A TAXONOMIC STUDY OF THE COOTER TURTLES, *PSEUDEMYS FLORIDANA* (LECONTE) AND *PSEUDEMYS CONCINNA* (LECONTE), IN THE LOWER RED RIVER, ATCHAFALAYA RIVER, AND MISSISSIPPI RIVER BASINS

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ABSTRACT

The taxonomy of the cooter turtles, *Pseudemys floridana* (LeConte) and *Pseudemys concinna* (LeConte) was studied in southwestern Louisiana to determine the relationship between these two turtles and to examine the validity of the taxonomic characters currently utilized.

One hundred and sixty-two turtles were examined from the lower Red River, the Atchafalaya River, and the Mississippi River basins. The color patterns and osteological characteristics were numerically scored. A discriminant analysis based on the characters of plastral pattern, carapace pattern, bridge markings, and the number of phalanges in the fifth toes of the hind feet, was conducted on these specimens. Two *a priori* groups of specimens with relatively "pure" characters were selected, one with *P. floridana* characters and one with *P. concinna* characters. From these *a priori* groups a set of discriminant coefficients was calculated for each character and all specimens were assigned Z-values based on these characters.

A linear plot of the Z-values showed most specimens in the sample were intermediate, with Z-values distributed between and overlapping both *a priori* groups. The four characters used had little or no taxonomic value in separating these turtles. The wide range of Z-values found within individual clutches indicated interbreeding of specimens with widely varying characteristics. Correlation coefficients for toe phalanx number and plastral pattern versus carapace length indicated these characters to be ontogenetic.

The results show that *Pseudemys floridana* and *Pseudemys concinna* should be synonymized under the senior synonym, *Pseudemys floridana*, pending discernment of quantitative characters that will distinguish *floridana* and *concinna* as species.

INTRODUCTION

The North American emydid turtles of the genus *Pseudemys* have had a long, confused taxonomic history. Relationships among many of the species complexes are neither understood nor agreed upon. *Pseudemys floridana* (LeConte) and *Pseudemys concinna* (LeConte) are members of one such complex. A taxonomic study of these two species was conducted in the lower Red River, the Atchafalaya River, and the Mississippi River basins in Louisiana (Fig. 1). The three subspecies reported to occur in this area according to Ernst and Barbour (1972), and Conant (1975) are *Pseudemys floridana hoyi* (Agassiz), *Pseudemys concinna hieroglyphica* (Holbrook), and *Pseudemys concinna mobilensis* (Holbrook). The purpose of this study was to determine the relationship between *Pseudemys floridana* and *Pseudemys concinna* in

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southern Louisiana and to examine the validity of the taxonomic characters currently being utilized to separate them.

Pseudemys concinna ranges throughout much of the southeastern United States and contains the subspecies *concinna, suwanniensis, mobilensis, texana* and *hieroglyphica. P. floridana* occurs in approximately the same geographic range and contains the subspecies *floridana, peninsularis*, and *hoyi* (Crenshaw, 1955; Ernst and Barbour, 1972; Conant, 1975). According to Ernst and Barbour (1972) *Pseudemys concinna* is an inland turtle that inhabits mainly rivers, preferring those with moderate currents, abundant aquatic vegetations, and rocky bottoms. It occurs, however, in almost any aquatic habitat such as lakes, ponds, swamps, tidal marshes, oxbows, and ditches. *P. floridana* inhabits any aquatic habitat in the coastal plains, preferring those with slow currents, soft bottoms, and abundant aquatic plants.

Figure 1. Study area which includes the Lower Red River, the Atchafalaya River, and the Mississippi River basins in Louisiana.

Taxonomic history. – The species were first described by LeConte (1830) as *Testudo floridana* and *Testudo concinna.* The early taxonomic literature (Bonaparte, 1831; Gray, 1831, 1855, 1863; Duméril and Bibron, 1835; Holbrook, 1836, 1838; Agassiz, 1857; Baur, 1893) involved primarily generic name changes and the addition of new subspecies.

Carr (1935) considered *Pseudemys floridana* and *P. concinna* to be northern and southern representatives of the same species. In LeConte's original description *P. floridana* had page priority so he selected it as the name of the species. Carr (1937) synonymized *P. mobilensis* with *P. floridana* and named a new subspecies *P.f. suwanniensis.* Stejneger (1938) recognized a new subspecies, *P.c. hoyi*, for the specimens which Agassiz had called *Ptychemys hoyi.*

Carr (1938) described *P.f. peninsularis* from Florida and included an analysis and key to the *P. floridana* group. He stated, "Due to inherent genetic instability, or to re-establishment of intercourse between previously isolated stocks, individual variation within a local population (even in a single litter) may result in phenotypes superficially more dissimilar than the actual races." He thought many descriptions stressed characters that were highly variable or sexually dimorphic and that because of this the original descriptions were inadequate. He described the *P. floridana* group as " . . . a *Rassenkreis* which extends westward in two limbs from the Atlantic coastal *floridana* – an inland series (*concinna, hieroglyphica, texana*), and another in the coastal plain (*peninsularis, suwanniensis, mobilensis*)." Carr (1952) redescribed the group and added *P.f. hoyi.*

Crenshaw (1955), in his study of the Florida races *P.f. floridana, P.f. peninsularis,* and *P.f. suwanniensis*, stated that

the relationships between all turtles of this complex were best shown by subdividing the complex into two species, *P. concinna* and *P. floridana*. The species *P. concinna* included the subspecies, *concinna, mobilensis, hieroglyphica, suwanniensis,* and *texana.* The species *P. floridana* included the subspecies *floridana, peninsularis,* and *hoyi.* The present status of these turtles is that suggested by Crenshaw (1955). Many authors include these turtles in the genus *Chrysemys* (McDowell, 1964; Weaver and Rose, 1967), however this has never been uniformly accepted (Holman, 1977) and data presented by Vogt and McCoy (1979) suggest that they should be placed in the genus *Pseudemys* and separated from *Chrysemys.*

Locality records and status. – Specimens of *P. floridana* are not easily distinguished from specimens of *P. concinna* on the basis of presently utilized taxonomic characters. Reported records for the three Louisiana subspecies show that many authors are unsure of the identity of specimens and unwilling to commit themselves as to the exact ranges for each subspecies. One aspect of the problem is the paucity of specimens. Another is the wide range of characters these turtles possess and the wide geographic range they occupy.

Three subspecies occur in Texas according to Brown (1950): *P.f. hoyi, P.c. texana*, and *P.c. mobilensis.* Brown referred to all as subspecies of *Pseudemys floridana*. He noted that the distribution of *P.c. texana* was unclear and that a number of specimens from Bastrop County might prove to be intergrades with *P.f. hoyi.*

Webb (1970) listed *Pseudemys f. hoyi* as occurring in eastern Oklahoma and remarked that *P.c. heiroglyphica* probably also ranged into eastern Oklahoma where the two "occasionally hybridize."

Two subspecies are reported from Arkansas, *C.c. hieroglyphica* and *C.f. hoyi* (Conant, 1975). Michael Plummer (pers. comm. November 17, 1976) has advised me that *P. concinna* appears to predominate in Arkansas populations but that most specimens appear to have intermediate characters.

The subspecies *C.c. hieroglyphica* and *C.f. hoyi* occur in the southern third of the state of Missouri where they hybridize in nature (Anderson, 1965).

Smith (1961) treated all Illinois specimens as hybrids of *P.c. concinna* x *P.f. hoyi.* His remarks included an opinion from Crenshaw which suggested that all southern Illinois turtles be regarded as hybrids because of introgression of *P. floridana* genes into the *P. concinna* populations of the lower Mississippi River Valley. Crenshaw believed this produced an intermediate form.

Two subspecies, *C.c. hieroglyphica* and *C.f. hoyi*, occur in Kentucky (Barbour, 1971). The ranges of these turtles in Kentucky appear to be sympatric and Barbour commented that the two hybridize freely with each other. Barbour (1971) and Conant (1975) showed *C.c. hieroglyphica* and *C.f. hoyi* as occurring in approximately the same ranges in Tennessee.

Three subspecies of *C. concinna* occur in Alabama; they include *C.c. concinna, C.c. hieroglyphica*, and *C.c. mobilensis* (Conant, 1975). One subspecies of *C. floridana, C.f. floridana*, occurs in Alabama (Conant, 1975; Mount, 1976). In dealing with the subspecies of *P. concinna*, Mount (1976) stated that, " . . . the geographic variation was found to be inconsistent with previous reports and assumptions" and nearly all characters used to distinguish the subspecies had wide areas of overlap. He felt the designation of subspecies was largely arbitrary. He chose to allocate all *P. concinna* in Alabama to the subspecies *P.c. concinna* and

noted that hybridization between *P. concinna* and *P. floridana* occurs frequently in the southeastern portion of the state.

Existing records for these turtles in Louisiana (Viosca, 1923, 1926; Cagle and Chaney, 1950) do not give a good indication of the species and subspecies which are found in various localities. Liner (1954) listed three Tulane specimens (TU-1104, 11046, 13618) as *P. floridana*. The first is from Vermilion Parish and the last two are from Terrebonne Parish. These specimens were examined and the data included in my statistical analysis of specimens.

Keiser and Wilson (1969) reported three subspecies of these turtles, *C.c. hieroglyphica*, *C.c. mobilensis*, and *C.f. hoyi*, from Louisiana, Keiser (1976) referred to the two species as the *Chrysemys floridana-concinna* complex and used the presence of a plastral pattern and the C-shaped mark on the second costal scutes of the carapace of *C. concinna* to separate the species. He also mentioned possible skeletal characters separating them, but noted that few Atchafalaya Basin specimens fit the descriptions of the subspecies given by Carr (1952). The localities and specimens cited by Keiser (1976) are included in this study as they constitute the core of the data from which the present study grew.

MATERIALS AND METHODS

Specimens examined. – The specimens used in this study were collected primarily from the Atchafalaya River Basin from 1975 to 1977. Specimens from the Red River and Mississippi River basins were borrowed from the Tulane University collection of amphibians and reptiles (TU). Atchafalaya River Basin specimens are from the University of Southwestern Louisiana collection of amphibians and repitles (USL). A total of 162 specimens was rexamined. All specimens collected during the course of this study were catalogued into the USL collection (Appendix I).

Method of collection. – Several types of traps (Legler, 1960) were used in the collection of adult turtles. Fish, chicken, cottonseed cakes, lettuce, and watermelon were tried as bait. Although no adult *P. floridana* or *P. concinna* were caught, adults of *P. scripta*, and *C. picta* were caught in traps. Most observations of feeding suggest that *P. floridana* and *P. concinna* are primarily vegetarian as adults (Allen, 1938; Carr, 1952; Ernst and Barbour, 1972). The abundance of natural plant foods may account for my inability to trap adult specimens even when plant materials were used as bait.

I obtained adult specimens by purchasing them from fishermen or by searching for nesting females along roads. Road collecting was most successful in the early morning from 5:00 to 8:00 A.M. (C.S.T.) and in late afternoon from 3:30 P.M. until dusk. Five adults from which I later obtained egg clutches were collected in this manner. A gill net was occasionally used in the collection of adult turtles, though with limited success.

Two methods used without success for the collection of juvenile turtles were night collecting and snorkeling. The most successful method of obtaining small turtles was to dip-net basking animals from a canoe or powerboat. Collection methods used in other areas with clear water (Chaney and Smith, 1950) did not work well in central Louisiana. The waters frequented by these turtles in central Louisiana usually are over 1 m deep and are often very turbid.

All eggs were collected from gravid females using Cagle's (1944) method. Specimens were pithed and the entire oviducts were removed. The eggs were removed from the oviducts and placed in an in-

cubator. Five clutches were incubated using Trotter's (1973) technique, with hatching success varying from 5% to 88%. Each clutch of hatchlings was kept alive for several months for observation and to allow color patterns to become distinct.

Osteological preparations. – Phalanges of the fifth toes of the hind feet were examined by X-ray (adult specimens) or clearing and staining (hatchlings and juveniles). The clearing and staining procedure was, with modifications, that of Hardaway and Williams (1975).

Description of taxonomic characters. – A number of taxonomic characters are presently used to differentiate subspecies of *P. floridana* and *P. concinna* in various parts of their ranges. They do not apply to all the subspecies and the reliability of each character varies depending on the subspecies and the locality. As many characters as possible were examined to determine which could possibly be used to separate *P. floridana* and *P. concinna* in the area studied.

Two characters used in this study and referred to in most present taxonomic literature (Carr, 1952; Crenshaw, 1955; Ernst and Barbour, 1972; Conant, 1975) are the plastral pattern and the carapace markings. *P. concinna* is reported to have a C-shaped yellow line on the second costal scute of the carapace (Fig. 2) and a plastral pattern that generally follows the seams of the plastral scutes (Fig. 3). *P. floridana* has either a straight line or an inverted Y-shaped line on the second costal scute of the carapace (Fig. 2) and an immaculate plastron (Fig. 3). Both of these characters are presently used as the major taxonomic characters separating these species. Both are based on pigmentation which, if used alone, is not a reliable taxonomic character at the species level. Variation in color and in the arrangement of pattern can result from non-genetic factors. Temperature may play an important role in pattern determinations especially during embryonic development (Fowler, 1970; Vinegar, 1973, 1974).

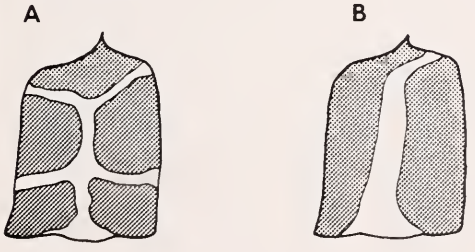

Figure 2. Pattern on the second costal scutes of the carapace; A. C-shaped pattern of *Pseudemys concinna*; B. Straight line pattern of *P. floridana*.

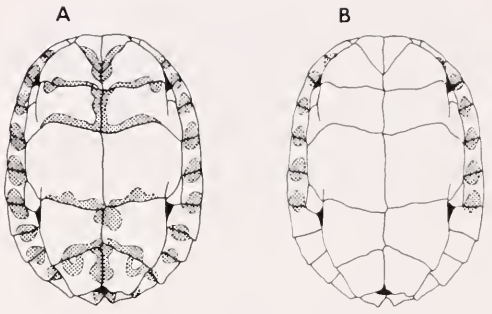

Figure 3. Typical plastral patterns; A. *Pseudemys concinna;* B. *P. floridana.*

Three characters that are used to distinguish various subspecies of *P. floridana* and *P. concinna* are neck stripe pattern, jaw serration, and the pattern on the ventral surface of the marginal scutes. All specimens in my sample were scored for each of these characters. These characters are, however, probably too qualitative and their range of variation too great to be useful in statistical analyses.

The pattern of stripes on the dorsal surface of the neck is used to distinguish *P.f. peninsularis* from *P.c. suwanniensis* in Florida. *P.f. peninsularis* has a hairpin

pattern while *P.c. suwanniensis* has a series of straight lines (Fig. 4). Sample specimens were scored as continuously lined (C), discontinuously lined (D), or hairpin patterned (H), for right and left sides of the neck. Many specimens possessed different combinations of these three categories and some possessed intermediate pattern types.

Jaw serration is used to distinguish *P.c. texana* from the other subspecies of *P. concinna* and *P. floridana*. This character can also be used to distinguish three Florida turtles, *P.f. peninsularis, P.c. suwanniensis,* and *P. nelsoni*, from each other. The sample specimens were scored on the basis of whether their jaws were serrated (S) or unserrated (U) and whether the upper jaw was notched (N) or un-notched (no symbol). The range of variation included that which was found in the above mentioned species long with other variations (Fig. 5).

The pattern on the ventral surface of the marginal scutes is used to distinguish *P. concinna* subspecies from *P. floridana* subspecies in Florida. *P. floridana* reportedly has few or no marginal markings while *P. concinna* may possess a variety of

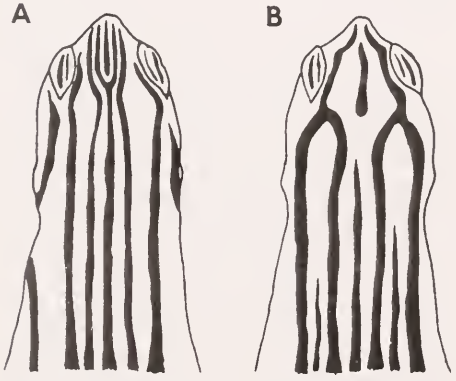

Figure 4. Neck stripe patterns; A. *Pseudemys concinna suwanniensis*; B. *P. floridana peninsularis.*

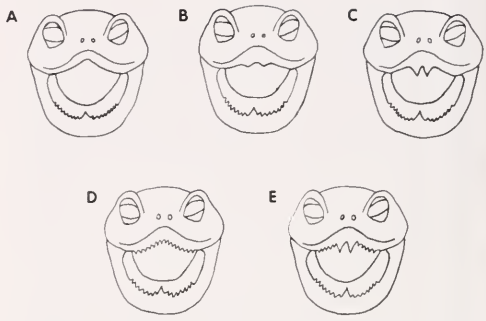

Figure 5. Jaw serrations found in various species and subspecies of *Pseudemys*; A. *P. concinna concinna*; B. *P. floridana hoyi*; C. *P. concinna texana*; D. a Louisiana variation; E. *P. nelsoni* (also found in some Louisiana specimens).

patterns (Fig. 6). Three predominant patterns occurred in the sample, but a fourth type, the absence of markings, was not observed. Patterns were scored as types one to four (Fig. 6).

A character I have analyzed in detail is the number of phalanges of the fifth toes of the hind feet (Weaver and Rose, 1967). Associated with this is the fusion or separation of the astragalus and calcaneum in the ankle (pers. comm. June 17, 1976, with unpublished manuscript attached from Francis L. Rose). These characters, when first used by Weaver and Rose (1967) in their study of the genus *Chrysemys*, appeared to be different for *P. floridana* and *P. concinna*. *P. floridana* reportedly had two toe phalanges and a fused astragalus and calcaneum. *P. concinna* reportedly had three toe phalanges and a separated astragulus and calcaneum (Fig. 7). These differences were theorized to be related to the degree of terrestrial or aquatic habits of each species (unpublished manuscript from Francis L. Rose). *P. floridana*, the more terrestrial turtle, has a shorter fifth toe and a more solid foot for better support while walking on land. *P. concinna* has a longer fifth toe which allows increased webbing; the separate astragalus and calcaneum al-

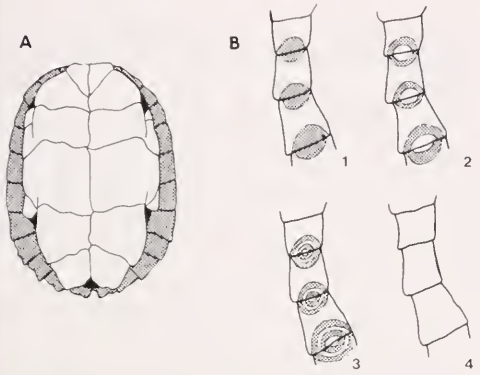

Figure 6. A. Locations of the pattern on the ventral surfaces of the marginal scutes. B. Pattern types found on the ventral surfaces of the marginals and the numerical scoring used to classify these.

so make its foot more flexible for swimming. Rose (pers. comm. October 11, 1976) has states that these characters may or may not be good taxonomic characters.

Penial morphology of *P. floridana* and *P. concinna* was shown to be identical with that of *P. scripta* and *P. nelsoni* (Zug, 1966). Osteological characteristics of the skulls of emydid turtles were analyzed and used for taxonomic purposes by McDowell (1964). He drew a distinction between a *rubriventris* series and a *floridana* series but did not identify any differences between *P. floridana* and *P. concinna*. Skull osteology and penial morphology were not examined in this study.

The precopulatory behavior reported for *P. floridana* (Cagle, 1950) appears to be similar to that reported for *P. concinna* (Marchand, 1944; C.G. Jackson, 1972). If there are subtle behavioral differences between *P. concinna* and *P. floridana* they have not been reported.

Statistical methods. – Markings from the following body and shell regions were recorded for each specimen: carapace, plastron, neck, bridge, and marginal scutes. Toe phalanx number on the fifth toes of the hind feet, fusion of the astragalus to calcaneum, jaw serration, and carapace length were also recorded. The color pattern data were qualitative and various systems of scoring patterns were devised for quantifying these data. The scoring systems used in this study were based on the key characters that have been used to separate *P. floridana* and *P. concinna* as species.

Plastral pattern was quantified by counting the number of plastral scutes that contained dark pigmentation. A number ranging from 0 to 12 was assigned to each turtle on the basis of the number of scutes containing dark pigmentation (Fig. 8). Most literature describes *P. floridana* as having an immaculate plastron, however, very few specimens in my sample completely lacked dark plastral pigmentation. I assumed individuals with low scores to be of *P. floridana* stock.

Pattern on the second costal scutes of the carapace was more difficult to score. When a large sample of specimens was examined, a gradation from the straight-line pattern of *P. floridana* to the C-shape of *P. concinna* could be observed. Five numbered categories were defined and numerical scores were assigned as follows: straight-line (1), branching (2), Y-shaped (3), X-shaped (4), and C-shaped

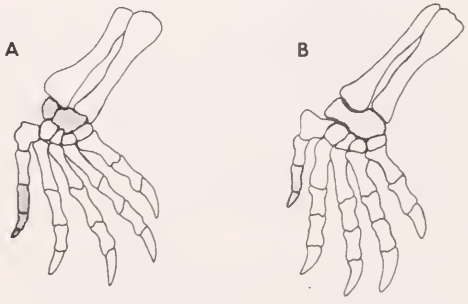

Figure 7. Bones of the hind feet; A. *Pseudemys concinna,* showing three phalanges on the fifth toe and separate astragalus and calcaneum; B. *P. floridana*, showing two phalanges on the fifth toe and a fused astragalus and calcaneum.

(5) (Fig. 9). The decision between an X-shaped and a C-shaped pattern was based upon whether the posterior branches touched the neural and marginal scutes (Fig. 9-4; X-shaped) or touched the third costal scute (Fig. 9-5; C-shaped). In some cases, especially in older specimens, this was difficult to accurately determine. If the branches were not complete a judgment as to their general direction had to be made. Right and left costal patterns were scored separately and later summed.

Four scutes make up the bridge that connects the plastron to the carapace. Specimens were scored 0 through 4 for left and right bridges separately, according to the number of scutes with dark pigmentation (Fig. 10). Scores for right and left sides were later summed. Neck striping and marginal markings were too qualitative and variable to be used in the statistical analyses.

Toe phalanx numbers on the fifth toes of the hind feet were recorded separately and later summed for use in the discriminant analysis. The astragalus fused to the calcaneum was not used since these bones were separate in all but three specimens.

A discriminant function based on four characters (plastral pattern, carapace pattern, bridge markings, and toe phalanx number) was computed using the

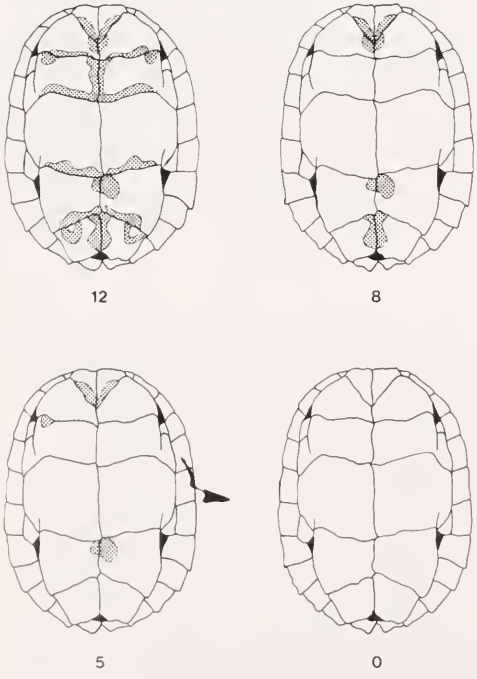

Figure 8. The scoring system for plastral patterns. Numbers indicate the number of plastral scutes containing dark pigmentation.

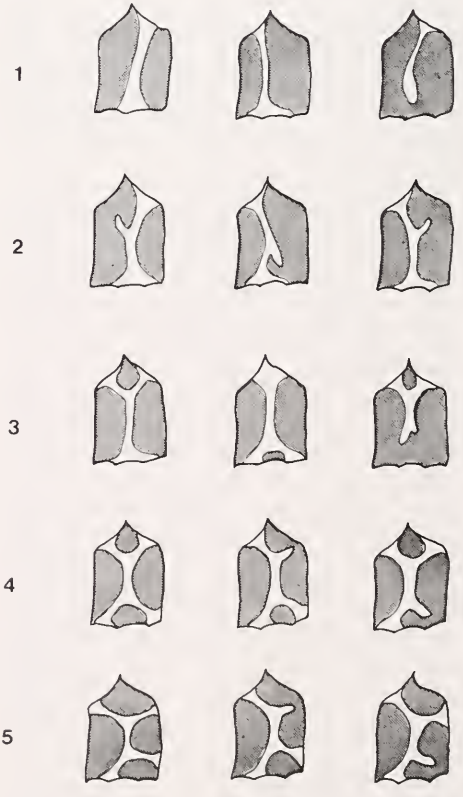

Figure 9. Scoring system used for the second costal scutes of the carapace; (1) Straight-line; (2) Branching; (3) Y-shaped; (4) X-shaped; (5) C-shaped. Three variations are shown for each category.

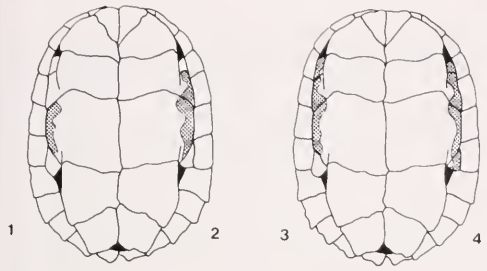

Figure 10. Scoring system used for scutes making up the bridge. Pattern categories 1 through 4 are shown through a 0 category could also be found.

BMD-04M program (Dixon, 1973). This program develops the linear function of the selected variables that gives the largest ratio of between-group variance to within-group variance. A series of discriminant coefficients is calculated to give this ratio and thus maximize discrimination between two *a priori* groups (Rao, 1952; Krishnaiah, 1966; Kendall, 1968; Gnanadesikan, 1977).

In accordance with this program, two *a priori* groups of twenty individuals each were selected from the total sample of 162 specimens; one group of specimens exhibited "pure" *P. floridana* characters, and the other "pure" *P. concinna* characters. Age and sex were not a basis for the selection of the *a priori* groups. From these *a priori* groups the set of discriminant coefficients was calculated. The sum of these coefficients times their respective character scores gave a value Z for each specimen. Using these Z-values, the program automatically classified into one group or the other all specimens not included in the *a priori* groups. By writing an addition to the program the Z-values themselves were obtained. Plotting individual Z-values on the discriminant axis showed which specimens in the unknown sample were within the range of either *a priori* group and which were intermediate (Rohwer and Kilgore, 1968; Thaeler, 1968; J.F. Jackson, 1973).

In addition to the discriminant analysis, correlation coefficients among several characters were computed using the BMD-02D program (Dixon, 1973). This program computes simple correlation coefficients. Early in this study I noticed that plastral pattern appeared to fade with age and that the number of toe phalanges on the fifth toes of the hind feet seemed to increase from 2 to 3 with age. Correlation coefficients between these characters and carapace length were computed to determine if this relationship actually existed.

RESULTS

Statistical analyses. – The results of the discriminant analysis (Fig. 11A) clearly show that, based on Z-values calculated from the four characters used, the sample does not fall into two distinct groups (species). There is also no large intermediate group that would indicate only F_1 hybridization. The sample is instead evenly distributed between, and overlaps, each *a priori* group. This indicates interbreeding of *P. concinna* and *P. floridana*, and backcrossing and interbreeding of the hybrids.

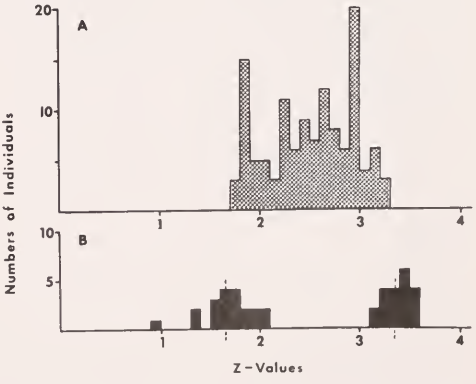

Figure 11. Histograms of specimen Z-values on discriminant axes; A. Plot of the Z-values of the unknown sample in the discriminant analysis; B. Plot of the Z-values of the *a priori* groups of *Pseudemys concinna* (mean 3.36) and *P. floridana* (mean 1.66). Dashed lines indicate the means of the *a priori* groups.

Table 1. Results of the discriminant analysis. Mean scores for each of the four characters used are shown for each a priori group along with the discriminant coefficient for each of the characters. Sample size, mean Z-value, and standard deviation for these Z-values are also given. Left and right scores have been summed for each character.

Character	P. floridana mean	P. concinna mean	Discriminant coefficient
1. Carapace pattern	3.150	9.650	0.149
2. Plastral pattern	4.850	9.750	0.037
3. Toe phalanx number	3.900	6.000	0.251
4. Bridge markings	5.350	7.750	0.007

a priori group	Sample size	Mean Z	Standard deviation Z
P. floridana	20	1.663	0.273
P. concinna	20	3.359	0.120

The mean Z-value of the *P. floridana* (1.66) and the *P. concinna* (3.36) *a priori* groups (Table 1) are well separated and the ranges of these groups have no overlap (Fig. 11B). The means for each character are also well separated (Table 1).

The range of the *P. floridana "a priori"* group was 1.14 (0.91 to 2.05) and that of the *P. concinna "a priori"* group was 0.38 (3.12 to 3.50). The range of the intermediate zone was 1.07 (2.05 to 3.12). This was slightly smaller than the range of the *P. floridana "a priori"* group. The unknown sample fills the intermediate zone, and overlaps and completely connects both *a priori* groups. Of the unknown individuals measured, 27 had Z-values that overlapped the *P. floridana "a priori"* group and 11 had Z-values that overlapped the *P. concinna "a priori"* group.

The Z-values for individuals from the five clutches hatched during this study were plotted, along with the Z-values of the females from which they were obtained, on separate discriminant axes (Fig. 12). In these figures the linear placement of genetically related individuals in the discriminant analysis is seen. In each plot the outlines of the *a priori* groups are shown. Specimens from the clutches used to make up part of the *a priori* groups are indicated by stippled squares.

Correlations computed on plastral pattern and toe phalanx number versus carapace length indicate these characters to be ontogenetically variable and not useable in taxonomy. The correlation of plastral pattern to carapace length was -0.40 which suggests a disappearance in the amount of plastral pattern as turtles grow. The correlation of toe phalanx number to carapace length was 0.45, which suggests that as turtles grow, a third phalanx on the fifth toes of the hind feet ossifies.

Qualitative characters. – Scoring of the characters jaw serration (Fig. 5), neck striping (Fig. 4), and marginal scute pattern (Fig. 6) is shown in Table 2. Jaw serration followed a gradient from strongly serrated to slighty serrated.

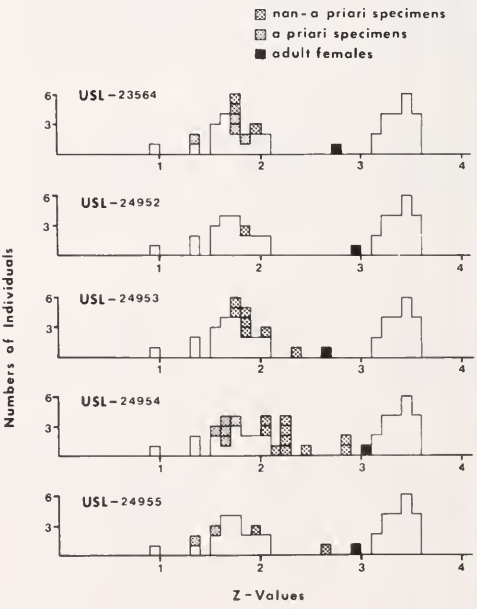

Figure 12. Plots on separate discriminant axes of the Z-values for the individual clutches from USL 23564, USL 24952, USL 24953, USL 24954, and USL 24955. Outlines of the *a priori* groups are shown. Individual specimens that were used to make up part of an *a priori* are shown by stippled squares and those not originally included in the *a priori* groups are shown by cross-hatched squares. The female from which each clutch came are shown as black squares.

For marginal scute patterns most specimens were scored as either type 2 (25.0%), with a doughnut-shaped mark, or type 3 (59.3%), with a double doughnut-shaped mark (Table 2; Fig. 6). Specimens were classified on the basis of the predominant pattern. Many specimens possessed several different types of markings.

Specimens scored for neck stripes (Fig. 4) possessed either continuous lines (31.4%) or hairpins (38.9%) on both sides of the neck. Fewer had discontinuous lines (12.5%) on both sides and the rest of the sample had mixed patterns (Table 2).

Table 2. Results of scoring the qualitative characters. Numbers of specimens for each category and percentages of the total sample are given for each character. Jaw serration and marginal scute pattern scoring systems are given in Figs. 5 and 6 respectively. Neck stripes were scored for left and right sides as: C - continuous lines, D - discontinuous lines, and H - Hairpin pattern.

Jaw serrations			
Serrated		Unserrated	
Notched (SN)	Un-notched (S)	Notched (UN)	Un-notched
54 / 33.5%	35 / 21.7%	10 / 6.2%	62 / 38.5%

Marginal Scute Pattern			
Type 1	Type 2	Type 3	Type 4
25 / 15.6%	95 / 59.3%	40 / 25.0%	0 / 0.0%

Neck Stripe Pattern					
C-C	H-H	D-D	C-H	C-D	H-D
50 / 31.4%	62 / 38.9%	20 / 12.5%	15 / 9.0%	3 / 1.8%	9 / 5.6%

Analysis of clutches. – Data from 34 hatchlings, obtained from the five gravid females, were included in the statistical analyses. Thirty-five eggs hatched, with an average incubation time of 60 days at 29° C. Many hatchlings had irregularities of shell scutes possibly caused by excessive incubation temperatures (Fowler, 1970; Vinegar, 1973, 1974). Details of each clutch are presented below:

USL 23564. – Eight individuals were hatched from the nine eggs of this female. The adult female predominantly resembled a *P. floridana*, however, the discriminant analysis placed this specimen as intermediate (Z-value of 2.70) and widely separated from its hatchlings. Seven of the hatchlings were used in discriminant analysis. One hatchling was lost. Four of the hatchlings were used to make up part of the *P. floridana* "*a priori*" group and the other three had Z-values that were clustered around the means of the *P. floridana* "*a priori*" group. Hatchlings Z-values ranged from 1.33 to 1.99 (Fig. 12). The hatchlings are catalogued as USL 24113–24119.

USL 24952. – Only one individual was hatched from 14 eggs taken from this female from Avoca Island, St. Mary Parish. The Z-value of the adult was 2.90 and close to the *P. concinna* "*a priori*" group's range though it superficially resembled a *P. floridana*. The hatchling had a Z-value of 1.87 which was within the range of the *P. floridana* "a priori" group (Fig. 12). The hatchling is catalogued as USL 24986.

USL 24953. – Seven individuals with scorable patterns hatched from 15 eggs of this female. The adult, also collected at Avoca Island, superficially resembled a *P. floridana*. All hatchlings possessed heavily pigmented plastra. The Z-values of the hatchlings ranged from 1.79 to 2.30 with all but one within the range of the *P. floridana* "*a priori*" group. The adult's Z-value was 2.60 which was well separated from all but that of one hatchling (Fig. 12). The hatchlings are catalogued as USL 24987 to 24993.

USL 24954. – The largest clutch came from this Avoca Island female. The adult possessed some *floridana*-like and some *concinna*-like characters. Fifteen hatchlings were obtained from 16 eggs. The hatchlings had a wide variety and combination of characters. The Z-values of these hatchlings ranged from 1.54 to 2.89. Five specimens from this clutch were used to make up part of the *P. floridana* "*a priori*" group. The majority of the hatchlings, however, had Z-values that placed them between the ranges of the

two *a priori* groups. The female had a Z-value (3.01) which was greater than all the hatchlings' and was well separated from all but two of the hatchlings (Fig. 12). The hatchlings are catalogued as USL 24967 – 24982.

USL 24955. – Seven eggs were taken from this female. From these, one hatchling was obtained and three embryos were removed from eggs in an advanced enough stage of development for their patterns to be scored. The adult was collected from the Atchafalaya River at Butte La Rose, St. Martin Parish. The Z-values for this clutch had the widest range of all the clutches analyzed (1.30 to 2.66). Here, as in the other clutches, the adult female had a Z-value (2.90) that was well separated from those of the hatchlings. Two of the hatchlings were used to make up part of the *P. floridana* "*a priori*" group (Fig. 12). The hatchlings are catalogued as USL 24982 – 24985.

DISCUSSION

The results from the discriminant analysis (Figs. 11 and 12; Table 1) show that the majority of the sample is intermediate on the basis of the four characters considered (plastral pattern, carapace pattern, bridge markings, and toe phalanx number). Other characters were not used in this analysis because of their wide and inconsistent range of variability. If the Z-values derived from these four characters can be assumed to be a measure of the genome then there is a complete gradation of characters from *floridana*-like to *concinna*-like individuals.

The *a priori* groups were selected by looking through the entire sample of 162 specimens and picking those whose characters nearly all were *floridana*-like or *concinna*-like. Age and sex were not used as criteria for the selection of the *a priori* groups. Calculations of Z-values show that some individuals from the unknown sample would evidently have been better choices for the *a priori* groups than some of the specimens selected. Using a sample size of 20 for each *a priori* group necessitated inclusion of some individuals whose characters were not all one extreme or the other.

If *P. floridana* and *P. concinna* were distinct species several results would be expected from the discriminant analysis. There would be a clustering of the unknown individuals around the *a priori* group means. There could be an F_1 hybrid peak somewhere between the two *a priori* groups but there should not be an even and continuous distribution of specimens from one *a priori* group to the other. The results are inconsistent with this and do not support the idea of separate species.

Figure 12 shows that all the clutches examined have a fairly wide range of characters. The clutches from USL 23564 and 24593 are grouped around the *P. floridana* "*a priori*" group. In the clutches from USL 24952, 24954, and 24955 the hatchlings' and adults' Z-values are widespread. The clutch from USL 24954 in particular has a wide range of Z-values that extend from one *a priori* group to the other. In each clutch the adult turtle's Z-value was separated from those of the majority of the hatchlings. The wide spread Z-values of these clutches and the separation of the majority of the hatchlings' Z-values from those of the adult females' are good indications of intergradation.

If *P. floridana* and *P. concinna* could be separated by a set of characters then the characters used to define each species should have a high degree of correlation. During the collection of data for this analysis I noticed that plastral pattern and toe phalanx number seemed to be related to the size of the individuals. The correla-

tion coefficients for these characters to carapace length also indicate this. Both toe phalanx number (correlation coefficient of -0.45) and plastral pattern (correlation coefficient of + 0.40) have a high correlation to shell length; this suggests that these characters are ontogenetic and of limited use as taxonomic characters. These characters were nevertheless used in the discriminant analysis since there were observable differences in them within the sample and no other characters were available.

The problem is whether these turtles should be regarded as separate species that are hybridizing or as subspecies that are intergrading. Perhaps as Carr (1952) stated, they do not fit well into our standard classification system. This problem has been compounded by several factors. Many of the original descriptions of these turtles are of limited use because the separation of species was based on locality and on sexually dimorphic characters. Their taxonomy at the present is based only on qualitative characters of color and pattern. Most studies of these species have dealt with only small segments of the ranges of these turtles.

In the original descriptions Le Conte (1830) described *Testudo floridana* and *T. concinna* and differentiated between them primarily on the basis of color and pattern. He mentioned differences in the shape of the carapacial scutes which can probably be attributed to the sex and size of the specimens used in his descriptions. The *T. floridana* he described was 15 inches (37.5 cm) long and the *T. concinna* was only 8 inches (20.3 cm) long. Carapacial scutes change shape as the turtles grow. Other than these scute differences LeConte differentiated between the two only by the pattern of yellow lines on the carapace.

Holbrook (1836 to 1838) described *Fmys hieroglyphica* and *E. mobilensis,* and also listed *E. concinna* and *E. floridana.* His descriptions, like those of LeConte, were based primarily on color and pattern. He also relied heavily on the location from which the specimens were taken for identification. His descriptions of all four turtles were similar; major differences were related mostly to sexually dimorphic and ontogenetic characters of the specimens.

All populations studied by Carr (1935, 1937, 1938, 1952) were considered by him to be subspecies of *P. floridana* since wherever any came into contact they interbred, and no characters could be used to reliably separate them. There appeared to be one exception to his uniform intergradation. Two of the subspecies, *P.f. peninsularis* and *P.f. suwanniensis*, seemed to maintain nearly complete reproductive isolation. The other subspecies *of P. floridana* were geographic subspecies; *P.f. peninsularis* and *P.f. suwanniensis* appeared to be ecological subspecies, separated by the preference of different habitats.

Crenshaw's (1955) division of the *P. floridana* complex into two species is based on the reproductive isolation maintained between *P.c. suwanniensis* and *P.f. peninsularis.* This division is founded upon an exception and not what normally occurs throughout the species ranges.

Crenshaw mentioned the occasional hybridization between *P.f. peninsularis* and *P.c. suwanniensis* but stated that it was believed to be secondary intergradation and rare. He also stated, "Evidence of introgressive hybridization and frequency of strongly intermediate specimens of the *floridana* and *concinna* groups increases progressively as one moves away from peninsular Florida into other areas of the U.S., however, relatively typical examples of each group occur throughout the area of geographic overlap of the two groups."

Crenshaw concluded that, "Relationships between members of the *P. floridana* complex will be more nearly reflected by subdividing the complex into two species." This was true for *P.f. peninsularis* and *P.c. suwanniensis* in Florida but not for the other subspecies throughout their respective ranges. Along with work of other researchers, my data indicate a large amount of intergradation in most areas of the ranges of these turtles (Smith, 1961; Pritchard, 1967; Barbour, 1971; Keiser, 1976; Mount, 1976). Crenshaw's work showed that *P. concinna* and *P. floridana* were closely related and intergrading but it did not conclusively show that they should be regarded as separate species.

Pritchard (1967) is the only recent author who has followed Carr's scheme. He mentioned difficulty in identification of subspecies because of extensive hybridization and the fact that some of the subspecies are not easily distinguishable from one another. He felt that separation into *P. floridana* and *P. concinna* was incorrect since the two intergrade completely.

Mayr (1963) defined species as, "groups of interbreeding natural populations that are reproductively isolated from other such groups." This definition is based primarily on reproductive isolation. Mayr listed various situations in which it would be difficult to apply this definition. Four of these situations are (1) morphological differentiation without reproductive isolation, (2) reproductive isolation dependent upon habitat isolation, (3) incompleteness of isolating mechanisms, and (4) the achievement of different levels of speciation within different populations. These four situations have possible application to the *P. floridana–concinna* complex.

Some authors (Ernst and Barbour, 1972; Conant, 1975) indicate that *P. floridana* and *P. concinna* occupy or once occupied different habitats. Possibly they have differentiated morphologically because of the different selective pressures in these habitats but have not developed any form of reproductive isolation before re-establishing contact with each other. Without reproductive isolation turtles differing morphologically may have interbred, producing offspring with a variety of characteristics. Many of these characteristics may not be useable as taxonomic characters to separate the two as species.

My data indicate that in the lower Red, Atchafalaya, and Mississippi river basins there is a large amount of interbreeding. Other workers (Brown, 1950; Smith, 1961; Anderson, 1965; Webb, 1970; Barbour, 1971; Mount, 1976) have also indicated the occurrence of interbreeding in other areas. The isolating mechanisms, if they exist, do not appear to be well established. Even in Florida the reproductive isolation of *P.f. peninsularis* and *P.c. suwanniensis* is not complete though interbreeding is rare (Crenshaw, 1952).

In nearly all areas of contact between *P. floridana* and *P. concinna* interbreeding has been observed, but in a few areas where there are distinct and separate habitats, interbreeding is rare (Smith, 1961; Pritchard, 1967; Barbour, 1971; Keiser, 1976; Mount, 1976). Contact between populations seems to be the most important limiting factor of reproductive isolation.

The lower Mississippi River drainage in Louisiana is an area where frequent contact between these turtles could be expected. Here the aquatic habitats are not as well defined as in many other areas of these species' ranges. Periodic flooding tends to mix geographically separated populations more often. Because of the increased contact *P. floridana* and *P. concinna* probably interbreed more in

this area than in many others and as a result have greater genetic similarity here.

Though Mayr (1963) stresses reproductive isolation as the prime factor separating species, it is not synonymous with noninterbreeding. Two species can interbreed and be reproductively isolated (Bigelow, 1965). Interbreeding can occur with little effect if the progeny are incompatible with the parent species. What is important is the flow or introgression of genes from one species to the other. My data indicate that introgression has taken place and implies a high degree of compatibility between *P. floridana* and *P. concinna*.

Grant (1963) described various population systems and used the term "semispecies" to refer to a population system having properties of both races and species. Following his classification system *P. floridana* and *P. concinna* would be classified as "sympatric semispecies" which are, "population systems intergrading discontinuously or partially and judged to be interbreeding on a restricted scale, they are sympatric and only partially isolated reproductively." Grant's classification offers a basis for argument that *P. floridana* and *P. concinna* are "ecological races" which are, "population systems intergrading continuously in morphological or physiological characters and judged to be interbreeding freely." Grant's classification would not classify *P. floridana* and *P. concinna* as separate species.

Both Grant's and Mayr's systems for classifying populations and species are useful as possible explanations of the relationship between *P. floridana* and *P. concinna*. The exact nature of the relationship cannot be determined except by long term breeding experiments. There is definite intergradation within the lower Red, Atchafalaya, and Mississippi river basins. The isolating mechanisms between *P. floridana* and *P. concinna* are weak if they exist. There is a complete gradation of characters and the characters presently used to separate these turtles into two species are probably useless. Apparently either a large hybrid swarm (a population that forms a continuous bridge between two parental species due to a breakdown in the isolating mechanisms) is present or two or more subspecies are merging within this area.

CONCLUSIONS

1. The discriminant analysis based on four characters (plastral pattern, carapace pattern, toe phalanx number, and bridge markings) has shown the following:
   - A. The specimens of the sample were not distinguishable as *Pseudemys floridana* and *P. concinna* but the majority were instead intermediate.
   - B. These four characters are of little or no taxonomic value in separating these turtles since there was found to be a complete and even gradation from *floridana*-like to *concinna*-like specimens.
   - C. The wide range of Z-values found within individual clutches indicates interbreeding of specimens with widely varying characteristics.
2. Plastral pattern was found to fade with age and was highly variable within individual clutches. This character is of little or no taxonomic value for the separation of *P. concinna* and *P. floridana*.
3. Toe phalanx number on the fifth toes of the hind feet appears to increase from two to three with age and is of little or no taxonomic value for the separation of *P. concinna* and *P. floridana*.
4. Because the majority of the sample of Louisiana specimens possesses inter-

mediate characters, and appears to be part of one continuously interbreeding population, I propose that the scheme of Carr (1952) be followed. Accordingly *Pseudemys concinna* and *Pseudemys floridana* are synonymized under the senior synonym, *Pseudemys floridana* until there may be quantitative characters to definitively distinguish the forms *floridana* and *concinna* as separate species.

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APPENDIX I

USL and Tulane University specimens used in the statistical analyses of this tudy. Specimens are listed by locality and parish alphabetically.

USL specimens. – Big Alabama Bayou (Point Coupee): 24034, 24094-24100, 25017. Little Alabama Bayou (Point Coupee): 23646, 23647, 24101-24106, 25018-25047, 25054-25057. East Outer Levee 5 mi. N. I-10 (Point Coupee): 25011-25013. False River (Point Coupee): 20195. Bayou Courtableau (St. Landry): 23566-23577, 24024-24026, 24028-24029, 24033, 25048-25052. Bayou Courtableau at West Outer Levee (St. Landry): 25014-25016. Indian Bayou Hunting Club (St. Landry): 22222. Krotz Springs (St. Landry): 23261. Atchafalaya River (St. Martin): 24955, 24982-24985. Butte La Rose (St. Martin): 25053. Butte La Rose Bayou (St. Martin): 14170, 14383, 14484, 15113, 23565, 25062. Whiskey Bay (St. Martin): 23564, 24113-24119, 25058. Avoca Island (St. Mary): 24952-24954, 24967-24981, 24986-24993.

Tulane specimens. – Caddo Lake (Caddo): 458, 632, 633, 647, 657, 658, 734, 735. Tensas River, Clayton (Concordia): 16042.0-16042.6. Lake Providence (East Carroll): 826. Waggamon Pond (Jefferson): 5772-5774, 5874, 5879, 5975, 5876. Lake Arthur (Jefferson Davis): 1104. Bayou Gauche (St. Charles): 13756.2. Lake Pontchartrain (St. Charles): 13571, 16038. Chauvin (Terrebone): 13618.

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ERRATA

Tulane Studies in Zoology and Botany Volume 22, number 2

In the article by Porras, McCranie and Wilson the following errors should be noted. The authors did not see final proofs and are not responsible for the errata.

P. 87, col. 1, line 42 — *Bothriopsis* should read *Brothriopsis*

P. 87, col. 1, line 44 — *Brothriopsis* should read *Bothriopsis*

P. 87, col. 2, line 11 — 1935: 22 should read 1935: 222

P. 87, col. 2, line 37 — 81.4% should read 81.6%

P. 87, col. 2, line 39 — 67.7% should read 69.7%

P. 87, col. 2, line 40 — x should read $\bar{x}$

P. 88, col. 2, line 12 — Xuantunich should read Xunántunich

P. 102, col. 2, lines 6 and 7 — Vanzolini and Williams, 70 should read Vanzolini and Williams, 1970

P. 102, col. 2, line 7 — Duellmn should read Duellman

P. 102, col. 2, line 8 — Duellmn should read Duellman

P. 103, col. 1, line 29 — UMNZ should read UMMZ

P. 103, col. 1, line 46 — USNM 22422 should read 22442

P. 104, col. 1, line 19 — Xuanantunich should read Xunántunich

P. 104, col. 1, line 22 — Posada-Arango, 1889 should read Posada-Arango, 1889a, 1889b

P. 105, col. 1, line 7 — Ophedia should read Ophidia

P. 105, col. 1, line 20 — 2Trimeresurus should read *Trimeresurus*

P. 105, col. 2, line 45 — *ophryomega* should read *ophryomegas*

P. 106, col. 1, line 41 — Buck should read Buckley

P. 107, col. 1, lines 1 - 5 — Information is out of place; it should come after Schmidt, 1933 as a continuation of the first two lines of that citation.

TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 22, Number 2 $3.50 May 3, 1981

LIFE HISTORY PATTERN OF *NOTROPIS SABINAE* (PISCES: CYPRINIDAE) IN THE LOWER SABINE RIVER DRAINAGE OF LOUISIANA AND TEXAS

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ABSTRACT

The life history of *Notropis sabinae* in two tributary streams of the lower Sabine River drainage system (Bayou Anacoco, Beauregard-Vernon Parish line, Louisiana; Big Cow Creek, Newton County, Texas) was studied from 1972 to 1977. The life history pattern observed for the two streams was similar. In Bayou Anacoco, the reproductive season extended from early April through late September; it was similar in Big Cow Creek except that reproduction ended earlier in September 1973. Counts of unovulated mature ova in females ranged from 113 to 423 for females 35-48 mm SL and were significantly correlated with female size. There was a low but significant correlation between the ovary weight-somatic weight ratio and body size among Bayou Anacoco females, but not among Big Cow Creek females. A low but significant correlation was found between mean mature ovum size and body size among females from both localities. The size of unovulated mature ova ranged from 0.55 to 0.88 mm diameter. There were no significant differences in slope or elevation of regression lines fitted to either fecundity or ova size data for each of the two localities. Sex ratios did not differ significantly from 1:1. Females matured at a slightly larger size than males; all females were mature by 32 mm in Bayou Anacoco and 33 mm in Big Cow Creek. Mean sizes of adult males and females did not differ significantly. Maximum age for most individuals of *Notropis sabinae* was about 1½ to 2 years. Maximum size was 49 and 47 mm SL for Big Cow Creek and Bayou Anacoco, respectively.

INTRODUCTION

Information on the life history of the Sabine shiner, *Notropis sabinae* Jordan and Gilbert, is almost completely lacking. Except for data on habitat and distribution, only ancillary comments are available (cf. Moore, 1944; Douglas, 1974; Pflieger, 1975). The reproduction, age and growth of *N. sabinae* are considered herein.

This species is a member of the *Notropis longirostris* species group (subgenus *Alburnops*; Swift, 1970), which also includes *N. longirostris* and an undescribed species in the Mobile Bay drainage system. The species in this group are common inhabitants of clear, small to moderate sized sand-bottomed streams of Gulf coastal plain drainages. *N. sabinae* occurs in such streams of the Calcasieu, Sabine and Neches river drainages of southwestern Louisiana and southeastern Texas; it is also present in the White and St. Francis river systems of Arkansas and Missouri (Moore, 1968; Pflieger, 1971, 1975; Buchanan, 1973; Douglas,1974). Douglas, (1974) also reported an isolated population in the Little River system of east-central Louisiana.

MATERIALS AND METHODS

Monthly collections were obtained from Bayou Anacoco below State Hwy. 111, Beauregard-Vernon Parish line, Louisiana (T. 2 S., R. 11 W., SE ¼ sec. 20). The stream receives Kraft papermill effluent above this locality; therefore,

another stream was sampled to provide a "check" on data from Bayou Anacoco. The second locality consisted of access points along Big Cow Creek for ca. 0.8 - 1.2 km from Farm Road 1416, Newton County, Texas. The sampling locality in Big Cow Creek was about 39 km SSW of that in Bayou Anacoco. Collections were made from December 1972 (March 1973 at Big Cow Creek) through November 1973 with 3-m long, 4.8-mm and 3.2-mm Ace mesh seines. Supplementary collections were made during the springs of 1974, 1976 and 1977. Fishes were initially preserved in 10% formalin and stored in 43% isopropyl alcohol. Specimens were deposited in the Tulane University Museum of Natural History.

Stream flow records were obtained from local offices of the United States Geological Survey (Baton Rouge, LA; Austin, TX). The gauging station on Bayou Anacoco was located at my sampling locality; however, the gauging station on Big Cow Creek was located at State Hwy. 87 ca. 35 km upstream from my sampling point. Water quality data for Bayou Anacoco were also secured; no such data were available for Big Cow Creek. Climatological and daylength data for nearby recording stations were obtained from the National Climatic Center, Asheville, North Carolina, and the Naval Obsrvatory, Washington, D.C., respectively.

Periodic changes in the reproductive condition of females were determined by measurements of ova, determination of ovarian weights, and gross examinations of ovaries of females in the monthly samples. Both ovaries were removed from each of 10 adult females (when available) chosen at random from each collection examined. The diameter of one of the larger eggs from each female was measured. Preserved ova were not spherical; thus diameters were estimated by averaging measurements of the largest and smallest dimensions. Measurements were made to the nearest 0.05 mm using an ocular micrometer in a dissecting microscope. Ovaries and specimens were dried to a constant weight at 100-105°C and weighed to the nearest 0.001 g; ovarian weight was calculated as a percentage of total body weight. Contents of the digestive tract were removed before drying to eliminate a possible source of variation in data. Gross assessments of reproductive condition were based on the classification of females into one of the following stages of ovarian condition: (1) Immature (IM) – ovaries very small, thin, transparent to slightly translucent. Larger, developing ova, if present, yolkless with nucleus visible. (2) Early maturing (EM) – ovaries small to moderate size, translucent to white in color. Larger eggs relatively small with nucleus obscured by yolk deposition, often numerous, and becoming white in color. (3) Late maturing (LM) – ovaries greatly enlarged, filling a large portion of the body cavity, white to cream color. Larger maturing ova often as large as mature ova but not easily differentiated from smaller maturing ova, usually cream colored. (4) Mature (MA) – ovaries greatly enlarged, filling a major portion of the body cavity and usually distending the abdomen, cream to yellow. Mature ova present, cream to yellow in color, easily differentiated from maturing ova on the basis of size and color, and relatively numerous. (5) Partially spent (PS) – ovary noticeably smaller than mature ovary, relatively small number of mature ova present, often translucent areas and/or areas of small maturing ova easily distinguishable among larger mature ova. All individuals capable of producing gametes were considered sexually mature adults. More specifically, females were considered sexually mature if they had at least three enlarged eggs with the nuclei obscured by yolk deposition in one ovary (usually left) examined from each specimen. Individuals classified as MA or PS were considered reproductive. Breeding coloration, tuberculation and enlargement of urogenital papillae were also noted.

To illustrate the ova development pattern in *N. sabinae*, an ova diameter histogram was prepared using a mature female. All eggs in one ovary with the nuclei obscured by yolk deposition were measured. The number in each 0.05 mm size group was plotted as a percentage of the total number measured.

Analysis of reproductive condition in males was based on tuberculation and gross examination of the testes. Maturity was assessed primarily on the basis of increased size and development of opaque white testes in comparison to the smaller transparent/translucent testes of immature males.

Fecundity was determined by direct counts of mature ova in ovaries of reproductively mature females. Generally the specimens examined were only those with abdomens distended as a result of the ovaries filling the body cavity. Mature ova were easily separated from maturing ova on the basis of size and color. For each of the females examined for the analysis of fecundity, ten mature ova were chosen at random and their diameters measured to determine mean mature ovum diameter. Ovaries and specimens were dried and weights determined for calculation of ovarian weight-somatic weight ratios. Covariance analyses of these data were conducted following Snedecor and Cochran (1967).

Analyses of size at sexual maturity, sex ratio and mean size of sexually mature males and females were based on a number of collections. Chi-square tests (X^2) were used in replicated tests for goodness of fit to determine if there were significant deviations from a 1:1 sex ratio ; average sizes of adult males and females were compared using the unweighted means analysis in a two-way analysis of variance (Steel and Torrie, 1960; Snedecor and Cochran, 1967; Sokal and Rohlf, 1969).

Estimates of age were made on the basis of length frequency and scale analyses. All individuals in each collection analyzed were measured to the nearest 0.1 mm standard length (SL) and length frequency histograms prepared by plotting the percentage frequency for each 1-mm size group. For scale analyses, about 10-20 scales were removed from the area above the lateral line and anterior to the dorsal fin insertion of each specimen examined. Scales were cleaned by rubbing between two fingers moistened with water, mounted between two glass slides, and observed by microprojection at 50X. Annuli were identified by various combinations of the following: cutting over of circuli in dorsal and ventral fields, discontinuity of circuli or ridge-spacing in the posterior field, thickening of circuli and bending of radii.

STUDY AREAS

The stream at the Bayou Anacoco locality normally ranged from ca. 15-38 m in width. The area consisted of flowing runs and/or riffles 0.6m or greater in depth; they stretched between sandbars which constituted about 30-40% of the total shoreline, the remainder being heavily wooded. The bottom was primarily comprised of white sand with some gravel intermixed in patches; at times it became covered with a light layer of silt and/or detritus. With a gradient of 0.5 m/km in the immediate area, stream flow was usually moderate or slightly greater. The average discharge for the period of August 1969 – September 1973 was 0.013 $m^3/s/km$ with an average annual runoff of 401 mm.

Bayou Anacoco was typically dark brown in color, presumably resulting largely from the papermill effluents. For example, monthly measurements of color for 1972-76 (excepting October 1972 – May 1973, August – October and December 1976) averaged 100 platinum cobalt color units, range from 20-400 units. Other physicochemical characteristics recorded over the same time period were as follows (mean followed by (range): dissolved oxygen, 7.4

ppm (5.3-10.0); pH, 6.9 (6.2-7.8); alkalinity 29 mg/1 (8-87); and specific conductance, 206 micromhos/cm(41-629).

The stream section sampled in Big Cow Creek was narrower and sandbars were much less extensive and more intermittent. This area probably represents the upper reaches of the tributary in which *N. sabinae* occurs in relatively large numbers. The stream usually ranged from ca. 15-24 m in width with a section of this area divided into two channels normally ca. 9-12 m wide. The stream bed was similar to that in Bayou Anacoco. Stream flow was usually moderate; the gradient in the immediate area was 0.5 m/km. Average discharge for the 24 year period April 1952 – September 1976 was 0.009 $m^3/s/km^2$, the average annual runoff 296 mm.

Mean annual temperature in the area (Kirbyville Forest Service, TX. and Elizabeth, LA, stations) was 19°C. Mean temperature in January was 10°C and in July 28°C. Average annual rainfall was 150 cm.

RESULTS

Species Associates — A total of 45 species was taken from Bayou Anacoco; 38 were taken from Big Cow Creek. *Notropis sabinae* was the second most abundant species in each area, constituting 31% and 23% of all specimens collected from Bayou Anacoco and Big Cow Creek, respectively. *Notropis venustus* was the most abundant species; it composed 37% and 33% of all samples from the two respective stations. An association similar to that of *Notropis longirostris, Notropis venustus* and *Ammocrypta beani* (Heins and Clemmer, 1975) existed between *N. sabinae, N. venustus* and *Ammocrypta vivax* in these streams. *Notropis sabinae* and *N. venustus* were always taken together; and although *A. vivax* was not as abundant (3% of all samples from each locality), it was taken frequently (94 and 92 percent frequency of occurrence, n=16, 13, respectively). Both *N. sabinae* and *A. vivax* occupied the same open sand bottoms along sandbars, although *A .vivax* tended to be more abundant in areas of mixed sand and gravel. Other species collected were not closely associated nor commonly taken with *N. sabinae.* A complete list of species taken at each locality (including relative abundance and frequency of occurrence) is available in Heins (1979).

Reproduction – Secondary sexual characteristics: The extent of tubercle development may vary considerably in reproductively mature *N. sabinae* males. Weakly tuberculate males had small to moderately large, fine tubercles scattered over the sides of the snout (separated by wide hiatus at the tip of the snout) and lateral areas of the head posteriorally from the anterior edge of the lacrimal to the anterior suborbital area; small widely scattered tubercles often extended to the angle of the preopercle. Tubercles on the side of the head were separated from those on the snout by a sometimes poorly defined hiatus along the anterior edge of the lacrimal. Highly tuberculate males (Fig. 1) had concentrations of large, slightly retrorse to erect tubercles on each side of the snout which were separated by a hiatus of variable size at the tip of the snout. Tubercles on the lateral areas of the head extended from the anterior edge of the lacrimal (large to moderately large, erect to slightly retrorse) posteroventrally to the angle of the preopercle, generally becoming smaller and erect and at times sparsely scattered. Tubercles in the anterior suborbital area also tended to be smaller. Small to moderate size tubercles occurred between the orbit and nares and were separated from the anterior suborbital tubercles; they extended to the antero-dorsal aspect of the orbital margin and were occasionally absent. Small to moderate size tubercles were variably developed in two small groups medial and slightly anterior to the nostrils; at times the groups were poorly

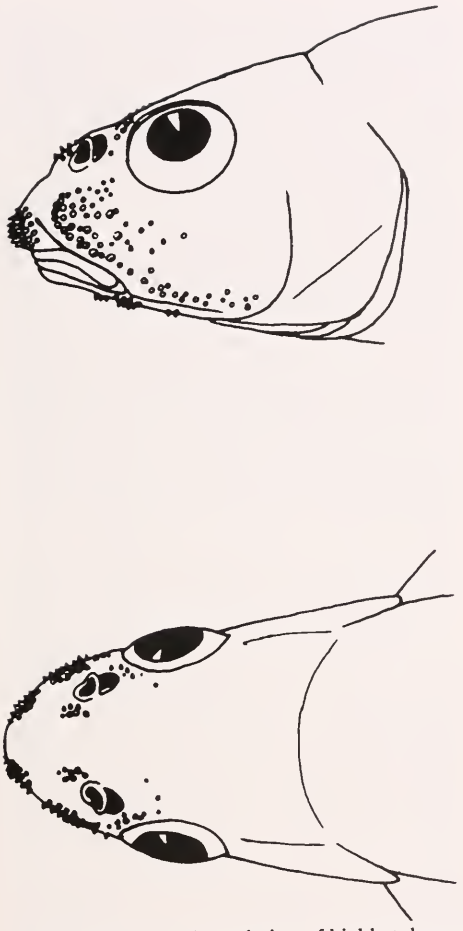

Figure 1. Head tuberculation of highly tuberculate *Notropis sabinae* males. The drawing is a composite of a number of specimens.

separated. Occasionally small scattered tubercles occurred between the orbits. Small to moderately large tubercles were variably developed on the posterior half of the mandibles of most males, forming one or two poorly defined rows in highly tuberculate males; occasionally a few also developed on the lower arm of the interopercle. Minute tubercles formed a shagreen on the pectoral rays of most males, the greatest development was generally on rays 2-6, less so on 7; they usually originated about one-fourth of the distance from the proximal end of the rays and extended to just past the first, major branching. Tubercles were occasionally scattered on other rays and the dital ends of hevily tuberculated rays. Tubercles also occured on dorsal, pelvic and anal fins but were poorly developed. No tubercles were noted on body scales.

Tuberculation in reproductively mature females was generally very weak. Some females developed small to fine tubercles that were scattered over the sides of the snout and head posteriorly to the suborbital areas. Tubercles occasionally extended to the angle of the preopercle or were on the mandible. Minute tubercles occasionally were also scattered along rays of the pectoral fins.

Reproductive coloration is poorly developed in both sexes, particularly in females. A faint lemon yellow color often develops in the dorsal and caudal rays of males, being strongest antero-basally. White pigmentation is also variably present in these and other fins, particularly the pectoral and anal. Breeding females have enlarged urogenital papillae which are absent in males.

Reproductive periodicity in females: Periodic changes in ova diameters and ovarian weights (Fig. 2) and gross ovarian examinations demonstrated a reproductive season extending from early April through late September in Bayou Anacoco. Diameters of ova and ovary weights were small from December 1972 through mid-March 1973 ($\bar{X}$ = 0.17—0.27 mm, 0.9-1.2% body weight). These measurements were slightly greater in late March 1976, but all females examined (n = 21) were still maturing as they were in 1973 (n = 18). No sample was available from April 1973 due to flooding during the scheduled sampling period. Females were in reproductive condition in early April of 1974 (93% MA&PS, n = 30) and 1976 (32% MA&PS, n = 37); diameters of ova averaged 0.71 and 0.53 mm and ovarian weights 6.1% and 3.7% of body weight, respectively. These data also indicate that reproductive activities began somewhat later in 1976. Females were in re-

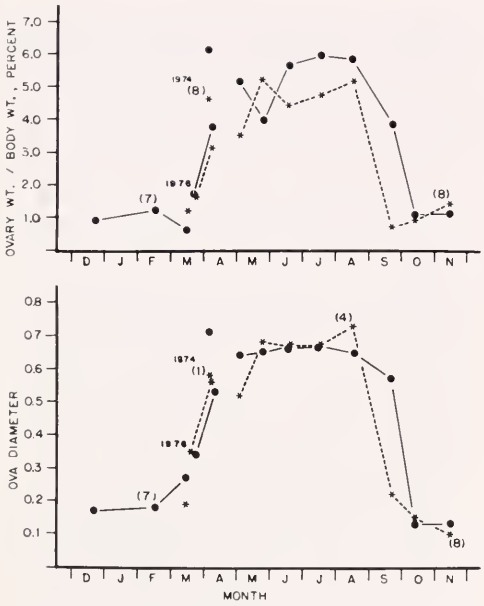

Figure 2. Mean diameter of largest ova (lower graph) and mean percentage ovary weight (upper graph) for *Notropis sabinae* from Big Cow Creek, Texas (dashed lines), and Bayou Anacoco, Louisiana (solid lines), 1972-73 (no April sample), April 1974, and March-April 1976. Lines connect only data points for sequential samples within the same year. Numbers in parentheses indicate the number of observations on the mean when less than ten. Statistics of variability are available in Heins (1979).

productive condition in early May 1973, (63% MA&PS, n = 30). Ova diameters and ovarian weights remained large from May through late September 1973 ($\bar{X}$ = 0.57 - 0.67 mm, 3.8% - 5.9% body weight). In September, 77% (n = 26) of the females were reproductive. Ova diameters and ovarian weights decreased to an average of 0.13 mm and 1.0% of body weight by mid-October, and almost all females were considered non-reproductive (98% IM&EM, n = 55). The reproductive periodicity of females in Big Cow Creek was similar to that in Bayou Anacoco (Fig. 2), but reproduction ended somewhat earlier in 1973. Diameters of ova and ovarian weights decreased to 0.22 mm and 0.7% of body weight by late September, and only 2 of 32 females (6%) were considered reproductive. The periodicity and variability in temperature, photoperiod and stream flow accompanying these cycles are shown in Figure 3.

After attaining reproductive condition, individual females remained reproductive throughout the spawning season. Maturing ova were present in reproducing females throughout the season. The ova development pattern of this species exhibits two complements of yolk-bearing ova, a stock of smaller maturing ova and a differentiated group of larger mature ova (Fig. 4). Such a bimodal distributions is indicative of a variable series of spawnings with complements of ova released periodically over an extended reproductive season (Hickling and Rutenberg, 1936; Prabhu, 1956; Qasim and Qayyum, 1961; MacGregor, 1970).

Reproductive periodicity in males: The cycles of testis and tubercle development were similar for both areas. Males taken in December and February had no tubercles although there were scars on a few; testes were small and cloudy to white in color. In March samples testicular activity was indicated by enlargement of the testes; tubercles also developed in March. Testes and tubercles were generally well developed from April into September; however, there was a decline of testis and particularly tubercle development in Big Cow Creek males in September, coincident with the decline of reproductive activity in females. Testes were small in October and November. Very small degenerating tubercles were still present in October but were generally absent in November, excepting tubercle scars in some males.

Reproductive effort and ovum size: There was a highly significant correlation between number of mature ova and standard length among females from both localities (Table 1). Regression lines expressing the relationship between counts of mature ova and body size did not differ in slope ($F = 0.14$; $df = 1, 60$; $p > .05$) or elevation ($F = 2.20$; $df =$

1, 61; $p > .05$) when tested by analyses of covariance; therefore, the data from both localities were combined. Counts of mature ova ranged from 113 to 423 for females 35.4 - 47.8 mm SL. The intercept, regression coefficient and correlation coefficient for the linear relationship between fecundity and standard length among females in the combined sample (Fig. 5, $r^2 = 0.57$) are also given in Table 1. Log-log and semi-logarithmic transformations yielded similar r^2 values, indicating that any of the three models adequately defined the relationship. However, logarithmic transformation of both variables stabilizes the variance along the regression line (Bagenal, 1967) and is important for use in prediction; the resulting equation is ($r^2 = 0.53$; F = fecundity, SL = standard length):

$$\log_{10}F = -2.8297 + 3.1953(\log_{10}SL).$$

There was a low but significant correlation between ovarian weight-somatic weight ratio and body size among females from Bayou Anacoco, but there was no significant correlation among females from Big Cow Creek (Table 1, Fig. 6). This notwithstanding, there was a low but highly significant correlation between ovarian weight-somatic weight ratio and body size among females in the combined samples. In general, these ratios ranged from 4.8 -15.2%.

There was a low but significant correlation between mean mature ovum size

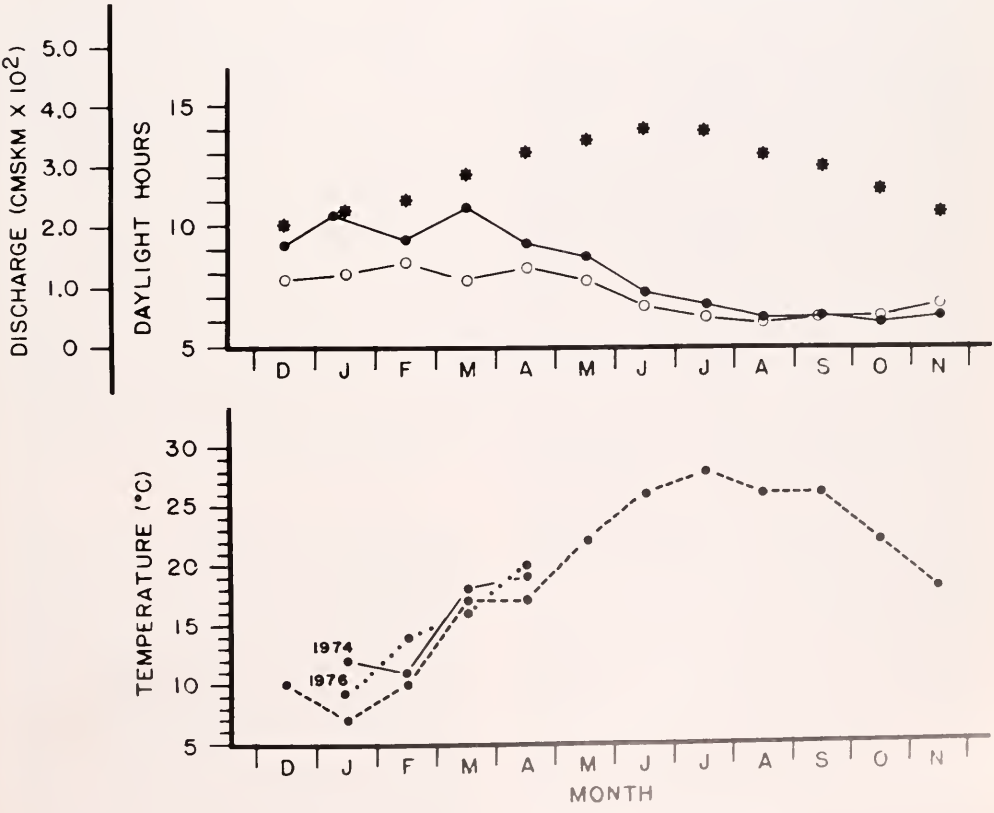

Figure 3. Environmental variability and periodicity for Big Cow Creek, Texas, and Bayou Anacoco, Louisiana. Upper graph: mean monthly number of daylight hours (bold asterisks, Lake Charles, LA) and mean monthly discharge as cubic meters per second per square kilometer for Big Cow Creek (1952-76, open circles, solid line) and Bayou Anacoco (1969-73, solid circles, solid line). Lower graph: mean monthly air temperature for 1973 (dashed line, DeRidder, LA), early 1974 (solid line), early 1976 (dotted line).

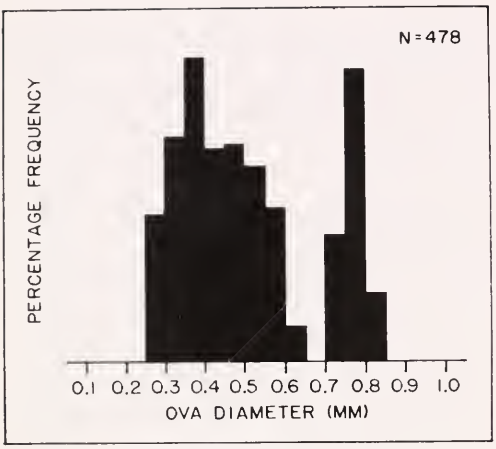

Figure 4. Size frequency distribution for vitellogenic ova in a reproductive *Notropis sabinae* female, indicating the typical pattern of ova maturation and recruitment.

and body size among females from both localities (Table 1, Fig. 7), indicating a tendency for larger females to produce larger ova. Data are missing for one specimen fromBayou Anacoco; the ovary was not well preserved and many eggs broke when teased from the follicles. Analysis of covariance showed that regression lines fitted to the data for each locality did not differ in slope ($F = 0.53$; $df = 1, 59$; $p > .05$) or elevation ($F = 2.03$; $df = 1, 60$; $p > .05$); therefore, data for both localities can be combined. The mean sizes of the mature ova measured ranged from 0.63 to 0.81 mm diameter and averaged 0.72 mm ($S = 0.0452$). Addition of mean mature ovum diameter to the linear equation for fecundity did not significantly increase the r^2 value ($F = 2.260$; $df = 1, 60$; $p > 0.05$).

Sex ratio, size at maturity and mean size of adult males and females: Chi-square tests indicated that there were no significant differences from a 1:1 sex ratio at either locality. The heterogeneity χ^2 was not significant ($p > .05$) for either Big Cow Creek (0.7485, $df = 4$) or Bayou Anacoco (5.3745, $df = 4$); similar results were obtained for the pooled χ^2 at the two respective stations (2.9823, $df = 1$; 1.6864, $df = 1$).

The number of specimens originally examined from Big Cow Creek to determine size at sexual maturity was insufficient; therefore, supplemental specimens taken in August 1973 and a portion of those taken in May 1977 were also examined. The supplemental specimens appeared to differ somewhat from those initially examined (May–July 1973) in that individuals seemed to mature at a

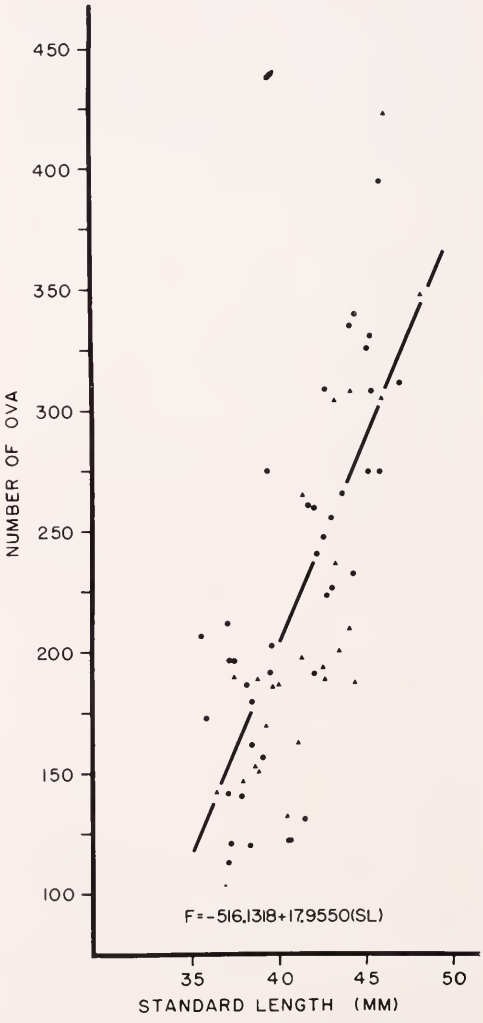

Figure 5. Relationship between number of mature ova and standard length for *Notropis sabinae* females from Big Cow Creek (triangles), Texas, and Bayou Anacoco (dots), Louisiana, 1973-74 and 1976-77.

Table 1. Summary of linear regression analyses of ova number-body size, ovary weight-somatic weight ratio--body size, and ova diameter-body size relationships for samples of *Notropis sabinae* from Big Cow Creek, Texas, and Bayou Anacoco, Louisiana, 1973-1974 and 1976-1977; ns = non-significant difference, * = significant difference at .05 level, ** = significant difference at .01 level.

Ova number-body size (SL)

Locality	n	Intercept	Regression Coefficient	r
Big Cow	24	−581.3956	19.2567	.772**
Anacoco	40	−497.7474	17.6721	.758**
COMBINED	64	−516.1318	17.9550	.753**

Ovary weight-somatic weight ratio--body size (SL)

Locality	n	Intercept	Regression Coefficient	r
Big Cow	24			.362^{ns}
Anacoco	40	−3.3558	0.3003	.364*
COMBINED	64	−4.3164	0.3282	.368**

Ova diameter-body size (SL)

Locality	n	Intercept	Regression Coefficient	r
Big Cow	24	0.4200	0.0075	.443*
Anacoco	39	0.5136	0.0049	.377*
COMBINED	63	0.4735	0.0060	.409**

smaller size. Despite this complication the data are useful for a approximate comparison of size at sexual maturity in the two populations. Males matured at a smaller size than females at both localities,completing maturation by 29 mm SL in Bayou Anacoco and 30 mm SL in Big Cow Creek. Females were not completely mature until 32 mm in Bayou Anacoco and 33 mm in Big Cow Creek.

The analysis of variance performed to test for significant differences in mean size of adult males and females from Big Cow Creek indicated a significant interaction between the effects of sex and month (Table 2); therefore, a test of simple effects was performed to determine when there were differences in mean size. This procedure indicated that females were significantly larger than males in July ($p. < .05$); all other differences were non-significant. The F-value for interaction was non-significant for the Bayou Anacoco samples, as was the F-value for sex, indicating that there were no significant differences in the mean sizes of adult males and females. Significant differences between monthly

samples were indicated for both localities but were not analyzed. The results for the July sample from Big Cow Creek are unexplained; however, they may be due to sampling error. It seems reasonable to conclude that there were generally no significant differences in the mean sizes of adult males and females at either locality.

Growth and Population Age Structure

Temperatures in the study area varied considerably over short periods (daily, weekly); but mean monthly temperature variation was moderate (Fig. 3). Therefore, annulus formation in this warm temperate region is quite variable. Further, annulus formation may be especially weak for smaller individuals experiencing their first winter. Thus, scale analyses were combined with length frequency analyses to obtain the most reliable age estimates. These analyses (Figs. 8, 9) indicate that the maximum age for most *N.sabinae* is about 1½ to 2 years. None of the scales examined from March or September 1973 Big Cow Creek samples (Fig. 8; n = 50, 54, respectively) had more than two annual marks. Some specimens examined from March appeared to be forming an annulus. These data, and examinations of a few larger specimens in April and May collections (a time of active annulus formation), suggest that some of the larger individuals (particularly those 44 mm SL) may enter a fourth growing season as three-year olds. Analysis of the length

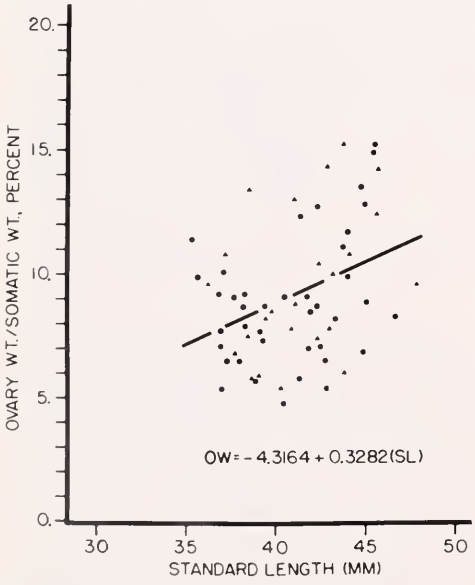

Figure 6. Relationship between ovary weight-somatic weight ratio and standard length for *Notropis sabinae* females from Big Cow Creek (triangles), Texas, and Bayou Anacoco (dots), Louisiana, 1973-74 and 1976-77.

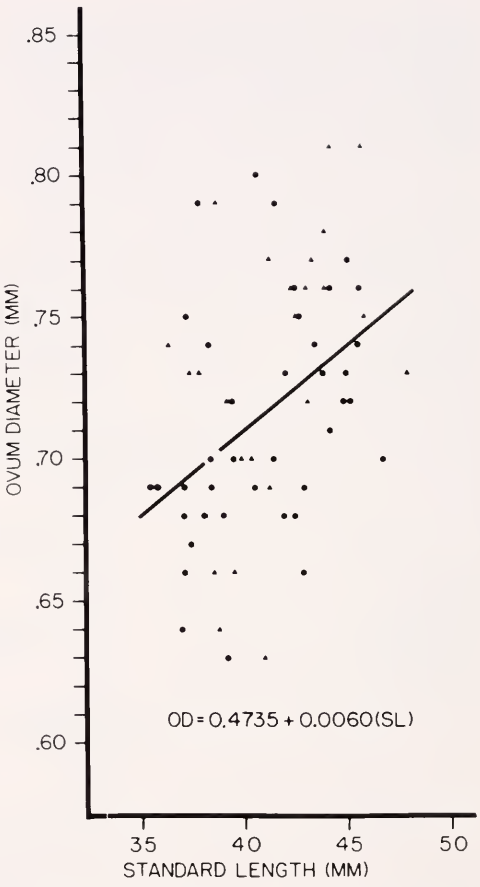

Figure 7. Relationship between mean size of unovulated, mature ova and standard length for *Notropis sabinae* females from Big Cow Creek (triangles), Texas, and Bayou Anacoco (dots), Louisiana, 1973-74 and 1976-77.

Big Cow Creek						
Sex	Date of Collection					Mean
	21 Mar 1976	2 May 1973	17 Jul 1973	21 Sep 1973	12 Oct 1973	
Male	36.834 (41)	37.225 (24)	38.673 (15)	39.796 (23)	39.943 (23)	38.5
Female	35.864 (50)	37.347 (32)	40.475 (16)	38.873 (33)	38.604 (25)	38.2

Analysis of Variance of Unweighted Means

Source	df	SS	MS	F-value
Sex	1	4.23760	4.23760	
Month	4	418.86419	104.71605	
Interaction	4	80.56889	20.14222	2.67303*
Error	272	2049.6125	7.53534	
Total	281			

Bayou Anacoco						
Sex	Date of Collection					Mean
	21 Mar 1976	2 May 1973	17 Jul 1973	21 Sep 1973	14 Nov 1973	
Male	38.670 (27)	37.942 (24)	37.782 (17)	34.929 (42)	37.053 (45)	37.3
Female	38.371 (21)	38.797 (31)	38.350 (18)	35.858 (24)	37.213 (38)	37.7

Analysis of Variance of Unweighted Means				
Source	df	SS	MS	F-value
Sex	1	12.65552	12.65552	1.66072^{ns}
Month	4	345.74802	86.43701	11.34271^{**}
Interaction	4	13.59546	3.39887	0.44602^{ns}
Error	277	2110.8763	7.62049	
Total	286			

Table 2. Mean size (mm SL), number of observations on the mean (in parentheses), and summary table for analysis of variance to test for presence of significant differences between mean size of adult (33 mm SL) male and female *Notropis sabinae* in various collections from Big Cow Creek, Texas, and Bayou Anacoco, Louisiana; ns = non-significant difference, * = significant difference at 0.05 level, ** = significant difference at 0.01 level. Adjustment of sums of squares for unequal numbers in the unweighted means analysis of variance was made to sums of squares for sex, month, and interaction.

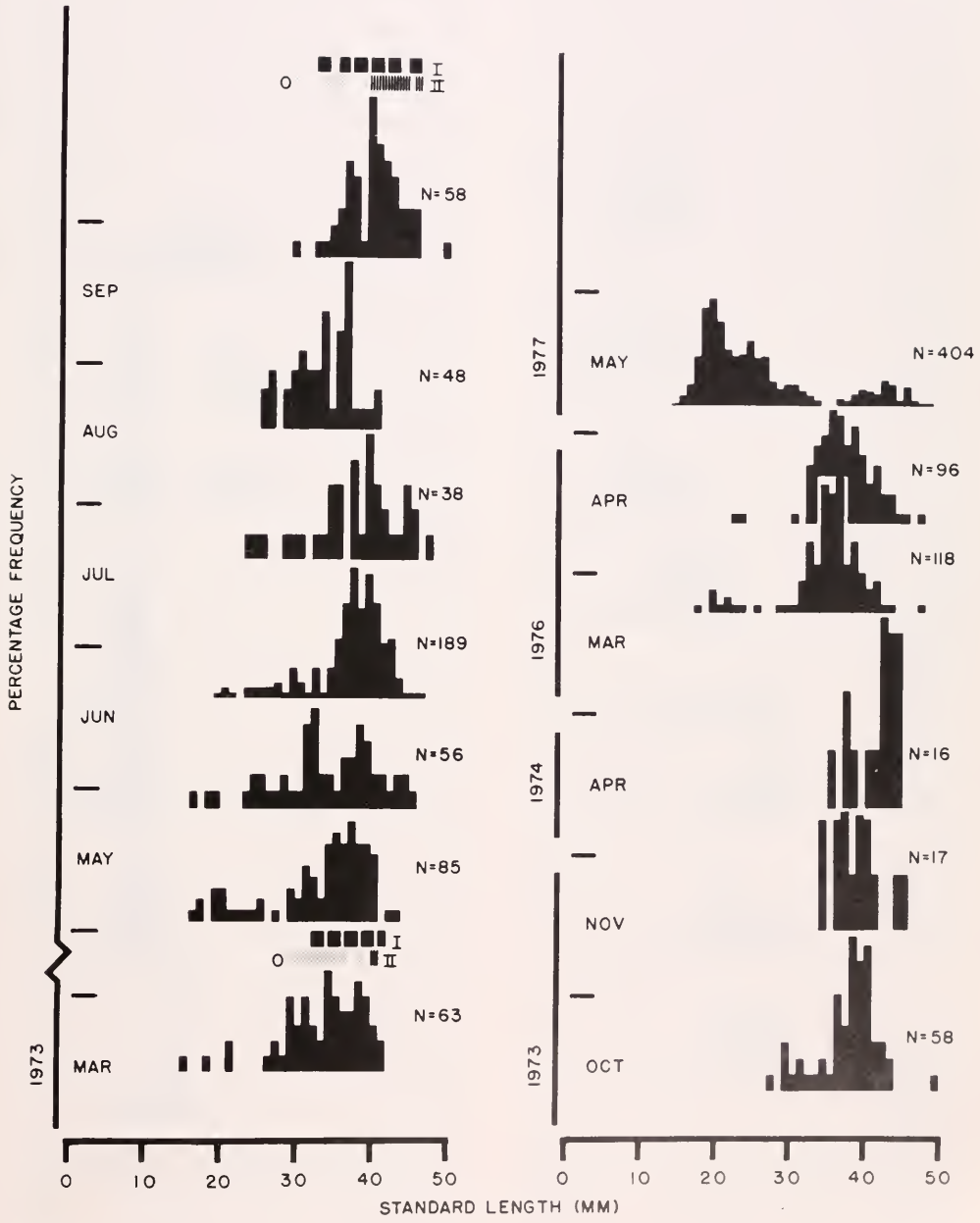

Figure 8. Length frequency histograms for collections of Notropis sabinae from Big Cow Creek, Texas. Horizontal bars are placed at beginning of each month; histogram bases are set at date of collection. Results of scale analyses are shown for March and September, 1973, collections. (0 = no annulus, I = 1 annulus, II = 2 annuli).

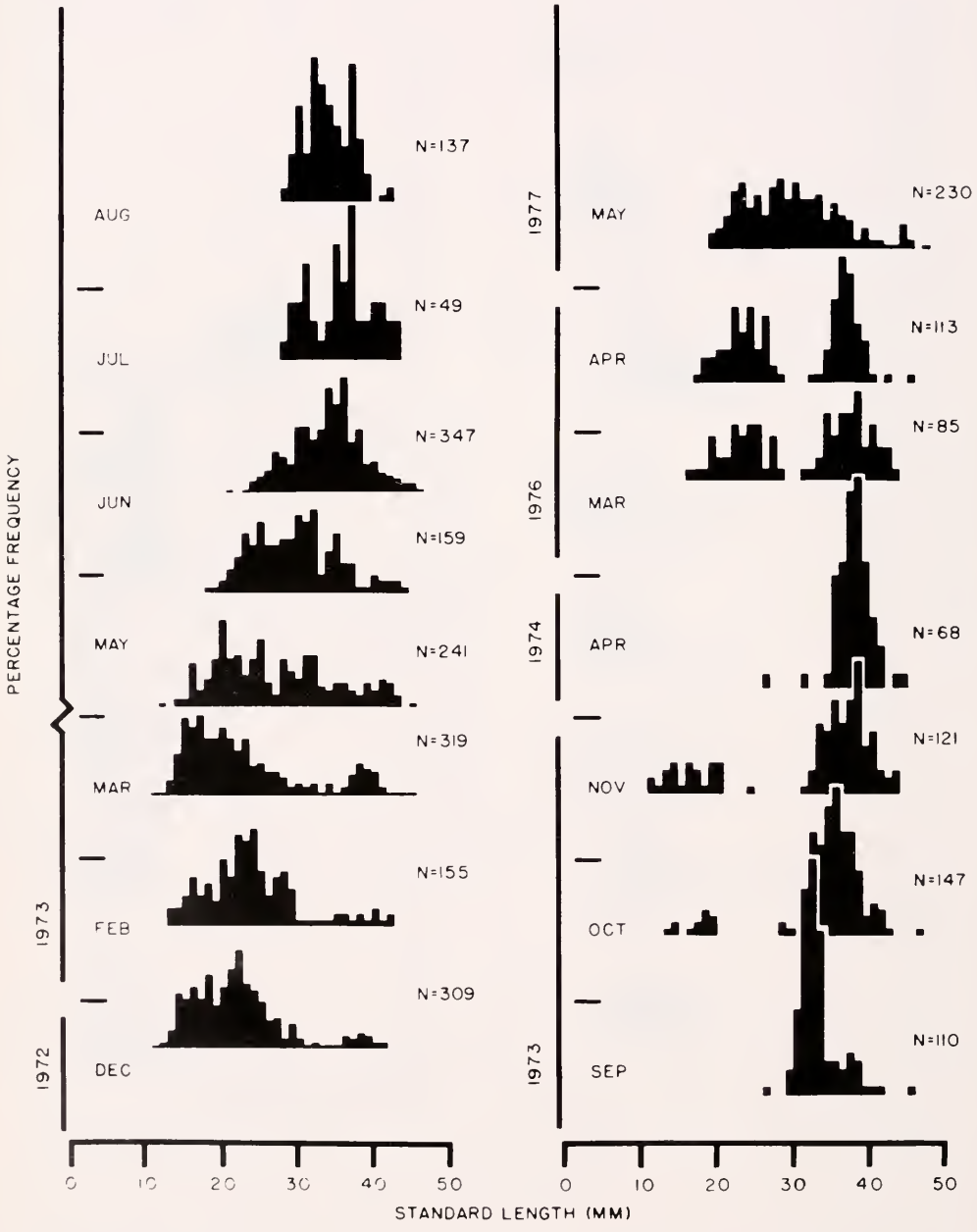

Figure 9. Length frequency histograms for collections of *Notropis sabinae* from Bayou Anacoco, Louisiana. Horizontal bars are placed at beginning of each month; histogram bases are set at date of collection.

frequency histograms for Big Cow Creek prior to and during the early part of the annual reproductive season demonstrates a bi-modal distribution. The origins and fates of these two groups suggest that the larger group is primarily comprised of one-year old individuals entering their third growth season as two-year olds. The number in this group dwindles considerably by the end of this season, suggesting that most individuals die by the age of two years. The group of smaller fish thus represents individuals having just completed a first winter and entering a second growth season as one year olds. Maximum size was about 49 mm and 47 mm SL in Big Cow Creek and Bayou Anacoco, respectively. Finally, these data and the data on size at maturity suggests that a small percentage of individuals might mature within their first growth season. However, at least the majority mature in their second season, at or within one year.

DISCUSSION

Notropis sabinae, along with other members of the *Notropis longirostris* species group (Heins and Clemmer, 1976; Heins, 1979; Heins et al., in press), has an extended reproductive season during which it seems a number of clutches of eggs are spawned. The long annual period of high temperatures and long photoperiods in the area (Fig. 3) probably facilitates the protracted reproductive season; temperature and photoperiod are two proximal factors that activate neuroendocrine centers controlling reproductive cycles in fishes (Schwassman, 1971; DeVlaming, 1972, 1974). Nevertheless, extended reproduction may be adaptive to a variable environment in that distributing reproductive activity over a long period of time may reduce the chance of losing a large portion of the annual recruitment (Starret, 1951; Tanyolac, 1973; Wallace,, 1973; Heins and Bresnick, 1975; Heins and Clemmer, 1976; Heins et al., in press). Protracted reproduction has also been observed in a number of southern species of *Notropis* (Mathur and Ramsey, 1974; Cowell and barnett, 1974; Beach, 1974; Cowell and Resico, 1975; Heins and Bresnick, 1975).

The protracted reproductive season and presumed production of multiple clutches of eggs indicates a relatively high seasonal reproductive effort for *Notropis sabinae*. Further, *N. sabinae* is a relatively small, short-lived member of the genus *Notropis* as are other members of the *N. longirostris* species group (cf. Hubbs and Hubbs, 1958; Carlander, 1969; Snelson and Jenkins, 1973; Hubbs and Miller, 1975; Heins and Clemmer, 1976; Heins, 1979; Heins et al., in press). *N. sabinae* also matures early, at about one year. Williams (1966) suggested that a small, short-lived species with high annual mortality should invest a greater effort in reproduction in a given season, as compared to a large, long-lived species. Additionally, strong selection for early maturity, that is within one year, should result from a short life expectancy (Tinkle, 1969).

The spawning of *N. sabinae* was not observed during this study; however, it presumably occurs over open sand as in *Notropis longirostris* (Hubbs and Walker, 1942). If this is so, *N. sabinae* would belong to the ecological guild of psammophilous fishes delineated by Balon (1975), as do other members of the *N. longirostris* species group.

Notropis sabinae, as with other members of the *N. longirostris* species group, exhibits life history traits conventionally considered characteristic of a relatively r-selected species (cf. Stearns, 1976; Balon et al., 1977). Nevertheless, some interspecific variation was observed among the life history patterns of members of the *N. longirostris* species group; variation was also noted among populations of *N. longirostris* which was more widely studied (Heins, 1979). This intra- and inter-specific life history variation will be considered in a forthcoming report. However, I will consider a distinc-

tive difference between *N. sabinae* and other members of the *N. longirostris* species group herein. Among those populations studied thus far, *N. sabinae* produces smaller mature, unovulated ova (cf. Heins and Clemmer, 1976; Heins, 1979; Heins et al., in press). The inter- and intra-specific variation observed in egg size appears to be related,at least in part, to stream flow patterns in southern North America (Fig. 10). Larger egg sizes were found in populations inhabiting areas of higher annual stream runoff (Heins, 1979). I postulate that there has been a selective advantage to larger egg size in those streams where average annual runoff is greater. Thus annual stream runoff values may indicate the relative severity of this factor in the respective stream environments. Svardson (1949) and Williams (1959) have argued that a reduction in fecundity could not be favored by natural selection unless it was a necessary consequence of some advantageous development such as increased egg size. Larger ova generally result in larger larvae that can be expected to be stronger, able to swim better, and less susceptible to damage (Blaxter, 1969). Thus, larger ova may result in larger larvae better able to survive in streams with greater average annual runoff. Heins and Clemmer (1976) had intimated this in their report on *N. longirostris*. This notion will be treated more fully along with other inter- and intra-specific variations in the life histories of members of the *Notropis longirostris* species group in a forthcoming paper.

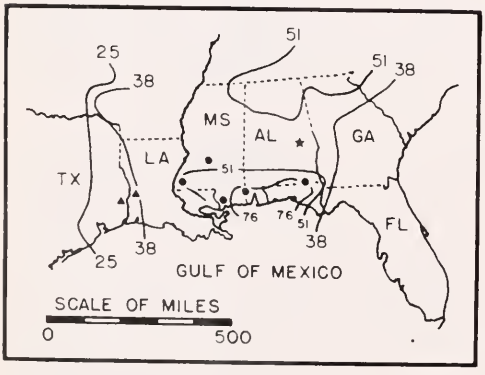

Figure 10. Map showing locations of various populations of *Notropis sabinae* (triangles), *Notropis longirostris* (dots), and *Notropis* species (cf. *N. longirostris*) (star) studied by Heins (1979) in relation to amount of annual stream runoff (cm). (After Geraghty et al. (1973), by permission.)

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THE SYSTEMATICS AND DISTRIBUTION OF THE HOGNOSE VIPER *BOTHROPS NASUTA*[1] BOCOURT (SERPENTES: VIPERIDAE)

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ABSTRACT

Variation in selected characters of scutellation, coloration, and body proportions in the Neotropical hognose viper, *Bothrops nasuta* Bocourt, is discussed and the speciied is redescribed. Analysis of this variation allows for the definition of three distinctive populations. No infraspecific taxa are recognized. The biogeographic history of the species is also discussed.

INTRODUCTION

Bothrops nasuta Bocourt, 1868, is a small, terrestrial pit viper occurring in humid lowland forests from Chiapas, México southward to Ecuador. It is a member of the *Bothrops lansbergi* group, a group of hognose vipers (*sensu* Burger, 1971), which was last revised by Amaral (1929a). The hognose viper group is in need of systematic study and the acquisition of an unusual specimen of *B. nasuta* from Ecuador by one of us (LP) prompted a review of the systematics of this species, the most widespread member of the group.

Amaral (1929a) had 32 specimens available to him. Since his revision more material has become available allowing for a more complete understanding of the systematics of this species.

MATERIAL AND METHODS

We examined 241 specimens of *Bothrops nasuta*. The single specimen of this species from Belize (Neill, 1965) was not available to us. The following scales were counted using the definition of Klauber (1972): intercanthals, prefoveals, preoculars, suboculars, and postoculars. We follow Burger (1971), with some modification, in defining and recording the following scales: postcanthals, interictals, interoculars, oculabials, and nasorostrals. The definitions of these latter scales are as follows:

Postcanthals. The undifferentiated marginal head scale(s) contacting the upper preocular between the canthal and supraocular.

Interictals. The supracephalic scales occupying the posterior portion of the head from oral rictus to oral rictus. For consistency, the interictals were counted between the last supralabials.

Interoculars. The irregularly disposed scales in the frontal region that were counted along the path between the supraoculars that traverses the fewest scales.

Oculabials. The rows of scales between

[1]According to Shreve (1957), Amaral (1964a, 1964b, 1976) and Schwartz and Thomas (1975), generic names ending in *-ops* are feminine in classical Greek usage. Thus, the specific name for this hognose viper is *nasuta*, not *nasutus*. For opinions to the contrary, see the 1964 edition of the International Code of Zoological Nomenclature and Smith and Larsen (1974).

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suboculars and supralabials but including neither.

Nasorostrals. The scales between the nasal and rostral.

The number of ventral scales was counted using the method of Dowling (1951). Due to the irregularity of scutellation in the nasofrontal area, the scales anterior to and including the interoculars, except for those bordering the edge of the head (rostral, internasals, canthals, postcanthals, and supraoculars), were counted and given the name nasofrontals. Postfoveals and median gulars were not counted due to their high degree of variability and consequent difficulty of accurate tabulation. The dorsal scale rows were counted one head length posterior to the interictals, at midbody, and at the vent. All measurements were made on preserved specimens, with the exception of those made on a record-length specimen from Ecuador in the senior author's live collection.

Statistical analyses were accomplished using the Student's *t* test, as described by Simpson, et al. (1960), using a probability value of .95.

Inasmuch as *Bothrops nasuta* has a basically linear distribution, we used, for the sake of convenience, the political boundaries within the animal's range as the basis for subdividing for analysis our data on variation. The populational groupings in the tables are defined in the discussion.

HISTORICAL SUMMARY

A considerable amount of confusion has existed in the literature concerning the hognose vipers. Much of the confusion was largely eliminated by Amaral's paper (1929a) on the *Bothrops lansbergi* group. In that paper Amaral redescribed *Bothrops nasuta* Bocourt and demonstrated its distinctness from *B. lansbergi* (Schlegel). He also snyonymized *B. brachystoma* (Cope) with *B. lansbergi*, thus terminating the application of the name *brachystoma* to specimens of *B. nasuta*. Moore (1962), however, incorrectly placed *brachystoma* as a synonym of *B. nasuta*.

Cope (1876) described *Bothriopsis proboscideus*. Later, he (1879) questioned the validity of *B. proboscideus* but continued to recognize it in a later paper (Cope, 1887). Amaral (1929a) placed *B. proboscideus* in the synonymy of *Bothrops nasuta*.

Posada-Arango (1889a) proposed a new genus of solenoglyph snakes, *Thanatos*, and described several new species, including *T. sutus*. Later in the same year (1889b) he introduced the generic name *Thanatophis*, without explanation (*fide* Vanzolini, 1977). Nicéforo María (1938) concluded that *Thanatophis sutus* is probably a synonym of *Bothrops nasuta*. His decision was tentative due to Posada-Arango's generalized description. García (1896), using the nomenclature of Posada-Arango, figured a specimen identified as *Thanatophis sutus*, which is actually a juvenile *B. nasuta*, supporting the contention that the two names are synonymous, a supposition supported by Daniel (1949, 1955), Burger (1971), and us. Peters and Orejas-Miranda (1970) and Vanzolini (1977) incorrectly place *Thanatophis* (or *Thanatos*) *sutus* as a synonym of *Bothrops lansbergi*.

Burger (1971) subdivided the various members of the genus *Bothrops* (*sensu lato*) into five genera. *Bothrops nasuta* was placed in the genus *Porthidium* as *P. nasutum*. This disposition was accepted by Smith and Smith (1976). Whereas we are in fundamental agreement with the generic limits proposed by Burger (1971), we prefer not to use them inasmuch as an adequate analysis of the basis for such a classification was not presented by him. In addition, Burger (1971) recognized two subspecies, *nasutum* and *sutum* (=*nasuta* and *suta*). This disposition was unsupported with any data and is not followed by us (see analysis of variation).

SPECIES ACCOUNT

Bothrops nasuta Bocourt

Bothrops lansbergii: Günther, 1863: 350; Dunn, 1928: 30 (part); Picado.1936: 392; E. H. Taylor, 1951: 178, 1954: 681.

Bothrops nasutus Bocourt, 1868: 202 (type locality: Panzós, on the banks of the Río Polochic, Guatemala; holotype: MNHN 1592 - *fide* Stuart, 1963), 1876: 410; Barbour and Loveridge, 1929: 3; Smith, 1943: 400, 1958: 224; Smith and Taylor, 1945: 182; Stuart, 1948: 87, 1950: 24, 1958: 29, 1963: 130; E. H. Taylor, 1954: 783; Moore, 1962: 62; Duellman, 1963: 245, 1966: 705; Klemmer, 1963: 408; Neill, 1965: 113; Hoge, 1965: 127; Savage, 1966: 751, 1973: 17; Heyer, 1967: 267; Moore, et al., 1968: 48, 61; Meyer, 1969: 415; Minton and Minton, 1969: 207; Scott, 1969: 232; Peters and Orejas-Miranda, 1970: 49; Hoge and Romano, 1971: 252; Alvarez del Toro, 1973: 158; R. T. Taylor et al., 1974: 384, 388; Henderson and Hoevers, 1975: 51; Campbell, 1976: 153.

Porthidium nasutus: Cope, 1871: 207.

Porthidium nasutum: Cope, 1871: 207, 1876: 151, 1879: 271, 1887: 89; Smith and Smith, 1976: S-B-16.

Bothriopsis proboscideus Cope, 1876: 150 (type locality: Sipurio, at base of mountains, Costa Rica; no holotype designated); Cope, 1879: 271.

Bothrops lansbergi: Müller, 1878: 703 (in error).

Bothrops brachystoma: Müller, 1882: 154; Amaral, 1925: 29, 1927a: 22, 1927b: 47; Loveridge, 1928: 63.

Bothriopsis (sic) *proboscideus*: Cope, 1887: 89.

Brothriopsis brachystoma: Cope, 1887: 89 (part).

Thanatos sutus Posada-Arango, 1889a: 45-49 (paper not seen).

Thanatophis sutus Posada-Arango, 1889b: 344 (type locality: "le district de Zea," Colombia; no holotype designated); García, 1896: 26.

Bothriechis lansbergii: Gunther, 1895: 190 (part).

Lachesis brachystoma: Boulenger, 1896: 547 (part); Boettger, 1898: 139.

Trimeresurus brachystoma: Mocquard, 1909, 945 (part).

Bothrops nasuta: Amaral, 1929a: 25. 26, 1929b: 237, 1931a: 89, 1931b: 94, 1935: 22, 1944a: 7, 10, 1944b: 18; Picado, 1931a: 69, 1931b: 104, 1936: 391; Dunn and Emlen, 1932: 32; Dunn, 1933: 79, 1944: 215; Schmidt, 1933: 19; Wettstein, 1934: 38; Nicéforo Maria, 1938: 419, 1942: 101; Prado, 1939: 1; Rendahl and Vestergren, 1941: 16, Daniel, 1949: 329, 1955: 80; Pifano and Römer, 1949: 302; E. H. Taylor, 1951: 177; Peters, 1960: 510; Villa, 1962: 50; Brattstrom 1964: 189; Medem, 1968: 194; Minton and Minton, 1969: 216; Wilson and Meyer, in press.

Trimeresurus nasutus: Dunn and Bailey, 1939: 20; Smith, 1941: 62.

Porthidium nasutum nasutum: Burger, 1971: 35, 132.

Porthidium nasutum sutum: Burger, 1971: 35, 132.

Description - The scutellation of this species is as follows: rostral higher than wide, the ventrolateral portion infrequently separated off as a nasorostral (5.0% of specimens examined); internasals paired, elongate, elevated anteriorly, usually in contact (81.4%); canthals usually single (96.6%); postcanthals often one (67.7%), sometimes two; intercanthals 3-7 (x=4.95); nasofrontals 20-59 ($\bar{x}$=37.23); interoculars 3-7 ($\bar{x}$=5.19); lateral edge of supraoculars flattened; interictals 19-28 ($\bar{x}$=24.58); nasal scale partially divided; prefoveals 2-12 ($\bar{x}$=5.60); subfoveals 1-7 ($\bar{x}$=2.26); loreal wider than high, upper preocular large, extending dorsally over the canthal ridge; middle preocular divided or not, infrequently absent, in contact with orbit or not; lower preocular single, in-

frequently absent, in contact with orbit or not; suboculars 1-4 ($\bar{x}$=1.66); postoculars 1-4 ($\bar{x}$=2.30); oculabials 1-4, usually 2 (88.8%); supralabials 8-11 ($\bar{x}$=9.34); infralabials 9-13 ($\bar{x}$=11.41), the first pair usually in contact; a single pair of chinshields; ventrals 123-145 ($\bar{x}$=135.80); anal plate single; subcaudals entire, 24-41 ($\bar{x}$=30.02); tail not prehensile; dorsal scale rows at neck 23-29, usually 25 (87.8%), at midbody 21-27, usually 23 (92.8%), at vent 17-21, usually 19 (96.6%); apical pits absent.

The hemipenis is divided with a bifurcate sulcus spermaticus, the sulcus dividing close to the base of the organ and each branch extending to the distal end of the apical lobe. The basal portion of the organ and the areas lateral to and between the branches of the sulcus are spinulate. The shoulders and the absulcate side of the organ are covered with spines which increase gradually in size proximally, terminating with a pair of enlarged basal spines situated on either side of the sulcus. Distal areas of the apical lobes are calyculate with papillate micro-ornamentation.

Distribution and Ecology - *Bothrops nasuta* is an inhabitant of the humid lowlands of Middle America and adjacent northwestern South America (Figs. 1 and 2). *Bothrops nasuta* belongs to the Eatern Mesoamerican Complex of Savage (1966) and the Humid Tropical Assemblage of Duellman (1966). It is distributed along the Caribbean lowlands from northern Chiapas, México, eastward through northern Guatemala, possibly to Belize (see discussion below), thence southward through Central America (Fig. 1) and onto the Pacific coastal plain of western Columbia to midwestern Ecuador (Fig. 2). The species probably also occurs in the mesic lowlands of eastern Veracruz, México, inasmuch as it has been recorded near the border in Chiapas in the same type of forest (Alvarez del Toro, 1973). A specimen (ANSP 4873) recorded from "Veracruz, Mexico" shows characters of specimens from much farther south in the range and we regard the data as questionable. The species probably also occurs in the southern portions of Tabasco.

The occurrence of *Bothrops nasuta* in Belize is questionable. Schmidt (1941) recorded a specimen of a hognose viper from Benque Viejo, Cayo District, Belize, which he identified as *Trimeresurus yucatanicus*. Neill (1965) recorded a specimen of *B. nasuta* from Xuantunich (=Benque Viejo), Cayo District, and speculated that Schmidt's specimen was probably of the latter species. This disposition was followed by Henderson and Hoevers (1975). McCranie and Porras (1978) examined the Schmidt specimen (USNM 61781), however, and determined it to be *Bothrops yucatanica*, thus reestablishing the occurrence of this species in Belize. The description of the specimen reported by Neill (1965) is ambiguous and will not distinguish *B. nasuta* from *B. yucatanica*.

In the northern part of its range (the Mexican and most of the Guatemalan portion), *B. nasuta* lives in the broadleafed forest or quasi-rainforest division of the evergreen forest (c.f. Duellman, 1966; also see Stuart, 1966). Duellman (1966) characterized these forests as having a marked dry season at which time some of the trees become leafless. However, some rain apparently falls throughout the year (Duellman, 1963). Stuart (1958) considered the forests of El Petén, Guatemala, as representing a transition from the wet forests of the south and the dry forests of the outer Yucatán Peninsula to the north. *Bothrops nasuta* apparently adapts to the drier conditions of the quasi-rainforest by living in thick woods around marshy areas (Alvarez del Toro, 1973), in the vicinity of rivers where the forests are more mesic (Chamá, 12 km NW Chinajá, Panzós, Piedras Negras, and Sayaxché, Guatemala), under similar conditions around Lago Miramar, Chiapas, México, and in the high forests surrounding the *aguadas*

of the Petén region of Guatemala. From extreme eastern Guatemala southward throughout Central America, the range of *B. nasuta* is within the more humid tropical rainforest division of the evergreen forest (c.f. Duellman, 1966). This forest differs from the quasi-rainforest in that the habitat is at least moderately moist throughout the year even though rainy and dry seasons are evident. These moist conditions are enhanced by the tendency of the forest to develop a continuous treetop canopy which provides abundant shade creating the "greenhouse effect" discussed by Duellman (1966). The only known occurrence of *B. nasuta* outside the evergreen forest is in the scrub forest (c.f. Duellman, 1966) of the Sula Plain near San Pedro Sula, Honduras. However, we believe these specimens came from gallery forest associated with the rivers of the region.

In several places in Costa Rica and Panamá, *Bothrops nasuta* crosses the Continental Divide onto the Pacific versant. The species has been collected on both sides of the divide in the Tilarán area of Guanacaste Province, Costa Rica. Along the Tilarán transect studied by heyer (1967), the range of *B. nasuta* is apparently continuous across the low divide (850 m) onto the Pacific versant, where the species has been collected approximately 4 km west of the divide. One

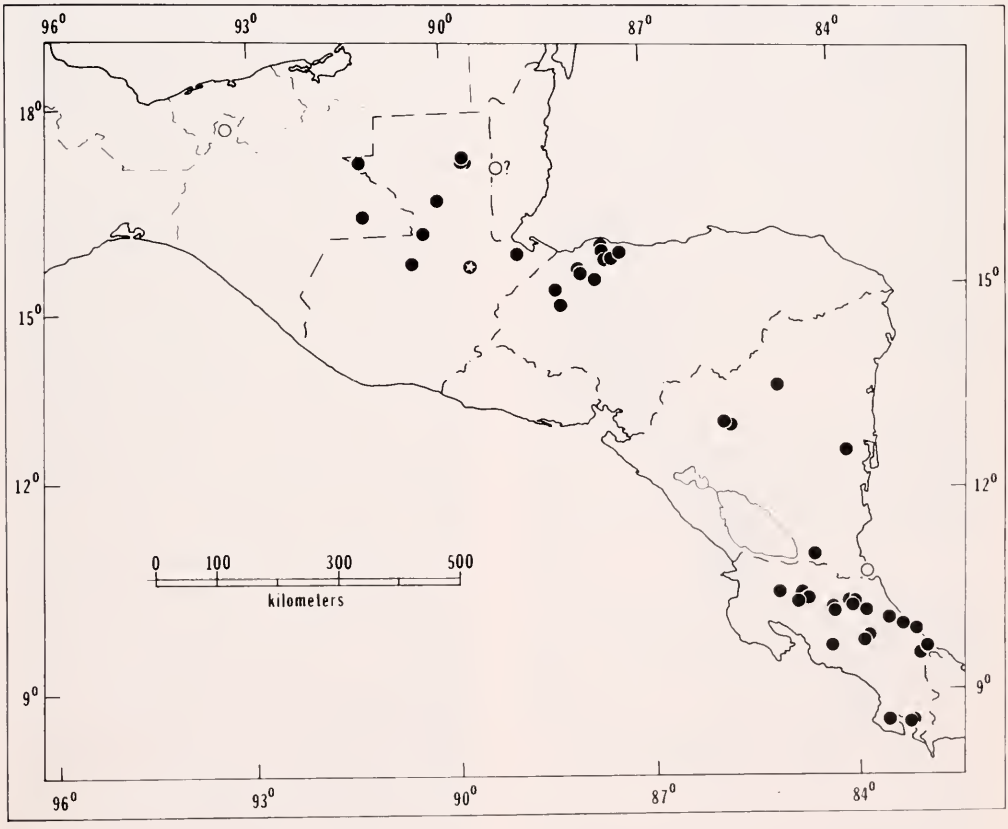

Figure 1. Distribution of *Bothrops nasuta* in Central America. Solid symbols represent localities of specimens examined. Hollow circles represent literature records (see section on distribution and ecology for discussion of questioned locality in Belize). The type locality is indicated by a star within a circle.

specimen (UCR 110) was collected on the Pacific versant at Puriscal (=Santiago), San José Province, Costa Rica. This specimen represents a relict population. An isolated population also occurs on the Pacific lowlands of the Golfo Dulce area of Costa Rica and probably adjacent Panamá. Savage (1966) and Savage and Vial (1974) discussed the factors creating the isolation of the vegetation of this region. However, the herpetofauna of the Golfo Dulce area resembles that of the Caribbean lowlands of Costa Rica and Panamá (Duellman, 1966; Savage, 1966; Savage and Vial, 1974). In Panamá, *B. nasuta* has been collected on the Pacific versant close to the Continental Divide in El Valle de Antón, Coclé Province. Dunn (1933), in a discussion of the El Valle area, stated that "Atlantic side conditions and fauna come a little way over the divide onto the Pacific versant." Two specimens collected by Herbert Clark (MCZ 37115-16) are recorded from Panama City, Panamá. Panama City is located in a savanna habitat (c.f. Duellman, 1966). These two specimens probably came from farther north in the mesic forests of the Canal Zone area where Clark obtained 13 other specimens. No specimens are available from Panamá east of the Canal Zone area, but it undoubtedly occurs in the Caribbean mesic forests of eastern Panamá.

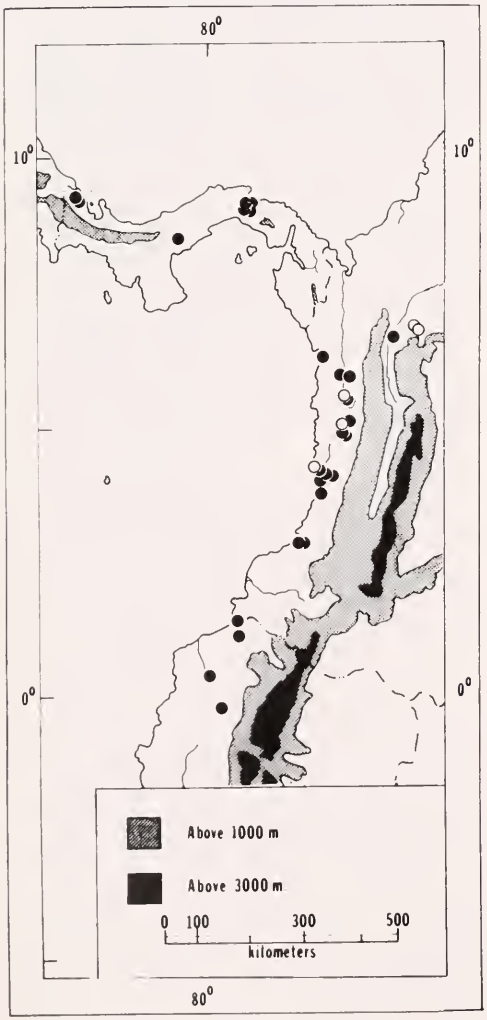

Figure 2. Distribution of *Bothrops nasuta* in Pananá, Colombia, and Ecuador. For explanation of symbols see Figure 1.

In South America *Bothrops nasuta* inhabits the lowland rainforests of Colombia west of the Andes southward to midwestern Ecuador. Dunn (1940), Duellman (1966), and Savage (1966) discussed the "crossover effect" occurring in the eastern Panamá-northwestern Colombia region, where the Caribbean mesic forms of lower Central America cross onto the wet Pacific lowlands of Colombia. However, the Pacific lowlands consist of a very narrow strip in northwestern Colombia. The lowland rainforests east of the Andes in the central portion of the department of Chocó and the adjacent western part of the department of Antioquia, Colombia, which are also inhabited by *B. nasuta*, are drained by the Río Atrato and its tributaries, which then flow northward into the Caribbean Sea. It is not until the Río San Juan drainage of southern Chocó is reached that *B. nasuta* becomes essentially a Pacific coastal plain animal, which it then remains to the terminus of its range in midwestern Ecuador. *Bothrops nasuta* also inhabits the low-

land rainforests of the rios Cauca and Porce in the department of Antioquia, Colombia. As with the Río Atrato, these latter two rivers flow northward into the Caribbean. The forests along the eastern edge of the Andes and on the Pacific coastal plain of Colombia are one of the most humid areas of the world and certainly the most humid of all of South America (Eidt, 1968; Haffer, 1970). The rains in the Quibdó area, Chocó, Colombia, fall year around (Haffer, 1970). Eidt (1968), in describing central Chocó, Colombia, stated that "only for a few days each year, usually when winds from the north disturb the general calm of the region, are there brief respites from the near constant rains." Myers et al. (1978) discussed the habitat at Quebrada Guanguí, Depto. Cauca, Colombia, where they collected a series of *B. nasuta* (AMNH 109794-811).

Bothrops nasuta occurs from near sea level to about 900 m in elevation, but is generally found below the 600 m contour. Of 112 specimens with elevational data, 49 (43.8%) were from below 200 n and 107 (95.5%) were from below 625 m The highest elevation datum available i 900 m for two specimens (UMMZ 116523, 117735) from near Matagalpa Nicaragua. Dunn (1944) gave an eleva tion of 1885 m for *B. nasuta* based on a record for Urrao, Antioquia, Colombia (Nicéforo María, 1938, 1942). We doubt that the specimen actually came from this elevation. Nicéforo Maria (1938) stated "que le fueron remitidos de. . .." This literally means "received from," which we interpret to mean "shipped from." We also question two other Nicéforo María (1938, 1942) records; Pueblo Rico, Depto. Caldas and Medellín, Depto. Antioquia. The elevations of these last two places are 1500 and 1538 m, respectively (Medem, 1965). Of 24 Colombian specimens with elevational data, all were from 200 m or below.

Bothrops nasuta is both terrestrial and nocturnal, although specimens can be found sunning themselves by day (Smith, 1943; pers. observ.). The species can also be found on low bushes or shrubs (E. H. Taylor, 1954; Medem, 1968). Posada-Arango (1889b) mistakenly believed that *B. nasuta* is arboreal, as did Amaral (1927b), when he said that *B. brachystoma* (=*B. nasuta*) "is a tree viper." Specimens have been found inside cavities in the trunks of trees, underneath roots of trees or rocks, on top of piles of rubbish (Alvarez del Toro, 1973), under rotting logs (Stuart, 1958), inside huts (Stuart, 1948), among loose rocks of ruins, (Smith, 1943), or simply on the forest floor (Duellman, 1963). We have collected *B. nasuta* under and lying near logs in the Turrialba area of Costa Rica.

Picado (1931a) reported that newborn *Bothrops nasuta* will eat earthworms and later will consume small lizards of the genus *Anolis*. Amaral (1927b) stated that the species feeds on lizards and Alvarez del Toro (1973) indicated that it feeds on anoles and mice. Picado (1931a) reported an instance of cannibalism involving juveniles. We have observed cannibalism among adults and juveniles in captivity. We have also observed them to eat leopard frogs (*Rana* sp.), anoles (*Anolis* sp.), and mice in captivity.

Bothrops nasuta has been reported to have 8 to 18 young (Picado, 1931a). A specimen in our collection (now LSUMZ 36898) from near Turrialba, Costa Rica, gave birth to 14 young in September, 1967.

Bites from *B. nasuta* are known to cause fatalities in human beings (Daniel, 1949), although Minton and Minton (1969) did not believe they are capable of doing so.

ANALYSIS OF VARIATION

Twenty-six characters were analyzed for geographic, sexual, ontogenetic, and individual variation. These characters are discussed below.

Internasals. - Typically, *Bothrops*

nasuta has the internasal scales in medial contact or separated by only one scale. One specimen (FMNH 68056), however, has the internasals separated by two scales. This specimen also has one shortened and one elongate internasal scale. Two specimens (LACM 45413, 45416) from Colombia do not have the internasal scales as elevated as do other *B. nasuta*, but are typical in all other respects.

The frequency of medial contact of the internasals varies geographically. All of the specimens of *B. nasuta* from México southward to Nicaragua have their internasals in mutual contact. Three specimens from Costa Rica and one from adjacent northwestern Panamá have their internasal scales separated by one scale, but two of these specimens are from the Península de Osa. The frequency of the mutual internasal contact is reduced in specimens from central Panamá southward to Ecuador (Table 1). In addition, specimens from central Panamá and Ecuador have the internasals in contact less frequently than do specimens from Colombia. In all of the specimens but one, which is a juvenile, from the Península de Osa, the internasals are less elevated and the snout is more attenuate.

Nasofrontals. - The numbers of nasofrontal scales in male *B. nasuta* average slightly lower than in females (Table 2) but the differences are not statistically significant.

Specimens from central Panamá exhibit a high average number of nasofrontal scales relative to other areas of the range (47.21 ± 2.63 as opposed to 37.79 ± 0.89).

Intercanthals. - Males average fewer intercanthals than do females (Table 3), except in central Panamá, but the latter differences will probably be reversed with study of additional material.

Central and western Panamanian specimens have a higher average number of intercanthals than do specimens from the remainder of the range (5.48 ± 0.36 vs. 4.92 ± 0.10).

Interoculars. - The average number of interoculars is higher in females than in males in the entire sample but the differences are not statistically significant (Table 3). However, specimens from the northern portion of the range (western Panamá northward), excepting the Península de Osa, show no statistically significant average difference between the sexes, whereas those from that point southward do (Table 3).

Interictals. - Generally, males have fewer interictals than do females but the differences are not statistically significant (Table 3).

Rostral. - Two specimens (AMNH 10981, UMMZ 91078) have the rostral scale horizontally divided. All other specimens have a single rostral scale.

Nasorostral. - A nasorostral scale is occasionally present in specimens from disparate parts of the range. The incidence of females possessing this scale appears to be greater than that of the males, inasmuch as ten of the twelve specimens having 1 or 2 nasorostrals are females.

Nasal. - All specimens of *B. nasuta* examined have a partially divided nasal scale, except for two, which have the scale completely divided. The usual condition is that of a partial crease at the upper and lower sections of the scale but a few specimens exhibit a complete division of this scale above or below the naris.

Prefoveals. - One specimen (UMMZ 117735) has the prefoveal scales extending to the rostral scale thus excluding the nasal scale from contact with the first supralabial.

Females have more prefoveals on the average than do males throughout the range (Table 4).

Subfoveals. - With respect to the sample as a whole, males have significantly fewer subfoveals than do females (Table 4).

Preoculars. - There are generally an upper, middle, and a lower preocular

Table 1. Variation in internasals, body blotches, and sex ratios in Bothrops nasuta (parenthetical numbers in first and last columns indicate sample size; middle columns indicate range, mean, confidence limits, and sample size, where applicable)

	Internasals	Body blotches		Sex ratios
	% in contact	Males	Females	% of females
México	100(2)	-	17	100(2)
Guatemala	100(13)	18-22(19.29±1.16)7	15-17(15.75±0.74)8	61.1(18)
Honduras	100(16)	17-20(18.50±19.06)2	15-18(15.88±0.94)8	81.3(16)
Nicaragua	100(7)	17-19(17.67±2.88)3	16	57.1(7)
Costa Rica	98.9(95)	16-22(18.36±0.63)25	15-20(17.22±0.48)36	60.0(95)
Western Panamá	90.0(10)	19-22(20.00±4.30)3	16-19(18.20±1.04)5	70.0(10)
(Northern Population)	98.6(148)	16-22(18.60±0.49)40	15-20(16.90±0.33)60	63.5(148)
(Osa Population)	71.4(7)	18-20(19.0±12.71)2	15-19(16.67±5.18)3	57.1(7)
Central Panamá	22.2(18)	19-23(19.00±4.68)4	16-19(17.77±0.70)13	78.9(19)
Colombia	66.7(57)	15-23(19.31±0.77)26	15-22(18.61±0.66)25	52.6(57)
Ecuador	22.2(9)	17-20(19.00±1.52)5	17-18(17.75±0.80)4	44.4(9)
(Southern Population)	52.4(84)	15-23(19.23±0.66)35	15-22(18.26±0.45)42	57.6(85)
Totals	81.6(239)	15-23(18.90±0.39)77	15-22(17.44±0.29)105	61.3(240)

(95.0% of the specimens examined). The contact of the preoculars with the orbit is inconsistent, expecially since there is often a fleshy rim of tissue interposed between the preoculars and the orbit. Individual specimens exhibit different preocular arrangements on either side of the head. There are occasional specimens that do not have a middle preocular. This condition usually occurs when the upper and lower preoculars are enlarged and in contact with each other, thus excluding the middle one from orbital contact. In one specimen (MCZ 55069) an enlarged supralacunal takes the place of the middle preocular.

Suboculars and Postoculars. - The subocular and postocular scales vary in number (see description). In many specimens counts varied widely from one side of the head to the other. Specimens had as few suboculars as one or as many as four and postoculars range from two to four on either side of the head of the same animal.

Oculabials. - The usual number of oculabials present in *B. nasuta* is two (88.8% of specimens examined).

Male *B. nasuta* from the entire range have significantly fewer oculabial scales than do females (Table 5).

The number of specimens in which the

Table 2. Variation in ventrals, subcaudals, and nasofrontals in Bothrops nasuta (parenthetical numbers indicate range, mean, confidence limits, and sample size, where applicable)

	Ventrals		Subcaudals		Nasofrontals	
	Males	Females	Males	Females	Males	Females
México	-	138	-	29-30(29.50±6.35)2	-	28-32(30.00±25.41)2
Guatemala	138-141(139.14±0.99)7	140-145(142.27±1.09)11	34-38(35.57±1.17)7	28-32(29.64±0.16)11	26-39(31.14±3.80)7	29-43(37.18±3.59)11
Honduras	135-139(137.33±5.17)3	135-142(139.67±1.47)12	33-35(34.33±2.88)3	26-30(27.91±0.70)11	26-46(36.00±127.06)2	29-48(34.92±3.52)12
Nicaragua	139-142(140.33±3.80)3	136-140(138.50±2.76)4	28-33(30.50±31.77)2	27-29(28.00±1.84)4	33-35(33.67±2.87)3	32-46(38.50±9.23)4
Costa Rica	129-143(136.37±0.84)38	128-144(137.35±0.42)57	27-41(32.67±0.72)36	24-35(28.46±0.18)54	22-43(33.53±1.69)38	25-54(35.05±1.54)56
Western Panama	133-138(136.00±6.60)3	129-139(135.29±3.65)7	34-36(35.00±2.48)3	25-31(27.86±1.63)7	39-42(41.00±4.30)3	33-46(40.86±4.61)7
(Northern Population)	129-143(136.98±0.71)54	128-145(138.14±0.55)92	27-41(33.22±0.65)51	24-35(28.49±0.46)89	22-46(33.77±1.48)53	25-54(35.78±1.20)92
(Osa Population)	136-137(136.67±1.43)3	136-139(137.25±2.39)4	33(33.00±0)2	25-27(26.25±1.52)4	20-34(28.33±12.95)3	33-40(36.25±4.75)4
Central Panamá	129-131(130.25±1.52)4	130-139(134.47±1.34)13	30-34(31.00±3.18)4	26-32(28.86±0.96)14	38-53(48.18±10.43)4	39-59(46.90±2.93)15
Colombia	123-141(130.54±1.37)26	127-143(132.83±1.31)29	28-35(32.00±0.60)27	24-31(28.07±0.59)30	25-56(39.22±3.37)27	29-58(41.43±2.56)30
Ecuador	127-137(131.00±4.65)5	132-136(133.50±3.05)4	31-35(33.00±1.96)5	28-29(28.50±0.92)4	32-44(39.20±5.72)5	31-45(40.25±10.18)4
(Southern Population)	123-141(130.57±1.10)35	127-143(133.35±0.92)46	28-35(32.03±0.55)36	24-32(28.33±0.45)48	25-56(40.14±2.77)36	29-59(42.84±1.92)49
Totals	123-143(134.53±0.28)92	127-145(136.56±0.58)142	27-41(32.73±0.44)89	24-35(28.38±0.33)141	20-56(36.09±1.54)92	25-59(38.17±1.12)145

Table 3. Variation in intercanthals, interoculars, and interictals in Bothrops nasuta (explanations as for Table 2)

	Intercanthals		Interoculars		Interictals	
	Males	Females	Males	Females	Males	Females
México	-	5(5.00±0)2	-	4-6(5.00±12.71)2	-	25-27(26.00±12.71)2
Guatemala	4-5(4.43±0.47)7	5-6(5.09±0.20)11	5-6(5.29±0.45)7	3-6(4.55±0.63)11	23-26(24.86±0.83)7	23-26(25.09±0.70)11
Honduras	4-5(4.33±1.40)3	4-6(4.92±0.46)13	3-5(4.33±2.87)3	3-7(4.31±0.71)13	25-27(25.67±2.87)3	23-27(24.85±0.73)13
Nicaragua	5(5.00±0)3	5-6(5.50±0.92)4	5(5.00±0)3	5-7(6.00±1.30)4	23-25(24.00±2.48)3	24-27(25.50±2.05)4
Costa Rica	3-6(4.53±0.23)38	4-7(4.89±0.15)57	4-7(5.21±0.26)38	3-7(5.35±0.20)57	19-27(24.00±0.53)38	19-28(24.51±0.41)57
Western Panamá	4-6(5.00±2.48)3	5-7(5.71±0.88)7	5-7(6.33±2.87)3	5-7(5.86±0.34)7	23-24(23.33±1.43)3	22-26(24.29±1.16)7
(Northern Population)	3-6(4.56±0.18)54	4-7(5.01±0.13)94	3-7(5.22±0.23)54	3-7(5.17±0.20)94	19-27(24.17±0.41)54	19-28(24.68±0.29)94
(Osa Population)	3-5(4.00±2.48)3	4-6(4.75±1.52)4	4-5(4.67±1.43)3	5-7(6.00±1.30)4	25(25.00±0)3	25-27(26.25±1.52)4
Central Panamá	5-7(5.75±1.52)4	3-7(5.40±0.55)15	4-5(4.75±0.80)4	5-7(5.47±0.35)15	22-25(23.75±2.00)4	22-25(24.33±0.50)15
Colombia	4-7(5.11±0.32)27	4-7(5.47±0.32)30	3-7(4.70±0.42)27	4-7(5.30±0.28)30	22-26(24.04±0.46)26	22-27(24.87±0.42)30
Ecuador	4.5(4.60±0.68)5	5-6(5.25±0.80)4	5(5.00±0)5	6-7(6.50±0.92)4	24-27(25.60±1.41)5	24-26(25.50±1.59)4
(Southern Population)	4-7(5.11±0.28)36	3-7(5.43±0.25)49	3-7(4.75±0.32)36	4-7(5.45±0.22)49	22-27(24.23±0.43)35	22-27(24.76±0.31)49
Totals	3-7(4.75±0.16)93	3-7(5.14±0.12)147	3-7(5.02±0.18)93	3-7(5.29±0.18)147	19-27(24.22±0.29)92	19-28(24.75±0.22)147

Table 4. Variation in prefoveals, subfoveals, and postcanthals in Bothrops nasuta (explanations as for Table 2).

	Prefoveals		Subfoveals		Postcanthals	
	Males	Females	Males	Females	Males	Females
Mexico	-	3-6(5.00±2.25)2	-	2-3(2.75±0.80)2	-	1(1.00±0)2
Guatemala	3-4(3.14±0.21)7	4-8(5.73±0.46)11	1-3(2.00±0.23)7	2-4(2.36±0.26)11	1(1.00±0)7	1-2(1.18±0.26)11
Honduras	3-8(4.80±2.39)3	4-9(6.00±0.50)13	2-3(2.40±0.68)3	2-5(2.62±0.29)13	1(1.00±0)3	1-2(1.08±0.55)13
Nicaragua	4-8(6.17±1.40)3	5-11(8.13±1.92)4	1-2(1.67±0.54)3	2-7(3.38±1.48)4	1-2(1.17±0.43)3	1-2(1.38±0.43)4
Costa Rica	2-9(4.62±0.35)37	3-12(6.11±0.28)57	1-4(2.09±0.14)37	1-5(2.42±0.14)57	1-2(1.14±0.08)37	1-2(1.61±0.09)57
Western Panama	5-7(6.17±0.79)3	4-10(6.64±1.00)7	2-3(2.33±0.54)3	2-4(2.29±0.35)7	1(1.00±0)3	1-2(1.79±0.25)7
(Northern Population)	2-9(4.61±0.30)53	3-12(6.15±0.22)94	1-4(2.09±0.11)53	1-7(2.48±0.11)94	1-2(1.10±0.06)53	1-2(1.47±0.07)94
(Osa Population)	3-8(4.67±0.96)3	3-7(5.00±1.09)4	1-3(2.00±0.66)3	2-3(2.13±0.37)4	1(1.00±0)3	1-2(1.25±0.39)4
Central Panama	5-8(6.13±1.13)4	3-11(6.23±0.78)15	1-3(2.13±0.54)4	1-3(1.97±0.11)15	1-2(1.50±0.45)4	1-2(1.43±0.19)15
Colombia	3-9(4.96±0.42)27	3-11(6.27±0.45)30	1-3(2.09±0.13)27	1-5(2.38±0.17)30	1-2(1.07±0.07)27	1-2(1.30±0.12)30
Ecuador	3-5(3.90±0.53)5	5-8(6.50±0.89)4	1-3(2.00±0.48)5	1-3(1.88±0.54)4	1-2(1.20±0.37)5	1-2(1.25±0.16)4
(Southern Population)	3-9(4.94±0.36)36	3-11(6.28±0.36)49	1-3(2.08±0.12)36	1-5(2.21±0.14)49	1-2(1.14±0.08)36	1-2(1.34±0.10)49
Totals	2-9(4.74±0.22)92	3-12(6.16±0.19)147	1-4(2.08±0.08)92	1-7(2.38±0.09)147	1-2(1.11±0.05)92	1-2(1.42±0.06)147

Table 5. Variation in supralabials, infralabials, and oculabials in Bothrops nasuta (explanations as for Table 2).

	Supralabials		Infralabials		Oculabials	
	Males	Females	Males	Females	Males	Females
Mexico	-	10-11(10.25±0.80)2	-	12-13(12.25±0.80)2	-	2(2.00±0)2
Guatemala	9-10(9.21±0.25)7	9-10(9.64±0.22)11	10-12(11.21±0.33)7	11-13(11.77±0.28)11	2(2.00±0)7	2(2.00±0)11
Honduras	9-10(9.33±0.54)3	9-11(9.92±0.30)13	10-12(11.00±0.94)3	10-13(11.92±0.28)13	1-2(1.60±0.68)3	1-2(1.92±0.11)13
Nicaragua	9(9.00±0)3	9-10(9.75±0.39)4	11-12(11.50±0.57)3	12-13(12.25±0.39)4	1-2(1.83±0.27)3	2(2.00±0)4
Costa Rica	9-10(9.22±0.10)38	8-11(9.56±0.01)57	10-12(11.04±0.16)38	10-13(11.76±0.12)57	1-3(1.89±0.08)37	2-3(2.04±0.04)57
Western Panama	9-10(9.17±0.43)3	9-10(9.46±0.31)7	10-11(10.33±0.54)3	10-12(10.86±0.50)7	2(2.00±0)3	2(2.00±0)7
(Northern Population)	9-10(9.20±0.08)54	8-11(9.64±0.09)94	10-12(11.05±0.14)54	10-13(11.75±0.10)94	1-3(1.90±0.07)53	1-3(2.02±0.03)94
(Osa Population)	8-10(9.00±0.66)3	9-11(10.00±0.45)4	10-12(10.67±0.86)3	11-13(12.00±0.45)4	2(2.00±0)3	2-3(2.25±0.48)4
Central Panamá	9-10(9.13±0.30)4	8-10(9.57±0.21)15	10-13(11.38±0.89)4	10-12(11.60±0.21)15	1-3(2.00±0.45)4	1-2(1.97±0.07)15
Colombia	8-11(9.15±0.12)27	9-10(9.52±0.13)30	10-12(10.65±0.16)27	10-13(11.73±0.18)30	1-3(1.94±0.13)27	1-4(2.20±0.13)30
Ecuador	9-10(9.10±0.23)5	9-10(9.25±0.39)4	9-11(10.30±0.48)5	11-12(11.63±0.43)4	2(2.00±0)5	2-3(2.38±0.43)4
(Southern Population)	8-11(9.14±0.10)36	8-10(9.51±0.10)49	9-13(10.68±0.17)36	10-13(11.68±0.13)49	1-3(1.96±0.11)36	1-4(2.14±0.09)49
Totals	8-11(9.18±0.06)93	8-11(9.60±0.07)147	9-13(10.89±0.11)93	10-13(11.73±0.08)147	1-3(1.92±0.06)92	1-4(2.06±0.04)147

oculabials are more than two is greater in Colombian and Ecuadorian specimens (21.2%) than in the remainder of the range (4.1%).

Supralabials and Infralabials. - The numbers of supralabials and infralabials average more in females than in males over the entire range (Table 5). All but one specimen (UMMZ 91078) have the first infralabials in contact.

Ventrals. - The number of ventral scales is slightly, but significantly higher in females than in males (Table 2) considering the range as a whole. A relatively high number of ventral scales is present in specimens of *B. nasuta* from western Panamá northward to México (129-145, $\bar{x} = 137.68 \pm 0.42$). A relatively low number exists in specimens from central Panamá southward to Ecuador (123-143, $\bar{x} = 132.15 \pm 2.58$).

Subcaudals. - As is usual in snakes, the subcaudals are more numerous in males than in females (Table 2), correlating with their greater relative tail length (Table 7).

Dorsal Scale Rows. - The dorsal scale rows usually number 25-23-19 (see description). Specimens from the Península de Osa are unusual, however, in possessing atypically high dorsal scale row counts (Table 6). Only one of the seven specimens available from there has the above-mentioned count. Two specimens have 25-25-19 rows, three have 27-25-19 rows, and a sixth has 29-27-19 rows. The latter specimen has the highest neck and midbody counts of any specimen examined.

Canthals. - All of the specimens that possess more than one canthal are from central Panama. Of 19 specimens from this area, 7 have two canthals on at least one side of the head; three specimens have two on both sides of the head.

Postcanthals. - Females show a higher incidence of two postcanthals (instead of one) than do males throughout the range (Table 4), with the exception of the sample from central Panamá. Viewed over the entire range, the differences are significant.

Color and Pattern. - Various aspects of color and pattern in *B. nasuta* vary individually, ontogenetically, sexually, and geographically.

There is considerable intrapopulational variation with some individuals being brightly marked on the head and body, whereas others are almost unicolor (see description).

The only series of specimens from a single locality from which adequate notes on ontogenetic color variation could be taken consists of twenty specimens from the Río Patia in southern Colombia (AMNH 107912-13, 109794-811). The juvenile specimens are noticeably brighter in color and more distinct in pattern than are the adults. In larger specimens the brownish gray ground color is basically the same but the brownish black to black dorsal blotches are faded and the whitish border of these blotches is indistinct. The fading of the pattern begins on the lateral portion of the dorsum and proceeds dorsad. The vertebral pale line is bright in the young and gradually fades in larger specimens, particularly females, until, in some specimens the line disappears altogether. In juveniles the dorsal blotches are discrete and well-defined, except for the first two or three blotches, which are reduced to small spots. As the animals increase in size, the blotches gradually fragment into two portions, which are laterally displaced from the middorsal line. This fragmentation and lateral displacement of the dorsal blotches proceeds from anterior to posterior.

Males generally possess a more contrasting facial and dorsal coloration than do females, although occasional dark male specimens are also seen. Males average more body blotches than do females and the values for the entire sample are significantly different (Table 1).

A living specimen from Ecuador in the senior author's private collection exhibits a peculiar temporary coloration prior to ecdysis. The animal is grayish

Table 6. Variation in dorsal scale rows in Bothrops nasuta (explanations as for Table 2).

	Males	Females
México	-	25(25.00±0)2
	-	23(23.00±0)2
	-	19(19.00±0)2
Guatemala	25(25.00±0)7	25-27(25.19±0.41)11
	23(23.00±0)7	23(23.00±0)11
	19-20(19.15±0.35)7	19(19.00±0)11
Honduras	25(25.00±0)2	25-27(25.36±0.49)12
	23(23.00±0)2	23-25(23.18±0.37)12
	19(19.00±0)2	19(19.00±0)12
Nicaragua	25(25.00±0)3	25(25.00±0)4
	23(23.00±0)3	23(23.00±0)4
	19(19.00±0)3	19(19.00±0)4
Costa Rica	23-27(24.92±0.52)39	23-27(25.08±0.14)57
	21-23(22.81±0.20)39	21-25(22.99±0.11)57
	19-20(19.03±0.32)39	17-21(19.01±0.10)57
Western Panamá	25(25.00±0)3	23-25(24.69±0.86)6
	23(23.00±0)3	23(23.00±0)7
	19(19.00±0)3	19(19.00±0)7
(Northern Population)	23-27(24.93±0.18)54	23-27(25.09±0.12)92
	21-23(22.85±0.14)54	21-25(23.02±0.08)93
	19-20(19.04±0.05)54	17-21(19.00±0.06)93
(Osa Population)	25-27(25.70±2.87)3	25-29(27.07±2.60)4
	23-25(24.37±2.87)3	25-27(25.53±1.60)4
	19(19.00±0)3	19(19.00±0)4
Central Panamá	23-25(24.53±1.60)4	23-25(24.75±0.39)15
	22-23(22.68±1.43)3	23(23.00±0)15
	19(19.00±0)4	19(19.00±0)15
Colombia	25(25.00±0)27	23-27(25.44±0.36)30
	23(23.00±0)27	23-25(23.22±0.11)30
	19(19.00±0)27	19-21(19.12±0.56)30
Ecuador	23-25(24.63±1.11)5	25-27(25.53±1.59)4
	21-23(22.63±1.11)5	23(23.00±0)4
	19(19.00±0)5	19-20(19.26±0.80)4
(Southern Population)	23-25(24.89±0.02)36	23-27(25.20±0.27)49
	21-23(22.91±0.13)35	23-25(23.13±0.14)49
	19(19.00±0)36	19-21(19.09±0.13)49
Totals	**23-27(24.94±0.13)93**	23-29(25.18±0.13)145
	21-25(22.92±0.12)92	21-27(23.12±0.10)146
	19-20(19.02±0.13)93	17-21(19.03±0.06)146

brown dorsally and powder gray ventrally. During the premolt period the ventrals and the first dorsal scale row and the ventral half of the second row turn a bright silver, contrasting markedly with the color of the remainder of the dorsum (Fig. 3).

Size and Proportions. - The average dimensions in head length, head width, head height, total length, and body length are greater in females than in males (Table 7; Fig. 4). Males possess a greater average relative tail length (Table 7), correlated with the higher average number of subcaudals (Table 2). Female specimens appear to be stouter than do males, but this feature is difficult to quantify because of variation caused by preservation.

Sex Ratios. - We sexed 240 specimens of *Bothrops nasuta*. A prevalence of females is present in collections from México southward through central Panamá (64.9% females vs. 35.1% males). The sex ratios in samples from Colombia and Ecuador are more evenly balanced (51.5% females vs. 48.5% males) (Table 1). Considering the number of specimens involved, it seems unlikely that these differences result simply from artifacts of collecting. The reasons for the greater percentage of females in samples from Panamá northward, however, remain obscure.

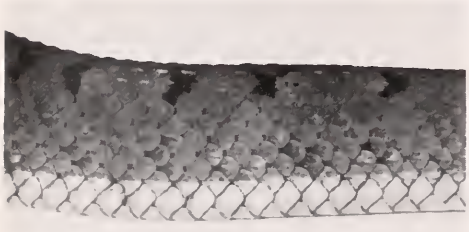

Figure 3. Section of body of a female *Bothrops nasuta* from Ecuador illustrating the marked contrast between the lower ventral color and that of the dorsum that is exhibited prior to ecdysis.

Figure 4. Adult male (lower) and female (upper) *Bothrops nasuta* from northern Honduras illustrating sexual dimorphism in size and the typical color pattern of members of the northern population.

DISCUSSION

On the basis of the foregoing analysis, the following characteristics have been shown to exhibit geographic variation in *Bothrops nasuta*: internasals; nasofrontals; intercanthals; interoculars; oculabials; ventrals; dorsal scale rows; canthals; color and pattern; sex ratios.

These characteristics show differing patterns of variation. The frequency of mutual internasal contact decreases markedly between samples from western and central Panamá. Ventral numbers are highest in the northern section of the range (western Panamá northward) and lowest in the southern section (central Panamá southward). Average numbers of interoculars are not significantly different between the sexes in samples from western Panamá northward, whereas the differenes are significant from that point southward. Central Panamanian specimens are distinctive in having a higher average number of nasofrontals, as well as being the only specimens possessing more than one canthal scale. Panamanian specimens have a higher average number of intercanthals than do specimens from the rest of the range. The preponderance of female specimens from the northern portion of the range south to and including central Panamá is

Table 7. Sexually dimorphic characters of size and proportions in *Bothrops nasuta* (measurements in millimeters - parenthetical numbers indicate range, mean, and sample size).

	Males	Females
Head length	11-24(17.0)93	12-37(22.6)147
Head width	7-15(11.3)93	8-28(14.9)147
Head height	4-10(6.6)93	4.14(8.6)147
Total length	162-463(291.1)88	156-635(349.0)139
Tail length	20-62(36.2)88	16-64(35.7)139
Body length	142-401(254.9)92	140-571(313.4)142
Tail/total length ratio	0.103-0.137(0.124)88	0.092-0.122(0.103)139

in marked contrast to the more even sex ratio in samples from Colombia and Ecuador. Specimens from Colombia and Ecuador have higher average numbers of oculabials than do specimens from the remainder of the range. The Península de Osa specimens are distinctive due to: (1) a higher number of dorsal scale rows on the neck and at midbody; (2) the juvenile tail color persisting into adulthood; (3) the shape and degree of elevation of the internasal scales, and (4) a distinctive dorsal body coloration.

Obviously, the most distinctive specimens are those occurring in the Península de Osa. Due to the small number of specimens available from this area, however, it remains an area in need of critical study. Other, less distinctive geographical groupings may be circumscribed as well. The patterns of variation in the samples of populations of *B. nasuta* outside of the Península de Osa are such that no clear cut distinctions can be drawn (i.e., the patterns of variation are discordant). On the other hand, the pattern of variation in several characters (frequency of mutual internasal contact; number of ventrals; nasofrontals, canthals, and intercanthals; sexual differences in average numbers of interoculars; and sex ratios) is such that a number of changes in those patterns occur in Panamá, with the most obvious changes occuring between western and central Panamá. Specimens from central Panamá, therefore, in general resemble specimens from South America, whereas those from western Panamá resemble specimens to the north (excluding those from the Osa Peninsula).

On the above basis, therefore, we prefer to recognize three distinctive populations of the hognose viper, *Bothrops nasuta*: the northern, Osa, and southern populations. Inasmuch as these populations do not exhibit equivalent levels of divergence, we do not recognize infraspecific taxa. We feel that to do so would tend to obscure the complex relationships we have detailed above. The populations are characterized below.

The Northern Population. - This population extends from southern México southward to the Boca de Almirante area of western Panamá, with the exception of the Península de Osa-Golfito area of southern Costa Rica. This population is characterized by having a greater incidence in the mutual contact of the internasal scales (98.6% of the specimens examined), a higher average number of ventral scales (males, 129-143, $\bar{x}$=136.98; females, 128-145, $\bar{x}$=138.14), a lower average number of nasofrontal scales (males, 22-46, $\bar{x}$=33.77; females, 25-54, $\bar{x}$=35.78), and a lower mean number of oculabials (96.6% of specimens having two or fewer). Typical examples from this population are illustrated in Figure 4.

The Osa Population. - This population is confined to the Península de Osa-Golfito area of southern Costa Rica and possibly adjacent western Panamá. This population is characterized by having a higher mean number of dorsal scale rows at the neck and midbody, the tendency of juvenile tail color to persist into adulthood (especially on the underside of the tail), a lesser degree of eleva-

tion of the anterior portion of the internasal scales, and a tendency for possession of transverse body bands (Fig. 5), as opposed to alternating blotches or spots.

The Southern Population. - This population occurs from Valle de Antón and the Canal Zone in central Panamá southward to Ecuador. This population is characterized by having a relatively low incidence of mutual contact of the internasal scales (52.4% of specimens examined), a lower average number of ventral scales (males, 123-141, $\bar{x}$=130.57; females, 127-143, $\bar{x}$=133.35), a higher average number of nasofrontal scales (males, 25-56, $\bar{x}$=40.14; females, 29-59, $\bar{x}$=42.84), and a higher mean number of oculabials (17.6% of specimens having three or more).

Biogeographic History. - Recently several authors have shown that alternating dry and humid climatic periods and sea level fluctuations occurring during the Pleistocene have had a marked effect on the evolution and distribution of Neotropical vertebrates (van der Hammen, 1961; Haffer, 1969; Vuilleumier, 1971; Duellman, 1979). In addition, several recent taxonomic studies on South American and Central American amphibians and reptiles have shown a close correlation between evolutionary events in the group in question and the paleogeographic events detailed in the above-cited papers (Vanzolini and Williams, 70; Duellmn, 1972; Heyer, 1973; Duellmn and Crump, 1974; Wilson and Mena 1980).

Figure 5. Adult female *Bothrops nasuta* (USCCRE 6391) from Rincón de Osa, Puntarenas Province, Costa Rica, illustrating the dorsal pattern of transverse bands.

Although the evolutionary relationships of the *Bothrops lansbergi* group, to which *B. nasuta* belongs, are imperfectly known, Burger (1971) expressed the opinion that the members of the *lansbergi* group, as well as those of the *godmani* and *nummifera* groups constitute a distinct genus, *Porthidium*. He stated that

"the *lansbergi* and *nummifera* groups diverged independently from the *godmani* group." In addition, he opined that "*Porthidium nasutum*, which is similar to *P. godmani* in some respects and specialized in others, is close to the ancestry of the *lansbergi* group." For these reasons we assume, for the present, that the point of origin of the species *B. nasuta* lies somewhere in Nuclear Central America and, most likely, southern México.

On the basis of information in the above-cited papers, we postulate the following sequence of events to account for the evolutionary history of *Bothrops nasuta*:

1. Movement of the *B. nasuta* stock from the north (probably southern México) into Central America during the upper Pliocene along the eastern humid corridor.
2. Movement of the stock of the Osa population into southern Pacific Costa Rica through low plateaus and/or narrow river canyons in the uplifting Talamanca range during the turn of the Pliocene-Pleistocene.
3. Isolation of the Osa population in the Península de Osa by rising sea levels during the interglacial periods of the Pleistocene.

4. Isolation of the northern and southern populations in wet forest refugia in Caribbean Central America and the Pacific side of Colombia, respectively, during a period of dry forest expansion in the Quaternary.

SPECIMENS EXAMINED

Locality data for each specimen examined are listed below. The data are arranged as follows: alphabetically by country, state (department or province), and locality; alphabetically by the first letter in the abbreviations for the museums, and numerically after each museum abbreviation. Specimens lacking precise locality data are listed in the first most restricted political unit possible. Localities enclosed by quotation marks are not mapped.

The localities and specimens are: COLOMBIA: "Boca de la Raspadura," AMNH 18298-300. *Antioquia*: "Medellín," AMNH 35735; Río Arquía, Belen, LACM 45413; Sabanalarga, Cauca Valley, AMNH 35795. *Cauca*: Quebrada Guanguí, 0.5 km above Río Patía, 100-200 m, AMNH 109794-811; Quebrada Guanguí, Río Patía, 100 m, AMNH 107912-13. *Chocó*: "no specific locality," AMNH 8067-68; Andagoya, MCZ 29255, USNM 124259, Andagoya-Condota area, UMNZ 121043-44; between Andagoya and Condota, UMMZ 121058; vic. Playa de Oro, upper Río San Juan, 200 m, AMNH 108460; Quebrada Taparal, 20 km N Palestina, CAS 119919; Río Atrato, S of Quibdó, USNM 140050; Río San Juan, USNM, 72352; Sierra de Baudó, ANSP 25573-78; trail between Quebrada Bochoramá and Río Tadocito, LACM 45416. *Valle*: Buenaventura, at Rockerfeller Lab, 12 m, TU 18712; km 13 from Buenaventura to Río Calima, 45 m, FMNH 165478, 165893; near Buenaventura on land of Cartón de Colón, TU 18711; Río Calima, Quebrada de la Brea, USNM 124260; Río Calima, 7 km from lumber camp, FMNH 165492, 165495, 165566, 165725-26, 165900; Rio Paposo, Virology Field Station, USNM 151711-12.

"COLOMBIA or ECUADOR": USNM 22422.

COSTA RICA: "Hospital San Juan de Dios," KU 34636; "Costa Rica,"UF 20627, 30709, UMMZ 133893, 133911. *Alajuela*: Cantón de San Carlos, Muelle San Carlos, 65 m, USC-CRE 2711; Cariblanco, UCR 1431; Cataratas de San Ramon, Lado San Carlos, USC-CRE 2754; Ciudad Quesada, 656 m, USC-CRE 2693; Ciudad Quesada, San Roque, 580 m, USC-CRE 2695; San Carlos, FMNH 191789, UMMZ 131327-29; Sarapiquí, 100m, UCR 109, 2990, USC-CRE 2691. *Cartago*: Pavones, nr. Turrialba, 819 m, KU 140087, LSUMZ 36898-99, USC-CRE 2710; Turrialba, 624 m, KU 30982-87, 34876, 34879-80, 35734-35, MCZ 55067-74, UCR 1870; Turrialba, IICA, 600-624 m, AMNH 69722, FMNH 179083, KU 25689, 34635, 34637-38, MCZ 56116, USC-CRE 646; Turrialba, 3 km from IICA on road to Pavones, 630 m, USC-CRE 190. *Guanacaste*: El Silencio de Tilarán, 825-850 m, USC-CRE 6217; 5 km ENE Tilarán, 600 m, KU 36693; Tilaran, 560-562 m, KU 35737-38, USC-CRE 2694, 2712, 7131, 7163. *Heredia*: "no specific locality," UF 30492, 30495, 30498, 31795-96; La Selva, central trail, 60 m, USC-CRE 8291. *Limon*: La Lola, 39 m, KU 34005, UMMZ 117736-37, USC-CRE 127 (2 spec.), 128 (3 spec.), 140 (2 spec.), 162, 203, 207, 655 (2 spec.); Limón, MCZ 19744; Los Diamantes, UMMZ 117738; nr. Penshurst, HSH/RSS 600; Penshurst, UCR 2721-22, 2738-39, 2940-41; Puerto Viejo, UCR 162; 4 km E Puerto Viejo, UCR 308; Suretka, nr. Mt. Mirador, KU 35736; Sipurio, Talamanca, AMNH 17332; Zent, MCZ 11457-58. *Puntarenas*: "no specific locality." UMMZ 83185; Golfito, 5 m, USC-CRE 836; 6.7 km E Golfito, LSUMZ 11652; Rincón de Osa, LACM 114153-54; vicinity of Rincon de Osa, 20-40 m, USC-CRE 6391; Rincon de Osa, Camino del Pacifico, UCR 3310, 3359. *San José*: Puriscal, UCR 110.

ECUADOR: *Esmeraldas*: Playa de Oro, Santiago River, USNM 20625-28; Quinindé, USNM 165317; Río Capapas, MCZ 11169. *Pichincha*: 18 km W Santo Domingo de los Colorados on Chono road, USNM 165320; 5 km W Santo Domingos de los Colorados, USNM 165321; 12 km NW Santo Domingo de los Colorados on Quinindé Road, USNM 165319. USNM 165319.

GUATEMALA: *Alta Verapaz*: Finca Chamá, UMMZ 91077-78. *El Petén*: 12 km NW Chinajá, 130 m, KU 55705; Piedras Negras, USNM 110415; Sayaxché, UCM 22367; Sojío (=Toocog), AMNH 69966-67, 69987; Tikal, 283 m, MCZ 55436-37, UF 13866, 13868-69, UMMZ 117944; 4.8 km S Tikal, KU 157665; 13.5 mi S Tikal, KU 157664; Valontun, 4 km SE Tikal, AMNH 100410. *Izabal*: 12.8 km SE Cayo Piedra, 153 m, ANSP 22149.

HONDURAS: *Atlántida:* Dakota, East Line, MCZ 20247; Jilamo, MCZ 34385; Lancetilla, AMNH 46958-60, MCZ 38781; Sonora Farm, Taujica District, MCZ 20493; Tela, AMNH 46961; Tela, Juliana Farm, MCZ 22023. *Cortés:* La Cumbre, nr. San Pedro Sula, MCZ 32028; San Pedro Sula, MCZ 33332-33. *Snata Barbara:* Santa Barbara, MCZ 27566; Trinidad, MCZ 27565. *Yoro:* Progreso, MCZ 22024, 26872-UMMZ 62522.

MÉXICO: *Chiapas:* Lake Miramar, USNM 136966-67. "Veracruz," ANSP 4873.

NICARAGUA: "vicinity of Poderoso," AMNH 12706. *Matagalpa:* "no specific locality," UMMZ 57654; Hacienda La Cumplida,

900m, UMMZ 117735; 19 km N Matagalpa, UMMZ 116523. *Río San Juan*: Los Sabalos, San Juan River, AMNH 28355. *Zelaya*: Eden Mine, AMNH 7411; Río Huahuashán, Papel Camp, AMNH 70247.

PANAMÁ: "Panama City," MCZ 37115-16. *Bocas del Toro*: Almirante, FMNH 83466, 153847, KU 80247, 112597; 11 km NW Almirante, FMNH 153849, 153851-52, 153999; 12 km NW Almirante, UU 5564. *Canal Zone*: Chico Limpio Divide, 470 m, MCZ 42767; Madden Dam, ANSP 23889; nr. Miramar River, 183 m, MCZ 42768; Pequeni-Esperanza Ridge, 214-610 m, MCZ 42772-81. *Coclé*: El Valle de Antón, 550 m, KU 112596; El Valle de Antón, Finca Acre, FMNH 68054-56. *Panamá*: nr. Boquerón, Candelaria, and Peluca Station, AMNH 68850.

LITERATURE RECORDS

BELIZE: Xuanantunich (Neill, 1965).

COLOMBIA: *Antioquia*: Segovia (Nicéforo María, 1942); "Urrao" (Nicéforo María, 1938, 1942); Zea District (Posada-Arango, 1889). *Caldas*: "Pueblo Rico" (Nicéforo María, 1938, 1942). *Chocó*: Cabeceras (Rendahl and Vestergren, 1941); Quibdó (Nicéforo María, 1942.

GUATEMALA: *Alta Verapaz*: Panzos (Bocourt, 1868).

MEXICO: *Chiapas*: Rancho Alejandría, Municipio de Juárez (Alvarez del Toro, 1973).

NICARAGUA: "Hacienda de Jericho [=Jerico], 991 m" (Gunther, 1895; Boulenger 1896); "Chontales" (Günther, 1895; Boulenger, 1896). *Río San Juan*: Greytown (Amaral, 1929a).

PANAMÁ: *Canal Zone*: "Cerro Bruja" (Amaral, 1929a; Schmidt, 1933; Dunn and Bailey, 1939).

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[2]Stated to have been from Progreso, Prov. Chiriqui, Panama by Loveridge (1928) and Amaral (1929a).

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SOME TREMATODES OF MAMMALS IN LOUISIANA

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ABSTRACT

The following trematodes were collected from mammals in southern Louisiana: Alaria mustelae Bosma, 1931 from the raccoon, *Procyon lotor* (Linn.); *Fibricola cratera* (Barker and Noll, 1915) Dubois, 1932 from raccoons, opossums (*Didelphis virginiana* Kerr), and a mink, *Mustela vison* Schreber; *F. lucida* (La Rue and Bosma, 1927) Dubois and Rausch, 1950 from a raccoon and a gray fox, *Urocyon cinereoargenteus* (Schreber); *Pharyngostomoides procyonis* Harkema, 1942 from the raccoon; *Heterobilharzia americana* Price, 1929 from raccoons and opossums; *Apophallus venustus* (Ransom, 1920) Cameron, 1936 from raccoons; *Parametorchis complexus* (Stiles and Hassal, 1894) Skrjabin, 1913 from raccoons; *Baschkirovitrema incrassatum* (Dies., 1850) Skrjabin, 1944 from an otter, *Lutra canadensis* (Schreber); *Brachylaima virginianum* Dickerson, 1930 from opossums; *Gyrosoma singulare* Byrd, Bogitsh, and Maples, 1961 from raccoons; *Hasstilesia texensis* Chandler, 1929 from swamp rabbits, *Sylvilagus aquaticus* (Bachman); *Maritreminoides nettae* (Gower, 1938) Rankin, 1939 from raccoons; and *Rhopalias macracanthus* Chandler, 1932 from opossums. *Brachylaima virginianum, Fibricola cratera, F. lucida, Hasstilesia texensis, Heterobilharzia americana,* and *Rhopalias macracanthus* have been previously reported from Louisiana; the other species are new locality records. The raccoon is a new host record for adult *Alaria mustelae*. Diagnoses are presented for species representing state records along with pertinent notes on the epidemiology and zoogeography of each.

INTRODUCTION

During our studies on the life cycle of *Alaria marcianae* (La Rue, 1917) Walton, 1949 in Louisiana we had the opportunity to examine other mammals for trematodes. All mammals reported herein were collected in southern Louisiana from an area bordered on the west by the Atchafalaya basin and on the east by Lake Maurepas. The mammals were collected by leg traps set in and around cypress-tupelo swamps.

The following mammals were examined for trematodes, one mink, *Mustela vison* Schreber; one gray fox, *Urocyon cinereoargenteus* (Schreber); one striped skunk, *Mephitis mephitis* (Schreber); two river otters, *Lutra canadensis* (Schreber); two swamp rabbits, *Sylvilagus aquaticus* (Bachman); twelve opossums, *Didelphis virginiana* Kerr; and thirty raccoons, *Procyon lotor* (Linn.).

Trematodes were fixed in steaming 10% formalin and stained in Semichon's aceto-carmine. All measurements are in micrometers unless otherwise stated; means are followed by the ranges in parentheses. Line drawings were prepared with the aid of a microprojector. Representative specimens for which diagnoses are given were deposited in the Manter Laboratory, University of Nebraska State Museum.

The following is a list of trematodes we found from mammals that have been previously reported from Louisiana: From the mink we found *Fibricola cratera* (Barker and Noll, 1915) Dubois, 1932 in the small intestine; both swamp rabbits harbored thousands of *Hasstilesia texensis* Chandler, 1929 in the small intestine; in opossums *F. cratera* and *Rhopalias macracanthus* Chandler, 1932 occurred in the small intestine of all twelve, *Brachylaima virginianum* Dick-

erson, 1930 in the small intestine of eight, and *Heterobilharzia americana* Price, 1929 in the mesenteric venules of three; from gray fox we have a single specimen of *F. lucida* (La Rue and Bosma, 1927) Dubois and Rausch, 1950 from the small intestine; no trematodes were found in the skunk; and in the raccoons we collected *F. cratera* and *F. lucida* from the small intestine of ten and one respectively, and *H. americana* in the mesenteric venules of four.

Lumsden and Zischke (1961) adequately described *Fibricola cratera, F. lucida, Hasstilesia texensis,* and *Brachylaima virginianum* from Louisiana mammals. Malek et al. (1961) studied *Heterobilharzia americana* in southern Louisiana and found the raccoon to be the principal definitive host. Kaplan (1964) was the first to report *H. americana* from the opossum and commented on its rarity in marsupials. In addition to these previously reported trematodes we have identified seven species, one from the otters and six from the raccoons, that have not been reported from Louisiana and are of importance from either epidemiological or zoogeographical standpoints.

Family DIPLOSTOMIDAE Poirier, 1886

Alaria mustelae Bosma, 1931
(Figure 1)

Synonyms: *Alaria freundi* Sprehn, 1932; *A. intermedia* (Olivier and Odlaug, 1938) Odlaug, 1940; *A. dubia* Chandler and Rausch, 1946; *A. minuta* Chandler and Rausch, 1946, *A. taxidea* Swanson and Erickson, 1946; *A. canadensis* Webster and Wolfgang, 1956.

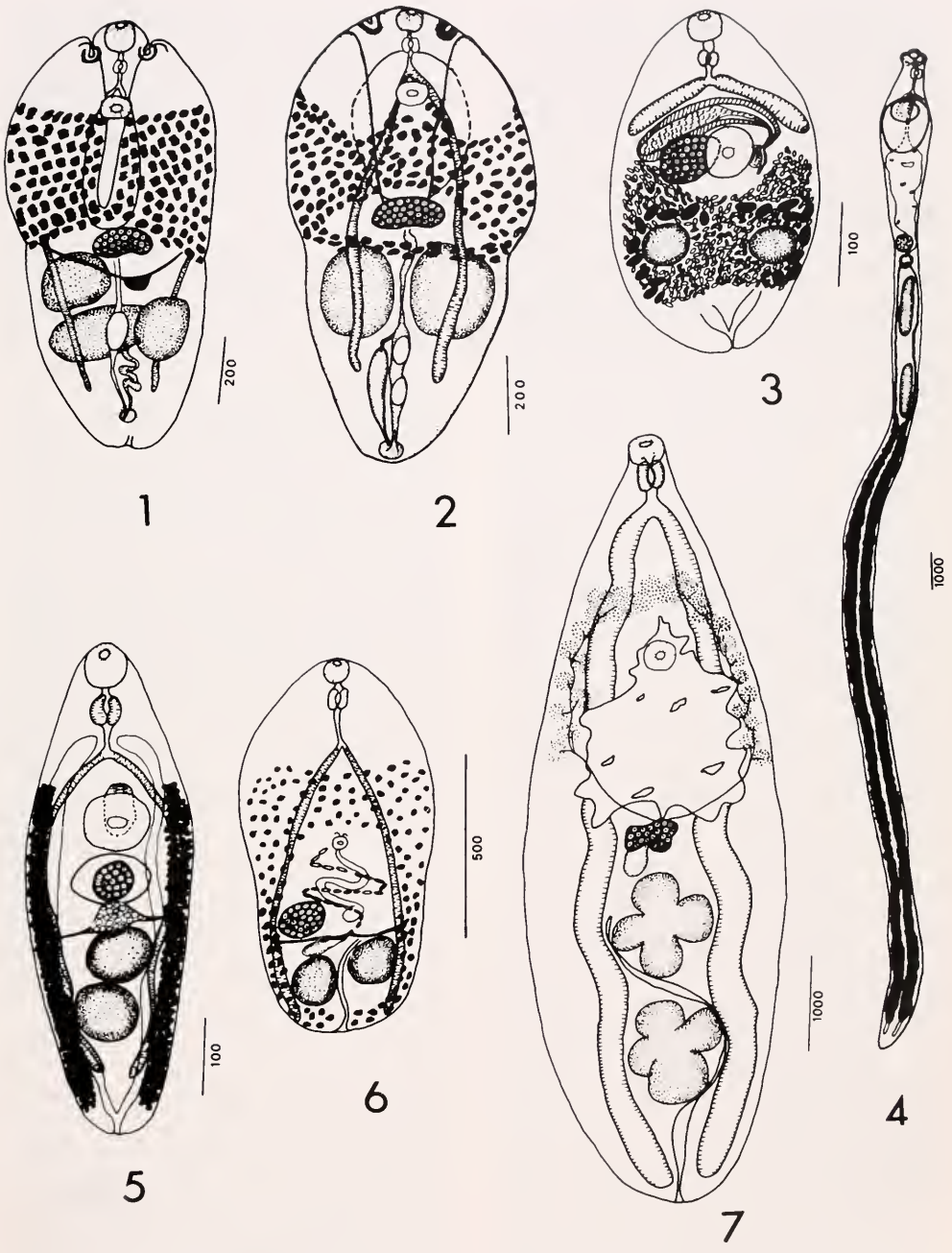
Hosts: *Procyon lotor* (Linn.).

Location: Small intestine.

Localities: Bayou Duplantier (East Baton Rouge Par.); 2 mi. N. of Hwy. 190 on Atchafalaya River (Pointe Coupee Par.). Univ. Nebraska State Mus., Manter Lab. Coll. No. 21194

Diagnosis (based on ten mature specimens): Body indistinctly bisegmented, 1250 (1160-1420) long; forebody scoop-shaped, 680 (650-770) long by 565 (500-580) wide, with pseudosuckers present on both sides of oral sucker; hindbody conical, 540 (460-650) long by 470 (450-530) wide, containing reproductive organs. Forebody cuticle completely covered with small spines; hindbody smooth. Oral sucker terminal, 86 (80-95) long by 81 (70-90) wide. Prepharynx present, short. Pharynx 66 (60-70) long by 48 (45-50) wide. Esophagus short, often not apparent. Ceca terminate near posterior end of body. Acetabulum wider than long, 73 (70-80) long by 90 (85-93) wide. Holdfast broadly oval, variable in size, anterior extension partially or completely covers the acetabulum. Testes two, not equal; anterior testis irregularly oval, laterally displaced on either side of midline, 188 (155-230) long by 206 (190-230) wide; posterior testis dumbbell-shaped, much wider than anterior testis, 183 (150-220) long by 335 (355-400 wide, posterior testis with ventro-medial groove to allow passage of ceca and uterus. Seminal vesicle expanded into a muscular ejaculatory duct. Ovary reniform, located at forebody-hindbody juncture, 94 (90-100) long by 147 (135-155) wide. Mehlis gland opposite anterior testis. Uterus makes an initial course into holdfast region and then passes posteriorly emptying into the genital atrium. Genital atrium posterior, subterminal on dorsal surface. Vitellaria occupies much of the forebody from the acetabulum to anterior testis, never observed posterior to anterior testis. Vitelline ducts unite to form a vitelline reservoir at the level of anterior testis. Eggs large, few, 106 (102-110) long by 63 (60-65) wide. Excretory pore subterminal on ventral side.

Discussion: Babero (1960) tentatively listed *Alaria taxidea* as an intestinal inhabitant of the skunk, *Mephitis mephitis*, in Louisiana. Johnson (1979) relegated



Figures 1-7. 1. *Alaria mustelae,* ventral view, from *Procyon lotor.*2. *Pharyngostomoides procyonis*, ventral view, from *Procyon lotor*. 3. *Maritreminoides nettae*, ventral view, from *Procyon lotor*. 4. *Baschkirovitrema incrassatum*, ventral view, from *Lutra canadensis*. 5. *Gyrosoma singulare*, ventral view from *Procyon lotor*. 6. *Apophallus venustus*, ventral view, from *Procyon lotor*. 7. *Parametorchis complexus,* ventral view, from *Procyon lotor*. Scale in micrometers.

A. taxidea to a junior synonym of *A. mustelae* based on life history and host specificity for mutelids. He demonstrated that specimens of *A. mustelae differed in size and morphology when recovered from different mustelid hosts. He found no natural A. mustelae* infection in the raccoons he examined, but 1000 mesocercariae fed to a single raccoon yielded 14 adults. They were similar morphologically to those from mustelid infections, but were decidedly smaller. Bosma (1934) stated that she recovered only *A. mustelae* metacercariae from raccoons.

This is the first report of natural infections of adult *Alaria mustelae* in raccoons. We found two of thirty raccoons infected. One infection consisted of fifteen worms whereas the second infection consisted of several hundred mature adults in the small intestine. Our specimens are smaller (1.160-1.420 mm) compared to the upper range (2.4 mm) of the species reported by Johnson (loc. cit.), but are larger than his specimens from the experimental infections in the raccoon (0.88-1.00 mm). Unfortunately Babero (loc. cit.) did not list measurements for his specimens from skunks and we were unsuccessful in gaining access to them. However, we concur that *A. taxidea* is a synonym of *A. mustelae* and that the low number of naturally infected raccoons, small size of worms, and the low number of adults recovered in experimental infections of raccoons indicates a physiological specificity for mustelids.

Of interest from an epidemiological standpoint, Beaver et al. (1977) reported a mesocercarial infection in a human in Louisiana. They believed the mesocercariae members of the genus *Alaria* and traced the infection to the consumption of an undercooked raccoon. Johnson (loc. cit.) has proven experimentally, and we have found in nature, that raccoons may serve as definitive hosts for *A. mustelae*. However, given the low specificity of *A. mustelae* for raccoons and the complex migration of all species of *Alaria* in the definitive host (gut to lungs and back to gut) some mesocercariae may lose their way and lodge in other tissues. We have evidence to this effect in other species of *Alaria* (to be presented elsewhere). This indicates that the raccoon is not only a definitive but a paratenic host as well.

Pharyngostomoides procyonis Harkema, 1942
(Figure 2)

Synonyms: *P. ovalis* Chandler and Rausch, 1946.

Hosts: *Procyon lotor* (Linn.)

Location: Small intestine.

Localities: St. Landry, Pointe Coupee, Iberville, St. Martin, East Baton Rouge, Ascension, and Livingston parishes.

Univ. Nebraska State Mus., Manter Lab. Coll. No. 21195.

Diagnosis (based on ten mature specimens): Body indistinctly bisegmented, 1160 (1080-1250) long; forebody scoop-shaped, 580 (520-620) long by 570 (520-630) wide, with pseudosuckers present on both sides of the oral sucker; hindbody conical, 580 (540-620) long by 506 (450-550) wide. Forebody cuticle completely covered with small spines; hindbody smooth. Oral sucker terminal, 74 (70-75) long by 90 (80-95) wide. Prepharynx 10 (5-15) long. Pharynx muscular, 57 (50-60) long by 51 (45-55) wide. Esophagus 22 (20-25) long. Ceca extend just posterior to testes, never reaching posterior end of body. Acetabulum spherical, posterior to intestinal bifurcation, 77 (75-80) long by 78 (75-80) wide, artially or completely covered by holdfast organ. Holdfast well developed, elongate, broadly oval, may reach as far as pharynx. Testes equal, spherical or oval, opposite but often diagonal, 237 (200-250) long by 200 (180-230) wide, located in hindbody dorsal to ceca. Seminal vesicle coiled,posterior to testes, expanded into a muscular ejaculatory pouch, that terminates in a genital cone. Genital atrium posterior, subterminal on dorsal side. Ovary reniform or trans-

versely oval, anterior to testes, 90 (85-100) long by 137 (125-160) wide. Uterus makes a short ascending loop into holdfast region, turns posteriorly and unites with ejaculatory pouch. Vitellaria mainly in forebody, extending from acetabulum to the anterior margin of testes. Vitelline ducts unite just posterior to ovary to form the vitelline reservoir. Eggs few, large, 92 (90-95) long by 60 (58-62) wide. Excretory pore subterminal on ventral side.

Discussion: *Pharyngostomoides* is a stenoxenic genus reported only from raccoons. Harkema (1942) described *P. procyonis* from raccoons in North Carolina and Texas. *P. ovalis* was subsequently described by Chandler and Rausch (1946) in Michigan and was later synonymized with *P. procyonis* by Dubois (1963). Harkema and Miller (1964) surveyed raccoons from North Carolina, South Carolina, Georgia, Florida, and Virginia and found *P. procyonis* present in each state. Further, they noted that there appeared to be two forms present in the raccoon. Beckerdite et al. (1971) raised both of these forms to full species. They described *P. adenocephala* and separated it from *P. procyonis* on the basis of: 1) larger size; 2) *shape (spathulate rather than scoop*-shaped); 3) presence of pseudosucker glands; 4) absence of an ejaculatory pouch; and 5) morphology of larval stages.

Based on our dignosis we conclude that our specimens belong to *P. procyonis*. We are not able to compare the morphology of the larval stages since the life history in Louisiana is unknown. We have found *P. procyonis* to be the most frequent parasite encountered in raccoons; 29 of 30 examined were infected with this worm. The only exception was a raccoon collected near a residential area of Baton Rouge. Infections ranged up to an estimated 5000 worms in one raccoon.

Family MICROPHALLIDAE Travassos, 1920

Maritreminoides nettae (Gower, 1938) Rankin, 1939

(Figure 3)

Synonyms: *Maritrema nettae* Gower, 1938; *Pseudospelotrema nettae* (Gower, 1938) Hunter and Vernberg, 1953.

Hosts: *Procyon lotor* (Linn.).

Location: Small intestine.

Localities: Atchafalaya R. at Krotz Springs (St. Landry Par.); 5 mi. N. of Butte La Rose on Atchafalaya R. (St. Martin Par.); 10 mi. S. of Ramah on East Atchafalaya Protection Levee (Iberville Par.).

Univ. Nebraska State Mus., Manter Lab. Coll. No. 21196

Diagnosis (based on ten mature specimens): Body small, pyriform, 407 (390-420) long by 231 (220-270) wide. Cuticle completely covered with small spines. Oral sucker subterminal, 45 (37-50) long by 57 (55-61) wide. Prepharynx 25 (15-33) long. Ceca short, thickwalled, bifurcating anterior to cirrus sac and extending toward edges of body; never extending past anterior level of acetabulum, 130 (120-143) long. Acetabulum pre-equatorial, larger than oral sucker, 63 (57-66) long by 63 (61-68) wide. Testes spherical, opposite, equal in size, 71 (60-83) long by 70 (60-77) wide. Cirrus sac crescent-shaped, transverse, preacetabular; walls of cirrus sac thick with well developed seminal vesicle, prostate, and ejaculatory duct; ejaculatory duct extends into a slender, protrusible cirrus. Genital atrium opens sinistral to acetabulum; atrium armed with small, stout spines. Ovary irregularly oval, usually overlapping acetabulum, 71 (64-81) long by 79 (75-80) wide. Uterus consists of loops between acetabulum and posterior stem of excretory vesicle. Vitellaria form a right angle to testes with the sides being anterior and lateral to each testis, a few follicles extend posterior to testes but never reach end of body. Eggs small,

numerous, 20 (20-22) long by 11 (10-11) wide. Excretory pore terminal; excretory vesicle V-shaped.

Discussion: Rankin (1939) erected the genus *Maritreminoides* for those microphallids with a long, protrusible cirrus and antero-lateral uterine coils. He placed in his genus *M. nettae* and two metacercarial forms from fishes; *M. obstipum* (Van Cleave and Mueller, 1932) and *M. medium* (Van Cleave and Mueller, 1932). Etges (1953) regarded the genus *Maritreminoides* valid, but transferred *M. obstipum* and *M. medium* into the genus *Maritrema* Nicoll, 1907 because they did not possess a protrusible cirrus. Sogandares-Bernal (1965) surveyed crayfishes in Louisiana for parasites and reported *Maritrema obstipum* from *Cambarellus shufeldti* (Faxon, 1881) and *Procambarus clarkii* (Girard, 1852). The metacercaria figured by Sogandares-Bernal is morphologically identical with the adult worms we have found in raccoons except for lacking a protrusible cirrus and being ovigerous. Presumably, Sogandares-Bernal assigned the metacercariae to the genus *Maritrema* based on the absence of a protrusible cirrus.

We believe the metacercariae found in crayfishes by Sogandares-Bernal (loc. cit.) to be the larval stage of the adults we have collected from raccoons. The fact that a cirrus was not figured for the metacercaria could well have been because the worms were immature. Functionally, a protruded cirrus in a metacercarial stage, unless progenetic, would be of dubious value. The location of the infected crayfishes, as reported by Sogandares- Bernal, is in the same basin as are the infected racoons. We have observed crayfish remains in many raccoons.

Though *Maritreminoides nettae* was described from ducks in Michigan (Gower, 1938), Harkema and Miller (1964) reported it from raccoons in North Carolina, South Carolina, and Georgia. We reported the finding of *M. nettae* in the small intestine of seven of thirty raccoons in Louisiana. We also report what we believe to be the second intermediate host, i.e. the crayfishes of Sogandares-Bernal (loc. cit.). If life histories of closely related forms are examined, the first intermediate host of *M. nettae* is most probably an amnicolid snail.

Family ECHINOSTOMATIDAE
(Looss, 1902) Poche, 1926.

Baschkirovitrema incrassatum (Diesing, 1850) Skrjabin, 1944
(Figure 4)

Synonyms: *Dipostomum incrassatum* (Diesing, 1850; *Echinostomum incrassatum* (Diesing, 1850) Stossich, 1891.

Hosts: *Lutra canadensis Schreber.*

Location: Small intestine.

Locality: Lake Verret (Assumption Par.)

Univ. Nebraska State Mus., Manter Lab., Coll. No. 21197.

Diagnosis (based on 14 mature specimens): Body elongate, slender, 27.5. (23-31) mm long. Maximum width at level of acetabulum, 1170 (1100-1300). Head color reniform, 546 (500-580) wide, bearing 27 spines; a double row of 4 corner spines on each side, 148 (140-160) long by 42 (35-50) wide; six lateral spines on each side are found in a single row and are increasingly larger from ventral to dorsal side, the largest lateral spine, 121 (100-145) long by 26 (25-30) wide; 7 dorsal, uninterrupted spines, 132 (120-150) long by 25 (24-26) wide. Oral sucker 262 (220-280) long by 287 (250-300) wide. Prepharynx 142 (130-150) long. Pharynx 240 (220-250) long by 170 (140-200) wide. Esophagus 690 (600-800) long. Ceca two, terminating near posterior end of body. Acetabulum very prominent, muscular, located in anterior fifth of body, 1190 (1100-1400) long by 990 (900-1050) wide. Testes tandem, elongate, oval, in anterior third of body; anterior testis 1190 (970-1450) long by 265 (200-320) wide; posterior testis 1090 (870-1400) long by 246 (200-310) wide.

Vas efferens originate on antero-lateral side of testes and unite at posterior margin of the acetabulum; cirrus sac dorsal, not extending posterior to the acetabulum, 1150 (1100-1400) long by 500 (400-550) wide; cirrus long, slender, and unarmed. Ovary round, dextral to midline, 300 (240-350) long by 260 (250-280) wide. Mehlis gland diffuse, immediately posterior to ovary. Uterus with short descending coil; ascending uterus forms transverse intercaecal loops between Mehlis gland and acetabulum; distal vessel of uterus forms a metraterm that opens at the common genital pore just anterior to acetabulum. Vitelline follicles extend from middle of anterior testis to posterior end of body, filling most of lateral space behind testes. Vitelline ducts originate at middle of anterior testis and unite to form a vitelline reservoir at level of Mehlis gland. Excretory pore terminal. Eggs abundant, 109 (105-115) long by 64 (60-66) wide.

Discussion: The geographical localities from which *Baschkirovitrema incrassatum* have been reported are of considerable interest. Braun (1901) described *B. incrassatum* from the otter, *Pteronura brasiliensis* Zimmerman, in South America; Beverly-Burton (1960) and Myers et al. (1960) report *B. incrassatum* from *L. maculicollis* Lichtenstein and *Aonyx capensis* (Schinz) from Africa; and Sawyer (1961), Harkema and Miller (1968), and Fleming et al. (1977) have identified *B. incrassatum* from *L. canadensis* in North America.

Harkema and Miller (loc. cit.) reported *B. incrassatum* from North Carolina and stated that they compared their specimens with those of Sawyer (loc. cit.) from Georgia and to specimens deposited in the National Museum by W. J. Hamilton from otters in New York. They reported all specimens from North America were similar and that they "compared favorably" with the measurements given by Beverly-Burton (loc. cit.) from Africa. The present report is the first to present measurements from North American material. We have found that our specimens from Louisiana are much larger than those reported from South America (Braun, 1901) and from Africa (Beverly-Burton, 1960) and with no apparent overlap (Table 1). In addition, the oral sucker and acetabulum of our specimens are proportionately larger than previously described.

As indicated by the measurements, our specimens are more closely aligned with the material from South America than those from Africa. Since life histories of any of these forms are enigmatic, it is difficult to ascribe differences at this time to intra- or interspecific variation.

Family PSILOSTOMIDAE Looss, 1900

Gyrosoma singulare Byrd, Bogitsh, and Maples, 1961

(Figure 5)

Synonyms: Originally described as *Grysoma singularis* Byrd et al., but Yamaguti (1971) emended the genus to *Gyrosoma.*

Hosts: *Procyon lotor* (Linn.).

Location: Small intestine.

Localities: Bayou Duplantier and Spanish Lake (East Baton Rouge Par.); Atchafalaya R. between Keith Lake and Krotz Springs (St. Landry Par.); and Head of Island (Livingston Par.).

Univ. Nebraska State Mus., Manter Lab. Coll. No. 21198.

Diagnosis (based on ten mature specimens): Body lanceolate, relatively thick, 632 (580-680) long; widest at level of acetabulum, 222 (200-265) wide. Cuticle thick, beset with short, stout spines; spines set in dense rows anteriorly and become less numerous behind the posterior testis. Oral sucker subterminal, 55 (52-59) long by 56 (52-59) wide. Prepharynx 15 (13-17) long. Pharynx barrel-shaped, 35 (30-41) long by 36 (33-39) wide. Esophagus distinct, 14 (22-41) long. Ceca bifurcating anterior to common genital pore, diverge laterally to acetabulum and terminate midway between posterior testis and caudal end of body. Acetabulum prominent, pre-

Table 1. Comparative measurements of *Baschkirovitrema incrassatum* from Africa, South America, and North America.

	Africa Beverley-Burton (1960)	South America Braun (1901)	North America (present study)
Body length	12.50-16.55 mm	7-19 mm	27.5 (23-31) mm
No. of head spines	27	27	27
Corner spines	108-154 X 28-37	104 X 31	148 (140-160) X 42 (35-50)
Lateral spines	105-130 X 28-32	–	121 100-145) X 26 (25-30)
Dorsal spines	109-144 X 30-34	83-93 X 21	132 (120-150) X 25 (24-26)
Oral sucker: length	190-220	166-250	262 (220-280)
Oral sucker: diameter	220-260	187-208	287 (250-300)
Acetabulum: length	870-1170	–	1190 (1100-1400)
Acetabulum: diameter	810-950	1000	990 (900-1050)
Pharynx: diameter	120-210	73-83	170 (140-200)
Testes: length	1120-1500	1000	1140 (870-1450)
Testes: diameter	320-480	400	256 (200-320)
Ovary: length	320-390	330	300 (240-350)
Ovary: diameter	320-370	266	260 (250-280)
Eggs	108-123 X 54-62	104 X 73	109 (105-115) X 64 (60-66)

equatorial, 89 (81-92) long by 82 (70-92) wide. Testes oval, diagonal (rarely tandem), contiguous and often overlapping; anterior testis 76 (66-88) long by 85 (81-96) wide; posterior testis 86 (72-96) long by 83 (77-94) wide. Cirrus sac prominent, dorsal to acetabulum, containing seminal vesicle, well developed prostate, and a short, muscular cirrus. Genital pore midventral between cecal bifurcation and acetabvulum; a well developed sphincter muscle is observed when the genital pore is constricted. Ovary ovoid, lying immediately postero-dorsal to acetabulum, 45 (42-48) long by 42 (40-44) wide. Uterus short, ascends directly to genital pore; usually only one egg observed in the uterus at one time, but occasionally two. Egg thick-shelled, large in comparison with body size, 105 (100-110) long by 64 (60-75) wide. Vitellaria extend laterally from the genital pore to caudal end of body; each follicle composed of large, clearly defined vitelline cells. Vitelline ducts extend medially between testes and acetabulum to form a large vitelline reservoir. Excretory system composed of a terminal excretory pore; a Y-shaped excretory vesicle that bifurcates at caudal end of ceca; and arms that extend anteriorly to level of the pharynx.

Discussion: The genus *Gyrosoma* was created by Byrd et al. (1961) to accommodate specimens collected from a single raccoon in Georgia. They considered these worms to be distinct from other psilostomids based on: 1) the diagonal arrangement of the testes; 2) triangular shape of the testes; 3) a short uterus; and 4) a single, large egg in the uterus. To our knowledge, the only other mention in the literature of *G. singulare* is that of Harkema and Miller (1964) who state that they have also found it in Georgia and South Carolina.

We have collected *G. singulare* from the small intestine of 24 raccoons in Louisiana. Infection ranged from a few to several hundred worms. This appar-

ently stenoxenic species is most easily distinguished by the presence of a large egg which may approach one fourth the size of the worm. No morphological data have been reported for this species other than that contained in the original description. Our measurements significantly extend the size range of this species (580-680 compared to 290-480) and we find that our specimens have more spherical shaped testes than the triangular or half-mooned shape reported by Byrd et al. (loc. cit.).

Family HETEROPHYIDAE (Leiper, 1909) Odhner, 1914

Apophallus venustus (Ransom, 1920) Cameron, 1936
(Figure 6)

Synonyms: *Cotylophallus venustus* Ransom, 1920; *C. similis* Ransom, 1920; *Rossicotrema venustum* Ciurea, 1924.

Hosts: *Procyon lotor* (Linn.).

Location: Small intestine.

Locality: 10 mi. S of Ramah on the East Atchafalaya Protection Levee (Iberville Par.).

Univ. Nebraska State Mus., Manter L2b. Coll. No. 21199

Diagnosis (based on ten mature specimens): Body elongate, oval with a slight constriction between acetabulum and ovary, 1018 (820-1150) long by 563 (450-650) wide. Cuticle with small spines over anterior two thirds; posterior devoid of spination. Oral sucker unornamented, subterminal, 56 (46-66)long by 70 (55-79) wide. Prepharynx distinct, 13 (11-24) long. Pharynx 54 (50-57) long by 52 (48-55) wide. Esophagus long and slender, 123 (99-132) long. Ceca extend to caudal end of body. Acetabulum small, weakly defined,located in genital sinus posterior to genital openings, 41 (31-44) long by 41 (39-44) wide. Testes oblique, globular or ovoid; anterior testis 129 (99-154) long by 163 (99-187) wide; posterior testis 133 (110-165) long by 180 (150-224) wide. Vas efferens unite at level of ovary to form a conspicuous sigmoid seminal vesicle. Cirrus absent. Ovary ovoid, dextral to midline, 104 (99-115) long by 110 (99-125) wide. Seminal receptacle large, transversely oval, and lying directly posterior to ovary. Uterus makes 3-4 transverse, intercaecal loops before entering genital sinus. Vitellaria unite across body between the intestinal bifurcation and acetabulum, then extend laterally to posterior end of body. Vitelline ducts unite to form a vitelline reservoir between seminal vesicle and testes. Eggs 35 (33-37) long by 20 (17-22) wide. Excretory pore terminal; posterior stem of excretory vesicle sigmoid as it courses between the testes.

Discussion: *Apophallus venustus* has, heretofore, been reported from eastern coastal states and provinces of North America (Cameron, 1936; Babero and Shepperson, 1958; and Harkema and Miller, 1964). Yamaguti (1971) considers *A. venustus* conspecific with its European relative *A. donicus* (Skrjabin and Lindrop, 1919) Price, 1931, but we prefer to follow Cameron (loc. cit.) and recognize *A. venustus* as a distinct species based on its greater anterior extent of vitellaria and its larger size.

The life history of *A. venustus* was studied by Cameron (1937,a) and consists of an operculate snail, *Goniobasis livescens* (Menke), as first intermediate host, a wide variety of fishes as second intermediate host, and any fish-eating mammal as the definitive host. Cameron (1937,b) reported a human infection in Canada with *A. venustus* eggs being found in the feces. The epidemiology was traced to the presumed ingestion of fish.

The presence of *A. venustus* in Louisiana is of epidemiological interest since many of its people subsist, to a large degree, off the land. Small infections may perhaps go unnoticed because adequate diets prevent loss of vigor. However, Africa et al. (1935), working in the Philippines, found a high correlation between cardiac alteration and heterophyid infection. Kean and Breslau (1964) state that a large number of cardiac fatalities (14.6%) in the Philip-

pines are attributed to heterophyid eggs which find their way into the circulation. These reports, coupled with the already mentioned human infection with *A. venustus* should alert epidemiologists and pathologists to the presence of this speies and its possible involvement inhuman infection in Louisiana.

We found four of thirty raccoons infected with *A. venustus*. The infections were located throughout the small intestine and not localized only in the jejunum and ileum as reported by Cameron (1937,a).

Family OPISTHORCHIIDAE Braun, 1901

Parametorchis complexus (Stiles and Hassal, 1894) Skrjabin, 1913

(Figure 7)

Synonyms: *Ditoma complexum* Stiles and Hassal, 1894.

Hosts: *Procyon lotor* (Linn.).

Location: Biliary system.

Localities: Sherburne (Pointe Coupee Par.); 10 mi. S. of Ramah (Iberville Par.).

Univ. Nebraska State Mus., Manter Lab. Coll. No.

Diagnosis (based on ten mature specimens): Body flat, elongate, anterior end attenuate and posterior rounded, 7.8 (6.0-10.5) mm long by 2.2 (1.6-2.9) mm wide. Entire cuticle spinous; spines less dense posterior to testes. Oral sucker terminal, 272 (230-320) long by 326 (330-400) wide. No prepharynx. Pharynx muscular, 253 (210-290) long by 233 (220-270) wide. Esophagus short, 113 (70-150) long. Ceca large, coursing sinuously around organs until reaching posterior end of body. Acetabulum weak, inconspicuous, located in anterior one fourth of body, 286 (260-330) long by 305 (280-330) wide. Testes tandem, lobate, located in posterior half of body; anterior testis 913 (670-1250) long by 956 (800-1150) wide; posterior testis usually larger and possessing more lobes, 994 (800-1400) long by 955 (730-1200) wide. Vas deferens enlarged to form seminal vesicle that courses anteriorly, dorsal to uterus, and empties into genital pore. Genital pore located ventrally, midway between acetabulum and medially positioned vitellaria. Ovary trilobed, pretesticular, 405 (300-500) long by 494 (390-610) wide. Seminal receptacle variable in shape, usually larger than ovary, lying immediately posterior to, and often overlaping, the ovary. Uterus voluminous, with tightly packed loops loosely bordered by the ceca, occupying most of the space between ovary and acetabulum. Vitellaria laterally displaced in anterior half of body; unite medially betwen intestinal bifurcation and genital pore. Vitelline ducts unite ventral to ovary to form a vitelline reservoir. Eggs oval, some constricted anteriorly, 28 (26-30) long by 16 (15-17) wide. Excretory pore terminal; posterior stem of excretory vesicle sigmoid as it passes between testes, eventually giving rise to a Y-shaped excretory vesicle.

Discussion: Stiles and Hassal (1894) originally described *P. complexus* from specimens found inthe biliary system of cats in Maryland and New York. Since that time, additional species have been described from the biliary system of carnivores: *P. noveboracensis* Hung, 1926 from the cat; *P. intermedius* Price, 1929 from the fox, *Vulpes fulva* (Desmarest); *P. canadensis* Price, 1929 from *Mustela vison*; and *P. manitobensis* Allen and Wardle, 1934 from the dog. Cameron (1944) examined the morphology of these worms and concluded that the latter four species were synonyms of *Metorchis conjunctus* (Cobbold, 1860) Looss, 1899. He based his separation on the anterior disposition of the vitellaria. In *M. conjunctus* the vitellaria are laterally displaced while the genus *Parametorchis* is characterized by the anterior union of the vitellaria. Cameron's proposal left *Parametorchis* a monotypic genus. Yamaguti (1971) incorrectly stated that Cameron synonymized *P. intermedius, P. canadensis, P. noveboracensis,* and *P. manitobensis* with *P. complexus.*

Harkema and Miller (1964) reported *P. complexus* from one of 320 raccoons they examined in the southeastern United States (the infected raccoon was found in North Carolina). We have found *P. complexus* in five raccoons in Louisiana. The worms inhabit all levels of the biliary system One raccoon harbored 91 mature *P. complexus* and the bile duct exhibited marked hypertrophy.

SUMMARY

The following trematodes were collected from small mammals in southern Louisiana: *Alaria mustelae* Bosma, 1931; *Fibricola cratera* (Barker and Noll, 1915) Dubois, 1932; *F. lucida* (La Rue and Bosma, 1927) Dubois and Rausch, 1950; *Pharyngostomoides procyonis* Harkema, 1942; *Heterobilharzia americana* Price, 1929; *Apophallus venustus* (Ransom, 1920) Cameron, 1936; *Parametorchis complexus* (Stiles and Hassal, 1894) Skrjabin, 1913; *Baschkirovitrema incrassatum* (Diesing, 1850) Skrjabin, 1944; *Brachylaima virginianum* Dickerson, 1930; *Gyrosoma singulare* Byrd, Bogitsh, and Maples, 1961; *Hasstilesia texensis* Chandler, 1929; *Maritreminoides nettae* (Gower, 1938) Rankin, 1939; and *Rhopalias macracanthus* Chandler, 1932.

Trematodes reported from Louisiana for the first time are: *Alaria mustelae, Pharyngostomoides procyonis, Maritreminoides nettae, Baschkirovitrema incrassatum, Gyrosoma singulare, Apophallus venustus,* and *Parametorchis complexus.*

The raccoon is a new definitive host for *A. mustelae. A.mustelae* shows a distinct specificity for mustelids rather than procyonids based on larger size of worms, low number of naturally infected raccoons, and the low number of adults recovered from experimentally infected raccoons. During migration of larval *A. mustelae* in the raccoon, mesocerariae may lose their way and lodge in other tissues. The raccoon is, then, both a definitive and paratenic host. This finding becomes important in light of the recent report of *Alaria* mesocerariae in man in Louisiana (Beaver et al., 1977).

Pharyngostomoides procyonis is the most frequently encountered trematode in raccoons in Louisiana. Though it has been reported from the eastern coastal states and Texas, it likely is found throughout the other Gulf Coast states as well.

Metacercariae reported in crayfishes as *Maritrema obstipum* by Sogandares-Bernal (1965) are identical to adult *Maritreminoides nettae* recovered from raccoons, except for a protrusible cirrus and being ovigerous. The infected crayfishes are found in the same river basin as are the infected raccoons. We propose that they are the same species based on morphological, geographical and ecological criteria.

Specimens identified as *Baschkirovitrema incrassatum* have been reported in otters from North America, South America, and Africa. Since speciation in otters has ocurred, these worms possibly may be in the process of pursuing distinct evolutionary pathways. Our specimens from North America are much larger than previously reported and with no apparent overlap. Based on reported measurement, our specimens notably are more closely aligned with the material from South America than from Africa.

The presence of *A. venustus* in Louisiana is of epidemiological significance since a human infection involving this species has been previously reported. The metacercariae of *A. venustus* is foundin fish and all fish-eating mammals are susceptible, including humans. Since other heterophyids have been found in be the cause of cardiac fatalities, both epidemiologists and pathologists should be aware of its presence and the possible involvement in human infection in Louisiana.

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