal and anal rays were counted at their bases. All rays were counted, rather than considering the last 2 rays as a single ray as is often done. This is the same method used by Brown (1956) and I have incorporated Brown's counts into my data. Caudal ray count is total branched rays plus 2. Since both species show early ontogenetic increase in the number of branched caudal rays this character was not recorded for individuals smaller than 30 mm standard length. Lateral-scale counts were made as described by Brown (1956). Head width was measured at the rear of the orbits, and body depth was taken as the vertical distance from the origin of the anal fin to the dorsal surface of the body. Caudal peduncle depth and length of depressed dorsal fin were taken as described by Hubbs and Lagler (1947).

Color pattern was recorded for specimens over 30 mm standard length. No attempt was made to quantify such patterns in more than a general manner except to estimate the number of dorsolateral spots for *F. olivaceus.* This estimate was obtained by counting the number of spots on the left side of the dorsum, above the lateral stripe, below the dorsal midline and within the standard length. Dorsum pattern was recorded as uniform, intermediate, or cross-hatched. Lateral stripe shape was recorded as smooth, rough, or with few, several or many vertical extensions. Tone of the band and extensions was recorded as dark, intermediate, or light. Dorsum spotting in *F. notatus* was recorded as none, few, many, or blotched. Spots in the dorsal, caudal and anal fins were recorded as many, normal, few, very few, and none. Predorsal line was recorded as absent, light, dashed, partial, or complete. These categories were not particularly satisfactory because of the high variability in coloration from sample to sample. However, their use helped guard against forming false impressions of the distribution of color patterns in a given sample.

Methods of statistical comparison follow those given by Cazier and Bacon (1949) and Mayr, Linsley and Usinger (1953). Meristic characters were compared with the use of a standard 2 x n Chi square test in addition to graphical comparison following Hubbs and Hubbs (1953).

### *Fundulus notatus*

Number of dorsal rays (Table 1, Fig. 2) and number of anal rays (Table 2, Fig. 2) serve to separate *F. notatus* into two groups: a western group which includes populations from the Guadalupe, Colorado, Brazos, San Jacinto, Trinity, Neches, and Sabine rivers; and an eastern group composed of populations from the Mississippi and Great Lakes drainages, Lake Pontchartrain drainage, Pearl River, and Tombigbee River. The differences between these two groups do not warrant the recognition of subspecies.

Samples from populations making up the western group have 10 as the modal dorsal ray number and an observed range of variation of 8 to 12. The modal dorsal ray number is 9 in all samples from the eastern group and the observed range of variation

TABLE 1
*Number of Dorsal Rays in Fundulus notatus*

| | Number of Dorsal Rays | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Populations | 8 | 9 | 10 | 11 | 12 | N | M | S.D. | 2S.E. |
| Guadalupe R., Tex. | | 8 | 39 | 20 | | 67 | 10.2 | .64 | .16 |
| Colorado R., Tex. | | 21 | 44 | 6 | | 71 | 9.8 | .59 | .14 |
| Brazos R., Tex. | | 25 | 68 | 7 | | 100 | 9.8 | .54 | .11 |
| San Jacinto R., Tex. | | 11 | 54 | 34 | 1 | 100 | 10.2 | .66 | .13 |
| Trinity R., Tex. | | 15 | 32 | 3 | | 50 | 9.8 | .57 | .16 |
| Neches R., Tex. | | 40 | 60 | | | 100 | 9.6 | .49 | .09 |
| Sabine R., Tex.-La. | 2 | 38 | 54 | 6 | | 100 | 9.6 | .63 | .13 |
| Total Western | 2 | 158 | 352 | 76 | 1 | 588 | 9.9 | .66 | .06 |
| Mississippi R. | 8 | 116 | 47 | | | 171 | 9.2 | .45 | .07 |
| L. Pontchartrain Dr. | 2 | 33 | 5 | | | 40 | 9.1 | .41 | .13 |
| Pearl R., La.-Miss. | 3 | 68 | 29 | | | 100 | 9.3 | .50 | .10 |
| Tombigbee R., Ala. | 3 | 24 | 9 | | | 36 | 9.2 | .57 | .19 |
| Total Eastern | 16 | 239 | 90 | | | 345 | 9.2 | .50 | .05 |

is from 8 to 10. A line drawn between 9 and 10 dorsal rays separates 73% of 588 western specimens from 74% of 345 eastern specimens; average separation 73.5%; coefficient of divergence 0.60.

The two groups are similar in observed range of variation (11 to 14) in anal ray number but have different modes. All samples from western populations except those from the Brazos River (mode 12) are modal at 13. All samples from eastern populations are modal at 12. A line drawn between 12 and 13 anal rays separates 63% of 588 western specimens from 85% of 337 eastern specimens; average separation 74%; coefficient of divergence 0.60.

Caudal ray number (Table 3) varies from 11 to 17. With the exception of the San Jacinto sample (mean 13.3, mode 13), the western group samples have a high average number of caudal rays (13.8 to 14.2). The Mississippi River sample (mean 14.2, mode 14) resembles the western group for this character. The rest of the eastern group samples are modal at 13. The Lake Pontchartrain drainage sample of 16 specimens (mean 13.4) is significantly different from the Mississippi River sample (Chi square 14.2, 4 degrees of freedom, P less than 0.01), but not from the Pearl River sample (mean 12.9) or the Tombigbee River sample (mean 13.4). The pattern of caudal ray number distribution roughly parallels the patterns seen in dorsal and anal ray number with the exception of the Mississippi River sample which has high mean caudal ray number and low mean dorsal and anal ray numbers.

Observed range of variation in lateral

TABLE 2
*Number of Anal Rays in Fundulus notatus*

| | Number of Anal Rays | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Populations | 11 | 12 | 13 | 14 | N | M | S.D. | 2S.E. |
| Guadalupe R., Tex. | | 6 | 39 | 20 | 67 | 13.2 | .58 | .14 |
| Colorado R., Tex. | | 26 | 41 | 4 | 71 | 12.7 | .53 | .12 |
| Brazos R., Tex. | 2 | 53 | 37 | 8 | 100 | 12.5 | .67 | .13 |
| San Jacinto R., Tex. | | 30 | 62 | 8 | 100 | 12.8 | .58 | .12 |
| Trinity R., Tex. | 1 | 16 | 29 | 4 | 50 | 12.7 | .64 | .16 |
| Neches R., Tex. | | 44 | 51 | 5 | 100 | 12.6 | .58 | .12 |
| Sabine R., Tex.-La. | 2 | 35 | 57 | 6 | 100 | 12.7 | .62 | .12 |
| Total Western | 5 | 210 | 316 | 51 | 588 | 12.8 | .65 | .05 |
| Mississippi R. | 7 | 124 | 16 | | 167 | 12.0 | .51 | .08 |
| L. Pontchartrain Dr. | 3 | 34 | 2 | | 39 | 12.0 | .36 | .12 |
| Pearl R., La.-Miss. | 3 | 68 | 29 | | 100 | 12.3 | .48 | .10 |
| Tombigbee R., Ala. | 2 | 23 | 10 | 1 | 36 | 12.3 | .94 | .52 |
| Total Eastern | 35 | 249 | 57 | 1 | 337 | 12.1 | .42 | .05 |

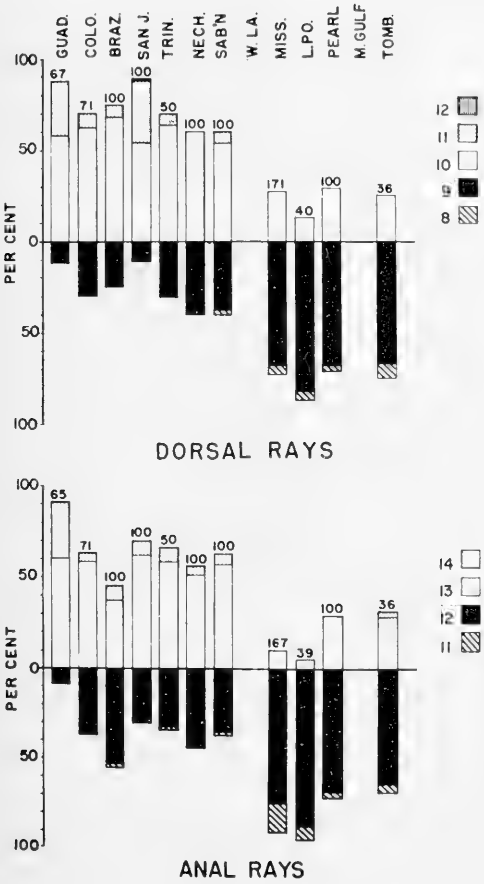

Figure 2. Distribution of dorsal and anal ray numbers in *Fundulus notatus*. Each bar represents 100% of the sample and is aligned on the break between 9 and 10 (dorsal rays) and 12 and 13 (anal rays), the most common numbers. Numbers above each bar are total sample size. The samples are arranged in order from west to east. These data are tabulated in tables 1 and 2.

scale number is 32 to 37 (Table 4); Braasch and Smith (1965, Fig. 2), however, reported a variation of 30 to 38 in their samples from the upper Mississippi Valley. Their method of counting gave counts 1 scale greater than the method I used. Most samples are modal at 34 or 35, but the Colorado River sample is modal at 36 and the Mississippi River sample is modal at 33. There is no broad pattern of geographic variation, such as those seen in ray number for the dorsal, anal and caudal fins.

Specimens from the upper Mississippi Valley and Great Lakes drainage tend to have broader heads, shorter snouts, and deeper caudal peduncles in comparison to specimens from other populations, but these characters are highly variable in all samples and do not seem to warrant the recognition of northern and southern groups. The Mississippi Valley and Great Lakes drainage populations seem to be similar throughout on the basis of dorsal, anal, and caudal ray numbers as well as lateral scale number.

In general, *F. notatus* may be divided into an eastern group characterized by a high percentage of low dorsal, anal and caudal ray numbers and a western group characterized by a high percentage of high numbers of dorsal, caudal and anal rays. No such pattern is seen in lateral scale number. The Mississippi River populations are characterized by low dorsal and anal ray numbers, high caudal ray number and low lateral scale lateral scale number.

### *Fundulus olivaceus*

Differences in dorsal ray number (Table 5, Fig. 3) may be used to divide *F. olivaceus* into three population groups. The most common dorsal ray number in samples from

TABLE 3

*Number of Caudal Rays in Fundulus notatus*

| | Number of Caudal Rays | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Populations | 11 | 12 | 13 | 14 | 15 | 16 | 17 | N | M | S.D. | 2S.E. |
| Guadalupe R., Tex. | | 2 | 5 | 17 | 5 | 1 | | 30 | 14.0 | .88 | .32 |
| Colorado R., Tex. | | 2 | 6 | 30 | 14 | 3 | | 55 | 14.1 | .89 | .24 |
| Brazos R., Tex. | | 4 | 5 | 27 | 13 | 1 | 1 | 51 | 14.1 | .99 | .28 |
| San Jacinto R., Tex. | 1 | 13 | 25 | 21 | 8 | | | 68 | 13.3 | 1.00 | .25 |
| Trinity R., Tex. | | 2 | 4 | 14 | 14 | 1 | | 35 | 14.2 | .91 | .31 |
| Neches R., Tex. | | 2 | 9 | 13 | 6 | | | 30 | 13.8 | .86 | .34 |
| Sabine R., Tex.-La. | | 2 | 9 | 21 | 10 | | | 43 | 13.9 | .80 | .24 |
| Mississippi R. | | 2 | 6 | 21 | 20 | 1 | | 50 | 14.2 | .85 | .27 |
| L. Pontchartrain Dr. | | | 10 | 6 | | | | 16 | 13.4 | .50 | .25 |
| Pearl R., La.-Miss. | 1 | 13 | 28 | 7 | 2 | | | 51 | 12.9 | .81 | .23 |
| Tombigbee R., Ala. | | 2 | 9 | 7 | 2 | | | 20 | 13.4 | .89 | .40 |

TABLE 4
*Number of Lateral Scales in Fundulus notatus*

| Populations | Number of Lateral Scales<br>32 | 33 | 34 | 35 | 36 | 37 | N | M | S.D. | 2S.E. |
|---|---|---|---|---|---|---|---|---|---|---|
| Guadalupe R., Tex. | | 2 | 24 | 11 | 1 | | 38 | 34.3 | .57 | .19 |
| Colorado R., Tex. | | 3 | 7 | 17 | 23 | 2 | 52 | 35.3 | .95 | .26 |
| Brazos R., Tex. | | 2 | 26 | 14 | 7 | 1 | 50 | 34.6 | .61 | .20 |
| San Jacinto R., Tex. | | 1 | 13 | 21 | 1 | | 36 | 34.6 | .61 | .20 |
| Trinity R., Tex. | 1 | 6 | 19 | 8 | | | 34 | 34.0 | .70 | .24 |
| Neches R., Tex. | 1 | 6 | 20 | 12 | | | 39 | 34.1 | .76 | .25 |
| Sabine R., Tex.-La. | | 5 | 11 | 21 | 6 | 2 | 45 | 34.8 | .99 | .30 |
| Mississippi R. | 6 | 24 | 9 | 3 | 1 | | 53 | 33.0 | .94 | .26 |
| L. Pontchartrain Dr. | | | 4 | 14 | | | 18 | 34.8 | .44 | .21 |
| Pearl R., La.-Miss. | | 18 | 32 | 1 | | | 51 | 33.7 | .47 | .23 |
| Tombigbee R., Ala. | | 9 | 13 | 3 | | | 25 | 33.8 | .44 | .18 |

the Navasota River population is 9. Samples from the Trinity, Neches, Sabine, western Louisiana drainage, Mississippi, Lake Pontchartrain drainage, Pearl, and Mississippi Gulf drainage are modal at 10 dorsal rays. There is clinal intergradation in this character from the Mississippi Gulf drainage population (mode 10) into the populations at the eastern limits of the range, where the mode is 9. Observed range of variation is from 8 to 11.

A line drawn between 9 and 10 dorsal rays separates 64% of 100 Navasota River specimens from 77% of 970 Trinity to Mississippi Gulf drainage specimens; average separation 70.5%; coefficient of divergence 0.37. A line drawn between 9 and 10 separates 77% of 970 Trinity to Mississippi Gulf specimens from 93% of 110 Choctawhatchee Bay specimens; average separation 85%; coefficient of divergence 0.89. The mean dorsal ray number of the Apalachicola population (9.2) is significantly higher than that of the Choctawhatchee Bay populations (8.9); Chi square (2 x 3, 2 degrees of freedom) 11.2, P less than 0.01.

A sample of 100 specimens from the southern Mississippi Valley is significantly different from a sample of 70 specimens from the northern Mississippi Valley populations; Chi square (2 x 4, 3 degrees of freedom) 11.7, P less than 0.01. A sample of 100 specimens from middle Mississippi tributaries (White River, Tennessee River) is intermediate between the northern and southern Mississippi Valley samples. These data indicate a clinal intergradation from low average dorsal ray number (9.6) in the southern Mississippi Valley to a higher average number (9.9) near the northern limits of the range in the upper Mississippi Valley. However Braasch and Smith (1965, Fig. 2)

TABLE 5
*Number of Dorsal Rays in Fundulus olivaceus*

| Populations | Number of Dorsal Rays<br>8 | 9 | 10 | 11 | N | M | S.D. | 2S.E. |
|---|---|---|---|---|---|---|---|---|
| Navasota R., Tex. | 2 | 62 | 35 | 1 | 100 | 9.4 | .54 | .11 |
| Trinity R., Tex. | | 13 | 68 | 19 | 100 | 10.1 | .56 | .11 |
| Neches R., Tex. | 1 | 20 | 70 | 9 | 100 | 9.9 | .56 | .11 |
| Sabine R., Tex.-La. | | 22 | 70 | 8 | 100 | 9.9 | .53 | .11 |
| Western La. Dr. | | 20 | 73 | 7 | 100 | 9.9 | .50 | .11 |
| S. Mississippi R. | 1 | 40 | 53 | 6 | 100 | 9.6 | .61 | .12 |
| M. Mississippi R. | | 22 | 73 | 5 | 100 | 9.8 | .45 | .09 |
| N. Mississippi R. | | 11 | 56 | 3 | 70 | 9.9 | .44 | .11 |
| L. Pontchartrain Dr. | | 19 | 77 | 4 | 100 | 9.8 | .56 | .11 |
| Pearl R., La.-Miss. | 1 | 30 | 64 | 5 | 100 | 9.7 | .56 | .11 |
| Miss. Gulf Dr. | | 25 | 73 | 2 | 100 | 9.8 | .47 | .09 |
| Total Trin. R.-Miss. G. | 3 | 222 | 677 | 68 | 970 | 9.8 | .53 | .03 |
| Alabama R. | 4 | 132 | 103 | 2 | 241 | 9.4 | .55 | .07 |
| Pensacola Bay Dr. | | 63 | 37 | | 100 | 9.4 | .49 | .10 |
| Choctawhatchee Bay Dr. | 18 | 84 | 8 | | 110 | 8.9 | .48 | .10 |
| Apalachicola R. | 5 | 69 | 26 | | 100 | 9.2 | .52 | .10 |

give a mean dorsal ray number between 9.6 and 9.7 for upper Mississippi Valley *F. olivaceus.* This suggests that Mississippi Valley populations are reasonably homogenous for this character. Further study is needed to clarify this point.

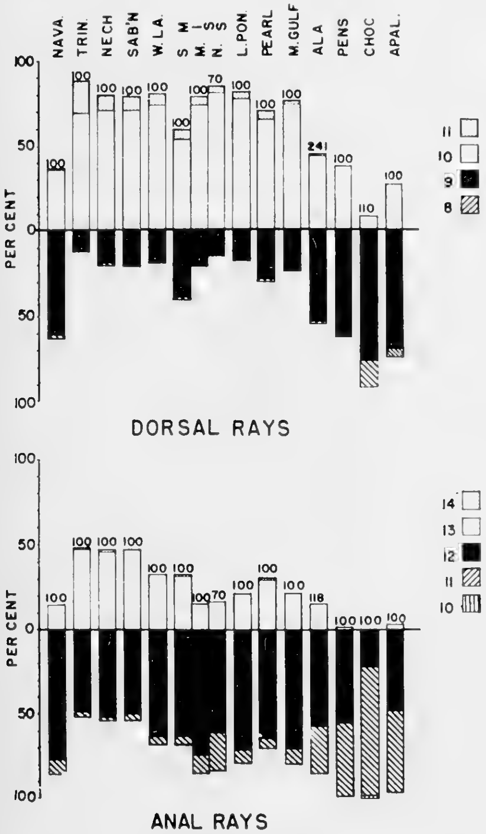

Figure 3. Distribution of dorsal and anal ray numbers in *Fundulus olivaceus.* Drawn as in fig. 2. These data are tabulated in tables 5 and 6.

Samples from eastern tributaries to the Mississippi were compared with those from the western tributaries. No significant differences were found.

The total observed range in variation in anal ray number is from 10 to 14 (Table 6, Fig. 3). Number of anal rays shows a pattern of variation similar to that seen in dorsal ray number, but the samples from the Mississippi Valley do not differ significantly. The sample from the Navasota River is modal at 12 as is the sample from the Trinity River, but a line drawn between 12 and 13 anal rays separates 86% of 100 Navasota specimens from 48% of 100 Trinity specimens; average separation 67%; coefficient of divergence 0.48.

Average number of anal rays drops from a high of 12.5 in the Trinity and Neches samples to a low of 11.2 in the Choctawhatchee Bay sample. This trend does not continue to the east. Although the average number (11.6) of the Apalachicola population is low, it is higher than the Choctawhatchee Bay average. The difference between the Choctawhatchee Bay and Apalachicola populations are probably real; Chi square (2 x 4, 3 d. f.) 13.0, P less than 0.01.

Two different rates of clinal intergradation are involved: (1) a change of average number of anal rays from 12.5 in the Trinity and Neches rivers into an average number of 12.1 for samples from the Mississippi Gulf drainage. This change in average number is the result of an eastward increase in percent of specimens with 12 anal rays and

Table 6
*Number of Anal Rays in Fundulus olivaceus*

| | Number of Anal Rays | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Populations | 10 | 11 | 12 | 13 | 14 | N | M | S.D. | 2S.E. |
| Navasota R., Tex. | | 9 | 77 | 14 | | 100 | 12.0 | .48 | .10 |
| Trinity R., Tex. | | 3 | 49 | 47 | 1 | 100 | 12.5 | .56 | .11 |
| Neches R., Tex. | | 2 | 52 | 45 | 1 | 100 | 12.5 | .56 | .11 |
| Sabine R., Tex.-La. | | 4 | 50 | 46 | | 100 | 12.4 | .59 | .12 |
| Western La. Dr. | | 5 | 63 | 32 | | 100 | 12.3 | .55 | .11 |
| Mississippi R. | | 32 | 180 | 57 | 1 | 270 | 12.1 | .58 | .07 |
| L. Pontchartrain Dr. | | 8 | 71 | 21 | | 100 | 12.1 | .51 | .10 |
| Pearl R., La.-Miss. | | 6 | 64 | 29 | 1 | 100 | 12.2 | .57 | .11 |
| Miss. Gulf Dr. | | 9 | 70 | 21 | | 100 | 12.1 | .53 | .11 |
| Alabama R., Ala. | | 33 | 67 | 18 | | 118 | 11.9 | .65 | .12 |
| Pensacola Bay Dr. | | 44 | 55 | 1 | | 100 | 11.5 | .52 | .10 |
| Choctawhatchee Bay Dr. | 2 | 76 | 22 | | | 100 | 11.2 | .45 | .09 |
| Apalachicola R. | | 50 | 48 | 2 | | 100 | 11.5 | .54 | .11 |

TABLE 7
*Number of Caudal Rays in Fundulus olivaceus*

| Populations | 11 | 12 | 13 | 14 | 15 | 16 | 17 | N | M | S.D. | 2S.E. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Navasota R., Tex. | | | 10 | 31 | 17 | 2 | | 60 | 14.2 | .75 | .20 |
| Trinity R., Tex. | | 4 | 6 | 22 | 28 | | 1 | 61 | 14.3 | .94 | .24 |
| Neches R., Tex. | | 1 | 1 | 10 | 36 | 12 | 1 | 61 | 15.0 | .65 | .16 |
| Sabine R., Tex.-La. | | | 3 | 18 | 18 | 1 | | 40 | 14.4 | .71 | .23 |
| Western La. Dr. | | 1 | 9 | 11 | 29 | 2 | | 52 | 14.4 | .89 | .25 |
| Mississippi R. | | | 11 | 35 | 86 | 9 | 3 | 144 | 14.3 | .69 | .11 |
| L. Pontchartrain Dr. | | 1 | 13 | 32 | 38 | 4 | | 82 | 14,3 | .79 | .17 |
| Pearl R., La.-Miss. | | 4 | 15 | 24 | 27 | 4 | 2 | 76 | 14.2 | 1.08 | .25 |
| Miss. Gulf Dr. | | | 8 | 22 | 28 | 1 | | 59 | 14.4 | .73 | .19 |
| Alabama R., Ala. | | 2 | | 12 | 14 | | | 28 | 14.4 | 1.07 | .41 |
| Pensacola Bay Dr. | | 5 | 26 | 2 | 6 | | | 39 | 13.2 | .87 | .28 |
| Choctawhatchee Bay Dr. | | 5 | 32 | 11 | 2 | | | 50 | 13.5 | .74 | .21 |
| Apalachicola R. | 1 | 1 | 16 | 13 | 11 | | | 42 | 13.8 | .96 | .30 |

a decrease in percent of specimens with 13 anal rays. The percentage of fish with 11 anal rays is reasonably constant in all these samples. (2) A reduction of average number of anal rays from 12.1 in the samples from the Mississippi Gulf drainage to an average number of 11.2 in the samples from the Choctawhatchee Bay drainage. This drop is the result of an eastward trend toward an increase in percent of specimens having 11 anal rays and a concurrent decrease in percent of specimens with 13 or 12 anal rays. A line drawn between 11 and 12 anal rays separates 91% of 100 specimens from the Mississippi Gulf drainage from 78% of 100 specimens from Choctawhatchee Bay drainage; average separation 84.5%; coefficient of divergence 0.92.

Observed range of variation in caudal ray number is 11 to 17 (Table 7). The Navasota River *F. olivaceus* sample is modal at 14, samples from the Trinity River east to the Alabama River are modal at 15, and samples from drainages east of the Alabama River are modal at 13. Though the modal numbers of the Trinity and Navasota samples are different, the means, 14.3 and 14.2 respectively, are not significantly different. A line drawn between 13 and 14 separates 93% of 28 specimens from the Alabama River from 79% of 39 specimens from the Pensacola Bay sample; average separation 86%; coefficient of divergence 0.64.

Lateral scale number ranges from 32 to 37 (Table 8) and 34 or 35 lateral scales are most common. Distribution of lateral scale number varies considerably from population to population. The Navasota, Trinity, Neches, and Sabine River samples are similar (mean: 34.4, 34.8, 34.4, 34.8 respectively). With the exception of the Neches sample, bimodal at 34 and 35, these samples are

Table 8
*Number of Lateral Scales in Fundulus olivaceus*

| Populations | 32 | 33 | 34 | 35 | 36 | 37 | N | M | S.D. | 2S.E. |
|---|---|---|---|---|---|---|---|---|---|---|
| Navasota R., Tex. | 1 | 6 | 19 | 22 | 2 | | 50 | 34.4 | .75 | .21 |
| Trinity R., Tex. | | 2 | 15 | 27 | 8 | | 52 | 34.8 | .75 | .21 |
| Neches R., Tex. | | 2 | 15 | 15 | | | 32 | 34.4 | .56 | .20 |
| Sabine R., Tex.-La. | | 5 | 11 | 21 | 6 | 2 | 45 | 34.8 | .98 | .29 |
| Western La. Dr. | 2 | 14 | 19 | 8 | 2 | | 45 | 33.9 | .92 | .28 |
| Mississippi R. | 6 | 37 | 107 | 41 | 3 | 1 | 194 | 34.0 | .78 | .11 |
| L. Pontchartrain Dr. | 2 | 15 | 26 | 28 | 3 | | 74 | 34.2 | .91 | .21 |
| Pearl R., La.-Miss. | | 5 | 32 | 29 | 7 | | 73 | 34.5 | .78 | .18 |
| Miss. Gulf Dr. | 1 | 17 | 31 | 11 | 4 | | 64 | 34.0 | .78 | .20 |
| Alabama R., Ala. | | 12 | 21 | 2 | | | 35 | 33.7 | .53 | .18 |
| Pensacola Bay Dr. | | 2 | 15 | 23 | 9 | | 49 | 34.8 | .79 | .23 |
| Choctawhatchee Bay Dr. | | | 4 | 37 | 11 | | 52 | 35.1 | .55 | .15 |
| Apalachicola R. | | | 2 | 17 | 30 | 3 | 52 | 35.7 | .66 | .18 |

modal at 35. The western Louisiana drainage sample is modal at 34 as is the Mississippi River sample. The Lake Pontchartrain drainage sample is almost bimodal at 34 and 35 (26 and 28 specimens respectively). These 3 samples have significantly lower means (33.9, 34.0 and 34.2 respectively) than the 4 western samples. There is a clinal decrease in average number of lateral scales from the Pearl River (34.5) east to the Alabama River (33.7) and a clinal increase in average lateral scale number from the Alabama River to a high of 35.7 for the Apalachicola River sample.

Brown (1956) contrasted Mississippi Valley specimens with specimens from the Gulf Coast. The former were said to have deeper and wider bodies and deeper caudal peduncles than the latter. He did not examine specimens from the lower Mississippi Valley. Southern Mississippi Valley fish resemble Gulf Coast drainage specimens and do not have the deep, wide body and deep caudal peduncle characteristic of northern specimens.

The following generalizations may be made. There is some correlation in variation in fin ray number in the unpaired fins. With the exception of the Navasota River population, western populations have a higher percentage of high fin ray numbers than eastern populations. The average dorsal ray number is nearly uniform from the Trinity River population east to the Mississippi Gulf drainage and drops off clinally to the east. Intergradation from high average anal ray number in the west to low average anal ray number in the east involves a low rate of clinal intergradation from the Trinity population to the Mississippi Gulf drainage population followed by a rapid rate of clinal intergradation eastward. Western populations (Navasota included) have high average caudal ray number and populations east of the Alabama River have low average caudal ray number. The Alabama River sample has the lowest average lateral scale number and the Apalachicola River sample has the highest, a reverse trend to those shown by fin ray numbers.

## Ecology

The published information available on the ecology and distribution of *F. olivaceus* and *F. notatus* is somewhat confusing, in part because each statement has been based on a study of either or both species in a limited area. In a study of the fishes of Tennessee, Kuhne (1939) stated, "Two subspecies occur in Tennessee, the northern (and more upland) *F. n. notatus* and the southern lowland *F. n. olivaceus* (Putnam). The latter has a flatter head and the body is marked by strong blackish spots." Moore and Paden (1950) noted that the two species sometimes occurred together in the Illinois River. Knapp (1953), in regard to *F. olivaceus* in Texas, stated: "Where its range overlaps with *F. notatus* the two are usually ecologically separated, *F. olivaceus* being typically a quiet water form. Near the coastal plain this species inhabits swifter water." He also stated, "In Texas *F. notatus* is to be expected in headwaters and fast streams." Braasch and Smith (1965) stated that *F. notatus* is more likely to be found in still water and *F. olivaceus* in fast water in the upper Mississippi Valley, and that the two seldom occur together in that area.

My examination of the hundreds of collections of the 2 species catalogued at Tulane University, University of Michigan Museum of Zoology and the Texas Natural History Collection at the University of Texas shows that in fact the two species are seldom collected at the same locality at the same time. When collections lumping specimens from several different habitats are excluded, it is clear that *F. notatus* and *F. olivaceus* are rarely syntopic (Rivas, 1964: 43).

Braasch and Smith (1965) reported mixed collections from the same general area taken 64 years apart, but my observations of two areas where syntopy has occurred indicate that syntopic associations at a particular locality are unstable and transient. One area is in the mainstream of the Amite River in Louisiana and the other is in a small tributary of the Navasota River in Texas. The first area was visited 4 times and the second 3 times (Table 9). Where numbers are given, all *Fundulus* seen were collected and the sample is probably an accurate reflection of the *Fundulus* population at that time. Where catalogue numbers are not given, specimens were retained alive and mixed with specimens from other localities for use in another study.

The differences in ecological preferences that are responsible for this separation of the two species are not clear at present. *Fundulus olivaceus* is abundant in the

TABLE 9

*Variation in relative abundance of Fundulus notatus and Fundulus olivaceus in 2 areas of occasional syntopy*

| Drainage and Date | *F. notatus* | *F. olivaceus* | Water Level |
|---|---|---|---|
| *Amite River* | | | |
| 28 Nov. 1963 | abundant | 0 | low |
| 14 May 1964 | — about equal numbers — | | high |
| 3 July 1964 | 2 | 0 | high, rising |
| 25 Oct. 1964 | 19 (TU 35697) | 22 (TU 35691) | low |
| *Navasota River* | | | |
| 30 March 1963 | 7 | 5 | low |
| 19 June 1964 | abundant | 0 | low |
| 19 Nov. 1964 | 1 (TU 37114) | 7 (TU 37116) | high, dropping |

"blackwater" streams along the Gulf Coast and *F. notatus* is rare in this type of stream, but neither species seems to show any preference for a particular type of habitat over a large area. Knapp (1953) has characterized *F. notatus* as a headwater form, but in the Guadalupe and Colorado rivers it is excluded from the headwaters. In the Pearl River drainage *F. notatus* is generally excluded from the small tributaries and is most abundant in the main channel of the river, but all the records I have from the Tombigbee River drainage are from small tributaries. Clark Hubbs (1957) pointed out that *F. olivaceus* in Texas is an eastern element of the Texas fauna whose western limits correspond primarily with the western limits of the Mixed Pine Oak Region. Exceptions to this statement are the records from the Navasota River in Brazos and Grimes counties (see *Material Examined*). These records are slightly west of the Mixed Pine Oak Region but from a drainage with previously recognized eastern faunal affinities (Knapp, 1953).

Where only one of the two species is present, it is able to occupy suitable habitats along the margins of lakes, rivers, ponds, and streams. Either species may inhabit large or small bodies of water and in the southern part of their ranges either *F. notatus* or *F. olivaceus* may be found at the edges of still or rapidly flowing water. Ordinarily neither species is found in riffle areas, although either may occur in quieter areas at the margins of riffles. In the area of sympatry the suitable habitats are divided between the two species and contact between the two is rare. With the exception of the general exclusion of *F. notatus* from "blackwater" areas, it appears that the macrohabitat occupied by *F. notatus* does not exhibit any consistent difference from the macrohabitat occupied by *F. olivaceus.*

In general, *F. notatus* is abundant in Texas and in the western and northern Mississippi Valley, and relatively rare in the southern Mississippi Valley and east of the Mississippi. *F. olivaceus* may be less abundant than *F. notatus* in Texas, but is by far the more common in the south, and is about as abundant as *F. notatus* in the middle Mississippi Valley. The abundance of *F. olivaceus* in the southern tier of states from Louisiana to western Florida is to some extent correlated with the occurrence of "blackwater" streams and swamp lakes in that area, but *F. olivaceus* is also abundant in other types of habitat.

## EXPERIMENTAL HYBRIDIZATION

In reference to *F. notatus* and *F. olivaceus*, Bailey, Winn, and Smith (1954) suggested: "It is possible that a more thorough study may prove them to be the genetic variants of a single species." Many individuals of both species have an intermediate appearance suggestive of either hybrid origin or introgression. The spotted individuals of *F. notatus* and the individuals of *F. olivaceus* which have very few, or very small spots could be interpreted as hybrids if opposing evidence were not available.

The most fruitful approach to this type of problem seemed to be the production of known hybrids for comparison with suspected natural hybrids. These experiments were intended to help determine the nature of the isolating mechanisms (if any) existing between the two forms in question. At the beginning of this study I believed *F. notatus* and *F. olivaceus* to be conspecific, but the results of these experiments render this position untenable.

### *Materials and Methods*

In February, March and April, 1964, 3 sets of hybridization experiments were performed: (1) a female *F. olivaceus,* from the Bogue Falaya River at the Delta Regional Primate Center near Covington, Louisiana, was crossed with a male *F. notatus* from the Colorado River at Austin, Texas; (2) a female *F. notatus,* from Hildebrandt Bayou near Beaumont, Texas, was crossed with a male *F. olivaceus* collected with the *F. olivaceus* female used in experiment one; and (3) a female *F. olivaceus* from a tributary to the Cahaba River in Alabama was crossed with a male *F. notatus* from Hildebrandt Bayou. The choice of fishes used in these experiments was governed by the necessity of using individuals unquestionably belonging to one species or the other.

Each cross was carried out in a 5 gallon Metaframe brand aquarium filled with aged New Orleans tap water. Some of the water used in changing or adding water came from a temporary rainwater pond near Lake Pontchartrain. This was necessary because New Orleans tap water was lethal to these fishes during late January and February, 1964. A nylon yarn mop weighted with a lead sinker was placed in a bottom inside corner of the aquarium to provide a spawning site. Both green and white mops were used with good results. Filtration and aeration were provided by a standard small inside box filter in each aquarium. These filters were charged with glass wool, charcoal and fine gravel. The fish were usually fed twice a day and at least once a day with Tetra-Min brand flake dry food, frozen raw beef liver, or frozen adult Artemia. Live mosquito larvae and cladocerans were fed when available. Each aquarium was illuminated with a 15 watt incandescent bulb in addition to daylight from an east window. A timer turned the lights on at 0530 and off at 2030 to simulate a 15 hour day.

The fishes spawned readily, generally in the late afternoon. Each morning the mops were removed from the aquarium, squeezed partially dry and inspected visually while running the strands of the mop through the fingers. Eggs were removed with the fingers and placed in clean aged aquarium water in a plastic container (11 cm square and 2 cm deep). Acriflavine dye was added to the incubation water to serve as a fungicide. Dead eggs were discarded and newly hatched fry (F-1) were transferred to small rearing tanks and fed twice daily on live newly hatched *Artemia* nauplii. Dead *Artemia* and detritus were removed from the rearing tanks periodically and the water was partially replaced with aged aquarium water.

When the fry began to show signs of crowding (differential and decreased growth rates) they were transferred to 10 or 20 gallon Metaframe brand aquaria and had scraped frozen beef liver, frozen adult *Artemia* and Tetra-Min added to their diet. The fry were distributed at the rate of about one fish per gallon of water.

The F-1's were transferred to outdoor concrete pools. The fry from experiment one were transferred on 28 May and the fry from experiments two and three on 22 July 1964. They were from 4 to 5 months old and averaged about 30 mm total length when transferred. The offspring from experiment one were removed from the pools on 20 September 1964, 21 were preserved on 21 September, and 5 pairs were retained for further experiments. The fish from experiment two were removed and preserved on 7 December 1964, and the fish from experiment three were transferred to a laboratory aquarium on 28 September 1964 and preserved 13 December 1964.

While in the pools, fish were fed daily with Tetra-Min or frozen adult *Artemia* to supplement natural foods present in the pools.

### *Results*

Experiment one resulted in 34 F-1 offspring; 2 died before reaching maturity, 1 was lost in transfer, 2 have been kept alive and 29 preserved for study. A comparison of the F-1 hybrids from experiment one with samples from the parent populations is given in Table 10. These hybrids are intermediate and distinctive in general appearance (Fig. 4). F-1 hybrids from experiment one were able to produce F-2 hybrids and backcrosses to both parent species with no sign of reduced sex drive or fertility. These experiments will be discussed further in a later paper.

Though the hybrids are intermediate in general appearance, analysis of individual characters (Table 10) shows that they are intermediate only in pattern of the dorsum and in number and shade of dorsolateral

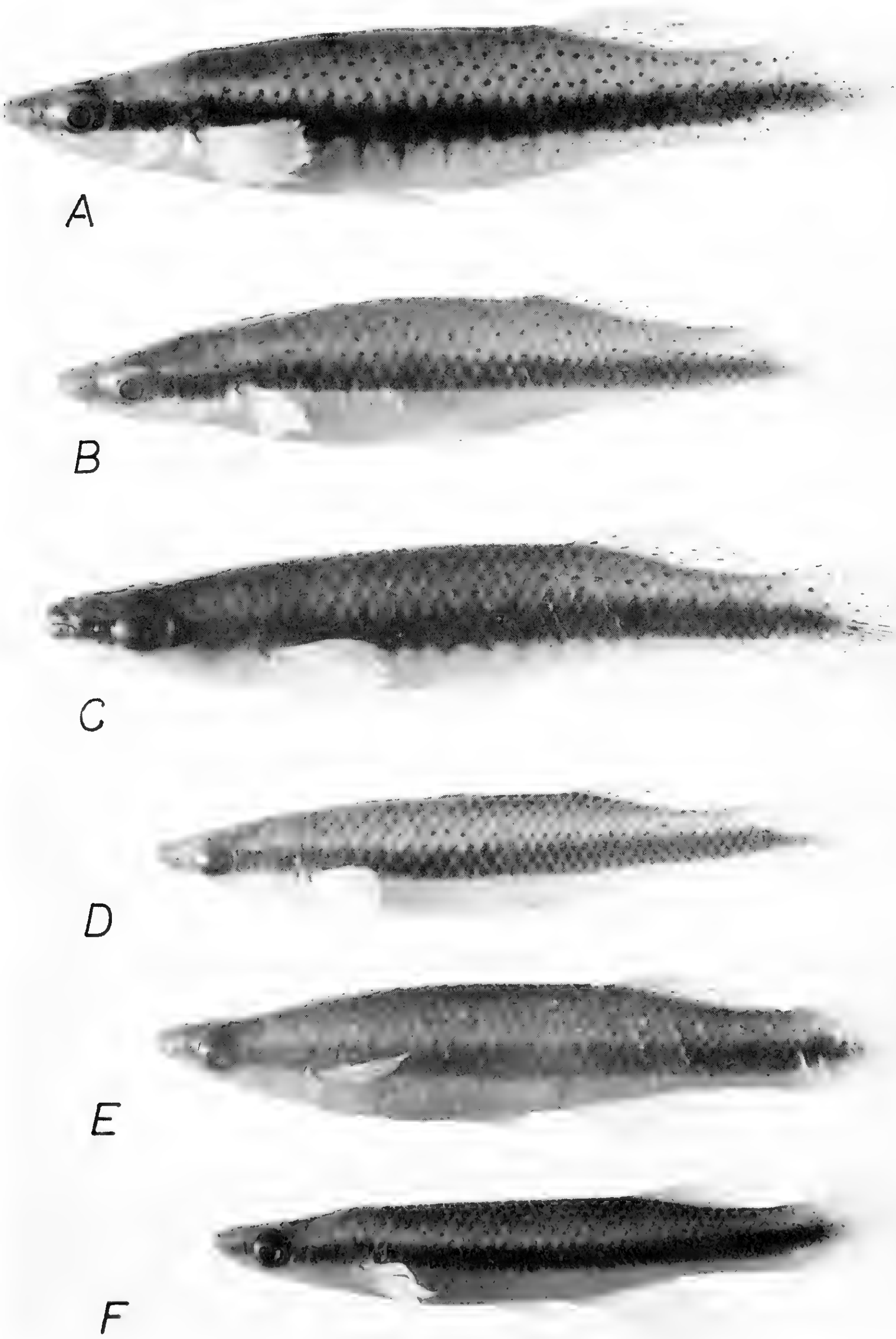

Figure 4. A. male *Fundulus olivaceus* (SL 54.9 mm) and B. a female *F. olivaceus* (SL 17.8 mm), from the Bogue Falaya River. C. a male, and D. a female F-1 hybrid from experiment one (SL 54.6 mm and 45.0 mm respectively). E. a male, and F. a female *Fundulus notatus* from the Colorado River (SL 49.4 mm and 42.8 mm respectively). Photographs by Forrest Jack Hurley.

spots. Other characters resemble one parent species, both parent species, or neither. The parent population samples and the F-1 hybrids do not show significant differences in dorsal ray number, caudal ray number, body depth, caudal peduncle depth of both males and females, or male dorsal fin length (see Fig. 5). The F-1 hybrids resemble Colorado River *F. notatus* in anal ray number and lateral scale number, but resemble Bogue Falaya River *F. olivaceus* in female dorsal fin length, female anal fin spotting, and number of lateral band extensions in males. Hybrid males have more heavily spotted anal fins than males from either parent population. The 29 F-1 hybrids are significantly broader-headed than samples from either parent population. This character seems to be intrinsic in the hybrids and not an artifact caused by laboratory conditions. Specimens of both parent species raised under similar conditions have not shown a similar effect. Of 16 characters studied, the F-1 hybrids from experiment one are intermediate in 3, extreme in 2, similar to both parent populations in 6, similar to *F. notatus* in 2 and similar to *F. olivaceus* in 3.

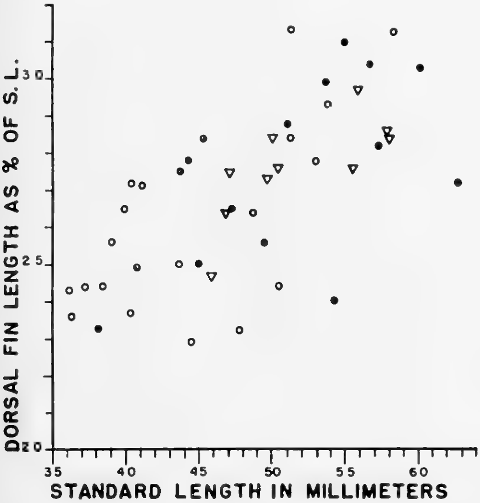

Figure 5. Comparison of dorsal fin length in *Fundulus notatus* (open circles), *Fundulus olivaceus* (solid circles), and F-1 hybrid (triangles) males. See Table 10 for comparison of females.

## DISCUSSION

*Fundulus olivaceus* generally has discrete, regular black spots on the dorsolateral surface of the body. *Fundulus notatus* may be immaculate or may have dusky spots or blotches. Though other characters may be of use in separating these species in a given area, this is the only one of the many proposed by Hubbs (in Moore and Paden, 1950: 88) and by Brown (1956: 131) which will serve to separate the two species everywhere. Head shape, snout length, body depth, caudal peduncle depth, shape of male dorsal and anal fins, shape and number of spots in the unpaired fins, color of the dorsum, predorsal stripe, and male lateral band extensions may be different for the two species at a given locality, but these characters are not conservative and their use as key characters confuses rather than clarifies.

The spots characteristic of *F. olivaceus* are generally more numerous in males than in females and large males tend to have more spots than small males. The spots vary from less than 0.2 mm to over 1.0 mm in diameter. They are usually round but may be dash-shaped or slightly irregular. The most striking development of these spots was seen on large males from the Pensacola Bay drainage samples. An attempt to use numbers of spots to define subpopulations of *F. olivaceus* failed because variation in most samples is too great.

This spotting characteristic, though the most reliable for use in separating *F. olivaceus* and *F. notatus*, breaks down in rare instances. A few collections from the southern states, from Texas to Florida, have included individuals of *F. olivaceus* with few dorsolateral spots. Braasch and Smith (1965) reported similar collections from the upper Mississippi Valley. Males in these collections have as few as 15 spots. Females usually have between 5 and 15 spots and some females have 4, 3, 2, 1, or none. These rare immaculate females may be morphologically indistinguishable from *F. notatus* females, and are identified as extreme variants of *F. olivaceus* rather than *F. notatus* because: (1) they sometimes occur outside the range (as presently known) of *F. notatus*, (2) they are not associated with immaculate males, and (3) they are associated with *F. olivaceus* which have a low number of dorsolateral spots. One of these females taken alone would certainly be identified as *F. notatus* and records of *F. notatus* based on single females should be critically examined.

*F. notatus* may have an immaculate dorsum or may have dusky spots or blotches on

TABLE 10

*Comparison of Parental Stocks of Fundulus notatus and Fundulus olivaceus with Artificially Reared F-1 Hybrids*

| Character | Colorado *F. notatus* |  |  |  | F-1 Hybrids |  |  |  | Bogue Falaya *F. olivaceus* |  |  |  | Hybrids Resemble |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | N | x̄ | S.D. | 2S.E. | N | x̄ | S.D. | 2S.E. | N | x̄ | S.D. | 2S.E. |  |
| Dorsal Rays | 71 | 9.8 | .59 | .14 | 29 | 9.9 | .49 | .19 | 100 | 9.8 | .56 | .11 | Both Parents |
| Anal Rays | 71 | 12.7 | .53 | .12 | 29 | 12.7 | .49 | .19 | 100 | 12.1 | .51 | .10 | *F. notatus* |
| Caudal Rays | 55 | 14.1 | .89 | .24 | 29 | 14.4 | .61 | .23 | 82 | 14.3 | .79 | .17 | Both Parents |
| Lateral Scales | 52 | 35.3 | .95 | .26 | 29 | 35.0 | .87 | .32 | 74 | 34.2 | .91 | .21 | *F. notatus* |
| HW/SL as % | 33 | 13.3 | .33 | .11 | 29 | 15.1 | .68 | .25 | 30 | 14.3 | .43 | .16 | Neither |
| BD/SL as % | 20 | 18.4 | 1.34 | .60 | 29 | 19.1 | .92 | .29 | 29 | 18.2 | 1.34 | .50 | Both Parents |
| CPD/SL ♂ | 16 | 11.5 | .80 | .40 | 10 | 10.9 | .30 | .19 | 16 | 11.2 | .58 | .28 | Both Parents |
| CPD/SL ♀ | 15 | 11.0 | .37 | .20 | 19 | 10.7 | .49 | .22 | 14 | 10.4 | .59 | .32 | Both Parents |
| DL/SL ♂ | No significant difference between samples, fig. 5. |  |  |  |  |  |  |  |  |  |  |  | Both Parents |
| DL/SL ♀ | 14 | 20.5 | 1.32 | .71 | 19 | 22.0 | .69 | .31 | 12 | 22.2 | .48 | .28 | *F. olivaceus* |
| Anal Fin Spots ♂ | very few or none |  |  |  | many |  |  |  | few |  |  |  | Neither |
| Anal Fin Spots ♀ | none |  |  |  | few |  |  |  | few |  |  |  | *F. olivaceus* |
| Stripe Extensions | 5 or less |  |  |  | 10 to 15 |  |  |  | 5 to 15 |  |  |  | *F. olivaceus* |
| Dorsum Pattern | cross-hatched |  |  |  | intermediate |  |  |  | uniform, dusky |  |  |  | Intermediate |
| Dorsum Spots, ♂ and ♀ | ♂ - none to few very light, ♀ - none |  |  |  | ♂ - intermediate<br>♀ - few, dusky |  |  |  | ♂ - many dark<br>♀ - few to many dark |  |  |  | Intermediate |

Figure 6. Two natural hybrids, both males. UMMZ 161253 (SL 39.5 mm, above) was the only *Fundulus* in the collection. TU 37120 (SL 31.2 mm, below)) was taken with both *Fundulus notatus* and *F. olivaceus*. Photographs by Forrest Jack Hurley.

the dorsum. Females are often more heavily spotted than males. Usually individuals with spots or blotches also have strong development of the predorsal line, which may be broken up into dashes or spots which complement the rest of the dorsal pattern. In contrast, *F. olivaceus* seldom has strong development of the predorsal stripe.

As has been pointed out by Clark Hubbs (1963) and others, closely related species generally are easier to cross than more distantly related ones. The ease with which these two species hybridize in the laboratory supports the idea that their close morphological similarity reflects close phylogenetic relationship. As the hybrids are intermediate in several characters and resemble one parent or the other in other characters, it is clear that the hybrids are not of gynogenetic origin nor are they "false hybrids" in which the paternal chromatin has no effect. The sex ratio of the hybrids (experiment one), 10 males to 21 females, is not significantly different from a theoretical 50:50 sex ratio of 15 males and 15 females. Hubbs and Drewry (1959) have discussed the pitfalls encountered in interpreting results of hybrid experiments.

That *F. notatus* and *F. olivaceus* are interfertile in the laboratory is not necessarily evidence that they are conspecific, but is evidence that isolating mechanisms (if any) which separate them in nature are ecological or behavioral rather than cytological.

My examination of some 12,000 specimens of *F. notatus* and *F. olivaceus* has uncovered two natural hybrids, both males (TU 37120 and UMMZ 161253, Fig. 6). The extreme rarity of *F. notatus* x *F. olivaceus* hybrids in nature is evidence of the effectiveness of isolating mechanisms. Paucity of natural hybrids may be due to hybrid non-survival but several lines of evidence point against this. Moore and Paden (1950) collected breeding pairs of *F. notatus* and *F. olivaceus* from an area of syntopy and found no heterospecific pairs. This observation indicates that when the ecological barriers which ordinarily separate the two species break down, isolation is maintained by the preference of the fish for mates of their own species. Heterospecific matings are easily obtained in the laboratory but seem to occur rarely in nature. The robust nature of the laboratory hybrids suggests that natural hybrids are probably able to compete with either or both parent species.

The paucity of natural F-1 hybrids suggests that introgressive hybridization is not at present an important contributor to variation in either species. Thus *F. olivaceus* with small spots, or few spots, or both, are probably not of hybrid origin. The same is true of heavily spotted or blotched *F. notatus*.

The two species are similar in range of variation in dorsal. anal and caudal ray numbers and in lateral scale number. Although there is considerable intraspecific variation in average number of caudal rays, populations of *F. notatus* are not significantly different from populations of *F. olivaceus* from the same area, with the exception of the populations from the Pearl River (compare Tables 3 and 6). Populations of the two species have significantly different distributions of lateral scale numbers in the Trinity, Mississippi, and Pearl rivers. Lateral scale number does not show a coordinated pattern of geographic variation in the 2 species. It is thus probable that local interspecific differences in this character are fortuitous and of little importance.

With the exception of the Navasota River population of *F. olivaceus,* western populations of *F. notatus* and *F. olivaceus* tend to have high dorsal ray number, and this character does not serve to separate them. The trend to high dorsal ray number extends to the Mississippi Gulf drainage in *F. olivaceus.* High dorsal ray number "western group" *F. olivaceus* and low dorsal ray number "eastern group" *F. notatus* show statistically significant differences in the Mississippi River (see also Braasch and Smith, 1965), Lake Pontchartrain drainage, and Pearl River. In the Alabama system populations of the two forms are not distinguishable on this character because *F. olivaceus* dorsal ray numbers are beginning to drop clinally toward the east.

With the exception of the Navasota River *F. olivaceus* both species tend to have high anal ray numbers in the west and low anal ray numbers in the east. Although there seems to be a slight difference in pattern of variation between the two species, this character serves only to separate the Navasota River *F. olivaceus* population from the Brazos River *F. notatus* population.

*Fundulus notatus* and *F. olivaceus* are two closely related species which are sympatric and occasionally syntopic over a large area. Both species have completely allopatric populations, *F. notatus* in the west and *F. olivaceus* in the east (Fig. 1). In this kind of distribution the phenomenon of character displacement is often seen. Brown and Wilson (1956) defined character displacement as follows: "Character displacement is the situation in which, when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone." The probable causes were said to be reinforcement of reproductive isolating mechanisms and ecological displacement. Character displacement would thus be the result of a long term process, and would be most pronounced where it was the result of relatively stable contact of populations of two closely related species over a period encompassing a large number of generations. My observations on areas of occasional syntopy do not support the hypothesis that *F. olivaceus* and *F. notatus* populations maintain stable contact over the period of time necessary for character displacement to occur. I suspect that individuals or populations of both species may migrate considerable distances. Individuals collected syntopically were perhaps allotopic the day before and vice versa.

Braasch and Smith (1965) were unable to show statistically significant differences between allopatric and sympatric samples from the upper Mississippi Valley, but they felt that apparent parallel divergence of two independent characters (dorsal ray number and lateral scale number) indicated some interspecific interaction between sympatric populations. My data do not support this conclusion because the patterns of geographic variation in either species seem to be independent of the presence or absence of the other species. I have been unable to see evidence of character displacement, either between syntopic populations and allotopic populations in the same drainage or between populations of one species inside and outside the range of the other. The possibility of character displacement in species recognition ability is presently being studied but results to date are inconclusive.

## MATERIAL EXAMINED

Complete locality data are given for only those collections which represent range extensions or other significant distributional data. Other collections are listed by drainage, state, county and museum number. Complete data on most collections are given by Thomerson (1965). The following museum abbreviations are used: University of Alabama Ichthyological Collection, UAIC; Florida State University, FSU; Private collection of William Smith-Vanez, WSV; Texas Natural History Collection, University of Texas, TNHC; Tulane University, TU; University of Michigan, Museum of Zoology, UMMZ. In addition to standard abbreviations for states and compass directions, the following are used: Co(s).—County(ies), Par(s).—Parish(es), Cr.—Creek, Dr.—Drainage, Hwy.—Highway, mi.—mile(s), R.—River, and trib.—tributary. In addition to the specimens listed here all specimens of the two species catalogued TNHC and TU (to

May 31, 1965), most of the specimens catalogued by UMMZ, and a few UAIC specimens were examined for verification of identification. Some 12,000 specimens of the two species were examined and counts were made on 933 *F. notatus* and 1621 *F. Olivaceus* from the material listed below. Distribution of these collections is shown in Fig. 1.

*Fundulus notatus*

*Guadalupe Dr.—Texas:* Medina Co.; TNHC 1865 (12)—Bexar Co.; TNHC 5336 (43)—Gonzales Co.; TNHC 301 (5)—Caldwell & Guadalupe Cos.; TNHC 86 (13), TNHC 177 (1), TNHC 235 (3), TNHC 330 (3)—Hays Co.; TNHC 3037 (13).

*Colorado Dr.—Texas:* Bastrop Co.; TNHC 3733 (11), TNHC 3795 (7), TNHC 5266 (16)—Travis Co.; TNHC 225 (4), TNHC 526 (2), TNHC 540 (22), TNHC 1078 (1), TNHC 1098 (2), TNHC 1895 (5), TNHC 2552 (2)—Llano Co.; Honey Cr. on Ray Smith Ranch midway between Llano and Marble Falls, TU uncatalogued (19).

*Brazos Dr.—Texas:* Grimes Co.; TU 37115 (1)—Bell Co.; TNHC 1021 (2), TNHC 3773 (12), TU 35996 (41)—McLennan Co.; TNHC 3467 (1), TNHC 4165 (4), TU 36002 (17)—Bosque & Hill Cos.; TNHC 4246 (1)—Bosque Co.; TU 2989 (9)—Erath Co.; TNHC 1992 (39)—Eastland Co.; TNHC 993 (20).

*San Jacinto Dr.*—Texas: Montgomery Co.; TNHC 1118 (42), TNHC 1199 (18)—San Jacinto Co.; TNHC 2377 (36), TNHC 2843 (4).

*Trinity Dr.—Texas:* Polk Co.; TNHC 5445 (3)—Madison & Walker Cos.; TU 4891 (13)—Ellis Co.; UMMZ 92385 (6), UMMZ 92388 (2)—Dallas Co.; UMMZ 120152 (4)—Tarrant Co.; UMMZ 97503 (7), UMMZ 170048 (1), UMMZ 170060 (5).

*Neches Dr.—Texas:* Anderson Co.; TU 3479 (6)—Cherokee Co.; TU 17686 (46), TU 17788 (11)—Rusk & Shelby Cos.; TU 3854 (6)— Shelby Co.; TU 3315 (20).

*Sabine Dr.—Louisiana:* Sabine Par.; TU 33312 (2), TU 33798 (1), TU 33938 (34), TU 34005 (6), TU 34078 (21), TU 35461 (11), TU 35567 (2)—De Soto Par.; TU 35544 (11)—*Texas:* Panola Co.; TNHC 6063 (10)—Harrison & Panola Cos.; TNHC 3190 (6).

*Mississippi and Great Lakes Dr.—Louisiana:* St. Charles Par.; Ponds in Bonnet Carre Spillway S of Hwy. 61, 20 mi. W New Orleans, TU 387 (5)—La Salle Par.; UMMZ 181940 (12)—*Oklahoma:* Nowata Co.; TU 15532 (39)—*Tennessee:* Lake Co.; UMMZ 103367 (2)— Davidson Co.; UMMZ 88106 (6), UMMZ 104498 (3), UMMZ 177568 (7)—Marshall Co.; UMMZ 121387 (13)—Jackson Co.; UMMZ 125113 (10)—*Michigan:* Washtenaw Co.; (Huron R.) UMMZ 72255 (19).

*Lake Pontchartrain Dr.*—Louisiana: East Baton Rouge Par.; Amite R. at Hwy. 190, 7 mi. E of intersection Hwy. 190 & Hwy. 61, TU 35697 (19)—Tangipahoa Par.; Tangipahoa R. at Hwy. 35, 1.5 mi. E Amite, UMMZ 182344 (1)—Tangipahoa Par. (?); Trib. to Natalbany R., UMMZ 182345 (20).

*Pearl Dr.—Louisiana:* Washington Par.; TU 37118 (54)—*Mississippi:* Marion Co.; TU 37119 (36)—Lawrence Co.; TU 26408 (29)—Hinds & Rankin Cos.; UMMZ 170728 (3).

*Tombigbee Dr.—Alabama:* Sumter Co.; TU 7497 (3), UMMZ 163741 (12)—*Mississippi:* Kemper Co.; UMMZ 157774 (3)—Noxubee Co.; TU 3755 (11), UMMZ 113885 (6).

*Fundulus olivaceus*

*Navasota Dr.—Texas:* Grimes Co.; Trib. to Navasota R. 5.1 mi. NE Navasota at Hwy. 190, TU 37116 (7)—Brazos Co.; Wickson Cr. UMMZ 129747 (3), Peachtree Cr. borrow pits 12 mi. S College Station, UMMZ 129764 (1), UMMZ 129951 (16), and UMMZ 138235 (5); Peach Cr. at Hwy. 6, UMMZ 129807 (80), Sand Cr. trib. to Navasota R. E of Kurten, UMMZ 129916 (3), Navasota R. and borrow pits 4 mi. E Kurten, UMMZ 129935 (7).

*Trinity Dr.—Texas:* San Jacinto Co.; TNHC 1169 (9)—Polk Co.; TNHC 5446 (29), TNHC 2415 (40), TNHC 6039 (20)—Anderson Co.; TU 3792 (2).

*Neches Dr.—Texas:* Hardin Co.; TU 21615 (57), TU 21761 (28)—Tyler Co.; TU 21686 (23).

*Sabine Dr.—Texas:* Newton Co.; TU 14045 (3)—Panola Co.; TU 3496 (10)—*Louisiana:* Vernon Par.; TU 777 (6) TU 5136 (6)—Sabine Par.; TU 793 (7), TU 5075 (21), TU 33764 (18), TU 33824 (13), TU 33941 (2), TU 3717 (1).

*Western Louisiana Dr.—Louisiana:* Allen Par.; TU 1327 (16), TU 14458 (4)—Rapides Par.; TU 1344 (11), TU 2059 (5), TU 2065 (13), TU 3459 (23), TU 4982 (19), TU 5769 (1), TU 5831 (11), TU 5871 (4).

*Southern Mississippi Dr.—Louisiana:* East Feliciana Par.; TU 5231 (19) TU 30884 (43)—*Mississippi:* Lincoln Co.; TU 28889 (7)—Holmes Co.; TU 3695 (10). *Middle Mississippi Dr., (Arkansas and Tennessee rivers)—Arkansas:* Garland Co; TU 14249 (12)—Yell Co.; TU 15487 (73)—Pope Co.; TU 13770 (13), TU 26925 (3)—*Mississippi:* Tishomingo Co.; TU 4197 (4)—*Tennessee:* Benton Co.; TU 14715 (5). *Northern Mississippi Dr.—Illinois:* Massac Co.; TU 3530 (25)—Johnson Co.; UMMZ 175870 (7).

*Lake Pontchartrain Dr.—Louisiana:* East Baton Rouge Par.; TU 35691 (22)—East Feliciana Par.; TU 4656 (39)—St. Tammany Par.; TU 967 (33), TU 9811 (14), TU 14512 (18).

*Pearl Dr.—Louisiana:* St. Tammany Par.; TU 25823 (25)—*Mississippi:* Pearl River Co.; TU 14107 (20), TU 23549 (40)—Marion Co.; TU 28415 (44)—Copiah Co.; TU 28872 (22).

*Mississippi Gulf Dr.*—Mississippi: Hancock Co.; TU 4771 (20), TU 7653 (6), TU 27078 (12)—Harrison Co.; TU 27094 (3)—Jackson Co.; TU 28087 (7)—Stone Co.; TU 16348 (21), TU 28095 (1)—Lamar Co.; TU 1622 (5)—Perry Co.; TU 1231 (5)—Covington Co.; TU 28582 (9), TU 28593 (1)—Lauderdale Co.; TU 7484 (3).

*Alabama (including Tombigbee) Dr.—Alabama:* Washington Co.; TU 33910 (2), UMMZ 163597 (84)—Clarke Co.; TU 32522 (11)—Monroe Co.; TU 2644 (15)—Crenshaw Co.; TU 2586 (8)—Wilcox Co.; TU 3065 (9), TU 3431 (14) Marengo Co.; TU 24544 (1)—Perry Co.; TU 25969 (19)—Bibb Co.; TU 19423 (6), TU 24688 (17)—Talapoosa Co.; TU 12174 (7)—Tuscaloosa Co; TU 27548 (4), TU 30192 (3), TU 30212 (6)—Blount Co.; UMMZ 168616 (18)—Marion Co.; TU 30235 (21)—*Mississippi:* Lee Co.; TU 2443 (10).

*Pensacola Bay Dr.—Florida:* Santa Rosa Co.; TU 20941 (7)—Okaloosa Co.; TU 23691 (30)—Walton Co.; TU 24762 (57).

*Choctawhatchee Bay Dr.—Florida:* Holmes Co.; TU 2277 (37)—*Alabama:* Dale Co; TU 2348 (28)—Henry Co.; TU 3902 (60).

*Apalachacola (Chatahoochee) Dr.—Alabama:* Russell Co.; UAIC 1097 (1), FSU 6591 (15), FSU 6656 (77), TU 10717 (3), WSV 6423-1 (2), WSV 6438-1 (3), WSV 6445-1 (44)—Lee Co.; FSU 6643 (11), TU 12099 (3), WSV 6414-3 (1)—*Georgia:* Early Co.; UAIC 1134 (1).

*Fundulus notatus x F. olivaceus*

*Mississippi Dr.—Louisiana:* Jackson Par.; Castor Cr. trib. to Little River at Chatham, UMMZ 161253 (1).

*Pearl Dr.—Mississippi:* Copiah Co.; Pearl River 3 mi. E Georgetown, TU 37120 (1).

## CONCLUSIONS

1. *Fundulus notatus* and *F. olivaceus* are highly interfertile in the laboratory and produce fertile and vigorous hybrids. Their ranges broadly overlap in nature and they are occasionally syntopic. The rare occurrence of natural hybrids (about 1 in 6000) indicates that strong isolating mechanisms separate the two species.

2. The exact nature of the isolating mechanisms is not known. The rare occurrence of syntopy indicates that isolating mechanisms are primarily ecological. However, no general statement of ecological parameters seems to have more than local validity and either species seems to occupy all favorable habitats when the other is absent.

3. Observations of syntopic populations indicate that strong behavioral isolation is operative. No evidence is available to suggest intergradation or introgressive hybridization.

4. Morphological character displacement is not demonstrated and is probably rare or absent as a result of the unstable nature of the syntopic associations.

5. A single character, the presence or absence of distinct, regular, dark black dorsolateral spots, separates specimens of *F. olivaceus* from specimens of *F. notatus* except in rare instances. Other characters may be used to separate local populations, but do not have range-wide utility. There is broad intraspecific overlap in all characters studied and the recognition of subspecies is not warranted.

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Volume 13, Number 2 August 30, 1966

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TULANE STUDIES IN ZOOLOGY

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# ANALYSIS OF A KEY ROLE IN A CAPUCHIN *(CEBUS ALBIFRONS)* GROUP[1]

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## ABSTRACT

A series of challenge situations was used to study the response patterns of group members in capuchin, rhesus, and pigtail monkey groups. Analysis and comparison of responses associated with key roles revealed important similarities in all groups despite the apparent absence of a status hierarchy among the capuchins. It is suggested that the "control animal" role is independent of the dominance or status hierarchies found in macaques. Further, it appears that it is this role and not dominance which is vital to the organization of many primate societies.

Analysis of the complex social organization of a primate group reveals a number of consitent response patterns which appear in only certain individuals within the group (Bernstein and Sharpe, 1966). These same response patterns can be recognized in other groups formed by animals of the same taxon, and often appear in similar form in several primate taxa. Such patterns may be referred to as "roles" in the restricted sense of consistent patterns of response shown by particular members of a society in specified situations. Although "role" as used by psychologists and sociologists refers to human societies, the societies of monkeys and apes approach the complexity of simple human societies with specialized patterns of responses associated with particular individuals within the group.

One of the most striking response patterns, or roles, in primate societies is that of the "dominant male" in certain macaque and baboon groups. The readily observable status hierarchies in these groups have led investigators to define the role by "priority to incentives". Recent field and laboratory studies, however, suggest that other aspects of social control may be the essential elements of this role (Bernstein 1964a, DeVore and Washburn 1963, Hall 1960, Reynolds 1963, and Schaller 1963).

In a series of experiments at the Yerkes Laboratories, three groups of rhesus *(Macaca mulatta)*, three groups of pigtails *(Macaca nemestrina)*, and one group of capuchins *(Cebus albifrons)* were tested in situations designed to elicit the expression of responses associated with the role of "dominant male". In addition, limited observations were made of Celebes black ape *(Cynopithecus niger)*, vervet *(Cercopithecus aethiops)*, gibbon *(Hylobates lar)*, mixed taxa and additional rhesus, pigtail, and capuchin groups. Groups consisted of 6 to 26 animals, with a median of 11.

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The basic test situations involved challenges to the group. In addition, feeding situations were contrived to maximize competition in order to test for "priority to incentives", and agonistic episodes were observed to measure responses to intragroup sources of challenge. Data on the macaques confirmed expectations derived from other observations (Bernstein 1964a). On the basis of observations of laboratory and wild groups of capuchins (Bernstein 1964b), it was hypothesized that many of the important response patterns found in macaque "dominant males" might also be present in certain capuchin males, despite the apparent absence of a status heirarchy in the latter. This paper reports the results of a series of laboratory tests with a capuchin group.

## METHOD

### *Subjects:*

Twelve *Cebus albifrons:* three adult males, six adult females, and three immature animals were used. The group was formed in November, 1962 and tests were conducted from April to July of 1963. The stabilization of social responses prior to testing is reported in Bernstein (in press).

### *Apparatus:*

An outdoor compound 48 x 24 x 8 ft, constructed of 2 x 4 in. welded wire over a lumber framework, was used to house the group. A 3 ft cubicle of similar construction could be extended into the compound from one side. A detailed description appears in Bernstein and Mason (1963).

### *Procedure:*

*Snake Test.* The first test consisted of placing a live 4 ft snake (tentatively identified as *Elaphe obsoleta quadrivitatta*) in a transparent plastic box within the 3 ft cubicle and presenting it to the group. Two observers scored all responses directed towards the snake and indicated which animals approached the box. Observations were made for 1000 sec from an enclosed observation post directly behind the cubicle, and for an additional 1000 sec from the opposite side of the compound.

*Human Intruder Test.* A human entered the compound and walked a fixed pattern waving a stick. Two complete circuits were completed in 100 sec and there were 10 such trials. Following this, a different human intruder remained passively seated in the compound for 1000 sec, then offered fruit every 100 sec, for the next 1000 sec.

*Cubicle Tests.* A group member was captured and placed in the 3 ft cubicle and presented to the group for 300 sec. Following this, the active human intruder entered the compound for 100 sec and departed for 100 sec, alternately, for 10 trials. During the first five intrusions observers remained in the observation post, and during the last five intrusions they moved to the opposite side of the compound. After completing this series, the subject was removed from the cubicle and held for 300 sec against the wire wall of the compound. The animal was then released into the compound and observations continued for an additional 300 sec. This procedure was repeated with each of the 12 group members.

Two observers scored all group responses and the responses of the captured animals. Approaches and contacts with the caged animal and the cage were scored in addition to social responses between animals and responses directed at the intruder or observers. Each response was scored to provide frequency counts, but duration was noted only for continuous vocalization (not more than 5 sec of silence between calls).

*Complex Space Test.* The final test consisted of modifying a 16 x 12 x 8 ft space in the compound by adding pieces of chain, rope, nylon net, wooden platforms, swings, and additional runways. A washtub of water was placed on the floor, a tether ball was hung, an infant "Busy Box" (a toy containing complex manipulanda) was attached to one wall, and several moveable pivoted platforms were placed in the space. For 2000 sec during each of the next nine days scores were kept identifying each animal in the test space, the duration of time spent in the test space, and new objects contacted. These observations continued each weekday thereafter for the next four weeks.

## RESULTS

*Snake Test.* Presentation of the snake produced visual orientation by most animals in the group. There were 14 instances of threat directed at the snake in the first 1000 sec. The largest male accounted for 3, an immature male for 8, its mother for 2, and another immature animal for 1.

Immediately following presentation, the two older immatures approached and threatened the snake. They were joined by the mother of one of them, and the largest male which placed his arm over the back of the more active immature animal—a response interpreted as aiding (Bernstein, in press). It was repeated three times. The largest male also groomed the immature animal's mother. These were the only animals to come within 8 ft of the snake during the first 1000 sec.

During the second 1000 sec three more animals approached but showed no directed responses to the snake. The two immature animals climbed onto the cubicle with one assuming the infant riding position on the other briefly.

*Human Intruder Test.* During 9 of the 10 trials when the intruder was active, the largest male threatened him and produced 95 percent of the 20 discrete threats counted. Many threats were prolonged (duration greater than 10 sec) and perhaps should be considered as multiple threats. The largest male was the only group member to approach the intruder; all other animals fled each time the intruder approached with the exception of one female who failed to flee twice. Considerable vocalization including the typical alarm call occurred, but the largest male repeatedly vocalized (in a distinctive barking voice) directly at the intruder whereas only one other adult male and an immature male ever vocalized directly at the intruder, and then only once each. The youngest immature never left its mother's back and another immature also rode its mother's back briefly.

In contrast, when the passive intruder was present an adult female threatened twice with the largest male joining her in threatening the intruder once. Other animals oriented towards the intruder and there was some vocalization. One immature nursed, a second threatened a female, and most animals remained in a far corner moving slowly.

Food offers immediately attracted the largest male, two immature animals, and a female. The female climbed onto the intruder and fed and one immature took food from the intruder, whereas other animals only took food dropped on the ground. The largest male threatened the intruder once and two females threatened the observers and the intruder. One of these females threatened twice more before taking food. Other animals took food from one another and the youngest immature moved independently near its mother.

*Cubicle Tests.* Caging a group member produced considerable vocalization, including alarm calling, which increased with the entry of the intruder. When the intruder was absent, group members gathered near the captive member and there was a great deal of reaching towards and contact with the caged animal. These activities and attempts to escape the cubicle decreased when the intruder was present.

Aggression towards the intruder was intensified when the captive animal was being held. Following release, the released animal often joined the group in further aggressive displays. Data are summarized in Table 1.

Examination of individual scores revealed a distinctive response pattern for the largest male. He threatened and charged the intruder 3 times more often than did any other animal, he was responsible for almost all the noisy demonstrations directed at the observers and intruder, and, he was on the ground next to the caged animal twice as often as was any other animal. Further, in addition to being in the area of caged animals, he contacted them twice as often as did any other group member whether the intruder was present or absent. He was also responsible for almost all vocalizations directed at the intruder. When confined to the cubicle, the largest male showed more aggression to the intruder and reached out towards and vocalized at the intruder more often than did any other animal. Finally, when group members were held, and following their release, the largest male was most active in threatening, charging and reaching towards the experimenters. Although he was sometimes joined by other animals, they seldom showed responses as persistently or as intensely, and did not respond when he was not present. When the largest male was confined to the cubicle, other group members clustered near him when the intruder was active.

One immature male was very vocal throughout testing and gave the alarm call continuously. He and another immature male were also most vigorous in attempts to escape the cubicle when confined. The third immature animal remained on its

TABLE 1

*Response frequencies when individuals were separated from the group and restricted in space.*

| | Human active | | Human hidden | | Subject held | | After release | |
|---|---|---|---|---|---|---|---|---|
| Response | group frequency | caged animal frequency | group frequency | caged animal frequency | group No. trials (of 12) | held animal No. trials (of 12) | group No. trials (of 12) | held animal No. trials (of 12) |
| Vocalization | 105 | 55 | 84 | 46 | 7 | 11 | 2 | 6 |
| Alarm call | 72 | 27 | 56 | 36 | 5 | 1 | 2 | 1 |
| Caged animal contacts | 23 | 0 | 132 | 18 | 3 | – | – | – |
| Aggressive to observers | 2 | 0 | 109 | 30 | 6 | – | 6 | 5 |
| Agressive to intruder | 44 | 39 | – | – | – | – | – | – |
| Approach experimenters | 35 | – | – | – | 5 | – | 2 | 3 |
| Group flees | 35 | – | – | – | – | – | – | – |
| Individual flees | 86 | – | – | – | – | – | – | – |
| Group follows one animal | 19 | – | – | – | – | – | – | – |
| Backtracking | 12 | – | – | – | – | – | – | – |
| Within 3 ft. of intruder | 13 | – | – | – | – | – | – | – |
| Demonstrating | 7 | 1 | 19 | 2 | 3 | – | 4 | 0 |
| Non directed responses | 1 | 0 | 7 | 2 | 0 | – | 0 | 0 |
| High location near cage | 10 | – | 337 | – | 2 | – | 0 | 0 |
| Medium location near cage | 8 | – | 141 | – | 2 | – | 0 | 0 |
| On ground near cage | 7 | – | 110 | – | 5 | – | 1 | 1 |
| Frequency enter cage area | 39 | – | 462 | – | 8 | – | 6 | – |
| Struggle for release | – | 12 | – | 19 | – | 4 | – | – |
| Reaching through cage wire, no contact | 1 | 35 | 0 | 8 | 7 | – | 0 | 0 |

Note: A dash indicates the response is not applicable.

mother's back during all trials and its mother fled the intruder more often than did any other animal. She also backtracked most often, but always did so while the largest male was between her and the intruder. (Backtracking by one or more animals was most common initially, i.e. quietly retracing the path that the full group had just covered in a noisy jumping flight from the intruder). When mother and infant were separated, both gave persistent alarm calls, but though the mother was aggressive towards the intruder when her infant was being held or confined (she showed few responses when other animals were involved) her infant showed little response when its mother was held or caged, but instead remained quietly with the group.

Trials with the human intruder became progressively less effective in producing avoidance responses. Whereas initially the group fled at the start of each approach of the intruder, they gradually tolerated closer approaches and some eventually remained on high platforms and did not flee. Advances by the largest male also increased in frequency, as did various demonstration responses such as shaking or banging objects. The cohesiveness of the group was most notable in early trials with the group fleeing as a unit, sometimes clearly following a single animal (a second adult male).

*Complex Space Test.* On the first day the complex space was available to the group, only the largest male and one female spent more than 10 sec in the area. On the second day another adult male and an immature male entered for short periods, and it was not until the third day that several animals spent any time in the area. Throughout the 29 observation days, some individuals spent significantly less time in the area than would be expected by chance (333 sec of each 2000 sec observation session since the complex space occupied one-sixth of the compound). Others gradually made increasing use of the new features and one adult male was in the area over one-half of the time (averaging

1262 sec per session). The least frequent entrant was the mother of the youngest immature animal (averaging 20 sec per session). Group scores fluctuated about chance with a mean of 449 sec per session.

*Intragroup Disturbances.* Although intragroups fighting was not frequent, when it occurred the largest male frequently responded and interfered in the interaction. During feeding tests, however, no status hierarchy could be detected, i.e. no consistent feeding order was observed when food was available from a single location, and few aggressive episodes occurred. Food was sometimes exchanged between animals and the exchanges were reciprocal. Detailed accounts are presented in Bernstein (in press).

## DISCUSSION

The data thus support the hypothesis that the consistent response pattern described as the role of the "dominant male" in macaque and baboon troop may occur in capuchin groups even when there is no evidence of a clear status hierarchy. Common responses include: assuming a position between an external disturbance and the group, attacking whatever appears to be distressing a captured group member, and approaching and terminating most cases of intragroup disturbance. Similar observations were obtained from studies of vervet, Celebes black ape, gibbon, and additional rhesus, pigtail, capuchin, and mixed taxa groups. I therefore suggest that the term "dominant male" be restricted to descriptions of a status heirarchy and another term selected for the described role. "Leader male" has been suggested, but in primate groups, animals fulfilling this role seldom travel first in group progressions, although they may exercise some control over troop movement. The key functions of this animal appear to be the control of intragroup disturbance, and the responses of the group to external challenges. "Control animal" is therefore suggested as a more appropriate term for the role.

Group members respond to the control animal in a distinctive fashion. They frequently enlist his aid in threatening both other group members and extra group targets. Further, when the control animal is confined in space, group members in distress may approach and remain in his immediate vicinity even if such approach increases their proximity to the cause of their distress. Approaches to the control animal are especially notable in the case of macaques where a status hierarchy exists and social distance is ordinarily enforced with subordinates avoiding the immediate vicinity of superiors. Control animals are also far more vigorous in attacking an external source of disturbance when the challenge is directed at the group rather than to the control animal as an individual and alone. In the capuchin group reported, the largest male often permitted friendly contact with humans when he was alone, whereas when the group was present and a human disturbed them, he was aggressive towards the human. Responses included: shaking and banging of objects, vocalization and bluffing, as well as direct attack.

In the present series, the relative lack of responsiveness to the snake can be interpreted as indicating that the snake so presented was not a serious challenge to the group. Other situations were perhaps more direct challenges. Certain complex relationships between group members could be observed in the course of testing in addition to the role of the control animal, and deserve future study.

Although the largest male capuchin approached and remained near all potentially challenging stimuli more than did any other animal, he was not simply the boldest animal in the group, as was revealed during tests when a passive person offered food. The largest male did not make contact with, or take food directly from the person although other members did so. When responding to challenges, the male shook and banged objects and engaged in other activities which attracted attention to himself. The responses were similar to those observed in wild troops when approached by a human (Bernstein 1964b).

The largest male frequently remained behind when the group fled and another adult male was usually the initiator of group movements. When the largest male did travel with the group, however, the other animals followed close behind him.

The responses of the macaque groups tested can be compared with the capuchin data and although the macaques were at times more intense and more successful in aggression towards the intruder, the differential size of capuchins and macaques may account for this. The size factor may be responsible for the relative caution with which capuchins approached new stimuli such as the complex space. The similarity of responses to challenges by control males in capuchin and macaque groups is striking and indicates that the protective function of the role is not necessarily associated with dominance or the existence of a status hierarchy. This conclusion was also supported by observations of the other groups mentioned. More data will be required, however, before any conclusions can be reached as to the differences between capuchin and macaque social organizations.

Among the macaques, and in the capuchin groups, particular animals (including some large females) at times supported the control animal in its activities. In larger groups several animals showed the same pattern of responses. In some groups, other animals, usually adult or subadult males, sometimes produced the pattern of responses associated with the control animal when it failed to respond for any reason. Removal of the control animal resulted in rapid substitution although return of the original control animal resulted in immediate resumption of the former pattern. This suggests that the functions of the control animal are essential to the society and failure to fulfill the function will elicit the responses in substitute animals.

Other roles in primate societies must also be carefully examined in order to understand the organization of a society and the differences between societies. The role of the control animal operates within the context of an organization of interrelated roles, some of which are briefly reflected in the present series of tests. We must be prepared, however, to find as much diversity in roles and role expressions as has been discovered in morphology. Morphological responses to ecological pressures have undoubtedly been paralleled in behavioral adjustments which may be reflected in the variety of organizations in primate societies.

## CONCLUSIONS

Analysis and comparison of the responses of control animals in capuchin and macaque groups revealed certain important similarities in the functions of these animals. Although the responses of these animals to challenges to the group were similar in both species, no evidence of a status hierarchy could be found in the capuchin group. The control animal role in some primate groups may therefore not be associated with the attributes of dominance. The control animal role does appear to be vital to the organization of some primate societies.

The term "control animal" is tentatively suggested for the distinctive role described.

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# RESURRECTED NAMES FOR MEXICAN POPULATIONS OF BLACK-NECKED GARTER SNAKES, *THAMNOPHIS CYRTOPSIS* (KENNICOTT)

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ABSTRACT

Three distinct subspecies of *Thamnophis cyrtopsis* occur in western Mexico. One subspecies, *T. c. cyrtopsis,* is restricted to the Mexican plateau. The other two subspecies previously masqueraded under the name *Thamnophis cyrtopsis cyclides.* Because the holotype of *cyclides* is from Arizona and indistinguishable from *T. c. cyrtopsis,* Cope's *Eutaenia pulchrilatus* 1885 is resurrected for snakes from the highlands, and Jan's *Tropidonotus collaris* 1863 is resurrected for snakes from the lowlands. *Thamnophis c. pulchrilatus* occurs in the boreal pine-oak forests of the highlands of the Transverse Volcanic Belt and of the southern parts of the Sierra Madre Oriental and Occidental, whereas *T. c. collaris* lives in tropical lowland and subtropical mountainous habitats from Sonora to Chiapas to Veracruz. The principal characters distinguishing the several subspecies include the number of supralabials, infralabial markings, and nape and ventrolateral pattern. It is suggested that the name *Eutaenia dorsalis* Baird and Girard, 1853 is applicable to the upper Rio Grande population of garter snakes currently designated as *Thamnophis sirtalis ornata.*

Recent studies made upon the reptiles indigenous to an area extending from southwestern Durango across the Sierra Madre Occidental to southern Sinaloa have indicated the presence of three distinct populations of the *cyrtopsis* group of garter snakes. An effort to determine the status of these snakes has resulted in the relegation of the name *cyclides* to the synonymy of *cyrtopsis,* and the recognition of three subspecies, namely, the restriction of *cyrtopsis* to the Mexican plateau population, the resurrection of Jan's *collaris* for garter snakes in the coastal lowlands of Sinaloa, and the use of Cope's *pulchrilatus* for those in the Sierra Madre highlands.

### *Applicability of the name cyrtopsis*

The specific name most recently proposed for the black-necked garter snakes of this complex is *Thamnophis dorsalis* (Fitch and Milstead, 1961). There is some suggestion, however, that *dorsalis* is applicable to the upper Rio Grande population of *Thamnophis sirtalis,* which was designated as *T.s. ornata* by Fitch and Maslin (1961:297). Fitch and Milstead (1961) presented arguments for applying the name *dorsalis* to the black-necked garter snakes previously known as *cyrtopsis,* principally on the basis of the itinerary of General Churchill and the stated type locality, "between Monclova, Mexico, and the Rio Grande," or simply "Rio Grande" (Baird and Girard, 1853:32). There is no contrary evidence regarding the type locality of *dorsalis,* but the original description requires close scrutiny.

Baird and Girard included two items that seem inapplicable to *cyrtopsis.* These are the middorsal stripe "covering one and two half-rows of scales, margined on each side for one scale continuously with black," and the "series of rather large spots . . . from head to anus, and ranged just above the lateral stripe." In *cyrtopsis,* the middorsal stripe, mostly confined to the vertebral row, may cover nearly half of the adjacent rows in some cases, but the stripe lacks continuous black borders. Specimens of *cyrtopsis* characteristically have a checkerboard pattern (mostly uniform brown posteriorly), but oc-

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casionally there are a few large black spots in a single row on the neck. Baird and Girard did not mention the conspicuous black nape blotches of *cyrtopsis.*

Since the time of the type description, the name *dorsalis* had been generally associated with the population of *Thamnophis sirtalis* in the upper part of the Rio Grande drainage (except Ruthven, 1908:158, footnote) until the reinterpretation by Fitch and Maslin (1961:299) and Fitch and Milstead (1961). The basis for applying *dorsalis* to snakes from the upper Rio Grande probably stems from a figure in Jan and Sordelli (1867:livr. 25, pl. 4, fig. 1), who applied the name *Tropidonotus sirtalis* var. *dorsalis* to their illustration of a snake from "Fort Conrad, nord du Mexique" (= west bank of Rio Grande, opposite Valverde, about 24 miles S Socorro, Socorro County, New Mexico). The characters of the snake illustrated fit the type description of *dorsalis* and resemble those of specimens of *sirtalis* from the upper Rio Grande. Individuals of *Thamnophis sirtalis* from the Rio Grande drainage in New Mexico have a single row of spots just above the lateral stripe. They also exhibit a wide middorsal stripe that occupies the vertebral row and halves of the adjacent rows, and which has narrow continuous black borders (although these are not one scale wide). In large specimens, the dorsolateral row of black spots tends to disappear and to be replaced by longitudinal dark lines. The black marks on the first dorsal scale row are lacking in some cases, contrary to the type description and the illustration of *dorsalis.* In spite of the stated type locality, it is likely that the name *dorsalis* belongs to the upper Rio Grande population of *Thamnophis sirtalis.* Cochran (1961:xi) and other authors have pointed out that data accompanying many specimens obtained during the early military or exploratory expeditions in the 1800's and deposited in the U.S. National Museum are in error.

If the name *dorsalis* is applied to the population of *sirtalis* of the Rio Grande it would replace the name *ornata* of Baird (1859). Regardless of the species to which *dorsalis* is applicable, the name *cyrtopsis* should be conserved for the black-necked garter snakes through application of the *nomen oblitum* rule of the 1961 International Code of Zoological Nomenclature (Smith and Williams, 1962; see also page 62 of present report concerning *nomina oblita.*) Duellman (1961:114-115) offered a brief summary of the principal taxonomic and nomenclatural changes involving *Thamnophis cyrtopsis.*

### *Status of the name cyclides*

The names *Thamnophis cyrtopsis cyrtopsis* and *T.c. cyclides* have both been applied to black-necked garter snakes from southern Durango and Sinaloa. While attempting to determine if the name *cyclides* applied to one of the three recognizable populations of that region, I discovered that the holotype of *cyclides* is from Arizona (Cochran, 1961: 218) and is indistinguishable from specimens of *T.c. cyrtopsis.*

Cope (1861:299) described *cyclides* as a variety of *Thamnophis cyrtopsis* on the basis of a single specimen, USNM No. 5023, stated to have been included in a collection from Cape San Lucas, Baja, California, that was sent to the Smithsonian Institution by Louis John Xantus. Since a type locality of Cape San Lucas obviously was in error, Smith and Taylor (1950:330) took the liberty of reassigning the locality as Guanajuato, Guanajuato. When the specific names of these garter snakes was subsequently changed from *eques* to *cyrtopsis* and northern and southern subspecies were recognized, the name *cyclides* was resurrected for snakes from the southern part of the Mexican plateau (see Smith, 1951).

The USNM catalog entry for No. 5023, dated October 10, 1861, seems to have been originally allotted to a *Thamnophis.* The locality and collector are indicated by ditto marks that refer to the preceding catalog entry of a *Cnemidophorus,* No. 5019, from Ft. Buchanan, Arizona, credited to Dr. B.J.D. Irwin. Subsequently, *Thamnophis* was crossed out, and, for some unknown reason, *Lichanura trivirgata* (Type), Cape San Lucas, and Xantus were inked in the appropriate places in the same catalog entry. Later, however, the *Lichanura* entry was crossed out and replaced by *Eutaenia cyrtopsis,* the locality was penciled in as Ft. Buchanan, Arizona, and the collector as Dr. Irwin (both written by Stejneger, according to Cochran, pers. comm.), and in the "Remarks" column the specimen was designated as *Thamnophis cyrtopsis cyclides* Cope = 5023 Type (written by Cochran). Leonhard Stejneger also initialed a penciled annotation in the "Remarks" column of the catalog entry that the "locality & collector [Cape San Lucas and Xantus] probably only refers to the type of *Lichanura trivirgata*, now entered as 15502." Cochran (1961:218) indicated Ft. Buchanan as the probable type locality of *cyclides*. *Cope* (1900) credited several species from Fort Buchanan to Dr. B.J.D. Irwin, but one species (represented by three specimens of *Holbrookia maculata*, USNM 5025, designated as paratypes of *pulchra* in the catalog) from that locality is erroneously credited to Xantus (*op. cit.*:296). The collector of the *Holbrookia* is indicated by ditto marks, which occur in all preceding entries from No. 5019, and which refer to Irwin; Cope referred to Xantus, which had been inked in the previous catalog entry No. 5023.

The holotype of *cyclides* (Fig. 1), bearing metal tag number 5023, is a young female, approximately 247 mm in body length (tail 78 mm); with 19-19-17 scale rows, 162 ventrals, 79 caudals, 8 supralabials (intercalary scale between 6th and 7th on right side), 10 infralabials, 3 postoculars, 1-2 and 1-3 temporals, and the 4th and 5th supralabials entering the orbit. The supralabial sutures are boldly black-marked, whereas black is lacking on the infralabial sutures, except between the 9th and 10th infralabials. The top of the head is gray, bears faint parietal spots, and contrasts with the black nuchal blotches. The two black nuchal blotches are separated from each other by the middorsal stripe, where it is slightly expanded to a width of three scales; the stripe extends anteriorly to the parietals. The dorsolateral area is uniform pale brown posteriorly, but exhibits a checkerboard pattern of rather small, separate, black spots anteriorly, with the most prominent spots just above the pale lateral stripe and the largest spots on the neck. The ventrolateral stripe (mostly on first scale row) is now faded, but it is slightly darker than the pale lateral stripe and is marked by two rows of paired, non-alternating black spots (upper row largest).

Figure 1. Holotype of *Thamnophis cyrtopsis* var. *cyclides* Cope, 1861, (= *Thamnophis cyrtopsis cyrtopsis*), from Fort Buchanan, Arizona. Photograph by Ralph W. Axtell.

The holotype of *cyclides* is similar to snakes herein designated as *Thamnophis cyrtopsis cyrtopsis*, and is unlike specimens of the species examined from the state of Guanajuato. *Thamnophis cyrtopsis* var. *cyclides* Cope, 1861, is thus considered to be a synonym of *Eutaenia cyrtopsis* (= *Thamnophis cyrtopsis cyrtopsis*) Kennicott, 1860, and the type locality as Fort Buchanan (= near Sonoita Creek above Patagonia, 45 mi. SE Tucson, Santa Cruz County), Arizona. Previously, Cope (1900:285) had noted "Fort Buchanan (Tucson), Arizona."

### *The subspecies of Thamnophis cyrtopsis in Western Mexico*

This report is not intended as a revision of *Thamnophis cyrtopsis*. Although specimens have been examined from several localities in Mexico, I have made no effort to examine all the available material of the species, and have not concerned myself with a study of related forms. My purpose has been only to establish the identity of the three recognizable populations of *T. cyrtopsis* in western Mexico.

Since the resurrection of *cyclides* (Smith, 1951), subsequent authors have applied that name to one or the other of two distinct populations. Because the name *cyclides* is a synonym of *cyrtopsis* and not applicable to either of these populations, Cope's *pulchrilatus* and Jan's *collaris* are resurrected for them.

The black-necked garter snakes considered in this paper are characterized by: 19-19-17 dorsal scale rows; pale middorsal stripe mostly confined to vertebral row; pale lateral stripe on second and third scale rows; black collar indented behind, or consisting of two separate black blotches on neck; seven or eight supralabials; ventrolateral stripe pale brown or blackish covering first scale row but encroaching on lower half of second scale row and lateral edges of ventrals; dark ventrolateral stripe absent in some cases, with pale lateral stripe broadened to cover first three dorsal scale rows; ventrolateral black markings usually largest on margins of first scale row and arranged irregularly or forming a pattern of paired spots; dorsolateral area (between pale middorsal and lateral stripes) uniformly black or brownish, or with checkerboard pattern of alternating rows of black spots; dorsolateral area often showing pattern of narrow, longitudinal, light lines that result from pale keels on some scales; ventral surface immaculate, except for occasional small black spots laterally on anterior edge of some ventrals; tongue red, black-tipped; peritoneum whitish to brownish; females larger than males; ventrals and caudals fewer in females than males. Ventral counts were made according to the Dowling method (1951).

### *Thamnophis cyrtopsis cyrtopsis* (Kennicott)

*E[utaenia] cyrtopsis* Kennicott, Proc. Acad. Nat. Sci. Philadelphia, [12]:333, 1860 (Rinconada, Coahuila, Mexico).

*[Thamnophis cyrtopsis]* Var. *cyclides* Cope, *Ibid.,* [13]:299, 1861 (Fort Buchanan, Arizona).

*Eutaenia aurata* Cope, Proc. U. S. Nat. Mus., 14:659, 1892 (Lake Valley, New Mexico).

*Thamnophis cyrtopsis cyrtopsis* Smith, Copeia, 1951(2):140, 1951.

*Type and type locality.*—Holotype, by original designation, USNM 8067; obtained by Lieut. Darius Nash Couch at "Rinconada Coahuila, Mexico," in 1853. The Rinconada where Couch collected is about 20 miles northeast of Ramos Arizpe, Coahuila, in the state of Nuevo León close to the Nuevo León-Coahuila state line (Conant, ms.).

Although Kennicott had at least three specimens before him (three localities are listed), the type description (1860:333) is based on No. 930 (USNM 8067), which is referred to as "the typical one," and is herein considered to be the holotype. In the USNM catalog, the entry for No. 8067 is *Eutaenia sirtalis (sirtalis* is crossed out in pencil), and it is designated in the "Remarks" column as "Type of *E. cyrtopsis* = old 930." The label accompanying the specimen jar is marked "Type. 930 (8067) *Eutaenia cyrtopsis* Kenn. Rinconada, Coahuila, Mex., Couch."

*Description of holotype.*—Some features of this specimen as observed by Roger Conant were transmitted to me. The specimen, a male, has 19-19-17 scale rows, 173 ventrals, 89 caudals, 8 supralabials, 11 infralabials, 2 postoculars, 1-2 temporals, 4th and 5th labials entering eye, and a total length of 622 mm (tail length 151 mm). The middorsal stripe is expanded to a width of three scales before terminating at a point five scales posterior to the parietals (nuchal collar complete). In the dark areas between the middorsal and lateral stripes are relatively faint dark spots. Apparently there was a continuous brown or dark gray stripe along the first row of scales and the edges of the ventrals, but this is now faded so that the dark spots along this stripe are prominent.

*Description.*—The top of the head usually is gray, occasionally brown, contrasting with the black nape blotches. There are two black blotches on the neck separated by the middorsal stripe that usually extends anteriorly to the parietals; occasionally the nape blotches are fused medially (as in the holotype) forming a black collar that is indented posteriorly or partly interrupted (among 11 young of one brood from Río Chico, Durango, three had indented collars, two had partly interrupted collars, and six had two separate nape blotches).

The yellowish middorsal stripe, expanded to a width of about three scales just behind the nuchal blotches, may have scalloped edges and be confined to the vertebral row or, in addition, may occupy small parts of the scales of the adjacent rows. There are eight, rarely seven, supralabials. The supralabial sutures are black, with the three posteriormost sutures often having the black twice as broad as those on the other sutures. All the infralabial sutures may be marked with black, some of the sutures in the middle of the lower lip may lack black, or all infralabial sutures may lack black except the posteriormost. Most of the dorsolateral area is uniform brown (sloughed scales gray), but occasionally black marks are adjacent to or intrude onto the pale stripes. There is either a checkerboard pattern of black spots or a single row of large black spots on the neck. Young specimens tend to have spotted patterns throughout the length of the body. Preserved specimens, because of sloughing of the brown scales, may show prominent spotted patterns throughout the length of the body, with the anterior pattern of large black spots becoming progressively disrupted into small flecks posteriorly.

A distinct ventrolateral stripe below the lateral light stripe is brownish, or pale gray, usually slightly paler than the dorsolateral area. It also includes a pattern of small black marks mostly arranged in pairs (two rows of non-alternating spots one above the other). The spots of the lower row cover the adjacent edges of the ventrals and scales of the first dorsal row, whereas spots of the upper row cover the adjacent edges of scales of the first and second dorsal rows. The ventrolateral spots may be fused into a large spot or streak on the neck, or fused into small hour-glass shaped marks, or may be small and virtually absent, especially posteriorly.

The specimen shown in Figure 2 is representative of Mexican specimens of *T. c. cyrtopsis* from Chihuahua and Durango.

Among 55 individuals, the number of ventrals averages 171.3 (157-184), and in 47 individuals, the number of caudals averages 88.7 (71-100). The sex of several specimens was not determined. Ventrals in 20 males average 171.4 (164-178) and in 15 females 166.8 (157-170). Caudals in 16 males average 90.6 (80-98) and in 12 females 83.0 (71-94). In 11 unsexed young removed from a gravid female (Río Chico, Durango), ventrals average 176.5 (173-184) and caudals average 90.7 (81-99). Supralabials counted on each side of the head are eight (93.5%), rarely seven.

*Remarks.*—The descriptive remarks pertain only to the specimens examined. Cursory examination of specimens from Coahuila and Texas suggests a wider middorsal stripe (vertebral row and halves of adjacent rows), and a more extensive spotted pattern in the dorsolateral areas on snakes from those states than among specimens from farther west.

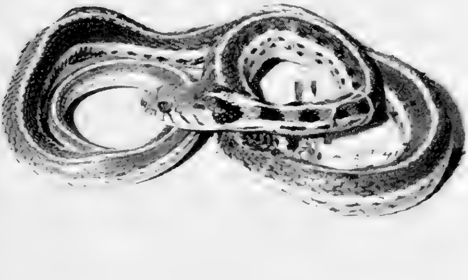

Figure 2. *Thamnophis cyrtopsis cyrtopsis*, UI 23432, from Mojárachic, Chihuahua, showing features generally characteristic of specimens from the Mexican plateau. Photograph by Isabelle Hunt Conant.

*Range.*—In Durango and Chihuahua, the subspecies *cyrtopsis* occurs on the plateau and on the east-facing slopes of the Sierra Madre to elevations of approximately 7000 feet. In Mexico, in general, the nominate race is principally a plateau form that is replaced to the south, west, and east in highland areas by *pulchrilatus* and in lowland or tropical areas by *collaris*. During this study, 55 Mexican specimens of *T. c. cyrtopsis* were examined from the states of Chihuahua, Durango, Sonora, and Zacatecas (Fig. 6). These specimens and their respective localities are:

**Chihuahua:** 4 mi. S and 1 mi. W Santo Tomás (KU 45330-33); 3 mi. S and 10 mi. E Pacheco (KU 44123); 1.5 mi. S and 2.5 mi. E Umira (KU 44287); 2 mi. SW San José Babicora (KU 47318); 2 mi. W Samachique (KU 47317); 3.5 mi. WNW Cocomarachic (KU 51943); 11 mi. WNW Cocomarachic (KU 51922); 7 mi. S Banderas (KU 47320-21); 2 mi. S and 5 mi. W San Francisco (KU 44289); 15 mi. N. Camargo (KU 53736); Presa Catalina, 15 mi. N Villa Ocampo, Durango (AMNH 88722); 15 mi. S and 6 mi. E Creel (KU 44290); 16 mi. S and 13 mi. W Creel (KU 51925); 23 mi. S and 1.5 mi. E Creel (KU 44288); Mojárachic (UI 23430-32); 12 mi. N Ciudad Chihuahua (RGW 2795); 20 mi. N Ciudad Chihuahua (RGW 3378). **Durango:** Río Chico (RGW 2482 and 11 young); 10 mi. W Metates (KU 68727); 1 mi. N Chorro (KU 39975); 12 mi. N Ciudad Durango (AMNH 88745); 22 mi. WSW Ciudad Durango (CAS 87349, 87356); 31 mi. SE Villa Ocampo (AMNH 88723); 4 mi. S Morcillo (MSU 4431-33); 4 mi. E Altar (LACM 7170); Buena Vista 4 mi. NNE Boquilla (MSU 3629); near Guanaceví (USNM 46367). **Sonora:** 5 mi. E Altar (LACM) 7170); Buena Vista (KU 47566); 3.5 mi. N. Ciudad Obregón (LACM 7171); 10 mi. N Guaymas (KU 73634); 9 mi. NNE Imuris (KU 48925). Zacatecas: 5 mi. SW Rancho Grande (AMNH 88744); Río Atotonilco, 2 mi. SE Sain Alto, (AMNH 88746); 2 mi. E Villa

Insurgentes (MSU 566); 5 mi. S. Ojo Caliente (UI 40355).

*Thamnophis cyrtopsis collaris* (Jan), new combination

*T(ropidonotus) collaris* Jan, Elenco Sist. Ofidi . . ., p. 69, 1863; Jan and Sordelli, Iconographie generale des ophidiens, 2:4, livr. 25, pl. 5, fig. 2, December 1867 (reprint 1961).

?*Thamnophis vicinus* Smith, Zoologica, 27:104, October 23, 1942 (near Temaxcal, about 20 kilometers east of Morelia, Michoacán).

*Thamnophis cyrtopsis cyclides* Smith (in part), Copeia, 1951(2):140, 1951.

*Type and type locality.*—Holotype, presumably by monotypy, originally deposited in museum in Bonn; probably lost (no inquiry made by author). The type locality is unknown other than "Messico," but was restricted to Guanajuato, Guanajuato, by Smith (1951:140).

*Description of holotype.*—The one-line description (Jan, 1863:69) is brief: "* T. collaris m. (8. 1. 3. 19) (M. Bonn) Messico." At the bottom of the page the asterisk indicates the following footnote: "(*) Le cifre posti fra parentesi indicano nell'ordine progressivo il numero normale dei sopralabiali, dei preoculari, dei postoculare, e delle serie longitudinali di squame, d'ogni specie."

The Inconographie, prepared to supplement the Elenco, shows a specimen of *collaris* that agrees with the description excepting for the occurrence of two postoculars (instead of three) on the left side of the head. The specimen illustrated in the Iconographie (1867:livr. 25, pl. 5, fig. 2) is from the "Collection Westphal-Castelnau, a Montepellier."

*Description.*—The top of the head is gray or brown (often blackish in preserved specimens), the color extending onto the neck in some cases and, contrasting with the black collar. The collar is partly interrupted in some cases by being indented posteriorly where the pale middorsal stripe terminates. The middorsal stripe, which has scalloped edges, is confined to the vertebral row or occasionally intrudes slightly onto scales of the adjacent rows; it may be slightly expanded just behind the nuchal collar. The sutures on the supralabials are narrowly marked with black, which is often lacking on the suture between the first and second labial. All infralabial sutures may lack black, but usually a small black mark occurs on the suture between the last (ninth and tenth) infralabials. The dorsolateral area between the pale middorsal and lateral stripes is pale to dark brown, having a checkerboard pattern of black spots the length of the body. The upper row of black spots touches the middorsal stripe, and the lower row touches the lateral stripe. In some specimens the dorsolateral area is almost uniform brown, especially posteriorly with the black spots small and indistinct. In the dorsolateral areas, parts of many scales (and skin between scales) are often flecked with white, and the light keels of the dark scales stand out as narrow, interrupted light lines. The dark ventrolateral stripe is lacking (first scale row same color as pale lateral stripe), but often there is a suggestion of a narrow, dim, brown line on the lower half of the first scale row and edges of the ventral scales. The first two rows and most of the third scale row are white, usually having two rows of black flecks and spots arranged alternately or in irregular fashion. Some specimens have some of the marks arranged in pairs, or they are virtually lacking except on the neck. The largest, and most consistent, spots occur on the lower half of the scales of the first row and on the adjacent edges of the ventrals. The specimens shown in Figure 3 are representative of *T. c. collaris.*

Coloration of a living juvenile (body length 213 mm; RGW 2887, 12 miles SE Alamos, Sonora) is as follows: top of head dark gray; nuchal collar black; middorsal stripe buff, with orange tint on neck and pale yellow just behind collar; dorsolateral areas brown with black spots and pale green to whitish flecks, and with brown-keeled scales contrasting across the black spots; first three scale rows pinkish buff with first scale row very pale brown anteriorly; venter white; iris reddish yellow; tongue red, black-tipped.

Among 121 individuals, the number of ventrals averages 155.0 (143-167), and in 85 individuals, the number of caudals averages 92.5 (76-109). The sex of several specimens was not determined. Ventrals in 38 males average 158.0 (149-166) and in 65 females 153.4 (145-167). Caudals in 28 males average 97.5 (77-109), and in 39 females 88.7 (76-103). Supralabials counted

Figure 3. *Thamnophis cyrtopsis collaris* showing variation in pattern—upper center, RGW 2394 from 8 mi. W El Palmito, Sinaloa; lower left, USNM 46605 from Huajuapan, Oaxaca; lower right, UI 23416 from 10 mi. NE Cuernavaca, Morelos. Photograph by Isabelle Hunt Conant.

on each side of the head are eight (94.3%), rarely seven (4.4%), or nine.

*Remarks.*—One of the specimens available to Kennicott in his preparation of the type description of *Eutaenia cyrtopsis* (=*Thamnophis cyrtopsis cyrtopsis*) was USNM 8066 from "Durango, Lieut. Couch." Mr. Roger Conant, who examined the specimen, sent me data indicating that it possesses characteristics applicable to *collaris.* Presumably the specimen is illustrated, but designated as USNM 8062, by Cope (1900: 1050), who referred two specimens to that number (*op. cit.*:1051). The enigmatic 8062 is also applied to an Illinois specimen of *Thamnophis* by Yarrow (1882:115, as *Eutaenia faireyi*) and Cope (1900:1024, as *Eutaenia proxima*).

In Durango, *collaris* is known only from the deep barrancas that dissect the Sierra Madre, and from the highest subtropical parts of the west-facing slopes; presumably USNM 8066 came from one of those two areas. Two specimens of *collaris* (BMNH 1882.11.15.21 and 1882.11.15.26), collected by Alphonse Forrer, are recorded from Ciudad (=La Ciudad) in the Durango highlands where the subspecies *pulchrilatus* occurs; Forrer also obtained BMNH specimens at Ventanas (=Villa Corona) in a subtropical habitat in a large barranca that is reached by trails and pack animals in about five hours from La Ciudad. The two BMNH specimens of *collaris* are doubtless from lower elevations, either along the trail to, or at, Ventanas (the problem of mixup of localities along this trail is discussed by Conant, ms).

Geographic variation seems to occur in the degree of black spotting on the first three white dorsal scale rows; black marks, however, almost always occur on the adjacent edges of the ventrals and scales of the first dorsal row. Specimens from Jalisco and northward usually have black marks irregularly arranged on the adjacent edges of scales of the first and second and second and third scale rows, whereas snakes from Michoacán and southward usually have these black spots reduced to specks, or in some cases they are indistinct and virtually lacking (see variation in Fig. 3). There seems to be no corresponding north-south variation in ventral and caudal counts. Of geographic interest, however, is a high frequency of seven supralabials in the state of Oaxaca (6 of 22 counts, or 27.3%).

Smith (1942:104) described *Thamnophis vicinus* from the highlands of Michoacán, and distinguished it from *Thamnophis cyrtopsis* by the absence of a pale middorsal stripe. Subsequent workers considered *vicinus* a pattern phase and junior synonym of *crytopsis* (see discussions by Bogert and Oliver, 1945:358-359; Milstead, 1953:349-350, 357; Duellman, 1961:114-115). This logical interpretation, however, is still largely theoretical and subjective; more specimens and further study are necessary to determine the status of *vicinus.* If *vicinus,* is assumed to be a pattern phase of *cyrtopsis,* it is necessary to place *vicinus* as a synonym of either *collaris* or *pulchrilatus.* But because *vicinus* has a dorsal pattern different from both *collaris* and *pulchrilatus,* and because all three forms occur in the same general area, it is somewhat questionable whether *vicinus* is a synonym of *collaris* or *pulchrilatus.* Based on Smith's data *(loc. cit.)* and the examination of one paratype of *vicinus* (UI 23435), the characteristics of *vicinus* most closely resemble those of *collaris* (caudal counts are most like *pulchrilatus*); specimens of *vicinus* also are recorded from the same locality (Morelia) as specimens of *collaris* (none of *pulchrilatus* are from same localities as specimens of *vicinus*). For the moment, I consider *vicinus* a synonym of *collaris.*

*Tropidonotus collaris* Jan, 1863, is the earliest name for the black-necked garter snakes in the coastal lowlands and subtropical highlands of western Mexico. That name, however, has not been used in scientific literature for over 50 years (last used by Cope, 1900:1062), and *collaris* thus is a *nomen oblitum* and unavailable according to the 1961 Code of International Nomenclature (Article 23b). It would seem then that the only junior synonym available, *vicinus,* should be used instead of *collaris.* For the reasons given below, however, I feel justified in using *collaris.*

Owing to published criticisms concerning the wording of Article 23(b) relative to *nomina oblita* (see Smith and Long, 1966, and references therein), I wrote Dr. Hobart M. Smith for his advice, to which he replied "I would urge that you use *collaris* and *pulchrilatus* if they happen to be applicable to either of the distinct populations you intend to recognize. These names are not really *nomina oblita,* for I am absolutely certain that the Commission did not intend for the definition of a *nomen oblitum* to come out as it did in the 1961 version of the Code. I have checked this with a sufficient number of those involved so that I am sure the definition would be more like this: a name *at whose expense* a junior synonym has been used for a period of at least fifty years prior to discovery of the error. Neither name qualifies by this definition, which is the only sensible one for a *nomen oblitum.* Regardless of definition, I have just been informed by the Commission's office that the *nomen oblitum* rule will no longer be invoked in any actions by the Commission until the matter can again be considered at the next International Congress of Zoology."

*Range.*—In western Mexico, the subspecies *collaris* occurs in the coastal lowlands, and on the west-facing slopes of the Sierra Madre to elevations slightly exceeding 6000 feet. Individuals of *collaris* also occur inland in the lowland tropical habitats of the numerous large barrancas that dissect the Sierra Madre. In southern Sinaloa and adjacent southwestern Durango, the habitats vary from thorny scrub forest, and tropical deciduous forest, to upper arid or mixed boreal-tropical (cloud forest) associations at the highest elevations.

In Mexico, in general, *collaris* seems to be characteristic of tropical or subtropical habitats, occurring in lowlands and in highland areas to elevations near 7000 feet (Zacualtipan, Hidalgo). For this study, 121 specimens of *collaris* have been examined from the states of Chiapas, Chihuahua, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Oaxaca, Sinaloa, Sonora, Veracruz, and Zacatecas (Fig. 6). Localities and specimens are:

**Chiapas:** Fenix, 3 mi. NW Monserrate (UI 6328). **Chihuahua:** Urique (KU 56233-35, 63739-40); 3 mi. NE Temores (KU 51926). **Durango:** 1.6 mi. E Sinaloa-Durango state line (LACM 7182); Huazamota (USNM 46482); "Durango" (USNM 8066, see page 61); La Ciudad (BMNH 1882.11.15.21, 1882.11.15.26, locality in error, see page 61); 4 mi. NE Mezquital (MSU 4435-36); 8 mi. N Mezquital (MSU 4434). **Guanajuato:** 4 mi. Acámbaro (UI 23413); Irapuato (UI 35059-61); "Guanajuato" (USNM 9892, 14434, 26147-48). **Guerrero:** vicinity *Chilpancingo* (KU 23797-98, UI 35014); 7 mi. E Chilpancingo (UI 23426); Omilteme (UI 23423). **Hidalgo:** S Zacualtipan (UI 23417); 5 mi. S Zacualtipan (UI 23422). **Jalisco:** Guayavas (LACM 1826); Rancho San Antonio, near Santa Clara (LACM 1824-25); Rancho El Rodeo, near San Marcos, Sierra de Ixtlán (MVZ 56318); Sierra de Cuale (KU 73631, 73633, 73652); 3 km. NE Talpa de Allende (KU 73629-30). **México:** Nochitongo Ditch, 30 mi. N Mexico City on Mex. Central Railroad (USNM 19003). **Michoacán:** Morelia (UI 23414); near Temaxcal, about 20 km. E Morelia (UI 23435, paratype of *vicinus,* formerly EHT-HMS 15897); Los Reyes (USNM 46463); Tacícuaro (USNM 110783). **Morelos:** 10 mi. NE Cuernavaca (UI 23416); Campo Agrícola, Progreso (UI 26062-65). **Oaxaca:** Cerro San Felipe (UI 52972, 53110-12); Huajuapan (USNM 46605); Cerro Pecho Blanco, Juchitán (UI 37184); San Felipe del Agua (UI 46762-63; Juquila Mixes (UI 52537); Oaxaca (UI 23424-25). **Sinaloa:** Rosario (USNM 46457); 3.8 mi. N La Cruz turnoff on Mex. Hwy. 15 (LACM 7172); 5.6 mi. W Mex. Hwy. 15 on La Cruz turnoff (LACM 7174); 13.6 mi. S Los Mochis turnoff on Mex. Hwy. 15 (LACM 7177); 29 mi. N los Mochis (KU 67725); 1 mi. E Santa Lucía (KU 40349, MSU 567); 2.2 km. NE Santa Lucía (KU 78923-24); 19.2 km. NE Santa Lucía (KU 78925-29); El Batel, 70 km. NE Mazatlán (MVZ 44704); Copala (MVZ 76568); 6.4 mi. S Mazatlán (CAS 95755); 0.7 mi. S. Terreros (LACM 7184); 4.1 mi. N Terreros (LACM 7176); 15.7 mi. S Terreros (LACM 7175); 5 mi. SW El Palmito (KU 75632-33, 80761); 8 mi. W El Palmito (RGW 2394); San José del Oro (KU 83413); 4.2-6.9 mi. S Culiacán (LACM 7178-80, 7183); 68.7 mi. N Cuiliacán (LACM 7173); 16.9 mi. S Culiacán (LACM 7181); Costa Rica, 16 mi. S Culiacán (UI 34903-13); El Dorado (UI 46961-71); 1 mi. NE El Fuerte (UI 40356). **Sonora:** 22.5 mi. NW Navajoa (UI 40357); Alamos (MVZ 66207); 12 mi. SE Alamos (RGW 2887); stream above Alamos, on Sonora-Chihuahua border (MVZ 74194). **Veracruz:** "Orizaba" (USNM 30496); "Mex. plateau, Mirador - Veracruz state" (USNM 25038). **Zacatecas:** Hacienda de San Juan Capistrano (USNM 46423).

### *Thamnophis cyrtopsis pulchrilatus* (Cope), new combination

*Eutaenia pulchrilatus* Cope, Proc. Amer. Philos. Soc. (for 1884), 22:174, 1885.

*Thamnophis cyrtopsis cyclides* Smith (in part), Copeia, 1951 (2):140, 1951.

*Type and type locality.*—Holotype by monotypy, USNM 9899, "one specimen from Dr. Dugès; locality uncertain but probably Guanajuato."

*Description of holotype.*—Cope's original description of *pulchrilatus* (1885:174) agrees with specimens here assigned to *pulchrilatus* except for his statement that, "There are no spots below the lateral light line, either on the neck or elsewhere." Later (1900:1062), Cope modified the type description mentioning that "There are sometimes spots below the lateral light line on the neck, due to interruptions in the lateral dark stripe."

The holotype of *pulchrilatus* (Fig. 4), bearing metal tag number 9899, is a female, with a body approximately 370 mm in length and a tail measuring 104 mm, 19-19-17 scale rows, 157 ventrals, 70 caudals,

Figure 4. Holotype of *Eutaenia pulchrilatus* Cope, 1885 (= *Thamnophis cyrtopsis pulchrilatus*), from "probably Guanajuato." Photograph by Ralph W. Axtell.

7 supralabials, 10 infralabials, 3 postoculars, 1-2 temporals, and with the 3rd and 4th supralabials entering the orbit. The supralabial sutures are marked with black pigment that reaches the edge of the lip in most cases; the infralabials lack black, except between the last two. Most scales have been sloughed off. A black nuchal collar is faintly interrupted by narrow median pale streaks that extend to the parietals. The middorsal stripe is scalloped and confined to the vertebral row. The dorsolateral area consists of a checkerboard pattern of black spots the length of the body; the median, keeled areas of each scale in the black spots are pale, producing a prominent narrow-lined effect. The pale lateral stripe occupies the adjacent halves of the second and third scale rows. The ventrolateral stripe is brown (where scales are not sloughed) with two distinct, non-alternating rows of black marks. The belly is immaculate except for occasional small black marks laterally on the anterior edges of some ventral scales.

*Description.*—The top of the head is dark brown or black, and often does not contrast with the black collar. The nuchal blotches are fused forming a black collar that occasionally may be partly interrupted, and it is indented posteriorly where the slightly expanded middorsal stripe terminates. The black collar often is confluent with the black dorsolateral areas. The pale middorsal stripe, which has scalloped edges, is confined to the vertebral scale row, but occasionally covers small parts of the adjacent rows. There are seven supralabials, rarely eight, having thin black lines or spots on the labial sutures. The black color usually is broadest on the suture between the sixth and seventh supralabials. The infralabial sutures lack black except for a small black mark that usually occurs on the suture between the last (ninth and tenth) infralabials. The dorsolateral area between the pale middorsal and lateral stripes is black, or brown, having an obscure checkerboard pattern of black spots the length of the body. The pattern is most

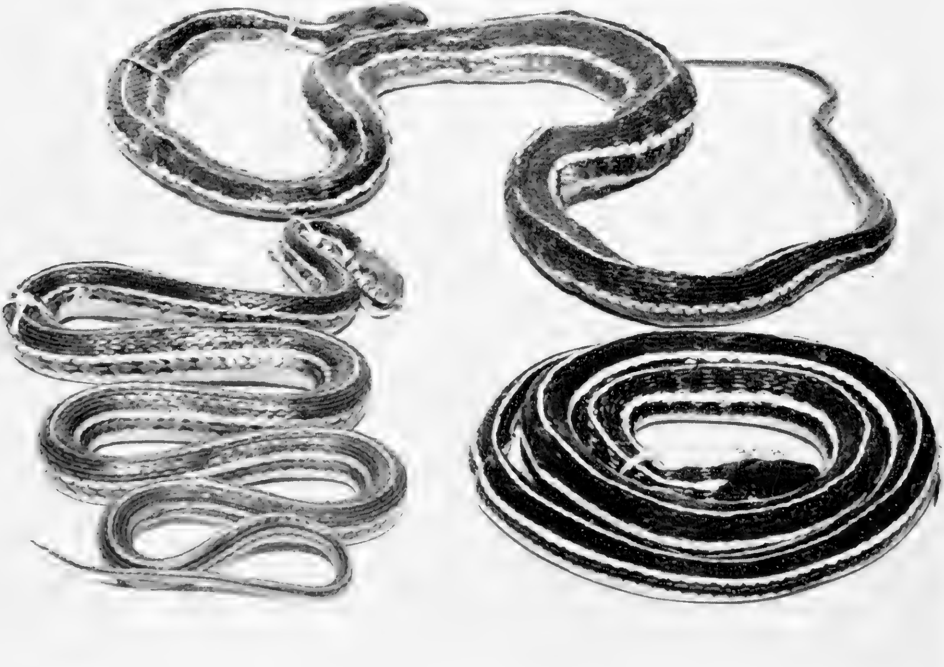

Figure 5. *Thamnophis cyrtopsis pulchrilatus* showing variation in pattern—upper center, USNM 46432 from Las Vigas, Veracruz; lower left, UI 23420 from "where to Chinapa branches," Michoacán; lower right, RGW 3718 from Hacienda Coyotes, Durango. Photograph by Isabelle Hunt Conant.

distinct in preserved specimens having sloughed scales. Dark scales often have contrasting pale keels that stand out as narrow, interrupted, light lines, and parts of some scales (and skin between scales) may be flecked with white. The keels and other parts of sloughed scales show pale flecks. The dark ventrolateral stripe below the lateral light stripe, if not mostly black, has two prominent rows of paired black spots (one above the other); the spots of each pair may be fused into hour-glass shaped marks, or fused into a single black spot. The body pattern of *pulchrilatus* is illustrated by Duellman (1961:115, fig. 10A). The specimens shown in Figure 5 are representative of *T. c. pulchrilatus.*

Coloration of a live female (body length 430 mm; RGW 3718 from Hacienda Coyotes, Durango) is as follows: top of head black, with tip of snout brown; nuchal collar black; middorsal stripe orange-yellow; dorsolateral areas black, with inconspicuous brown keels on some scales; lateral stripe yellow on neck, white elsewhere; ventrolateral stripe mostly black with brown flecks aligned to form narrow line posteriorly, but alternating with black spots anteriorly; sides of head and underside of head and neck, pale yellow; belly pale blue-white, having pale yellow on posterior margins of ventrals and tending to form midventral line, especially on tail; iris black and orange-brown; tongue red, black-tipped.

Among 31 individuals, the number of ventrals averages 162.8 (151-173), and in 27 individuals, the number of caudals averages 79.4 (68-94). The sex of several specimens was not determined. Ventrals in 15 males average 164.6 (157-173), and in 12 females 162.7 (151-170). Caudals in 13 males average 82.5 (76-94), and in 10 females 76.1 (68-86). Supralabials counted on each side of the head are seven (95.4%), rarely eight; one specimen (USNM 110780, from Tacícuaro, Michoacán) is unusual in lacking all the sutures (all supralabials fused), except for the suture between the second and third labial on both sides of the head.

*Remarks.*—Geographic variation occurs in the darkness of the dorsolateral area and ventrolateral stripe. Snakes from high elevations in the Sierra Madre Occidental (Durango) and Sierra Madre Oriental (Veracruz and Puebla) have almost solid black dorsolateral and ventrolateral areas, whereas most snakes from the Trans-Mexican Volcanic Belt Michoacán) have paler ground colors and more conspicuous patterns (see Fig. 5). The ground color of one specimen from Morelos in the Volcanic Belt is black, and the difference in pattern is perhaps correlated with altitude (black at highest elevations, paler at lower elevations). Conant (1963:494) mentioned some of the black individuals from Durango.

Among eight specimens from Tacícuaro, Michoacán, seven are *pulchrilatus* and one a *collaris:* none shows characteristics of both subspecies. The one specimen of *collaris* probably is from a different area and lower elevation than the seven *pulchrilatus.* Of seven snakes recorded from "Guanajuato" (city or state unknown), four are *collaris* and three are *pulchrilatus* (including the holotype). The exact geographic provenance of these seven snakes is unknown. Cope (1879:266) listed one of the snakes, USNM 9892, from Guadalajara, and Dr. Edward W. Nelson believed that at least some of Alfred Dugès' specimens sent to the USNM "labeled as coming from Guanajuato, . . . were given him by students and that the specimens may not have come from that locality" (Kellogg, 1932:8).

*Eutaenia pulchrilatus* Cope, 1885, is the earliest and only name (senior synonym) available for this recognizable population, but the name has remained unused in the scientific literature for over 50 years (last usage by Cope, 1900:1062). If the wording of Article 23(b) is to be rigidly construed, the name is a *nomen oblitum* according to the 1961 International Code of Zoological Nomenclature. The name *pulchrilatus,* however, is employed because there is no junior synonym available, and because of criticism and probable revision of Article 23(b) (see page 62 of present report concerning *nomina oblita*).

*Range.*—In Durango, the subspecies *pulchrilatus* occurs in the highest parts of the Sierra Madre Occidental in the boreal, nontropical, pine-oak forest, and, judging from other records, *pulchrilatus* is also found in corresponding habitats in the Sierra Madre Oriental of eastern Mexico and the interconnecting Transverse Volcanic Range or Cordillera Volcánica across southern Mexico. In Mexico, *pulchrilatus* seems to be characteristic of mountainous pine-oak regions at elevations exceeding a general level of 7000 feet. Some of these regions may be isolated. In this study 33 specimens have been examined from the states of Durango, Guanajuato, México, Michoacán, Morelos, Nayarit, Puebla and Veracruz (Fig. 6). Localities and specimens are:

**Durango:** 2 mi. NE El Salto (MVZ 67426); 3 mi. E El Salto (CAS 91855); Hacienda Coyotes (RGW 3718); 1.5 mi. W San Luis (MSU 562-64); Rancho Las Margaritas, 28 mi. E and 17 mi. W Vicente Guerrero (MSU 559, 561, 578). **Guanajuato:** "Guanajuato" (USNM 25363, 14433). **Mexico:** near Zitácuaro, 2 mi. S San Martín (UI 23411-12); Villa Victoria (UI 23415); "Valley of Mex and Toluca" (USNM 32279-80). **Michoacán:** 17 mi. W Jiqualpan (AMNH 87570); "where road to Chinapa branches" (UI 23420-21); Tacícuaro (UI 23418-19, USNM 110777-81). **Morelos:** 2 mi. W Huitzilac (KU 61179). **Nayarit:** Santa Teresa (USNM 46420-21). **Puebla:** Totalco, San Antonio Limon (UI 23427); Río Octapa, 2.5 mi. NNE Teziutlán (AMNH 88794). **Veracruz:** Las Vigas (USNM 46432); 2 km. E Las Vigas (KU 25901).

### *Comparisons and Relationships*

The populations recognized in this paper—*cyrtopsis, collaris,* and *pulchrilatus*—are subspecifically related; they are distinguished from one another by combinations of characteristics, and they show intergradation. The geographic distribution of the specimens examined is shown in Figure 6.

Ventral and caudal counts overlap; ventral counts show a transition from the highest counts in *cyrtopsis,* through intermediate counts in *pulchrilatus,* to the lowest counts in *collaris,* whereas the caudal counts are

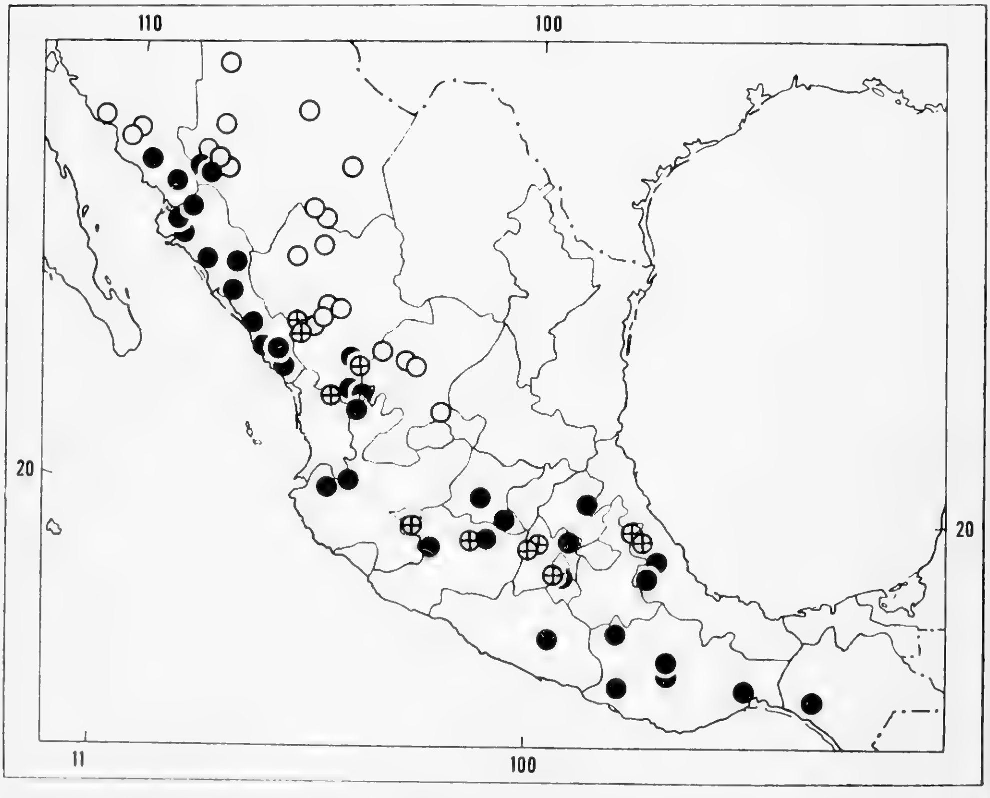

Figure 6. Map of Mexico showing geographic distribution of specimens examined of three subspecies of *Thamnophis cyrtopsis*—*T. c. cyrtopsis*, open circles; *T. c. collaris*, solid circles; *T. c. pulchrilatus*, crosses in circles. Intergrades are assigned to the subspecies they most closely resemble. Specimens representing localities a short distance apart share the same circle.

highest in *collaris,* intermediate in *cyrtopsis* and lowest in *pulchrilatus.* Four principal distinguishing characters—nape and ventrolateral pattern, number of supralabials, and infralabial markings—occur in different combinations in the three subspecies. The subspecies *collaris* and *pulchrilatus* share two characters (black collar and black lacking on infralabial sutures) not found in *cyrtopsis,* and seem more closely related to each other than to *cyrtopsis.* The subspecies *pulchrilatus* possesses one character in common with *cyrtopsis* (paired spots in ventrolateral stripe), and *cyrtopsis* has one character possessed by *collaris* (eight supralabials). The subspecies *collaris* and *pulchrilatus* each have one character not shared with *cyrtopsis* (dark ventrolateral band lacking with irregular arrangement of black spots in *collaris*, and seven supralabials in *pulchrilatus*). The most distinct subspecies seems to be *cyrtopsis,* for it possesses two characters shared by neither *collaris* nor *pulchrilatus* (blotches on nape and black infralabial sutures). The subspecies *cyrtopsis* and *collaris* possibly attain a larger maximum size than *pulchrilatus.* The largest *collaris* is about 800 mm, and the largest *cyrtopsis* about 702 mm, whereas the largest *pulchrilatus* is about 560 mm in body length.

### *Intergradation*

Some specimens have characteristics indicating intergradation. In Durango, intergradation between *cyrtopsis* and *pulchrilatus* is expected on the high east-facing slopes of the Sierra Madre where *cyrtopsis* of the *plateau* and foothills is replaced by *pulchrilatus* in the pine-oak forest at the higher elevations. Two specimens from 22 miles WSW Ciudad Durango, Durango, taken at about 7500 feet elevation, suggest that intergradation between *cyrtopsis* and *pulchrilatus* occurs in that region; one specimen (CAS 87349) is referable to *cyrtopsis,* but the other (CAS 87356) is most like *cyrtopsis* although it resembles *pulchrilatus* in having seven supralabials (right side only), a nuchal collar, black dorsolateral areas, and in having the paired black spots of the ventrolateral band larger than those in *cyrtopsis.*

In western Mexico, contact between *cyrtopsis* and *collaris* seems to occur in highland areas where the tropical west-facing slopes merge with the temperate east-facing slopes and there is no interposition of a boreal pine-oak forest, and also in the numerous tropical barrancas and canyons that dissect the Sierra Madre. Five specimens (KU 56233-35, 63739-40) from Urique in a large barranca in western Chihuahua are most like *collaris,* but resemble *cyrtopsis* in having a pale brown ventrolateral stripe with paired black spots; the black collar is partly interrupted in three specimens, and the middorsal stripe notably expanded just behind the collar in two specimens.

In western Mexico specimens of *collaris* often show paired black spots on the first scale row like *cyrtopsis,* but in *collaris* the ventrolateral brownish stripe is lacking. Some specimens of *collaris* having ventrolateral patterns resembling *cyrtopsis* occur in areas of expected intergradation. Among three *collaris* from near Mezquital in the shallow tropical valley of the Río Mezquital in southwestern Durango, one (MSU 4434) has paired ventrolateral black spots (some fused) on the anterior part of the body. Another specimen (KU 83413) from San Jose del Oro, Sinaloa, has a partly divided collar and many ventrolateral black marks paired as in *cyrtopsis;* near El Palmito, Sinaloa, at an elevation of 6100 feet, two of three specimens (KU 75633, 80761) resemble KU 83413, except that the collar is uninterrupted in 80761.

Northward in coastal regions of Sonora, intergradation between *cyrtopsis* and *collaris* occurs near Ciudad Obregón. One specimen (LACM 7171) from 3.5 miles N Ciudad Obregón is most like *cyrtopsis,* but it has dark brown dorsolateral areas with black spots throughout the length of the body, and a ventrolateral pattern (some black spots paired as in *cyrtopsis*) like *collaris.*

Two specimens of *collaris,* from the states of Veracruz (USNM 25038) and México (USNM 19003), have ventrolateral patterns in which the spots are mostly or partly arranged in two rows as in *cyrtopsis* and *pulchrilatus.* One specimen of *collaris* from Guanajuato (USNM 23413) seems to be intermediate in having 7-8 supralabials and paired ventrolateral spots as in *pulchrilatus.*

Most Mexican specimens of the three subspecies of *Thamnophis cyrtopsis,* with further aid provided by the descriptions and illustrations, can be readily identified by the following combinations of characters in the key below:

1. Eight supralabials; black collar or two separate blotches on neck; ventrolateral stripe pale brown or gray or absent 2

1a. Seven supralabials; black collar indented behind and usually confluent with black dorsolateral areas; ventrolateral stripe, on first scale raw below pale lateral stripe, black or brownish with black spots arranged in pairs (one above the other); infralabial sutures not black. *pulchrilatus* (highlands in boreal pine-oak forest)

2. Two black blotches on neck separated by middorsal stripe; ventrolateral stripe pale brown, having small black spots arranged in pairs (one above the other); dorsolateral area, except for spots on neck, mostly uniform brown; infralabial sutures often black. *cyrtopsis* (plateau and adjacent foothills)

2a. Black collar indented behind where middorsal stripe terminates; first three scale rows whitish (dark ventrolateral stripe lacking), either mostly uniform, or having small scattered black marks with the largest on the lower edge of the first scale row and the adjacent edge of the ventrals; dorsolateral area mostly uniform brown or with a black-spotted checkerboard pattern; infralabial sutures not black. *collaris* (lowlands and highlands in tropical habitats)

### *Discussion*

The recognition of *pulchrilatus* and *collaris* represents a return to the nomenclature used in the mid to late 1800's. Cope (1885: 173), in a key prefacing the description of *pulchrilatus*, distinguished the previously named *collaris* as having a "lateral stripe not defined below" from *pulchrilatus* as having a "lateral stripe bordered below by a brown stripe." The presence or absence of this dark ventrolateral stripe is one of the principal characters distinguishing *collaris* from *pulchrilatus*. Cope (loc. cit.) also noted that the scales of the first dorsal row were keeled in *collaris* and smooth in *pulchrilatus*, but I am unable to ascribe any taxonomic value to this character. Later, Cope (1887:73) noted that *collaris* was, "Perhaps the same as *E. cyrtopsis*." Cope was the last person to recognize *pulchrilatus* (1900:1062) and *collaris* (*op. cit.*:1051), but he misapplied the latter name. Both Boulenger (1893-209) and Ruthven (1908:158, footnote) treated *pulchrilatus* and *collaris* as synonyms in their accounts of *Tropidonotus ordinatus* Var. *eques* and *Thamnophis eques*, respectively. Both *pulchrilatus* and *collaris* have since remained indistinguishable from *eques* (=*cyrtopsis*); Ruthven (*op. cit.*:162), however, noted that *pulchrilatus* was based upon specimens having seven supralabials, a distinctive feature of *pulchrilatus*.

Study of neotropical garter snakes was revitalized by Smith (1942), who recognized a northern race, *eques cyrtopsis*, and a southern race, *eques eques*. Later, Smith (1951) discovered that the name *eques* is applicable to a different species of garter snake, whereupon the northern race became known as *cyrtopsis cyrtopsis* and the southern race as *cyrtopsis cyclides*. This arrangement has been utilized by subsequent authors. The present study, however, demonstrating that the name *cyclides* has been misapplied, has necessitated reviving the names *pulchrilatus* and *collaris* from the synonymy of *cyclides*, which was a composite of those two forms as visualized by Smith (1942) and Milstead (1953).

The name *sumichrasti* has been linked subspecifically with *cyrtopsis* (Milstead, 1953: 365). Rossman (1965), however, demonstrated that the name *sumichrasti* has long been misapplied, and is properly identified with a little-known, montane species. None of the specimens examined by me are nonstriped or obscurely striped, a pattern ascribed to *sumichrasti*, and many snakes previously referred to *sumichrasti* from southern Mexico are perhaps *T. cyrtopsis collaris*. Specimens examined from Guerrero and Oaxaca and designated as intergrades between *cyclides* and *sumichrasti* by Milstead (1953:370) are herein assigned to *collaris;* he also referred specimens from the city of Oaxaca to *sumichrasti* (*op. cit.*:368), a locality from which I examined specimens of *collaris*. *Thamnophis sumichrasti* probably is ecologically sympatric with *T. cyrtopsis;* Rossman's comments *(loc. cit.)* suggest that *T. sumichrasti* and *T. c. collaris* occur together (both from near Zacualtipan, Hidalgo, and Orizaba, Veracruz; see also Ruthven, 1908:163, 165) and that *T. c. pulchrilatus* and *T. sumichrasti* are found in the same place (both from near Teziutlán, Puebla). In the Mexican highlands, it is not unusual to find several sympatric species of *Thamnophis;* five different kinds of garter snakes can be found together in the Durango pine-oak highlands, and three of them closely resemble one another.

*Thamnophis cyrtopsis collaris* resembles the population in the Tepalcatepec Valley of Michoacán known as *Thamnophis cyrtopsis postremus,* especially in lacking the dark stripe on the first dorsal row of scales. However, *collaris,* seems to differ from *postremus* (data from Duellman, 1961:116-117) in having more ventrals (average 155.0 and not fewer than 143 in *collaris;* average about 141.5 and not exceeding 151 in *postremus*) and caudals (average 92.5 and no fewer than 76 in *collaris;* average about 71.0 and not exceeding 79 in *postremus*), in having dorsolateral rows of large black spots, instead of small ones (contrast two illustrations in Duellman, *op. cit.*:115, fig. 10A and B), and in having scattered black spots and flecks on the first three, whitish dorsal scale rows (black markings small or usually lacking on first three rows in *postremus*), In the two last-mentioned characteristics, however, some specimens of *collaris* resemble *postremus.* Specimens of *collaris* may have the spots in the dark dorsolateral and pale ventrolateral areas reduced in size and distinctness, the patterns corresponding to remarks concerning *postremus* by Duellman (1961:116), who stated that some specimens have "small dark flecks on the first row of dorsal scales," and by Smith (1942: 109), who, in the type description of *postremus,* wrote that the "outer row of dark spots on first and second scale rows [are] greatly reduced, generally scarcely visible." Fouquette and Rossman (1963:197-198) also mentioned the resemblance in pattern of Oaxacan specimens of *T. cyrtopsis* and *postremus.*

The recognition of *pulchrilatus* and *collaris* brings to five the number of subspecies of *Thamnophis cyrtopsis.* These are as follows:

*Thamnophis cyrtopsis collaris* (Jan)—east and west coast of Mexico in tropical lowlands and highlands.

*Thamnophis cyrtopsis cyrtopsis* (Kennicott)—southwestern United States and Mexican plateau.

*Thamnophis cyrtopsis ocellata* (Cope)—Edwards Plateau of central Texas.

*Thamnophis cyrtopsis postremus* (Smith)—Tepalcatepec Valley of Michoacán.

*Thamnophis cyrtopsis pulchrilatus* (Cope)—highland mountainous areas in Mexico.

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August 30, 1966

# SKELETAL AGE CHANGES IN THE CHIMPANZEE[1]

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## ABSTRACT

The skeletons of thirty chimpanzees of known ages from birth through thirty-five years were examined for gross, radiographic, and microscopic changes that could be associated with age. Anthropometric measurements were taken, and standardized radiograms of the stripped bones were measured for correlation with age, sex, and constitutional variations.

The age ranges during which certain epiphyses were found in the process of fusion are presented. These data extend the ability to determine age in the chimpanzee by epiphyseal closure through adolescence into adulthood. Additional changes in the costal cartilages and sternal ends of the ribs, the pubic symphysis, and the inferior angle of the scapula cover the age period of late adolescence and young adult life. Changes in the microscopic structure and resorptive patterns of bone provide additional information regarding age that supplements gross and radiographic appearance.

As part of a long range investigation into the effects of age, sex, and constitutional variations on skeletal structure in the chimpanzee, age changes in the gross, radiographic, and microscopic structure of bone have been examined in thirty chimpanzees of known age from birth through thirty-five years. Routine anthropometric measurements were obtained on sixteen of these chimpanzees just prior to exsanguination at the Yerkes Laboratory of Primate Biology in Orange Park, Florida. These were standard measurements according to Martin (1928), Hooton (1946), and Hrdlicka (Stewart, 1952), except that they were made with the chimpanzees anesthetized and supine. A few special measurements were added to demonstrate specific relationships among anatomic areas and body regions.

After they were fixed in formalin, the stripped skeletons were sent to the Armed Forces Institute of Pathology, where the individual bones were X-rayed by standardized procedure.[3] These radiograms were ex-

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[1] The condensed form of a paper presented November 5, 1964 as part of a symposium on primates at the Tulane University Delta Regional Primate Research Center in Covington, Louisiana.

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[3] The stripped bones of each chimpanzee were placed on a cardboard cassette at a fixed distance of 42 inches from tube to cassette and radiographed in both anterior-posterior and lateral planes. Since anatomic structure was of primary interest rather than radio-density, exposure time varied with the size of the bones, but the basic 55 kilovolt and 50 milliampere settings of the machine remained constant. All radiographic metric comparisons were of measurements of radiographs made in this same standardized manner, but certain radiographic measurements were checked against comparable gross bone measurements to determine the amount of enlargement resulting from x-ray dispersion. Since the stripped bones were in contact with the cassette at their lowest point and less than four inches away from it at their maximum distance, enlargement was generally less than 5% even at the edges of the film.

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amined, and the state of epiphyseal closure was recorded. The long bones were measured from the radiograms to establish growth rates and differences in relative size. Diameters, widths, and cortical thicknesses were measured in addition to bone lengths. Since long bones derive most of their length from the metaphyseal growth plates, the inter-metaphyseal lengths were measured, as were the functional lengths between the articular surfaces of each long bone. Indices were devised that would show the ratios of long bone length to height, width and cortical thickness to length, and bone size to body weight. Skeletal structure was related to the anthropometry and ponderal index as well (Table 1).

After they were X-rayed, the bones were cut on a bandsaw into blocks appropriate for standardized microscopic sections. The ends of the major long bones were cut in a longitudinal plane to provide information about the metaphyseal growth plate, the articular cartilage and subchondral plate, and the cancellous bone. Ground cross-sections were made of the middle portion of the diaphyses of the major long bones to examine variations in the microscopic structure. In man, the cancellous bone undergoes changes related to age in the metaphyseal and epiphyseal ends of some long bones (Schranz, 1959) (Hansen, 1953-54), and there are microscopic changes in the structure of the mid-shaft area that have been well-correlated with age (Amprino and Bairati, 1936) (Jowsey, 1960) (Kerley, 1965).

Sections of the clavicle, ribs, vertebrae, pelvis, hand, and foot also were made. These were chosen to examine differences in bone growth and metabolism, and because they represent areas that have known variations in man. Vertebrae show differences in density with age in man (Broman, Trotter and Peterson, 1958) (Trotter, Broman and Peterson, 1959), and with sex (Trotter, Broman and Peterson, 1959) (Seale, 1959). The pelvis exhibits a high degree of sexual dimorphism in man (Boucher, 1957) (Hoyme, 1957) (Washburn, 1948); the pubic symphysis (Todd 1920-21) (Brooks, 1955) (McKern and Stewart, 1957) and sternal end of the clavicle (Todd and D'Errico, 1928) have variations that are correlated with age, as do the sternal ends of the ribs (McKern and Stewart, 1957). These gross and microscopic skeletal variations that have been correlated with age and sex in man serve as guide-posts for examining age changes in the chimpanzee, one of man's closest relatives, which should exhibit age variations similar to those found in man.

## RESULTS

Although the bulk of this research was designed as a long-term project that is in process, certain results are of immediate interest to researchers in primatology and can be presented for the first thirty chimpanzees of documented age in the larger series. These results will present the age ranges during which certain skeletal changes occurred in this series of thirty chimpanzees whose ages were recorded from birth.

Figures 1-4 show the rates of growth in length for the major long bones of the arm and leg from birth until well past the age

TABLE I.

*Anthropometric and Radiographic Indices*

Sitting height/stature
Stature/arm span
Thoracic index
Hip width/chest width
Abdominal/chest girth
Biacromial/sitting height

Femur length/stature
Femoral shaft width/length
Femoral cortex/length
Femoral shaft width/stature
Tibia length/stature
Tibial shaft width/length
Tibial cortex thickness/length
Tibial shaft width/stature
Clavicle/humerus length
Clavicle width/length

Forearm/upper arm girth
Lower/upper leg girth
Leg length/arm length
Thigh/lower leg length
Foot width/leg length
Hand width/arm length

Humerus length/stature
Humeral shaft width/length
Humeral cortex/length
Humeral shaft width/stature
Radius length/stature
Radial shaft width/length
Radial cortex thickness/length
Radial shaft width/stature
Bi-iliac/stature
Bi-iliac/bi-acromial

when growth in length has been completed. These measurements were made from radiographs of bones that had been disarticulated, stripped of most of the soft tissue, and include the bony parts of the epiphyses. They represent the maximum length of the bone on the radiographs and include the width of the metaphyseal growth plates. The rates

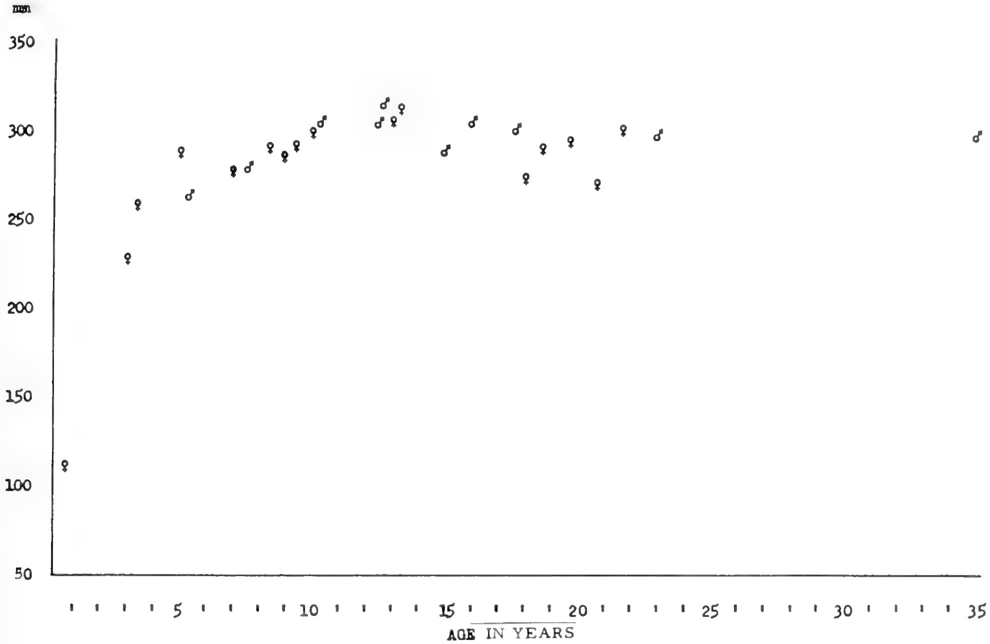

Figure 1. Rate of growth in overall length of the humerus.

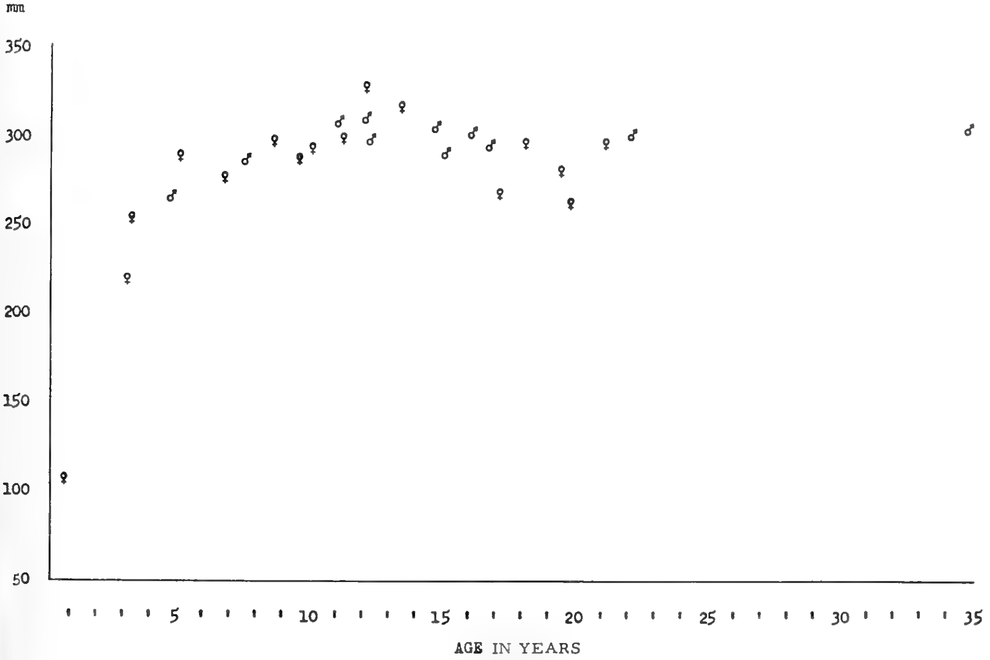

Figure 2. Rate of growth in overall length of the femur.

of growth in length level off at about ten years of age and there is little additional growth in length after age twelve. These results are in general agreement with those previously reported by Gavan (1953) from a study of anthropometric measurements of living chimpanzees. Some of the same chimpanzees measured by Gavan were included

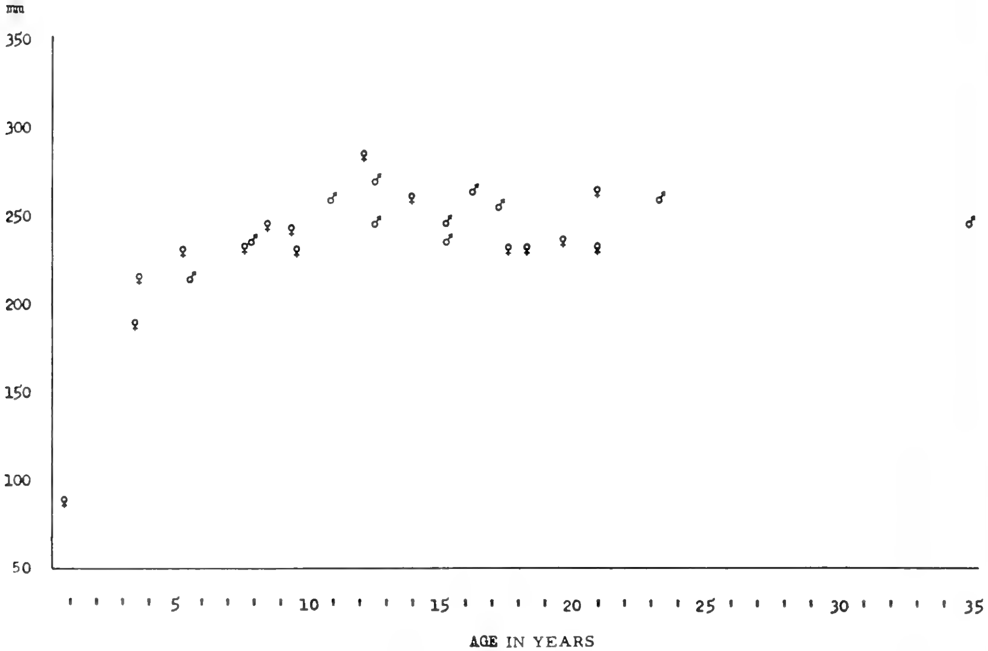

Figure 3. Rate of growth in overall length of the tibia.

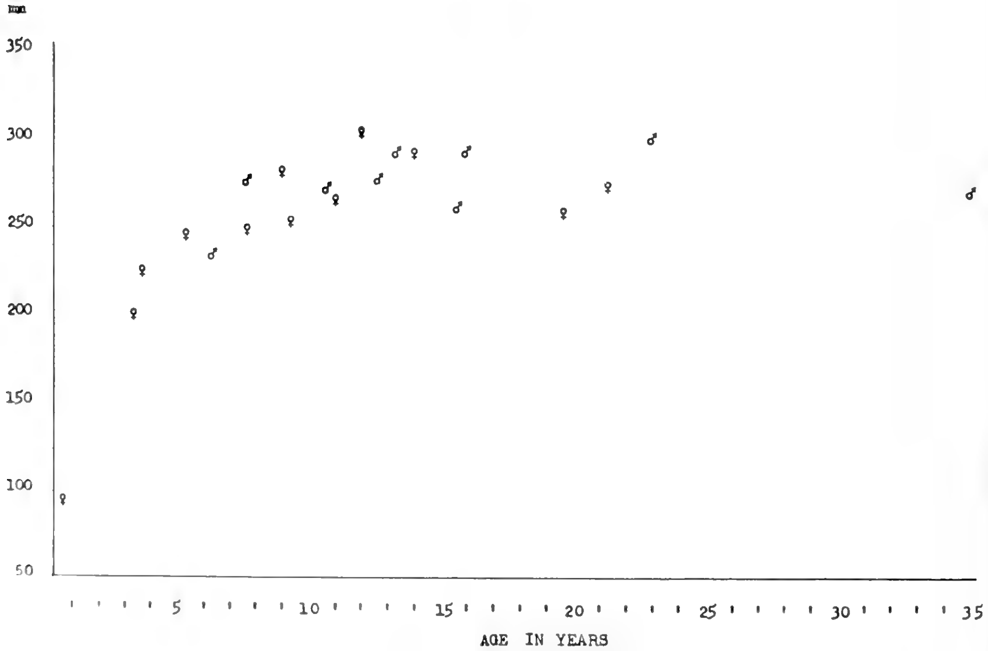

Figure 4. Rate of growth in overall length of the radius.

in the present study. However, they were measured at the time of death in this study at later ages than when Gavan measured them. In this report, growth rate curves were derived from a cross-sectional study of thirty chimpanzees rather than a longitudinal study of the continuing growth at periodic intervals in individual animals, as in Gavan's study. In both types of growth study the rates of growth are determined by plotting size against age. In the present study, the overall lengths of the major long bones were derived from radiographic measurements.

The ages at which various epiphyses fuse to the diaphyses of long bones and the segments of certain other bones fuse together were recorded within the limits of the sam-

TABLE II. AGES OF EPIPHYSEAL UNION

| AGE IN YEARS | 0 | | | | 5 | | | | | | 10 | | | | | | | 15 | | | | | | | 20 | | | | 25 | 30 | 35 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SEX | ♂ | ♂ | ♀ | ♀ | ♀ | ♂ | ♀ | ♂ | ♀ | ♀ | ♀ | ♀ | ♀ | ♂ | ♀ | ♀ | ♂ | ♂ | ♂ | ♂ | ♂ | ♂ | ♀ | ♀ | ♀ | ♀ | ♀ | ♂ | | | ♂ |
| EPIPHYSES & SEGMENTS | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| PROXIMAL HUMERUS | - | - | - | - | - | - | - | - | - | C | X | C | C | C | C | C | X | | X | C | X | X | X | X | X | X | X | X | | | X |
| DISTAL HUMERUS | - | - | - | - | C | C | C | X | X | X | X | X | X | X | X | X | X | | X | X | X | X | X | X | X | X | X | X | | | X |
| MEDIAL EPICONDYLE | - | - | - | - | - | - | C | C | X | X | X | X | X | X | X | X | X | | X | X | X | X | X | X | X | X | X | X | | | X |
| PROXIMAL RADIUS | - | - | - | - | - | - | - | - | - | C | X | X | X | X | X | X | X | | X | X | X | X | X | X | X | X | X | X | | | X |
| DISTAL RADIUS | - | - | - | - | - | - | - | - | - | - | - | C | C | C | X | C | X | | X | X | X | X | X | X | X | X | X | X | | | X |
| PROXIMAL ULNA | - | - | - | - | - | - | C | | - | X | X | X | X | X | X | X | X | | X | X | X | X | X | X | X | X | X | X | | | X |
| DISTAL ULNA | - | - | - | - | - | - | - | - | - | - | | C | C | C | X | C | X | | X | X | X | X | X | X | X | X | X | X | | | X |
| METACARPALS | - | - | - | - | - | - | - | - | - | X | | X | X | X | X | X | X | | X | X | X | X | X | X | X | X | X | X | | | X |
| PHALANGES | - | - | - | - | - | - | - | - | C | X | | X | X | X | X | X | X | | X | X | X | X | X | X | X | X | X | X | | | X |
| SCAPULAR BORDER | - | - | - | - | - | - | - | - | - | - | C | - | | C | C | - | C | | C | C | X | X | X | X | X | X | | X | | | X |
| ACROMIAL PROCESS | - | - | - | - | - | - | - | - | - | - | X | | | X | X | X | | | X | X | X | X | | X | X | | | | | | X |
| CORACOID PROCESS | - | - | - | - | | - | | - | - | X | X | | | X | X | X | | | X | X | X | X | | X | X | | | | | | X |
| STERNAL CLAVICLE END | - | - | - | - | - | - | - | | - | - | - | - | | - | - | - | - | | - | - | C | C | X | C | X | X | | X | | | X |
| STERNUM | - | - | - | - | - | | - | - | - | - | - | | | - | C | C | C | | C | C | C | C | C | C | C | | | | | | X |
| RIBS | - | - | - | - | - | - | - | | - | - | X | | | X | X | | X | | X | X | X | X | X | X | X | X | X | X | | | X |
| CERVICAL VERTEBRAE | - | - | - | - | - | - | - | - | - | - | | C | X | X | X | | X | | X | X | X | X | X | X | X | X | | X | | | X |
| THORACIC VERTEBRAE | - | - | - | - | - | - | - | - | - | C | - | C | C | C | X | C | C | | X | X | X | X | X | X | X | X | X | X | | | X |
| LUMBAR VERTEBRAE | - | - | - | - | - | - | - | - | - | C | - | C | C | C | X | C | C | | X | X | X | X | X | X | X | X | X | X | | | X |
| SACRUM | - | | - | - | - | - | - | - | - | - | - | - | C | C | C | C | C | C | C | C | C | C | C | C | C | C | C | C | | | X |
| ILIAC CREST | - | - | - | - | - | - | - | - | - | C | C | C | - | | C | - | C | C | C | X | X | X | X | X | X | X | X | X | | | X |
| TRI-RADIAL PLATE | - | - | - | - | - | - | C | - | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| ISCHIUM | - | - | - | - | - | - | - | - | - | C | - | C | - | C | X | C | X | C | C | X | X | X | X | X | X | X | X | X | | | X |
| FEMORAL HEAD | - | - | - | - | - | - | - | - | C | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| GREATER TROCHANTER | - | - | - | - | - | - | - | - | C | C | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| LESSER TROCHANTER | - | - | - | - | C | | | - | | C | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| DISTAL FEMUR | - | - | - | - | - | - | - | - | - | C | X | C | X | X | | C | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| PROXIMAL TIBIA | - | - | - | - | - | - | - | - | - | C | X | C | X | X | | C | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| DISTAL TIBIA | - | - | - | - | - | - | - | - | - | C | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| PROXIMAL FIBULA | - | - | - | - | - | - | - | - | - | C | X | X | X | X | | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| DISTAL FIBULA | - | - | - | - | - | - | - | - | - | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| CALCANEUS | - | - | - | - | - | - | - | - | | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| METATARSALS | - | - | - | - | - | - | - | - | - | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| PHALANGES | - | - | - | - | - | - | - | - | C | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | | | X |
| AGE IN YEARS | 0 | | | | 5 | | | | | | 10 | | | | | | | 15 | | | | | | | 20 | | | | 25 | 30 | 35 |

Explanation of symbols: - - epiphysis open C = epiphysis in the process of closing X = epiphysis completely closed ple from the examination of Roentgenograms of the stripped bones. Radiographic obseravtions were confirmed by histologic sections of the epiphyseal-metaphyseal areas in the long bones. The results are presented in Table II. The sequence of epiphyseal closure in this sample is similar to that reported by Schultz (1940). The distal end of the humerus begins to fuse around five years of age and is the first epiphysis to complete fusion. The proximal end of the ulna and the triradiate cartilage separating the three elements of the innominate begin fusing shortly afterwards. Some epiphyses, such as those in the hand, ankle, and foot, complete the process of fusion shortly after they begin it, while others, those of the proximal humerus and the iliac crest, may take several years to complete fusion. There appears to be relatively little variability in the age range during which fusion occurs in some areas, as in the elbow, while fusion in the epiphyses of the knee and proximal humerus occurs over a much longer time span.

The approximate ages of chimpanzees of unknown age can be determined by the data that have been published on age changes in dental eruption (Nissen and Riesen, 1964) and by the appearance of secondary ossification centers (Nissen and Riesen, 1949a, 1949b) (Schultz, 1956). The data that have been published permit the determination of age in the chimpanzee up to about eleven or twelve years—the same range covered by Gavan's growth study. The data presented in Table II extend the ability to determine age up through adolescence and well into adulthood.

Direct observation of radiographs of monkeys of various skeletal ages has shown that the costal cartilages of most monkeys, both New World and Old World, begin to calcify while deciduous dentition is still present.[4] The calcium is deposited in the center of the costal cartilages in the form of flat bars that almost connect the ribs and sternum. The process begins early in childhood in some monkeys. In man, the costal cartilages calcify in middle and old age, and in some aged humans the calcified cartilage has been resorbed and replaced by bone. When radiographs of the chimpanzee costal cartilages were examined, those of the older chimpanzees showed typical patterns of calcification (Figure 5). These patches of calcified cartilage became radiographically discernible as early as seventeen years of age, which is about fourteen years later than they appear in monkeys, and much earlier than calcification can be seen in the costal cartilages of man. The age distribution of discernible costal calcification in the chimpanzee is presented in Table III.

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[4] The skeletons of about 100 other primates of undocumented age including both Old World and New World monkeys were made available for study by the Delta Regional Primate Research Center of Tulane University. These have been x-rayed and histologic slides have been prepared for selected representative specimens. Not all of the radiographs or histologic slides of these other primates have been measured or analyzed yet, but it is apparent that several of the age changes described in the chimpanzee in this paper occur earlier in other primates while much of the deciduous dentition is still present and before many of the epiphyses have begun to fuse.

TABLE III.

RADIOGRAPHIC AGE CHANGES IN THE CHIMPANZEE

| AGE IN YEARS | 0 ' ' ' ' 5 ' ' ' ' 10 ' ' ' ' 15 ' ' ' ' 20 ' ' ' ' 25 ' ' ' ' 30 ' ' ' ' 35 |
|---|---|
| PUBIC SYMPHYSIS IN THE PROCESS OF FUSION | - - -- --- - --- ------- - --XXX X - X X |
| CALCIFICATION IN THE COSTAL CARTILAGE | - - -- --- - --- --- - -XXXX X XX |
| OSSIFICATION OF THE STERNAL RIB ENDS | - - -- --- - --- --- - --XXX - XX |
| SEX | ♀ ♂ ♀♀ ♀♂♀ ♂ ♀♀♀ ♀♀♂♀♂♀♂ ♂ ♂♂♂♀♀ ♀ ♀♀ ♂ ♂ |

\- No radiographic evidence of fusion, calcification, or ossification.
X Radiographic evidence of progressive fusion, calcification, or ossification.

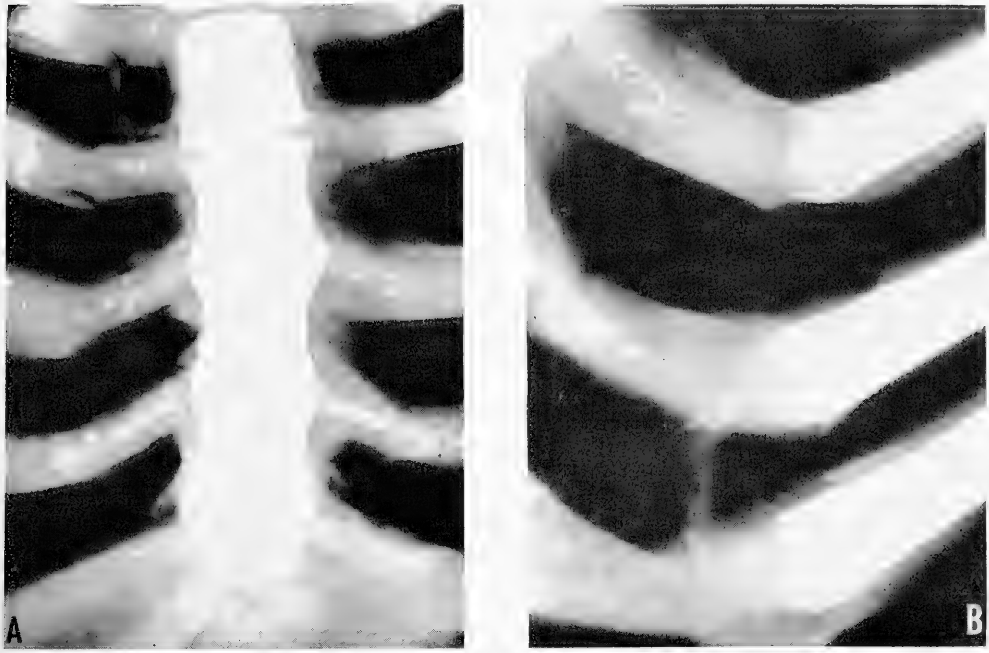

Figure 5. Age changes in the sterno-costal area. **A.** Calcification in the costal cartilage of an 18 year old female chimpanzee. **B.** Progressive ossification of the rib ends of a 21 year old female chimpanzee.

An additional change occurs in adult chimpanzees in the area of the sternal ends of the ribs that is also correlated with age. There is a continuation of ossification from the periosteal surface of the rib at the costo-chondral junction that produces a progressive deepening, or cupping, of the end of the rib. This is accompanied by ossification from the center of the costo-chondral junction which projects into the costal cartilage (Figure 5). The age distribution for radiographically discernible costo-chondral ossification follows the same basic pattern as the calcification of the costal cartilages with regard to age (Table III).

The two halves of the pubic symphysis begin to fuse at about eighteen years of age in the chimpanzee (Figure 6), and there is bony ankylosis across the upper third of the symphysis by age thirty-five. The ages at which this fusion can be seen both radiographically and microscopically are shown in Table III. In man, the two halves of the pubic symphysis do not normally fuse at any age, but in other animals, including many of the primates, the symphysis fuses over as much as half its length at a fairly early age. Symphyseal union in the chimpanzee has been noted before (Schultz, 1956), but the age at which fusion occurs has not been documented.

There are age changes in the microscopic structure of the mid-shaft area of chimpanzee long bones that are quite similar to those found in man (Kerley, 1965). Osteones increase in number and complexity of arrangement with the increasing age of the chimpanzee as they replace circumferential lamellar bone in the cortex. Osteoclasts burrow channels along the length of the bone through the circumferential bone beginning shortly after birth. These channels are gradually filled in turn with concentric layers of lamellar bone and become osteones. As the osteones become numerous, fragments of old osteones are left surrounding newer ones where osteoclastic resorption had removed portions of them. In old age, there is very little circumferential lamellar bone, and most of the cortex is composed of densely-packed osteones and fragments of old osteones.

The areas of the cortex that undergo intensive resorptive activity at any given time also vary with age. The resorptive channels that run longitudinally along the shafts of long bones and fill in with concentric lamellae to form osteones later are diffusely spaced throughout the thickness of the cortex in infancy and early childhood (Figure 4).

During late childhood and early adolescence in man, between 10 and 17 years of age, there is a concentration of resorptive channels in the peripheral part of the cortex near the periosteal surface, as a result of increased osteoclastic activity prior to the replacement of the remaining sheets of subperiosteal lamellar bone by osteones in late adolescence. This peripheral concentration of resorptive cavities can be seen in chimpanzee long bones between five and ten years of age. In the normal chimpanzee slides examined, from around eleven years until age thirty-five there is little cortical resorption and the cortex is rather homogeneously osteon bone that is more densely packed with osteones and fragments of old osteones as age increases.

Histologic age changes in resorptive patterns have been described in the long bones of the leg in man (Kerley, 1962), a close relative of the chimpanzee. The patterns of resorption are quite similar in both, except that the inner third of the cortex undergoes extensive resorption in man beginning about age sixty-five in males and earlier in females, whereas the oldest chimpanzee (age 35) in this series showed no evidence of medullary resorption. However, it is reasonable to predict that the same pattern of meduallary resorption might be present in more aged male or aging female chimpanzees. Comparable stages in the patterns of resorption are shown in Figure 7 for chimpanzee (E-H) and human (A-D) femurs.

There is relatively little change in proportion that can be related to age in the chimpanzee after about three years of age. The most notable exceptions are in the width of the hip and shoulder areas, the ratio of forearm to upper arm, and the relative thickness of the cortex in long bones. The clavicle continues to grow slightly after the humerus has completed its growth in length. The length of the clavicle was about 38% of the length of the humerus at three years of age and increased to 45% by age 22 in this series. In the hip region, the biiliac width increased from 76% of the length of the femur at one-and-a-half years of age to 96% by age twenty-two. The length of the forearm decreased from 106% of the length of the upper arm at one year of age to 95% by age twenty-three. The

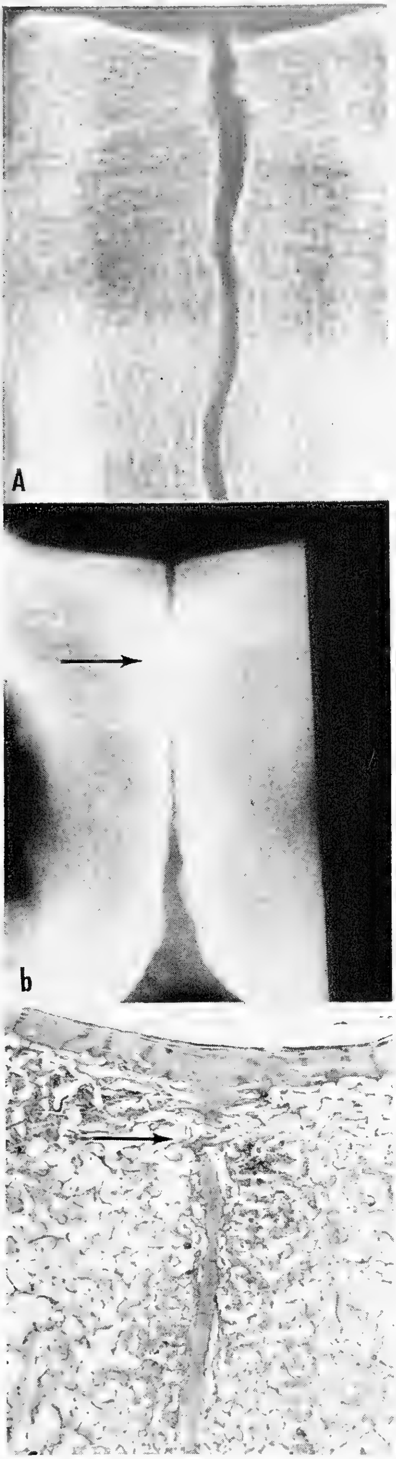

Figure 6. Fusion of the pubic symphysis. **A.** Radiograph of the pubic symphysis of a 14 year old male chimpanzee. **B.** Radiograph of the pubic symphysis of an 18 year old male chimpanzee. **C.** Histologic section of the pubic symphysis of a 35 year old male chimpanzee.

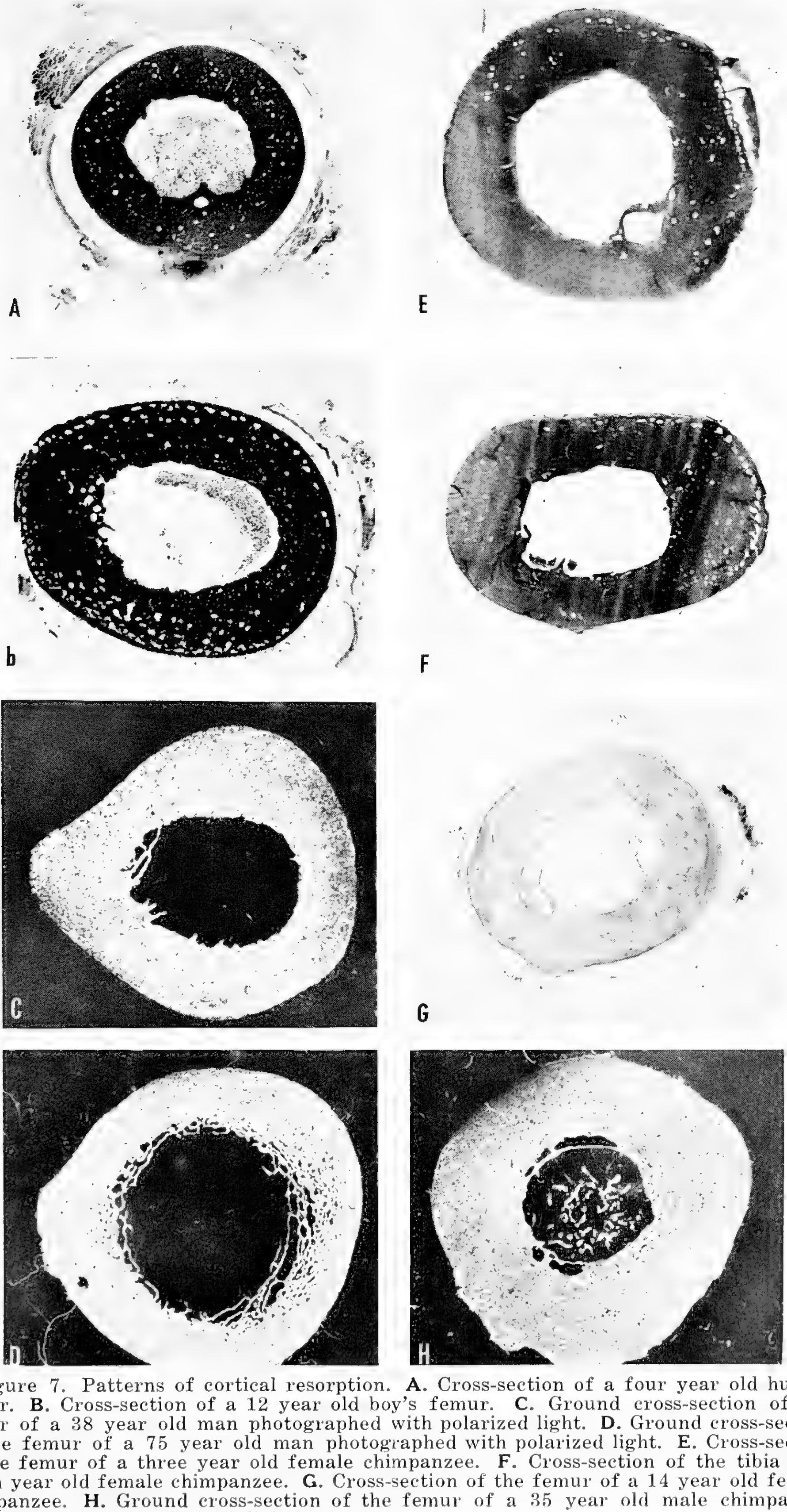

Figure 7. Patterns of cortical resorption. **A.** Cross-section of a four year old human femur. **B.** Cross-section of a 12 year old boy's femur. **C.** Ground cross-section of the femur of a 38 year old man photographed with polarized light. **D.** Ground cross-section of the femur of a 75 year old man photographed with polarized light. **E.** Cross-section of the femur of a three year old female chimpanzee. **F.** Cross-section of the tibia of a seven year old female chimpanzee. **G.** Cross-section of the femur of a 14 year old female chimpanzee. **H.** Ground cross-section of the femur of a 35 year old male chimpanzee photographed with polarized light.

lateral diameter of the midshaft of the major long bones of the arm and leg increased with age to adulthood. The relative lateral diameter of the mid-shaft of the femur, where the change was the most pronounced, increased from 7% of the total length of the femur at 3½ years of age to 10% by fourteen. From birth to three years of age the mid-shaft diameter decreased from 12% of the length at birth to 7% at three years, as the bones lengthened rapidly, and developed thin shafts.

There were rather minor differences in skeletal structure or proportions between male and female chimpanzees. As might be expected, the most notable differences occurred in the areas of the pelvis that are involved in parturition. The bi-ischial width as measured from radiographs is wider in proportion to the bi-iliac width in females, reflecting a relatively larger pelvic outlet than male chimpanzees have. In addition, the bi-iliac width is greater in proportion to the length of the femur in females than in males, making the pelvis wide relative to the thigh length in females. The hip width is greater in females when related to the sitting height, whereas males have a larger average chest circumference relative to the sitting height.

Of all the indices computed, the only significant variation that did not vary with age or sex but appeared related to body type was the thickness of the femoral cortex relative to the total length of the femur. The relative cortical thickness of the femur was greater in endomorphic and mesomorphic chimps than in those that were ectomorphic. The ponderal index (height divided by the cubic root of the weight) is a measure of the compactness or linearity of an individual. Compact chimps with an index under 40 had relatively thick femoral cortices, whereas the linear ones with an index over 40 had relatively thin femoral cortices. Thus the weight bearing and muscle action seemingly directly affect the relative thickness of the femoral cortex. Additional factors not apparent from this study seem to affect the cortical thickness of the humerus.

The epiphysis of the inferior angle of the scapula ossifies and fuses to the scapula in a distinctive manner in the chimpanzee, and the formation and fusion of this epiphysis provide the basis for an additional parameter in estimating chimpanzee age in the range from six to eighteen years. This epiphysis is a large one in the chimpanzee, and it ossifies over a period of several years, beginning as one or several small centers in the outer

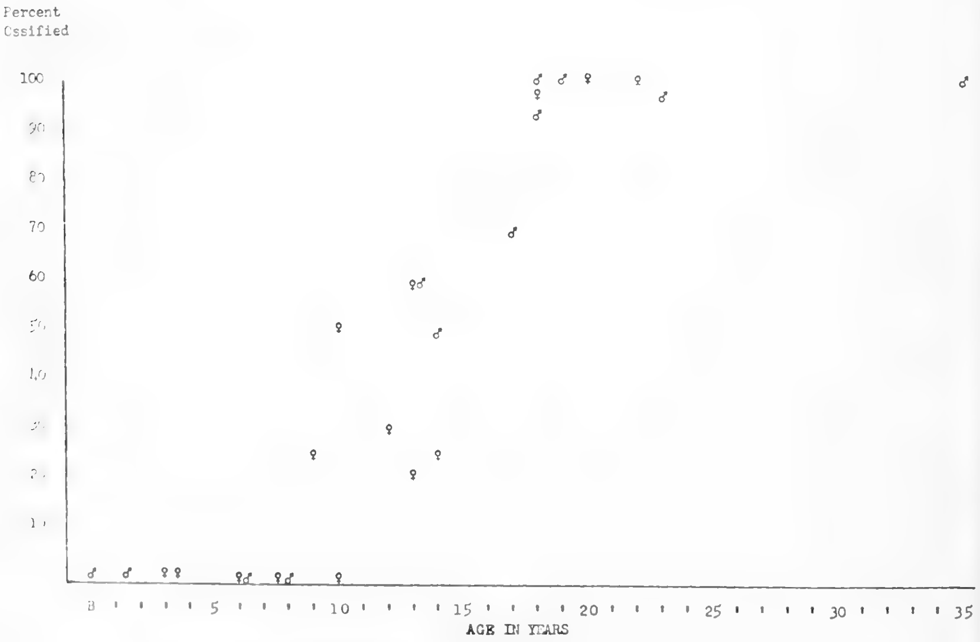

Figure 8. Epiphysis of the inferior scapular angle.

rim of the cartilage that forms the inferior angle. The outer part of the epiphysis ossifies first, forming a border of bone around a large area of cartilage at the inferior angle. As the epiphysis matures, the center part ossifies and the whole epiphysis fuses to the scapula. Owing to the size and manner of ossification, the percentage of the total epiphysis that is ossified at a given time can be estimated from radiographs or from the ossified portion of the epiphysis itself. There is a positive relationship between age and the percentage of the epiphysis that is ossified in the chimpanzee (Figure 8). In recording the data used in Figure 8, complete bony formation and the fusion of the epiphysis to the scapula with obliteration of the growth plate separating them was considered 100% ossification.

## DISCUSSION

The manner in which age changes occur and the times of epiphyseal union indicate that chimpanzees have a closer phylogenetic relationship to man than to either New World or Old World monkeys. Certain age changes in the pubic symphysis, sternum, and costal cartilages are found in monkeys from childhood on, whereas in chimpanzees they are modified and begin around seventeen years of age. In monkeys and other mammals these changes are much more extensive than they are in the chimpanzee and begin rather early in life, while in man they occur in middle age, and no fusion occurs at the pubic symphysis. The microstructure of the diaphyses of long bones of chimpanzee resembles that of man more than it does that of monkeys by microscopic comparison of histologic cross sections. As might be expected, all of these factors indicate that the chimpanzee falls between man and the monkeys phylogenetically, with a stronger resemblance to man than to monkeys.

These age changes in the costo-chondral areas, epiphyseal union, the age changes in microscopic structure of long bone diaphyses and the regression of cancellous bone in metaphyses all suggest that the chronologic age in years for a given skeletal age in the chimpanzee is between two and three times that of most monkeys and about two-thirds that of humans of the same skeletal age. After growth in length of the long bones of the extremities has been completed, a small amount of growth continues in the width of the shafts of the long bones, at the ends of ribs, at the sternal end of the clavicle, and in the lateral dimensions of the pelvis.

There is relatively little sexual dimorphism in chimpanzees other than differences in size between male and female. The skeletal variations that do exist between the sexes are greater relative width in the pelvic area of females and relatively larger chests in the males. These differences perhaps have some selective advantage in mate acquisition for males and in parturition for females. Chimpanzees exhibit remarkably little sex differentiation in the skeleton when compared to other large anthropoids.

## SUMMARY AND CONCLUSIONS

The bones of thirty chimpanzees ranging in age from birth to thirty-five years were examined, X-rayed, and made into histologic sections. The radiographs and histologic sections were then compared with the gross skeleton, and information obtained from all three sources was correlated with age and sex. The ages at which various epiphyses began fusing with the metaphyses and the ages which fusion had been completed in all chimpanzees were recorded. Additional age changes were found in the costal cartilages, pubic symphysis, and the sternal ends of the ribs. These all began about eighteen years of age, when the epiphyses of most of the long bones had just completed fusion.

Microscopically, there were age changes in the structure of the long bones that are comparable to those found in man. Osteones and fragments of old osteones increased in number with advancing age, while lamellar bone and non-Haversian canals decreased. In addition, there were variations in the resorptive patterns of the mid-shaft areas of long bones that were associated with age and were very similar to those found in the long bones of man.

1. The state of epiphyseal union can be determined by gross examination, X-ray, or histologic slides, but the most reliable data are derived from all three when the epiphyses are in the process of fusing.
2. Specific age changes in the scapula, pubic symphysis, and costo-chondral areas add further information useful in determining age in the difficult period after the epiphyses have all fused.
3. Changes in the microscopic structure

and patterns of resorption are the normal result of advancing age in chimpanzees as well as in man. These changes must be taken into account in assessing any experimental results from an examination of the skeleton —particularly those that propose to evaluate nutritional results.

## ACKNOWLEDGMENTS

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Volume 13, Number 3 September 1, 1966

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TULANE STUDIES IN ZOOLOGY

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# THE WESTERN ATLANTIC SWIMMING CRABS *CALLINECTES ORNATUS*, *C. DANAE*, AND A NEW, RELATED SPECIES (DECAPODA, PORTUNIDAE)

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## ABSTRACT

Former understanding concerning limits of variation and geographic range in the species *Callinectes ornatus* Ordway and *C. danae* Smith is altered by recognition of a new, closely related species, *C.* **similis,** from the Carolinian zoogeographic subregion. The two established species are redescribed and illustrated along with the new. Tables of measurements and comparisons, as well as a map, are included for easy reference.

## INTRODUCTION

Specific differences between the Western Atlantic littoral portunid crabs *Callinectes ornatus* Ordway, 1863, and *C. danae* Smith, 1869, seemed well delineated by Rathbun (1930) until recently. People studying these crabs along the coast of the Carolinas and points southward in the United States found that many specimens seemed to share characters attributed to both species by Rathbun, and Lunz (1958) questioned whether or not what had been uncritically called *C. ornatus* for many years along the Carolinas was in reality *C. danae.* He sought counsel from other carcinologists, but received inconsistent determinations. Lunz reluctantly called his specimens *C. ornatus,* but left the question of their identity open.

Blue crab investigations initiated by the Bureau of Commercial Fisheries of the U. S. Fish and Wildlife Service at Beaufort, N. C., in 1957, were hindered by the same difficulty, for *Callinectes* species other than *C. sapidus* Rathbun contribute to commercial catches along this coast in a minor degree and occur in samples of crabs from commercially fished waters. Moreover, life history studies involving identification of *Callinectes* larvae from plankton, as well as studies on rearing the larval stages, depend on accurate identification. In view of these needs and problems, large series of the questionable *Callinectes* species were collected from the east coast of Florida in 1962 by Bureau personnel and turned over to me for study in an attempt to clarify the taxonomic confusion.

This material, together with that in the University of North Carolina Institute of Fisheries Research Collection (UNC-IFR), selected material from the U. S. National Museum (USNM), and types of both *C. ornatus* and *C. danae* from the Museum of Comparative Zoology, Harvard University (MCZ), and Peabody Museum of Natural History, Yale University (YPM), formed the basis for comparisons.

*Callinectes ornatus* and *C. danae* appear to be valid species. However, their striking structural similarities led to confusion in distinguishing between them in the past, and the hitherto unrecognized existence of a third species in North and Middle America added to the puzzle. One apparent source of

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confusion is the series of line drawings given by Rathbun (1930: Figs. 15b, d; 16a, b; 17a, b; 18b, d). Not all specimens fall clearly into categories suggested by these figures. In addition, Hay and Shore (1918) listed *C. ornatus* as common in the Carolinas, and in that area this became the identification of choice almost by neglect, with Williams (1965) perpetuating the error. The following discussion should clarify the status of previously known species, establish their geographic ranges insofar as available material allows, and stabilize identity of the undescribed northern form.

Anatomical features most helpful in distinguishing these species, features emphasized in the diagnoses following, are: shape of the intramedial area, a central dorsal, roughly trapezoidal configuration on the carapace, which in the genus *Callinectes* is a combination of the metagastric and urogastric regions; sizes of the median pair of interocular teeth on the frontal margin; sculpture on the carpus of the chelipeds; shape and position of the T-shaped male abdomen; and finally, shape of the first male pleopods. The pleopods are most diagnostic for the species, and in descriptions of them I have decided to broaden a terminology used by Stephenson and Campbell (1959). They spoke of the basal bulb, distal portion, and extreme tip. Each first pleopod can be described more minutely as consisting of a broad basal bulb, a narrowing intermediate portion, a slender distal portion of variable length designated after this as the shank, and the extreme tip. Aside from these features, there are no consistently distinctive spines, teeth, grooves, angles, proportions, or tufts of hair on any of the remaining legs or mouthparts among the three species.

### *Callinectes ornatus* Ordway

Figs. 1; 4A, B.

*Callinectes ornatus* Ordway, 1863, p. 571.—Rathbun, 1896, p. 356 (in part); pl. 15; pl. 24, fig. 3; pl. 25, fig. 2; pl. 26, fig. 2; pl. 27, fig. 2.—1901, p. 48.—Verrill, 1908, p. 366.—Rathbun, 1930, p. 114 (in part); pl. 50; text-figs. 15b, 16a, 17a, 18b.

*Callinectes diacanthus* A. Milne Edwards, 1879, p. 225 (variety).

*Diagnosis.*—Six frontal teeth including inner orbitals, submedian teeth often obsolete.

Intramedial area broad laterally and relatively short anteroposteriorly as compared with *C. danae.*

Anterolateral teeth, except outer orbital and slender lateral spine, acute to progressively more acuminate laterally; first five with posterior margins longer than anterior margins, and distinctly separated by narrow-based, rounded notches; last two with margins approximately equal in length, with separating notches broader, next to last tooth distinctly more acuminate than last. Outer orbital and infraorbital teeth acute. Lateral spine trending definitely forward.

Carpus of chelipeds almost smooth dorsally; inferior lateral ridge terminating in a low tooth occasionally followed by an inconspicuous eminence.

Penultimate (fifth) segment of male abdomen relatively narrow, sides slightly constricted, not parallel; usually with distal segments 5 and 6 recessed below plane of sternum in retracted position. First pleopods of male each tapering from inflated basal bulb to slender tip reaching about level of suture between third and fourth thoracic sterna; curved in such manner that intermediate portion and proximal portion of shanks of each side overlap in situ (no overlap among young, but very close together); shanks becoming membranous distally, each with lanceolate tip on its own side of median sagittal plane of crab. Portion proximal to tip armed with short, backward pointing spinules quite visible at low magnification, somewhat more numerous and longer distally than proximally with tendency to arrangement in rows near tip on ventral and mesial margin; spinules extending proximally along shank to level of intermediate portion near basal bulb; spinules more numerous on mesial than on lateral edge near tip, but more numerous on lateral than on mesial edge proximally (small males with no spines proximally).

*Measurements.*—See Table 1.

*Variations.*—The median pair of interocular teeth are developed well enough in the dried syntype from Haiti to impair identification based on this character alone. Specimens from Bermuda have blunter anterolateral teeth than this dry specimen. Among young males especially, the sternoabdominal surface may be plane and not recessed as in many adults.

From adult material in USNM, this spe-

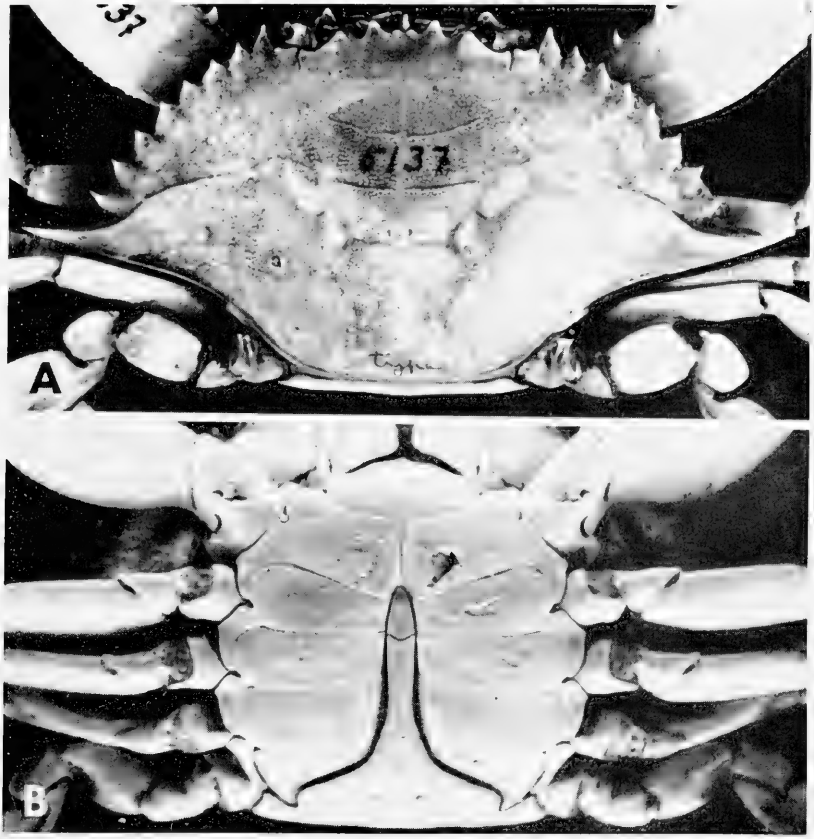

Figure 1. *Callinectes ornatus* Ordway, syntype male, Gonaives, Haiti, MCZ No. 5137; A, dorsal view of carapace, X 1; B, ventral view of sternal area slightly enlarged.

cies apparently shows far less variation than *C. danae.*

*Color.*—Adult males, Bermuda: Carapace dull olive to dark brown, usually with a large, ill-defined, roundish spot of orange or orange red on each side posteriorly; lateral spines and denticles light blue or whitish, white tipped. Eyestalks purple. Chelipeds proximally similar to carapace, spotted with blue and with spines pale blue, joints red; inner surface of palm white but with a large bright red patch bordered with purple; fingers mostly purple, tipped with red. Walking legs bright blue above, with a band of scarlet at each joint and a patch of paler blue or green on posterior and lower side of each article; dactyls red. Swimming legs similar in color but with red articular bands wider, a patch of orange or yellow on each article; dactyl with proximal blue band separated from distal scarlet band by an orange band. Abdomen light blue posteriorly.

Many individuals less brilliantly colored, juveniles often dull or plain olive-yellow to greenish above. Some males more melanistic, exhibiting shades of dark brown and purple with accents of yellow and brownish red. Albinistic (or light hued) forms not uncommon. (After Verrill, 1908.)

*Material examined.*—Syntypes, MCZ, seven specimens; nine lots of adults from 140 lots, mostly juveniles or specimens returned to sender, USNM; two 5-gallon and some smaller lots from Florida collected by U. S. Fish and Wildlife Service Bureau of Commercial Fisheries personnel.

*Type localities.*—Gonaives, Haiti; Cumana, Venezuela; Bahamas; Tortguas [Florida]; Charleston, South Carolina.

*Known range.*—The species as here restricted has a geographic distribution extending from an extreme northern limit at Charleston, South Carolina, along eastern and southern Florida, and the Atlantic continental coast from the eastern shore of Yucatan Peninsula to Surinam; throughout the Lesser and Greater Antilles and Bahama Islands; and Bermuda (Fig. 5).

*Remarks.*—Though type material from Charleston appears to be *C. ornatus,* (immature males and females, and small adult females), it is a matter of some concern that the stated origin of these specimens is from a locality representing an apparent extreme northern limit of geographic range. No other specimens of this species are known to me from the Carolinas, though I have seen immature specimens from near Jacksonville in northern Florida. The species is much more abundant in the Miami area nearer its geographic center in the Caribbean Sea.

### *Callinectes danae* Smith

Figs. 2; 4C, D.

*Lupa dicantha* Dana, 1852, p. 272.—1855, pl. 16, figs. 7a-c.

*Callinectes diacanthus:* Ordway, 1863, p. 575.—A. Milne Edwards, 1879, p. 226 (variety).

*Callinectes danae* Smith, 1869, p. 7.—Rathbun, 1896, p. 357, pl. 16; pl. 24, fig. 4; pl. 25, fig. 3; pl. 26, fig. 3; pl. 27, fig. 3. —1901, p. 48.—Verrill, 1908, p. 370 (?). —Rathbun, 1930, p. 118 (in part); pl. 51; text-figs. 15d, 16b, 17b, 18d.—Lemos de Castro, 1962, p. 39; pl. 2, fig. 9.

*Diagnosis.*—Six frontal teeth including inner orbitals, submedian pair short but distinct.

Intramedial area narrow laterally and relatively long anteroposteriorly as compared with *C. ornatus.*

Anterolateral teeth, except outer orbital and slender lateral spines, intermediate in length between *C. ornatus* and new species described below; tips of first three teeth nearly rectangular with posterior margins somewhat longer than anterior margins, teeth separated by narrow-based rounded notches; remaining teeth, especially sixth and seventh, acuminate, resembling those of *C. ornatus.*

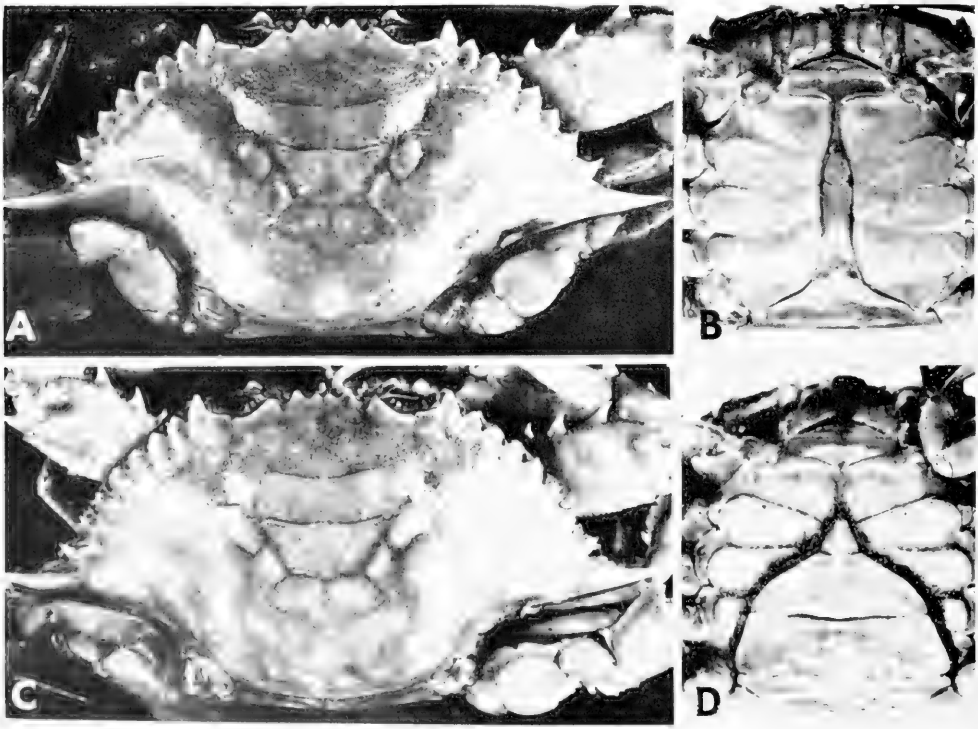

Figure 2. *Callinectes danae* Smith, syntypes, Recife (= Pernambuco), Brazil, YPM No. 824. Male, A, carapace in dorsal view, B, sternal area in ventral view; female, C, carapace in dorsal view, D, sternal area in ventral view, slightly reduced.

having anterior edges concave, and posterior edges somewhat convex. Outer orbital and infraorbital spines somewhat blunted. Lateral spine extending straight laterally or curved slightly forward.

Carpus of chelipeds with upper surface bearing slightly developed, interrupted ridges trending longitudinally with axis of limb, ridges bearing obsolescent granules often better developed in males than in females; inferior lateral ridge terminating in a strong lateral spine or tooth often followed by a strong eminence.

Penultimate (fifth) segment of male abdomen with sides almost parallel, only a slight constriction in proximal half preceded and succeeded by converging margins; distal segments 5 and 6 only somewhat recessed below plane of sternum in retracted position. First pleopods of male each tapering from inflated basal bulb to slender tip reaching about level of suture between second and third thoracic sterna; curved in intermediate portion in such manner that shanks of each side are either somewhat overlapping or almost contiguous in situ; shanks becoming membranous, narrow and trough-shaped distally with tips bent ventrolaterally. Distal half of each shank with minute spines hardly visible at low magnification on dorsal aspect and, in addition, two well separated, exceedingly slender longer spines on bent portion distally.

*Measurements.*—See Table 1.

*Variations.*—The first pleopods of males vary somewhat in length individually, being either a little longer or more often shorter than as diagnosed above. The tips of these appendages, too, are subject to individual variation, usually curving ventrolaterally, but often ventromesially, laterally, mesially, or seldom straight, asymmetrical, or sinuously curved. Some specimens have the prominent, sparse, terminal setae; some do not. In some, the lateral fine setae are more evident than in others. Usually the cross suture between abdominal segments 5 and 6 is anterior to the suture between the second and third thoracic sterna. Constriction of abdominal segment 5 appears to be more pronounced in large mature males than in immatures in which the segment is not only more nearly parallel sided but also relatively broader than in older crabs.

*Color.*—Half grown male, Ilha São Sebastião, State of São Paulo, Brazil (USNM No. 61002): Carapace a sort of sage green [grayish green] and medium brown with porcelain white patches, frontal area dark red, teeth yellow grading through whitish to white tips. Chelipeds similar, medium brown with greenish tinge, spines nearly all porcelain white, entire outer margin, and inner margin of carpus, dark brown; inner surface of hand and carpal articulation china blue; fingers all white. Articles of walking legs china blue, merus more heavily stippled from distal end to middle, a sort of cinnamon color mixed with white between legs; dactyls orange-red to scarlet. Swimming legs like chelipeds, margins of articles salmon near articulations; dactyl transparent but reddish to brownish yellow distally, white on proximal half and adjacent propodus. Underparts whitish. (Modified after Schmitt *in* Rathbun, 1930.)

*Material examined.*—Types, MCZ and YPM; 24 to 96 lots, USNM.

*Type locality.*—Recife (= Pernambuco), State of Pernambuco, Brazil.

*Known range.*—The species as here restricted has a geographic distribution extending from the northern coast of Cuba, through the Greater and Lesser Antilles, as well as along the Atlantic continental coast, from British Honduras to the State of Santa Catarina, Brazil (Fig. 5).

## *Callinectes* **similis** sp. n.

Figs. 3; 4E, F.

*Callinectes ornatus:* Rathbun, 1896, p. 356 (in part).—Hay and Shore, 1918, p. 433; pl. 34, fig. 2.—Rathbun, 1930, p. 114 (in part).—Williams, 1965, p. 172, fig. 152.

*Callinectes danae:* Rathbun, 1930, p. 118 (in part).

*Diagnosis.*—Six frontal teeth including inner orbitals, submedian pair short but distinct.

Intramedial area narrow laterally and relatively long anteroposteriorly, intermediate in shape between *C. ornatus* and *C. danae.*

Anterolateral teeth, except outer orbital and slender lateral spine, broad, distinctly separated by narrow-based, rounded notches, tips of first five nearly rectangular; tips of sixth, and especially seventh, acuminate with separating notches broader. Outer orbital and infraorbital spines prominent and, especially outer orbital, acuminate at tip. Lateral spine strong, curved forward.

Carpus of chelipeds with upper surface

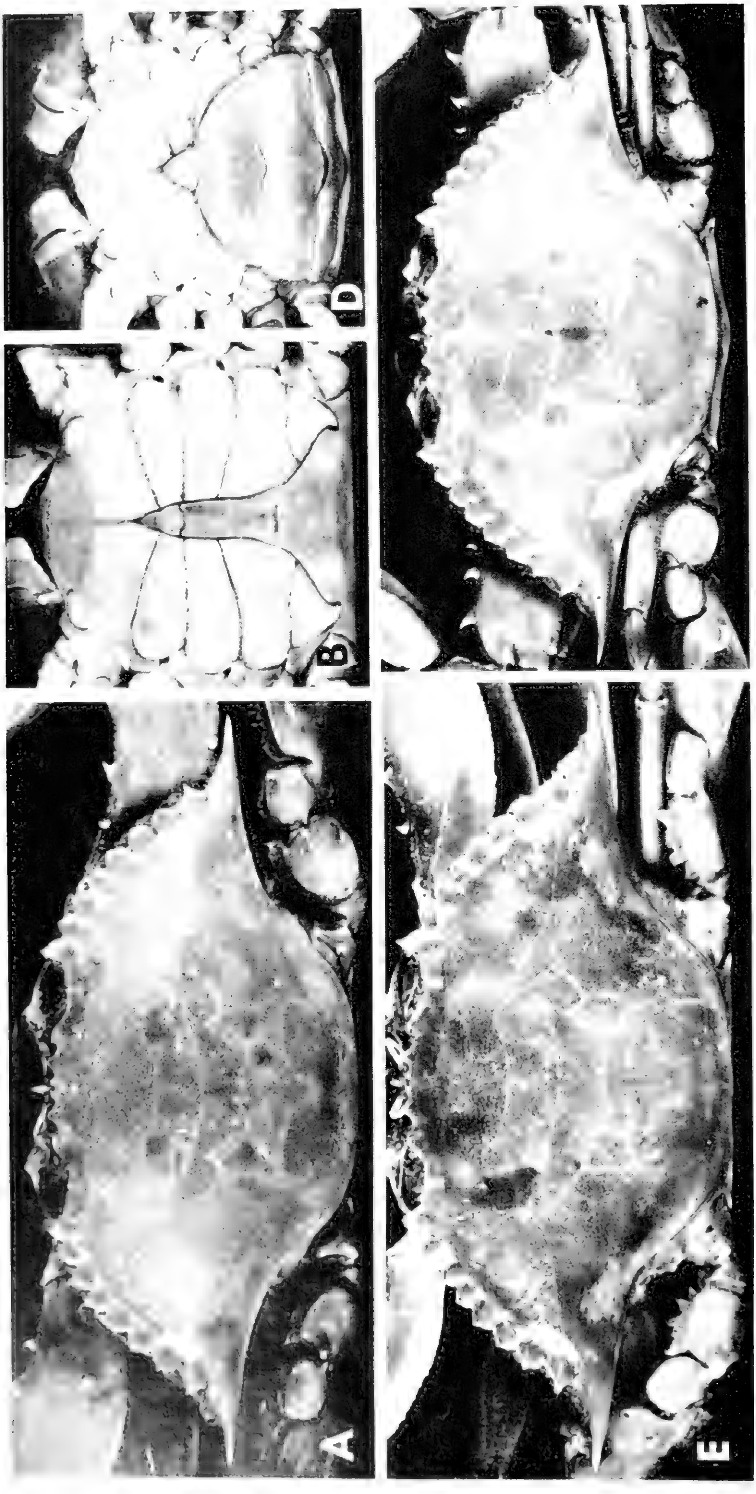

Figure 3. *Callinectes similis* sp. n., holotype male, A, carapace in dorsal view, B, sternal area in ventral view; paratype female, C, carapace in dorsal view, D, sternal area in ventral view; paratype male, near Beaufort Inlet, N. C., E, carapace in dorsal view; X 1.

bearing two obsolescent granulate ridges and suggestion of others; inferior lateral ridge terminating in a strong anterior spine followed by a low, oblique, granulate, dorsoventrally flattened eminence.

Penultimate (fifth) segment of male abdomen having an extremely slight constriction in proximal half preceded by converging margins; distal segments 5 and 6 not recessed below plane of sternum in retracted position. First pleopods of male each tapering from inflated basal bulb to slender tip reaching zone at level of fourth thoracic sterna; pleopods widely separated in situ. Basal bulb narrowing through intermediate portion to slender shank more abruptly than in *C. ornatus,* often giving rise to a slight shoulder on mesial border just proximal to constriction on intermediate portion. Shank slender, nearly straight and parallel sided to near unadorned, somewhat membranous tip bent slightly mesiad. Shank armed with scattered, mintue, backward pointing spinules, less numerous and somewhat smaller than in *C. ornatus;* most dense and largest distally, becoming very small and scattered proximally in intermediate portion, spinules more dense laterally than mesially.

*Description, holotypic male.*—Carapace, including lateral spines, about 2.2 times as wide as long, moderately convex, lightly and almost uniformly granulate dorsally except smooth along posterolateral and posterior slopes of dorsum, nearly smooth along anterolateral and anterior margins, especially between teeth and along orbits; smooth areas with tendency to iridescence; a symmetrically sinuous granulate line extending from side to side and a shorter arcuate line between this and frontal margin; intramedial area moderately long and narrow, resembling *C. danae* more than *C. ornatus.* Six frontal teeth including inner orbitals; submedian teeth short but distinct, intermediate teeth exceeding inner orbitals. Anterolateral teeth broad, each pair distinctly separated by a narrow-based, rounded notch; tips of first five nearly rectangular with anterior margins shorter than posterior; tips of sixth, and especially seventh, acuminate with separating notches broader; notches between teeth each with a shallow pit on adjacent dorsal surface. Lateral spine strong, slender, curved forward, scarcely as long as space occupied by three preceding teeth. Outer orbital spines acuminate, inner edge straight, outer sinuous;

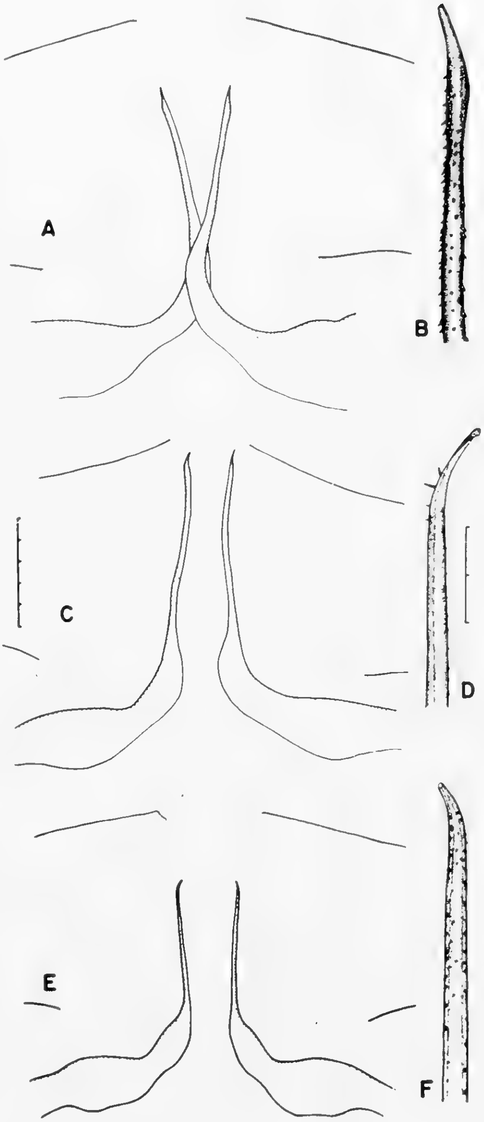

Figure 4. Outlines of first pleopods of males in situ with abdomen removed, flanked on right by enlarged views of left pleopod tips in ventral view. *Callinectes ornatus* Ordway, A, B, specimens from Florida off Biscayne Bay. *C. danae* Smith, C, Cardenas Bahia, Cuba (specimen showing shorter and more widely spaced pleopods than "typical"); D, MCZ syntype No. 5143. *C. similis* sp. n., E, paratype from type locality; F, paratype from near Beaufort Inlet, N. C. Each subdivision on scales = 1 mm.

infraorbital spines prominent and projecting beyond level of slender rostrum.

Chelipeds large and powerful, armed with sharp strong spines and with pincers asymmetrically modified as a crusher (right) and cutter (left). Merus with three spines in front and a single small one at distal end behind, proximal to this a transverse groove and spiniform shoulder. Carpus with two lateral granulate ridges, the inferior terminating in a strong spine followed by a low, oblique, granulate, dorsoventrally flattened ridge continuous with condyle articulating with palm; dorsal side with two obsolescent, granulate ridges, a long radial ridge and a shorter faint superior ridge with suggestion of still others trending longitudinally with axis of limb. Hand strong, prominently ribbed with longitudinal, granulate ridges; three superior ridges continued on superior surface of dactyl; a strong proximal spine at superior articulation with carpus and a low distal spine on palmar portion of superointernal ridge; median internal and external ridges confined to body of hand; external inferior ridge strongest at base of immovable finger. Fingers nearly straight and strongly toothed, with incurved pointed tips crossing each other when closed.

Abdomen in form of inverted T; basal segments broad, distal segments narrow. Terminal segment (sixth) approximately oblong-lanceolate in outline, separated from penultimate (fifth) segment by a symmetrically sinuous movable suture at level slightly advanced beyond suture between second and third thoracic sterna; penultimate segment slightly sinuous sided but broader at all levels than terminal segment, proximal half slightly constricted laterally and less indurated than other parts, suture forming connection to proximal portion of abdomen almost completely fused; distal segments 5 and 6 not recessed below plane of sternum in retracted position. First pleopods each narrowing from broad basal bulb, through definite intermediate portion more abruptly than in *C. ornatus,* to slender tip reaching zone at level of fourth thoracic sterna; pleopods widely separated in situ. Shank slender, nearly straight and parallel sided to near unadorned, somewhat membranous tip bent slightly mesiad. Shank armed with scattered, minute, backward pointing spinules, less numerous and somewhat smaller than in *C. ornatus:* most dense and largest distally, becoming very small and scattered proximally near intermediate portion, spinules more dense laterally than mesially.

First, second, and third walking legs, as well as modified paddlelike last legs, with no features distinctive from other *Callinectes* species; first to third each with conspicuous fringe of hairs on posterior edge of propodus and dactyl, a shorter fringe on anterior edge of dactyl; paddlelike last leg with hairy fringe on all edges except posterior of carpus and merus and edges of more proximal articles.

*Mature and immature paratypic females.*—Abdomen of mature female broad, rounded, loosely covering much of posterior sternal plastron, terminal segment approximately in shape of equilateral curvilinear triangle lodged anterior to sternal suture between first and second walking legs. Immature female with abdomen triangular; terminal segment borne at same level as adult, shape between that of mature male and female; proximal segments fused, not movable as in adult. Carapace more inflated dorsally, yet proportionally no more deep bodied than male; lateral spines and chelipeds relatively weaker than in male.

*Measurements.*—See Table 1.

*Variations.*—Width of the gap between the first pleopods of males is subject to variation but the pleopods never lie in contiguity. There is some variation in length of the male pleopods, in relative development of the median interocular teeth, and especially in shape of the intramedial area. In addition to individual variation, this feature changes in shape with age.

*Color.*—Adult male, Beaufort Inlet, North Carolina: Carapace green dorsally, irregular areas of iridescence at bases of, and between, anterolateral teeth, and on posterior and posterolateral borders. Chelipeds and portions of legs similar in color or more tannish green dorsally, with iridescent areas on outer and upper edges of carpus and hands; chelae white on outer face, blue to fuchsia on inner surface, with fuchsia on tips of fingers and teeth of opposed edges. Lateral spines and some anterolateral teeth, as well as spines on chelipeds, white tipped. Walking legs grading from fuchsia distally through violet blue to light blue mottled with white proximally, pubescence on legs beige. Swimming legs variably mottled with white; all legs

## TABLE 1.

*Measurements for type material of three closely related, partially sympatric species of* **Callinectes.**

| Measurements in mm | *C. ornatus* | | | | | | | *C. danae* | | | | *C. similis* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Gonaives, Haiti, 1860, Coll. A. Hilchenbach. MCZ No. 5137 | Cumana, Venezuela. 1859, Coll. Capt. Couthouy. MCZ No. 5136 | Charleston, S. C. Coll. L. Agassiz. MCZ No. 5128 | | | Charleston, S. C. MCZ No. 5210 | | Pernambuco, Brazil, 1867, Coll. C. F. Hartt. YPM No. 824 | | Pernambuco, Brazil, 1867, Coll. C. F. Hartt. MCZ No. 5143 | | 2 to 3 miles off beach between St. Johns River jetties and Jacksonville Beach, Florida, 18 June, 1962. USNM Nos. 113341 (holotype) & 113342 (mature ♀ paratype). | | | | Off Beaufort Inlet Carteret County, North Carolina, 31 October, 1962. | |
| | Syntype | Syntype | Syntypes | | | Labelled "Types" | | | | Syntypes | | Holotype | Paratypes | | 113341 | Paratypes | |
| | ♂ | ♂ | ♂ ‡ | † | ♀ | ♀ | ♀ | ♂ | ♀ | ♂ | ♀ ‡ | ♂ | ♂ | ♀ | ♀ | ♂ | ♀ § |
| Length in midline excluding rostrum | 47 | 40.3 | 27.3 | 26.5 | 37 | 30.1 | 31.6 | 42.6 | 42.2 | 40.3 | 40.4 | 45.7 | 34.7 | 31 | 40 | 45.5 | 39.8 |
| Width including lateral spines | 103 | 80 | 58* | 58.5 | 79 | 62* | 67.1 | 97.5 | 95 | 93.4 | 92 | 101.3 | 77.4 | 67.4 | 88.9 | 104.3 | 86.6 |
| Width to base of lateral spines | 82 | 65.9 | 48 | 45.6 | 62.9 | 49.8 | 53.3 | 77 | 74.5 | 73.1 | 71 | 80.4 | 61.5 | 52.6 | 69 | 81.2 | 79 |
| Width between outer orbitals | 38 | 32 | 23.3 | 22.6 | 30 | 24.9 | 25.8 | 35 | 36 | 33.2 | 33.3 | 36.5 | 27.5 | 24.8 | 31.5 | 37* | 32 |
| Width between inner orbitals | 18 | 14 | 10.6 | 9 | 13 | 10.2 | 11.4 | 14 | 15 | 12.7 | 13.5 | 14.5 | 11 | 9 | 12.5 | 14.5 | 12.5 |
| Width between infraorbitals | 21 | 17.5 | 12.7 | 11.7 | 16.5 | 13.6 | 13.9 | 18.6 | 20.5 | 18 | 18 | 20.5 | 15 | 13.3 | 17.3 | 19.5 | 16* |
| Width between prominent interorbitals | 8.5 | 6.9 | 5 | 4.6 | 5.8 | 4.8 | 5.4 | 6.7 | 7 | 6.4 | 6.5 | 7 | 5.5 | 5 | 6.9 | 6.8 | 6.2 |
| Maximum height of body | 27 | 22.3 | 15.6 | 15.3 | 21.8 | 17.2 | 17.8 | 23.4 | 24.3 | 21.7 | 22 | 24.8 | 19.3 | 18.8 | 22.8 | 25.5 | 23 |
| Male Abdomen | | | | | | | | | | | | | | | | | |
| Width 3d segment | 34.5 | 27.9 | | | | | | 27.2 | | 27.6 | | 32.5* | 26.5 | | | 33.6 | |
| Length fused segs. 3 and 4 in midline | 13.4 | 11.1 | | | | | | 11.2 | | 10.9 | | 11.8 | 9.8 | | | 29.7 | |
| Length 5th segment in midline | 11.5 | 9.2 | | | | | | 12.4 | | 10.3 | | 12 | 9.2 | | | 12.5 | |
| Narrowest width 5th segment | 3.3 | 2.7 | | | | | | 3.4 | | 3.2 | | 5.1 | 4.6 | | | 4.7 | |
| Mature Female Abdomen | | | | | | | | | | | | | | | | | |
| Width basal (1st) segment | | | | | 29.2 | 24.6 | 25.9 | | 32.1 | | 30.5 | | | | 31.1 | | 33 |
| Width 2d segment | | | | | 30.5 | 24.8 | 26 | | 31.6 | | 30.5 | | | | 32.6 | | 34 |
| Width largest (4th) segment | | | | | 27.1 | 21.1 | 27.7 | | 29 | | 28 | | | | 30.5 | | 29.7 |
| Length 4th segment in midline | | | | | 7.4 | 5.7 | 6 | | 8.4 | | 8 | | | | 8.2 | | 8.6 |
| Length segment 2-6 in midline | | | | | 23.9 | 18.3 | 19.5 | | 26.8 | | 26.4 | | | | 27 | | 27 |
| Intramedial Area | | | | | | | | | | | | | | | | | |
| Anterior width | 22 | 18 | 12.4 | | | 14.3 | 15.5 | 17 | 18 | 16 | 17.4 | 20.5 | 14.5 | 14 | 18.5 | 20 | 19 |
| Posterior width | 14 | 10.8 | 7.9 | | | 9.1 | 9.4 | 10 | 10.5 | 9.5 | 10.7 | 11.5 | 9 | 8 | 11 | 12.5 | 10.4 |
| Median length | 7 | 5.8 | 3.8 | | | 4.7 | 5.4 | 7.5 | 7.5 | 7.4 | 7.5 | 7.1 | 5.8 | 5 | 6.7 | 6.8 | 6.7 |
| Lateral, angular, length | 8.8 | 7.6 | 5.5 | | | 5.4 | 6.5 | 8.5 | 8 | 8 | 8.2 | 9 | 7 | 6.5 | 8.5 | 9 | 9 |

* Estimated measurement † Immature ‡ Badly broken specimen § Ovigerous female

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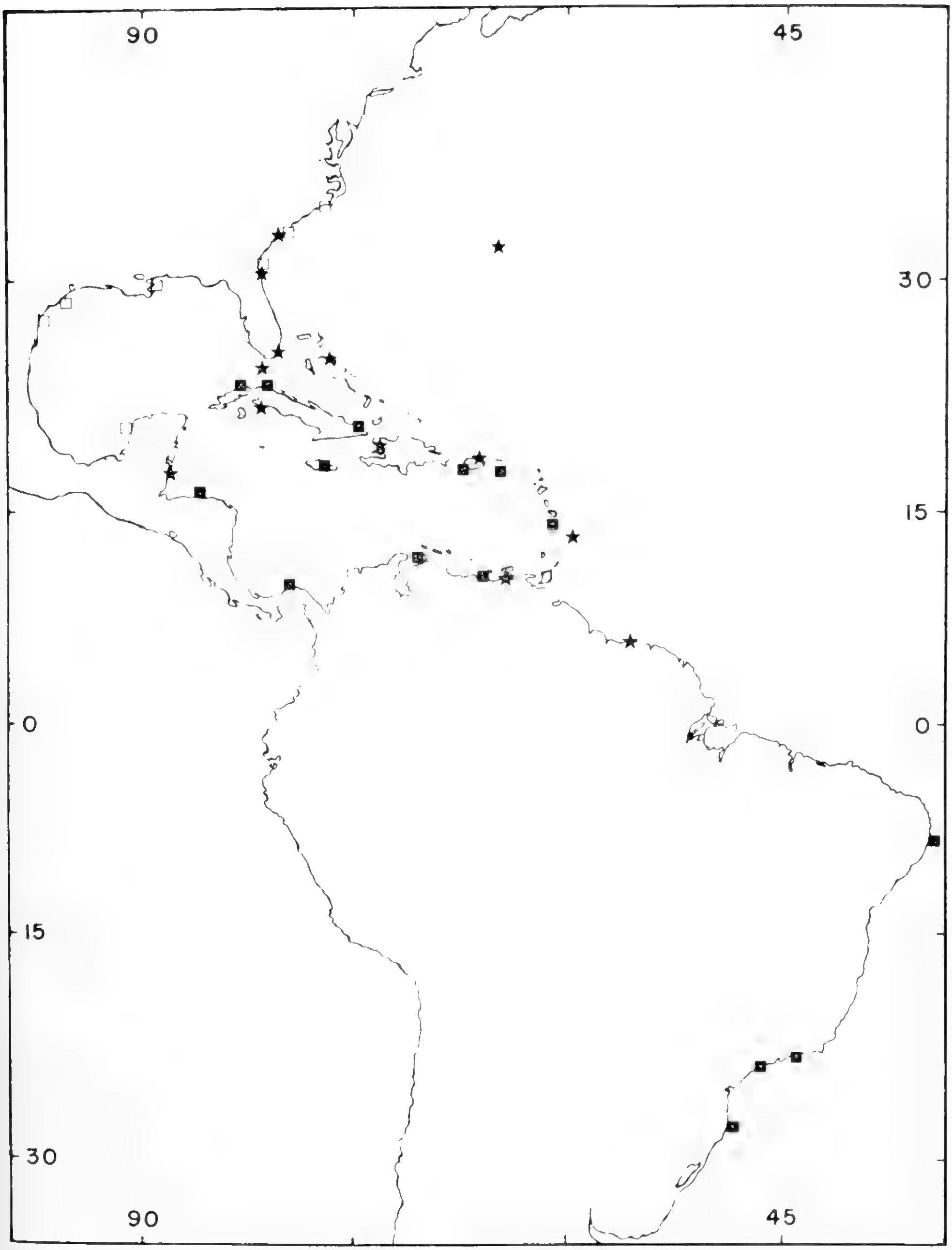

Figure 5. Geographic ranges represented by specimens studied; □ *Callinectes similis* sp. n.; ★ *C. ornatus* Ordway; ■ *C. danae* Smith.

with stellate fuchsia markings at articulations. Underparts white and blue.

Ovigerous female, Beaufort Inlet, North Carolina: Similar to male except with more violet blue on inner surface of chelae; fingers either with white teeth or fuchsia colored teeth. Legs with dactyls reddish orange grading abruptly to blue on propodi, pubescence brown to beige. Abdomen with iridescent areas. (After Williams, 1965.)

*Material examined.*—Several 5-gallon and smaller lots collected by U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries personnel; 17 lots in UNC-IFR; several lots labelled "*C. ornatus*" in USNM.

*Type locality.*—Two to three miles off beach between St. Johns River jetties and Jacksonville Beach, Florida.

*Known range.*—New Jersey to State of Campeche, Mexico.

*Disposition of types.*—The male holotype (No. 113341), female paratype (No. 113342), and a series of paratypes have been placed in the USNM; also, series of paratypes have been placed in the MCZ, YPM, and UNC-IFR.

*Relationships.*—*Callinectes similis* appears to be most closely related to *C. ornatus* and *C. danae.*

*Remarks.*—The great similarity of this species to its congeners suggested the name *similis.*

In Texas, Daugherty (1952) reported both a spring and fall breeding season for *C. similis* (=*danae*) with egg mass formation occurring in Gulf waters of 15 to 40 fathoms and in bays when salinities were comparable to those of the Gulf. Lunz's (1958) report of ovigerous females from South Carolina in May, August, and September, their occurrence as late as November in North Carolina (Williams, 1965), and in June and July among paratypes from northeastern Florida suggests that spring and fall may represent only peaks in occurrence of egg-bearing females along the Atlantic shore.

## Discussion

For rapid identification, a list of comparisons is given in Table 2. These char-

Table 2
*Distinctive features exhibited by three closely related partially sympatric species of* **Callinectes.**

| | *C. ornatus* | *C. danae* | *C. similis* |
|---|---|---|---|
| Intramedial area. | Wide & short. | Narrow & long. | Intermediate between other two. |
| Median pair interocular teeth. | Slightly developed or absent. | Present. | Present. |
| Carpal teeth & dorsal ridges. | Low lateral tooth.<br>Smooth dorsally. | Strong lateral tooth or teeth.<br>Dorsal ridges present. | Strong lateral tooth & a distal lateral eminence.<br>Low dorsal ridges present. |
| Male 1st pleopods. | Often crossed near base.<br>Flared portion of tip lanceolate.<br>Spines on narrow shank quite visible at low magnification.<br>Tips reaching to about level of suture between 3d & 4th thoracic sterna. | Somewhat crossed to somewhat separated.<br>Trough-shaped tip bent usually ventrolaterally.<br>Few spines on narrow shank hardly visible at low magnification.<br>Tips reaching to level of suture between 2d & 3d thoracic sterna. | Not crossed, well separated.<br>Plain tip bent mesially.<br>Few minute spines on narrow shank.<br>Tips reaching to zone at level of 4th thoracic sterna. |
| Male abdomen. | Usually recessed below plane of sternum.<br>Sides not parallel. | Somewhat recessed.<br>Sides almost parallel. | Not recessed.<br>5th segment slightly constricted. |
| Geographic distrib. | S. C. (?), Fla.; Caribbean area to northern South America; Bermuda. | Caribbean area to southern Brazil. | New Jersey to Campeche, Mexico. |

acters distinguish almost all of the specimens examined by me. However, two areas from which doubtful specimens were found should be mentioned. Some individuals from northern Cuba (Fig. 4C) and others from near the Canal Zone in Panama present puzzling combinations of *similis-danae* characters. Both of these areas are beyond the known range of *C. similis* but within that of *C. danae.* Such specimens, few in number, may represent extremes in variation of *C. danae,* but no solutions are possible until more are available for study.

Finally, a high incidence of the sacculinid parasite, *Loxothylacus texanus* Boschma was noted in a large series of *C. ornatus* from Biscayne Bay, Fla. Reinhard (1950) discussed occurrence of this parasite on *C. sapidus,* but never on *C. similis* (=*danae*) in the Gulf of Mexico, and also noted its occurrence on *C. marginatus* in Panama. I have not seen *L. texanus* on *C. similis.*

## ACKNOWLEDGMENTS

A number of people gave me aid in preparation of this study. Fenner A. Chace, Jr., counseled with me on a number of occasions and both he and Raymond B. Manning of the USNM made study space available and loan of specimens possible. William A. Newman, MCZ, and Willard D. Hartman, YPM, arranged loan of type series. I am indebted also to G. R. Lunz, D. H. B. Ulmer, Jr., A. E. Smalley, G. H. Rees, M. Judy, and D. Dudley for ideas presented in conversation, and to the men who collected crabs specifically for this study. Mrs. Erika Kohlmeyer drew views of pleopods in situ and inked all of Figure 4.

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September 1, 1966

# *ETHEOSTOMA RUBRUM*, A NEW PERCID FISH OF THE SUBGENUS *NOTHONOTUS* FROM BAYOU PIERRE, MISSISSIPPI

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and
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## ABSTRACT

*Etheostoma (Nothonotus)* **rubrum** is described from 209 specimens taken from Bayou Pierre or its tributary, White Oak Creek, Mississippi River System, Copiah County, in southwestern Mississippi. *Etheostoma rubrum* is a diminutive species. It is the smallest, except for *tippecanoe*, in the subgenus *Nothonotus*. The closest relative of *rubrum* is *moorei*. *E. rubrum*, *E. moorei*, and an undescribed species from the Cumberland and Tennessee Rivers form a species group in the subgenus *Nothonotus*. A comparison of *rubrum* and *moorei* shows that the differentiation in most meristic characters is at a relatively low level, but is sharpest in number of lateral line scales. Like other species in the subgenus *Nothonotus*, color pattern is an important species character. The major pattern differences are described.

*E. rubrum* is known only from the type-locality. The preferred riffle habitat is probably limited thus yielding a restricted range.

Shortly after our description of *Etheostoma moorei* (1964:131), a related species was found more than two hundred miles distant from any other species of the subgenus *Nothonotus*. *E. rubrum* was noted by Raney and Timothy Zorach during a study of *Etheostoma camurum* (Cope) when a single specimen which had been collected by Ralph W. Yerger and students, Florida State University, was examined. At our request John S. Ramsey and Michael D. Dahlberg, Tulane University, visited the type-locality of *rubrum* and collected 107 specimens. Later five additional series were collected. We are especially indebted to Dr. Ramsey who made careful color descriptions, habitat notes, and vertebral counts, and to Timothy Zorach, who made most of the counts given in Tables 1 and 2. Measurements (by Raney) and most counts were made in the manner following Hubbs and Lagler (1958:8-15). Scale rows "Anal to first dorsal fin" were counted from a point just laterad of the origin of the anal fin forward and upward to the first dorsal fin base. Scale rows from the "second dorsal to anal fin" were counted from a point just laterad of the origin of the second dorsal fin downward and backward to the anal fin base or to, but not including, the midventral scale. In the text, the genus *Etheostoma* is understood when the generic name has been omitted.

This study was supported by National Science Foundation grants G 9038 and GB 650 to Raney and by NSF G 9026 and National Institutes of Health grant WP-82 (C2) to Suttkus.

### *Etheostoma (Nothonotus)* **rubrum**,
### new species
### Bayou Darter
### (Fig. 1)

*Material:* The type-material consists of seven series totaling 209 specimens. All are from Bayou Pierre or its tributary, White

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*Photographs by Clyde D. Barbour*

Fig. 1. Top. *Etheostoma rubrum*, new species. Paratype adult male, 42.9 mm in standard length, from Bayou Pierre, 8.6 mi SW Utica, Copiah Co., Mississippi, 2 April 1966, TU 40368. Bottom. *Etheostoma rubrum*, new species. Paratype, adult female, 35.9 mm in standard length from the same locality. TU 40368.

Oak Creek, the Mississippi River System, Copiah Co., in southwestern Mississippi. The holotype, Cornell University no. 48232, an adult male 34.9 mm standard length (S.L.), was collected with 106 paratopotypes, 26-40 mm S.L., CU 48233 (53 spec.), and Tulane University 30171 (47 spec.), U. S. National Museum 188899 (6 spec.), on 7 December 1963 by Ramsey and Dahlberg, at Highway 18 crossing, 8.6 mi SW of Utica (junction of Highways 18 and 27). One paratopotype, Florida State University 9275, 35.5 mm S.L., was collected at the same locality on 4 July 1963 by Yerger, R. Birdsong, and T. Fraser. The above specimens were used in the counts which appear in the tables.

Other specimens taken at the type-locality include: CU 46665, 21 paratopotypes, 28-41 mm, 1 February 1964 by Raney and Suttkus; TU 32264, 11 paratopotypes, 28-35 mm, 17 May 1964 by Suttkus and Ramsey; TU 37305, 4 paratopotypes, 30-36 mm, 19 March 1965 by Suttkus and Larry Ogren; TU 37451, 53 paratopotypes, 21-39 mm, 28 April 1965 by Suttkus and Francis Rose; TU 40368, 10 paratopotypes, 32-46 mm, 2 April 1966 by Suttkus and G. H. Clemmer.

Two additional paratypes, TU 31341, 32-36 mm, were collected 1 February 1964 in White Oak Creek, a tributary to Bayou Pierre, 2.7 mi S of Utica at Hwy. 18 crossing, Hinds Co., Mississippi by Raney and Suttkus. The data for the comparative materials of *moorei* and *camurum* used in Tables 1 and 2 are given in Raney and Suttkus (1964:132-133).

*Diagnosis:* A diminutive species. Smallest, except for *tippecanoe,* in subgenus *Nothonotus.* Closest relative is *moorei.* Snout moderately sharp; branchiostegal membranes moderately conjoined; frenum broad; lower jaw included. Body moderately streamlined, anterior two-thirds with

Table 1.
Scale counts in *Etheostoma rubrum* (Bayou Pierre, Miss.), *E. moorei* White River Dr., Ark.) and *E. camurum* (Ohio River Dr.)

| Species | Lateral Line Scales | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 |
| *rubrum* | 1 | 2 | – | 4 | 7 | 13 | 19 | 27 | 23 | 6 | 6 | – | – | – | – | – | – | – |
| *moorei* | – | – | – | – | – | – | 1 | 2 | 9 | 7 | 14 | 13 | 9 | 3 | 3 | 1 | – | – |
| *camurum* | – | – | – | – | – | 1 | 1 | 3 | 7 | 6 | 4 | 2 | 4 | 2 | – | 2 | 2 | 1 |

| | Caudal Peduncle Scales | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Above Lateral Line | | | | Below Lateral Line | | | | | Total | | | | | |
| | 7 | 8 | 9 | 10 | 8 | 9 | 10 | 11 | 12 | 18 | 19 | 20 | 21 | 22 | 23 |
| *rubrum* | 1 | 65 | 41 | 1 | – | 39 | 59 | 9 | 1 | 1 | 28 | 47 | 22 | 9 | 1 |
| *moorei* | – | 29 | 31 | 2 | – | 5 | 35 | 22 | – | – | 4 | 22 | 18 | 16 | 2 |
| *camurum* | 2 | 22 | 11 | – | 1 | 11 | 19 | 4 | – | 3 | 9 | 11 | 9 | 3 | – |

| | Diagonal Scale Rows | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Above Lateral Line | | | | | | Anal to 1st Dorsal Fin | | | | | | | | 2nd Dorsal to Anal Fin | | | | | |
| | 4 | 5 | 6 | 7 | 8 | 9 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 12 | 13 | 14 | 15 | 16 | 17 |
| *rubrum* | – | – | 60 | 48 | – | – | 3 | 4 | 44 | 36 | 19 | 2 | – | – | 1 | 37 | 49 | 20 | 1 | – |
| *moorei* | 3 | 6 | 42 | 10 | 1 | – | – | – | 1 | 12 | 25 | 18 | 6 | – | – | 3 | 20 | 30 | 8 | 1 |
| *camurum* | – | 2 | 15 | 12 | 5 | 1 | – | – | 3 | 11 | 8 | 9 | 2 | 2 | – | 4 | 9 | 11 | 9 | 2 |

nearly horizontal ventral contour. Caudal fin truncate. Nape, breast, and anterior fourth of belly naked. Cheek naked except for patch of six to nine exposed scales behind eye. Opercle scaled. Lateral line complete. Oblique subocular bar complete, but with a lighter section immediately below eye and a forward extention toward upper tip of maxillary. Pronounced double basicaudal spot. Only complete vertical bar on body encircles posterior end of caudal peduncle. Sexual dimorphism marked; male larger; male with few red spots on side of body; female with many such spots and with spotted fins; horizontal dark lines on posterior sides of body poorly developed in male, absent in female.

*E. rubrum* differs from *moorei* in many details of color and pattern and has more vertebrae, anal and pectoral rays, and fewer lateral line scales, transverse body scales, caudal peduncle scales and dorsal fin rays.

*Description:* Small with compressed and moderately streamlined body like *moorei*. Greatest body width close behind head. Greatest body depth at or close to dorsal fin origin. Snout moderately sharp. Caudal peduncle deep (Fig. 1).

In large adults, angle formed by upper and lower profiles of head varies from 26 to 43°, entering angles of muzzle 65-69°. Eyes located high on head; head, viewed laterally, slightly interrupted above by fleshy margin of orbit. Anterior and posterior profiles of top of head meet at angle of 147 to 155°. Profile of snout a straight line from eye to upper edge of premaxillary. Length of pelvic base much greater than pelvic interspace. In 10 adults ratio of pelvic interspace/pelvic base .40 to .50. Head length contained in standard length 3.2 to 3.4 times. Head longer than deep; depth at occiput contained in head length 1.5 to 1.7 times. Measurements of holotype (length in mm and in parentheses expressed as thousandths of standard length) are as follows: standard length 34.9, body depth at dorsal origin 7.3 (209); caudal peduncle depth 4.2 (120); body width 4.5 (129); caudal peduncle length 8.0 (229); highest dorsal spine 4.4 (126); highest dorsal soft ray 5.6 (106); caudal fin length 6.8 (195); first anal spine 3.9 (112); highest anal ray 4.9 (140); longest pectoral ray 8.4 (241); pelvic fin length 8.6 (246); pelvic fin base 1.6 (46); interpelvic space 0.7 (20); head length 10.1 (289); head depth (at occiput) 6.2 (178); head width 4.9 (140); snout length 2.3 (66); orbit length 2.2 (63); fleshy interorbital width 1.8 (51); upper jaw length 3.3 (94); lower

TABLE 2.
Fin-ray and vertebral counts in three species of *Etheostoma*

| Species | First Dorsal | | | | Second Dorsal | | | | | | Total Dorsal Rays | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10 | 11 | 12 | 13 | 9 | 10 | 11 | 12 | 13 | 14 | 20 | 21 | 22 | 23 | 24 | 25 | 26 |
| *rubrum* | 26 | 76 | 6 | – | – | 6 | 67 | 34 | 1 | – | 3 | 23 | 47 | 31 | 4 | – | – |
| *moorei* | 2 | 57 | 3 | – | 1 | 2 | 38 | 21 | – | – | 1 | 4 | 35 | 20 | 2 | – | – |
| *camurum* | – | 5 | 28 | 2 | – | – | 4 | 23 | 7 | 1 | – | – | 1 | 6 | 20 | 6 | 2 |

| | Anal Soft Rays | | | | | Left Pectoral | | | | Vertebrae | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 5 | 6 | 7 | 8 | 9 | 12 | 13 | 14 | 15 | 35 | 36 | 37 | 38 | 39 |
| *rubrum* | 1 | – | 52 | 54 | 1 | 1 | 34 | 72 | 1 | 1 | 54 | 49 | 1 | – |
| *moorei* | – | 1 | 49 | 12 | – | 5 | 46 | 11 | – | 3 | 34 | 6 | – | – |
| *camurum* | – | – | 11 | 23 | 1 | – | 1 | 26 | 8 | – | – | 10 | 30 | 1 |

jaw to juncture of branchiostegal membranes 5.4 (155); pelvic insertion to juncture of branchiostegal membranes 6.9 (198).

Body scaled except for breast and nape, and midline of belly for a distance extending one-fourth to one-third distance to anus. Opercle scaled; cheek naked except for patch of six to nine scales located immediately behind eye. One or two (usually embedded) scales in same region in some paratypes of *moorei* (CU 41966). Lateral line usually complete but occasionally a scale in advance of hypural poreless. Usually one or two normal-sized scales followed by three to five smaller scales behind hypural. Supratemporal canal complete, with three pores; supraorbital complete, with four pores; infraorbital complete, with eight pores; preopercularmandibular canal complete, with ten pores. Jaws, vomer and palatines well toothed. Branchiostegals are 6-6.

*Coloration:* Color differences are important in separating closely related species in the subgenus *Nothonotus*. Sexual dimorphism is pronounced. The following description is modified after one made by Dr. Ramsey based on specimens which had been in formalin for two days after their capture on 7 December 1963 and on notes made from live and freshly preserved specimens collected by Raney and Sutkus on 1 February 1964.

In the male the head from the posterior interorbital area to the midfrenum has russet vermiculations on a field of dusky yellow. The area is bounded ventrally by a dark brown, thin preorbital bar, which originates just below the anterior midpoint of eye and slants forward and slightly downward to the maxillary and beyond to the upper lip. Here the two preorbital bars do not coalesce, but extend posteriorly on the lip. The top surface of the snout is lighter than the head behind the eyes. The top of head from the posterior, interorbital region to the nape and downward to the upper posterior edge of opercle is russet-brown. The scaled portion of the opercle is dusky brown. A short, narrow, black postorbital bar covers part of the scaled portion of upper anterior cheek at the level of the lower edge of the pupil. A dark spot behind the upper part of the eye tends to circle upward and usually crosses the top of the head. The upper two-thirds of the cheek is yellow-orange and the lower one-third except for the very lower edge, is immaculate white. Fine black spots are scattered over the cheek and adjacent lower head except immediately before and after the suborbital bar. A black subocular bar extends obliquely backward from lower midpoint of eye to lower edge of the subopercle. Just below the eye a black spur from the suborbital bar extends forward beyond the posterior tip of the maxillary but does not reach the upper lip. The underside of the lower jaw has scattered melanophores which appear as a dark line. The area between the lower jaws has melanophores interspersed with yellow-orange chromatophores. In life this area is superficially iridescent pale green extending from the lower jaw symphysis to the subocular bar. The branchiostegal membranes are pale blue along the inner and posterior edges. Pupil amber and ringed by an iridescent golden iris.

The dark-brown nape is interrupted by a narrow, russet band which extends downward to about the level of the third scale row above the lateral line just behind the posterior edge of the opercle. A short, sharply-defined humeral bar barely extends downward to a point slightly below the upper edge of the pectoral fin. The prepectoral region has diffuse melanophores on a pale orange background. The breast, to a point between the pelvic fins, is pale blue in life. The belly is white. The anus is encircled by yellow-orange.

The dorsum and upper sides of the body are brownish; the lower sides are lighter than the upper sides and olivaceous. In both sexes dark punctulations are scattered along the dorsum. In life about one-third of the males had one to 12 (mostly 1-3) bright red spots on the lower sides and occasionally there were yellow spots. Eight brownish saddles across the dorsum. Nine to 11 vague, vertical, brownish bars cross the body; the terminal bar at the posterior end of the caudal peduncle is best defined and encircles the caudal peduncle below. The penultimate bar is next best developed. The other bars tend to be interrupted and appear as diffuse dark blotches along the midside (see Fig. 1). A small area of the lower caudal peduncle at the anteriormost procurrent rays is yellow, as is the venter just anterior to the dark band which encircles the caudal peduncle. The dorsal procurrent rays are dark brown.

Females resemble males in coloration of the head and body, except there are more bright crimson dots forming irregular rows on the side of the body. These dots number from 26 to 56, and each covers the anterior one-third of a scale. Other spots are russet or brownish. The red dots are distributed from just before the tip of the appressed pectoral to the caudal peduncle and usually extends from four scale rows above to three scale rows below the lateral line. The female also has whitish dots on the body.

Narrow, dark horizontal lines are present on the posterior side of the body in the male (mostly on the caudal peduncle) but are faint in many specimens. They are fainter or absent in the female and are much less distinct than in other described species of the subgenus *Nothonotus.* In both sexes, but especially in the female (Fig. 1), the dark markings on the side of the body are outlined by irregularly shaped or rectangular light areas.

The fins of the sexes differ in coloration. In the male the first dorsal fin has a narrow dark margin which is most noticeable on the posterior two-thirds of the fin. A narrow subterminal light band reaches close to, or to, the margin anteriorly. Beneath this is a broad red or orange-red band which is sharply defined anteriorly but posteriorly diffuses over the lower half of the fin. This band is brightest on the posterior edge of each spine and contrasts with the duller interradial membrane. The extreme base of the fin fades to yellow-brown. In large adults particularly, the larger melanophores usually are distributed evenly on the basal two-thirds of the membranes. There is a spot at the base of each membrane.

In the female the first dorsal fin has a very narrow dark margin but in some specimens this margin is only partially developed; in a few, particularly small individuals, it is absent. Below the dark margin is a light area which is most prominent behind each spine and which forms an ill-defined horizontal band. A reddish band which is brightest anteriorly extends near the lower base of the fin and grades into dusky-brown at the base. This fin tends to be somewhat more spotted than in the male but basically the coloration in life or in freshly preserved specimens is the same. Superficially the first dorsal fin appears red on the lower half of the fin, has a thin dark margin and an intermediate light area.

The edge of the second dorsal fin in the male is bordered by a blackish band but the very tips of the rays are light. The blackish band is narrowest anteriorly. A narrow, submarginal, whitish band parallels the blackish band. A broad red or red-orange band extends through the middle of the fin. The lower third or fourth of the fin is olive. At the very base of the membranes there are dark spots.

The second dorsal in the female also has a moderately defined, dark terminal band. A red band is absent but red or russet spots are scattered over the fin. In addition, black spots are located mostly on the rays and appear in four or five irregular rows. A row of brownish spots is present on the base of the membranes. In life the red spots are prominent.

The anal fin of the male is much like the second dorsal fin. The former has a narrow light margin and a blue-black submarginal band in the soft-rayed portion of the fin.

The membranes associated with the first two rays (spines) were blue-green for their entire length except for a narrow vertical orange slash; the area is clear in preserved specimens. A red band extends through the middle of the anal. The base of the fin is olive or yellowish with dark spots at the base of the membranes.

In the female the anal fin is also like the second dorsal fin. An inner band in life is a red or red-orange. Usually three or four brown or red quadrate spots are found adjacent to each ray.

The caudal fin of the male has a very narrow terminal clear area and a subterminal black band of about the same width. Anterior to the latter is a yellowish band about half again as wide as the black band; the remainder of the fin is reddish with some yellow on the fin rays. A prominent character is the two dark basicaudal spots which tend to coalesce in some specimens.

In the female the caudal fin has a narrow terminal clear band and a blue-black subterminal band which is better developed in some specimens than others. The remainder of the fin is crossed by four or five wavy rows of spots which are russet or red in life and which in preserved specimens appear as small dark spots. As in the male there are two prominent dark basicaudal spots.

The posterior third of the pectoral fin in the male is clear. The lower rays are thickened near the tip. The basal two-thirds of the pectoral is pink or red; the latter is more pronounced on the rays and presents a streaked appearance. The fleshy base bears a prominent pink crescent. The prepectoral area lacks a strongly developed bar.

The pectoral fin of the female is colored much like that of the male. The outer one-fourth or one-third is clear; the extreme base is crossed by a pink crescent and the fin is red on the basal half. The rays are yellowish throughout. In preservative the rays bear scattered dark spots. There is no strong prepectoral bar.

The pelvic fin spine of the male has a whitish opaque tip. The tips of the lower rays are thickened and milky in color in both sexes. The basal two-thirds or three-fourths of the fin is red or orange-red and the color is concentrated mostly on the rays. The distal third or fourth of the fin is clear.

In the female the posterior tip and a small area at the base of the pelvic fin are clear. The central portion is yellowish with scattered brown and red spots. In preserved specimens there are two to three dark spots on the inner rays.

The urogenital papilla in the male taken February 1 is flattened and subtriangular with the apex pointing posteriorly; the apex does not reach the anterior base of the first anal spine. In the female the papilla is rounded posteriorly and in both sexes parallel grooves line the lower surface.

Males average slightly larger than females and in each of the six collections which contained more than one specimen a male was the largest specimen taken. Large young and yearlings have female-like spotted fins. Some yearlings were 21-22 mm in standard length and this size may represent the largest individuals at one year. *E. rubrum* probably spawns when two years old, and three years may be the maximum length of life as judged from a study of the length frequency distributions. A 46 mm male was the largest specimen captured.

*Comparisons and relationships:* Contrary to our statements in Copeia, 1964 (1):138, *E. rubrum* is closely related to *moorei* and they and an undescribed species from the Cumberland and Tennessee rivers form a species group in the subgenus *Nothonotus*. In these species the male is larger. *E. rubrum* is smaller than the other species. A comparison of *rubrum* with *moorei* (Tables 1-3) shows that the differentiation in most meristic characters is at a relatively low level, but is sharpest in number of lateral line scales. Like other species in the subgenus *Nothonotus* color pattern is an important species character. The major pattern differences are given in Table 3. Bright red color in females is unusual in darters where the males usually are more brilliantly colored.

Superficially *rubrum* resembles *camurum* in meristic characters but differs most in dorsal, anal, and pectoral rays and vertebral counts. However, *camurum* is recognized by us as a complex of subspecies and species and a generalized comparison is difficult. Data for *camurum* given in Tables 1 and 2 are for specimens taken from the Ohio River System as are the pattern differences noted below. The female of *rubrum* has prominent dark spots on the fins which are lacking in *camurum*. Both sexes in the former have the double dark basicaudal spot; none is present in *camurum*. A sharp, oblique, dark

TABLE 3.

A comparison of *Etheostoma rubrum* and *E. moorei*

| Character | *rubrum* | *moorei* |
|---|---|---|
| Patch of scales behind eye | From 6 to 9 large exposed scales | None, or one or 2 small scales |
| Eye | Longer than snout | Equals or shorter than snout |
| Prominent red spots on sides of body | Present; more so in ♀ | Absent or few in either sex |
| Dark punctulations on dorsal 3rd of body | Abundant | Absent or few |
| Dark horizontal streaks on posterior 3rd of body | Poorly developed; very faint in ♀ | Moderate in both sexes, but fainter in ♀ |
| Dark edge of dorsal and caudal fins | Weak or moderately developed | Prominent |
| Red bands in dorsal fins | Present in both sexes | Absent |
| Dark suborbital bar | Narrow and sharp | Wide and diffuse posteriorly |
| Cheek | Light | Dusky |
| Dark spot in procurrent caudal rays | Small | Large |
| Usual number of: | | |
| 1st dorsal spines | 10-11 | 11 |
| 2nd dorsal soft rays | 11-12 | 11-12 |
| Total dorsal rays | 21-23 | 22-23 |
| Left pectoral rays | 13-14 | 13-14 |
| Anal soft rays | 8 (often 7) | 7 (sometimes 8) |
| Vertebrae | 36-37 | 36 |
| Usual number of scales: | | |
| Lateral line | 50-53 | 53-57 |
| Anal to 1st dorsal | 15-17 | 16-18 |
| 2nd dorsal to anal | 13-15 | 14-16 |
| Around caudal peduncle | 19-21 | 20-22 |

suborbital bar is present in *rubrum* but is absent in *camurum.* Dark horizontal streaks are found in both sexes in *camurum* but are poorly developed in *rubrum.* The body of *camurum* is huskier and the snout is blunter than in *rubrum.* The cheek is naked in *camurum,* whereas rubrum has some large exposed scales behind the eye.

*Distribution:* E. rubrum is known only from the type-locality in Bayou Pierre and from its major tributary, White Oak Creek. Attempts by us and others to take it elsewhere in the same and nearby stream systems have failed. The preferred riffle habitat probably is limited and the range thus is restricted.

*Ecology and associates:* On 1 February 1964, *E. rubrum* was taken by Raney and Suttkus in a long riffle at the type-locality using a 12x6 foot nylon seine with 1/4 inch mesh. At this time the flow was moderate and the riffle-pool habitat varied in width from 60 to 100 feet. The depth in the deeper sections of the riffles approached three feet and that in the pools exceeded five. The water was slightly turbid. No vegetation was present.

The bottom was bedrock and was partly covered by loose gravel with an occasional sand bar or a mixture of sand and small gravel. *E. rubrum* was usually taken over gravel near, but not in, the swiftest current. Earlier at the same place on 7 December 1963, Dr. Ramsey took both juveniles and adults in moderately swift current over packed gravel. He noted that adults were most abundant near the head of riffles in water less than one foot deep but that some were found in the more turbulent areas. *E. rubrum* was taken most often in the same seine haul with *Etheostoma zonale* (Cope) and *Noturus hildebrandi* (Bailey and Taylor) but *E. rubrum* frequently was found in deeper water. *E. rubrum* was taken infrequently in the same set with *Percina uranidea* (Jordan and Gilbert) and rarely with *Percina sciera* (Swain). Other species taken in the same riffles or nearby pools were: *Dorosoma cepedianum* (LeSueur), *Hypentelium nigricans* (LeSueur), *Moxostoma* *poecilurum* (Jordan), *Ericymba buccata* Cope, *Hybognathus nuchalis* Agassiz, *Hybopsis amblops* (Rafinesque), *Hybopsis bellica* (Girard), *Notemigonus crysoleucas* (Mitchill), *Notropis atherinoides* Rafinesque, *Notropis camurus* (Jordan and Meek), *Notropis chrysocephalus isolepis* Hubbs and Brown, *Notropis longirostris* (Hay), *Notropis lutrensis* (Baird and Girard), *Notropis v. venustus* (Girard), *Notropis volucellus* (Cope), *Pimephales notatus* (Rafinesque), *Pimephales vigilax perspicuus* (Girard), *Ictalurus punctatus* (Rafinesque), *Noturus miurus* Jordan, *Noturus funebris* Gilbert and Swain, *Fundulus notatus* (Rafinesque), *Chaenobryttus gulosus* (Cuvier), *Lepomis megalotis* (Rafinesque), *Micropterus p. punctulatus* (Rafinesque), *Ammocrypta asprella* Jordan and Meek, *Ammocrypta beani* Jordan, *Ammocrypta vivax* Hay, *Etheostoma histrio* Jordan and Gilbert, *Etheostoma stigmaeum* (Jordan), and *Etheostoma whipplei artesiae* (Hay).

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September 1, 1966

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Volume 13, Number 4 February 24, 1967

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TULANE STUDIES IN ZOOLOGY
Volume 13, Number 4 February 24, 1967

# A REVIEW OF THE COLUBRID SNAKE GENUS *CEMOPHORA* COPE

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## ABSTRACT

The monotypic genus *Cemophora* occurs throughout most of the southeastern United States, from southeastern Missouri, southern Illinois, and southern Indiana, southward to the Gulf of Mexico and eastward to the Atlantic coast as far north as New Jersey, excluding most of the Appalachian Mountain Chain; to the west the range extends to eastern Oklahoma and eastern Texas, with a population occurring in southern Texas separated by a hiatus of some 300 miles from the nearest eastern Texas locality. The genus is considered to be most closely related to *Lampropeltis*, especially the *Lampropeltis triangulum* group. The nomenclatural history of *Cemophora coccinea* is reviewed. An analysis of sexual dimorphism, ontogenetic variation, individual variation, and geographic variation is presented. Three subspecies may be distinguished on the basis of number of ventrals, supralabials, and pattern. The name *C. c. coccinea* is applied to the peninsular Florida population, *C. c. lineri* is the southern Texas race, and *C. c. copei* is used for the wide-ranging northern subspecies. It appears that the nominate race and *lineri* are closely related, suggesting a Pleistocene climatic condition that caused a split in the population and withdrawal into Texas and Florida (and adjacent areas) refugia. Later, as climatic conditions become favorable, the species reinhabited the southeast from Florida (and adjacent areas). The Suwanee Straits of northern Florida allowed the isolation necessary for the differentiation of *copei* from *coccinea*.

The scarlet snake was described as *Coluber coccineus* by Blumenbach (1788) from a Florida specimen. Gmelin (1789) repeated Blumenbach's description in the 13th edition of Linnaeus' *Systema Naturae.* Sowerby in 1804 described a specimen of a snake reportedly from Dumfrieshire, Scotland, as *Coluber dumfrisiensis.* Allocation of this name to the synonymy of *Cemophora coccinea* was made somewhat hesitatingly by Schmidt (1954). Merrem in 1820 treated *coccinea* under the genus *Elaps.* In 1837 Schlegel placed *coccinea* in the genus *Heterodon* on the basis of the enlarged maxillary teeth. Holbrook (1842) disagreed with Schlegel and placed it in the genus *Rhinostoma.* Duméril, Bibron, and Duméril (1854) placed *coccinea* in the genus *Simotes* (a junior synonym of a mammalian genus; apparently = *Oligodon*).

Cope (1860) considered the scarlet snake to be generically distinct and described a new genus, *Cemophora,* for it. He distinguished *Cemophora* from *Simotes* primarily on the basis of the form of the rostral scale. Unaware of Cope's work, Jan (1862) made the same distinction between the scarlet snake and the snakes of the genus *Simotes* and placed it in a new genus, *Stasiotes.* Cope's name has priority, however, hence the name stands as *Cemophora coccinea.*

Jan (1862) described *Cemophora copei* from Tennessee, based primarily on the fact that his specimen had the loreal entering the eye and had a greater number of body blotch-

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es than typical *C. coccinea.* Garman (1884) considered *copei* a variety of *coccinea.* Cope (1900), however, placed *copei* in the synonymy of *coccinea,* where it has remained.

There has been much controversy in the last fifty years over the correct specific name for the scarlet snake (and, consequently, the specific name of the scarlet king snake). Stejneger (1918) was the first to comment on this problem, and suggested that the name *Coluber doliatus* Linnaeus, 1766, was not applicable to the scarlet king snake. He also pointed out the inapplicability of Schlegel's (1837) *Coronella coccineus* to either the scarlet snake or the scarlet king snake. *Coronella coccineus* probably is applicable to the same form described by Holbrook a year later as *Coluber elapsoides,* although Schlegel cited *Coluber coccineus* Latreille, 1802. Latreille, however, had reference to the scarlet snake *Coluber (=Cemophora) coccineus* of Blumenbach, 1788, and Schlegel's description makes it apparent that he was referring to the scarlet king snake *(Lampropeltis triangulum elapsoides).*

Klauber (1948), in contrast to Stejneger, felt that the name *Coluber doliatus* Linnaeus, 1766, could be correctly allocated and that it applied to the scarlet king snake and not to the scarlet snake. His beliefs were based on the fact that only two species in the Carolinas have both the ringed pattern and the ventral and caudal counts to satisfy Linnaeus' description. Since the original description also stated that the paired black rings do not quite surround the body, it could only apply to the scarlet king snake inasmuch as the scarlet snake has an immaculate venter.

Mittleman (1952) upheld Stejneger's disposition of the name *Coluber doliatus,* examining each of Klauber's main points in some detail, demonstrating that a different interpretation could be made, and that his (Mittleman's) interpretation would have the added advantage of retaining a well-established name. He demonstrated that there was little chance that a specimen of the scarlet king snake from the Carolinas would have 164 ventral scutes inasmuch as the highest numbers of ventrals in the scarlet king snake occur in the northern portion of the range and that out of a sample of 84 specimens of the scarlet king snake only three had 164 ventrals or less and these three were all from Florida. He also showed that a 164 count would be typical for *Cemophora* from the Carolinas. H. M. Smith (1952), in a short paper on the same subject, essentially agreed with Mittleman.

Smith, Lynch, and Puckette (1964 and 1965) took up the problem in an application to the International Commission on Nomenclature. They utilized data from ventral counts and information from the original description of *Coluber doliatus* by Linnaeus (1766), translated for them by a noted Linnaean scholar, Dr. Donald P. Rogers, Department of Botany, University of Illinois, and presented a convincing argument for placing the name *Coluber doliatus* Linnaeus, 1766, in the synonymy of *Cemophora coccinea.* They then requested that the name *doliatus* as used in the combination *Coluber doliatus* Linnaeus, 1766, be suppressed for the purposes of the Law of Priority. The basis for this is that the name *doliatus* has been too closely associated in the literature with the scarlet king snake. Although a decision on this problem is still pending, we are following the suggestions outlined by Smith, Lynch, and Puckette (op. cit.).

## CEMOPHORA Cope, 1860

*Cemophora* Cope, 1860: 244.
*Stasiotes* Jan, 1862: 75 (type species, *Coluber coccineus* Blumenbach).

*Type species.—Coluber coccineus* Blumenbach, 1788.

*Generic diagnosis.*—A small to medium-sized snake with the rostral enlarged and projecting beyond the lower jaw, with the last two maxillary teeth distinctly enlarged and saber-like (Fig. 1), and with a dorsal pattern of red saddles bordered by black, between which are white or light yellow interspaces. The venter is immaculate; the snout is red. Pattern alone will separate this genus from all other North American genera with the possible exception of *Lampropeltis*

Figure 1. Left maxilla of *Cemophora coccinea,* showing enlarged posterior teeth.

(some races of *L. triangulum*) from which *Cemophora coccinea* differs by having enlarged posterior maxillary teeth and the large rostral.

### *Description*

*Scutellation and size.*—Rostral wider than high, strongly projecting, visible above for a distance equal to three-fourths the width of rostral. Rostral projecting between internasals for a distance equal to one-half the greatest length of internasals. Internasal suture equal in length to that of prefrontal suture, but internasals much smaller than prefrontals. Canthus rostralis rounded. Frontal almost hexagonal, almost as wide as long. Supraoculars small, their length equal to one-half the length of frontal. Eye distinctly visible from above. Parietals truncate to slightly rounded behind. Length of parietal suture almost one-half the length of frontal. Nasal scale divided; naris situated approximately in center of scale. Loreal single, small, about twice as long as high. Preoculars normally one. Postoculars normally 2, the lower somewhat smaller. Temporals usually 1 + 2. Supralabials usually 6 or 7; 2nd and 3rd supralabial entering the eye when the number is 6, the 3rd and 4th entering the eye when the number is 7. Infralabials usually 7, sometimes 6, 8, or 9. Three infralabials touching the anterior chin shields; 4th infralabial largest. Dorsal scales smooth, with two apical pits, usually in 19 rows throughout. Ventrals 149 to 195 (mean 168.9, 236 counts). Subcaudals in two rows, 31 to 50 (mean 40.7, 235 counts). Anal scale single. Females ranging from 148-705 mm total length, males 152-823 mm. Tail length/total length ratio range: females 0.111 to 0.163, mean 0.138, 83 counts; males 0.126 to 0.180, mean 0.148, 99 counts.

*Color.*—Color pattern consists of a series of black-bordered, red to red-orange blotches on a light gray, cream, or white background. Red blotches number 12 to 28 on the body

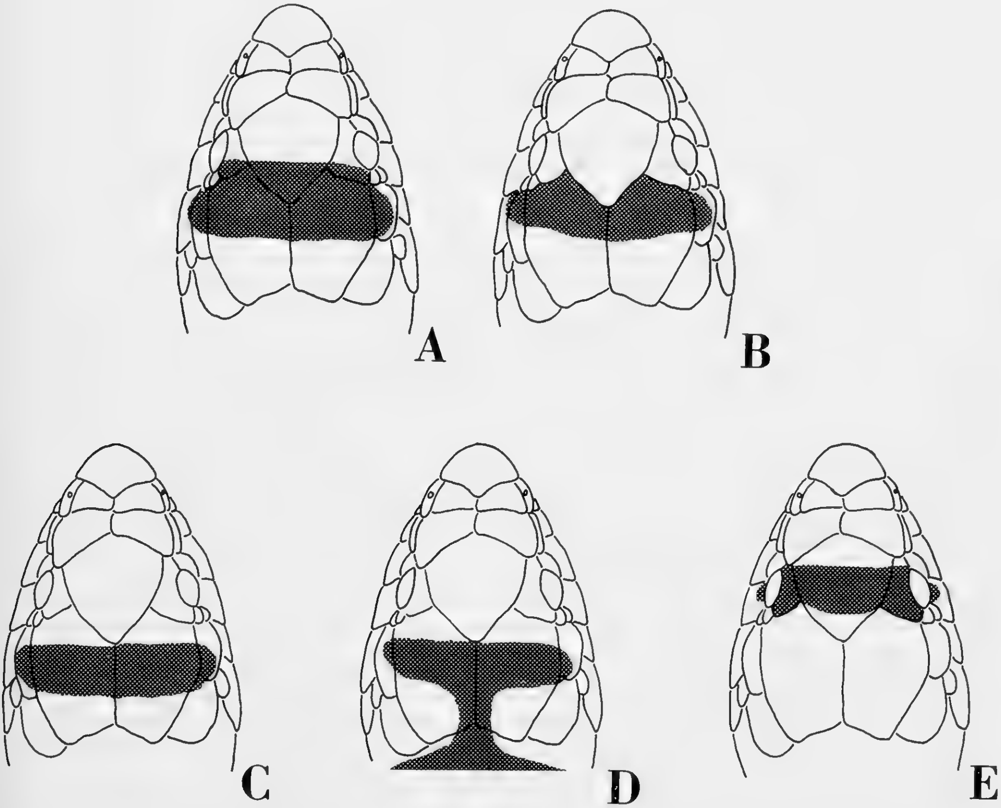

Figure 2. Diagrammatic representation of variation in head pattern of *Cemophora coccinea*. The most frequent pattern is represented by "A."

and 1 to 8 on the tail. Red blotches are usually longer than the black or white areas. The first red blotch ranges from 4½ to 12 scales in length and the fifth or sixth red blotch is from 1½ to 9 scales long. Both the first and the fifth or sixth white rings range from 1 to 4 scales in length. The venter is cream with an occasional slight invasion of the black rings into the lateral edges of the ventrals. The black band (Fig. 2) on the head varies in position from the middle of the frontal to the middle of the parietals; the rest of the head is red. This black band may be broken up or modified in any number of ways. The black band is followed by a white ring, then a black ring, and finally by the first red blotch. The lower portion of the side of the head is usually cream as is the chin.

*Hemipenis.*—This description was taken from an everted right structure (LSUMZ 7277). The hemipenis (Fig. 3) is bilobed with a single sulcus spermaticus extending onto the lateral lobe. The proximal area is naked. Distally a spinose area grades into a calyculate area that extends to the apices of the organ. Microornamentation of the calyces is papillate. The area between the lobes is naked. No apical differentiation occurs. Cope (1900, pl. 17, fig. 11) illustrates the *in situ* organ.

*Osteology.*—That *Cemophora* is a highly modified burrower is readily apparent from the anatomy of the skull. The overall appearance of the skull is one of smoothness. The premaxilla has a prominent anterior knob and is closely applied to the nasals, which are fused. The parietal shield is very weakly delimited. Both the prefrontals and postorbitals articulate with the maxillae. The quadrate is comparatively short and broad. Otherwise, the most interesting feature of the skull is the pair of enlarged posterior maxillary teeth on each side that are long, thin, and saber-like. Ranges in tooth counts are: maxilla 9-10 (6 counts), pterygoid 9-11 (4 counts; a fifth example having 3 teeth probably exhibits aberrant development), palatine 9-10 (4 counts), dentary 9 (6 counts).

## *Individual Variation*

*Supralabials.*—The number of supralabials varies from three to eight. Counting each side separately the following percentages of frequency were obtained: 6 (61.9), 7 (31.7), 5 (5.7), 8 (0.2), 4 (0.2), 3 (0.2). Considering both sides of the head the following combinations were observed: 6-6, 6-7, 7-7, 7-8, 5-6, 5-5, and 4-3. When the number of supralabials is 6, the 2nd and 3rd enter the orbit. When the number is 7, the 3rd and 4th enter the orbit. When the number is 5, the 2nd and 3rd enter the orbit, indicating that the point of reduction is behind the eye. In the one specimen (FMNH 22665) that has 8 supralabials on one side of the head, the 3rd and 4th enter the eye, indicating the addition is behind the eye. In the one specimen (MCZ 1344) with a supralabial count of 4-3, only the 2nd supralabial enters the eye. The significance of the high percentage of 6 and 7 supralabials will be discussed below.

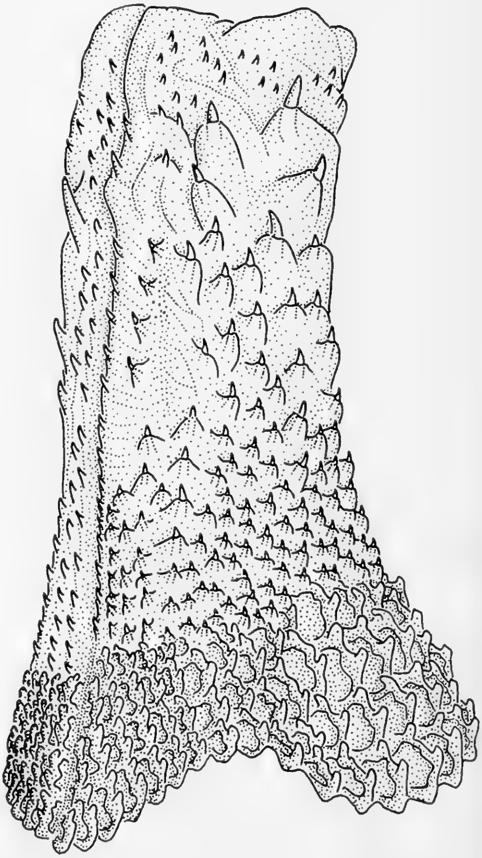

Figure 3. Sulcate view of right hemipenis of a *Cemophora coccinea* x *copei* intergrade (LSUMZ 7277) from 4 mi. WSW Otter Creek, Levy Co., Florida.

*Infralabials.*—The number of infralabials varies from 5 to 9. Counting each side separately the following percentages were obtained: 7 (57.1), 8 (27.3), 9 (9.9), 6 (5.4), 5 (0.2). Considering both sides of the head the following combinations were observed: 7-7, 9-9, 8-8, 7-8, 8-9, 6-7, 7-9, 6-8, 5-6, 6-6. When the number of infralabials is 6 or 7, the 4th is the largest, and three infralabials touch the anterior chin shields. When the number of infralabials is 8 or 9, the 5th is the largest, and usually 4 infralabials touch the anterior chin shields.

*Loreal.*—The loreal normally abuts against the lower portion of the preocular but occasionally protrudes beneath it and enters or nearly enters the orbit. There is no variation in the number of loreals, all counts being 1-1.

*Preoculars.*—Preoculars are invariably 1-1 with a single exception, that being 1-0.

*Postoculars.*—The number of postoculars is normally 2-2 (90.9) but there is some variation, as follows: 1-1 (6.6), 2-1 (1.4), and 3-2 (.95).

*Dorsal scale rows.*—There is considerable variation in the number of dorsal scale rows. The most common count is 19-19-19 (54.4). The following combinations also occur: 19-19-17 (14.6), 21-19-19 (12.1), 19-19-18 (5.1), 20-19-19 (1.9), 17-17-17 (1.9), 21-19-18 (1.3), 21-19-17 (1.3), 19-19-17 (1.3), 18-19-17 (1.3), 21-20-19 (0.07), 20-19-18 (0.07), 19-18-14 (0.07), 19-17-16 (0.07), 17-19-17 (0.07), 17-17-15 (0.07). Anterior counts were made one head length posterior to the first row of dorsal scales; middle counts were made approximately at mid-body; posterior counts were made just anterior to the anus.

*Head pattern.*—An attempt was made to categorize the variation of the black band on the head into several "basic types." We have designated five of these (Fig. 2). The most frequent type of head pattern (Fig. 2, A) is one in which the black band covers the posterior one-third of the frontal and anterior one-third to one-half of the parietal. The four remaining types are: (B) the black band is on the anterior one-third of the parietals and abuts against the posterior border of the frontal and supraoculars; (C) the black band crosses the middle of the parietal; (D) the black band of the head is joined with the first black band of the body; (E) the black band crosses the middle of the frontal and supraoculars. However, intermediate conditions between these types do occur and no two snakes have exactly the same head pattern.

The snout is normally red but occasionally scattered black pigment is present.

*Albinism.*—Brimley (1942) reported an albino specimen from between Reidsville and Leaksville, Rockingham County, North Carolina, with the comment that "It was about fifteen inches long and had the black bands replaced by white, the red spots reduced in size and the white (for black) and yellow ones widened."

### *Sexual Dimorphism*

Sexual dimorphism occurs in number of ventrals, in tail length/total length ratios, and to a lesser extent in number of body blotches. Considering the entire geographic range of the species, females have a larger mean number of ventrals (170.3, 96 counts) than do males (165.8, 110 counts). Mean differences in caudal number is very slight, the means being 41.7 (111 counts) in males and 40.4 (94 counts) in females. Males have a proportionally longer tail (tail/total length = 0.148) than do females (0.138). Males also tend to have a higher number of body blotches (mean for males 18.3, 111 counts; for females 17.6, 101 counts). The only characteristic significant at the .05 level using the "t" test is the number of ventrals.

### *Ontogenetic Variation*

Perhaps the most striking ontogenetic variation in *Cemophora* is the change in coloration. Neill's report (1950:62) of this phenomenon is quoted in full: "In the newly hatched *Cemophora* the back bears a row of scarlet saddles that extend downward on the sides to the second or third scale rows above the ventral plates. The saddles are bordered anteriorly and posteriorly with black, and are separated by clear white interspaces. The white of the venter extends upward on the sides to include one or two scale rows and is also continuous with the white of the dorsal interspaces. Extending the length of the body along the ventrolateral region is an irregular row of black flecks, which form narrow lateral borders to the red saddles, and which tend to form a black spot just above the ventrals at the level of each white interspace. The degree of ventrolateral flecking is subject to considerable individual variation.

"Specimens of about 12 inches length begin to show a faint yellowish suffusion in the vertebral portion of each transverse white marking. As the snake grows older the yellow intensifies and spreads laterally. The ventrolateral black flecking is reduced, while the transverse black bands extend farther down on the sides and on to the ventral plates. The red likewise extends laterally, and also becomes richer and deeper. The fully adult scarlet snake is marked with deep red transverse bands that extend upon the tips of ventrals, and these red bands are bordered with narrower black ones that encroach even farther upon the abdominal scutes. The black-bordered red bands are separated by bright yellow interspaces, the yellow fading into white in the ventrolateral region. Often, but not invariably, there is a black spot on each side, just above the ventrals, at the level of each yellow interspace. The adult scarlet snake, viewed even from the side, appears to be ringed with red, yellow, and black; this is not the case with young examples. In favorable ecological areas the herpetologist may collect a series of large adults that appear to differ from the more familiar (and smaller) specimens generally encountered elsewhere.

"In very old specimens there is a general darkening and dulling of the entire pattern, the red becoming dark red-brown, and the yellow becoming tan or even light gray-brown. The darkening begins in the vertebral region and progresses laterally with age."

Woolcott (1959: 263), mentioned that newly hatched *Cemophora* have, "soft pink colored saddles rather than the characteristic red."

### *Ecological and Life History Notes*

Aside from a few miscellaneous notes on food and food habits, habitat, and activity, there is little information available on the ecology of *Cemophora.*

*Food.*—The data available in the literature have been placed in tabular form (Table 1). Small lizards and reptile eggs appear to form the bulk of the diet, with insects, small amphibians, and young mammals making up a lesser portion. No detailed stomach content studies have been undertaken in this species, but should prove worthwhile if enough material can be obtained.

Feeding on eggs may be correlated with the enlarged posterior maxillary teeth of *Cemophora* (Minton and Bechtel, 1958). Neill (1951), however, surmised that *Cemophora* may puncture eggs with its pointed snout.

TABLE 1.
Food records of *Cemophora coccinea.*

| Type of Food | Reference |
|---|---|
| Probably worms and insect larvae | Minton, 1944 |
| Small frogs, lizards, and insects | Haltom, 1931 |
| *Acris* | Brode and Allison, 1958 |
| Anole | Wilson, 1951 |
| Small lizards and snakes | Brimley, 1942 |
| *Lygosoma, Eumeces, Haldea,* young of *Diadophis,* and young of wild mice | Ditmars, 1936 |
| Eggs of *Terrapene c. bauri* | Dickson, 1948 |
| Eggs of *Elaphe g. guttata* | Minton and Bechtel, 1958 |
| Eggs of *Graptemys* and *Pseudemys* (?) | Neill, 1951 |
| Eggs of *Cemophora* (in captivity) | Ditmars, 1936 |
| Hard orange or yellow substance in digestive tract (=solidified egg yolk?) | Palmer, *pers. comm.* |

*Habitat.*—Scarlet snakes are fossorial or semifossorial snakes coming to the surface primarily at night. Specimens have been collected in leaf litter, rotten logs, in various types of soil, especially sandy soil, and under rocks.

With respect to macrohabitat, scarlet snakes have been collected in pine forest, hardwood forest, and in mixed forest.

*Burrowing.*—Wilson (1951: 172) discussed burrowing behavior of the scarlet snake. "Placed in a container with several inches of loose soil, the snake soon began burrowing movements, thrusting the head to right and left until the head and neck were concealed. The procedure then was altered, the snake forcing the snout deeper into the soil and lifting it upward. This continued until the snake was completely concealed. It remained several days in concealment before again emerging."

### *Distribution*

*Cemophora coccinea* is mainly Austroriparian in distribution (Fig. 4), which fits Savage's (1960) map of the herpetological provinces of North America fairly well for this region. The main discrepancies are in the Ohio Valley region where the scarlet snake ranges farther north than Savage's boundary and in the western portion of the range where the species extends into Savage's Desert and Plains Province in eastern Oklahoma.

The range of the scarlet snake extends along the Atlantic coast from New Jersey southward to the southern tip of Florida, westward including all the Gulf coast states at least as far as Kenedy County, Texas; the range extends northward including eastern Texas, eastern Oklahoma, Arkansas, Tennessee, and Kentucky to southern Indiana, southern Illinois, and southeastern Missouri. Records for the Florida Keys (Carr, 1940) were discounted by Duellman and Schwartz (1958).

Physiographically speaking, the scarlet snake is primarily found on the Coastal Plain (Fenneman, 1949). The range of *C. coccinea* extends onto the Piedmont and as far north as the Interior Low Plateau. The scarlet snake apparently is absent in the main portion of the Appalachian chain.

Auffenberg (1948: 212) was the first to report the scarlet snake in Texas. He stated, however, that "there is no doubt that these snakes were accidentally brought in from Pensacola, Florida." We have corresponded with Dr. Auffenberg, hoping to borrow the specimens and perhaps pin down more precisely the provenance of these specimens, but he reported that the specimens have apparently been discarded. It is likely that the

Figure 4. Distribution of *Cemophora coccinea* and subspecies. Squares represent *C. c. coccinea;* circles, *C. c. copei;* triangles, *C. c. lineri;* square-circle combination, *coccinea-copei* intergrades; open symbols, literature records.

specimens represented the southern Texas race.

*C. coccinea* has been recorded from central and southeastern Missouri (Anderson, 1965; Nickerson, in press). Anderson reported scarlet snakes from Dunklin and Phelps counties, although the Dunklin specimen is not available for confirmation. Nickerson reported three additional specimens from Miller and Camden counties.

A specimen of *C. coccinea* collected at Wolf Lake Swamp, Union County, Illinois (Bennett, 1953) represents the single record for that state. The specimen cannot now be found in the collections of Southern Illinois University, according to Dr. Ronald Brandon (pers. comm.). P. W. Smith (1961) accepted the record as valid.

Three specimens were reported from extreme southeastern Indiana, by Minton and Bechtel (1958) who drew attention to the interesting fauna found on the bare slopes at the southern end of the Knobstone Escarpment. This area is also the only portion of that state where *Tantilla c. coronata, Cnemidophorus sexlineatus,* and a large trap-door spider have been found.

Kentucky records have recently been reviewed by Fuller and Barbour (1962) and Collins (1964).

Records from the Delmarva Peninsula (Delaware, and the peninsular parts of Maryland and Virginia) have been summarized by Conant (1958).

Scarlet snakes apparently are widespread in Louisiana. Their actual abundance is uncertain; prior to the summer of 1966 only about twelve specimens were known from the state. However, during June, 1966, one of us (Williams) collected seven specimens in Natchitoches Parish, six in two nights, suggesting that the species may not be as rare as formerly thought.

The scarlet snake is not common anywhere in its range, but appears to reach its greatest abundance in Florida and North Carolina, where it is not infrequently encountered in some localities. Impressions of abundance, however, simply reflect availability of material.

## *Generic Relationships*

The affinities of the scarlet snake, *Cemophora coccinea,* apparently are with a group of five North American genera *(Lampropeltis, Rhinocheilus, Stilosoma, Arizona,* and *Pituophis)*, which all agree in being generalized colubrids of constricting habits and in having a long intrapulmonary bronchus (Underwood, 1966). The hemipenis in these genera, consists of a bilobed structure with a single *sulcus spermaticus* ending obliquely in one lobe, with apical calyces of variable extent, and with nonenlarged spines on the medial portion. The basal area typically is smooth or with small spinules. The genus *Cemophora* appears to be most closely related to *Lampropeltis* (Tables 2 and 3). It differs from that genus in having a more prominent rostral, enlarged posterior maxillary teeth, and a smaller number of maxillary teeth.

To show the generic relationships of *Cemophora,* we have attempted to set up a system similar to that set up by Norris (1958: 294) showing specific relationships within the lizard genus *Uma.* These data are presented in Tables 2 and 3. By this method the following relationships are shown, from the closest to the most distant: *Lampropeltis, Arizona* and *Rhinocheilus* (equally close), *Stilosoma,* and *Pituophis.* The genus *Stilosoma,* although exhibiting certain unique features, appears to be more closely related to *Cemophora* than to any of the other genera.

*Cemophora coccinea* most closely resembles certain members of the *Lampropeltis triangulum* group (particularly *L. triangulum syspila*) in terms of color pattern. It resembles *L. t. elapsoides* (= *L. doliata doliata* of many authors) most closely in development of the rostral plate, numbers of ventrals and caudals, numbers of supralabials and infralabials, and number of temporals. The scarlet snake differs from *L. t. elapsoides* in not having the rings of the dorsal pattern continued onto the venter. There is a possibility of convergence of the various characters involved between these species. In our present state of knowledge, however, it seems best to consider the genus *Cemophora* to be a derivative of some member of the *triangulum* group, which became adapted to a more fossorial existence and to a more specialized diet consisting in large part of the eggs of reptiles.

TABLE 2.
*Comparison of Cemophora with related genera*[1]

| | *Lampropeltis* | *Rhinocheilus* | *Arizona* | *Pituophis* | *Stilosoma* | *Cemophora* |
|---|---|---|---|---|---|---|
| Ventrals | 152–254 | 181–218 | 185–241 | 205–262 | 239–277 | 149–195 |
| Subcaudals | 27–79 | 41–61[2] | 39–63 | 47–84 | 33–48 | 31–50 |
| Supralabials | 7–8 | 8(6–9) | 8(7–9) | 8–9(7–10) | 6 | 6–7 |
| Infralabials | 9–10 | 9(8–11) | 11–15 | 10–15 | 6–7(5–8) | 7(6–9) |
| Internasals | 2 | 2 | 2 | 2 | 2 | 2 |
| Prefrontal | 2 | 2 | 2 | 2–4 | 2 | 2 |
| Nasal | divided | divided | semidivided | divided | single | divided |
| Loreal | 0–1 | 1 | 1 | 0–1 | none | 1 |
| Preocular | 1 | 1–2 | 1(2) | 1–2(3) | 1(0) | 1 |
| Postocular | 2 | 2 | 2(1) | 2–4 | 2 | 2 |
| Temporals | 2 + 3 + 4 | variable | 2 + 3 | variable | 1 + 1 | 1 + 2 |
| Anal plate | entire | entire | entire | entire | entire | entire |
| Dorsal Scales[3] | 17–27(2) | 23–25(1–2) | 25–31(1) | 27–37(2) | 19(0) | 19(2) |
| Total length/ tail ratio | 0.09–0.18 | 0.12–0.17 | 0.11–0.17 | 0.10–0.19 | 0.07–0.10 | 0.11–0.18 |

[1] Data obtained from the following sources: *Lampropeltis* (Blanchard, 1921), *Rhinocheilus* (Klauber, 1941), *Arizona* (Klauber, 1946), *Pituophis* (Stull, 1940), *Stilosoma* (Highton, 1956).

[2] Most subcaudals undivided; in five other genera they are divided.

[3] All genera except *Pituophis* have smooth dorsal scales; number in parenthesis refers to number of apical pits, preceding figures refer to number of scale rows at midbody.

TABLE 3.
*Relationships of the Lampropeltis-like Genera*

| | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| | *Lampropeltis* | *Rhinocheilus* | *Arizona* | *Pituophis* | *Stilosoma* | *Cemophora* |
| Ventrals | 2,3,6 | 1,3,6 | 1,2,6 | 5 | 4 | 1,2,3 |
| Caudals (number) | 2,3 | 1,3 | 1,2 | – | 6 | 5 |
| Caudals (divided or not) | 3,4,5,6 | – | 1,4,5,6 | 1,3,5,6 | 1,3,4,6 | 1,3,4,5 |
| Supralabials | – | 3 | 2 | – | – | – |
| Infralabials | 2 | 1 | 4 | 3 | 6 | 5 |
| Internasals | 2,3,4,6 | 1,3,4,6 | 1,2,4,6 | 1,2,3,6 | – | 1,2,3,4 |
| Prefrontals | 2,3,6 | 1,3,6 | 1,2,6 | – | – | 1,2,3 |
| Nasal | 2,4,6 | 1,4,6 | – | 1,2,6 | – | 1,2,4 |
| Loreal | 4 | 3,6 | 2,6 | 1 | – | 2,3 |
| Preocular | 6 | 3,4 | 2,4 | 2,3 | – | 1 |
| Postocular | 2,3,5,6 | 1,3,5,6 | 1,2,5,6 | – | 1,2,3,6 | 1,2,3,5 |
| Temporals | 2,3 | 1,3 | 1,2 | – | – | – |
| Anal plate | – | – | – | – | – | – |
| Dorsal scales | 2,3,4 | 1,3,4 | 1,2,4 | 1,2,3, | 6 | 5 |
| Total length/ tail length ratio | 2,3,4,6 | 1,3,4,6 | 1,2,4,6 | 1,2,3,6 | – | 1,2,3,4 |
| Color pattern | 6 | 5 | 4 | 3 | 2 | 1 |
| *Lampropeltis* | – | 10 62% | 9 56% | 6 38% | 2 12% | 9 56% |
| *Rhinocheilus* | 10 62% | – | 11 69 | 5 31 | 2 12 | 7 44 |
| *Arizona* | 9 56 | 11 69 | – | 7 44 | 2 12 | 7 44 |
| *Pituophis* | 6 38 | 5 31 | 7 44 | – | 2 12 | 5 31 |
| *Stilosoma* | 2 12 | 2 12 | 2 12 | 2 12 | – | 5 31 |
| *Cemophora* | 9 56 | 7 44 | 7 44 | 4 25 | 5 31 | – |

We have patterned this method of showing relationships after Norris (1958: 294). Each genus is assigned a number and by the use of these numbers, similarities of one or more genera to any one genus can be noted. A blank space generally reflects the lack of affinities with any of the other genera.

The lower portion of this table summarizes the above information. For example, *Cemophora* exhibits 9 characters out of 15 in common with, or a 58 per cent similarity to, *Lampropeltis* and links it most closely with that genus.

## *Discussion of Subspecies*

### *Cemophora coccinea coccinea*
(Blumenbach)
(Figure 5)

*Coluber coccineus* Blumenbach, 1788: 11; Gmelin *in* Linnaeus, 1788: 1097; Daudin, 1803: 43 (part); Harlan, 1827: 356 (part).

*Elaps coccineus:* Merrem, 1820: 145 (part).

*Heterodon coccineus:* Schlegel, 1837: 141 (part).

*Rhinostoma coccineus:* Holbrook, 1842: 125, pl. 30 (part); Baird and Girard, 1853: 118 (part).

*Rhinostoma coccinea:* Baird, 1859: pl. 33, fig. 89.

*Simotes coccineus:* Duméril, Bibron, and Duméril, 1854: 637; Günther, 1858: 26.

*Stasiotes coccineus:* Jan, 1862: 75 (by inference; part).

*Cemophora coccinea:* Cope, 1860: 244 (part); Jan, 1863a: 45 (part); Garman, 1884: 78 (part); Cope, 1888: 381 (part); Cope, 1892: 602 (part); Boulenger, 1894: 214 (part); Cope, 1900: 928 (part); Brown, 1901: 85 (part); Duellman and Schwartz, 1958: 306.

*Cemophora doliata coccinea:* Mittleman, 1952: 25.

*Cemophora doliata:* H. M. Smith, 1952: 26 (part).

*Cemophora coccinea coccinea:* Williams, Brown, and Wilson, 1966: 85 (part).

*Holotype.*—Apparently nonexistent. Type locality, "Florida."

*Range.*—The Florida peninsula south of approximately 29°5′ degrees of latitude.

*Diagnosis.*—A subspecies of *Cemophora coccinea* usually with 7 supralabials (91 percent have at least 7 on one side), with 4th and 5th supralabials entering orbit; ventrals 158-185, mean 174.0 (69.9 percent have 170 or more); body blotches 12-22, mean 17.6; black bands of dorsal pattern extending laterally to dorsal scale rows 1 or 2, and enclosing dorsal red blotches; black band of first body blotch not touching parietals (85.5 percent separated by 2 or more scales).

*Variation.*—Supralabials 6-8, mean 6.9 (118 counts). Ventrals 158-185, mean 174.0

Figure 5. Upper, *Cemophora coccinea coccinea* from Tampa, Hillsborough County, Florida (UF 1514). Photograph by J. Harvey Roberts. Lower, *C. c. lineri* from 34.5 miles S Riviera, Kenedy County, Texas (AMNH 75307), photograph by Gerald C. Schaefer.

(59 counts); subcaudals 36-50, mean 42.7 (61 counts). Body blotches 12-22, mean 17.6 (61 counts). In *C. c. coccinea* populations first black band on body never touching parietals, separated from parietals by 1-4 scales, means 2.3 (62 counts).

*Remarks.*—Duellman and Schwartz (1958: 306) mentioned that the number of body blotches in *Cemophora coccinea* in peninsular Florida decreases from north to south. Our data tend to support their contention, although the cline is not so clear-cut. Eighteen specimens from Alachua and Marion Counties (here considered as intergrades between *C. c. coccinea* and *C. c. copei*) have 10 to 25 dorsal blotches, mean 18.3. Fourteen specimens from Lake and Pinellas Counties have 16 to 22 dorsal blotches, mean 18.1. Twelve specimens from Dade and Collier Counties have 12 to 21 dorsal blotches, mean 16.2.

That the peninsular Florida animals might be distinct from the mainland form has been suggested by Neill (1950) and Mittleman (1952). Neill pointed out the low number of dorsal body blotches (discussed above) in southern Florida (Dade County) and the high number in Georgia (our data for 18 specimens show a mean of 18.4 for this state). He also mentioned some difference in head pattern, Georgia specimens having a straight black head band and southern Florida specimens having a black band in the form of a wide V, with the apex directed backwards. We have, however, found this character to be highly variable and of little geographic significance.

## *Cemophora coccinea copei* Jan

(Figure 6)

*Coluber coccineus* Daudin, 1803: 43 (part); Harlan, 1827: 356 (part).
?*Coluber dumfrisiensis* Sowerby, 1804: 5, pl. 3 (here considered a *nomen dubium*).
*Elaps coccineus:* Merrem, 1820: 145 (part).
*Heterodon coccineus:* Schlegel, 1837: 102 (part).
*Rhinostoma coccineus:* Holbrook, 1842: 125 (part); Baird and Girard, 1853: 118.
*Rhinostoma coccinea:* Baird, 1859: pl. 33, fig. 89.
*Simotes coccineus:* Duméril, Bibron, and Duméril, 1854: 637 (part); Günther, 1858: 26 (part).
*Cemophora coccinea:* Cope, 1860: 244; Jan, 1863b: 230; Jan, 1863a: 45 (part); Bocourt, 1883: 567; Garman, 1884: 78 (part); Cope, 1888: 381 (part); Cope, 1892: 602 (part); Boulenger, 1894: 214 (part); Cope, 1900: 928 (part); Brown, 1901: 85 (part); Stejneger, 1918: 99 (part).
*Stasiotes coccineus:* Jan, 1862: 75 (by inference; part).
*Cemophora copei* Jan, 1863b: 231; Jan, 1863a: 45.
*Cemophora coccinea* var. *copei:* Garman, 1884: 78.
*Cemophora doliata doliata:* Mittleman, 1952: 25.
*Cemophora doliata:* H. M. Smith, 1952: 26 (part); P. Smith, 1961: 223.

*Holotype.*—Presumably in the Geneva Museum, if designated. Type locality, "Tennessee."

*Range.*—New Jersey, southern Indiana, southwestern Illinois, and southeastern Missouri southward to the Gulf coast, including northern Florida, westward to eastern Texas. The scarlet snake apparently does not pene-

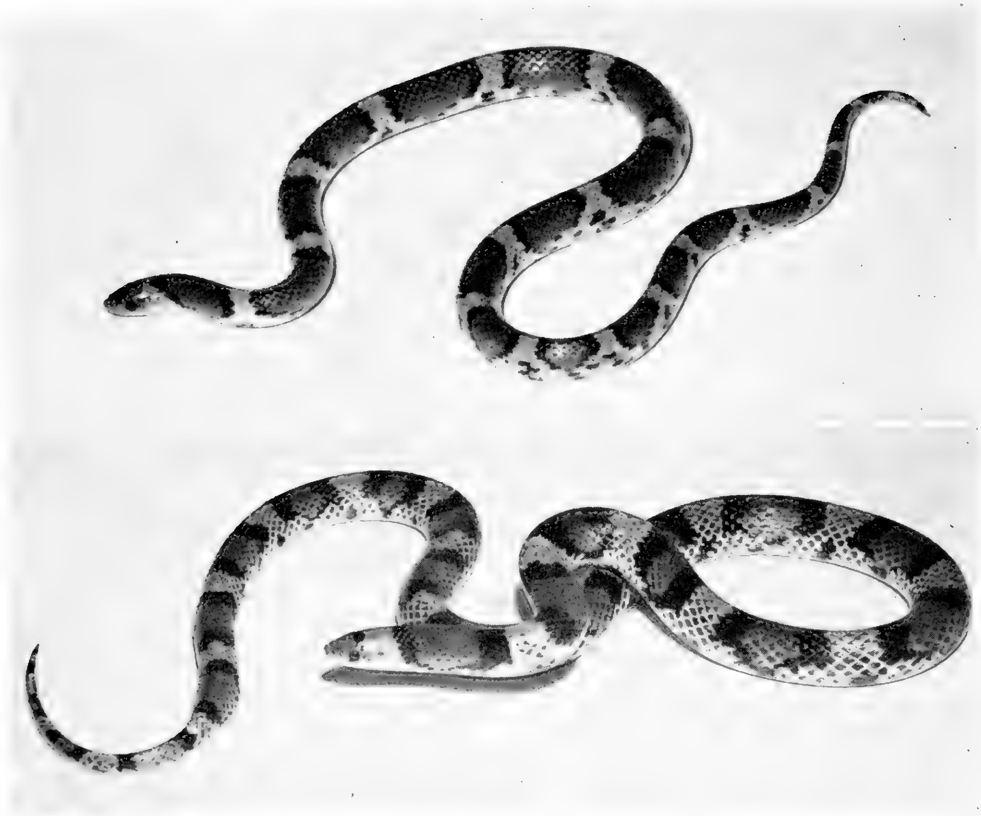

Figure 6. Upper, *Cemophora coccinea copei* from Lake Pine, Burlington County, New Jersey (AMNH 96127), showing juvenile pattern. Lower, *C. c. copei* from Blountstown, Calhoun County, Florida. Both photographs by Isabelle Hunt Conant.

trate far into the Appalachian Mountain chain.

*Diagnosis.*—A subspecies of *Cemophora coccinea* usually with 6 supralabials (82.4 percent have at least 6 on one side while lacking 7), the 3rd and 4th supralabials entering orbit; ventrals 150-180, mean 165.3 (70 percent 169 or less); body blotches 13-28, mean 18.6; black bands of dorsal pattern extending laterally to dorsal scale rows 1 or 2, and enclosing dorsal red blotches; black band of first body blotch usually touching parietals in 88 specimens, joining or approaching junction with black band of head in 77 specimens (85.1 percent touching, joined or separated from parietal by one or less scales).

*Variation.*—The subspecies *C. c. copei* exhibits considerable variation, some of which is of geographic interest (Table 4) and is discussed below.

Ventrals range from 150-180, mean 165.3 (180 counts), increasing clinally from north to south along the coastal plain. The means range from a low of 158.6 in New Jersey to a high of 170.0 in northern Florida. The mean number of ventrals remains approximately the same as that of northern Florida in those states bordering the Gulf of Mexico. The high ventral number in the peninsular Florida population apparently represents a southward extension of this cline. Inland there is a slight increase in ventral number from southwest (Oklahoma and Arkansas) to northeast (Indiana and Kentucky).

Caudals range from 30-48, mean 39.5 (161 counts). No clinal differences in the number of caudals comparable to those found in number of ventrals are apparent, the mean numbers for the states involved exhibiting a rather erratic pattern.

TABLE 4.
*Geographic variation in C. c. copei.* N = number of counts, R = range, X = means, T = first body blotch touching parietal, J = first body blotch joined with dark head band, NT = first body blotch not touching parietal.

| Locality | Ventrals | | | Subcaudals | | | Supralabials | | | Body blotches | | | First body blotch | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | R | X | N | R | X | N | R | X | N | R | X | T | J | NT |
| New Jersey | 16 | 153–162 | 156.9 | 16 | 35–43 | 38.3 | 31 | 5–7 | 5.9 | 17 | 14–19 | 16.0 | 11 | 0 | 6 |
| Maryland | 3 | 150–170 | 160.3 | 2 | 38–40 | 39.0 | 4 | 6 | 6.0 | 3 | 14–18 | 16.0 | 2 | 1 | 0 |
| Washington, D. C. | 1 | 161 | 161.0 | 1 | 41 | 41.0 | 2 | 5–6 | 5.5 | 1 | 15 | 15.0 | 1 | 0 | 0 |
| Virginia | 5 | 162–167 | 163.6 | 6 | 34–42 | 37.8 | 10 | 6 | 6.0 | 5 | 16–20 | 17.8 | 4 | 1 | 0 |
| North Carolina | 48 | 154–172 | 161.2 | 51 | 32–46 | 39.4 | 81 | 3–7 | 5.9 | 54 | 13–20 | 17.0 | 36 | 2 | 5 |
| South Carolina | 18 | 157–178 | 165.3 | 18 | 34–44 | 40.2 | 35 | 5–6 | 5.9 | 19 | 14–20 | 17.2 | 12 | 3 | 3 |
| Georgia | 17 | 154–174 | 166.3 | 17 | 38–48 | 41.8 | 40 | 5–7 | 6.0 | 18 | 14–22 | 18.4 | 12 | 3 | 4 |
| Northern Florida | 9 | 159–176 | 170.0 | 9 | 36–45 | 39.9 | 17 | 5–7 | 6.1 | 9 | 14–19 | 17.4 | 1 | 1 | 6 |
| Alabama | 6 | 162–171 | 167.8 | 6 | 36–40 | 38.5 | 12 | 5–6 | 5.8 | 6 | 15–20 | 18.2 | 1 | 3 | 2 |
| Mississippi | 15 | 161–177 | 170.0 | 12 | 33–46 | 40.7 | 30 | 5–7 | 6.2 | 16 | 16–21 | 18.7 | 0 | 4 | 1 |
| Louisiana | 10 | 161–184 | 170.2 | 10 | 35–42 | 38.3 | 19 | 5–7 | 6.1 | 11 | 16–27 | 23.4 | 1 | 3 | 7 |
| Eastern Texas | 1 | 174 | 174.0 | 1 | 43 | 43.0 | 2 | 6 | 6.0 | 1 | 25 | 25.0 | 0 | 0 | 1 |
| Arkansas | 6 | 156–176 | 161.0 | 6 | 36–40 | 37.7 | 12 | 6–7 | 6.1 | 6 | 18–27 | 22.5 | 2 | 1 | 3 |
| Oklahoma | 7 | 156–176 | 164.4 | 6 | 34–43 | 38.0 | 10 | 6–7 | 6.4 | 7 | 18–28 | 22.4 | 0 | 4 | 3 |
| Missouri | 1 | 149 | 149.0 | 1 | 40 | 40.0 | 2 | 6 | 6.0 | 1 | 19 | 19.0 | 0 | 0 | 0 |
| Illinois | 1 | 161 | 161.0 | 1 | 41 | 41.0 | 2 | 6 | 6.0 | 1 | 19? | 19.0? | 0 | 0 | 0 |
| Indiana | 3 | 163–168 | 165.0 | 2 | 33–40 | 36.5 | 6 | 6 | 6.0 | 3 | 19–22 | 20.3 | 1 | 2 | 0 |
| Kentucky | 9 | 161–180 | 167.5 | 6 | 36–40 | 37.8 | 17 | 5–7 | 5.8 | 9 | 15–23 | 19.4 | 1 | 3 | 2 |
| Tennessee | 4 | 155–171 | 163.8 | 4 | 38–41 | 39.8 | 8 | 6–7 | 6.1 | 4 | 17–23 | 20.0 | 1 | 3 | 0 |

Supralabials usually number 6 (74.8 percent have 6 on both sides, an additional 7.6 percent have 6 on one side and 7 on the other; 7.6 percent have 6-5, the remaining 10 percent are either 5-5, 7-7, or 4-3). Supralabials range from 3-7, mean 5.9 (340 counts). There is a tendency for a greater number of specimens to have 5 supralabials in the coastal area rather than the inland area, but this apparently lacks significance.

The number of body blotches ranges from 13-28, mean 18.6 (191 counts). There is a distinct difference in the mean number of body blotches between the inland and coastal states (including only that part of Louisiana east of the Mississippi River). The range in number of body blotches for the coastal area is 13-22, mean 17.5. The range in number of body blotches for the inland area is 15-28, mean 21.8. There appears to be a clinal increase in number of body blotches from north to south within the coastal area. The discrepancies in this cline may be due to lack of specimens. The cline reverses itself in peninsular Florida (see discussion of variation in *C. c. coccinea*). There is some indication that there is a clinal increase in number of body blotches from northeast (Indiana and Kentucky) to southwest (Oklahoma, Arkansas, and Louisiana west of the Mississippi River). This is uncertain, however, and these differences may instead be indicative of a difference between the inland states east of the Mississippi River (Illinois, Indiana, Kentucky, and Tennessee) and those west (Arkansas, Oklahoma, Louisiana, and extreme eastern Texas).

In the Atlantic coastal states the first black body band usually touches the parietals. The position of the first black body band becomes highly variable in the Gulf coastal states and the inland area. It may either touch (53.8 percent) or be separated from the parietals (23.4) or joined with the black head band (22.8). The number of dorsal scales separating the first black band from the parietals usually is 1 or 2 (range 1 to 3, mean 1.5) in this area, whereas in the peninsular Florida population it is usually 2 or 3 or more (see discussion of *C. c. coccinea*).

### *Cemophora coccinea lineri* Williams, Brown, and Wilson

(Figure 5)

?*Cemophora coccinea* Auffenberg, 1948: 212.

*Cemophora coccinea lineri* Williams, Brown, and Wilson, 1966: 85.

*Holotype.*—AMNH No. 75307, collected 34.5 miles S. Riviera, Kennedy County, Texas, on 29 June 1963 by Ernest A. Liner and Richard Whitten.

*Range.*—Known only from Kenedy County, Texas.

*Diagnosis.*—A subspecies of *Cemophora coccinea* with 7 supralabials (100 percent in known specimens), the 4th and 5th supralabials entering orbit; ventrals 188-195, mean 191.5; body blotches 17; black bands of dorsal pattern extending laterally to dorsal scale rows 3, 4, or 5, and not enclosing dorsal red blotches; black band of first body blotch not touching parietals.

*Variation.*—Little is known of variation in this subspecies, only two specimens being available for examination.

*Remarks.*—As stated in the original description (Williams, Brown, and Wilson, 1966: 85) we believe that *Cemophora coccinea* is a natural resident in the area around Corpus Christi, Texas. It is unfortunate that the specimens reported by Auffenberg (1948) were lost inasmuch as they might represent *C. c. lineri* or perhaps intergrades between *C. c. lineri* and the population to the north. Additional specimens from this area are much needed.

### *Intergradation Between Subspecies*

Nineteen specimens from Levy, Alachua, and Marion Counties, Florida are considered to be intergrades between *Cemophora c. coccinea* and *C. c. copei.* Comparative data for *C. c. coccinea, coccinea-copei* intergrades, and *C. c. copei* are presented in Table 5.

The intergrades show strong tendencies toward *coccinea,* especially in ventrals and caudal counts. The number of body blotches shows influence of *copei* both in mean and in upper range. The mean number of supralabials is close to *coccinea:* however the occurrence of 6 supralabials on both sides occurs in 21 per cent of the intergrade populations (18 counts) and only 9 percent of *coccinea* (59 counts), while in *copei* 74.8 percent have 6 on both sides (130 counts).

Head pattern in the intergrades is obviously closer to *coccinea* since 95 percent do not have the first blotch touching the parietal (100% in *coccinea*).

No intergrades are known between *C. c. copei* and *C. c. lineri.*

### *Subspecific Comparisons and Relationships*

As noted in the description of *Cemophora coccinea lineri* (Williams, Brown, and Wilson, 1966) there appears to be a close relationship between the south Texas race, *lineri* and the nominate subspecies, which occurs in peninsular Florida. Similarities are reflected in number of supralabials (normally 7 in both), in number of ventrals (both have distinctly higher means than *C. c. copei,* the higher mean occurring in *lineri*), and in low number of body blotches (the Atlantic coast population of *copei* agrees with them in this feature. *C. c. copei* appears to be more closely related to the nominate race than to *lineri,* as reflected by its mean number of ventrals and its possession of laterally complete body blotches (not closed laterally in *lineri*). The nominate subspecies may be separated from *C. c. copei* by the following characteristics: supralabials normally 7, as opposed to 6; a larger number of ventrals (mean for *coccinea* 174.0, for *copei* 165.3); and first body blotch separated from parietal by 2 or 3 scale lengths, whereas in *copei* the first body blotch usually in contact with parietal or, if not, separated from it by less than 2 scale lengths.

The similarity between the nominate form and *C. c. lineri* suggests a Pleistocene withdrawal of the species into eastern and western refugia. Additional examples of this phenomenon were given by Blair (1958). With the re-establishment of favorable conditions for this species there was a reinvasion of the southern United States from the Florida refugia. Differentiation of the mainland subspecies was probably aided by the opening of the Suwannee Straits (see Neill, 1957, for influence of the Suwannee Straits on the Florida fauna). The possibility that *lineri* represents a Gulf circumferential migrant from Florida is a distinct possibility (see Auffenberg and Milstead, 1965, for more details on this Pleistocene route).

### *Key to Subspecies of Cemophora coccinea*

1. Ventrals 188 or more; body blotches not closed laterally ................ *Cemophora coccinea lineri*
1. Ventrals 185 or less; body blotches closed laterally ............ 2
2. Supralabials normally seven, first black body blotch not touching parietals ............ *Cemophora coccinea coccinea*
2. Supralabials normally six, first black body blotch usually touching parietals or joined with black head band ............ *Cemophora coccinea copei*

### *Specimen List*

The following is a list of the abbreviations used in this study for collections from which we examined specimens: AMNH American Museum of Natural History, New York;

TABLE 5.
*Comparison of intergrades (coccinea x copei) with C. c. coccinea and C. c. copei*

| | *coccinea* | intergrades | *copei* |
|---|---|---|---|
| Ventrals | 174.0(59)[1]<br>(158–185) | 175.2(19)<br>(160–179) | 165.3(180)<br>(150–180) |
| Caudals | 42.7(61)<br>(36–50) | 43.0(19)<br>(37–47) | 39.5(161)<br>(30–48) |
| Supralabials | 6.9(118)<br>(6–8) | 6.7(37)<br>(6–8) | 5.9(340)<br>(6–7) |
| Body blotches | 17.6(61)<br>(12–22) | 18.3(19)<br>(15–25) | 18.6(191)<br>(13–28) |
| First black body band percent not touching parietal | 100% (62)<br>(2.3)[2] | 95% (19)<br>(2.3) | 23.4% (163)<br>(1.5) |

[1] Means are followed by sample number in parenthesis; number in parenthesis below is sample range.

[2] Figure in parenthesis (below) for the last character is mean number of scale rows separating anterior edge of first black band from parietal.

BCB Bryce C. Brown personal collection, Baylor University, Waco, Texas; CNHM Chicago Natural History Museum, Chicago, Illinois; EEB Elmer E. Brown personal collection, Davidson College, Davidson, North Carolina; GCS Gerald C. Schaefer personal collection, University of Richmond, Richmond, Virginia; CU Cornell University, Ithaca, New York; JTC Joseph T. Collins personal collection, 5807 Montgomery Road, Cincinnati, Ohio; KLW Kenneth L. Williams personal collection (to be deposited in the Northwestern Louisiana State College collection, Natchitoches, Louisiana); KU University of Kansas Museum of Natural History, Lawrence, Kansas; LSUMZ Louisiana State University Museum of Zoology, Baton Rouge; MCNP Mammoth Cave National Park, Mammoth Cave, Kentucky; MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MSC Mississippi State University, State College; NCSM North Carolina State Museum, Raleigh; NM Newark Museum, Newark, New Jersey; RB Roger Barbour personal collection, University of Kentucky, Lexington; SAM Sherman A. Minton, Jr. personal collection, Indiana University Medical Center, Indianapolis; TCF Tom C. Fuller personal collection, 1247 S. Floyd St., Louisville, Kentucky; TU Tulane University, New Orleans, Louisiana; UCM University of Colorado Museum, Boulder; UF University of Florida, Gainesville; UIMNH University of Illinois Museum of Natural History, Urbana; UMMZ University of Michigan Museum of Zoology, Ann Arbor; UO University of Oklahoma, Norman; USM University of Southern Mississippi, Hattiesburg; USNM United States National Museum, Washington, D.C.; USWL University of Southwestern Louisiana, Lafayette; UT University of Texas, Austin.

*Cemophora coccinea coccinea* (specimens examined). **FLORIDA.** *Brevard County:* Cape Canaveral, AMNH 8442-8443; Eau Gallie, MCZ 7026. *Citrus County:* Floral City, CU 5403; 0.7 mi. E Inverness, UMMZ 109357. *Collier County:* Marco Island, UMMZ 109356; 3 mi. SE Naples, UF 8600. *Dade County:* 18 mi. W Florida City, UMMZ 108343; 7 mi. N Homestead, UMMZ 111363; Lemon City, USNM 26304, 30947-30948, 38161; Miami, UIMNH 447; Ojus, USNM 25265; Paradise Key, USNM 85320-85321; Royal Palm State Park, Everglades, UIMNH 34664. *Hillborough County:* Tampa, CNHM 427, UF 1514. *Indian River County:* Sebastian, MCZ 16160, 38579, 43845. *Lake County:* Astor Park, UCM 18915-18917; 3 mi. W Astor Park, UF 4580; Eustis, CU 1732, USNM 24355, 24359; Leesburg, UMMZ 77468; Umatilla, UF 84; 3 mi. W Umatilla, UF 304. *Lee County:* Bonita Springs, CU 5653-5654; near Fort Myers, USNM 36962-36963. *Highlands County:* Lake Placid, Archibald Station, AMNH 65410. *Orange County:* No other data, USNM 56430; Oakland, UF 5937; Orlando, SAM 780, USNM 84885; near Orlando, USNM 124140. *Palm Beach County:* Palm Beach, MCZ 13656-13657. *Pinellas County:* Clearwater, USNM 10741; Gulfport, CNHM 8571-8572; Maximo Point, St. Petersburg, CU 956, UMMZ 79920. *Sarasota County:* 4 mi. E Sarasota, SAM 198. *Seminole County:* 8.5 mi. NE Geneva, UF 4579; 12 mi. E Sanford, UF 7060. *Volusia County:* 6 mi. E De Land, UF 7061; 1 mi. S. Lake Helen, UF 4582; 5.5 mi. E Ostean, UF 4576-4577. *No county data* (localities not mapped): Citronville, MCZ 6368; Eureka, CU 1299; Fairchild Gardens, UMMZ 118518; Georgiana, USNM 14828; Port Jackson, CU 2604.

Specimens not examined (plotted on map as open symbols). **FLORIDA.** *Brevard County:* Micco (Ditmars, 1936). *Dade County:* Coral Gables (Duellman and Schwartz, 1958); Fort Biscayne (Duellman and Schwartz, 1958). *Lake County:* Okahumpka (Neill, 1951). *Monroe County:* Pinecrest (Duellman and Schwartz, 1958). *Pinellas County:* Tarpon Springs (Brimley, 1910). *Putnam County:* Crescent City (Neill, 1951). *Sumter County:* Only data (Carr, 1940).

*Cemophora coccinea copei* (specimens examined). **ALABAMA.** *Dale County:* Ozark, CU 4050. *Lee County:* near Auburn, UMMZ 83196. *Mobile County:* Mobile, MCZ 56. *Walker County:* No other data, TU 17145. *No specific data* (not mapped): "north Alabama," USNM 5221. **ARKANSAS.** *Drew County:* Monticello, CNHM 40767. *Greene County:* 3.5 mi. SE Paragould, UMMZ 78182. *Hempstead County:* No other data, UMMZ 84171. *Lafayette County:* No other data, CNHM 21986-21987. *Union County:* near Louisiana-

Arkansas border, UMMZ 95920; 3 mi. S Eldorado, TU 18023. **FLORIDA.** *Calhoun County:* 6 mi. W Blountstown, UF 9666. *Clay County:* Orange Park, KU 60973-60974. *Columbia County:* Watertown, AMNH 8255. *Duval County:* Arlington, AMNH 22396. *Escambia County:* Pensacola, UMMZ 51762; vicinity of Pensacola, CNHM 53677-53678. *Jackson County:* 3 mi. SE Marianna, UMMZ 73939. *Liberty County:* near Wilma Ranger Station, LSUMZ 6173. *Okaloosa County:* 10 mi. SW Niceville, TU 13433. **GEORGIA.** *Bibb County:* near Macon, GCS 609. *Brooks County:* 5 mi. W Quitman, UMMZ 81177. *Camden County:* St. Mary's USNM 16701. *Charlton County:* Cheeser Island, Okefinokee Swamp, CU 354-355; Billy's Island, Okefinokee Swamp, CU 120, 6102. *Chatham County:* Savannah, CU 3920. *Chattahoochee County:* Fort Benning, CU 4669, 4754-4755. UIMNH 34266. *Fulton County:* Rosswell, MCZ 260. *Grady County:* Beechton, "the Hall," CNHM 8121. *Liberty County:* Riceboro, USNM 131709. *McIntosh County:* middle of Sapelo Island, KU 69906. *Meriweather County:* outskirts of Greenville, UMMZ 98041. *Thomas County:* Thomasville, CNHM 35449; Greenwood Plantation, Thomasville, CNHM 35980. **INDIANA.** *Floyd County:* 3.5 mi. W New Albany, SAM 8; 5 mi. W New Albany, SAM 520; Bald Knob, 5.5 mi. N New Albany, UMMZ 117522. **KENTUCKY.** *Bell County:* Pine Mountain State Park, TCF 193. *Calloway County:* Blood River at route 121 crossing, UIMNH 64658. *Edmonson County:* near Turnhole, Mammoth Cave National Park, MCNP 46. *Hopkins County:* 5 mi. W Mortons Gap, RB collection. *Jefferson County:* Mt. Holly near Harrison Lane south of Fairdale, TCF 192. *McCreary County:* 7 mi. W Cumberland Falls, JTC 282, 329. *Marshall County:* camp grounds, Camp Bear Creek, TCF 188. *Pulaski County:* 1.5 mi. S Burnside, TCF 166. **LOUISIANA.** *Grant Parish:* 10 mi. S Colfax, TU 5532, 11797; Fishville, USWL collection; near Pollock, TU 6383. *Jackson Parish:* 5.5 mi. E Jonesboro at Beech Springs, UCM 18631. *Lincoln Parish:* Dubach, TU 13264. *Morehouse Parish:* Prairie Mer Rouge, USNM 2185 (2). *Natchitoches Parish:* 3.2 mi. N Bellwood, KLW 2525; 6 mi. N Bellwood, KLW 2513; 7.7 mi. N Bellwood, KLW 2509; 7.3 mi. S Bellwood, KLW 2510; 8.2 mi. S Bellwood, KLW 2494; 0.3 mi. N Kisatchie, KLW 2511; 2.6 mi. SW Natchitoches, KLW 2474. *Sabine Parish:* Fort Jesssup, USNM 6298. *St. Tammany Parish:* 0.5 mi. N Hickory, LSU 14138. *Union Parish:* Oakland, TU 12994, 13477. **MARYLAND.** *Anne Arundel County:* Mill Creek, USNM 141395. *Baltimore County:* Baltimore, MCZ 750. *Wicomico County:* Salisbury, AMNH 77104. **MISSISSIPPI.** *Forrest County:* 18.5 mi. S Collins, UIMNH 29118; Hattiesburg, 2 mi. S on 28th Avenue, USM 55.237. *Harrison County:* Biloxi, CNHM 21556; near Bixoli, AMNH 46749; 4 mi. E Gulfport, LSUMZ 282; Handsboro, AMNH 78998; Mississippi City, USM 53.1087. *Jackson County:* Daisy-Vestery, near Red Creek Baptist Church, USM 57.434. *Jones County:* Laurel, MSC 1669-1671. *Lamar County:* near Hattiesburg, USM 55.236; 4.5 mi. NW Hattiesburg, USM 57.405. *Lauderdale County:* 8 mi. S Meridian, USM 53.1053. *Lawrence County:* Monticello, USNM 2189. *Newton County:* about 2 mi. N Decatur, MSC 2200. *Perry County:* Beaumont, USM 53.151. **NEW JERSEY.** *Atlantic County:* Albor's Blueberry Plantation, near Pleasant Mills, NM collection; Sweetwater, AMNH 96131. *Burlington County:* Green Bank, AMNH 96122; Mt. Misery, AMNH 69056; Fieldsboro Bridge, south of Mt. Misery, AMNH 96130; Ockanickon, south of Medford, AMNH 96123; Taunton Lakes, AMNH 96128-96129; near Taunton Lakes, AMNH 96124-96126; Taunton Lakes, near Lake Pine, AMNH 96127; intersection of route 70 and old Lakehurst road, east of Upton, AMNH 96121; Whitesburgh, AMNH 58070-58071; Woodmansie, 8 mi. SW Whiting, AMNH 96120. *Cumberland County:* north part of Millville, AMNH 96132; east part of Millville, AMNH 96133; Vineland, AMNH 63858. **NORTH CAROLINA.** *Beaufort County:* Belhaven, NCSM 704; Washington, CU 2205. *Brunswick County:* Oak Island, EEB 2168; Caswell Beach road, Oak Island, EEB 2175; Long Beach road on Oak Island, EEB 2169; near Southport on Long Beach road on Oak Island, EEB 2429; between Southport and Supply, Highway 130, EEB 2177-2178; intersection 130 and Long Beach road, Southport, EEB 2174; 6 mi. N Southport on North

Carolina route 303, EEB 2176; 13 mi. E Supply on North Carolina route 130, EEB 462; 16 mi. N Southport, NCSM 1735; 19 mi. N Southport, NCSM 1736; Wilmington, USNM 145608. *Burke County:* 8 mi. NW Morgantown on N. C. route 181, EEB 2268. *Carteret County:* Beaufort, MCZ 1344; Morehead City, NCSM 1024, 1026; between Morehead City and Newport on U. S. 70, EEB 474. *Clay County:* Hayesville, NCSM 706. *Cumberland County:* Fayetteville, CNHM 135178, EEB 927, USNM 137574. *Dare County:* Roanoke Island, AMNH 38157. *Iredell County:* Harmony, NCSM 701. *Mecklenburg County:* Davidson EEB 475. *New Hanover County:* near Carolina Beach, NCSM 705, 1021; 7 mi. S Wilmington, LSUMZ 13598. *Pitt County:* 1 mi. NW Greenville, NCSM 1028; 6 mi. S Grimesland, NCSM 1025. *Robeson County:* Maxton, AMNH 65586. *Scotland County:* No other data, NCSM 703. *Wake County:* no other data, NCSM 699; Cary, NCSM 708; Garner, NCSM 1022; near Holly Springs, NCSM 1027; near Milbrook, NCSM 707; Raleigh, CU 4312, NCSM 700, 702. *Wayne County:* 1.5 mi. NW Seven Springs, NCSM 1261. *Wilson County:* Wilson, NCSM 1023. **OKLAHOMA.** *Creek County:* Drumright, USNM 125119. *Okmulgee County:* no other data, UO 399, 3630, 12161, 12279. *Pittsburg County:* no other data, UO 28342. *Tulsa County:* Tulsa, UMMZ 84442. **SOUTH CAROLINA.** *Aiken County:* 2 mi. N Wagoner on route 39, EEB 1194. *Anderson County:* no other data, USNM 2387. *Beaufort County:* Bluffton, MCZ 5613; Lady Island, MCZ 4426, 13066. *Charleston County:* Charleston, USNM 2307. *Chesterfield County:* McBee, EEB 1286; 1 mi. SW Patrick on U. S. 1, EEB 3014. *Horry County:* Highway 90 in eastern part of county, EEB 361; near Myrtle Beach, UMMZ 94165; 1 mi. West of jct. with U. S. 17 on S. C. 544, north of Murrem's Inlet, EEB 1287. *Lexington County:* Leesville, CNHM 65160; 5 mi. SE Leesville, UMMZ 84441; near Leesville, USNM 89393, 91398. *Orangeburg County:* Norway, USNM 31179. *Sumter County:* Manchester State Forest Headquarters, EEB 670; Manchester State Forest, east end of the Rosemary Tower road, EEB 3202; 2.7 mi. S Wedgefield on S. C. 261, EEB 3051. **TENNESSEE.** *Cumberland County:* 8 mi. W Crossville, UMMZ 84439. *Decatur County:* Perryville, KU 2473. *Hardeman County:* 11 mi. NE Bolivar, UMMZ 79214. *Monroe County:* 7.9 mi. E Tellico Plains, Cherokee National Forest, UF 10822. **TEXAS.** *Hardin County:* 2.1 mi. NW Loeb, UT 22492. **VIRGINIA.** *Amelia County:* Amelia courthouse, USNM 145823. *Fairfax County:* Mt. Vernon, UMMZ 56260. *Hanover County:* Beaverdam, USNM 129361. *King William County:* West Point, USNM 144530. *Nottoway County:* 4 mi. W. Burkesville, USNM 145824. *Southampton County:* 4 mi. NW Courtland, UF 14471. *No data:* "Virginia," MCZ 13063. **WASHINGTON, D. C.** Anacostia, USNM 35308.

Specimens not examined (plotted on map as open symbols). **ALABAMA.** *Dale County:* Ozark (Snyder, 1945). **ARKANSAS.** *Pike County:* no other data (Dowling, 1957); *Sebastian County:* Fort Smith (Dellinger and Black, 1938); *Washington County:* No other data (Dowling, 1957). **FLORIDA.** *Duval County:* Jacksonville (Deckert, 1918). **GEORGIA.** *Richmond County:* No other data (Neill, 1948). **ILLINOIS.** *Union County:* Wolf Lake Swamp (Bennett, 1953). **KENTUCKY.** *Caldwell County:* Pennyrile Forest State Park (Collins, 1964). *Laurel County:* No other data (Fuller and Barbour, 1962). *Rowan County:* Area near Morehead (Collins, 1964). **MISSISSIPPI.** *Forrest County:* Brooklyn (Cliburn, 1958). *Hancock County:* Bay Saint Louis (Brimley, 1910). **MISSOURI.** *Dunklin County:* Kennett (Anderson, 1965). *Phelps County:* near Rolla (Anderson, 1965). **NEW JERSEY.** *Burlington County:* Whitesbog (Kauffeld and Trapido, 1944). **NORTH CAROLINA.** *Duplin County:* No other data (Brimley, 1942). *Durham County:* No other data (Brimley, 1942). *Forsyth County:* No other data (Brimley, 1942). *Guilford County:* No other data (Brimley, 1942). *Rockingham County:* Between Reidsville and Leaksville (Brimley, 1942). *Rowan County:* No other data (Brimley, 1942). **OKLAHOMA.** *Creek County:* Parthenia Park (Force, 1930). *Pittsburg County:* Just off route 6 near McAlester (Carpenter, 1954). **SOUTH CAROLINA.** *Georgetown County:* Georgetown (Jobson, 1940). *Richland County:* Columbia (Corrington, 1929). **TENNESSEE.** *Sevier County:* Cades Cove (King, 1939). **VIR-**

**GINIA.** *Princess Anne County:* No other data (Werler and McCallion, 1951).

*Cemophora coccinea lineri* (specimens examined). **TEXAS.** *Kenedy County:* King Ranch, BCB 10993; 34.5 mi. S Riviera (holotype), AMNH 75307.

Specimens not examined (plotted on map as open symbols). **TEXAS.** *Nueces County:* U. S. Naval Air Station, Corpus Christi (Auffenberg, 1948).

Intergrades (*C. c. coccinea* x *C. c. copei*, specimens examined). **FLORIDA.** *Alachua County:* Gainesville, CNHM 8573-8575, UF 454, 2504; 4 mi. S Gainesville, UF 4585; Payne's Prairie, UF 2731, 7062; 2.2 mi. S Hawthorne on U. S. 301, EEB 1193. *Levy County:* No other data, KU 74111; 4 mi. WSW Otter Creek, LSUMZ 7277. *Marion County:* No other data, CNHM 3388, KU 80997, UMMZ 52257; Ocala, USNM 142092; Silver Springs, CNHM 22665, 28483, 48443-48444.

## SUMMARY

The nomenclatural history of the genus is reviewed. *Cemophora* is the name utilized for the monotypic genus. We follow Smith, Lynch, and Puckette (1964) in using the name *Cemophora coccinea* (Blumenbach), 1788. These authors considered *Coluber doliata* Linnaeus, 1766, a senior synonym of *Coluber coccinea* but have asked for the former's suppression under the Plenary Powers of the International Commission on Zoological Nomenclature on the grounds of its long association with the milk snakes *(Lampropeltis triangulum).*

*Cemophora coccinea* may be distinguished by pattern alone from all other North America snakes, with the possible exception of some *Lampropeltis triangulum;* from the latter the scarlet snake may be distinguished by its large rostral and enlarged posterior maxillary teeth. The relationship of *Cemophora* to 5 genera *(Lampropeltis, Rhinocheilus, Stilosoma, Pituophis, Arizona)* usually considered as having phylogenetic affinities is examined. The scarlet snake appears to be most closely related to *Lampropeltis,* specifically to certain members of the *L. triangulum* group.

Selected characters were analyzed for individual, sexual, ontogenetic and geographic variation. Sexual differences were found in number of ventrals, proportional tail length, and to a lesser extent in number of body blotches. Ontogenetic variation occurs in pattern. The red blotches are lighter or even pinkish in young. The white interspaces on the dorsal pattern are immaculate in young and acquire dark pigment as the individual ages.

Three geographic races are distinguished on the basis of ventral number, supralabial number, and pattern. *Cemophora c. coccinea* (Blumenbach) of peninsular Florida is distinguished by a large number of ventrals (mean 174.0), normally 7 supralabials, and the 1st black blotch not touching pareitals (usually separated by 2 or more scales). *C. c. copei* Jan occurs along the Atlantic and Gulf coasts from New Jersey to eastern Texas, and inland to southern Illinois, southern Indiana, and southeastern Missouri; this race has a smaller number of ventrals (mean 165.3), normally 6 supralabials, and the 1st black blotch touching parietals or separated by less than 2 scales. *C. c. lineri* Williams, Brown, and Wilson of southern Texas (Kenedy County) has a large number of ventrals (mean 191.5), 7 supralabials, and the dorsal black blotches open ventrolaterally (closed in other two races). *C. c. coccinea* is closely related to *lineri,* as is evidenced by ventral and supralabial numbers. It would appear that Pleistocene climatic conditions caused a splitting of the range of *C. coccinea* driving the species into southern refugia in Texas, where *lineri* evolved, and Florida (and adjacent areas). When climatic conditions again became favorable *C. coccinea* moved northward into the Austroriparian region of southeastern United States. The Suwanee Straits barrier in northern Florida allowed the isolation necessary for the differentiation of *copei* from *coccinea.*

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# STUDIES ON AMERICAN PARAGONIMIASIS. V. Further observations on the presence of *Paragonimus* in fresh-water crabs from Costa Rica, with notes on susceptibility to cercariae of *P. kellicotti*.*

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## ABSTRACT

The fresh-water crabs *Ptychophallus tristani* (Rathbun, 1896) Smalley, 1964, and *Potamocarcinus magnus* (Rathbun, 1896) Pretzmann, 1965, are reported as natural second intermediate hosts for *Paragonimus* from two localities in Costa Rica. The incidences and intensities of infection and their localities by host, sex, and size are reported. The metacercariae of *Paragonimus* were found on the hearts of the infected crabs. Nine specimens of three species of wild-caught fresh-water crabs from Costa Rica were exposed to cercariae of *Paragonimus kellicotti* from Louisiana, but only one specimen was infected, suggesting that the affected specimen had acquired its infection previous to exposure in the laboratory, or that *P. kellicotti* cercariae are not as infective to fresh water crabs as to crayfishes, perhaps reflecting upon the evolutionary biology of this host-parasite relationship. Metacercariae of *Paragonimus* from Costa Rica were fed to an uninfected domestic cat and the infection became patent on 67th day, but was lost after 202 days.

A larval microphallid trematode, possibly the metacercaria of *Maritrema prolixum* Caballero and Montero, 1961, was also found in the Costa Rica crabs.

## INTRODUCTION

In a previous note (Sogandares and Smalley, 1965) we reported metacercariae of *Paragonimus* from preserved specimens of the Costa Rican fresh-water crab *Ptychophallus tristani* (Rathbun, 1896) Smalley, 1964 (=*Pseudothelphusa tristani*). We also examined preserved immature *Potamocarcinus magnus* (Rathbun, 1896) Pretzmann, 1965 (=*Pseudothelphusa magna*), but found these to be uninfected. Since our report *(op. cit.)* we have visited different sites in Costa Rica for purposes of examining additional fresh-water crabs for paragonimiasis, and to determine where the metacercariae locate in their host. Some crabs were brought to our laboratories to attempt infections of domestic cats with Costa Rican *Paragonimus,* and to test the susceptibility of these crabs to *Paragonimus kellicotti* Ward, 1908, from Louisiana. Since we do not plan to return to Costa Rica in the near future, we have decided to present our somewhat limited findings.

## METHODS

Fresh-water crabs were collected from under rocks in streams from different localities in Costa Rica. These were identified with the aid of Smalley's (1964) keys. The crabs were cut open and carefully dissected with needles under a binocular dissection microscope in our examinations for metacercariae. The cyst membranes of some of the metacercariae were dissected with needles and the metacercariae identified visually under a compound microscope. Thereafter, the cysts of *Paragonimus* metacercariae were easily separated from another species (Microphallidae) found. Crabs from localities where *Paragonimus* had not been found were placed in fingerbowls containing a small amount of dechlorinated tap-water. A crushed *Pomatiopsis lapidaria* (Say) bearing a seventh generation laboratory infection of *P. kellicotti* from Louisiana was placed overnight, at room temperature, in

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each fingerbowl containing the crab to be exposed. This procedure has been reliable in our laboratory to infect Louisiana crayfishes, *Procambarus clarkii* (Girard, 1853), of medium size (about 50 mm) with from 30 to 100 metacercariae. The snail infections were maintained as described by Sogandares (1965). Three metacercariae of *Paragonimus* recovered from one *Ptychophallus tristani* from 3 mi E Atenas, Alajuela Province (580 m elevation) were intubated *per os* into a domestic cat which had been judged to be free of paragonimiasis by several fecal examinations using sedimentation concentration and Telemann's (1908) techniques.

## RESULTS

Table I shows that 1 of 5 *Ptychophallus tristani,* all from a locality where *Paragonimus* metacercariae had not been found previously, harbored an infection by *Paragonimus* metacercariae after exposure to cercariae of *Paragonimus kellicotti* from Louisiana. Two specimens each of *Ptychophallus tumimanus* and *P. montanus* were refractory to Louisiana *P. kellicotti.*

Table II shows that *Ptychophallus tumimanus* and *P. montanus* from a swift mountain stream at 1200 m elevation were uninfected with *Paragonimus* metacercariae. One of 15 *Ptychophallus tristani* collected in three different localities, ranging from 580 to 900 m elevation, was naturally infected with three metacercariae of *Paragonimus.* Two of 13 *Potamocarcinus magnus* from two relatively close localities, ranging from 450 to 580 m elevation, were each infected with one *Paragonimus* metacercaria. In all cases the *Paragonimus* metacercariae were found on or in the heart tissues of the affected crabs.

Eggs were first detected in the feces of the domestic cat exposed to three metacercariae of *Paragonimus* from *Ptychophallus tristani* on the 67th day. Eggs could not be detected, even with Telemann's technique, in the feces of the infected cat by the end of 202 days. The cat was then killed and examined. Post-mortem examination revealed two hemorrhagic spots in the lungs, but no worms were recovered. Further examination of the entire animal, including brain and brain case, sinuses, other organs and muscles, *etc.,* failed to reveal the presence of *Paragonimus* or other trematodes or cestodes.

The hepatopancreas of *Potamocarcinus magnus* and *Ptychophallus tristani* from 3 mi E Atenas, Alajuela Province, and also *P. tristani* from 0.5 mi S Cebadilla, Alajuela Province, were not infrequently infected with a microphallid metacercaria which may be *Maritrema prolixum* Caballero and Montero, 1961.

## DISCUSSION

The numbers of cercariae of Louisiana *P. kellicotti* to which each crab in Table I was exposed would have been sufficient to produce heavy infections of 30 to 100 metacercariae in medium size (about 50 mm) Louisiana crayfishes such as *Procambarus clarkii.* Only one of five *P. tristani* harbored 3 metacercariae of *Paragonimus* after such a massive exposure, suggesting that the affected specimen had acquired its infection previous to exposure in the laboratory or that *P. kellicotti* cercariae are not as infective to fresh-water crabs as to crayfishes, perhaps reflecting upon the evolutionary biology of this host-parasite relationship.

The Central and South American form *(P. rudis)* of *Paragonimus* and the North American form *(P. kellicotti)* have been synonymized by Caballero and Montero

TABLE I.
*Results of exposures of Costa Rican fresh-water crabs to* Paragonimus kellicotti *cercariae from Louisiana.*

| Species | No. Specimens Exposed | Locality of Origin and Elevation | Incidence | Intensity[1] |
|---|---|---|---|---|
| *Ptychophallus tristani* (Rathbun, 1896) Smalley, 1964 | 5 | 0.8 mi. W Piedades, San Jose Prov., 900 m | 1/5 | 3 |
| *Ptychophallus tumimanus* (Rathbun, 1898) Smalley, 1964 | 2 | 2 mi. S Cariblanco, Heredia Prov., 1200 m | 0/2 | 0 |
| *Ptychophallus montanus* (Rathbun, 1898) Smalley, 1964 | 2 | 2 mi. S Cariblanco, Heredia Prov., 1200 m | 0/2 | 0 |

[1] Number of metacercariae recovered after 6 wks.

TABLE II.
*Incidence and intensity of natural infections of Costa Rican fresh-water crabs by* Paragonimus.

| Species | Sex | Numbers/ size[1] | Number infected | Intensity[2] | Locality and Elevation |
|---|---|---|---|---|---|
| *Ptychophallus tristani* (Rathbun, 1896) Smalley, 1964 | ♀ | 1/17 | 1 | 3 | 3 mi. E Atenas, Alajuela Prov., 580 m |
| | ♂ | 1/27 | 0 | 0 | |
| | ♂ | 3/15–38 | 0 | 0 | 0.5 mi. S Cebadilla Alajuela Prov., 600 m |
| | ♂ | 5/20–31 | 0 | 0 | 0.8 mi. W Piedades, San Jose Prov., 900 m |
| | ♀ | 5/18–31 | 0 | 0 | |
| *Ptychophallus tumimanus* (Rathbun, 1898) Smalley, 1964 | ♂ | 4/30–41 | 0 | 0 | 2 mi. S Cariblanco, Heredia Prov., 1200 m |
| | ♀ | 2/24–27 | 0 | 0 | |
| *Ptychophallus montanus* (Rathbun, 1898) Smalley, 1964 | ♂ | 2/17–24 | 0 | 0 | |
| *Potamocarcinus magnus* (Rathbun, 1896) Pretzmann, 1965 | ♂ | 6/60–70 | 2 | 1, 1 | Rio Grande de Tarcoles on Atenas Hwy, Alajuela Prov., Approx. 450 m |
| | ♂ | 7/24–61 | 0 | 0 | 3 mi. E Atenas, Alajuela Prov., 580 m |

[1] Carapace width in mm.
[2] Numbers of metacercariae recovered from individual crabs.

(1961) and others, yet they seem to possess different biological characteristics insofar as infectivity to the second intermediate host is concerned.

It is yet premature to discuss the distribution of infections of fresh-water crabs by *Paragonimus* in Costa Rica. However, the infections found by us were confined to Alajuela Province at elevations ranging from 450 to 580 m (Table II), and adults and juveniles of *Ptychophallus tumimanus* and adults of *Potamocarcinus magnus* are susceptible to natural infections. The overall incidence and intensity of natural infections in crabs from the localities visited by us is low. Natural infections seem to be discontinuous rather than widespread, but further collections of large series of crabs may prove otherwise.

The loss of the cat infection is indeed puzzling, especially since careful effort was made to examine the host and to recover the worms. A possible explanation is that the worms could have localized in a pedunculated cyst, protruding into the gastrointestinal tract, which may have broken off and ruptured, releasing the worms into the lumen of the host gut where they were passed in the feces. There is also a possibility that the worms could have located in the maxillary sinus, as do some other troglotrematids (*Troglotrema acutus* (Leuckart, 1842) in Europe, *Archillurbainia nouvelli* Dollfus, 1939, from Malaysia, and *A. recondita* Travassos, 1942, from Brazil and the Lesser Antilles), migrated out of their cavity, and then have been passed by the host, though no evidence for this was found.

The adults of the microphallid metacercariae from the crabs, tentatively identified as *Maritrema prolixum*, are known from *Philander opossum fuscogriseus* (Allen) (Caballero and Montero, 1961), the same host from which *Paragonimus rudis* (Diesing, 1850) has been recovered in the general area (Caballero and Montero, 1961) where the infected crabs were collected.

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# *PERCINA AUROLINEATA*, A NEW PERCID FISH FROM THE ALABAMA RIVER SYSTEM AND A DISCUSSION OF ECOLOGY, DISTRIBUTION, AND HYBRIDIZATION OF DARTERS OF THE SUBGENUS *HADROPTERUS*

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## ABSTRACT

A new species of *Percina* (subgenus *Hadropterus*) from the Alabama River system is described and compared with *nigrofasciata, sciera* and *lenticula*. The new species P. *aurolineata* is closest to *P. sciera*, but differs in average number of lateral-line scales and vertebrae and in color pattern. Samples for comparison of the species of the subgenus were obtained from co-inhabiting populations. Range extensions are given for *Percina lenticula* and *P. sciera*. Hybridization between *P. nigrofasciata* and *P. sciera* is described and discussed.

## INTRODUCTION

The first specimen of *Percina aurolineata* was taken from the Cahaba River, 2.2 miles north of Centerville, Bibb County, Alabama on 17 March 1957, by R. D. Suttkus, R. J. Miller, H. V. Miller, and J. L. deAbate along with *Percina lenticula* Richards and Knapp,[1] 1964 and *Noturus munitus* Suttkus and Taylor, 1965.

The other 58 specimens were collected during 1962, 1965 and 1966 from the Cahaba and Coosawattee Rivers.

We gratefully acknowledge: assistance in collecting by Dr. C. Robert Shoop, Glenn H. Clemmer, William T. Mason, and the students of the 1965 and 1966 Tulane University Summer Program in Environmental Biology; the loan of material from the University of Alabama (UAIC) by Dr. Herbert T. Boschung, Jr. and James D. Williams; assistance by Dr. Reeve M. Bailey, University of Michigan Museum of Zoology (UMMZ), in making counts and measurements on a specimen of *Percina lenticula;* permission by Dr. Donald Scott, University of Georgia (UG), to examine 3 specimens of *P. lenticula;* and the aid of collecting and loan of comparative material from Cornell University (CU) by Dr. Edward C. Raney; and loan of material from the United States National Museum (USNM) by Dr. Ernest A. Lachner; photographs are by Dr. Clyde D. Barbour.

We particularly are indebted to Dr. Gerald E. Gunning for assisting the authors in the collection of many of the samples of comparative material from the Pearl River. Nearly all collections were obtained at night and often under severe weather conditions. Assistance in field work and laboratory studies was made through National Institutes of Health grants WP-00082-04, 05 and 3-T1-Es-27-02S1, -03S1, and National Science Foundation NSF G-9026.

## *Percina aurolineata*, new species
## Goldline Darter
## (Figs. 1-2)

The description is based on 59 specimens, all of which were taken from the Alabama River drainage.

*Material.* The holotype, Tulane University 39573, an adult male 70.0 mm in standard length, was collected from the

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[1] The date given by Richards and Knapp (1964: 695) for RDS field number 2594 should read 17 March 1957 rather than 17 May 1957.

TABLE 1
Measurements of *Percina aurolineata* and *Percina sciera* expressed as thousandths of standard length.

| | *aurolineata* Coosawattee | | | *sciera* Tombigbee | |
|---|---|---|---|---|---|
| | TU 39573<br>Holotype | TU 38507 CU 50388 USNM 199733<br>TU 38320 | | TU 37584 | TU 34603 |
| Number, sex, standard length (mm) | ♂ (70.0) | 5♂ 5♀ (49.6–74.1) | | 5♂ 5♀ (42.0–76.5) | |
| | | $\bar{x}$ | Range | $\bar{x}$ | Range |
| Body length | 161 | 173 | 163–191 | 182 | 162–202 |
| Body width | 128 | 129 | 118–142 | 137 | 125–152 |
| Caudal peduncle depth | 81 | 78 | 74–81 | 90 | 84–98 |
| Caudal peduncle length | 250 | 246 | 233–255 | 236 | 214–259 |
| Longest D. spine length | 97 | 103 | 95–115 | 111 | 104–118 |
| Longest D. soft ray length | 127 | 130 | 121–136 | 134 | 116–145 |
| First A. spine length | 61 | 72 | 59–77 | 79 | 69–85 |
| Longest A. ray length | 141 | 152 | 136–162 | 142 | 126–160 |
| Longest P$_1$ ray length | 213 | 215 | 197–229 | 215 | 208–226 |
| Caudal fin length | 176 | 173 | 167–189 | 185 | 168–197 |
| P$_2$ fin length | 184 | 193 | 179–202 | 197 | 173–211 |
| P$_2$ fin base length | 31 | 31 | 29–35 | 37 | 31–42 |
| Transpelvic width | 74 | 74 | 65–80 | 76 | 69–81 |
| Head length | 237 | 242 | 236–252 | 253 | 247–259 |
| Head width | 128 | 124 | 119–128 | 133 | 119–149 |
| Head depth | 128 | 136 | 128–145 | 146 | 133–159 |
| Snout length | 64 | 60 | 54–65 | 60 | 52–66 |
| Orbit length | 53 | 54 | 51–60 | 58 | 52–64 |
| Least fleshy interorbital width | 41 | 39 | 36–41 | 47 | 43–51 |
| Upper jaw length | 60 | 57 | 53–60 | 66 | 62–73 |
| Juncture of branchiostegal membranes | | | | | |
| to tip of lower jaw | 124 | 134 | 124–151 | 135 | 119–150 |
| to P$_2$ insertion | 143 | 147 | 138–153 | 154 | 146–162 |

TABLE 2
Number of lateral line scales for the species of *Percina* (Subgenus *Hadropterus*). Values for holotype in boldface.

| Species and Drainage | 46 | 47 | 48 | 49 | [illegible] | [illegible] | [illegible] | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | N | x̄ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *n. nigrofasciata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Cahaba R. | | | | | | | 1 | 1 | 6 | 4 | 10 | 9 | 9 | 12 | 10 | 9 | 8 | 3 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | 83 | 58.4 |
| Black Warrior R. | 1 | 1 | – | – | | | [illegible] | 6 | 8 | 9 | 10 | 3 | 4 | 2 | – | 2 | – | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 51 | 55.0 |
| Tombigbee R. | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| Leaf R. | | | | | | | | | 2 | 1 | 2 | 2 | 1 | 1 | 1 | – | – | – | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | 11 | 57.3 |
| Pearl R. | | | | | | | | | 1 | – | 1 | 5 | 3 | 5 | 5 | 5 | 1 | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | 28 | 59.2 |
| *aurolineata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Coosawattee R. | | | | | | | | | | | | | | 1 | – | – | 1 | 1 | 4 | 4 | **10** | 5 | 5 | 4 | 1 | 6 | 2 | 1 | 1 | | | | | | | | | | | | | | | | | 46 | 67.3 |
| Cahaba R. | | | | | | | | | | | | | | | | | | 1 | – | 1 | 2 | 2 | 2 | 3 | – | 2 | | | | | | | | | | | | | | | | | | | | 13 | 67.6 |
| *sciera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Black Warrior R. | | | | | | | | | | | | | | | 1 | – | – | 1 | 1 | 2 | 1 | 1 | – | – | – | 1 | – | – | 1 | | | | | | | | | | | | | | | | | 9 | 66.1 |
| Tombigbee R. | | | | | | | | | | | | | 2 | 2 | 2 | 3 | 4 | 4 | 2 | 3 | 6 | 2 | 1 | 2 | – | 1 | | | | | | | | | | | | | | | | | | | | 34 | 63.7 |
| Leaf R. | | | | | | | | | | | | 1 | 1 | 3 | 3 | 4 | 6 | 1 | 5 | 7 | 2 | 4 | 4 | | | | | | | | | | | | | | | | | | | | | | | 41 | 63.4 |
| Pearl R. | | | | | | | | | | | 1 | 4 | 5 | 6 | 14 | 13 | 18 | 24 | 28 | 21 | 16 | 11 | 6 | 1 | 2 | – | – | 1 | | | | | | | | | | | | | | | | | | 171 | 63.3 |
| *lenticula* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Etowah R.[1] | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | 1 | 2 | – | – | 2 | 1 | 8 | 86.5 |
| Coosa R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | 1 | |
| Cahaba R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | 1 | – | 2 | 2 | 1 | – | 2 | – | – | 2 | – | – | 1 | 13 | 82.1 |
| Tombigbee R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | – | 1 | | | | | | | | | 3 | 80.3 |
| Leaf R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | 1 | 3 | 1 | – | – | 2 | 1 | 10 | 85.8 |
| Pearl R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | 1 | – | 1 | 3 | – | – | 2 | 1 | 1 | | | | 11 | 82.3 |

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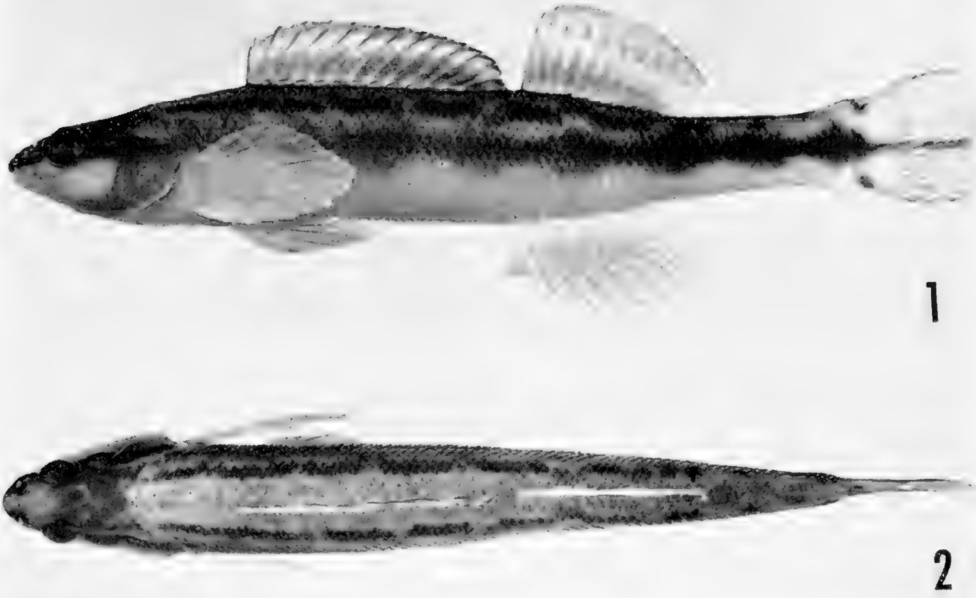
[1] Data from Richards and Knapp, 1964.



Figures 1 and 2. Lateral and dorsal views, *Percina aurolineata*, sp. nov. Holotype, adult male, 70.0 mm in standard length (TU 39573).

Coosawattee River about 200 yards below the mouth of a small spring tributary 4.2 miles southwest of the center of Ellijay, Gilmer Co., Georgia, 18 June 1966, RDS 3910, by Suttkus and 1966 Environmental Biology class.

Paratypes: Taken with the holotype were 3 paratypes, TU 41049 (2♂, 1♀, 57-70 mm in S.L.). Other paratypes include TU 38507 (6♂, 9♀, 38-59), Cornell University 50388 (2♂, 1♀, 50-65), United States National Museum 199733 (2♂, 1♀, 47-57), all from Ga., Gilmer Co., Coosawattee R. 4.2 mi SW of Ellijay, 22 June 1965, RDS 3707, Suttkus and Environmental Biology class; USNM 199817 (3♂, 3♀, 48-68) Ga., Gilmer Co., Coosawattee R., 3 mi S of Ellijay, 9 September 1965, William Smith-Vaniz and Wilmer A. Rogers; TU 38320 (3♂, 2♀, 41-74) Ga., Gilmer Co., Cartecay River, near the mouth of a tributary 3.1 mi SE of Ellijay, near Ga. Hwy 52, 18 June 1965, RDS 3695, Suttkus and Environmental Biology class; TU 40714 (4♀, 55-65), 15 April 1966, RDS 3881, Suttkus and Glenn H. Clemmer; TU 41053 (3♂, 3♀, 37-64) 17 June 1966, RDS 3909, Suttkus and Environmental Biology class.

Other material, all from Alabama: TU 15284 (♀, 47), Bibb Co., Cahaba R. 2.2 mi N of Centerville, just E of Hwy 5, 17 March 1957, RDS 2594, Suttkus, Miller, Miller and deAbate; TU 29116 (juveniles, 34 and 28), Bibb Co., Cahaba R. 8.5 mi NE of Centerville, Hwy 27, 17-18 July 1962, RDS 3132, Suttkus and Mason; TU 37656 (♀, 49), Shelby Co., Cahaba R., 5.4 mi W of Pelham, Hwy 52, 10 May 1965, RDS 3669, Suttkus and Clemmer; TU 37676 (4♂, 62-70), Bibb Co., Cahaba R., 2.2 mi N of Centerville, just E Hwy 5, 11 May 1965, RDS 3670, Suttkus and Clemmer; UAIC 1611 (♂, 60), Bibb Co., Cahaba R. at Pratt Ferry bridge, 5 June 1965, J. D. Williams et al; TU 38197 (2♀, 47 and 51), Shelby Co., Cahaba R., 5.4 mi W of Pelham, Hwy 52, 24 June 1965, RDS 3709, Suttkus and Environmental Biology class; TU 40800 (2♀, 51 and 54), Bibb Co., Cahaba R., 8.5 mi NE of Centerville, Hwy 27, 19 April 1966, RDS 3887, Suttkus and Clemmer.

Methods of counting and measuring described by Hubbs and Lagler (1958) and Richards and Knapp (1964) were followed.

*Diagnosis.* A slender species (Table 1) of the subgenus *Hadropterus* with moderate sized scales (lateral line scales 59-74, usually 64-72); moderate number of vertebrae (40-44, usually 41-43); low number of dorsal soft rays (10-13, usually 10 or 11); slender caudal peduncle, depth less than one third of length of peduncle; narrow least fleshy interorbital width; short upper jaw; mid-dorsal saddles absent or indistinct; dorsolateral pigmentation is a continuous or interrupted stripe (bright amber or russet during nuptial condition), straight at the anterior end, not turned dorsad toward the occiput.

*Description. Percina aurolineata* is the most slender of the four species now included in the subgenus *Hadropterus* (Figure 1 and Table 1; also see Table 7, Richards and Knapp, 1964: 698). Measurements and counts are given for the holotype, paratypes, and other material in Tables 1-6. In males the belly is fully scaled with scales in the midventral row enlarged. The nape is completely covered with scales, which are somewhat reduced in size and embedded anteriorly. The opercle, temporal region, and cheek are completely covered with scales. Those on the cheek are usually partially embedded. The entire breast and prepectoral area are covered with embedded scales or a combination of embedded and exposed scales.

Some females have the belly completely covered with scales although the anterior ones are usually embedded. Other females have scattered embedded scales on the belly, leaving small naked areas. The nape, opercle, cheek and breast are covered with scales, but the scales are smaller and more embedded on the nape, cheek and breast than in the males. There are a few small embedded scales on the prepectoral area.

The branchiostegal membranes are somewhat more narrowly conjoined in *P. aurolineata* than in *P. lenticula,* and are more broadly conjoined than in *P. sciera* (Table 1). The values for the ratio of distance from tip of lower jaw to juncture of branchiostegal membranes divided by distance from the juncture to insertion of pelvic fins are: holotype 0.86, ten paratypes 0.84 - 1.00 ($\bar{x} = 0.91$); *P. lenticula* 0.87-1.05 ($\bar{x} = 0.94$); *P. sciera,* ten specimens from Tombigbee River 0.76 - 1.00 ($\bar{x} = 0.87$).

The preopercle typically has a serrate margin, and 51 of the 59 specimens have one to three pored scales on the caudal fin base (average for 51 specimens is 1.72).

*Coloration in alcohol.* The dark lateral band is composed of seven to nine linearly connected black, oval, or quadrate blotches. The dark band continues anteriorly on the upper edges of the opercle and cheek and on the snout to the lateral parts of the frenum and on the adjoining part of the upper lip.

TABLE 3
Number of vertebrae in the species of *Percina* (Subgenus *Hadropterus*).

| Species Drainage | 39 | 40 | 41 | 42 | 43 | 44 | N | $\bar{x}$ |
|---|---|---|---|---|---|---|---|---|
| *n. nigrofasciata* | | | | | | | | |
| Cahaba R. | | 22 | 35 | 2 | | | 59 | 40.7 |
| Tombigbee R. | | 1 | | | | | 1 | |
| Leaf R. | | 15 | 15 | 1 | | | 31 | 40.5 |
| Pearl R. | | 18 | 19 | 1 | | | 38 | 40.5 |
| *aurolineata* | | | | | | | | |
| Coosawattee R. | | | 2 | 18 | 14 | 2 | 36 | 42.4 |
| Cahaba R. | | 2 | 6 | 3 | | | 11 | 41.1 |
| *sciera* | | | | | | | | |
| Black Warrior R. | | | 4 | 2 | | | 6 | 41.3 |
| Tombigbee R. | | 10 | 18 | 4 | | | 32 | 40.8 |
| Leaf R. | 3 | 29 | 47 | 1 | | | 80 | 40.6 |
| Pearl R. | 1 | 44 | 75 | 1 | | | 121 | 40.6 |
| *lenticula* | | | | | | | | |
| Etowah R.[1] | | | | | 4 | 4 | 8 | 43.5 |
| Cahaba R. | | | | 1 | 8 | | 9 | 42.9 |
| Tombigbee R. | | | | | 2 | | 2 | 43.0 |
| Leaf R. | | | | 1 | 6 | 3 | 10 | 43.2 |
| Pearl R. | | | | | 5 | 5 | 10 | 43.5 |

[1] Data from Richards and Knapp, 1964.

Posteriorly the lateral band is separated slightly from the mid-basal caudal dark spot. The top of the head is dusky except on the anterior portion of the interorbital region and the middle of the frenum which are much lighter. Superimposed on the dusky pigmentation are several scattered brown spots. The lower part of the head below the forward extension of the lateral band is dusky in the males. There is an intensification of the pigmentation below the eye in most males which forms an indistinct suborbital bar. The lower part of the head of the female is much less pigmented than in the male. There are a few melanophores along the posterior part of the upper lip, along the rami of lower jaws, the anterior tip of the lower lip and a few extend posteriorly from the symphysis. An elongate cluster of melanophores forms a poorly developed suborbital bar in the female although the bar is quite noticeable because the surrounding areas of the cheek are devoid of pigment. The ventral part of opercle, cheek, and snout as well as the gular region and the branchiostegal membranes are devoid of pigment in the female. One large female has a few melanophores on the outer part of the left branchiostegal membrane.

Mid-dorsal blotches (saddles) are lacking or indistinct in both sexes. The two juveniles (TU 29116) are exceptions in that dorsal saddles are distinct. Some specimens have a mid-dorsal stripe with slight intensification of pigment just in front of the first dorsal, at posterior end of first dorsal, another extends from base of fourth to seventh soft dorsal ray, another is found on the caudal peduncle under the posterior part of the extended second dorsal fin, and a posterior intensification occurs on the caudal peduncle at the base of the upper procurrent caudal rays. The intensifications are sometimes saddle-like but are not sharply defined as are similar dorsal blotches in *P. sciera*, which, moreover, are separated by light areas. The sharp contrast between dark saddles and light intervening areas in the male of *P. sciera* is masked by the overall darkening at breeding time. The middorsal stripe extends from the anterior base of the first dorsal fin to the occiput in all specimens. Most specimens have a small, well defined, dark-brown spot at the base of the first dorsal spine and at the base of the first dorsal soft ray.

A single brown dorsolateral stripe extends from the lateral aspect of the occiput to the anterior lateral region of the caudal peduncle. In some specimens it continues

TABLE 4
Number of dorsal rays in the species of *Peroina* (Subgenus *Hadropterus*);
Values for holotype in boldface.

| Species | Dorsal Spines | | | | | | Dorsal Soft Rays | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Drainage | 11 | 12 | 13 | 14 | N | $\bar{x}$ | 10 | 11 | 12 | 13 | 14 | N | $\bar{x}$ |
| *n. nigrofasciata* | | | | | | | | | | | | | |
| Cahaba R. | 3 | 69 | 12 | | 84 | 12.1 | 3 | 53 | 26 | 2 | | 84 | 11.3 |
| Black Warrior R. | 15 | 26 | 10 | | 51 | 11.9 | 2 | 28 | 20 | 1 | | 51 | 11.4 |
| Tombigbee R. | | | 1 | | 1 | | | 1 | | | | 1 | |
| Leaf R. | 3 | 8 | | | 11 | 11.7 | 1 | 7 | 3 | | | 11 | 11.2 |
| Pearl R. | 3 | 21 | 4 | | 28 | 12.0 | 4 | 13 | 11 | | | 28 | 11.2 |
| *aurolineata* | | | | | | | | | | | | | |
| Coosawattee R. | | 6 | **35** | 5 | 46 | 13.0 | 16 | **28** | 1 | 1 | | 46 | 10.7 |
| Cahaba R. | | 5 | 7 | 1 | 13 | 12.7 | 7 | 5 | 1 | | | 13 | 10.5 |
| *sciera* | | | | | | | | | | | | | |
| Black Warrior R. | | | 7 | 2 | 9 | 13.2 | 1 | 4 | 4 | | | 9 | 11.3 |
| Tombigbee R. | | 11 | 18 | 5 | 34 | 12.8 | 1 | 18 | 13 | 2 | | 34 | 11.5 |
| Leaf R. | 2 | 14 | 23 | 2 | 41 | 12.6 | 2 | 15 | 23 | 1 | | 41 | 11.6 |
| Pearl R. | 4 | 77 | 84 | 6 | 171 | 12.5 | 1 | 56 | 106 | 8 | | 171 | 11.7 |
| *lenticula* | | | | | | | | | | | | | |
| Etowah R. | | 1 | 6 | 1 | 8 | 13.0 | | | | 4 | 4 | 8 | 13.5 |
| Coosa R. | | 1 | | | | | | | | 1 | | | |
| Cahaba R.[1] | | 2 | 10 | 1 | 13 | 12.9 | | | 4 | 8 | 1 | 13 | 12.8 |
| Tombigbee R. | | | 3 | | 3 | 13.0 | | | | 3 | | 3 | 13.0 |
| Leaf R. | | | 9 | 1 | 10 | 13.1 | | | 2 | 7 | 1 | 10 | 12.9 |
| Pearl R. | | 3 | 8 | | 11 | 12.7 | | | 1 | 5 | 5 | 11 | 13.4 |

[1] Data from Richards and Knapp, 1964 (in part).

anteriorly on the head to the posterior rim of the orbit. This stripe is usually continuous anteriorly but frequently interrupted posteriorly. In most specimens the stripes are linear but may curve slightly with the dorsal contour of the body. However, in some individuals the stripes undulate, especially posteriorly. The intervening spaces between the dorsolateral stripe and the dorsum and the black lateral band are light in the female and slightly dusky in the male.

The entire ventral region of the male is uniformly dusky. With magnification most males are seen to have dark-edged scales. In contrast the female is nearly immaculate below the dark lateral band. The female has a few small patches of brown or black pigment scattered along the lower side of the body, along base of anal fin, on the ventral side of caudal peduncle, on the prepectoral area, and on the breast. Large females have a dark triangular patch just anterior to the anus.

The first dorsal fin of the male has a moderately wide distal dark band. Proximal to this outer band is a clear band of about the same width which is crossed by pigmented spines. Some large males have brown blotches superimposed on some spines (at the intermediate zone). The proximal half to two thirds of the first dorsal fin is uniformly black except for a narrow light area at the extreme base.

In the female the first dorsal fin is sparsely pigmented. There is a very narrow incomplete distal dark band with the major part of the pigment on the spines. An intermediate band, scarcely developed in some individuals, and a proximal band are composed almost entirely of pigmentation on the spines with very little on the intervening membranous areas.

In the male the second dorsal fin is dusky except for around the rays at their first branching. These nonpigmented areas form a row of light spots across the fin. There are superimposed brown spots on the anterior edge of the first ray and on the membrane between the two branches of each ray just distal to the nonpigmented part of each ray.

In the female the membranous part of the entire second dorsal is essentially without pigment. A few scattered melanophores are present on the membrane next to the rays just distal to their first branching and, in some individuals, next to the heavily pigmented portions of the rays, and at the extreme basal part of the membranes. The basal third of each ray is heavily pigmented;

TABLE 5
Caudal peduncle scale counts for species of *Percina* (Subgenus *Hadropterus*); Values for holotype in boldface.

| Species<br>Drainage | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | N | $\bar{x}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *n. nigrofasciata* | | | | | | | | | | | | | | | | | |
| Cahaba R. | 3 | 4 | 19 | 31 | 24 | 2 | | | | | | | | | | 83 | 22.9 |
| Black Warrior R. | 4 | 15 | 14 | 16 | 2 | | | | | | | | | | | 51 | 21.9 |
| Tombigbee R. | | | 1 | | | | | | | | | | | | | 1 | |
| Leaf R. | 1 | 3 | 7 | | | | | | | | | | | | | 11 | 21.5 |
| Pearl R. | 1 | 8 | 10 | 6 | 3 | | | | | | | | | | | 28 | 22.1 |
| *aurolineata* | | | | | | | | | | | | | | | | | |
| Coosawattee R. | 1 | 7 | 12 | **24** | 1 | 1 | | | | | | | | | | 46 | 22.4 |
| Cahaba R. | | | 2 | 5 | 4 | 1 | 1 | | | | | | | | | 13 | 23.5 |
| *sciera* | | | | | | | | | | | | | | | | | |
| Black Warrior R. | | | 3 | 4 | 1 | – | 1 | | | | | | | | | 9 | 23.1 |
| Tombigbee R. | | | 3 | 7 | 15 | 5 | 3 | – | 1 | | | | | | | 34 | 24.0 |
| Leaf R. | | 1 | 9 | 9 | 16 | 6 | | | | | | | | | | 41 | 23.4 |
| Pearl R. | | 7 | 31 | 47 | 42 | 32 | 10 | 2 | | | | | | | | 171 | 23.6 |
| *lenticula* | | | | | | | | | | | | | | | | | |
| Etowah R.[1] | | | | | | | | | | | | 3 | 3 | 2 | | 8 | 31.9 |
| Cahaba R. | | | | | | | | | | | 1 | – | 2 | 8 | 2 | 13 | 32.8 |
| Tombigbee R. | | | | | | | | | | | | 1 | 1 | 1 | | 3 | 32.0 |
| Leaf R. | | | | | | | | | | | 2 | 4 | 4 | | | 10 | 31.2 |
| Pearl R. | | | | | | | | | | | | 6 | 4 | – | 1 | 11 | 31.6 |

[1] Data from Richards and Knapp, 1964 (in part).

next distally is a narrow clear or sparsely pigmented portion which is bordered by another narrow heavily pigmented area. These pigmented parts of each ray extend to the first branching of the rays. The pigmentation at the crotches of the branched rays forms the most pronounced band across the second dorsal fin. In some females the pigment extends along the rays from the first branching to their distal tips but in other specimens there is no pigmentation distal to the branching or only along the anterior rays of the fin.

The caudal fin of both sexes has three basal dark spots. The middle spot is the largest; it is triangular, and only slightly separated from the posterior end of the lateral band. The upper and lower spots are usually distinct; however, in a few individuals the lower basal caudal spot is coalesced with the middle spot. There are upper and lower rounded light areas immediately posterior to the basal caudal spots. The remainder of the caudal fin is dusky except for one or two narrow vertical light areas which appear as wavy vertical bars.

The anal fin of the male is uniformly dusky except at the proximal branching of the rays where a series of light areas forms an interrupted band across the fin.

In the female the pigmentation of the anal fin is similar to that of its second dorsal. There is little or no pigment on the membranes and the pigment along the soft rays forms three narrow bands or two bands with a narrow one distally and a broad one proximally. Both spinous rays and adjoining membranes are usually clear although a few females have two or three melanophores on the posterior margin of the second spine.

The base and all rays of the pectoral fin of the male are dusky. Some males have a crescentic light area distal to the dusky base. Most of the membranes are clear.

The pectoral fin of the female is lighter than that of the male. Part of the prepectoral region and the base of the pectoral are pigmented.

Both the membranes and the rays of the pelvic fins are uniformly dusky in the male. The anterior edge of the fleshy covering over the spine and the swollen tips of the succeeding soft rays are lightly pigmented or milky.

The pelvic fins of small females are im-

TABLE 6
Number of left pectoral rays and anal soft rays in the species of *Percina* (Subgenus *Hadropterus*); Values for holotype in boldface.

| Species | Left Pectoral Rays | | | | | | Anal Soft Rays | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Drainage | 12 | 13 | 14 | 15 | N | x̄ | 7 | 8 | 9 | 10 | N | x̄ |
| *n. nigrofasciata* | | | | | | | | | | | | |
| Cahaba R. | | 14 | 68 | 2 | 84 | 13.8 | | 16 | 62 | 6 | 84 | 8.9 |
| Tombigbee R. | | 27 | 20 | 1 | 48 | 13.4 | | 15 | 27 | 9 | 51 | 8.9 |
| Black Warrior R. | | | 1 | | 1 | | | | 1 | | 1 | |
| Leaf R. | | 3 | 8 | | 11 | 13.7 | | 1 | 10 | | 11 | 8.9 |
| Pearl R. | | 2 | 19 | 7 | 28 | 14.2 | | 7 | 20 | 1 | 28 | 8.8 |
| *aurolineata* | | | | | | | | | | | | |
| Coosawattee R. | | 2 | **38** | 6 | 46 | 14.1 | | 15 | **26** | 5 | 46 | 8.8 |
| Cahaba R. | 3 | 9 | 1 | | 13 | 12.8 | 1 | 3 | 9 | | 13 | 8.6 |
| *sciera* | | | | | | | | | | | | |
| Black Warrior R. | | 4 | 4 | 1 | 9 | 13.7 | 1 | 3 | 5 | | 9 | 8.4 |
| Tombigbee R. | | 9 | 21 | 4 | 34 | 13.8 | 2 | 24 | 8 | | 34 | 8.2 |
| Leaf R. | | 7 | 19 | 5 | 31 | 13.9 | 2 | 26 | 13 | | 41 | 8.3 |
| Pearl R. | 3 | 36 | 117 | 15 | 171 | 13.8 | 5 | 92 | 73 | 1 | 171 | 8.4 |
| *lenticula* | | | | | | | | | | | | |
| Etowah R.[1] | | | 5 | 3 | 8 | 14.4 | | | 6 | 2 | 8 | 9.2 |
| Cahaba R. | | | 8 | 5 | 13 | 14.4 | | | 11 | 2 | 13 | 9.1 |
| Tombigbee R. | | | 1 | 2 | 3 | 14.7 | | | 2 | 1 | 3 | 9.3 |
| Leaf R. | | | 2 | 8 | 10 | 14.8 | | | 6 | 4 | 10 | 9.4 |
| Pearl R. | | | 7 | 3 | 10 | 14.3 | | | 6 | 5 | 11 | 9.4 |

[1] Data from Richards and Knapp, 1964.

TABLE 7

Records of catches of members of the subgenus *Hadropterus* and *Percina palmaris* from areas of known coinhabitation in the Pearl, Pascagoula, Tombigbee and Alabama drainages.

Numbers in parentheses are Tulane University Fish Collection catalogue numbers.

| | *auroli-neata* | *lenti-cula* | *nigro-fasciata* | *sciera* | *palmaris* |
|---|---|---|---|---|---|
| Pearl R. drainage | | | | | |
| Pearl R.: lower part | | | | | |
| Sept. 10, 1963 (31463, 31452) | – | 1 | – | 4 | – |
| June 11, 1964 (33244, 33250) | – | 1 | – | 21 | – |
| July 9, 1964 (33621, 33625) | – | 2 | – | 4 | – |
| Jan. 16, 1965 (27696, 27697, 27699) | – | 1 | 3 | 39 | – |
| Mar. 25, 1965 (37316, 37309, 37334) | – | 1 | 3 | 92 | – |
| Strong R. at rapids 2.3 mi W of Pinola, Miss. | | | | | |
| Apr. 3, 1958 (17733) | – | – | – | 11 | – |
| May 3, 1958 (18079) | – | – | – | 12 | – |
| July 3, 1958 (18727) | – | – | – | 8 | – |
| May 8, 1959 (19787) | – | – | – | 33 | – |
| July 4, 1960 (23740, 23737) | – | – | 2 | 7 | – |
| Dec. 29, 1962 (28806, 28805) | – | – | 1 | 51 | – |
| Nov. 6, 1963 (30143, 30148) | – | – | 15 | 153 | – |
| Feb. 1, 1964 (31702, 31700) | – | 1 | – | 17 | – |
| May 17, 1964 (32875, 32867, 32883) | – | 3 | 11 | 162 | – |
| Dec. 13, 1965 (39459, 39460) | – | – | 8 | 39 | – |
| Pascagoula R. drainage | | | | | |
| Leaf R. at rapids 1 mi W of Moselle, Miss. | | | | | |
| Dec. 29, 1962 (28645, 28624) | – | – | 5 | 58 | – |
| Nov. 2, 1963 (30074, 30053, 30057) | – | 10 | 11 | 31 | – |
| Dec. 12, 1965 (39407, 39408) | – | – | 4 | 3 | – |
| Tombigbee R. drainage | | | | | |
| 0.5 mi above and below Hwy 50 bridge, 10 mi NW of Columbus, Miss. | | | | | |
| Sept. 9, 1964 (34603) | – | – | – | 21 | – |
| May 6, 1965 (37580, 37590, 37584) | – | 1 | 1 | 11 | – |
| June 26, 1965 (38543, 38546) | – | 1 | – | 3 | – |
| Dec. 12, 1965 (39429) | – | – | – | 7 | – |
| Alabama R. drainage | | | | | |
| Cahaba R. | | | | | |
| Mar. 17, 1957 (15284, 15291, 15286) | 1 | 7 | 17 | – | – |
| July 17-18, 1962 (29116, 29133) | 2 | – | 2 | – | – |
| May 10, 1965 (37656, 37665) | 1 | – | 36 | – | – |
| May 11, 1965 (37676, 37679) | 4 | – | 19 | – | – |
| June 24, 1965 (38197, 38196) | 2 | – | 16 | – | – |
| Apr. 19, 1966 (40800, 40790) | 2 | – | 15 | – | – |
| Coosawattee R. | | | | | |
| June 22, 1965 (38507*, 38508) | 21 | – | – | – | 114 |
| June 18, 1966 (41049 + 39573, 41044) | 4 | – | – | – | 23 |
| Cartecay R. | | | | | |
| June 18, 1965 (38320, 38321) | 5 | – | – | – | 51 |
| Apr. 15, 1966 (40714, 40713) | 4 | – | – | – | 45 |
| June 17, 1966 (41053, 41055) | 6 | – | – | – | 39 |
| Talking Rock Cr. | | | | | |
| June 19, 1965 (38351, 38350) | – | – | 74 | – | 5 |
| Apr. 15, 1966 (40726, 40728) | – | – | 53 | – | 26 |

* Plus Cornell Univ. 50388 and U.S. National Museum 199733.

maculate. Large females have scattered dusky spots along the rays.

*Color in Life.* Color notes were recorded for the four male specimens (TU 37676) obtained from the Cahaba River on 11 May 1965 soon after they were collected. Each had three or four bright amber or russet spots on the dorsal part of the snout and four or five similar spots on the top of the head between the interorbital region and the occiput. Yellowish blotches were present in the intervening areas and the rim of the orbit was yellowish. The iris appeared to be a mixture of amber and orange. The dorsolateral stripe on either side of the body was bright amber. Each spine in the anterior half of the first dorsal fin had an elongate bright amber blotch in the submarginal band. This submarginal band which was described as a nonpigmented (membranous areas) intermediate band in the alcoholic specimens was bright canary yellow in life. The marginal band and the basal zone were dusky. The second dorsal fin was mostly dusky but the light areas (as described for alcoholic specimens) at the branching of the rays were bright yellow in life. The basal part of each interradial membrane was bright yellow. A small bright russet spot was present at the anterior base of the second dorsal fin.

The dorsolateral area above and below the amber dorsolateral stripe was bright yellow. This bright yellow shaded to olive at the superior margin of the lateral band. An elongate suborbital patch, an elongate area below the preorbital band on the snout, and the upper part of the upper lips were yellow. The base of the caudal fin and the area around the basal caudal spots were bright yellow. The one or two wavy vertical areas on the caudal fin were bright yellow. The anal fin was bluish-gray with yellowish on some rays; the distal margin had a narrow milky white edging. The pectoral fins were yellowish, especially the crescentic area distal to the dusky base. The pelvics were bluish-gray with a milky white edging on the distal margin.

Below the lateral dark band the body was pale with a bluish-olive hue. The ventral surface of the lower jaw, the interopercular surface and the ventral surface of the cheek were iridescent blue.

Color notes for a paratypic series (RDS 3707, taken 22 June 1965) were recorded by the junior author on July 17, 1965. Some fading had occurred, but the males were yellow to yellow-olivaceous above, and a pale yellow submarginal band was present on the first dorsal fin. The other fins were colored as follows: second dorsal and caudal yellowish; pelvics dusky, with some with yellow on anterior half; anal dusky and pectorals yellowish, especially near the base. The lips were yellow and the ventral part of the body was pale with dusky overlay.

Females were more yellow above the lateral line. The cheeks and lips were yellow. The first dorsal fin lacked a submarginal yellow band. The ventral part of the body was white with scattered patches of dark-edged scales. The caudal was yellow, as in the males, but the anal and pelvics were clear. These fins were clear except for scattered dark patches, mainly on the rays.

Specimens collected from the Cartecay River on 15 April 1966 were somewhat emaciated and did not exhibit any yellow, golden or amber coloration. Obviously these specimens were in winter condition and had not started to develop nuptial coloration.

*Variation.* Geographic variation is apparent between Cahaba and Coosawattee populations. The Coosawattee specimens have a higher average number of vertebrae, dorsal spines, dorsal soft rays, pectoral rays, and anal soft rays, but average fewer rows of scales around the caudal peduncle (Tables 2-6). A parallel pattern of variation is shown for *P. lenticula* in data presented by Richards and Knapp, 1964. Specimens of *lenticula* from the Etowah River (higher elevation) differ from Cahaba River specimens also in having higher meristic counts. An exception is noted in the caudal peduncle scale row count, which is lower in the upstream population of *lenticula.*

*Relationships.* Richard and Knapp (1964: 690) indicated the Pearl River drainage as the eastern limit of the range of *Percina sciera* along the Gulf Coast. They gave comparative information and suggested relationships (1964: 698, 699) for the three species which they included in the subgenus *Hadropterus.*

Meristic characters, proportional measurements, and color patterns support the view that *aurolineata* and *sciera* are closely related, and furthermore that *sciera* is probably more closely related to *aurolineata* than to *lenticula.* Both *lenticula* and *aurolineata* occur together in the Cahaba River and may occur together in other parts of the Alabama system. Specimens of *sciera* from the Tombigbee, Leaf and Pearl rivers were selected for comparison because they were taken with *lenticula* at the same sites. Thus Table 7 summarizes coinhabitation by geographical areas; *sciera, lenticula,* and *nigrofasciata* are coinhabitants in the Pearl, Leaf, and Tombigbee rivers; *sciera* and *nigrofasciata* in the Black Warrior River (it is likely *lenticula* will be collected there eventually); and *aurolineata, lenticula* and *nigrofasciata* in the Cahaba River. Perhaps future collections will reveal coinhabiting populations of *aurolineata* and *lenticula* in the upper part of the Alabama River drainage.

In some characters (e.g. in number of lateral line scales and number of vertebrae) *aurolineata* is intermediate between *lenticula* and *sciera. Percina aurolineata* is closer to *sciera* and *nigrofasciata* than to *lenticula* in most meristic characters. *Percina lenticula* has the highest values for most meristic characters. Of the meristic characters considered, the number of lateral line scales (Table 2) shows the greatest divergence among the four species. *Percina nigrofasciata* has the lowest average number of scales and *lenticula* has the highest. *Percina sciera* is nearly intermediate between *aurolineata* and *nigrofasciata* in this character. On the basis of many meristic characters, *sciera, aurolineata,* and *nigrofasciata* form a close group distinct from *lenticula.*

In body proportions (Table 1) and color pattern, *aurolineata* seems to be more closely related to *sciera* than to either *nigrofasciata* or *lenticula.*

The complementary distribution of *aurolineata* and *sciera* suggests that *aurolineata* represents an eastern isolate of *sciera* stock and that *sciera* has not redispersed into *aurolineata* range. The reverse movement seems less likely because *aurolineata* apparently has a lower maximum temperature tolerance than *sciera. Percina aurolineata* has been encountered only above the Fall Line, and thus may represent a population derived from a former *sciera* stock which invaded the upper Alabama system from the Tennessee drainage when they were connected in the past. (Hayes and Campbell, 1900: 131-33; Simpson, 1900: 133-136).

*Comparisons. Percina aurolineata* and *sciera* differ primarily in coloration. The dorsal saddles are lacking or indistinct in *aurolineata,* while *sciera* invariably has well defined median dorsal saddles which are visible even on darkened nuptial males. *P. aurolineata* has a single linear, continuous or interrupted stripe on the dorsolateral area whereas *sciera* has oval or quadrate blotches or if narrow spots are present, they are not arranged in a linear fashion, but instead undulate between the lateral margins of the dorsal saddles and dorsal margins of lateral blotches. In *aurolineata* it continues anteriorly to the lateral aspect of the occiput, and in some specimens is continuous with the postorbital bar, whereas in *sciera* it typically curves toward the middorsal part of the occiput, and frequently joins with that on the opposite side to form a V-shaped pattern at the occiput.

All (faint in some specimens such as the holotype) *aurolineata* specimens have a middorsal stripe which extends from the origin of dorsal fin to the occiput. Although some specimens have a predorsal blotch, it is not encircled anteriorly by a light area. *Percina sciera* has a dorsal saddle just in front of the first dorsal fin and this saddle is separated from the convergent dorsolateral stripes by a lightly pigmented area. The bright yellow, amber or russet coloration of *aurolineata* is not seen in *sciera.* Nuptial males of *sciera* are generally dark over the entire body. Sometimes the females of *sciera* are yellowish on the dorsolateral area, but lack the bright amber or russet.

*P. sciera* from the Tombigbee River has more of the belly, breast, and prepectoral area naked than does *aurolineata* from any part of its range. Also more of the scales of *sciera* are small and embedded.

Average differences are shown in several proportional measurements between *aurolineata* and *sciera* (Table 1). However, there is no overlap in range of variation in depth of caudal peduncle, least fleshy interorbital width, and upper-jaw length.

*Ecology and distribution. P. aurolineata* is an inhabitant of the main channels of rivers, as is *P. lenticula.* The rivers at collection sites ranged from 50 to 200 feet in width. All localities were "white water" rapids four inches to three feet deep with small to extensive bottom areas of bedrock, boulder, rubble and gravel. River weed, *Podostemum,* grew at all localities, and was particularly luxuriant at the Cartecay and Coosawattee sites. In addition to *Podostemum* there were extensive beds of water willow, *Justicia,* at the three Cahaba River sites. Although there may be a general association of *aurolineata* with plants, none was observed in the clumps of *Podostemum* or *Justicia. Percina aurolineata* was observed on the sand between the *Podostemum*-covered boulders at the Cartecay River locality, over gravel between *Podostemum*-covered boulders at the type locality, and over gravel next to beds of *Justicia* at the lower Cahaba River locality.

Water temperatures ranged from 12.5 to 25°C: 18°C at the Cartecay River site at 1330 hrs on 18 June 1965, 12.5°C at 1250 hrs on 15 April 1966; 20°C at Coosawattee River at 1730 hrs on 22 June 1965; 23°C at two localities on the Cahaba River at 2330 hrs on 10 May 1965 and at 1030 hrs on 11 May 1965; and 25°C at upper Cahaba River locality at 1430 hrs on 24 June 1965.

The known occurrences of *Percina aurolineata* and *P. lenticula* (Fig. 3) are such as to suggest the probability that both species occurred throughout the upper Alabama drainage in the past, and that they may be present in a few localities in this area at the present time. However, pollution and extensive impoundment probably have eliminated these species from much of the area.

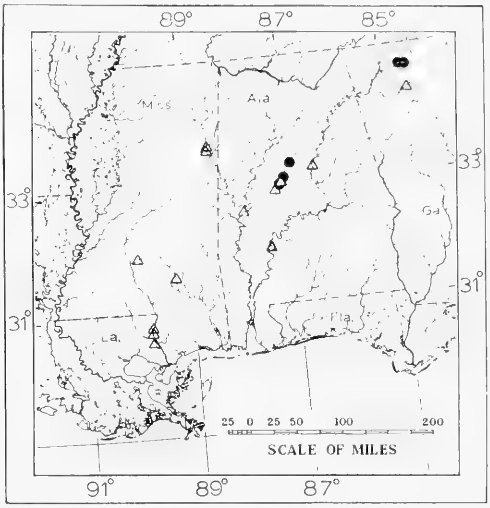


Figure 3. Distribution of collections of *Percina aurolineata* (solid circles) and *Percina lenticula* (open triangles).

Toward achieving a more detailed analysis of distributional interrelations, we have tabulated (Table 7) the catch statistics of all collections of *aurolineata* and *lenticula* made by us, along with statistics for other species of the subgenus *Hadropterus* taken with *aurolineata* and *lenticula.* Additional statistics for *sciera* and *nigrofasciata* are presented for comparison. Catch records for *Percina palmaris* (Bailey) are presented along with data for *aurolineata* because *palmaris* was the only other species of *Percina* taken at the Cartecay and Coosawattee localities, which drain the region above Coosawattee Falls. Talking Rock Creek is a small tributary entering the Coosawattee below the falls. Perhaps the indicated switch in dominance, based on number of individuals caught by seine, is coincidental or a reflection of biased sampling, but the figures may indicate a relationship of dominance through competition in the two kinds of habitats, river *(palmaris* vs. *aurolineata)* and creek *(nigrofasciata* vs. *palmaris)* or the specific relationship between each species and the particular habitat. During the April 15, 1966 collection from Talking Rock Creek the water was 15°C and there was an obvious difference in number of the two species in the different habitats. *Percina palmaris* was common in the riffles and rare along the banks in still water. However *nigrofasciata* was common in the latter area which apparently is its wintering habitat.

Associated fish species taken with *Percina aurolineata* at the type locality were *Hypentelium etowanum, Campostoma anomalum, Nocomis micropogon, Notropis callistius, Notropis stilbius, Notropis trichroistius, Notropis zonistius, Micropterus coosae, Micropterus punctulatus henshalli,* *Etheostoma jordani, Percina palmaris* and *Cottus carolinae zopherus.* Associates at the Cartecay locality were *Ichthyomyzon gagei, Hypentelium etowanum, Moxostoma duquesnei, Campostoma anomalum, Nocomis micropogon, Notropis callistius, Notropis stilbius, Notropis trichroistius, Notropis zonistius, Semotilus atromaculatus, Lepomis auritus, Micropterus coosae, Percina palmaris* and *Cottus carolinae zopherus.* Fish species taken with *aurolineata* at the three Cahaba River localities were as follows: *Alosa alabamae, Alosa chrysochloris, Dorosoma cepedianum, Hypentelium etowanum, Moxostoma duquesnei, Campostoma anomalum, Ericymba buccata, Hybopsis aestivalis, Hybopsis amblops winchelli, Hybopsis storeriana, Notropis caeruleus, Notropis callistius, Notropis chrysocephalus isolepis, Notropis stilbius, Notropis uranoscopus, Notropis venustus stigmaturus, Notropis volucellus, Phenacobius catostomus, Pimephales vigilax perspicuus, Noturus leptacanthus, Noturus munitus, Anguilla rostrata, Fundulus olivaceus, Ambloplites rupestris ariommus, Lepomis cyanellus, Lepomis macrochirus, Lepomis m. megalotis, Micropterus coosae, Micropterus punctulatus henshalli, Ammocrypta beani, Ammocrypta vivax, Etheostoma jordani, Etheostoma rupestre, Etheostoma stigmaeum, Percina caprodes carbonaria, Percina copelandi, Percina lenticula, Percina n. nigrofasciata, Percina shumardi, Cottus carolinae zopherus.*

*Ecology and relationships of lenticula, nigrofasciata and sciera outside of range of aurolineata.* *Percina sciera* seems to be tolerant of a greater range of habitat with regard to size of stream than either *aurolineata* or *lenticula. Percina sciera* is a common inhabitant of small rivers and large tributaries as well as of large rivers in the Tombigbee, Pascagoula, and Pearl river drainages. Outside of the central Gulf Coastal area, that is west of the Mississippi River and north in the Mississippi basin area, *sciera* lives in small streams as well as rivers. *Percina nigrofasciata* is abundant along the eastern Gulf and southern Atlantic Coastal Plain, primarily in small streams. It occurs in the small streams in the Piedmont region above the fall line in the Alabama, Apalachicola, Savannah, and Edisto systems (Crawford, 1956: 17). Often *nigrofasciata* is associated with a gravel bottom or with emergent or submerged aquatic vegetation or debris (snags) in the small-stream habitat. Invariably, when living in a river habitat, *nigrofasciata* is associated with bedrock, boulders, rubble, or gravel bottom where *Podostemum* or *Justicia* usually grows. *Percina sciera* seems to be more tolerant of other types of bottom (sand, silt-covered sand, or gravel) where aquatic plants are absent. Perhaps there is considerable interspecific competition between the two species in the river habitats and *sciera* is more successful in the deep, swift waters and non-vegetated areas.

Thirty-seven monthly night collections for the period April 1963 through April 1966 from a sand bar along the Pearl River, 1.4 miles east of Bogalusa, Louisiana, did not produce any *nigrofasciata.* However, *sciera* (26 specimens) was taken in ten collections. Thirty-seven concurrent night collections, plus nine additional collections (during March and April, 1965 and February, March and April, 1966), were made immediately below a low dam four miles south of Bogalusa. The bottom at this part of the Pearl River was composed of gravel with a very sparse growth of *Podostemum.* In the parts sampled the current was more swift than at the sand bar locality. In the 46 samples, *nigrofasciata* was taken 11 times (28 specimens), *sciera* 29 times (789 specimens) and hybrids four times (11 specimens). *Percina sciera* was present in greater number in every collection which also yielded *nigrofasciata.* Most specimens of both species were collected during the cooler months. Very few were taken from the shallows during the summer when water temperature exceeded 25°C.

Based on the tabulation in Table 7, *Percina sciera* appears to be more successful in the river habitats than is *nigrofasciata.* The periodicity and duration of the monthly sampling period for the lower Pearl River localities eliminates the possibility of missing a peak in abundance of *nigrofasciata* because several samples were obtained during the peak of spawning. Moreover, *nigrofasciata* is found more often in the shallow parts of the riffles and rapids than is *sciera* and so any sampling bias would have favored *nigrofasciata.*

A comparison of catch records from the

Strong River area with those from the lower Pearl River at the dam south of Bogalusa shows that frequency of occurrence and number of specimens of *nigrofasciata* were higher at the former locality. The Strong River rapids had a thick carpet of *Podostemum*, and usually there were more extensive shallow areas than present at the dam locality. Thus the Strong River area seemed to be a better habitat for *nigrofasciata* but even there *sciera* dominated.

*Percina lenticula* adults typically inhabit the deepest and fastest parts of rapids, and this is the likely reason so few specimens have been collected. The November 2, 1963 collection from Leaf River came from the fastest (10 feet per second) and deepest (2.5 feet) part of the rapids. During the December 12, 1965 visit, high water prevented collecting in midstream and collecting was limited to the edge; this probably accounted for the lack of *lenticula* and for the predominance of *nigrofasciata* over *sciera* in the collection.

An interesting species association was noticed during the November 1963 collecting from the Leaf River. The bedrock in the rapids area was very uneven, with numerous potholes. We assumed (not being able to see the bottom because of turbulence and turbidity) that most of the fishes caught in the seine were chased out of the holes by our kicking. In more than half of the nine or ten sets in which we obtained *lenticula* we also captured one or two specimens of *Etheostoma histrio* and *Anguilla rostrata*.

*Hybridization*. Swain (1884: 252) stated in his description of *Hadropterus scierus* that *scierus* and *nigrofasciatus* are evidently closely related. Hubbs and Black (1954: 202) noted Swain's observation about the relationship between the two species and stated that both species sometimes occur together in the central part of the Gulf lowland, that their morphological and ecological relationships had not been determined, and that no indication of intergradation between them had been observed. Neither Hubbs and Black (1954), nor Hubbs (1954) in his description of a new subspecies of *scierus* specifically mentioned or used specimens from the Pearl, Pascagoula or Tombigbee rivers in their tabulations of meristic characters. Crawford (1956: 27, 33) mentioned coinhabiting populations of *sciera* and *nigrofasciata* in the Pearl River and in drainages flowing into Lake Pontchartrain. He compared the two species (op. cit.: 27, 29) and (:33) stated that there is no evidence of intergradation and that the respective forms seem to be relatively unsuccessful in invading each others range. He suggested that this is further evidence for the close relationship between the two forms.

Intensive studies of the fishes of the Pearl River at Pools Bluff Sill, Washington Parish, Louisiana, have revealed the presence of hybrids between *Percina nigrofasciata* and *Percina sciera*.

The fast flowing, turbulent waters over the extensive gravel beds below the low dam support an abundance of fishes and seventy-three species have been recorded.

During January through April high water condition is typical for the Pearl River at Pools Bluff Sill. Although some darters do not move into temporary flooded areas behind the curtains of the dam, both *nigrofasciata* and *sciera* do and apparently spawn over sand bottom and gravel. Because of the turbidity and turbulence, direct observations on behavior usually are impossible. Both species spawn from the middle of February to about the middle of April at the Pools Bluff locality. The following observations were made in 1965; January 16, both *nigrofasciata* and *sciera* were collected, no ripe individuals of either species, water temperature 13°C at 1:48 AM; March 18, *sciera* males ripe, water 15°C at 8:00 PM; March 25, *sciera* males ripe, females not ripe, water 17°C at 10:20 PM; April 8, *sciera* male nearly spent, water 20°C at 9:15 PM. During the spring of 1966 the following data were recorded: February 18, *sciera* female ripe, water 11°C at 12:00 midgnight; February 24, *nigrofasciata* female ripe, *sciera* males ripe, water 10°C at 12:15 AM: March 4, *nigrofasciata* male ripe, *sciera* males and females ripe, water 12°C at 1:30 AM; March 10, *sciera* males and females ripe, water 12° C at 5:30 PM.

Physical and biological conditions at Pools Bluff that appear to be conducive to hybridization between *nigrofasciata* and *sciera* are: (1) a barrier (dam); (2) restricted preferred spawning areas; (3) presumably a marginal habitat for *nigrofasciata;* (4) overlap in spawning time, and (5) extremes in relative abundance (*nigrofasciata* relatively scarce and *sciera* common).

The *Percina nigrofasciata* x *Percina sciera* hybrids (Figs. 7-9) exhibit an intermediacy especially in number, shape, and size of lateral blotches (Figs. 4-12, Table 8). The lateral and vertical dimensions of the major lateral blotches were determined for 10 specimens of *nigrofasciata* (TU 27697, 2 specimens; TU 37309, 2; TU 39550, 1; TU 39681, 1; TU 39725, 4); for 10 hybrids (TU 39380, 2; TU 39726, 4; TU 40000, 2; TU 40887,1; TU 40888,1) for 10 specimens of *sciera* (TU 39724). The basicaudal blotch, although not measured, was considered as the first blotch, the penultimate as the second and so on forward. The average ratios (lateral dimension of blotch, as measured along lateral line, divided by vertical dimension) are consistently intermediate in the hybrids (Table 8). The number of lateral blotches is also intermediate for the hybrids.

The hybrids are also intermediate in number of scales (Table 9). In number of vertebrae and fin rays the parental species are too similar to provide a satisfactory test for hybrid intermediacy (Table 10).

*Supplementary material.* The material examined in this study for comparison of meristic characters is listed in abbreviated form.

*Percina lenticula. Pearl River drainage:* TU 31463 (1, 72 mm S.L.) La., St. Tammany Parish, Wilson Slough at West Pearl River, 3.5 mi E Talisheek, RDS 3329, 10 Sep. 1963. TU 27696 (1, 73) La., Washington Par., Pearl R. just below dam at Pools Bluff, 4 mi S Bogalusa, RDS 3623, 16 Jan. 1965. TU 33621 (2, 48 and 49) La., Washington Par., Pearl River just above dam at Pools Bluff, 4 mi S Bogalusa, RDS 3526, 9 July 1964. TU 37316 (1, 100) La., Washington Par., Pearl River just below dam at Pools Bluff, 4 mi S Bogalusa, RDS 3644, 25 Mar. 1965. TU 33244 (1, 38) La., Washington Par., Pearl River at River Mile 54, 2.3 mi SE Bogalusa, RDS 3479, 11 June 1964. UMMZ 173953 (1, 154) Miss., Strong R., 1954. TU 31702 (1, 106) Miss., Simpson Co., Strong R., 2.3 mi W Pinola, Hwy 28 (formerly Hwy 20) RDS 3376, 1 Feb. 1964. TU 32875 (3, 98-117) Miss., Simpson Co., Strong R. 2.3 mi W of Pinola, Hwy 28, RDS 3431, 17 May 1964. TU 41970 (1, 74)[1] La., St. Tammany Par., Pearl R. at River Mile 52, 11.5 mi below Pools Bluff Sill, RDS 4024, 18 October 1966. TU 41990 (1, 76)[1] La., St. Tammany Par., Pearl R. at River Mile 51.5, 12 mi below Pools Bluff Sill, RDS 4025, 18 October 1966. *Pascagoula River*

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[1] Specimen was not used in comparison but collection site is represented on map.

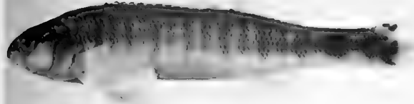
TABLE 8

Ratios of lateral dimension divided by vertical dimension of lateral blotches in ten each of *Percina nigrofasciata*, hybrids, and *Percina sciera* from the Pearl River.

Lateral Blotches

| | 12th | 11th | 10th | 9th | 8th | 7th | 6th | 5th | 4th | 3rd | *Penultimate*[1] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Percina sciera* | | | | | | | | | | | |
| Number of specimens | | | | 3 | 7 | 10 | 10 | 10 | 10 | 10 | 10 |
| Average | | | | 0.34 | 0.39 | 0.59 | 0.83 | 0.99 | 1.10 | 0.99 | 1.18 |
| *P. sciera* × *P. nigrofasciata* | | | | | | | | | | | |
| Number of specimens | | 2 | 8 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| Average | | 0.25 | 0.30 | 0.29 | 0.37 | 0.33 | 0.39 | 0.50 | 0.58 | 0.70 | 0.94 |
| *P. nigrofasciata* | | | | | | | | | | | |
| Number of specimens | 5 | 9 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| Average | 0.17 | 0.17 | 0.16 | 0.16 | 0.17 | 0.17 | 0.21 | 0.26 | 0.37 | 0.56 | 0.79 |

[1] Lies just ahead of the central basicaudal spot.



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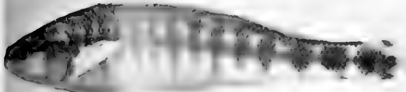

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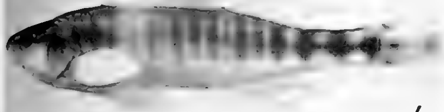

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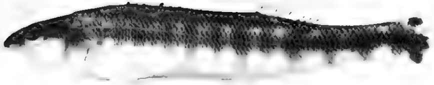
Figures 4-6. *Percina nigrofasciata.* 4 TU 39806 5. TU 39725 6. TU 27697.



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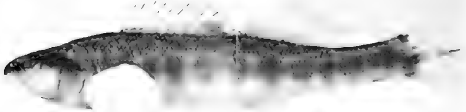
Figures 7-9. *Percina nigrofasciata* X *Percina sciera.* 7. TU 40000 8. TU 39380 9. TU 39380.



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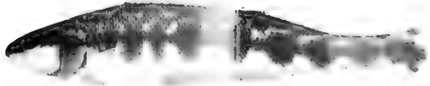

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Figures 10-12. *Percina sciera.* 10. TU 39801 11. TU 39801 12. TU 39801.

*drainage:* TU 30074 (10, 103-141) Miss., Jones Co., Leaf River about 1 mi W Moselle, RDS 3354, 2 Nov. 1963. *Tombigbee River drainage:* TU 37580 (1, 82) Miss., Lowndes Co., Tombigbee R. 9 mi NW Columbus, 0.5 mi above Hwy 50 bridge, RDS 3663, 6 May 1965. TU 38543 (1, 30) Miss., Clay Co., Tombigbee R. 9 mi NW Columbus, 0.5 mi below Hwy 50 bridge, RDS 3712, 26 June 1965. UG 660 (1, 33) Ala., Marengo and Sumter County line, Tombigbee R., 9-10 July 1959. *Alabama River drainage:* UG 140 CR-3 (1, 48), Ala., Shelby Co., Coosa R., 30 Aug. 1949. UAIC 2036 (3, 24-28) Ala., Bibb Co., Cahaba River 2.5 mi SE of Harrisburg, 4 June 1966. TU 40939 (1, 37[1]): Ala., Wilcox Co., Alabama R. at Tait Bar, River Mile 122.4, RDS 3920, 28 June 1966. In addition, all material listed by Richards and Knapp (1964) from Cahaba River and up-

TABLE 9
Comparison of scale counts.

| | Lateral Line Scales | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 |
| *Percina nigrofasciata* | 1 | 1 | – | 1 | 3 | – | 3 | 1 | | | | | | |
| *Percina nigrofasciata* × *Percina sciera* | | | | | 2 | 2 | 1 | 1 | 1 | – | 2 | 1 | | |
| *Percina sciera* | | | | | | 1 | 1 | – | 2 | 2 | 1 | 1 | – | 2 |

| | Transverse Scales (From origin of anal upward to base of first dorsal fin) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | Mean |
| *Percina nigrofasciata* | 2 | 1 | 5 | 2 | | | | | | 19.7 |
| *Percina nigrofasciata* × *Percina sciera* | | | 2 | 4 | 2 | – | 2 | | | 21.4 |
| *Percina sciera* | | | 1 | 1 | 2 | 2 | – | 3 | 1 | 23.1 |

| | Caudal Peduncle Scales | | | | | |
|---|---|---|---|---|---|---|
| | 21 | 22 | 23 | 24 | 25 | Mean |
| *Percina nigrofasciata* | 3 | 3 | 4 | | | 22.1 |
| *Percina nigrofasciata* × *Percina sciera* | 2 | – | 5 | 3 | | 22.9 |
| *Percina sciera* | | 5 | 1 | 1 | 3 | 23.1 |

TABLE 10
Comparison of Fin Ray counts and number of vertebrae.

| | Dorsal Rays | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Spines | | | | | Soft Rays | | | | |
| | 11 | 12 | 13 | 14 | Mean | 10 | 11 | 12 | 13 | Mean |
| *P. nigrofasciata* | 1 | 6 | 3 | | 12.2 | 1 | 6 | 3 | | 11.2 |
| *P. nigrofasciata* × *P. sciera* | | 4 | 5 | 1 | 12.7 | | 2 | 8 | | 11.8 |
| *P. sciera* | | 4 | 6 | | 12.2 | | 4 | 5 | 1 | 11.7 |

| | Anal Soft Rays | | | | | | |
|---|---|---|---|---|---|---|---|
| | Anal Soft Rays | | | | Vertebrae | | | |
| | 8 | 9 | 10 | Mean | 40 | 41 | 42 | Mean |
| *P. nigrofasciata* | 3 | 7 | | 8.7 | 7 | 4 | 2 | 40.6 |
| *P. nigrofasciata* × *P. sciera* | 4 | 6 | | 8.2 | 5 | 7 | 1 | 40.7 |
| *P. sciera* | 7 | 2 | 1 | 8.4 | 4 | 12 | 2 | 40.8 |

| | Left Pectoral Soft Rays | | | |
|---|---|---|---|---|
| | 13 | 14 | 15 | Mean |
| *P. nigrofasciata* | 1 | 8 | 1 | 14.0 |
| *P. nigrofasciata* × *P. sciera* | 1 | 8 | 1 | 14.0 |
| *P. sciera* | 2 | 8 | | 13.8 |

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[1] Specimen was not used in comparison but collection site is represented on map.

per Alabama River drainage was used in this paper.

*Percina n. nigrofasciata. Pearl River drainage:* The following material was collected from La., Washington Par., Pearl R. just below dam at Pools Bluff, 4 mi S of Bogalusa: TU 27630 (1, 56) RDS 3617, 18 Dec. 1964; TU 27697 (2, 60 and 79) RDS 3623, 16 Jan. 1965; TU 27837 (2, 63 and 67) RDS 3629, 12-13 Feb. 1965; TU 37309 (2, 70 and 81) RDS 3644, 25 Mar. 1965; TU 37377 (4, 58-77) RDS 3645, 3 Apr. 1965; TU 39550 (2, 49-66) RDS 3830, 21 January 1966; TU 39681 (1, 70) RDS 3832, 18 February 1966 and TU 39725 (4, 62-80) RDS 3833, 24-25 February 1966. The following material was collected from Miss., Simpson Co., Strong R. 2.3 mi W Pinola, Hwy 28: TU 23740 (2, 34 and 34) RDS 2917, 4 July 1960; TU 28806 (1, 34) RDS 3193 29 Dec. 1962; TU 30143 (15, 38-94) RDS 3357, 6 Nov. 1963; TU 32867 (10, 44-59) RDS 3431, 17 May 1964, and TU 39459 (8, 38-68) RDS 3825, 13 Dec. 1965. *Pascagoula River drainage.* TU 28581 (5, 30-68) Miss., Covington Co., Leaf R. 1 mi upstream from US Hwy 84, 10 mi ENE Collins, RDS 3185, 23 Nov. 1962. TU 28601 (10, 28-69) Miss., Covington Co., Leaf R. 0.75 mi upstream from US Hwy 84, 10 mi ENE Collins, RDS 3186, 23 Nov. 1962. TU 28654 (5, 35-54) Miss., Jones Co., Leaf R. 1 mi W Moselle, RDS 3192, 29 Dec. 1962. TU 30053 (11, 33-74) Miss., Jones Co., Leaf R. 1 mi W Moselle, RDS 3354, 2 Nov. 1963. TU 39407 (4, 43-70) Miss., Jones Co., Leaf R. 1 mi W Moselle, RDS 3822, 12 Dec. 1965. *Tombigbee River drainage.* TU 37590 (1, 58) Miss., Lowndes Co., Tombigbee R. 9 mi NW Columbus, 0.5 mi upstream from Hwy 50 bridge, RDS 3663, 6 May 1965. *Black Warrior River drainage.* UAIC 1060 (38, 32-57) Ala., Tuscaloosa Co., Black Warrior River below Oliver Dam at Tuscaloosa, 28 October 1963. UAIC 1594 (6, 32-62) Ala., Tuscaloosa Co., Black Warrior River below Oliver Dam at Tuscaloosa, 7 May 1965. UAIC 1766 (4, 34-44) Ala., Tuscaloosa Co., Black Warrior River below Oliver Dam at Tuscaloosa, 29 September 1965. *Cahaba River drainage.* TU 15286 (17, 42-73) Ala., Bibb Co., Cahaba R., 2.2 mi N Centerville, RDS 2594, 17 Mar. 1957. TU 35091 (3, 40-68) Ala., Bibb Co., Cahaba R. 2.2 mi N Centerville, RDS 3504, 26 June 1964. TU 37679 (19, 37-76) Ala., Bibb Co., Cahaba R. 2.2 mi N of Centerville, RDS 3670, 11 May 1965. TU 29133 (2, 31 and 35) Ala., Bibb Co., Cahaba R. 7 mi NE Centerville, Hwy 27, RDS 3132, 17-18 July 1962. TU 32721 (10, 50-72) Ala., Shelby Co., Cahaba R. 5.4 mi W Pelham or 3.2 mi SW Helena, Hwy 52, RDS 3461, 31 May 1964. TU 37665 (36, 45-80) Ala., Shelby Co., Cahaba R. 5.4 mi W. Pelham, Hwy 52, RDS 3669, 10 May 1965. TU 38196 (16, 25-70) Ala., Shelby Co., Cahaba R. 5.4 mi W Pelham, Hwy 52, RDS 3709, 24 June 1965.

*Percina nigrofasciata* × *Percina sciera.* The following were collected from La., Washington Par. Pearl R. just below dam at Pools Bluff, 4 mi S Bogalusa: TU 39380 (2, 64 and 69), RDS 3821, 10 Dec. 1965; TU 39726 (6, 59-82), RDS 3833, 24-25 February 1966; TU 40000 (2, 63 and 68), RDS 3837, 10 March 1966; TU 40887 (1, 68), RDS 3623, 16 January 1965 and TU 40888 (1, 71), RDS 3644, 25 March 1965.

*Percina sciera. Pearl River drainage.* TU 27849 (32, 53-86) La., Washington Par., Pearl R. just below dam at Pools Bluff, 4 mi S Bogalusa, RDS 3629, 12-13 Feb. 1965. TU 27911 (23, 48-80) La., Washington Par., Pearl R. just below dam at Pools Bluff, 4 mi S Bogalusa, RDS 3640, 4 Mar. 1965. TU 37337 (24, 51-89) La., Washington Par., Pearl R. just below dam at Pools Bluff, 4 mi S Bogalusa, RDS 3641, 18 Mar. 1965. TU 39724 (131, 49-89) La., Washington Par., Pearl R. just below sill at Pools Bluff, 4 mi S Bogalusa, RDS 3833, 24-25 February 1966. TU 30148 (153, 33-88) Miss., Simpson Co., Strong R. 2.3 mi W Pinola, Hwy 28, RDS 3357, 6 Nov. 1963. TU 32883 (162, 39-75) Miss., Simpson Co., Strong R. 2.3 mi W Pinola, Hwy 28, RDS 3431, 17 May 1963. *Pascagoula River drainage.* TU 28624 (58, 36-77) Miss., Jones Co., Leaf R. 1 mi W Moselle, RDS 3192, 29 Dec. 1962. TU 30057 (31, 45-84) Miss., Jones Co., Leaf R. 1 mi W Moselle, RDS 3354, 2 Nov. 1963. *Tombigbee River drainage.* TU 34603 (21, 42-55) Miss., Lowndes Co., Tombigbee R. 9 mi NW Columbus 0.5 mi downstream from Hwy 50 bridge, RDS 3583, 9 Sept. 1964. TU 37584 (11, 34-76) Miss., Lowndes Co., Tombigbee R. 9 mi NW Columbus, 0.5 mi upstream from Hwy 50 bridge, RDS 3663, 6 May 1965. TU 38546 (3, 19-27) Miss., Clay Co., Tombigbee R. 9 mi NW of Columbus, 0.5 mi downstream from Hwy 50 bridge, RDS 3712, 26 June 1965. *Black Warrior drainage.* CU 45968 (4, 34-47) Ala., Tuscaloosa Co., North R. 6 mi W Hwy 69 on Hwy 38, TZ 17, 14 Aug. 1963. TU 30203 (2, 37 and 42) Ala., Tuscaloosa Co., trib. to North R. and North R. 8 mi N Northport, Hwy 69, RDS 3214, 10 Apr. 1963. UAIC 1594 (3, 51-68) Ala., Tuscaloosa Co., Black Warrior River below Oliver Dam at Tuscaloosa, 7 May 1965.

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