

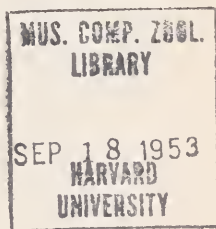
TULANE STUDIES IN ZOOLOGY

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A NEW BURROWING CRAWFISH OF THE GENUS
PROCAMBARUS FROM LOUISIANA AND
MISSISSIPPI
(DECAPODA, ASTACIDAE)

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TULANE UNIVERSITY
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A NEW BURROWING CRAWFISH OF THE GENUS
PROCAMBARUS FROM LOUISIANA AND
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(DECAPODA, ASTACIDAE)

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The new species of *Procambarus* described herein occurs over a fairly wide geographic area, however, it has never been found in large numbers and is a rarely encountered form. Ecologically it may be included among the secondary burrowers (Hobbs, 1942: 20). The relationships of this new species are not clear and will be discussed following the description.

PROCAMBARUS PLANIROSTRIS, *sp. nov.*

Holotype male, form I.—Body subovate, appearing somewhat compressed; abdomen about equal to length of cephalothorax (29.0-27.5 mm). Height of cephalothorax (figs. 1, 2) slightly less than width in region of caudodorsal margin of the cervical groove (12.5-13.0 mm); greatest width of cephalothorax slightly caudad of caudodorsal margin of the cervical groove.

Areola narrow (20 times longer than width), with a single punctation in the narrowest part; cephalic portion of cephalothorax about 1.75 times as long as the areola; length of areola about 36 percent of total length of cephalothorax.

Rostrum without lateral spines; widest at base, margins slightly raised and only slightly thickened, converging at acumen. Upper surface almost flat, moderately punctate. Acumen small, directed dorsally at tip.

Postorbital ridges reduced, terminating anteriorly without spines; lateral surface excavate. Branchiostegal spine small. Cervical groove interrupted laterally; lateral spine reduced to the size of a large tubercle. Lateral surfaces of cephalothorax granulate, dorsal surface moderately granulate.

Cephalic region of telson with spines in each caudolateral angle, three on right, five on left.

Epistome (fig. 3) slightly more than twice as wide as long, with slightly concave center; cephalic margin with a small spine.

Antennae nearly equal to total length of the crawfish; of normal form. Antennal scale (fig. 4) narrow; widest a little distad of middle; lateral margin inflated, straight and terminating distally in a small spine; total length less than length of areola (8.5-10.0 mm).

Chela (fig. 5) with palm inflated; fingers slightly depressed; setiferous punctations present over dorsal surface of most of palm and both fingers. Inner margin of palm with a row of eight prominent

tubercles. Both fingers terminating in short corneous tips, that of the dactyl overhanging the other when the fingers are closed. Thirteen rounded tubercles at base and one distally-located corneous tubercle on opposable margin of immovable finger; fourteen rounded tubercles in corresponding positions on the dactyl. Upper surface of dactyl with seven strong tubercles basally.

Carpus (fig. 5) with five strong spines on distal end in a semi-circular arrangement extending medioventrally from dorsal to ventral condyles which articulate with the chela. Upper surface with smaller tubercles toward inner margin and scattered setiferous punctations generally.

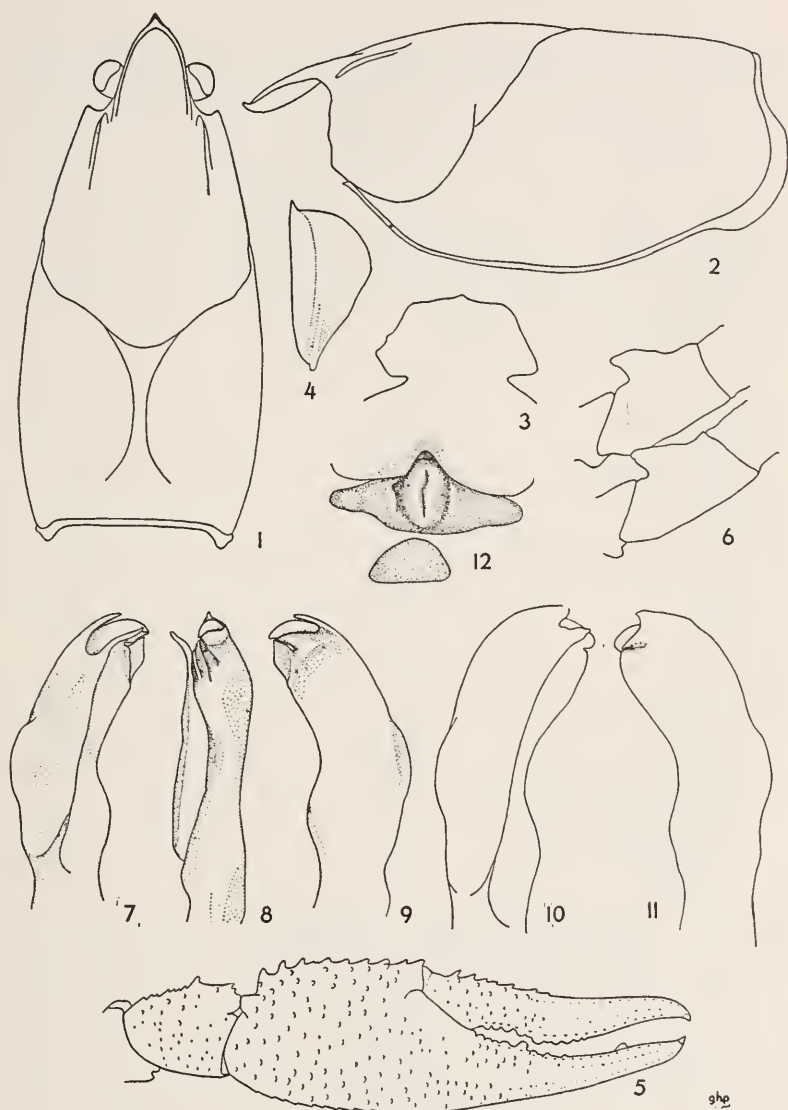
Simple hooks (fig 6) present on ischiopodites of third and fourth pereopods; length of each greater than half the diameter of the respective ischiopodites.

First pleopod (figs. 7, 8, 9) reaching to anterior side of the coxopodite of the third pereopods when the abdomen is flexed. Apex terminating in four distinct parts which as a unit extend caudad at about a 40° angle to the shaft of the pleopod. Mesial process non-corneous, spiniform, directed caudodistad, and not extending beyond the other terminal parts; cephalic process corneous, arising on mesial side of the central projection, directed caudodistad, excavate on caudolateral surface, and closely applied to the central projection; central projection corneous, compressed, "beak-like" in shape, with apex directed caudad; fusion line of centrocaudal and centrocephalic components clearly indicated. Caudal process consisting of two corneous parts: mesially a low, longitudinal ridge flanked laterally by a leaf-like element which extends distally, its apex coming in contact with the overhanging central projection. Cephalic margin of the shaft of the pleopod with a distinct shoulder.

Morphotype male, form II.—Very similar to holotype in general appearance; chelae and hooks on ischiopodite of the third and fourth pereopods greatly reduced. First pair of pleopods (figs. 10, 11) reaching to middle of coxopodites of third pereopods when the abdomen is flexed; all processes reduced and non-corneous.

Allotype female.—Very similar to holotype in general appearance; chelae greatly reduced. Annulus ventralis (fig. 12) immovable, roughly spindle-shaped with center produced into a cone-shaped protuberance on either side of which is a shallow groove. The sinus originates on the center line a short distance removed from the anterior margin then proceeds through a gently zigzag course to the apex of the central, cone-shaped protuberance. The sternum of the preceding thoracic segment is slightly produced so that its posterior margin underhangs the anterior margin of the annulus.

Color.—The following color notes were made from living mature specimens collected at the type locality. In general this is a drab-colored species. The effect is that of a light tan overcast with olive



Figures 1-12. *Procambarus planirostris*, sp. nov.: 1, 2, cephalothorax of the holotype; 3, epistome of the holotype; 4, antennal scale of the holotype; 5, chela and carpus of the holotype; 6, hooks on ischiopodites of the third and fourth pereopods of the holotype; 7, 8, 9, mesial, caudal and lateral views of the first pleopod of the holotype; 10, 11, mesial and lateral views of the morphotype; 12, annulus ventralis of the allotype. Pubescence removed from all structures illustrated.

dorsally on the cephalothorax; the rostrum tan only. Abdomen dorsally with an inconspicuous wide stripe of olive-tan which tapers to a point on the base of the telson; background color of abdomen on either side of the dorsal stripe is a light tan with very fine flecks of darker reddish-tan; this background color extends also onto the dorsal surface of the telson and uropods. On the dorsolateral parts of the abdominal tergites there is a row of spots of olive, one on the anterior margin of each tergite, and connected longitudinally by a faint line of olive. Chelae of the same basic color as the background color of the abdomen, but tubercles capped with black or dark brown, giving the chela and carpus a fine-spotted appearance. One specimen had a faint bluish cast to the fingers.

Measurements.—As follows, in millimeters:

	Holotype	Allotype	Morphotype
Cephalothorax:			
Length	27.5	20.0	29.0
Width (greatest)	13.5	10.0	14.0
Height (greatest)	12.5	9.5	13.5
Areola:			
Length	10.0	7.5	10.5
Width (at narrowest point)	0.5	0.5	0.7
Rostrum:			
Length	5.5	4.0	6.5
Width at base	5.5	3.5	5.5
Abdomen:			
Length (to tip of telson)	29.0	22.0	29.0
Right chela:			
Length of outer margin			
of hand	25.5	11.0	21.0
Length of dactyl	15.0	6.0	12.0
Width of palm (greatest)	8.5	4.0	7.5
Thickness of palm			
(greatest)	6.0	2.5	5.0
Length of inner margin			
of palm	10.0	4.0	8.0

Type locality.—The holotype and allotype were collected from a low area of mixed hardwood, pine and palmetto flatwoods one mile south of Walker (on Louisiana highway 336), Livingston Parish, Louisiana. The holotype was taken on February 17, 1951 by Dr. R. D. Suttkus when the area was inundated by about a foot of water; the allotype was collected on August 29, 1952 by the author and C. E. Biggs from a simple burrow with a neat chimney, around the base of which there was about six inches of standing water. The soil here is a whitish clay and the burrow extended to about twelve inches beneath the soil surface. At the same place there were numerous burrows of *Cambarus hedgpethi* Hobbs and *Orconectes clypeatus* (Hay).

The morphotype was collected from a small creek three miles south of Janice, Perry County, Mississippi on January 28, 1951 by Dr. Fred R. Cagle. No other crawfishes were found at this locality.

Disposition of types.—The holotype, allotype and morphotype are deposited in the United States National Museum, catalogue numbers 95674, 95675, and 95676 respectively. The paratypes are in the following collections: Academy of Natural Sciences, Philadelphia (1 ♂₁, 2 ♂♂ juv., and 1 ♀), the personal collection of Dr. Horton H. Hobbs Jr. at the University of Virginia (1 ♂₁, 1 ♂ juv., and 1 ♀), and Tulane University (2 ♂♂₁, 7 ♂♂ juv., 4 ♀♀, and 6 ♀♀ juv.).

Geographic distribution.—The type series of *Procambarus planirostris* was collected from the "Florida" parishes of southeastern Louisiana and southern Mississippi. These records and a summary of the deposition of these specimens are as follows. LOUISIANA: *East Baton Rouge Parish*: 9 mi. s. Baton Rouge, January 26, 1949, G. H. Bick and L. L. Ellis (TU 910); *Livingston Parish*: 1 mi. s. Walker, February 17, 1951, R. D. Suttkus (USNM, TU 2278), same locality, July 19, 1952, G. H. Penn, R. D. Suttkus and C. E. Biggs (ANS, HHH), same locality, August 20, 1952, G. H. Penn and C. E. Biggs (USNM); *St. Tammany Parish*: Lake Pontchartrain at Mandeville, February 22, 1935, P. Viosca, Jr. and H. B. Chase (TU P-610); *Washington Parish*: 6 mi. nw. Enon, August 10, 1948, G. H. Penn and M. H. Penn (ANS), Franklinton, March 27, 1949, F. R. Cagle (ANS, HHH), 2 mi. n. Varnado, March 3, 1953, F. R. Cagle (TU 2894). MISSISSIPPI: *Perry County*: 3 mi. s. Janice, January 28, 1951, F. R. Cagle (USNM, TU 2853).

Relationships.—*Procambarus planirostris* appears not to belong definitely in any of the sections of *Procambarus* as currently recognized, but has certain characteristics of each of two sections, and apparently occupies a somewhat intermediate position between the two. It shows affinities with the *Barbatus* Section (Hobbs, 1942: 35-36) in its general body conformation and in that the cephalic process of the first pleopod arises from the mesial side of the central projection, but differs from members of this section in lacking the accessory cephalo-distal ridge or knob-like prominence. It shows closer affinities with the *Clarkii* Subgroup of the *Blandingii* Section as defined by Hobbs (1942: 93, 98-99) in possessing a distinct shoulder on the cephalic margin of the first pleopod, and in the general configuration of the annulus ventralis.

Because *P. planirostris* exhibits this peculiar combination of characteristics a new section to accommodate it could be justified. However, because of its assumed closer relationship to the species of the *Clarkii* Subgroup of the *Blandingii* Section than to those of the *Barbatus* Section, I am placing it in a separate subgroup, the *Planirostris* Subgroup in the *Blandingii* Section. This action necessitates the modification of Hobbs' diagnosis (1942: 93) with regard to the cephalic process of the first pleopod to the following: cephalic process when present arises from cephalic or cephalolateral margin in all species except those of the *Planirostris* Subgroup in which it arises from the mesial side of the central projection.

REFERENCE CITED

- HOBBS, HORTON H., JR. 1942. The crayfishes of Florida. *Univ. Fla. Publ., Biol. Sci. Ser.*, 3(2): 1-179.

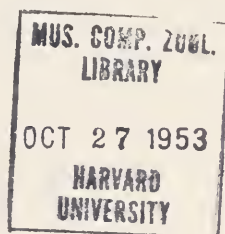
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THE LIFE HISTORY OF THE CRAWFISH
ORCONECTES (FAXONELLA) CLYPEATUS (HAY)
(DECAPODA, ASTACIDAE)

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George Henry Penn, *Editor*,
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THE LIFE HISTORY OF THE CRAWFISH
ORCONECTES (FAXONELLA) CLYPEATUS (HAY)

(DECAPODA, ASTACIDAE)

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The details of the life histories of comparatively few species of crawfishes in the United States have been studied, however the life history of at least one species in each of the four major genera is fairly well known. Within the genus *Orconectes* two species of the subgenus *Orconectes* have been well studied: *O. propinquus propinquus* (Girard) by Creaser (1933a) in Michigan, and by Van Deventer (1937) and Bovbjerg (1952) in Illinois; and *O. immunis immunis* (Hagen) by Tack (1941) in New York. The subject of the present study, *O. clypeatus*, a member of the subgenus *Faxonella*, has a somewhat distinctive life cycle which might prove to be characteristic of this subgenus alone.

When this study was begun practically nothing had been published concerning either the ecology or life cycle of the species. The entire literature may be summarized in a few sentences. Hay (1899) described it as *Cambarus clypeatus* on the basis of a single female collected from a skiff at Bay St. Louis, Hancock County, Mississippi. From the date of this inauspicious first scientific recognition, *clypeatus* remained a species of questionable affinities (*c.f.* Faxon, 1914) until Creaser (1933b) described the first and second-form males and redescribed the female from two series of specimens collected in Louisiana and Alabama. He also included brief notes describing the "pools along the roadside" and "pools in a bog or swamp" respectively in which it was collected and included the statement that "many burrows were found along the edge of these pools . . . no doubt this species is a burrower, for the pools certainly dry at certain seasons of the year." Later the same year, Creaser and Ortenburger (1933) recorded *O. clypeatus* from Oklahoma and repeated Creaser's notes on its ecology. Lyle (1938) recorded it from Mississippi without comment. Hobbs (1942) recorded it from Florida, Georgia, Alabama and Arkansas and described its burrows along the sides of a roadside ditch in Jackson County, Florida as "marked by small, neatly constructed chimneys, simple, and ranging in depth from six inches to a foot." Penn (1942) recorded the species as abundant in a "pine barren pond" in Louisiana. Finally, Penn (1952) published a compilation of the data of the distribution and ecology of the species in Louisiana.

Within the boundaries of Louisiana *O. clypeatus* is one of the commonest species of crawfishes, and occurs in the following variety of habitats as listed by Penn (1952); temporary situations (58%), including roadside ditches, pineland sloughs, puddles and borrow pits, potholes in dry creek beds, and burrows; permanent situations (42%),

¹ Present address: Savannah, Georgia.

including ponds, creeks, rivers, swamps and swamp ponds. Within the state it occupies these habitats in all physiographic regions except the recent alluvial lands and coastal marshes. The overall distribution of the species as presently known includes the Coastal Plain from southeastern Oklahoma to northeastern Arkansas and Georgia.

THE STUDY AREA

The life history of *O. clypeatus* was studied from October 1949 through January 1951 by means of field observations and statistical analyses of periodic samples of a natural population. The population which was studied and from which the samples were collected was located in a pineland ditch 2.4 miles south of Hickory, St. Tammany Parish, Louisiana. The ditch itself lay to the south side of an unused logging road which formed a retaining levee for an extensive, permanently inundated slough on its north side. The ditch was about 200 feet long, from one to two-and-one-half feet deep, and from three to five feet wide. On the bottom and along the sides, the ditch was covered with a thick carpet of *Juncus repens* Michx. throughout the entire year, and at least some parts of the ditch were shaded throughout each day.

Drought conditions, characterized by the complete absence of standing water anywhere in the ditch, and wet conditions characterized by the presence of standing water throughout the ditch, both occurred periodically during the study period (Table 1). During the wet periods the water level fluctuated with the amount of local rainfall, occasionally overflowing the banks. Usually either one or the other situation obtained when sampling was done, but an intermediate condition existed in which the deeper parts of the ditch were wet and the shallower parts dry. At such times separate samples were collected from each situation. Other crawfishes present in the ditch were numerous *Cambarellus shufeldtii* (Faxon) and occasional *Procambarus blandingii acutus* (Girard).

METHODS OF STUDY

The primary approach to the study was the analysis of periodic samples removed from the population. Collections of samples were originally planned for four week intervals over a period of sixteen months, but it was not practical to adhere strictly to this schedule. A total of sixteen samples on fourteen dates was collected; however, samples for six of the sixteen months are not represented (Table 1). During November and December 1949, drought conditions prevailed and, although field trips were made, the burrowing population was not found. During the other four months, January, March, August and November 1950, no field trips were made because of transportation difficulties.

The samples were collected by dipnet during the wet periods and by digging during the dry periods. Both methods were used along the sides of and in the middle of the ditch for each collection. From one-fourth to one-third of the length of the ditch was sampled when the ditch was wet, but during drought conditions the slower and more

TABLE 1.
BASIC DATA FOR HICKORY, LA. SAMPLES OF *Orconectes clypeatus*.

Lot Number	Date of Collection	Condition of Ditch	Type of Sample		Maximum Water Depth (in inches)	Number (and percentages) of Specimens in Sample			Total
			Water	Burrows		♂ I	♂ II	♀	
1583	1949: Oct. 16	Wet	X		15	3 (4.4)	48 (70.5)	17 (25.1)	68
—	Nov. 25	Dry		X	0	0	0	0	0
—	Dec. 6	Dry		X	0	0	0	0	0
1799	1950: Feb. 24	Wet	X		12	28 (3.6)	343 (44.2)	405 (52.2)	776
1885	Apr. 9	Wet	X		10	46 (10.2)	194 (42.8)	213 (47.8)	453
1946	May 12	Intermediate		X	6	5 (2.7)	102 (53.1)	85 (44.2)	192
1972	June 2	Dry		X	0	4 (2.9)	83 (60.6)	50 (36.5)	137
1980	June 13	Wet	X		12	16 (4.9)	158 (47.9)	156 (47.2)	330
2017	July 12	Dry		X	0	5 (8.5)	22 (37.3)	32 (54.2)	59
2022	July 15	Intermediate	X		3	37 (22.0)	58 (34.5)	7~ (43.5)	168
2207	Sep. 29	Intermediate	X		6	88 (67.1)	7 (5.4)	36 (27.5)	131
2208	"	"		X	6	1	1	2	4
2218	Oct. 16	Dry		X	0	0	3	1	4
2229	Oct. 27	Dry		X	0	13 (86.6)	1 (6.7)	1 (6.7)	15
2246	Dec. 1	Dry		X	0	1 (7.0)	2 (10.7)	14 (82.3)	17
2255	Dec. 29	Wet	X		12	7 (1.7)	163 (47.3)	177 (51.0)	347
2261	1951: Jan. 24	Wet	X		12	18 (1.9)	422 (44.2)	515 (53.9)	955

laborious digging was restricted to from one-sixteenth to one-eighth of the length of the ditch.

The first sample made from burrows was taken in the second dry period (May 1950) after the study was begun. The burrows were found over the bottom and along the sides of the ditch and each was marked only by an inconspicuous entrance hole, usually less than three-fourths of an inch in diameter; chimneys were never seen. Below the entrance each burrow branched off into several tunnels, which eventually led to individual pockets or "cells" from eight to fifteen inches beneath the surface. Each pocket was occupied by one crawfish only.

Although this collection established the fact that the population burrowed during dry periods, the possibility that a portion of it might migrate during such times remained to be determined. Accordingly, each time a visit was made to Hickory, the slough across the road was checked with a dipnet for a migrating part of the population. Only six individuals of *O. clypeatus* were found in the slough and these only during wet periods following times when the ditch could have overflowed and flooded the road. If drought is a necessary factor for the completion of the life cycle of this species then the facts that the road was seldom flooded and that the unpopulated slough always contained water explains the scarcity of this species in collections from the slough. It was felt therefore that the absence of *O. clypeatus* from collections during the October-November 1949 drought was a result of faulty technic in sampling, not of an absence of the burrowing population.

The majority of the samples was preserved in alcohol either in the field or immediately upon return to the laboratory. Some first-form males, collected December 1, 1950, and some ovigerous females, collected between September and December 1950, were kept alive for observation in the laboratory.

In the laboratory the length of the cephalothorax was measured on all specimens. This measurement was taken on an observed mid-dorsal line from the tip of the rostrum to the end of the cephalothorax. All measurements were made with an ocular micrometer calibrated for a stereoscopic microscope. Each measurement was estimated to the nearest part of a micrometer unit but was converted for recording only to the nearest one-tenth (0.1) of a millimeter. As it was measured and recorded each specimen was assigned a sub-lot number and kept in an individual vial until the entire lot (*i.e.*, sample) had been completely studied.

A series of females was selected for the study of ovarian egg growth and production. After an ovary had been removed, the eggs were teased from it in a dish of water. Eggs were measured along their longest diameters and recorded to the nearest hundredth of a millimeter (0.01). Total ovarian egg count was recorded for only a few of the females so analysed.

A few specimens, in addition to certain samples, were collected separately and kept alive for observation in the laboratory. Such in-

dividuals were placed each in separate bowls or small aquaria containing rain water, sand, and usually some vegetation. All were fed Pabulum.

STATISTICAL ANALYSES

A detailed discussion of the statistical analyses used in this study is not included in this paper. However, since the conclusions and interpretations of the life cycle are based largely on statistical methods, a brief summary of the methods employed and the steps of the various analyses is included here.

Methods used in the statistical analyses were modeled closely on those given by Peatman (1947) and Cazier and Bacon (1949). The measurement of cephalothorax length was taken as the criterion of age, but sexual maturity was based on other well-established biological criteria, *i.e.*, attainment of first form in the males, and maturation of ovarian eggs or the ovigerous condition in the females.

Since it was anticipated that each sample would give a clue to the stage of development of the entire population during a given time fragment in its annual cycle, it was necessary first to determine the homogeneity or extent of heterogeneity of the apparent age components (*i.e.*, size groups) of each sample. This was done following the grouping of measurements according to the following criteria: (1) each sample was kept separate according to time and place (*i.e.*, either aquatic or burrowing); (2) females, first-form males, second-form males, and unsexed young were separated into sub-groups respectively whenever they occurred in any one sample. At this point the sub-groups of the samples were each considered to be homogeneous on the fundamentals of location, time, and sex, but not on age.

Determination of homogeneity of age of these groups was based on three hypotheses: (1) that the frequency distribution of the cephalothorax length describes the form of the normal curve when the group is homogeneous; (2) that those groups which do not fit the normal curve, do not because of the presence of more than one age group within the group tested, and vice versa, those groups that do, do so because of the presence of only one age group; and, (3) that the heterogeneous groups (according to age only) can be resolved into their homogeneous components under certain conditions.

Grouped data were used throughout the study for all calculations of mean, standard deviation, and for those other statistics that were based upon the mean or standard deviation. The criteria for class groupings of the samples were: one-tenth millimeter (the very youngest crawfishes); two-tenths millimeter (the maturing groups), and five-tenths millimeter (the adult groups).

The first hypothesis was proved by using a set of young crawfish removed from the pleopods of their mother, thus of a known uniform (or homogeneous) age (Table 2, Dec. 1, group "j"). The second and third hypotheses, dependent on the proof of the first, were resolved by applying the chi-square Test of Significance to the separate frequency distributions of each of the sub-groups already known to be homogeneous except for age. The results (chi-square probabilities)

TABLE 2.
BASIC STATISTICS FOR GROUPS OF FEMALES
AND UNSEXED JUVENILES

Date	Group	Number of Specimens	Cephalothorax Length in Millimeters		P
			Actual Range	Mean	
1949:					
Oct. 16	Q	1	18.8	—	—
	R	16	13.4 — 16.1	14.9	.50
1950:					
Feb. 24	a	5	5.2 — 5.8	—*	—*
	A	333	6.0 — 10.0	8.0	.02
	I	17	10.3 — 12.7	11.0	.50
	S	46	13.8 — 18.6	15.7	.99
Apr. 9	b	6	7.8 — 8.8	—	—
	B	141	8.9 — 12.3	10.6	.30
	II	39	13.0 — 16.9	15.1	.50
	T	30	15.5 — 18.2	16.7	.50
	V	3	19.0 — 19.6	—	—
May 12	c	1	8.1	—	—
	C	80	9.8 — 13.3	11.5	.90
	III	8	13.6 — 14.6	—	—
June 2	D	50	10.6 — 13.3	12.0	.90
June 13	d	4	8.6 — 10.2	—	—
	E	148	10.5 — 13.8	12.2	.10
	IV	8	14.1 — 16.5	—	—
July 12	F	32	10.9 — 13.8	12.4	.50
July 15	G	73	9.6 — 14.4	12.4	.10
Sep. 29	H	36	12.3 — 15.4	13.7	.50
Oct. 15	g	6	4.8 — 5.2	—	—
	J	1	14.7	—	—
Oct. 27	h	3**	2.1 — 2.3	—	—
	K	1	14.8	—	—
Dec. 1	j	50***#	2.4 — 2.8	2.6	.20
	k	44***	2.0 — 3.2	2.7	.50
	m	2**	3.8 — 4.2	—	—
	e	1	11.2	—	—
	M	12	13.1 — 15.2	—	—
Dec. 29	n	6	2.8 — 3.4	—	—
	o	148	3.5 — 4.7	4.2	.50
	N	23	11.5 — 18.0	14.2	.50
1951:					
Jan. 24	p	30	3.0 — 3.4	3.2	.90
	q	155	3.7 — 4.6	4.1	.30
	r	174	4.5 — 5.8	5.2	.50
	s	119	5.6 — 6.6	6.1	.50
	t	5	6.7 — 7.6	—	—
	f	4	10.8 — 11.7	—	—
	P	52	13.8 — 19.0	16.7	.02

* Mean and chi-square probability not calculated for groups of less than 15 specimens. A chi-square probability of 0.10 (10%) and above estimates with confidence that the groups are homogeneous.

** Unsexed juveniles.

Attached to pleopods of mother.

gave estimates only of the occurrence of significant deviations or the lack of deviations of any of the distributions from the normal distribution. A significant deviation was interpreted as the result of the inclusion of more than one age group within a distribution. Accordingly, the frequency distributions of the thus-established heterogeneous age groups were re-observed and subdivided into apparent smaller homogeneous groups (*i.e.*, at apparent modal breaks, or de-

TABLE 3.
BASIC STATISTICS FOR GROUPS OF MALES

Date	Group		Number of Specimens	Cephalothorax Length in Millimeters		P
	♂ II	♂ I		Actual Range	Mean	
1949:						
Oct. 16	R		48	11.9 — 16.6	14.4	.50
		1	2	13.7 — 13.9	—*	—*
		Q	1	19.2	—	—
1950:						
Feb. 24	a		6	3.7 — 5.8	—	—
	A		310	6.0 — 10.2	8.1	.50
	I		27	10.4 — 14.8	12.4	.20
		S	28	12.6 — 17.3	14.8	.09
Apr. 9	b		5	7.2 — 8.5	—	—
	B		168	8.9 — 12.4	10.4	.50
	II		20	12.5 — 15.4	13.6	.50
	T		2	16.1 — 16.4	—	—
		2	36	11.9 — 14.8	13.6	.50
		W	10	15.1 — 17.5	—	—
May 12	c		1	8.7	—	—
	C		99	9.5 — 13.4	11.5	.50
	III		2	14.2 — 14.7	—	—
		3	5	11.5 — 13.8	—	—
June 2	D		83	9.8 — 13.8	11.6	.20
		4	4	12.0 — 13.6	—	—
June 13	d		3	8.4 — 9.8	—	—
	E		153	10.0 — 13.2	11.7	.50
	IV		3	13.7 — 14.5	—	—
	V		1	16.1	—	—
		5	16	11.8 — 13.6	12.8	.20
July 12	F		22	11.1 — 13.1	12.1	.50
		6	5	11.3 — 13.6	—	—
July 15	e		1	9.2	—	—
	G		56	10.4 — 14.2	12.1	.50
	VI		1	15.3	—	—
		7	37	11.0 — 14.2	12.5	.10
		8	1	18.2	—	—
Sep. 29	H		7	12.8 — 14.6	—	—
		9	88	10.8 — 15.3	12.9	.50
		10	1	16.4	—	—
Oct. 15	J		3	13.0 — 13.8	—	—
Oct. 27	K		1	14.0	—	—
		11	12	11.9 — 14.1	—	—
		12	1	16.4	—	—
Dec. 1	M		2	12.9 — 13.3	—	—
		13	1	13.5	—	—
Dec. 29	n		6	3.3 — 3.6	—	—
	o		140	3.7 — 4.6	4.2	.50
	N		17	10.7 — 15.8	13.3	.50
		14	6	11.8 — 14.5	—	—
		15	1	16.6	—	—
1951:						
Jan. 24	p		30	3.0 — 3.6	3.4	.90
	q		146	3.6 — 4.4	4.0	.50
	r		81	4.5 — 5.1	5.0	.95
	s		121	5.2 — 6.1	5.7	.30
	t		47	6.1 — 6.8	6.4	.50
	f		10	13.4 — 13.9	—	—
	P		23	14.0 — 18.4	15.8	.90
		16	18	11.6 — 18.5	14.2	.50

* Mean and chi-square probability not calculated for groups of less than 15 specimens. A chi-square probability of 0.10 (10%) and above estimates with confidence that the groups are homogeneous.

pressions in the frequency distributions) and the chi-square test applied to each new sub-group. In the majority of cases the heterogeneous age groups could be subdivided by this procedure into homogeneous age groups with an acceptable degree of confidence.

When all lots had been subdivided into their component homogeneous age groups (Tables 2 and 3), the data were plotted as bars (actual ranges and means) on time graphs and the major facts of the annual cycle of this species were ready for interpretation. Reference to these graphs (figs. 1 and 2) will be made repeatedly in connection with the elaboration of the life cycle which follows.

THE LIFE CYCLE

Females.—The maturing females (fig. 1, series A, B, C . . . P) increased significantly in size from February to early June at which time they reached a growth plateau that was maintained through July. Between July and September another significant increase in growth was evident. Since ovigerous females were first seen in September this last increase in size is interpreted as representing the "maturity molt" of the spawning population of females and probably compares to the male maturity molt (*i.e.*, transformation from second- to first-form) which must occur prior to copulation. From September to December the mature females did not show any additional significant change in size.

The December adult females (group "N") appeared to have increased again in January forming part of group "P", indicating that at least one molt had taken place. That females molt after the young leave them was substantiated by laboratory observations. In terms of the life history this molt may be interpreted as marking the end of the active reproductive season. Tack (1941) with *Orconectes immunis* and Penn (1943) with *Procambarus clarkii* both found that females molted after their young had left, although not immediately.

Group I (fig. 1, series I-IV) is assumed to have been a continuation of a 1949 group comparable to group "f" of January 1951, and was probably about a year old. Although not represented by large numbers, this series was definitely represented in the samples through June, but by September seemed to have disappeared, reappearing presumably in December and January to form the upper ranges of groups "N" and "P".

In view of the facts that representatives of Series I-IV were not in the samples from July to December and that several large females were collected in September showing signs of having already completed spawning (*i.e.*, with remains of hatchlings' exuviae on their pleopods) it is thought that other individuals also had been ovigerous before September and had been overlooked because they were already in burrows.

Individuals of the series "Q" through "W" were not evident in the samples from April on, and it is assumed that they had died by this date. It is assumed that group "P", representing the terminus of two combined series (A-P and I-IV) which were one and two years old

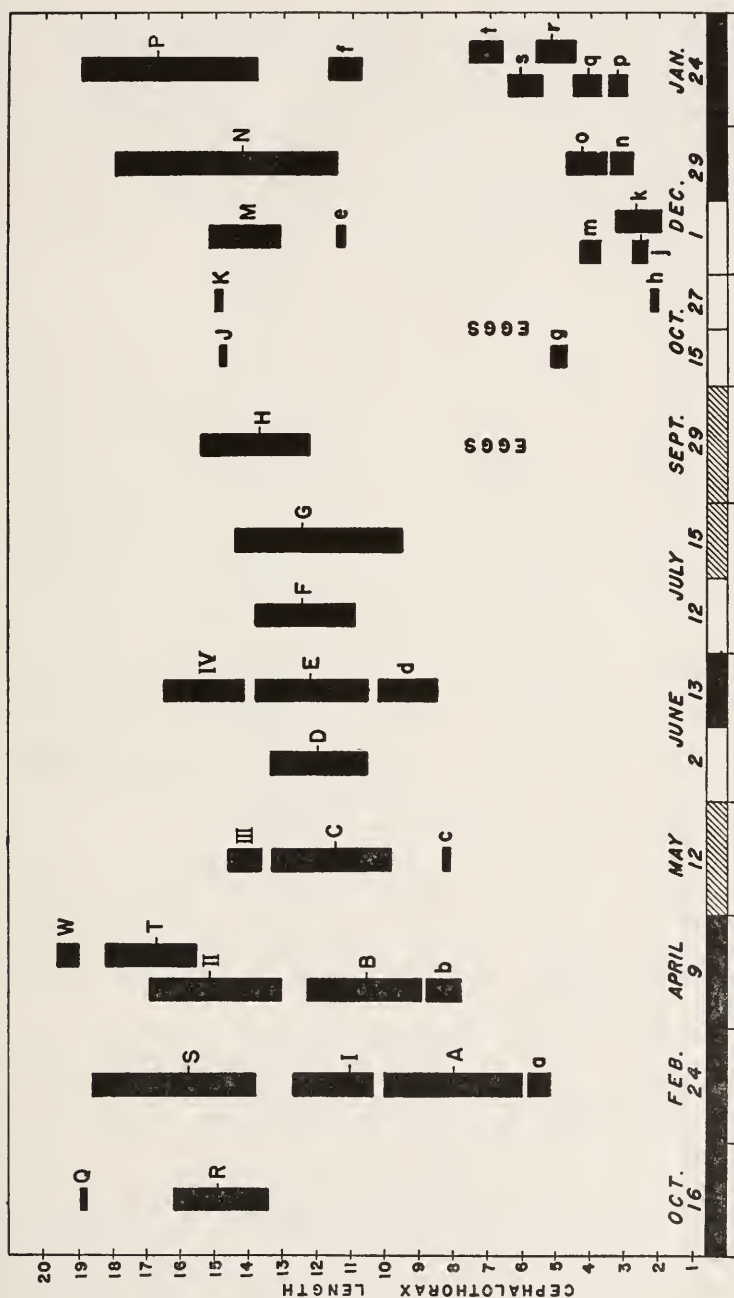


Figure 1. Females. Vertical bars represent age groups, horizontal lines represent the means of the groups. Those groups for which the means are not given contain less than fifteen individuals. Horizontal bar at bottom of graph indicates the condition of the ditch: solid = wet; cross-hatched = intermediate; open = dry.

respectively, followed the same trends as groups "Q" thru "W" and died in the spring of 1951.

The presence of various groups of juveniles (fig. 1, series a, b, c . . . f) from October through January indicates that egg maturation and embryonic development of the entire population was spread over a period of several months. The growth trends of each of these groups cannot be clearly understood from the analyses. The latest juveniles added to the free-swimming population (group "p") probably represented the offspring of the few late-spawning females found in December with young still attached to their pleopods. It is assumed that the January juvenile groups eventually gave rise to groups comparable to groups "a" and "A" of February 1950.

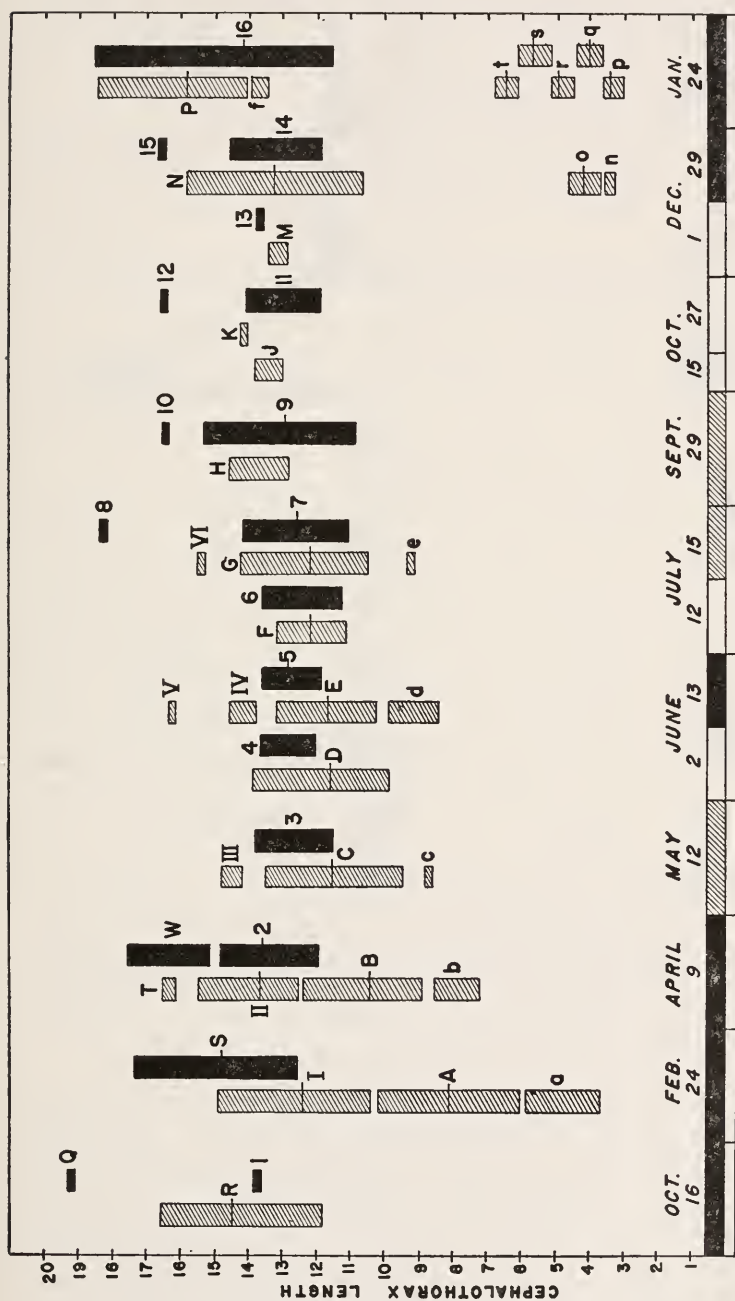
Males.—As might be expected the growth of the male population as a whole paralleled that of the females in most respects, but the interpretation is complicated by the shifts in groupings accompanying the maturation molt from second- to first-form. The maturing second-form males (fig. 2, series A, B, C . . . P) increased significantly from February to May; from May through July they endured a growth plateau as did the maturing females of the same time period. Sometime between May and July some of the larger second-form males apparently matured and molted to first-form, and there is evidence that the greater percentage actually transformed by May. The period from February to May was characterized by significant growth increases, and, if the male population exactly paralleled the female a maturity molt should not have occurred during this time. However, with the advent of the summer growth plateau and because of the overlap of size groups of second- and first-form males in May and June (fig. 2, groups "C" with "3", and "D" with "4") it is inferred that some of the larger second-form males had molted into first-form by May (fig. 2, group 3), and that others molted and became parts of the groups "4", "5" and "6", and most of the groups "7" and "9" when the climax of breeding was reached in September.

The majority of group "9" is thought to have continued as first-form males to December. Groups "H" through "M" represent either second-form males that had already molted back to first-form (*i.e.*, from group "3" through "7") and/or those which would molt to first-form later in January. From the statistics comparing these groups the latter assumption seems most justified.

Groups "11", "13" and "14" represent, at least in part, a continuation of group "9". By December and January, individuals of these groups molted back to the second-form and constituted the upper parts of groups "N" and "P". Those individuals of groups "N" and "P" which had not yet molted to first-form apparently did so in January and constituted the upper part of group "16".

The fact that first-form males molt back to second-form was established by laboratory observations of first-form males of the December sample, most of which had molted back to second-form by January 27th.

Group "e" (fig. 2, series a, b, c . . . e) appears to have developed by December into the lower part of group "N". By January the lower part of group "N" is thought to have molted into first-form and



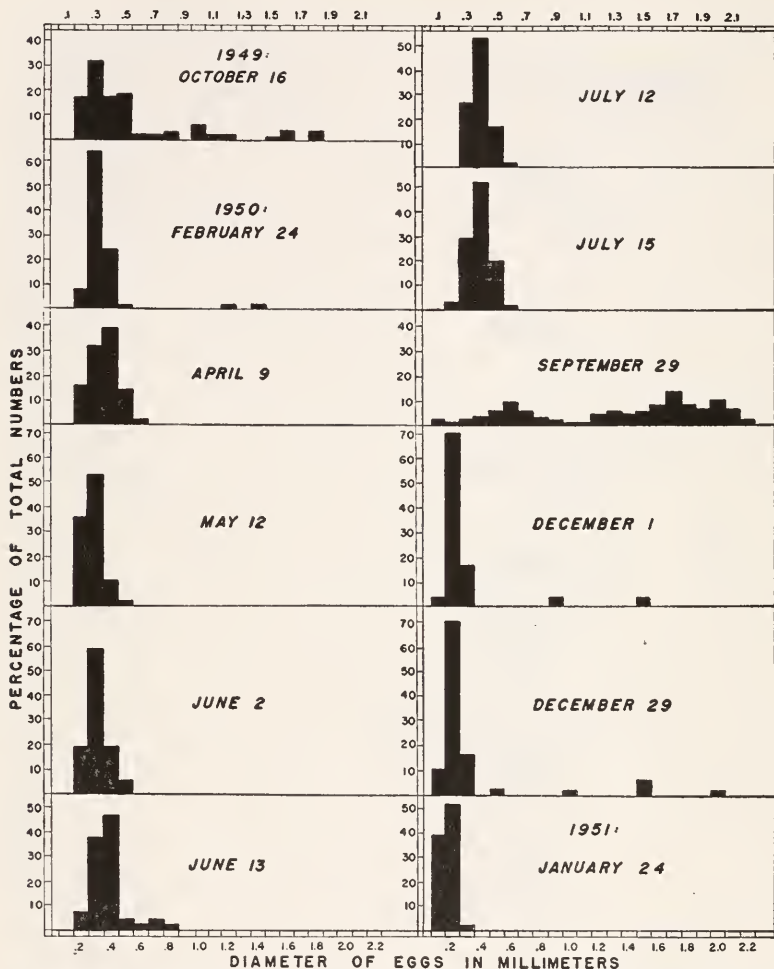


Figure 3. Maturation of ovarian eggs. Each sample is represented by a percentage frequency histogram in which each bar represents the percentage of the total number of individuals within the histogram.

then constituted at least the lower part of group "16".

Group I of February (fig. 2, series I-VI) apparently was constituted of contributions from group "R" (its upper range) and from a group comparable to group "f" of January (its lower range). Representatives of this series were in each sample from February through July 15th. Prior to February some individuals molted to first-form (group "I") and from February through July the majority also molted to first-form contributing to the groups "S" and "2" through "7". From September through December the remaining few molted to first-form and were represented by groups "10", "12" and "15".

Groups "Q" and "W" and the upper part of "S" apparently died in

the spring as indicated by the absence of the proper size in the May and June samples. The upper range of group "R" was probably composed of males recently molted from first- to second-form. Group "T" was a continuation of this group which apparently died by May.

From these conclusions the fate of the January adult group may be stated. The upper ranges of groups "P" and "16" should have died first and the remainder of these groups probably died before the next major reproductive period in 1951. Group "f" should have formed a group comparable to group "I" of February and lived to be about two years old.

The growth trends of the male juveniles (fig. 2, series n, o, p . . . t) were assumed to be essentially similar to those of the female juveniles.

Ovarian Egg Development.—The trend of ovarian egg development for the year 1950 was determined quantitatively from a comparative study of percentage frequency histograms (fig. 3) made for each sample, in which the measurements of ovarian eggs were grouped into 0.10 mm size classes.

Prior to July 12th the ovarian eggs seemed to have been static in size and in this stage did not show any tendency toward maturing at different rates as might have been expected from the study of the egg-laying and rates of development of the young.

Except for the samples of February and June 13th the upper ranges of these did not exceed 0.6 mm (fig. 3). Only two percent of the February sample fell within the higher range, and since it was concluded previously that most of the females had already undergone a molt terminating the major reproductive period, it is inferred that these larger eggs in February were eventually resorbed. Penn (1943) for *Procambarus clarkii* gave evidence that a greater number of eggs may be developed in the ovary than are laid, and Stephens (1952) showed that ovarian eggs are readily resorbed by female *Orconectes virilis* under experimental conditions.

By September the majority of the eggs were in the large size group with peaks at 1.3, 1.7 and 2.0 mm. The presence of these large eggs within the ovaries coincided with the presence of eggs on the pleopods. Within the range below 1.0 mm the peak of 0.6 mm occurred. It is thought that these eggs eventually matured and were laid.

In September another small peak was noted at the 0.10 mm size. These are believed to represent recently developed ovarian eggs of females which had already spawned prior to the date of the sample.

In October females carrying eggs were still present in the samples. Although no ovarian study was made for this month, due to the inadequacy of the sample, it is assumed that the results of the October 1949 analysis would roughly apply. Although apparently egg-laying was still in progress, the majority of the mature female population had already spawned, as indicated by the higher percentages of small eggs.

The December samples showed that at least ninety percent of the population had already laid eggs prior to this date. The large eggs still present in the ovaries represented either those that were eventually resorbed, or that were eventually laid at the individual erratic spawn-

ing times. In general composition this sample compared with that of February 1950.

By January 1951 the ovarian eggs of the females were all immature, indicating that the reproductive period for the population as a whole had definitely terminated.

The reproductive potential was determined from a total count of the ovarian eggs of all mature non-ovigerous females (nineteen) of the September sample. The average of these counts is 14.2 eggs per female within the relatively wide extremes of 9 and 21 (Table 4).

Sex Ratio and Burrowing Responses.—Although burrowing during drought was adequately confirmed by field observation, these activities could not be observed directly during the wet periods and an analysis of the sex ratio of these collections was relied on to furnish these data. It was assumed that if the water samples, which were apparently representative of the water population, did not contain the expected sex ratio, then a significant absence or predominance of one or the other sex for any particular sample would indicate a burrowing component.

The "theoretical sex ratio" was based on the actual sex ratio of the younger male and female homogeneous groups of the February 1950 sample (figs. 1 and 2, groups "A"). The sex ratio for this group was females/males=333/310 or 1.07. This group was chosen because the specimens were large enough to sex easily and all of the young population was assumed to be in the water at this time of the year. To determine the chance differences and real differences between this ratio and the sex ratio of any other group or sample, the limits of a continuum of likely hypothesis (differences due to chance) and the limits marking off two continua of unlikely hypothesis (real differences) were established from the percentage of males to females in the young February groups.

The results of the comparison (Table 5) show that the females were not significantly different from the theoretical sex ratio during the months of February and December 1950 and January 1951, and possibly April 1950. For these months either both sexes were burrowing or both were not and the fact that both sexes were responding alike obscures the issue. However, since all these samples were large in numbers and taken from the ditch during decidedly wet periods (Table 1) it is assumed that most of the population was probably in the water.

Those collections in which the percentages of females were significantly less than the theoretical ratio were the samples of October 1949 and June 13, July 15 and September 1950. Since the females were not in the water samples it is assumed that they were burrowing. Since burrowing coincided in September with the presence of large eggs in the ovaries (fig. 3) or the presence of eggs on the pleopods, it is concluded that the egg-laying activity was a stimulus to burrowing. This conclusion lends corroboration to the possibility of erratic or pre-seasonal reproductive activities of the June 13 and July 15 samples as already indicated (fig. 3) from the study of ovarian eggs.

Analyses of the samples taken from burrows indicates that with one

TABLE 4.
OVARIAN EGG PRODUCTION

Cephalothorax Length (mm)	Number of Eggs of Individual Females	Total Number of Females of Size Class	Total Number of Eggs of Size Class	Average Number Eggs per Female
13.1	11	1	11	11.0
13.3	12, 16	2	28	14.0
13.5	10, 11, 12	3	33	11.0
13.7	9, 12, 16, 20, 21	5	78	15.6
13.9	15, 15, 18	3	48	16.0
14.1	13, 14	2	27	13.5
14.3	12, 15, 18	3	45	15.0
		—	—	—
	GRAND TOTAL	19	270	14.2

exception (July 12) there was a significant absence of females in each of the dry samples. Since it has been established that the entire population burrowed during drought there is no logical reason why the females should not have been collected except that the technic of dry sampling was inadequate. The only other conclusion would be that of a mass death of only the females during drought times and this is biologically unacceptable.

SUMMARY AND DISCUSSION OF LIFE CYCLE

During the dry periods the crawfishes burrowed along the sides of and in the bottom of the ditch instead of migrating to the adjacent slough, a permanent body of water. There was no evidence during the course of this study to indicate that the crawfish ever migrated over dry land; however, dispersal was possible and evidences of it were observed during periods of flooding rains. Ovigerous females were found in burrows regardless of the conditions in the ditch. Indeed, the first ovigerous females collected were dug from burrows alongside the flooded ditch in September. It may be significant that immediately following this observation a drought period ensued and the remainder of the population was forced to burrow. The females carrying the vulnerable eggs were thus, by natural instincts, already in protected burrows when the drought conditions began. It would seem that an ovigerous female could not be so agile or successful a burrower as one unencumbered by eggs. However, it is not known whether spawning females burrowed before or after laying their eggs.

The eggs of *O. clypeatus* are surprisingly large in comparison to the relatively small size of the females carrying them. This certainly is correlated with the low average of 14.2 eggs per female, and perhaps the whole concept is correlated with the burrow habitat of the ovigerous females. It is interesting, and possibly significant, that a very low reproductive potential also obtains in *Procambarus hagenianus* (Faxon) in which the females similarly shun free-water when ovigerous (Lyle, 1938).

Ovigerous females were collected on September 29 and October 15, 1950. No collections at all were made in November, but females collected on December 1st were carrying young still clinging to their pleopods. Although the length of time between oviposition and hatching, and the time that females normally carry their young was not determined it is assumed that both time periods were of short duration since free-living young first appeared in the population in the October 15th sample, about two weeks after the first ovigerous females were collected.

The juveniles of January 1951 were represented by five overlapping age groups. Three groups comparable to the three larger groups of this sample probably participated in the major spawning period (September-October) of 1950. Groups comparable to the two younger groups of January 1951 may have given rise to groups that spawned erratically (*i.e.*, post-seasonal: November-December) during 1950.

As a group the maturing females increased significantly in size from February to early June. From this date until July 15th they

TABLE 5.

SEX RATIOS

Date	Range	Total Crawfish	Males	Females	Percent of Females
1949:					
Oct. 16	All	68	51	17	25
1950:					
Feb. 24	Adults	122	55	67	55
	Juveniles	654	316	338	52
Apr. 9	All	453	240	213	47
May 12	All	192	107	85	44
June 2	All	137	87	50	36
June 13	All	340	184	156	46
July 12	All	59	27	32	54
July 15	All	169	96	73	43
Sep. 29	All	131	95	36	27
Dec. 29	Adults	47	24	23	49
	Juveniles	300	146	154	51
1951:					
Jan. 24	Adults	107	51	56	52
	Juveniles	848	389	459	54

remained nearly static in size, but between mid-July and September they again increased significantly in size, presumably undergoing a maturity molt. Another molting period ensued during December and January marking the termination of the active reproductive period for the majority of the mature females. Apparently most of these females lived about a year and a half, dying before the next major spawning period. The females that were already a year old in early 1950 probably constituted an erratic pre-seasonal (July-August) spawning group in 1950 and died in the first months of 1951 at an age of about two years.

As a group the males were similar to the females in growth patterns. The maturing second-form males increased significantly in size until May at which time the growth plateau was reached. During May a few of this group molted into first-form males. By September the majority of them molted into first-form except the very youngest. These latter apparently transformed towards the end of December and formed an erratic post-seasonal spawning group among the males. Many of the first-form males molted back to second-form during December and January. The participants of the major spawning group lived to be about one year old, while the participants of the post-seasonal spawning period lived to be about two years old.

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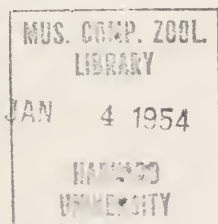
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MARINE PELECYPODS IN LOUISIANA
(COPEPODA, CYCLOPOIDA)

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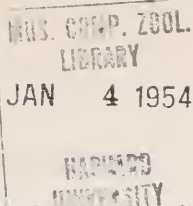
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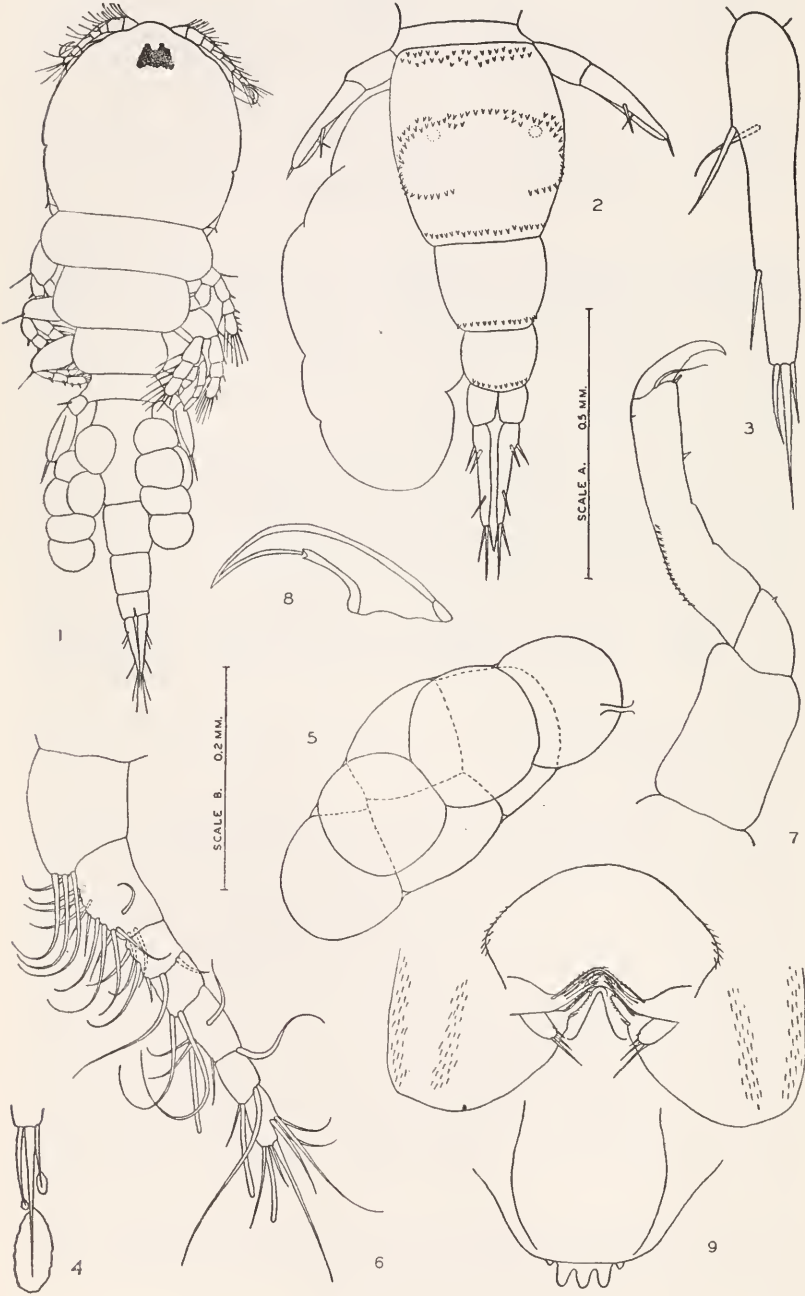
In June, 1947, a parasitic copepod, *Ostrincola gracilis* C. B. Wilson (1944), was discovered in the mantle cavity of four species of pelecypods from the Barataria Bay region of Louisiana. The hosts were the Virginia oyster (*Crassostrea virginica* Gmelin), the ribbed mussel (*Modiolus demissus granosissimus* Sowerby), the recurved mussel (*Mytilus recurvus* Rafinesque), and the hard shelled clam or quahaug (*Venus mercenaria mercenaria* Linné.).

A study of the copepods thus obtained has revealed certain important omissions and inaccuracies in the original description. The holotype and allotype specimens, U. S. National Museum No. 79697, have not been available for dissection and study, but a male and a female, U. S. National Museum No. 79698, having the same collection data as the holotype and allotype and apparently paratypes though not designated as such by Wilson, have been compared in detail with the Louisiana forms. The specimens from Louisiana proved to be conspecific with the actual specimens of *O. gracilis* as identified by Wilson.

For helpful suggestions in connection with this paper I am indebted to Mrs. Mildred S. Wilson.

Female.—The body (fig. 1) in living specimens is colorless, except for a dark reddish-black median eye and a brownish intestine. (In glycerine and polyvinyl alcohol mounts the eye is bluish.) The total length (from the tip of the head to the posterior end of the caudal rami), based on an average of five specimens, is 1.083 mm and the greatest width of the cephalothorax is 0.274 mm. The abdomen is three-segmented. The ventral surface of the genital segment and abdomen bears minute spines arranged as in figure 2, but the dorsal surface lacks spines. The caudal ramus (fig. 3) bears three terminal setae and three along its outer edge. The terminal setae in many specimens show brownish accretions around their tips (fig. 4). The egg sacs (fig. 5) both contain about seven eggs and are attached dorsolaterally. The first antenna (fig. 6) has seven podomeres and bears several aesthetes. The arrangement of the setae on the distal podomere suggests a subdivision into two podomeres

¹ The material upon which this paper is based was collected while the author was a guest investigator at the Louisiana State University Marine Laboratory at Grand Isle, Louisiana.



but there is no articulation. The second antenna (fig. 7) has a notch-like interruption on the inner margin of the claw (fig. 8).

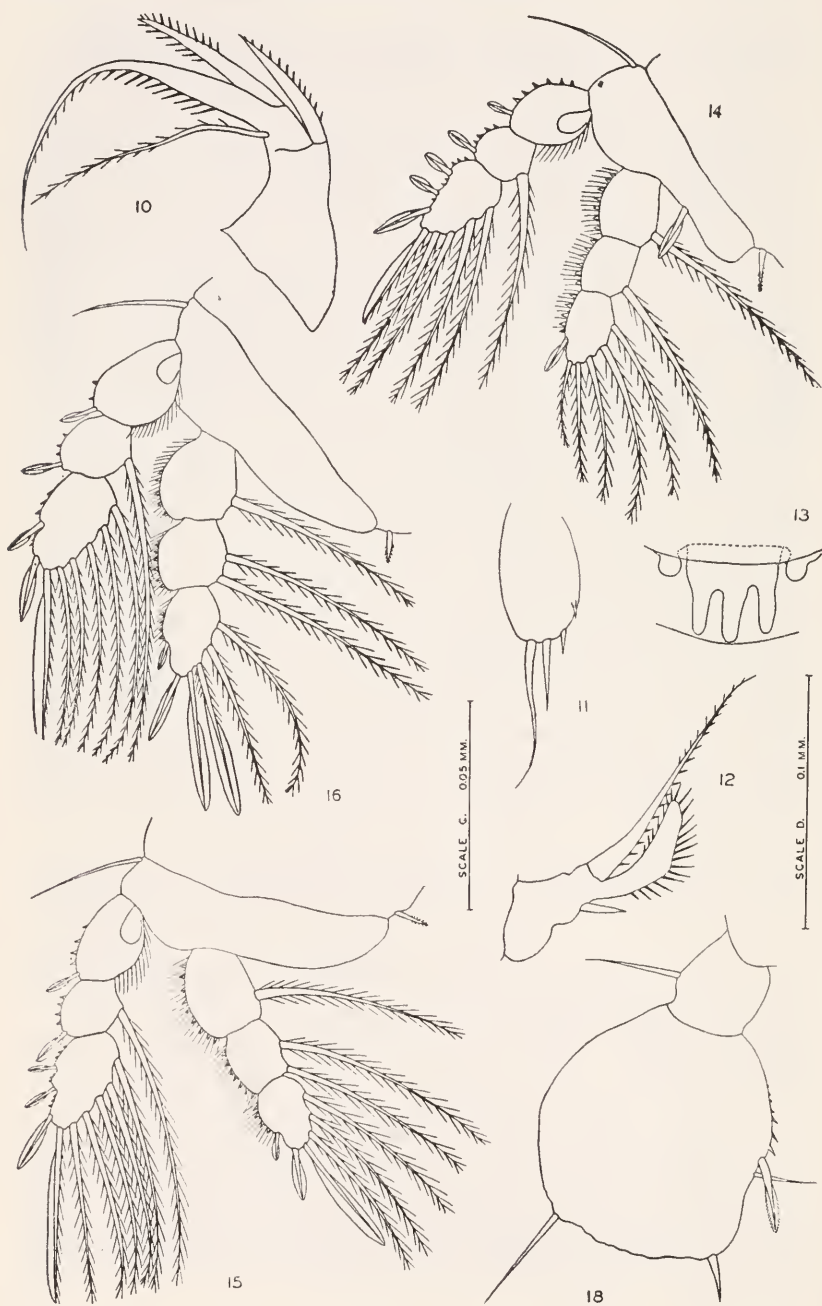
The mouthparts (fig. 9) are much reduced. The labrum is wider than long and bears on each side a group of small spines. Its posterior edge seems to be entire and not deeply incised, although this feature is difficult to ascertain because of the impinging of the labrum and the mouthparts. The mandible (fig. 10) has a somewhat elongated base with an apical armature of four elements. The first maxilla (fig. 11) is minute and arises from a point along the distal half of the basal part of the mandible. In unmounted specimens the first maxillae extend nearly vertically from the ventral body surface, but in pressed whole mounts they appear to be directed more posteriorly. Each first maxilla consists of a single lobe bearing four setae which are progressively shorter toward the midline of the body. The second maxilla (fig. 12) has a much inflated basal part and a relatively small apex with tripartite armature. The distal portions of both the mandibles and the second maxillae in unmounted specimens are directed vertically from the ventral body surface and somewhat anteriorly. The mandibles and both pairs of maxillae are minute and closely appressed, so that it is only with great care that they can be isolated for study. The labium is small and rather poorly delimited, with a longitudinal concavity on its posterior surface. The maxillipeds are lacking. In the median region of the head posterior to the labium there is a prominent postoral protuberance, especially conspicuous in lateral view. In the midline of the body on the anterior surface of the ridge between the bases of the first pair of legs there is a trilobed structure (fig. 13). In pressed specimens this trilobed area appears to be overlapped by the posterior edge of the postoral protuberance.

The first, second, third, and fourth swimming legs are shown in figures 14-17 respectively. The spine and setal formula is as follows:

	leg 1		leg 2		leg 3		leg 4	
	exp	end	exp	end	exp	end	exp	end
first podomere	1:0	0:1	1:0	0:1	1:0	0:1	1:0	0:1
second podomere	1:1	0:1	1:1	0:2	1:1	0:2	1:1	0:2
third podomere	8	6	9	6	8	6	8	5

The fifth leg (fig. 18) has two podomeres, the proximal one small with a single outer seta, the distal one expanded into a broad, in-

Figures 1-9. *Ostrincola gracilis*, female: 1, dorsal view; 2, genital segment and abdomen, ventral view; 3, caudal ramus; 4, terminal setae of caudal ramus with accretions; 5, egg sac; 6, first antenna; 7, second antenna; 8, detail of claw of second antenna; 9, area of mouthparts.



wardly concave disk with four marginal setae.

Male.—The color in life resembles that of the female. The total length, based on an average of five specimens, is 0.760 mm and the greatest width of the cephalothorax is 0.200 mm. The abdomen is four-segmented (fig. 19). The ventral surface of the genital segment and abdomen bears minute spines as in figure 20. The caudal rami are like those of the female. The first antenna (fig. 21) has seven podomeres, with all but the proximal one having an aesthete.

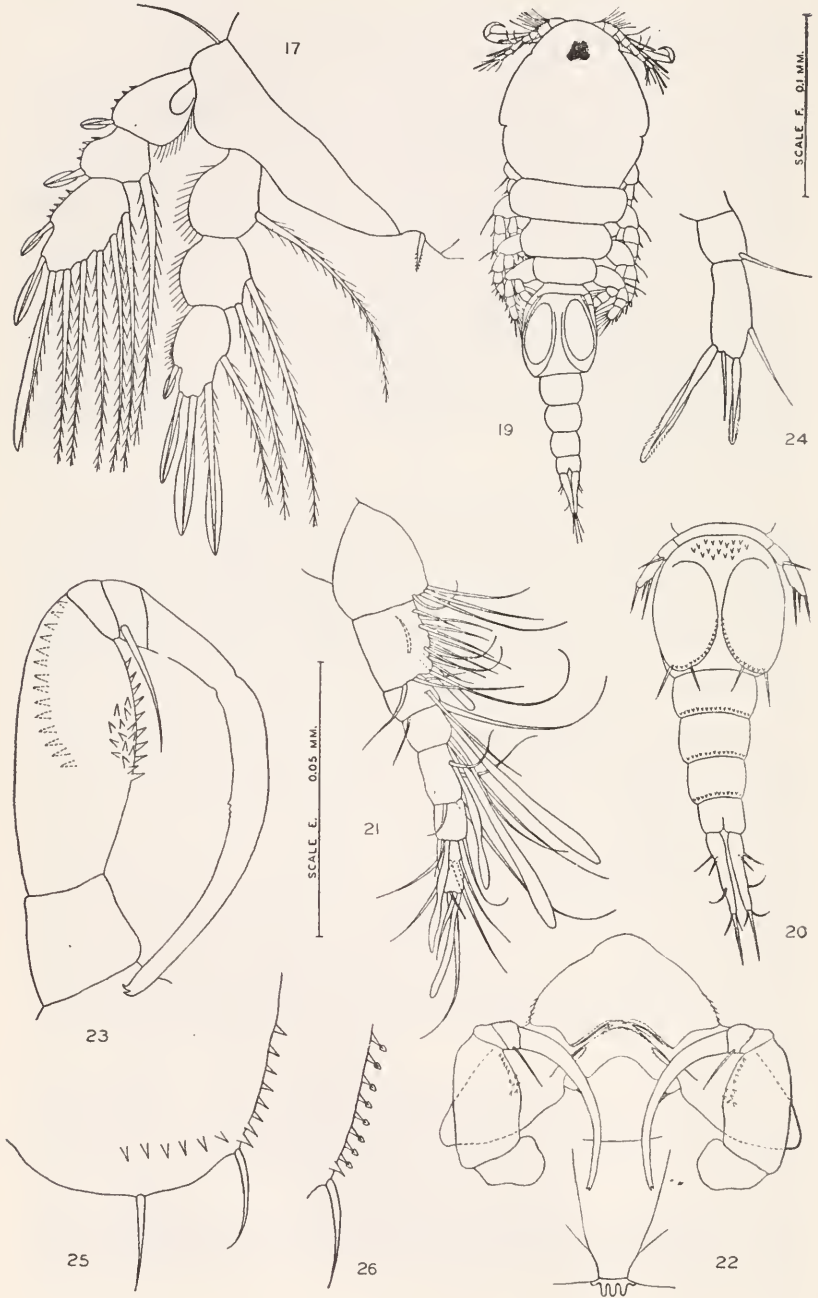
The second antennae, mandibles, first maxillae, and second maxillae are like those of the female. The maxilliped (figs. 22, 23) has five podomeres, the proximal one short, the second large and spinose on its outer and inner margins, the third short, the fourth short also with an inner seta, and the last elongated, arcuate, and slender. The last podomere is as long as or slightly longer than the rest of the podomeres together.

The four pairs of swimming legs are identical in structure with those of the female, having the same spine and setal arrangement. The fifth leg (fig. 24) has two podomeres, the first with a single outer seta, the second longer, not expanded, but with more or less parallel margins, and with four marginal setae. The sixth leg (figs. 20, 25) consists of two setae at the posterior corner of the genital segment. In a few males some of the spines near the sixth legs show brownish caps covering their tips (fig. 26).

Remarks.—*Ostrincola* seems to stand between the ergasilid genus *Myicola* Wright (1885) and the Lichomolgidae as represented by the genus *Pseudomyicola* Yamaguti (1936). The segmentation and armature of the first antenna, the mandible, the first and second maxilla, the male maxilliped, and the segmentation and armature of legs 1-4 resemble *Myicola metisiensis* Wright. In two respects at least *Ostrincola* differs from *Myicola*. The second antenna is rather elongated and slender, while in *Myicola* it is shortened and robust. The distal podomere of the fifth leg in the female is much expanded, while in *Myicola* it has nearly subparallel margins. In both these characters *Ostrincola* resembles the condition in *Pseudomyicola*, differing from that genus, however, in the first antenna, the mandible, and other features.

The generic validity of *Ostrincola* seems to rest upon the future discovery of other related species. In the meantime, however, the original generic description may be emended as follows:

Figures 10-16, 18. *Ostrincola gracilis*, female: 10, mandible; 11, first maxilla; 12, apex of second maxilla; 13, trilobed structure between bases of first legs; 14, first leg; 15, second leg; 16, third leg; 18, fifth leg.



OSTRINCOLA Wilson 1944, *emended diagnosis*

Body cyclopoid with head and first thoracic segments fused. Thoracic segments 2-5 diminishing regularly in width. Genital segment longer than wide. Abdomen three-segmented in the female, four-segmented in the male. Caudal rami much elongated and sub-cylindrical. Sexual dimorphism not pronounced. Attachments of egg sacs dorsolateral; eggs relatively few in number.

First antenna in both sexes with seven podomeres. Second antenna uniramous, with four podomeres, the penultimate relatively long and slender and the last a curved claw. Mandible with a moderately long basal portion bearing an apical armature of four parts, directed anteriorly. First maxilla a minute somewhat posteriorly directed lobe arising from the area immediately behind the distal half of the base of the mandible and bearing four unequal setae. Second maxilla with a much inflated basal part and a small apical portion with tripartite armature, directed anteriorly. Anterior to the mouthparts a swollen labrum without a deeply incised posterior edge, and posterior to them a rather weakly developed labium. Behind the labium a swollen postoral protuberance. Maxillipeds lacking in the female. The male maxilliped large, with five podomeres, the second podomere elongated and relatively stout, the last podomere slender, arcuate, and about as long as the other four podomeres together.

Legs 1-4 biramous, the rami with three podomeres, and the spine and setal formula as in *Myicola*. Fifth leg uniramous in both sexes, with two podomeres; the distal podomere in the female expanded into a broad, inwardly concave disk armed along the margin with four setae, in the male elongated with subparallel margins, similarly armed.

Genotype.—*Ostrincola gracilis* Wilson 1944.

The major points in the emendation concern the number of abdominal somites, the number of first antennal podomeres, the nature of the mouthparts, and the number of podomeres in the fifth legs.

Occurrence.—In Barataria Bay *O. gracilis* was found near Chene Fleurie in *Mytilus* and *Crassostrea*, in Sugarhouse Bend Bayou at Grand Terre in *Mytilus* and *Crassostrea*, and in the tidal marsh back of Grand Isle in *Venus*, *Crassostrea*, and *Modiolus*. The collection data are summarized in Table 1.

Figures 17, 19-26. *Ostrincola gracilis*, female: 17, fourth leg. Male: 19, dorsal view; 20, genital segment and abdomen, ventral view; 21, first antenna; 22, area of mouthparts; 23, maxilliped; 24, fifth leg; 25, sixth leg; 26, setae of sixth leg with cap-like coverings.

TABLE 1
INCIDENCE OF *Ostrincola gracilis* IN PELECYPODS OF THE BARATARIA
BAY REGION OF LOUISIANA.

Clam Host	Number Examined	Number with <i>O. gracilis</i>	Percent Parasitized	Average Number Per Host
<i>Crassostrea virginica</i>	399	157	39.3	1.88 (1-11)
<i>Modiolus demissus</i> <i>granosissimus</i>	241	89	36.9	1.73 (1-7)
<i>Mytilus recurvus</i>	45	7	15.5	1.14 (1-2)
<i>Venus mercenaria</i> <i>mercenaria</i>	1	1	100	2
	686	254	37.0	1.81 (1-11)

Ecological notes concerning the four species parasitized are to be found in the publication of Harry (1942). According to observations previously made (Humes, 1942) the water in Barataria Bay seldom exceeds ten feet in depth, except in the passes leading to the open Gulf. The bottom is largely composed of sand and silt with extensive areas devoted to oyster beds. The summer water temperature ranges from 25.8 to 29.8° C. The salinity at Chene Fleurie is 9.18 grams per liter, while at the eastern end of Grand Terre near Sugarhouse Bend Bayou it is 25.30. Although no ecological information was given by Wilson (1944) regarding the type specimens at Beaufort, North Carolina, it seems probable on the basis of the Louisiana material that this copepod will be found as a parasite in pelecypods living in shallow-water, estuarine regions which are protected from the open sea.

EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida. Scale **A** applies to figures 1 and 19; scale **B** to figures 2, 5, and 20; scale **C** to figures 3, 4, 13, 23, 25, and 26; scale **D** to figures 6, 7, 14-18, 21, and 24; scale **E** to figures 8, and 10-12; and, scale **F** to figures 9 and 22.

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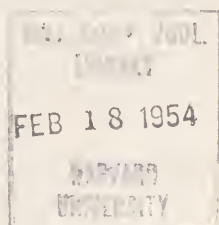
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HYBRID INVIABILITY BETWEEN *RANA PIPIENS* FROM
WISCONSIN AND MEXICO

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HYBRID INVIABILITY BETWEEN *RANA PIPIENS* FROM WISCONSIN AND MEXICO¹

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Laboratory crosses among individuals of various populations of the widely-distributed meadow frog, *Rana pipiens*, have revealed the extent to which intraspecific gene exchange is possible. The occurrence of abnormalities in hybrids between certain geographical populations of *R. pipiens* has been demonstrated by Moore (1949a). In general, the intensity of hybrid defects is inversely proportional to the north-south distance between the localities of the parents employed in the laboratory hybridizations. It has also been shown (Moore, 1949b) that the geographically extreme northern and southern populations of this species differ in embryonic rate of development and embryonic temperature tolerance. Moore has inferred that these embryological differences represent differential adaptations to environmental temperatures, and he further surmises that the embryonic defects in hybrids between northern and southern individuals may be associated with the different temperature adaptations of the parental eggs.

The most severe abnormalities have been observed in hybrids between *R. pipiens* from Alburg, Vermont and two localities in eastern Mexico, Monterrey in Neuvo Leon and Axtla in San Luis Potosi (Moore, 1947).

In the present investigation, meadow frogs obtained simultaneously from a different northern locality, Oshkosh, Wisconsin and several localities in the State of Tamaulipas, Mexico provided the opportunity to hybridize the respective groups, and thus contribute additional information on the problem of geographical differentiation and the development of isolating mechanisms in populations of *R. pipiens*.

EXPERIMENTAL

A comparison was made of the rate of embryonic development and embryonic temperature tolerance of *R. pipiens* from Mexico and Wisconsin to determine if differences existed, and reciprocal hybrid crosses were conducted to ascertain the extent of developmental compatibility. The methods of experimentation were essentially similar to those employed in other work of this type (Moore, 1946, 1949b; Volpe, 1952, 1953). The technique, and the modifications introduced, will be brought out during the discussion of the experiments.

Embryonic temperature adaptations.—Ovulation of Mexican and Wisconsin meadow frogs was induced by pituitary injection. The

¹ Aided by a grant from the Tulane University Council on Research. I am indebted to Dr. R. M. Darnell of Tulane University for collecting the meadow frogs from Mexico, and to Miss Vera Morel for the drawings used in illustrating this paper.

eggs were stripped from the females into sperm suspensions prepared by macerating the testes of a male in 10-20 cc. of 0.1% Ringer's solution. Eight artificial fertilizations, in groups of two, were conducted. Each fertilization of a Mexican ♀ X Mexican ♂ was carried out simultaneously with a cross Wisconsin ♀ X Wisconsin ♂. By conducting parallel fertilizations, differences in rate of development of Mexican and Wisconsin embryos were readily apparent. The four ovulated Mexican females were derived from four different localities, as follows: (1) Storm's Ranch, 7 km. northeast of Gomez Farias, Tamaulipas; (2) La Union, 9½ km. north of Gomez Farias, Tamaulipas; (3) El-Mante-Tampico Highway, 29 km. east of El Mante, Tamaulipas; (4) El Mante-Tampico Highway, 72 km. east of El Mante, Tamaulipas. All four Wisconsin mating pairs employed came from Oshkosh, Wisconsin.

The egg masses from any single fertilization were cut into small clusters of 9 to 13 eggs to permit more surface for respiration. The eggs clusters were placed in finger bowls, each finger bowl containing ten clusters (referred to as a "group") in 200 cc of 0.1% Ringer's solution. The finger bowls were then distributed to constant temperature units, which maintained temperatures accurate to $\pm 0.2^{\circ}\text{C}$. Development of four groups of Wisconsin eggs and four groups of Mexican eggs was observed at 18.9°C ., 21.1°C ., 27.5°C ., 29.5°C ., and 33°C .

The eggs derived from the Mexican females were larger than those obtained from the Wisconsin females. Measurements of the eggs (vitellus diameter) prior to first cleavage were made by means of an ocular micrometer calibrated from a 1/100 millimeter-ruled stage micrometer. The diameters of 86 Wisconsin eggs ranged from 1.60 mm. to 1.95 mm., the mean and standard deviation being 1.73 ± 0.08 . Similar measurements of 101 Mexican eggs indicated a range of 1.95 mm. to 2.20 mm. (2.10 ± 0.06). The difference is significant (the difference of the means is three times the standard error of the difference). Although a few of the Wisconsin eggs approached the size of the Mexican eggs, a *cluster* of the latter could be readily distinguished with the unaided eye from a *cluster* of the former. This detectable difference in egg size (recall the relation of the volume of a sphere to its radius) made it possible to keep both the Mexican and Wisconsin clusters of eggs in the same finger bowl containing Ringer's solution at a desired temperature. This procedure reduced the error of developmental deviations due to any temperature variations which may have been encountered if each group of eggs had been kept in separate finger bowls. No difficulty was experienced in identifying the two groups of eggs while they developed within the jelly membranes. To obviate any difficulty in later development, the embryos of each group just prior to hatching were separated into individual finger bowls containing fresh 0.1% Ringer's solution which previously had been brought to the desired temperature.

TABLE 1.
A COMPARISON OF DEVELOPMENT IN EGGS OF *Rana pipiens* FROM MEXICO AND WISCONSIN
AGE IN HOURS BETWEEN STAGES 3 AND 20

Experiment 1			18.9° C.		Experiment 2			18.9° C.		Experiment 3			21.1° C.		Experiment 4			21.1° C.	
Age in Hours	La Union, (110) ^a	Oshk., Wisc. (104)	Age in Hours	El Mante 29 km. e, Mex. (115)	Oshk., Wisc. (111)	Age in Hours	Storms Ranch, Mex. (111)	Oshk., Wisc. (105)	Age in Hours	El Mante 72 km. e, Mex. (116)	Oshk., Wisc. (109)	Age in Hours	Storms Ranch, Mex. (111)	Oshk., Wisc. (105)	Age in Hours	El Mante 72 km. e, Mex. (116)	Oshk., Wisc. (109)	Age in Hours	El Mante 72 km. e, Mex. (116)
0	3 ^b	3	0	3	3	0	3	3	0	3	3	0	3	3	0	3	3	0	3
11.0	7	7	18.2	9	9	6.0	7	7	8.2	8	8	8.2	8	8	8.2	8	8	8.2	8
13.2	8	8	24.5	10L	11E	13.5	9	9	18.2	11E	10M	18.2	9	9	18.2	11E	10M	18.2	11E
16.2	9	9	31.2	12E	12L	16.5	10E	10E	24.2	12M	12E	24.2	10E	10E	24.2	12M	12E	24.2	12M
20.5	10E ^c	10E	40.5	13E	13M	23.2	12E	11M	29.0	13E	12L	29.0	12E	11M	29.0	13E	12L	29.0	13E
32.5	12M	12L	44.0	13L	14E	26.5	12L	12M	31.5	13M	13E	31.5	12L	12M	31.5	13M	13E	31.5	13M
38.5	12L	13E	46.5	14E	14M	38.7	14L	14M	35.0	14M	14E	35.0	14L	14M	35.0	14M	14E	35.0	14M
44.5	13L	14E	49.2	14M	14L	41.0	16E	14L	47.2	16L	16M	47.2	16E	14L	47.2	16L	16M	47.2	16L
56.7	16E	16M	52.2	15	16E	45.5	16M	16E-M	55.0	17E-M	17E	55.0	16M	16E-M	55.0	17E-M	17E	55.0	17E-M
64.0	16L	17E	64.5	16L	17E	50.5	16L	16M	66.2	18M-L	18E-M	66.2	16L	16M	66.2	18M-L	18E-M	66.2	18M-L
70.5	17M	17L	70.5	17M	17L	64.0	18M	18E	69.5	18L	18M	69.5	18M	18E	69.5	18L	18M	69.5	18M
81.0	18E	18M	76.7	17L	18E	71.5	19E	18L	78.0	19M-L	19E	78.0	19E	18L	78.0	19M-L	19E	78.0	19M-L
93.0	19E	19M	91.2	18L	19E	76.2	19L	19E	80.0	20E	19L	80.0	19L	19E	80.0	20E	19L	80.0	19L
96.7	19M	19L	95.0	19E	19M-L	79.0	20E	19L	83.0	—	—	83.0	20E	19L	83.0	—	—	83.0	—
101.0	19L	20E	98.5	19M	19L	82.5	—	20E	—	—	—	—	—	20E	—	—	—	—	—
105.0	20E	—	102.0	19L	20E	—	—	—	—	—	—	—	—	—	—	—	—	—	—
			104.7	20E	—														

^a The number in parentheses indicates the number of embryos examined.

^b The embryos were considered to be in a given stage when 50 percent or more of them exhibited the characteristics for that stage.

^c The stages are described in Pollister and Moore (1937); the letters E, M, and L signify early, middle and late.

The rate of development was determined by examining the groups of embryos at each of the constant temperatures at frequent intervals from first cleavage to gill circulation. Certain problems arise in obtaining an adequate measure of the time required by a group of embryos to reach a given stage. Even when special precautions are taken to provide as uniform an environment as possible, eggs within a group exhibit variation in the speed with which they reach a given point in development. Thus, to permit statistical comparison between two groups of developing eggs, it would be desirable to make repeated observations to determine when 100 percent of the eggs had reached a particular morphological stage. This is laborious and tedious and even if this procedure were practical, it would be necessary to break the continuous embryonic development into a series of extremely minute discontinuous steps to permit an accurate determination of the extent of variation. The problem was attacked by selecting morphological stages at which recognizable specific processes begin, and the onset of a given stage was taken as the time at which 50 percent or more of the eggs within a group entered that stage. The stages drawn up by Pollister and Moore (1937) were employed, with the further refinement of designating the stages as early (E), middle (M), and late (L). In comparing two groups of eggs which were developing at different speeds, an estimate of the variability was obtained by noting the percent of embryos in the more slowly developing group which were as advanced as the majority of embryos in the second group which exhibited the faster rate of development. In all experiments, it was found that only five percent or less of the more slowly developing group of embryos were as advanced as the majority (50 percent or more) of the faster developing group of embryos; nor were there more than five percent of the faster developing group of embryos in as early a stage as the majority (50 percent or more) of the more slowly developing group of embryos. Moreover, the arbitrary criterion of 50 percent was found to be a conservative figure. From fertilization to stage 17 (tail bud stage) 80 percent or more of the embryos reached a given stage simultaneously; from stage 18 (muscular contraction) onward, 70 percent or more of the embryos entered a particular stage at the same time. Thus, although it is difficult to analyse the spectrum of variation, the ascertainment at any one reading of the norm of a group and the extreme variants of that group (in relation to the other group being compared) permits an accurate determination of comparative rates of development.

No differences could be detected in the rate of development of the four groups of Mexican embryos at each of the experimental temperatures. However, the groups of Mexican embryos differed in rate of development from those derived from Wisconsin. In Table 1 a comparison is made of the time in hours required by 50 percent or more Mexican and Wisconsin embryos within a group to reach the experimental end-point, stage 20, at two temperatures, 18.9°C

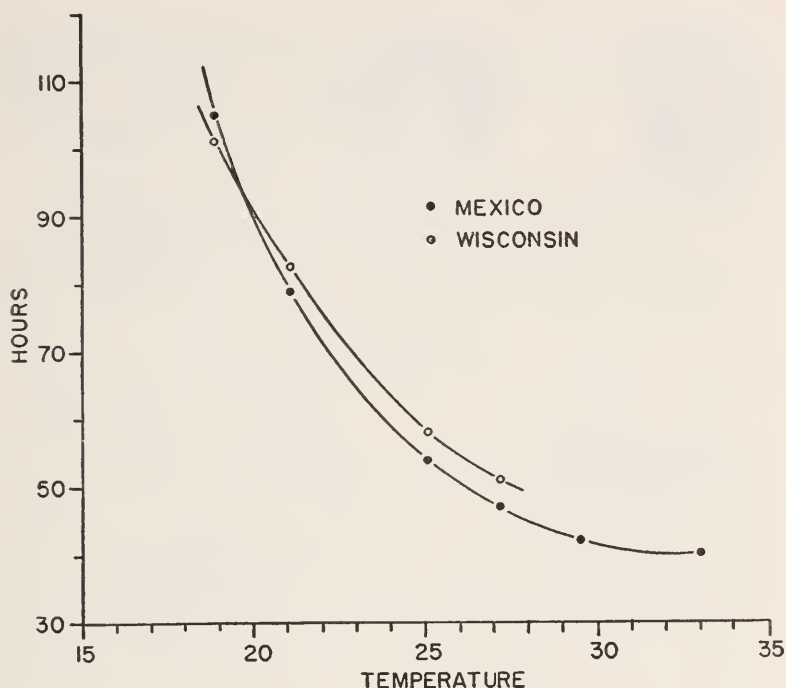
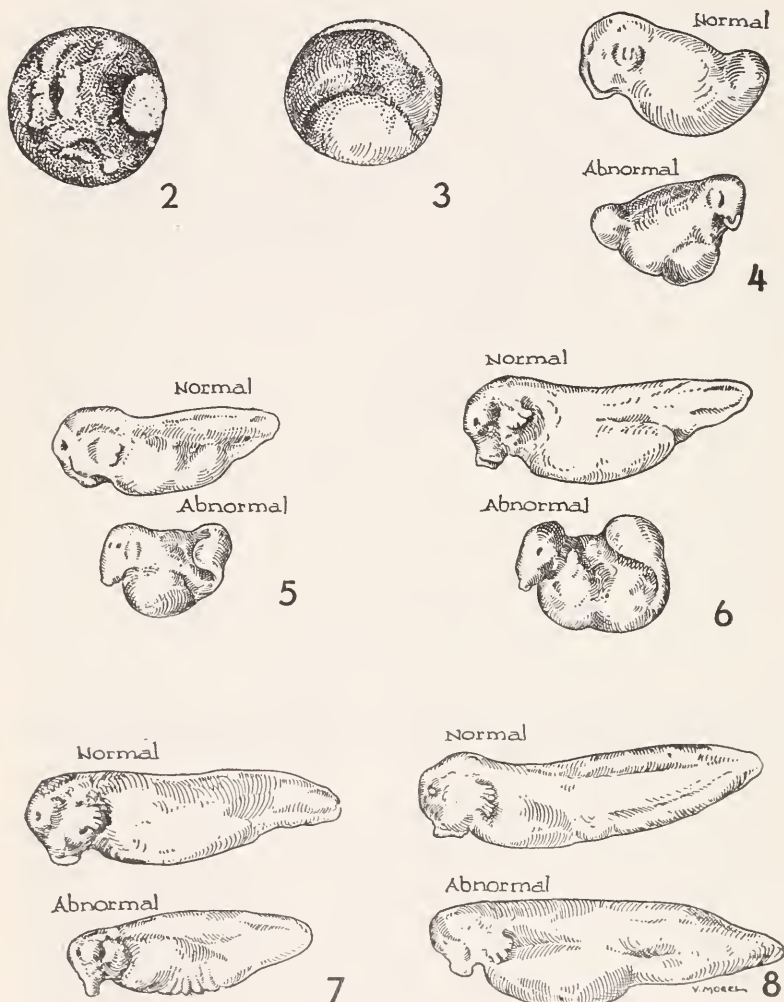


Figure 1. A comparison of the mean time, in hours, between stages 3 and 20 at different temperatures, in degrees Centigrade, of embryos of *Rana pipiens* from Mexico and Wisconsin.

and 21.1°C. At 18.9°C, the embryos from each of the different localities in Mexico developed more slowly than the Wisconsin embryos. At 21.1°C. (and higher temperatures), the Mexican embryos developed more rapidly. Figure 1 shows a plot of the mean time in hours between stages 3 and 20 required by four groups of Mexican embryos and four groups of Wisconsin embryos at the different temperatures employed. The faster rate of development of Mexican embryos at higher temperatures may be associated with the greater tolerance of these embryos to high temperatures.

To estimate temperature tolerance, records were made of the types and proportions of embryonic abnormalities at each temperature. The Mexican embryos are decidedly better adapted to the higher temperatures. At 33.0°C, early death of all of the Wisconsin embryos was evidenced by irregular cleavage furrows. At this same temperature, the Mexican eggs cleaved normally, but the majority of the eggs later exhibited defects in gastrulation. However, an average of 13 percent for the four groups of embryos (57 of a total of 437 eggs) developed to the gill circulation stage (stage 20). At 29.5°C,



Figures 2-8. Development of hybrid embryos from the cross La Union, Mexico ♀ X Oshkosh, Wisconsin ♂. Control embryos (La Union, Mexico ♀ X La Union, Mexico ♂) are shown in some figures for comparison. For full explanations, see text. 2. The pitted appearance of the ectodermal surface of an early hybrid gastrula; 3. The furrow encircling the hybrid egg and the narrow depression on the dorsal side representing the neural groove; 4. *Top*: normal appearance of the tail-bud stage (stage 17) in a control embryo; *Bottom*: hybrid embryo with extreme reduction of head, fused oral suckers projecting from head, and the ventral abdominal bulge; 5. *Top*: heart beat stage (stage 19) in a control embryo; *Bottom*: shrivelled appearance of hybrid embryo showing abbreviated head,

only a few developmental irregularities (total average of nine percent for four groups of embryos) were noted in the Mexican embryos. In contrast, the Wisconsin embryos developed only as far as the neurula stage. Moreover, development was normal in the Mexican embryos at 27.5°C, whereas 85 percent (390 of a total of 460 eggs) of the Wisconsin tadpoles were distorted.

At the low temperature extreme, adequate temperature control was not available. However, some indication of the differential effects of low temperature on the embryos was obtained by placing the developing eggs in a refrigerator which fluctuated from 6°C to 9°C. Four groups of Mexican eggs (total of 392 eggs) failed to cleave and 436 Wisconsin eggs developed normally up to stage 17 (300 hours), at which time the experiment was terminated. It appears that the embryos of *R. pipiens* from Wisconsin behave like those of other northerly distributed amphibians in being able to tolerate low temperatures.

In all probability, the differences in rate of development and temperature tolerance of Mexican and Wisconsin eggs represent adjustments that adapt the eggs to their respective environments. However, data on prevailing environmental conditions, particularly temperatures of their breeding waters, are lacking. Also, it seems reasonable to suspect that the improper interadjustments of morphogenetic movements observed in hybrid development (discussed below) are attributable, at least in part, to conflicting modes of action of temperature-related processes.

Reciprocal artificial hybridizations.—The procedure in artificial hybridization consisted of fertilizing the eggs of one female from a particular locality in two batches: the first with the sperm of a male derived from the same locality ("control"), and the second with the sperm of a male from a different locality ("hybrid"). Eight hybrid crosses were conducted, four of which involved a Mexican *pipiens* egg and a Wisconsin *pipiens* sperm each with controls ("Type A" cross); the others were reciprocal crosses each with controls ("Type B" cross). The hybrid embryos from the two types of crosses were

ventral abdominal bulge, and the curved tail (the confining inner jelly membrane is not shown); 6. *Top*: gill circulation stage (stage 20) in a control embryo which has hatched from the jelly membranes; *Bottom*: hybrid embryo showing little progress made over previous stage (fig. 5); the hybrid embryo is still trapped within the inner jelly membrane, but this is not shown in the illustration; 7. *Top*: gill circulation stage (stage 20) in a control embryo; *Bottom*: an exceptional hybrid embryo which has hatched, showing the wrinkled blastocoele roof in the ventral abdominal region and the microcephalic condition with the downward projecting fused oral suckers; 8. *Top*: tail fin circulation stage (stage 22) in a control embryo; *Bottom*: a surviving hybrid embryo in which considerable reorganization has taken place: the ventral abdominal bulge has disappeared and the head tends toward a normal condition; however, mouth and eye formations are atypical.

characterized by retarded developmental rates and extensive structural abnormalities. Within each type of cross the results were essentially similar; thus only a single cross of each type will be described in detail.

Type A, Cross 1:

La Union, Mexico ♀ X Oshkosh, Wisconsin ♂

La Union, Mexico ♀ X La Union, Mexico ♂ (Control)

Conducted at 18.9°C.

The rate of development in the early cleavage stages was maternal and the cleavage furrows were normal. The first indication of hybrid abnormality appeared during gastrulation. The surface of the presumptive ectoderm area overlying the blastocoele became wrinkled and presented a pitted appearance (fig. 2). During the closure of the blastopore and the subsequent formation of the neural folds, the series of pits arranged themselves in the form of a groove or furrow encircling the ventral portion of the egg (fig. 3). The groove marked externally the floor of the blastocoele. This was determined by puncturing a few eggs with a needle slightly below the groove. Blastocoele fluid escaped and yolk cells occupied the internal area at the level delimited externally by the groove. Thus the blastocoele failed to become completely obliterated during the gastrular movements. The persistent blastocoele later assumed the shape of a bulge in the ventral abdominal region of the developing hybrid embryos. The neural folds that formed in the hybrid embryos were narrower and closer together than in the control embryos. This condition foreshadowed the future reduction of the head. Figure 4 shows the extreme reduction and abnormalities of the anterior region of hybrid embryos at the tail bud stage. The oral suckers were greatly reduced in size and fused; the olfactory pits were absent or, if present, approached one another toward the mid-line; the stomadeal groove was absent; the gill plate showed no visible differentiation into arches; and the ventral abdominal bulge filled with blastocoele fluid was prominent. By late stage 19, the control embryos had already hatched (fig. 5). The majority of the hybrid embryos remained curled within the inner jelly membrane and failed to hatch. The structural abnormalities in the hybrid embryos were pronounced. The ventral abdominal bulge remained relatively large; the fused oral suckers projected downward; no stomadeal pit was present; and the gill plates remained undifferentiated and drawn close to the head. The hybrid embryos appeared arrested at this time. When the controls reached stage 20 (gill circulation), no advances were made by the hybrid embryos over the prior stage (fig. 6). Most of them cytolized within the inner jelly mass. However, some of the hybrids hatched. In those hatching, either the bulge in the ventral ectoderm became wrinkled and cytolysis ensued, or, in a very small percent, the bulge became reduced in size (fig. 7). Of the latter a few continued development into stage 22 (fig. 8). In these surviving hybrid embryos, the small fused suckers began to disappear, but the development of the mouth structures and eyes were much delayed and small.

These hybrids were transferred to a balanced aquarium, but all failed to live. Death was associated with reduced heads, abnormal eyes and atypical mouthparts, as control embryos placed in the same tank at the same time continued developing.

The hybrid abnormalities described above were also noticed in the other crosses of Mexican ♀ X Wisconsin ♂ ("Type A"). Hybrid embryos of this type of cross characteristically exhibited reduced heads with fused suckers and fused olfactory pits. In each of the four "Type A" crosses conducted, all hybrid embryos died.

Type B, Cross 1:

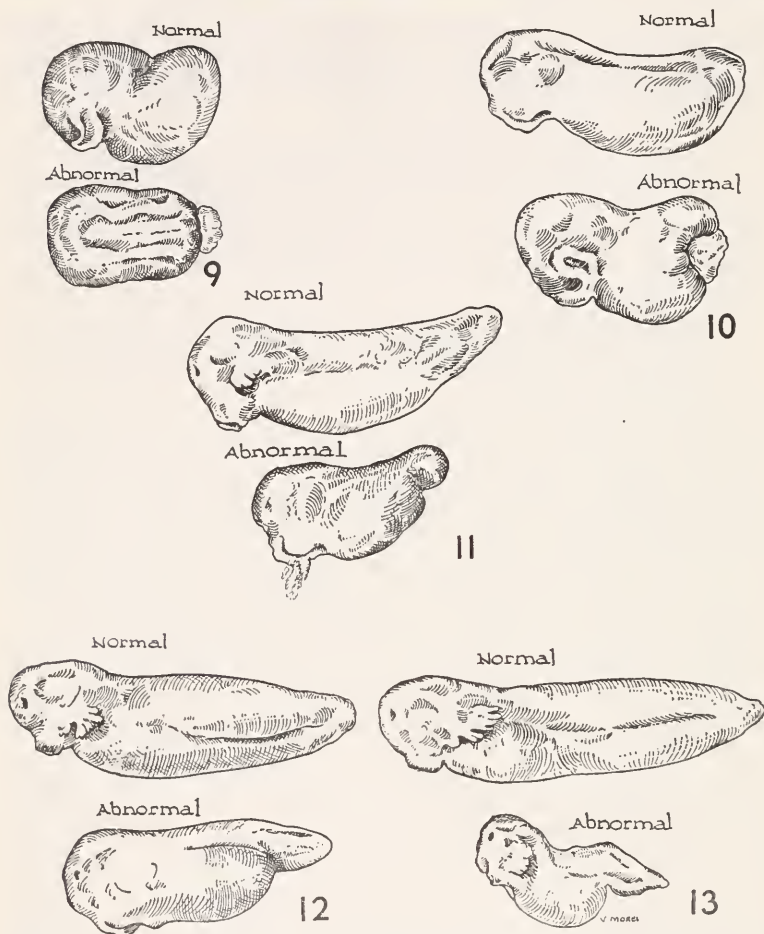
Oshkosh, Wisconsin ♀ X 29 km. e. El Mante, Mexico ♂

Oshkosh, Wisconsin ♀ X Oshkosh, Wisconsin ♂ (Control)

Conducted at 18.9°C.

The defects observed in these hybrid embryos were different, in fact almost opposite to those described in the "Type A" cross. Many embryos failed to recover from the effects of abnormal gastrulation. The disintegrating gastrulae exhibited open blastopores with extruding yolk plugs. However, a fair percent formed neural plates though the blastopore remained open (fig. 9). The neural folds that developed in the anterior end of the hybrid embryos were more divergent than encountered in the controls. This foreshadowed the enlarged head that appeared in later development. As shown in figure 9, the hybrid embryos were markedly retarded in development (the controls were in late stage 16). During later development (fig. 10), the hybrid embryos showed open blastopores of varied sizes. An atypical tail bud developed from the median dorsal lip of the open blastopore. Characteristic defects, other than the persistent yolk plug and shortened tail, were the enormous head, the abbreviated body form, and the unusually immense, widely-separated oral suckers. When the controls reached stage 19 (fig. 11), the surviving hybrid embryos were considerably retarded. An unnatural mucus mass filled the space between the huge oral suckers. As the controls progressed to stage 20 (fig. 12) the hybrids showed little developmental advance. The oral suckers remained large and divergent, and the blastopore beneath a shortened tail remained open in most embryos. By the time the controls were in stage 22 (fig. 13) all the hybrid embryos died. Cytolysis appeared to begin first in the yolk cells of the exposed yolk plug. The cytolyzing embryos showed enlarged heads, immense oral suckers, curved tails, and poorly differentiated gill plates. A few, prior to death, showed the earliest beginnings of external gills, but corpuscles were never observed coursing through them.

The hybrid embryos in the three other "Type B" crosses were characterized by the same kind and intensity of abnormalities. Not a single functional tadpole was obtained in all the crosses involving Wisconsin eggs and Mexican sperm.



Figures 9-13. Development of hybrid embryos from the cross Oshkosh, Wisconsin ♀ X Tampico, Mexico ♂. Control embryos (Oshkosh, Wisconsin ♀ X Oshkosh, Wisconsin ♂) are shown in all figures for comparison. For full explanation, see text. 9. *Top*: a control embryo approaching tail bud stage (stage 17); *Bottom*: retarded hybrid embryo in medullary plate stage (stage 13), showing the open blastopore with the large, extruding yolk plug; 10. *Top*: tail bud stage (stage 17) in a control embryo; *Bottom*: hybrid embryo showing the exposed yolk plug and the large, divergent oral suckers; 11. *Top*: heart beat stage (stage 19) in a control embryo; *Bottom*: hybrid embryo with an enlarged head, stubby tail, and a thick mucus mass projecting from the overactive oral suckers; 12. *Top*: gill circulation stage (stage 20) in a control embryo; *Bottom*: a hybrid embryo arrested in development; abnormal in those respects previously noted; 13. *Top*: tail fin circulation stage (stage 22) in a control embryo; *Bottom*: appearance of a hybrid embryo just prior to cytolysis; note the enlarged head, shortened body form, and poorly differentiated tail.

DISCUSSION

It is clear that isolation through hybrid inviability has reached a high intensity between Oshkosh, Wisconsin *Rana pipiens* and those from the area of Tamaulipas, Mexico. Moore (1947) demonstrated a similar high degree of incompatibility between Alburg, Vermont and eastern Mexico meadow frogs. It may have been argued that the observed hybrid abnormalities were due to certain characteristics unique only to Vermont meadow frogs among northern *pipiens* or to an equally peculiar property of those meadow frogs from the particular Mexican localities studied by Moore. Similar results in this investigation utilizing *pipiens* from another northern locality and different Mexican localities suggest the likelihood that all northern meadow frogs could not cross with their southerly-distributed low-land relatives in Mexico. The geographically extreme members of the species range have built up different adaptive gene complexes to the extent that they are incapable of producing viable hybrids in the laboratory.

It must be admitted that the probability of a Wisconsin meadow frog crossing with a Mexican frog in nature is extremely remote. Yet it is just this point which emphasizes the fact that incipient isolating mechanisms do not develop initially for the effect itself, but are simply the inevitable consequence of two populations accumulating sufficient adaptive genetic differences during a period of geographical separation. Muller (1942) was among the first to favor this concept that isolating mechanisms arise as a by-product of genetic divergence of allopatric populations. The genetic changes which arise to better adapt one population to particular environmental factors may also be instrumental in isolating to varied degrees that population from other populations which may possess different adaptive, incidentally isolating, pleiotropic alleles. In our case, genetic differentiation of the allopatric *pipiens* populations has proceeded to such a marked degree that isolation is almost complete. Presumably the genes or gene complex governing different temperature requirements of the two types of eggs also have very strong isolating effects. If the Wisconsin and Mexican *pipiens* were ever to meet in nature, natural selection would probably reinforce the isolation thru hybrid inviability by additional mechanisms which would guard against the production of hybrids and thus prevent the wastage of reproductive energy. Recently, Koopman (1950) has demonstrated experimentally an increase in the amount of reproductive isolation between two species of *Drosophila* as a result of continual artificial selection.

Of embryological interest is the demonstration that the results of hybridization between the two geographically extreme groups are very dissimilar in the reciprocal crosses. The gastrulation process is differentially affected in each type of hybrid development. In

the cross Mexican *pipiens* ♀ X Wisconsin *pipiens* ♂, the invaginative phase (internal rearrangement of groups of cells) of gastrulation is most seriously hampered, whereas in the reciprocal cross the progress of the blastopore lips over the yolk (epiboly of gastrulation) appears to be most disturbed. These early defects in the gastrular movements are responsible for the major subsequent abnormal form changes in each type of cross. In the cross Mexican *pipiens* ♀ X Wisconsin *pipiens* ♂, restriction of internal yolk movement results in the failure of the blastocoele to be completely obliterated. As the persistent blastocoele offers resistance to the involuting chorda-mesoderm, the latter is abnormally disposed in the anterior head region and this probably accounts for the subsequent microcephaly. In the reciprocal cross (Wisconsin *pipiens* ♀ X Mexican *pipiens* ♂), restriction of the epibolic spreading of the animal hemisphere results in a permanently open blastopore. The exposed yolk-plug later cytolyzes under the irregularly curved, shortened tail. Although the abnormalities in the posterior region of these hybrid embryos are traceable back to an open blastopore, the origin of macrocephaly in the anterior region is not apparent from the observations made.

As has been shown, normally fertilized eggs of Wisconsin and Mexican *pipiens* differ considerably in their rate of development. This is the most obvious physiological difference between the two eggs, and one may be tempted to propose that an asynchronous developmental rate in the hybrid egg is the factor initially responsible for the observed abnormalities. It is hazardous, however, to suggest that this may be the actual causative mechanism. The hybridization experiments were conducted at 18.9°C and 21.1°C; temperatures at which the developmental rates of Wisconsin and Mexican eggs differ. It would have proved interesting to run the hybridization experiments at 19.8°C, a temperature at which (interpolated from figure 1) the rates of development are the same. An insufficiency of frogs from Tamaulipas, Mexico frustrated efforts along this line, but it appears likely that the same types and intensity of developmental abnormalities would have been encountered if the reciprocal crosses were conducted at 19.8°C. The causative mechanism thus remains problematic. Others have attributed heterogenic hybrid abnormalities to a variety of factors: altered activity or inactivation of the sperm nucleus, disturbance of the nucleo-plasmic ratio, competition of enzymes for limited substrates, etc.

Successful interpretation of our case and others is further complicated by the demonstration that modifications in amphibian development produced by direct action of a variety of chemical and physical agents simulate in many ways inhibitions in hybrid development (see Child, 1941).

SUMMARY

1. The geographically extreme members of *Rana pipiens* from Tamaulipas, Mexico, and Oshkosh, Wisconsin, are characterized by different embryonic rates of development and embryonic temperature tolerances, which may represent differential adaptations to the water temperatures in nature to which the eggs of each group are subjected.

2. Experimental hybrids between Wisconsin and Mexican meadow frogs show such marked embryonic abnormalities that none would survive if the respective parental populations were to become sympatric and hybridize in nature. The evolutionary tenet that the earliest indication of reproductive isolation appears as a by-product of the genetic divergence of allopatric populations is supported.

3. The types of embryonic abnormalities in the reciprocal hybrids follow definite patterns. Hybrid embryos derived from the cross Mexican ♀ X Wisconsin ♂ exhibit persistent blastocoeles, microcephaly, fused suckers and olfactory pits, reduced mouthparts, and atypical eyes. Hybrid embryos from the reverse cross, Wisconsin ♀ X Mexican ♂, possess enlarged yolk plugs, macrocephaly, overdeveloped suckers, shortened bodies, and curved tails.

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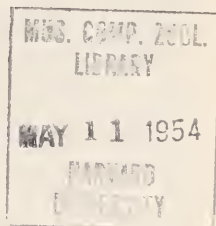
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THE BUTTERFLIES AND SKIPPERS OF LOUISIANA

EDWARD NELSON LAMBREMONT,
NEW ORLEANS.



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THE BUTTERFLIES AND SKIPPERS OF LOUISIANA¹

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New Orleans

Prior to the summer of 1948 when a project to survey the butterflies and skippers of Louisiana was started there existed only scattered records and four parish lists. The oldest of these was published as a catalog of the Lepidoptera of New Orleans and its vicinity by Ludwig von Reizenstein in 1863. As originally published the records of von Reizenstein could not have been included in this paper because the basis of von Reizenstein's determination of species was unknown. Twenty-six of the species, however, were checked against Morris (1862) and are included with the other records. Six species, as yet unidentifiable, are listed for general interest in Table 1.

Kopman (1903) published a popular account of the butterflies of Louisiana in the *New Orleans Times Democrat*. Of the 24 species recorded only three have definite localities noted and are included herein. Hine (1904, 1906) listed the Lepidoptera of Cameron parish in the southwestern corner of the state, including valid records for 15 species, and Montgomery (1932) listed 15 species from Madison and Tensas parishes in the northeastern corner. Glick (1939) listed eight species from Madison parish. All other publications deal with only a few species.

From these publications a small, highly localized list may be compiled consisting of 43 species, including four type localities, in the state.

The best and most recent local study was published since the initiation of this survey. It consists of collections and notes made by Jung (1950) within Orleans, Jefferson, Plaquemines, and St. Bernard parishes. Thirty-seven species of butterflies and skippers are recorded, 17 of which had not been reported from the state previously.

Taking Jung's paper (1950) into consideration the state list numbered 60 species and subspecies. The present survey, concluded in March 1951, adds 38 previously unrecorded species and subspecies, bringing the total to 98 (Table 2). This is by no means to be considered all the species that should be found, for many that are known to occur in nearby areas have not been taken within Louisiana's borders. The rich fauna of Texas and Mexico undoubtedly overlaps part of Louisiana, particularly the southwest, and many of the Texas-Mexican forms have been taken short distances from the Louisiana-Texas line. In all probability the number of species would have reached about 140 if the survey had been continued. Completion of the survey would require considerable collecting in the state during certain seasons of the year, particularly in the spring. On the basis

¹ From a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science of the Graduate School of Tulane University.

TABLE 1.

SPECIES RECORDED BY VON REIZENSTEIN (1863) WHICH WERE UNIDENTIFIABLE. NOTES ARE PRESENTED EXACTLY AS THEY APPEAR IN THE ORIGINAL; COMMENTS BY THE WRITER ARE IN PARENTHESES.

Goniopteryx Eclipsis.

Xanthidia Sylvatica, MSS Rare.

Heliconia diaphona Drur. Rare Western Lake Shore.
(Probably *H. charitonius*)

Euptoieta hegesia? Cram. City Park. On Passiflorae.
(Probably *E. claudia*)

Apatura myops, MSS. On elm trees.

Thecla io, MSS. City Park, rare. On camomilla.

of their overall distributional patterns approximately 40 additional species may be anticipated to occur in Louisiana. These are listed in Table 3, but otherwise are not mentioned in this paper.

AREA STUDIED

Including islands in the Gulf of Mexico the total area of Louisiana is 48,506 square miles, of which 3,097 square miles are water surface (1,060 square miles of landlocked lakes). The entire state is within Merriam's Austroriparian life zone; the northern portion within the Carolinian area, and the southern portion in a semi-tropical region called the Gulf Strip.

Viosca (1933) divided Louisiana into four main physiographic areas which are illustrated in figure 1. Each of these supports a characteristic flora. As will be noted later the distribution of certain butterflies and skippers is correlated with these areas to some extent. In addition to the natural vegetation there are many man-made communities which tend to obscure the relation between natural vegetation and physiographic areas. Such man-made disturbance communities are: pine-hardwood, scrub-oak grassland, successional changes on abandoned farmlands, and undeveloped agricultural land-reclamation projects. These man-made disturbance areas support many small flowering plants, both natural and horticultural, which are attractive to butterflies and skippers.

With the exception of the coastal ridge and delta division all major physiographic regions of Louisiana were sampled intensively during the two-and-one-half year term of this survey. Those places within short distances from New Orleans were concentrated upon, but three major trips totalling more than 50 days in the field were taken to collect in the northern uplands. The accompanying map (fig. 2) shows the distribution of collections. To facilitate travel and increase the range only a few areas were sampled over any length of time. These include the Sabine parish area; Caddo and neighboring

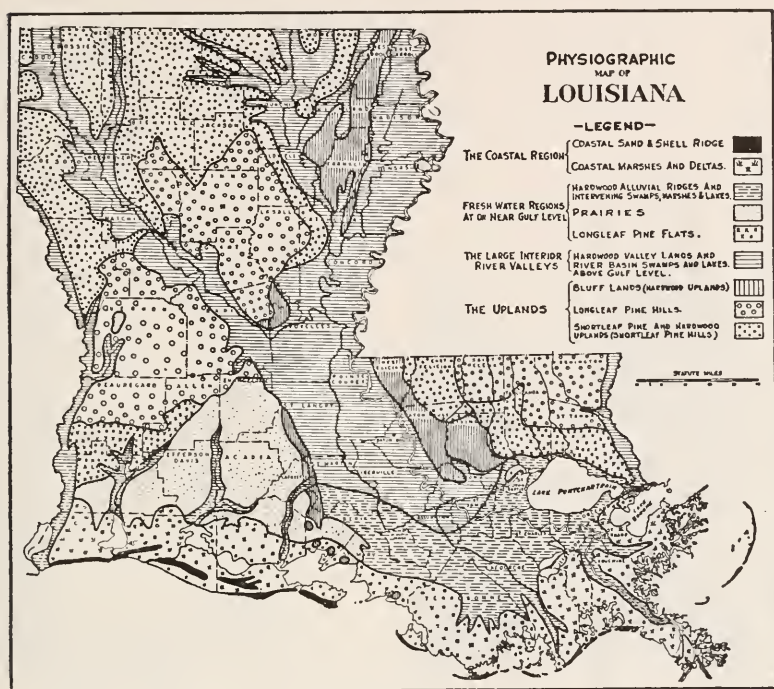


Figure 1. Physiographic map of Louisiana from Viosca (1933). Reprinted by permission of the copyright owner.

parishes; Lincoln-Jackson-Union parish area; Ouachita-Morehouse and parishes east; Concordia parish and surrounding area; Allen parish and all parishes east to the Mississippi river, excluding West Baton Rouge; the Florida parishes; and New Orleans and vicinity.

Most of the collections were made during the summer months. The only heavily collected sections during other times of the year were the Jackson-Lincoln-Union area in the spring, Allen parish and all parishes east to the Mississippi river in the fall, and the Florida parishes and New Orleans and vicinity throughout the year.

The majority of the butterflies and skippers were taken by the author from June 1948 to April 1951; records previous to this time were contributed by other members of the Tulane University zoology staff.

SYSTEMATIC TREATMENT

Each species is considered individually. Each such treatment includes a summary of observations and Louisiana distribution records. The arrangement of species follows Klots (1951).

Where specific data are required the records are listed alphabetically by parish, each including the following: locality (within five miles

TABLE 2
LIST OF LOUISIANA SPECIES CONTRASTING PREVIOUSLY REPORTED
MATERIAL WITH THE NEW RECORDS ADDED HEREIN.

From Literature	New Records
Lethe portlandia (Fabricius)	
Euptychia hernes sosybius (Fabricius)	
	SATYRIDAE
	Euptychia gemma gemma (Hübner)
	Euptychia areolata areolata (J. E. Smith)
	Euptychia cymela cymela (Cramer)
	Cercyonis pegala pegala (Fabricius)
	Cercyonis pegala alope (Fabricius)
	DANAIDAE
Danaus plexippus plexippus (Linné)	
Danaus plexippus melanippe (Linné)	
Danaus gilippus berenice (Cramer)	
	Nymphalidae
Heliconius charitonius tuckeri Comstock & Brown	
Agraulis vanillae nigrior Michener	Dryas julia delila (Fabricius)
Euptoleta claudia claudia (Cramer)	Speyeria cybele (Fabricius)
Phyciodes gorgone (Hübner)	Melitaea nycteis nycteis Doubleday
Phyciodes tharos tharos (Drury)	Nymphalis antiopa antiopa (Linné)
Polygonia interrogationis (Fabricius)	
Vanessa atalanta atalanta (Linné)	
Vanessa cardui cardui (Linné)	
Vanessa virginensis (Drury)	
Precis evarete coenia (Hübner)	
Limenitis archippus watsoni (dos Passos)	
Limenitis arthemis astyanax (Fabricius)	
Anaea andria (Scudder)	
Asterocampa clyton clyton (Boisduval & LeConte)	
Asterocampa celtis celtis (Boisduval & LeConte)	
Asterocampa celtis alicia (Edwards)	
	LIBYTHEIDAE
Libytheana bachmannii bachmannii (Kirtland)	
	RIODINIDAE
Calephelis virginensis (Guerin)	
	LYCAENIDAE
Atides halesus halesus (Cramer)	Strymon ontario autolytus (Edwards)
Strymon cecrops (Fabricius)	Strymon liparops liparops (Boisduval & LeConte)
Strymon melinus melinus (Hübner)	Hemiargus isolus (Reakirt)
Incisalia irus (?) (Godart)	Celastrina argiolus pseudargiolus (Boisduval & LeConte)
Feniseca tarquinus tarquinus (Fabricius)	
Everes comyntas comyntas (Godart)	

PAPILIONIDAE

Papilio polyxenes asterias Stoll
Papilio crespontes crespontes Cramer
Papilio glaucus glaucus (Linné)
Papilio troilus troilus Linné
Papilio palamedes palamedes Drury
Graphium marcellus marcellus (Cramer)
Battus polydamus lucayus (Rothschild & Jordan)
Battus philenor philenor (Linné)

Colias eurytheme eurytheme Boisduval
Zerene cesonia (Stoll)
Phoebis sennae sennae (Linné)
Phoebis sennae eubule (Linné)
Euremia nicippe nicippe (Cramer)
Euremia lisa (Boisduval & LeConte)
Nathalis iole Boisduval
Pieris rapae (Linné)
Pieris protodice protodice Boisduval & LeConte
Ascia monuste phileta (Fabricius)

PIERIDAE

Anthrocharis genutia genutia (Fabricius)
Colias philodice philodice (Latrielle)
Phoebis philea (Linné)
Phoebis agarithe maxima (Neumoegen)
Euremia dairaira dairaira (Latrielle)

HESPERIIDAE

Epargyreus clarus (Cramer)
Urbanus proteus (Linné)
Pyrgus communis communis (Grote)
Celotes nessus (Edwards)
Erynnis horatius (Scudder & Burgess)
Ancyloxypha numitor (Fabricius)
Hesperia leonardus stallingsi H. A. Freeman
Hylephila phyleus (Drury)
Poanes viator (Edwards)
Oligoria maculata (Edwards)
Lerema accius (J. E. Smith)
Lerodea eufala (Edwards)
Calpodetes ethlius (Stoll)
Panoquina panoquin (Scudder)

Achalarus lyciades (Geyer)
Thorybes bathyllus (J. E. Smith)
Thorybes confusus Bell
Pholisora hayhurstii (Edwards)
Erynnis juvenalis (Fabricius)
Copaoides minima (Edwards)
Atalopodes campestris (Boisduval)
Polites manataqua manataqua (Scudder)
Polites themistocles (Latreille)
Polites vibex brettus (Boisduval & LeConte)
Wallengrenia otho otho (J. E. Smith)
Atrytone argos argos (Boisduval & LeConte)
Atrytone dukesi Lindsey
Atrytone ruricola metacomet (Harris)
Amblyscirtes vialis (Edwards)
Amblyscirtes textor (Hübner)
Lerodea l'herminieri (Latreille)
Panoquina ocola (Edwards)

TABLE 3
SPECIES EXPECTED TO OCCUR IN LOUISIANA BUT NOT YET RECORDED

Lethe creola (Skinner)	SATYRIDAE	Lethe eurydice (Johannson)
Melitaea ismeria (Boisduval & LeConte)	NYMPHALIDAE	Asterocampa clyton flora (Edwards)
Phyciodes texana semiole (Edwards)	LYCAENIDAE	Mitoura gryneus (Hübner)
Strymon m-album (Boisduval & LeConte)		Incisalia nippon nippon (Hübner)
Strymon titus mopsus (Hübner)		Hemiargus ceranus antibastus (Hübner)
Strymon favonius (J. E. Smith)		Brephidium pseudofea (Morrison)
Strymon ontario (Edwards)	PIERIDAE	
Strymon falacer (Godart)		
Eurema mexicana (Boisduval)	HESPERIIDAE	Polites peckius (Kirby)
Thorybes pylades Scudder		Poanes yehl (Skinner)
Pholisora catullus (Fabricius)		Problema byssus (Edwards)
Erynnis icelus (Scudder & Burgess)		Atrytone logan logan (Edwards)
Erynnis brizo brizo (Boisduval & LeConte)		Atrytone alabamae Lindsey
Erynnis martialis (Scudder)		Atrytone dion (Edwards)
Erynnis baptisiae Forbes		Atrytonopsis hianna (Scudder)
Erynnis zarucco (Lucas)		Amblyscirtes alternata (Grote & Robinson)
Hesperia sassacus (Harris)		Amblyscirtes belli H. A. Freeman
Hesperia meta (Scudder)		Lerodea neamathla Skinner & Williams
Hesperia attalus (Edwards)		Megathymus yuccae Boisduval & LeConte
Hesperia meskei (Edwards)		Megathymus cofaqui Strecker
Polites verna (Edwards)		

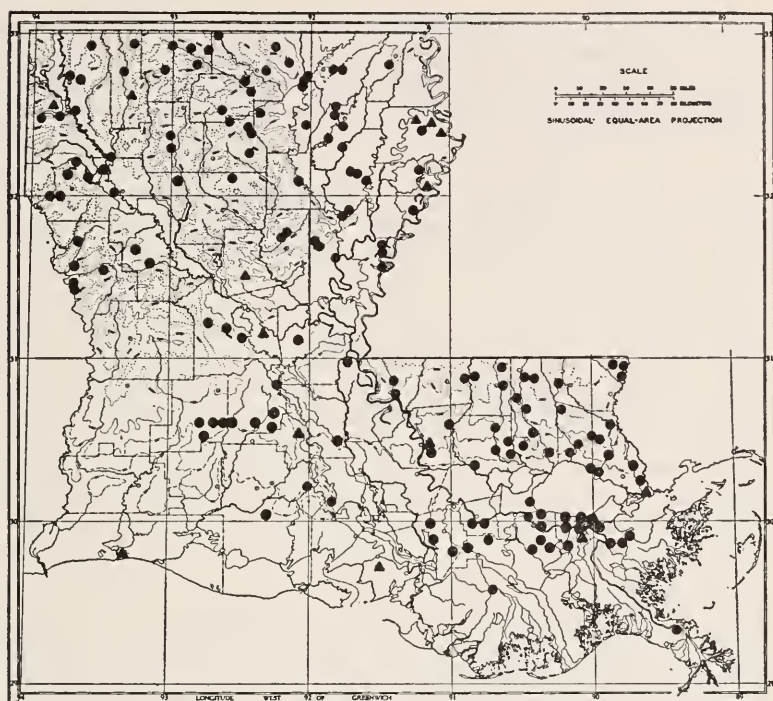


Figure 2. Map showing distribution of localities from which material was examined, or previously recorded; triangles = localities from the literature; dots = localities from the present survey.

of nearest Post Office), date of collection, number and sex of specimens, and institutional location of specimens in parentheses. Unless otherwise specified all specimens are in the Tulane collection. Abbreviations of the institutions are: LPI = Louisiana Polytechnic Institute, Ruston; LSM = Louisiana State Museum, New Orleans; SLI = Southwestern Louisiana Institute, Lafayette; TU = Tulane University ("P" series are collections prior to 1947 with sparse data; lot numbers P-955 through P-1101 consist of the James M. McArthur Collection).

Superfamily PAPILIONOIDEA, The Butterflies
Family SATYRIDAE

LETHE PORTLANDIA PORTLANDIA (FABRICIUS), the Pearly Eye.—The writer has not taken this species; however, Skinner (1897) described a specimen captured in Louisiana as *L. creola*. Dr. Austin H. Clark informed the writer (in correspondence) that this supposed *creola* is actually *portlandia*. Skinner's record is: *St. Landry*: Opelousas, VII-3-1897.

EUPTYCHIA CYMELA CYMELA (CRAMER).—The Little Wood-satyr

is rather common in Louisiana during the spring and early summer; earliest and latest dates recorded are April 1, 1950 (8 ♂♂) and June 24, 1950 (1 ♀). It is most often seen in woody places, particularly in pinelands, and most of the specimens have been taken in the upland pine areas of the state.

E. cymela cymela has not been recorded from Louisiana previously. Twenty-four specimens (12 ♂♂, 12 ♀♀) have been examined from 14 localities in the following parishes: Catahoula, Jackson, Lafayette (SLI), LaSalle, Lincoln, Morehouse, Ouachita, St. Tammany, Union and Washington.

EUPTYCHIA HERMES SOSYBIUS (FABRICIUS).—The Carolinian Satyr is undoubtedly the most abundant satyrid; it is probably rivaled by only two other species, *Eurema lisa* and *Phyciodes tharos*, in being the most common butterfly in Louisiana. This satyrid is particularly abundant in woody areas, especially in pinelands and oak forests, where it remains in quiet shaded spots rather than in the sunny habitats of most other butterflies. This subspecies flies the year round; specimens have been collected in all months except January and August. Earliest and latest dates are February 10, 1943 (1 ♂) and December 25, 1949 (1 ♀).

One hundred and nine specimens (64 ♂♂, 45 ♀♀) have been examined from 51 localities in the following parishes: Allen, Assumption, Catahoula, Claiborne, Evangeline, East Feliciana, Jackson, Jefferson, Lafayette (SLI), Lincoln, Livingston, Morehouse, Orleans, Ouachita, Pointe Coupee, Richland, Sabine, St. Helena, St. Landry, St. Tammany, Tangipahoa, Union, Washington, West Carroll and West Feliciana. Previously it had been recorded from Cameron (Hine, 1906) and Orleans parishes (von Reizenstein, 1863).

EUPTYCHIA AREOLATA AREOLATA (J. E. SMITH), the Georgia Satyr.—All specimens were collected in the longleaf pine flats north of Lake Pontchartrain. Supposedly the species ranges as far west as Texas, but the results of this survey indicate it must be rare west of the Mississippi river, although it localizes and can be overlooked. It resembles *E. hermes* in habits and flight by keeping close to the ground.

E. areolata areolata has not been recorded from Louisiana previously. The 31 specimens (15 ♂♂, 16 ♀♀), examined were collected from the following localities: *Livingston*: Springville, IX-6-50 (TU 2184); *St. Tammany*: St. Tammany, V-12-49 (TU 1219); Hickory, V-12-50, VI-2-50, VI-29-50, IX-30-50 (TU 1948, 1973, 2000, 2198); Covington, IX-5-50, IX-8-50 (TU 2180, 2197); Folsom, IX-7-50 (TU 2187); Talisheek, IX-13-50 (TU 2200); *Tangipahoa*: Ponchartroula, IX-6-50 (TU 2182); Robert, IX-6-50 (TU 2185); *Washington*: Angie, VI-5-50 (TU 2034).

EUPTYCHIA GEMMA GEMMA (HUBNER), the Jeweled Brown.—This beautiful woodland butterfly resembles *E. hermes* closely in habits, but it is considerably less common for only three specimens (all females) have been taken in Louisiana. From the writer's expe-

rience the species occurs in pinelands, and several which eluded capture were seen in the longleaf pine flats of St. Tammany parish.

This species has not been recorded from Louisiana previously. The three records are: *Richland*: Girard, VI-27-50 (TU 2081); *St. Tammany*: Mandeville, X-26-49 (TU 1599); *Tangipahoa*: Tangipahoa, IX-7-50 (TU 2192).

CERCYONIS PEGALA PEGALA (FABRICIUS).—The Southern Wood-nymph probably has a better protective coloration than any other butterfly except its allied subspecies, *C. pegala alope*. The insect usually may be found sitting on the sides of pine trees, and unless disturbed it is often mistaken for a loose piece of bark. The undersides of the wings are colored in such a way that they blend with the surroundings so well that one must "beat" the trees with a stick to flush them from hiding. When disturbed the butterfly quickly flies a short distance to another tree, and the same procedure must be repeated. To add to this collecting difficulty they are exceptionally hard to capture in flight. Only a few have been collected in Louisiana, perhaps because of their deceptiveness.

C. pegala pegala has not been recorded from Louisiana previously. The three records are: *St. Tammany*: Covington, IX-8-50, 1 ♂ (TU 2197); Hickory, IX-13-50, 1 ♀ (TU 2198); *Tangipahoa*: Amite, IX-7-50, 1 ♀ (TU 2195).

CERCYONIS PEGALA ALOPE (FABRICIUS), the Common Wood-nymph.—In the past, authors have treated this subspecies as a separate species along with other forms of *C. pegala*. More recently some have chosen to combine all as one large clinal species. Until the *pegala-alope* complex is understood fully the writer prefers to consider them as separate subspecies. The observations given for typical *pegala* are much the same as those for *alope*.

C. pegala alope has not been recorded from Louisiana previously. The only record is: *LaSalle*: Summerville, VI-12-50, 1 ♂ (TU 2048).

Family DANAIDAE

DANAUS PLEXIPPUS PLEXIPPUS (LINNÉ).—The Monarch is one of the most interesting butterflies of our fauna, and has attracted considerable attention because of its migrations. For many years they have been known to swarm (Saunders, 1871) and migrate.

The Louisiana collections show two annual peaks of abundance of this subspecies: one in April, and the other during October and November. Judd (1950) reported a congregation of Monarchs on the north shore of Lake Erie which occurred during the last four days of August 1949, and Saverne (1908) reported swarms in Michigan which lasted from September 4 through 15. Williams (1930) quoted Shannon in saying that one of the four main routes of migrating butterflies in North America is from Canada along Lake Ontario and Lake Erie southward. Travelling at a speed of five to seven miles per hour (Park, 1948), a swarm of monarchs leaving

Canada in late August should reach the Gulf states in about a month providing there are no high winds against them. This correlates somewhat with our recorded peak of October-November, and also with a large flight which the writer observed headed southward October 10, 1949 near New Orleans, and one noted in November 1941 by Percy Viosca (newspaper article).

Originally this insect was more or less confined to North America, but with time it has spread throughout the islands of the Atlantic, and to most of the Pacific islands, including New Zealand and Australia (Williams, 1930, 1937).

Forty-five specimens have been examined (27 ♂♂, 18 ♀♀) and hundreds more have been observed in migratory flight. Collections have been made throughout the year, except January and February; earliest and latest dates are March 18, 1950 (1 ♂) and December 15, 1949 (1 ♂). The monarch has been recorded from 24 localities in the following parishes: Avoyelles (SLI), Franklin, Jefferson, Lafayette (SLI), Lincoln, Livingston, Morehouse, Orleans, Ouachita, Richland, St. Bernard, St. Charles, St. Helena, St. James, St. John the Baptist, St. Landry, St. Tammany, Tangipahoa and West Feliciana. Previously the monarch had been recorded from Cameron (Hine, 1906) and Orleans parishes (von Reizenstein, 1863; Shufeldt, 1884; Jung, 1939, 1950).

DANAUS PLEXIPPUS MELANIPPE (HUBNER), the South American Monarch.—This subspecies has caused much controversy in recent years for the figure in Holland (1898; 1931 revised) given to represent *D. plexippus plexippus* is actually the subspecies *melanippe*. Although *melanippe* is not typical for most of North America it has been captured as an occasional visitor as far north as Illinois and New York (Clark, 1941).

The Louisiana record is: *Orleans*: New Orleans, VIII-8-25, 1 ♂ (TU P-967). Previously it had been recorded from St. Tammany parish by Clark (1941).

DANAUS GILIPPUS BERENICE (CRAMER).—The Queen is a rare danaid in Louisiana. The few records show that this species flies mostly during the warmer months. One female, however, was taken in March, 1950, probably because the winter of that year was very mild. Unlike the monarch this species is not migratory.

The six specimens examined were from the following localities: *Jefferson*: Metairie, VIII-7-47 (TU 92); *Bridgedale*, VIII-25-50 (TU 2123); *Orleans*: New Orleans, XI-26-27, VII-1-32, III-25-50 (TU P-970, P-982, 1825); *St. Tammany*: Mandeville, X-11-49 (TU 1566). Previously it had been recorded from Cameron (Hine 1906) and Orleans parishes (Jung, 1939, 1950).

Family NYMPHALIDAE

HELICONIUS CHARITONIUS TUCKERI COMSTOCK AND BROWN.—The Zebra is not common in Louisiana, but it is seen occasionally during the summer and early autumn in the southernmost parishes.

The few records from the state were obtained in August and October. Although the writer has never seen this butterfly in the field, a few of them were reported to him from the Mississippi delta region, the southern extremity of Louisiana. Comstock and Brown (1950) recorded it from Texas. The larvae feed on passion flowers.

The few records are as follows: *Jefferson*: Mississippi river bank opposite New Orleans, X-18-1894 (Kopman, 1903); *Orleans*: New Orleans (von Reizenstein, 1863); *Terrebonne*: Houma, VIII-9-19 (LSM).

AGRAULIS VANILLAE NIGRIOR MICHENER, the Gulf Fritillary.—This is the commonest fritillary in Louisiana. During the hot summer months swarms of them may be seen hanging on blades of grass in open fields. It flies from spring to early fall; earliest and latest dates are March 22, 1950 and November 7, 1919.

The flight is exceptionally fast, and efforts at chasing this insect on the wing usually prove unsuccessful. One trick it uses in eluding capture is to fly up to about eight feet and suddenly reverse its direction. It can change its course much faster than a running man, and the writer has often found himself giving "chase" in the opposite direction from which the butterfly was traveling. However, many specimens may be taken while they are resting. According to Williams (1937) this butterfly is migratory.

The species apparently is more abundant in the southern parishes of Louisiana. Forty-seven specimens (30 ♂♂, 17 ♀♀) have been examined from 18 localities in the following parishes: Allen, Jefferson, Lafayette (SLI), Livingston, Orleans, Plaquemines, Pointe Coupee, Rapides, St. Bernard, St. Landry, St. Tammany and Terrebonne (LSM). Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863; Michener, 1947; Jung, 1950).

DRYAS JULIA DELILA (FABRICIUS), the Julia Butterfly.—McDunnough (1938) listed this species as of doubtful North American occurrence, but Holland (1931) stated that it is an occasional visitor in the extreme South. The genus is primarily a tropical one.

D. julia delila has not been recorded from Louisiana previously. The one record is: *Lafayette*: Lafayette, XI-5-41, 1 ♂ (SLI).

EUPTOIETA CLAUDIA CLAUDIA (CRAMER).—The Variegated Fritillary is very common in Louisiana from early spring throughout the summer; earliest and latest dates are March 31, 1950 (1 ♀) and October 16, 1949 (1 ♀). The larvae feed on passion flowers and violets. Several years ago, in early July, the writer's attention was called to a vacant lot in uptown New Orleans which was literally "seeded" with chrysalids of this butterfly. Previous to the time that this lot was infested there was a dense growth of passion flowers, but after the feeding of thousands of caterpillars nothing remained but bare twigs covered with chrysalids. Needless to say the emergence of adults was sensational, and a good series of pupae was collected and reared.

Within Louisiana, *E. claudia claudia* appears to be more abundant in the southern areas. Thirty-nine specimens (20 ♂♂, 19 ♀♀) have been examined from 15 localities in the following parishes: Assumption, Concordia, Evangeline, Jefferson, Lafayette (SLI), Lafourche, Orleans, Ouachita, St. Bernard, St. Landry (SLI) and St. Martin (SLI). Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863; Jung, 1950).

SPEYERIA CYBELE (FABRICIUS), the Great Spangled Fritillary.—The single Louisiana specimen was taken in the coastal area in early October, and as the species is not common to the state, perhaps it was a straggler southward during the cooler months.

S. cybele has not been recorded from the state previously. The one record is: *Lafayette*: Lafayette, X-2-31, 1 ♂ (SLI).

MELITAEA NYCTEIS NYCTEIS DOUBLEDAY, the Silvery Checkerspot.—Holland (1931) stated that *M. nycteis* ranges from Maine to western North Carolina, and westward to the Rocky Mountains. He did not say whether it comes below the latitude of North Carolina, or stays north of there. Klots (1951) also did not mention its occurrence south of the mountains of North Carolina, Missouri and Kansas. The Louisiana records may be considered southern range extensions, but since the species is not abundant in the state it appears that Louisiana is at the southern tip of its range. A single specimen was collected in the Sabine river area (near Texas), and another near the Pearl river (near Mississippi), at opposite sides of the state. Three specimens were seen at the latter location, but only one was taken. The flight is fast and erratic.

M. nycteis nycteis has not been recorded from Louisiana previously. The two records are: *Sabine*: Zwolle, VIII-2-49, 1 ♀ (TU 1381); *Washington*: Richardson, IX-7-50, 1 ♂ (TU 2188).

PHYCIODES GORGONE (HUBNER), the Gorgone Crescent-spot.—This crescent-spot, though closely allied to it, cannot begin to approach *P. tharos* in abundance. It flies from spring to early fall in sunny places, but does not seem to be restricted to any part of the state. Earliest and latest dates are March 7, 1951 (1 ♂) and October 16, 1949 (1 ♂).

Twenty-three specimens (14 ♂♂, 9 ♀♀) have been examined from 14 localities in the following parishes: Allen, Assumption, Bossier, DeSoto, Evangeline, Natchitoches, Pointe Coupee, Rapides, St. Charles, St. Tammany and Union. Previously it had been recorded from Cameron (Hine, 1906) and Orleans parishes (Jung, 1950).

PHYCIODES THAROS THAROS (DRURY).—The Pearly Crescent-spot is by far the most abundant butterfly in Louisiana. With the exception of the coldest days it flies throughout the year (it has been collected in all twelve months), not only in bright open fields, but in densely shaded forests as well, and is known to cluster around wet spots on the ground (Scudder, 1889). When at rest this butterfly

has the peculiar habit of slowly raising and lowering its wings. The larvae feed on plants of the family Compositae, particularly the asters.

One hundred and thirty-one specimens (74 ♂♂, 57 ♀♀) have been examined from 68 localities in the following parishes: Allen, Assumption, Catahoula, Claiborne, Concordia, DeSoto, East Baton Rouge, East Feliciana, Evangeline, Jackson, Jefferson, Lafayette (SLI), Lafourche, LaSalle, Lincoln, Livingston, Morehouse, Natchitoches, Orleans, Ouachita, Pointe Coupee, Rapides, Richland, Sabine, St. Charles, St. Helena, St. James, St. Landry, St. Tammany, Tangipahoa, Union, Washington, Webster and West Carroll. Previously it had been recorded from Madison (Montgomery, 1932) and Orleans parishes (Jung, 1950).

POLYGONIA INTERROGATIONIS (FABRICIUS), the Question Mark.—This species is exceptionally nervous and fast in flight, which perhaps accounts for the scarcity of records. In the writer's opinion each record obtained equals at least two or three uncaught butterflies, and from sight-records it appears that this species is rather abundant in Louisiana during the spring and summer months. Earliest and latest dates are March 10, 1949 (1 ♀) and October 15, 1926 (1 ♀).

This butterfly frequents open spots and forest edges. Scudder (1889) notes that it often sucks the sap flowing from wounded trees and decaying fruits, and the writer has taken adult specimens feeding on decaying fish and turtle meat. The larvae feed on a great variety of plants, particularly of the family Urticaceae.

Eighteen specimens (7 ♂♂, 11 ♀♀) have been examined from eight localities in the following parishes: Jefferson, Lafayette (SLI), Orleans, Ouachita, Sabine, Terrebonne (LSM), Washington and West Carroll. Previously it had been recorded from Orleans parish by Jung (1950).

NYMPHALIS ANTIOPA ANTIOPA (LINNÉ), the Mourning Cloak.—This beautiful butterfly is primarily a species of the northern states, appearing only occasionally in Louisiana during the late summer and fall months. It has not been recorded from the state previously.

The three records are: *Lincoln*: Ruston (LPI); *Orleans*: New Orleans, IX-25-31, 1 ♀ (TU P-977), and VIII-25-32, 1 ♀ (TU P-983).

VANESSA ATALANTA ATALANTA (LINNÉ), the Red Admiral.—This species is well-named *atalanta* for it is one of the speediest of the nymphalids. All of the specimens were caught while occupied with feeding. The larvae feed on nettles (*Urtica* spp.)

In Louisiana, *V. atalanta atalanta* is never too abundant, but it may be seen almost throughout the year, although more often during the warmer months. Earliest and latest dates are January 30, 1950 (3 ♂♂, 2 ♀♀) and October 28, 1928 (1 ♀). Jung (1950) stated that he found it to be abundant in drained swamp areas near New Orleans.

Twenty-one specimens (8 ♂♂, 13 ♀♀) have been examined from eight localities in the following parishes: Claiborne, Jefferson, Lafayette (SLI), Orleans, Ouachita, St. Tammany, Webster and West Feliciana. It had been reported previously from Orleans parish by Jung (1939, 1950).

VANESSA CARDUI CARDUI (LINNÉ), the Painted Lady.—In Louisiana this butterfly is not quite as abundant as the related species *atalanta* and *virginiensis*, the few records indicating that it flies from spring throughout the summer and autumn. Earliest and latest dates are May 3, 1924 (1 ♀) and October 18, 1949 (1 ♂).

Williams (1937) described the migrations of *cardui*, noting that in 1931 their abundance in the northern states brought help to the farmers because of the vast destruction of thistles, the food plant of their larvae. Yet in other years they do considerable damage to artichokes.

The specimens taken in the state were from open, sunny fields, and on the shrubs bordering forests. Only one was taken on thistle.

The localities are: *Caddo*: Shreveport, VIII-5-49, 1 ♀ (TU 1432); *Orleans*: New Orleans, V-3-24, 1 ♀ (TU P-957); *St. Bernard*: Shell Beach, X-18-49, 1 ♂ (TU 1595); *St. Landry*: Cortabieu, X-16-49, 1 ♀ (TU 1580). Previously it had been recorded from Cameron (Hine, 1906) and Orleans parishes (von Reizenstein, 1863).

VANESSA VIRGINIENSIS (DRURY).—Hunter's Butterfly is fairly common in Louisiana through most of the year; earliest and latest dates are January 21, 1950 (3 ♂♂) and October 10, 1930 (1 ♀). Most of the specimens were taken while feeding, for like its ally, *V. atalanta*, this species is a strong flier. The larvae feed on various species of the family Compositae.

Nineteen specimens (11 ♂♂, 8 ♀♀) have been examined from nine localities in the following parishes: Catahoula, East Feliciana, Jackson, Lafayette (SLI), Orleans, St. Charles, St. Tammany, Washington and West Feliciana. Previously it had been recorded from Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863; Jung, 1939, 1950).

PRECIS EVARETE COENIA (HUBNER), the Buckeye.—This common butterfly of the southern states probably is familiar to everyone. In Louisiana it is very abundant throughout the spring, summer and autumn; earliest and latest dates are January 21, 1950 (1 ♂) and November 8, 1949 (1 ♂, 1 ♀). Of all that were collected in the state only a few were obtained while they were flying or feeding, for the insect seems to prefer to sit on hard, dry mud in full sunlight, slowly moving its wings. During a recent visit to Lacombe, La. the writer saw hundreds of buckeyes sitting on a large mound of dry, yellow clay.

Holland (1931) stated that the larvae in the later stages feed on plantains and Scudder (1889) reported them on *Gerardia purpurea* and on other species of the family Scrophulariaceae.

Forty-seven specimens (31 ♂♂, 16 ♀♀) have been examined from 31 localities in the following parishes: Allen, Claiborne, East Baton Rouge, Evangeline, Jefferson, Lafayette (SLI), Livingston, Natchitoches, Orleans, Ouachita, Rapides, St. Bernard, St. Charles, St. James, St. John the Baptist, St. Landry, St. Tammany, Tangipahoa, Union and Washington. Previously it had been recorded from Madison (Glick, 1939) and Orleans parishes (von Reizenstein, 1863; Jung, 1950).

LIMENITIS ARTHEMIS ASTYANAX (FABRICIUS), the Red-spotted Purple.—This butterfly is very fast in flight, and if disturbed will soar into the air. Most of the specimens were obtained in damp, swampy places where they often sit on soft mud, or upon the leaves of shrubs and small trees. The larvae feed on cherry, apple, hackberry, willow and related shrubs and trees (Holland, 1931).

The species flies throughout the summer and early fall; earliest and latest dates are May 31, 1949 (1 ♀) and October 15, 1949 (1 ♀).

Thirteen specimens (6 ♂♂, 7 ♀♀) have been examined from nine localities in the following parishes: Catahoula, Claiborne, East Feliciana, Livingston, Orleans, Tangipahoa, Terrebonne (LSM) and West Feliciana. Previously it had been recorded from St. Tammany parish by Jung (1950).

LIMENITIS ARCHIPPUS WATSONI (DOS PASSOS), the Viceroy.—This butterfly exhibits one of the best known examples of protective mimicry. It looks almost exactly like the monarch, *Danaus plexippus*, a species protected from insectivores by the unpleasant taste it possesses from feeding on milkweeds. An interesting fact concerning the viceroy is that throughout its range are found subspecies each of which mimics the prevalent danaid of the area (Chermock, 1947).

L. archippus ranges throughout North America into the Gulf States where the subspecies *floridensis*, in the east, and *watsoni*, in the west, occur. The latter was described by Dos Passos (1938) from specimens caught at Alexandria, La. In the state this subspecies is very common during the spring, summer and autumn months; earliest and latest dates are April 24, 1948 (1 ♂) and November 12, 1949 (1 ♀).

The flight, usually within five feet of the ground, is fast, but leisurely, and the butterfly is not too difficult to capture as it flies, or when it feeds on flowers. The larvae feed on various species of willows, although occasionally they feed on plum and cherry (Scudder, 1889).

Thirty-three specimens (24 ♂♂, 9 ♀♀), have been examined from 22 localities in the following parishes: Allen, Assumption, Claiborne, Evangeline, East Baton Rouge, Jefferson, Lafayette (SLI), Lafourche, Livingston, Orleans, Pointe Coupee, St. Bernard, St. Charles, St. Helena, St. James, St. Landry and Tangipahoa. Previously it had been recorded from Orleans (Jung, 1950), Rapides (Dos Passos, 1938) and Tensas parishes (Montgomery, 1932).

ANAEA ANDRIA (SCUDDER).—The Goatweed Butterfly is very common in Louisiana during the spring and early summer, but because of its rapid flight and protective coloration it is difficult to capture. Earliest and latest dates are February 2, 1929 (1 ♀) and October 20, 1939 (1 ♂). When resting this butterfly usually sits on the ground among dead leaves showing the under surfaces of the wings which blend well with the surroundings. Several individuals have been taken on the trunks of sycamore trees; others undoubtedly blended with the loose bark and were not seen. The caterpillars feed on the goatweed (*Croton capitatum*).

A. andria appears to be slightly more abundant in northern Louisiana. Most of the specimens were taken in the hardwood areas. Eighteen specimens (9 ♂♂, 9 ♀♀) were examined from 13 localities in the following parishes: Catahoula, Claiborne, Concordia, Evangeline (SLI), Lafayette (SLI), Morehouse, Orleans, Pointe Coupee, Winn and Union. Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932), Orleans (Jung, 1950) and Rapides parishes (Johnson and Comstock, 1941).

ASTEROCAMPA CLYTON CLYTON (BOISDUVAL AND LECONTE).—The Tawny Emperor is not very common in Louisiana. The writer has seen two females, and von Reizenstein (1863) and Jung (1950) reported it from New Orleans. The butterfly is very fast in flight and is difficult to catch. The larvae feed on leaves of the hackberry (*Celtis mississippiensis*).

The Louisiana records are: *Lafayette*: Lafayette, VII-20-41, 1 ♀ (SLI); *Ouachita*: Sterlington, VI-23-50, 1 ♀ (TU 2072).

ASTEROCAMPA CELTIS CELTIS (BOISDUVAL AND LECONTE).—In Louisiana the Hackberry Butterfly is very common during the hot summer months, but due to the difficulty of capturing it only a few have been taken. Earliest and latest dates are June 8, 1947 (1 ♂) and August 3, 1931 (1 ♂). The flight is exceptionally rapid, high around the tops of bushes and trees. The larval food is hackberry.

Twenty-one specimens (9 ♂♂, 12 ♀♀) have been examined from seven localities in the following parishes: Concordia, Lafayette (SLI), Ouachita, Richland, and Sabine. Previously it had been recorded from Orleans parish by von Reizenstein (1863) and Jung (1950).

ASTEROCAMPA CELTIS ALICIA (EDWARDS).—Apparently in Louisiana this subspecies of the hackberry butterfly is quite restricted in its range, whereas *A. celtis celtis* is the dominant subspecies throughout the state.

The writer saw many of these butterflies darting among the branches of hackberry trees along the Mississippi river batture near New Orleans. On that occasion two males were captured, but not without considerable effort. The three specimens examined were all taken in Orleans parish as follows: VII-10-32, 1 ♀ (TU P-982) and IX-1-48, 2 ♂♂ (TU 1258).

Family LIBYTHEIDAE

LIBYTHEANA BACHMANNII BACHMANNII (KIRTLAND), the Snout Butterfly.—This species is very abundant in Louisiana during the hot summer months, but appears to fly at least occasionally even during the winter as the writer has observed a few individuals in December and January. Other than these "off season" observations the earliest and latest dates are May 19, 1950 (1 ♂) and August 27, 1949 (1 ♂). They may be found in swarms along roadside pools of water and damp places on the ground. Williams (1937) described a southeasterly migration of these "snouts" in September, which extended over a front of 250 miles. He estimated that one and a quarter million butterflies passed every minute on the whole front. The larvae feed on hackberry trees.

Twenty-four specimens (17 ♂♂, 7 ♀♀) have been examined from 14 localities in the following parishes: Catahoula, Concordia, East Feliciana, Lafayette (SLI), Morehouse, Orleans, Sabine, St. Bernard, Vermilion (SLI), Washington and West Feliciana. Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932) and Orleans parishes (Jung, 1939, 1950).

Family RIODINIDAE

CALEPHELIS VIRGINIENSIS (GUERIN), the Little Metal-mark.—The writer has captured a single male of this tiny butterfly from the Florida parish area, in the easternmost section of the state. Little is known of the immature stages of this species.

The lone record is: *St. Tammany*: St. Tammany, III-29-51, 1 ♂ (TU 2349). Previously it had been recorded from Opelousas in St. Landry parish by Holland (1931) under the synonym *C. louisiana*.

Family LYCAENIDAE

ATLIDES HALEUS HALEUS (CRAMER), the Great Purple Hair-streak.—The writer has not taken this beautiful insect, but Jung (1950) reported it from New Orleans. The one specimen examined was also collected in New Orleans, November 11, 1933, 1 ♂ (TU P-991).

STRYMON CECROPS (FABRICIUS).—The Cecrops Hair-streak is common in Louisiana during the spring and summer months, and is easily taken while it feeds on flowers. Earliest and latest dates are January 30, 1950 (1 ♂) and October 16, 1949 (1 ♂). A habit peculiar to the lycaenids consisting of "cleaning" or rubbing together the upper surfaces of the wings while at rest, is practiced strongly by this species.

Twelve specimens (10 ♂♂, 2 ♀♀) have been examined from twelve localities in the following parishes: Allen, East Feliciana, Franklin, Lafayette (SLI), Madison, Orleans, Ouachita, Pointe Coupee, Sabine, St. Tammany and Tangipahoa. Previously it had been recorded from Caddo (Field, 1941) and Madison parishes (Montgomery, 1932).

STRYMON MELINUS MELINUS (HUBNER), the Common Hair-streak.—This species is very common in Louisiana. The butterfly is very

swift in flight but is taken easily while feeding on wild flowers. It flies throughout the spring, summer and early fall; earliest and latest dates are March 10, 1943 (1 ♂) and October 14, 1949 (1 ♀). Howard (1895) described the damage to bean plants caused by the larvae.

Twenty-three specimens (15 ♂♂, 8 ♀♀) have been examined from 16 localities in the following parishes: Catahoula, Evangeline, Jefferson, Lafayette (SLI), Lincoln, Livingston, Natchitoches, Orleans; St. Bernard, St. Tammany, Tangipahoa and Washington. Previously it had been recorded from Cameron (Hine, 1906) and Orleans parishes (Jung, 1950).

STRYMON ONTARIO AUTOLYCUS (EDWARDS).—The Northern Hair-streak has been taken only once in Louisiana. Klots (1951) stated that it is not common, but may be caught easily while it feeds. The larva feeds on oak.

S. ontario autolytus has not been recorded from Louisiana previously. The Louisiana record is: *Orleans*: New Orleans, V-5-51, 1 ♀ (TU 3010).

STRYMON LIPAROPS LIPAROPS (BOISDUVAL AND LECONTE), the Striped Hair-streak.—Scudder (1889) stated that this butterfly is usually localized near thickets and swamps. The only specimen from Louisiana was taken in a dense upland hardwood forest with a very thick undergrowth of vines.

S. liparops liparops has not been recorded from Louisiana previously. The lone record is: *LaSalle*: Summerville, VI-12-50, (TU 2049).

INCISALIA IRUS (GODART), the Hoary Elfin.—This species is included on the basis of Skinner's report (1907), of it from the state, although the record is rather dubious. Holland (1931) stated that the species is always rather rare, but has a wide east-west distribution in the latitude of New England. This means that Skinner either published an exceptional range extension, or that he was confused with other nearly related species; most likely his specimen was *I. henrici*, with which *irus* has often been confused.

FENISECA TARQUINIUS TARQUINIUS (FABRICIUS), the Harvester.—The writer has taken only one specimen of this species, a female which was captured in a dense hardwood forest on the banks of the Ouachita river in northeastern Louisiana. The butterfly was flying about four feet from the ground in a very nervous manner and was taken with difficulty. The larvae of this butterfly are of some economic importance because they feed on woolly aphids, particularly those of the alder and beech.

The single record is: *Richland*: 7 miles north of Girard, VI-27-50, 1 ♀ (TU 2084). Previously the species was recorded from Caddo (Scudder, 1889), Orleans (von Reizenstein, 1863) and Webster parishes (Johnson, 1886).

HEMIARGUS ISOLUS (REAKIRT), Reakirt's Blue.—Klots (1951)

gives the range as "Mexico, north to Nebraska, almost entirely west of the Mississippi river." The few specimens collected in Louisiana certainly appear to be at the eastern edge of the species' range, and may be considered an extension as far as the southern portion of the range is concerned.

H. isolus has not been recorded from Louisiana previously. The records are: *Concordia*: 13 miles northwest of Ferriday, VI-16-50, 1 ♂ (TU 2056); *Morehouse*: 12 miles east of Mer Rouge, VI-19-50, 3 ♂ ♂, 1 ♀ (TU 2063).

EVERES COMYNTAS COMYNTAS (GODART).—The Eastern Tailed-blue is very abundant in Louisiana during the spring and summer months; earliest and latest dates are January 2, 1950 (1 ♀) and October 14, 1949 (1 ♂). The writer has seen most specimens along the edges of forests in partly shaded areas and on the ground around moist places. Their quick flight and small size make them hard to catch.

Sixty-five specimens (38 ♂ ♂, 27 ♀ ♀) have been examined from 25 localities in the following parishes: Catahoula, Evangeline, East Feliciana, Lafayette (SLI), LaSalle, Lincoln, Madison, Morehouse, Natchitoches, Ouachita, Richland, Sabine, St. Charles, St. Tammany, Union, Washington and West Carroll. Previously it had been recorded from Madison parish by Montgomery (1932).

CELASTRINA ARGIOLUS PSEUDARGIOLUS (BOISDUVAL AND LE-CONTE).—The Spring Azure apparently is rare in Louisiana. The few specimens collected were taken in the longleaf pine flats of the Florida parishes. Scudder (1889) stated that the range does not touch the Gulf of Mexico; hence this species may not be found in the coastal parishes.

C. argiolus pseudargiolus has not been recorded from Louisiana previously. The two records are *East Feliciana*: Felixville, VI-8-50, 3 ♂ ♂ (TU 2037); *Washington*: Angie, VI-4-50, 1 ♂ (TU 2032).

Family PAPILIONIDAE

PAPILIO POLYXENES ASTERIAS (STOLL).—The Common American Swallowtail apparently is not confined to any particular part of Louisiana. It is rather abundant throughout the spring and summer; earliest and latest dates are January 1, 1950 (1 ♂) and September 7, 1926 (1 ♀). It is a frequent visitor to flowers; specimens have been taken on roses, clover and numerous umbelliferous plants. It has some economic importance as the caterpillars may feed on celery, dill, parsnip, carrots, caraway and parsley.

Twenty-three specimens (14 ♂ ♂, 9 ♀ ♀) have been examined from ten localities in the following parishes: Claiborne, Franklin, Jefferson, Lafayette (SLI), Orleans, Richland, St. Charles, Tensas, Vermilion (SLI) and Washington. Previously it had been recorded from Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863; Jung, 1939, 1950).

PAPILIO CRESPHONTES CRESPHONTES (CRAMER).—The Giant Swallowtail, one of largest of the North American butterflies, is of eco-

onomic importance to fruit growers for the caterpillar, the "Orange-puppy," feeds on citrus trees. In Louisiana it is more abundant in the southernmost areas. Rothschild and Jordan (1906) record the species from "Louisiana."

Saverner (1908) reported badly damaged *P. cresphontes* and *P. troilus* migrating southward along with monarchs during August; this may have been the situation of two *cresphontes* captured in north Louisiana during August which were accompanying a southerly migration of monarchs. In Louisiana the species flies from spring to early fall; earliest and latest dates are March 2, 1949 (1 ♂, 1 ♀) and November 13, 1911 (1 ♀).

Twenty-six specimens, (13 ♂♂, 13 ♀♀) have been examined from eleven localities in the following parishes: Claiborne, Jefferson, Lafayette (SLI), Livingston, Orleans, Plaquemines, St. Tammany, Terrebonne (LSM) and Vermilion (SLI). Previously it had been recorded from Cameron (Hine, 1906) Orleans (von Reizenstein, 1863; Jung, 1939, 1950) Plaquemines (Jung, 1950), St. Bernard (Jung, 1950) and Terrebonne parishes (Comstock, 1882).

PAPILIO GLAUCUS GLAUCUS (LINNÉ).—The Tiger Swallowtail displays strong sexual dimorphism. In the southern part of its range some of the females are dark brown rather than black and yellow. According to Klots (1951) this melanism occurs in about 50 percent of the females, but he states that the brown form is less common or nonexistent in the extreme south. All of the females that the writer has seen from Louisiana show this dark brown coloration. Some of the males are larger and tend to show the darker yellow color of *P. glaucus australis*, although none of the specimens appear clearly to be that subspecies.

The species is a strong flier and is difficult to catch in flight; however, the writer found them easy to collect while they were feeding on the thistle (*Cirsium horridulum*). Riley and Howard (1895) reported the caterpillars feeding on the leaves of camphor trees in Louisiana.

The species has been collected in all months of the year except January and December; earliest and latest dates for adults are February 18, 1950 (2 ♂♂) and November 16, 1939 (1 ♀).

Twenty-three specimens (17 ♂♂, 6 ♀♀) have been examined from twelve localities in the following parishes: Assumption, Bossier, Claiborne, Lafayette (SLI), Madison, Morehouse, Natchitoches, Orleans, Sabine, St. Charles, St. Tammany and Washington. Previously it had been recorded from Jefferson (Jung, 1950), Morehouse (Riley and Howard, 1895), Orleans (von Reizenstein, 1863) and St. Tammany parishes (Jung, 1950).

PAPILIO TROILUS TROILUS (LINNÉ).—The Spicebush Swallowtail is the most common member of its genus in Louisiana. It flies from early spring to late summer; earliest and latest dates are February 23, 1949 (3 ♂♂) and September 16, 1945 (1 ♂). The larvae and adults feed on spicebush, sassafras and other Lauraceae.

Saverner (1908) stated that *P. troilus* was seen migrating southward with the monarch (*Danaus plexippus*) in August, but no evidence of migrations of this swallowtail have been noted as yet in Louisiana.

Forty-one specimens (27 ♂♂, 14 ♀♀) have been examined from eleven localities in the following parishes: Caddo, DeSoto, Jackson, Jefferson, Lafayette (SLI), LaSalle, Orleans, Ouachita, Sabine, St. Tammany and Union. Previously it had been recorded only from Orleans parish by von Reizenstein (1863) and Jung (1939, 1950).

PAPILIO TROILUS ILIONEUS J. E. SMITH.—While many of the spicebush swallowtails from Louisiana are more typical of the subspecies *troilus*, three specimens possess very definite characteristics of subspecies *ilioneus*. However, the majority collected have characteristics common to either or both of the subspecies, due to the clinal nature of the species.

P. troilus ilioneus has not been recorded from Louisiana previously. The records are: *Orleans*: New Orleans, III-4-49, 2 ♀♀ (TU 1110); *Ouachita*: Sterlington, VI-23-50, 1 ♂ (TU 2072).

PAPILIO PALAMEDES PALAMEDES (DRURY).—The Palamedes Swallowtail is a rather rare insect in Louisiana, records of this species being confined to the coastal parishes. As this butterfly is a strong flier and difficult to capture, adults are more readily obtained by rearing them from the larval stage. The few specimens collected were taken in the months of April, June, July, August and October; earliest and latest dates are April 1, 1918 and October 13, 1934.

Nine specimens (5 ♂♂, 4 ♀♀) were examined from three localities in the following parishes: Lafayette (SLI), Orleans and Terrebonne (LSM). Previously it had been recorded from Orleans parish by von Reizenstein (1863), Rothschild and Jordan (1906) and Jung (1950).

GRAPHIUM MARCELLUS MARCELLUS (CRAMER), the Pawpaw Butterfly.—Although this species is fairly common in Louisiana during the early summer months it is exceedingly difficult to take with a net. A few specimens were obtained, however, after many others had eluded capture. Earliest and latest dates were April 1, 1950 (1 ♂) and September 10, 1947 (1 ♀). Late in the survey it was learned that this butterfly usually picks an orbit to follow in its flight, and if the collector misses it on the first try he has only to wait a few minutes for the same individual to return, flying almost exactly the same course.

Within Louisiana *marcellus* apparently is rare in the coastal and Florida parish areas, and all of the specimens were obtained from the vicinity of the Mississippi river westward and northward. It is more abundant in the upland areas of the state. Its scarcity in southern Louisiana may be due to the lack of its food plant, the pawpaw (*Asimine triloba* and *A. parviflora*), in the coastal region.

Eleven specimens (6 ♂♂, 5 ♀♀) were examined from five local-

ities in the following parishes: Catahoula, Lafayette (SLI), Sabine, Union and West Feliciana. Previously it had been recorded from Orleans parish by Kopman (1903) under the name *Papilio ajax*.

BATTUS PHILENOR PHILENOR (LINNÉ).—The Pipe-vine Swallowtail is most common during the summer months in Louisiana, but it has a long flying season; earliest and latest dates are February 1, 1949 (1 ♂) and October 16, 1940 (1 ♀). Holland (1931) states that *philenor* has been observed ovipositing as late as October. The species is exceptionally fast in flight, perhaps accounting for the scarcity of records. The larvae generally feed on Dutchman's pipe or pipe-vine (*Aristolochia serpentaria* and *A. durior*).

Seventeen specimens (13 ♂♂, 4 ♀♀) have been examined from eleven localities in the following parishes: Bossier, Lafayette (SLI), Morehouse, Ouachita, Rapides, Sabine, St. Tammany, Union and Washington. Previously it had been recorded from Cameron (Hine, 1906), Orleans (von Reizenstein, 1863), St. John the Baptist (Jung, 1950), St. Mary (Kopman, 1903), and St. Tammany parishes (Jung, 1950).

BATTUS POLYDAMUS LUCAYUS (LINNÉ), the Polydamus Butterfly.—The writer has not seen this butterfly in Louisiana, but von Reizenstein (1863) reported it from New Orleans. According to his observations it was very rare, usually found feeding on Virginia snake root and Dutchman's pipe. McDunnough (1938) doubted its occurrence in North America, but Klots (1951) stated that it occurs in the Gulf states from Florida to Texas.

Family PIERIDAE

ANTHOCHARIS GENUTIA GENUTIA (FABRICIUS), the Falcate Orange-tip.—In Louisiana this species apparently is confined to the upland regions of the northern part of the State. Scudder (1889) stated that the butterfly has never been very abundant. From the writer's experience it seems that this species is a very weak flier, and is easy to collect, although Scudder (1889) reported otherwise.

A. genutia has not been recorded from Louisiana previously. The three records are: *Jackson*: Kelleys, IV-1-50, 1 ♂ (TU 1846); *Chatham*, IV-1-50, 2 ♂♂ (TU 1849); *Lincoln*: Downs ville, IV-1-50, 1 ♂, 1 ♀ (TU 1859).

COLIAS EURYTHEME EURYTHEME BOISDUVAL.—The Eurytheme Sulphur can be found in all parts of Louisiana, but it is not as abundant in the coastal area as it is in the pinelands and uplands, especially in open grass or clover-covered fields. This species flies throughout most of the year; earliest and latest dates are January 21, 1950 (2 ♂♂) and November 8, 1939 (1 ♀). The larvae feed occasionally on *Trifolium repens* and other related species of this genus, but Scudder (1889) reported that the caterpillars would not eat red clover. The favorite food, however, is the introduced alfalfa (*Medicago sp.*), on which it is a serious pest.

With the exception of *C. a. pseudargiolus*, a lycaenid, *C. eurytheme*

is probably the most variable species in our butterfly fauna. The literature is filled with descriptions of the many sexual and seasonal forms. These have been considered at times to be distinct species, and as such have presented a very puzzling problem. However, in recent years much has been done by Hovanitz (1943, 1944) to study the *Colias* complex; hybridization and female albinism have been studied also by Gerould (1946).

Sixty specimens (26 ♂♂, 34 ♀♀) have been examined from 22 localities in the following parishes: Assumption, Claiborne, Concordia, East Baton Rouge, Evangeline, Lafayette (SLI), Morehouse, Natchitoches, Orleans, Ouachita, Rapides, Richland, and St. Charles. Previously it had been recorded from East Baton Rouge (Floyd, 1941), Madison (Montgomery, 1932; Glick, 1939) and Orleans parishes (Scudder, 1889; Jung, 1939, 1950).

COLIAS PHILODICE PHILODICE (LATREILLE), the Common Sulphur.—The common name of this butterfly implies abundance, but it is rather rare in Louisiana, and although it has a wide range throughout North America one specimen has thus far been taken in the state. From what can be discerned from Scudder (1889) it is not numerous at the southern extremities of its range.

C. philodice philodice has not been recorded from Louisiana previously. The lone record is: *Lafayette*: Lafayette, XI-30-36, 1 ♂ (SLI).

ZERENE CESONIA (STOLL), the Southern Dog-face.—The writer has examined only one specimen from Louisiana, and it has been recorded by von Reizenstein (1863) from New Orleans. The fact that this butterfly flies very fast and often high off the ground may account for the scarcity of records. The species frequents pinelands, and has been seen by the writer in the pine flats of the Florida parishes in August, but on that occasion the individuals were flying fast and high above the ground, and none were caught.

The single record is: *Lafayette*: Lafayette, XI-12-28, 1 ♂ (SLI).

PHOEBIS SENNAE EUBULE (LINNÉ).—The Cloudless Sulphur is very abundant during most of the year throughout Louisiana. Earliest and latest dates are March 4, 1934 (1 ♀) and November 1, 1949 (1 ♂). It is an exceptionally strong flier, and is migratory. Great swarms of them have been observed far out at sea, flying just above the waves (Williams, 1937). During courtship when the male and female "pinwheel" high above the ground they are especially hard to capture, yet when feeding they are so occupied that the writer has taken many by hand. The larvae feed on *Cassia* spp.

Forty-six specimens (25 ♂♂, 21 ♀♀) have been examined from 32 localities in the following parishes: Allen, Assumption, Bossier, Claiborne, Concordia, East Baton Rouge, Evangeline, Franklin, Jefferson, Lafayette (SLI), Orleans, Ouachita, Pointe Coupee, Rapides, Red River, Richland, Sabine, St. Bernard, St. Helena, St. Tammany, Tangipahoa (SLI, TU) and Washington. Previously it had been recorded from Madison (Montgomery, 1932) and Orleans parishes

(von Reizenstein, 1863; Jung, 1939, 1950).

PHOEBIS SENNAE SENNAE (LINNÉ).—This subspecies is included on the basis of Klots' (1951) mention that "in southern Florida and Louisiana many very *sennae*-like specimens occur." He describes the color as being a warmer yellow than that of *eubule*. Indeed, in the Tulane and Southwestern Louisiana Institute collections there are specimens of *P. sennae* that fit this description, particularly those from the Lafayette area. Since the subspecific classification is very complex and for the most part a matter of statistics the writer has chosen to include the "*sennae*-like" specimens in the records for *eubule*. One female taken at Lafayette on November 2, 1950 comes closest to fitting the description of warm yellow.

PHOEBIS PHILEA (LINNÉ), the Red-barred Sulphur.—The writer has never collected *P. philea* although several specimens from Louisiana have been available for examination. In addition to these the writer has information from Dr. Wm. T. M. Forbes (in personal communication) that he had taken this species in New Orleans on January 1, 1933. The species is known to be migratory.

P. philea has not been recorded from Louisiana previously. The few records are: *Allen*: Kinder, VI-12-41, (SLI); *Orleans*: New Orleans, X-11-32, 1 ♂ (TU P-978), and VII-15-32, 1 ♀ (TU P-982).

PHOEBIS AGARITHE MAXIMA (NEUMOEGER), the Large Orange Sulphur.—As this butterfly is mainly tropical, only three specimens have been caught in Louisiana, and these are from the southern parishes. The species is migratory according to Williams (1937).

It has not been recorded from the state previously. The few records are: *Lafayette*: Lafayette, 1 ♀ (SLI); *Orleans*: New Orleans, VIII-24-26, 1 ♀ (TU P-965), IX-19-31, 1 ♀ (TU P-977), and X-2-31, 1 ♀ (TU P-978).

EUREMA DAIRA DAIRA (LATREILLE), the Fairy Yellow.—This is a very variable species; some have all, others only one-half the border of the hind wings black, and individuals of the latter type often have the undersides of the hind wings white. These two forms for a long time were held as two species, but Dr. R. L. Chermock (personal correspondence) considers them to be variations of one species.

In Louisiana the species apparently is not widespread, nor does it fly during as great a part of the year as does *E. lisa*. With the exception of one male from the southwest, all specimens were taken during the summer in the Florida parishes. Though the species apparently is not evenly distributed, the writer found a dense population of what appeared to be a southwesterly migration September 6-8, 1950, near Covington, La. All the butterflies were flying in one direction a few feet from the ground stopping only occasionally to feed at conspicuous flowers.

E. daira daira has not been recorded previously from Louisiana.

The records are: *Lafayette*: Lafayette, IX-25-36, 1 ♂ (SLI); *Livingston*: Springfield, IX-6-50, 2 ♂♂, 1 ♀ (TU 2183, 2184); *St.*

Helena: Liverpool, IX-7-50, 3 ♂♂, 1 ♀ (TU 2193); Greensburg, IX-7-50, 2 ♂♂ (TU 2194); *St. Tammany*: Folsom, IX-7-50, 1 ♂, 2 ♀♀ (TU 2187); Covington, IX-8-50, 2 ♂♂ (TU 2196); *Tangipahoa*: Lee Landing, IX-6-50, 1 ♂ (TU 2181); Robert, IX-6-50, 1 ♂, 1 ♀ (TU 2185); Tangipahoa, IX-7-50, 1 ♀ (TU 2191); Amite, IX-7-50, 2 ♀♀ (TU 2195); *Washington*: Angie, VI-5-50, 1 ♂, 1 ♀ (TU 2034); Richardson, IX-7-50, 1 ♂, 2 ♀♀ (TU 2188).

EUREMA NICIPPE NICIPPE (CRAMER).—The Nicippe Sulphur is common throughout Louisiana during most of the summer months. However, it has a relatively long flying season; earliest and latest dates are April 8, 1950 (1 ♀) and December 8, 1949 (1 ♀).

This butterfly is not usually common everywhere throughout the summer, but occurs in small swarms in sunny places in the pinelands. When it is flying it is rare to see only one at a time, as usually several are in flight short distances from each other.

Forty-eight specimens (30 ♂♂, 18 ♀♀) have been examined from 26 localities in the following parishes: Avoyelles (SLI), Catahoula, Claiborne, Concordia, Evangeline, Lafayette (SLI), Livingston, Morehouse, Ouachita, Plaquemines, Pointe Coupee, Rapides, Richland, Sabine, St. Helena, St. Landry (SLI), St. Tammany, Tangipahoa, Vermilion (SLI) and Washington. Previously it had been recorded from Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863).

EUREMA LISA (BOISDUVAL AND LECONTE).—The Little Sulphur is the most abundant pierid in the state. In Louisiana it is most abundant in mid-summer, although it flies from early spring well into the autumn. Earliest and latest dates are January 2, 1950 (2 ♀♀) and October 16, 1949 (4 ♂♂, 4 ♀♀). Scudder (1889) stated that the butterfly will fly in heavily clouded weather, but the writer believes this to be unlikely as it has always been observed to take cover when clouds hide the sunlight.

E. lisa is not a strong flier and is easy to capture. Usually they fly close to the ground in open places, and congregations of them are often seen sucking water from moist ground. However, in spite of its frailness and weak flight, it has been known to migrate in great clouds for remarkable distances (Scudder, 1889). The larvae feed on *Cassia* spp.

One hundred and eleven specimens (73 ♂♂, 38 ♀♀) have been examined from 56 localities in the following parishes: Allen, Assumption, Bienville, Catahoula, Claiborne, Concordia, DeSoto, Evangeline, Franklin, Lafayette (SLI), Lafourche, Livingston, Morehouse, Natchitoches, Orleans, Pointe Coupee, Rapides, Richland, Sabine, St. Bernard, St. Charles, St. Helena, St. Landry, St. Tammany, Tangipahoa, Washington, Webster and West Feliciana. Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932) and Orleans parishes (Jung, 1950).

NATHALIS IOLE (BOISDUVAL), the Dwarf Yellow.—Jung (1950) reported this species as very common about fields in New Orleans,

but I have not found it in great numbers at any one time as it is very local and easily overlooked. It flies in sunny, grassy places along the sides of roads, and in open fields. It is most abundant in the warmer months, but stragglers have been taken as late as October in Louisiana.

The few records are: *Claiborne*: 8 miles east of Lisbon, VIII-6-49, 1 ♂, 1 ♀ (TU 1457); *Lafayette*: Lafayette, X-2-36, 1 ♀ (SLI); *Pointe Coupee*: McCrea, X-14-49, 1 ♂ (TU 1568); *Sabine*: Negreet, VII-7-50, 1 ♀ (TU 2101); 10 miles west of Negreet, VII-8-50, 1 ♀ (TU 2106).

PIERIS RAPAE (LINNÉ).—The Cabbage Butterfly was not originally a member of the North American fauna, but was introduced on this continent at Quebec in 1860 from Europe. From there the species has spread throughout the continent inflicting damage to crops totalling hundreds of thousands of dollars annually. Scudder (1889) gave an excellent account of its spread, but gave no definite date for its introduction into Louisiana. However, it had reached Bastrop, Texas by 1881.

In Louisiana the species is abundant during the spring and early summer months, but may be seen flying during late fall and winter. Earliest and latest dates are January 2, 1950 (5 ♂♂, 1 ♀) and November 30, 1950 (1 ♂). The writer has seen many adults feeding on the blossoms of clover (*Trifolium repens*).

Twenty-one specimens (13 ♂♂, 8 ♀♀) have been examined from nine localities in the following parishes: Catahoula, Lafayette (SLI), Ouachita, St. Charles, Washington and West Feliciana. Previously it had been recorded from Orleans and St. Bernard parishes by Jung (1939, 1950).

PIERIS PROTODICE PROTODICE (BOISDUVAL AND LECONTE).—The Common White has a wide range over the continent and it is not scarce in Louisiana where it flies during the hot summer months. Earliest and latest dates are June 16, 1950 (5 ♂♂, 1 ♀) and September 5, 1938 (1 ♀). The flight is easy and rather methodical, and adults are easily collected.

Twelve specimens (8 ♂♂, 4 ♀♀) have been examined from seven localities in the following parishes: Catahoula, Concordia, Lafayette (SLI), Morehouse, Orleans and Ouachita. Previously it had been recorded from Cameron (Hine, 1906), Madison (Montgomery, 1932) and Orleans parishes (von Reizenstein, 1863; Jung, 1939, 1950).

ASCIA MONUSTE PHILETA (FABRICIUS), the Great Southern White.—Much has been written concerning the migration and immature stages of this butterfly by Nielsen and Nielsen (1950) who found eggs deposited on saltwort (*Batis maritima*), nasturtium (*Tropaeolum majus*), spider-wisp (*Cleome* spp.) and other plants. In spite of its wide range and abundance in the Gulf states only two males and one female have been caught in the state. However, the writer saw many of them flying along the shore and over the water of Lake Pontchartrain at New Orleans (May 10, 1950), but speci-

mens were not obtained.

The few records are: *Lafayette*: Lafayette, VI-25-28, 1 ♀ (SLI) and VII-8-50, 1 ♂ (SLI); *Orleans*: New Orleans, VI-30-31, 1 ♂ (TU P-974). Previously it had been recorded from Orleans parish by von Reizenstein (1863) and Jung (1939, 1950).

Superfamily HESPEROIDEA, the Skippers

Family HESPERIIDAE

EPARGYREUS CLARUS (CRAMER), the Silverspotted Skipper.—The flight of this species is very fast, and although it is common it is not easily caught. All specimens were captured while they fed on flowers, particularly blossoms of the buttonball bush (*Cephalanthus occidentalis*). Caterpillars feed on *Robina*, *Wisteria*, *Pueraria* and other leguminous plants.

Jung (1950) reported it common within residential New Orleans, but the writer has taken specimens only in sunny fields and bordering areas of woods.

The few Louisiana records are: *Caldwell*: Columbia, VIII-3-48, 1 ♂ (TU 429); *Sabine*: Negreet, VII-7-50, 1 ♂ (TU 2101); *St. Tammany*: Folsom, IX-7-50, 1 ♂ (TU 2187); Covington, IX-8-50, 1 ♂, 1 ♀ (TU 2196). Previously it had been recorded from Madison (Glick, 1939) and Orleans parishes (von Reizenstein, 1863; Jung, 1950).

URBANUS PROTEUS (LINNÉ), the Longtailed Skipper.—In Louisiana this species is seen almost throughout the year flying from flower to flower in open sunny places. Earliest and latest dates are February 23, 1949 (1 ♂) and November 6, 1949 (1 ♂). This skipper often picks a resting place and returns to the same spot time and time again after being disturbed. One such individual, whose tails were broken in such a way as to make it easily recognizable, favored a lead pipe in the writer's garden. Day after day for almost a month the same skipper headquartered around the pipe, occasionally flying a few feet away to feed on lantana flowers. The larvae feed on certain species of the Leguminosae, particularly *Wisteria* and *Clitoria*.

Twelve specimens (10 ♂♂, 2 ♀♀) have been examined from eight localities in the following parishes: Allen, Assumption, Orleans, Pointe Coupee, St. Bernard, St. Charles, St. Tammany and Tangipahoa. Previously it had been recorded from Orleans parish by Shufeldt (1884) and Jung (1950).

ACHALARUS LYCIADES (GEYER), the Hoary-edge.—Only three individuals have been taken in Louisiana, and these during the summer. One was captured while it was feeding on flowers of the buttonball bush (*Cephalanthus occidentalis*). The larvae feed on various leguminous plants.

The species has not been recorded from Louisiana previously. The few records are: *Sabine*: Negreet, VII-7-50, 1 ♂ (TU 2102); 10 miles west of Negreet, VII-8-50, 1 ♂ (TU 2106); *Union*: Marion, VI-24-50, 1 ♂ (TU 2075).

THORYBES BATHYLLUS (J. E. SMITH).—The Southern Dusky-wing is more abundant in Louisiana than its ally, *T. confusus*, and flies from early spring throughout the summer. Earliest and latest dates are February 24, 1950 (1 ♂) and September 8, 1950 (2 ♂♂, 1 ♀). The larvae feed on various species of the family Fabaceae.

T. bathyllus has not been recorded from Louisiana previously. The ten specimens examined (6 ♂♂, 4 ♀♀) are from the following localities: *Bienville*: Bienville (TU 1459); *Sabine*: Negreet (TU 2101); *St. Tammany*: Hickory (TU 1800); Covington (TU 2196); *Tangipahoa*: Ponchatoula (TU 2182); Robert (TU 2185); *Union*: 7 miles east of Farmerville (TU 1863); *Washington*: Richardson (TU 2188).

THORYBES CONFUSUS BELL.—The Northern Dusky-wing is found occasionally in Louisiana during the summer months but records of it are not numerous. According to Scudder (1889) it frequents open fields and sunny places visiting flowers, often clovers. Little is known of the immature stages.

T. confusus has not been recorded from Louisiana previously. The few records are: *Catahoula*: 5 miles southwest of Lee Bayou, VI-11-50, 1 ♀, (TU 2044); *Claiborne*: Scottsville, VI-29-50, 1 ♂ (TU 2086); *Sabine*: Belmont, VIII-2-49, 1 ♂ (TU 1379); Negreet, VII-10-50, 1 ♂ (TU 2103).

PYRGUS COMMUNIS COMMUNIS (GROTE).—The Common Checkerspot Skipper is one of the commonest skippers of Louisiana, often seen flying a few inches from the ground on hot, dusty roads. Earliest and latest dates are January 24, 1950 (1 ♂) and October 16, 1949 (3 ♂♂). Most specimens have been taken during flight, which is very rapid and elusive. The collector must not lose sight of the insect for a second if he wishes to catch it, for its checkerboard pattern blends very well with the background.

There is no apparent localization in the state, the species having been collected in all the major areas. The larvae feed on various species of the family Malvaceae.

Twenty-one specimens (18 ♂♂, 3 ♀♀) have been examined from 18 localities in the following parishes: Catahoula, East Feliciana, Evangeline, Jefferson, Lafayette (SLI), Natchitoches, Orleans, Ouachita, Pointe Coupee, Rapides, Sabine, St. Bernard, St. Charles, St. Landry, St. Tammany, Washington and West Feliciana. Previously it had been recorded from Orleans parish by Jung (1950).

CELOTES NESSUS (EDWARDS), the Streaky Skipper.—The writer has not seen this species in Louisiana but it was reported from Madison parish by Glick (1939) who did extensive work with traps carried by airplanes. A single specimen was taken during the day at an altitude of twenty feet.

PHOLISORA HAYHURSTII (EDWARDS), Hayhurst's Skipper.—A single specimen of this species has been taken in Louisiana, flying near the ground in a dense oak-hardwood stand on the front lands of the

Mississippi river. Little is known concerning the immature stages.

The species has not been recorded from Louisiana previously. The single record is: *Jefferson*: Kenner, III-9-51, 1 ♂ (TU 2298).

ERYNNIS HORATIUS (SCUDDER AND BURGESS), Horace's Dusky-wing.—Most of the individuals were captured in hot, sunny spots in and along dense forests, but none were seen feeding. The flight is rapid and fleeting, the insect staying about ten feet away from the collector, alighting on the ground, and darting to a new resting place if disturbed. Three males collected on June 4th, and 5th were sitting on the hot, dry surface of a sand bar along the Pearl river. Earliest and latest dates are June 1, 1950 (1 ♂) and September 7, 1950 (1 ♂). Little is known about the immature stages.

Eleven specimens (9 ♂♂, 2 ♀♀) were examined from nine localities in the following parishes: Assumption, DeSoto, East Feliciana, LaSalle, St. Tammany, Union and Washington. Previously it had been recorded from Orleans parish by Jung (1950).

ERYNNIS JUVENALIS (FABRICIUS).—Only three specimens of this skipper have been taken in Louisiana. The larvae feed on oaks and various legumes according to Scudder (1889).

This species has not been recorded from Louisiana previously. The records are: *Orleans*: New Orleans, II-4-50, 1 ♀ (TU 1782); *St. Tammany*: Covington, IX-8-50, 2 ♀♀ (TU 2196).

ANCYLOXYPHA NUMITOR (FABRICIUS).—The Numitor Skipperling apparently is never abundant in Louisiana. According to Scudder (1889) the flight is slow and feeble and it is one of the easiest skippers to capture in flight. The larvae feed on grasses (Klots, 1951). Earliest and latest dates are February 18, 1950 (1 ♂) and October 19, 1949 (1 ♀).

Eight specimens (3 ♂♂, 5 ♀♀) have been examined from seven localities in the following parishes: Allen, Evangeline, Jefferson, St. Bernard, St. Charles, St. Tammany and Washington. Previously it had been recorded from Jefferson parish by Jung (1950).

COPAEODES MINIMA (EDWARDS), the Tiny Skipperling.—This is probably the smallest skipper in North America. It is very common but its size and ability to blend into its surroundings make it difficult to see. The majority were taken while feeding on daisies in open, sunny fields throughout the state. Earliest and latest dates are March 2, 1949 and October 18, 1949. Nothing is known of the early stages.

C. minima has not been recorded from Louisiana previously. Twenty-four specimens (13 ♂♂, 11 ♀♀) have been examined from 14 localities in the following parishes: Claiborne, Evangeline, Jefferson, Livingston, Morehouse, Orleans, Ouachita, Pointe Coupee, Rapides, Richland, St. Bernard and Tangipahoa.

HESPERIA LEONARDUS STALLINGSI H. A. FREEMAN.—A single specimen of the Leonardus Skipper was taken in Madison parish by Glick (1939) in an airplane trap at an altitude of twenty feet. The

writer has no other information concerning the occurrence of this species in Louisiana.

HYLEPHILA PHYLEUS (DRURY).—The Fiery Skipper is often taken while it frequents flowers along the borders of woods, and in open places in dense forests. The flight is not rapid, hence the species is easily captured. Earliest and latest dates are March 2, 1949 (1 ♀) and October 16, 1949 (1 ♂, 1 ♀). The larvae supposedly feed on crab grass (Scudder, 1889).

Twenty-one specimens (13 ♂♂, 8 ♀♀) have been examined from 15 localities in the following parishes: Catahoula, East Feliciana, Evangeline, Jefferson, Morehouse, Orleans, Richland, Sabine, St. Landry, Tangipahoa, Union and Washington. Previously it had been recorded from Cameron parish by Hine (1904).

ATALOPEDES CAMPESTRIS (BOISDUVAL), the Sachem.—The few Louisiana specimens are all from the eastern parishes near the Mississippi river. From what the writer has observed the flight is rather rapid and jerky, the skipper flitting from flower to flower; however, when it is feeding it may be caught easily. The larvae feed on Bermuda grass.

The species has not been recorded from Louisiana previously. The records are: *East Feliciana*: Felixville, VI-8-50, 2 ♀♀ (TU 2039); *LaSalle*: Summerville, VI-12-50, 1 ♂ (TU 2048); *Morehouse*: 10 miles west of Twin Oaks, VI-26-50, 1 ♂, 1 ♀ (TU 2079); *Ouachita*: Perryville, VI-23-50, 1 ♂ (TU 2071); *Sterlington*, VI-18-50, 1 ♂ (TU 2060) and VI-23-50, 1 ♀ (TU 2072); *Union*: Marion, VI-24-50, 1 ♂, 1 ♀ (TU 2075).

POLITES MANATAAQUA MANATAAQUA (SCUDDER), the Manataaqua Skipper.—Lindsey, Bell and Williams (1931) stated that this subspecies occurs from the northeastern United States to Alabama, and westward to South Dakota and Nebraska. Klots (1951) described its range as above, but included Arkansas and Georgia. The species is rare in Louisiana, but nevertheless the six specimens taken constitute what appears to be a southern range extension. All were captured in moist, grassy openings in the pine flats of the Florida parishes north of Lake Pontchartrain. The larvae feed on common grasses.

The subspecies has not been recorded from Louisiana previously. The records are: *St. Tammany*: Hickory, IX-13-50, 1 ♂ (TU 2198); *Tangipahoa*: Ponchatoula, IX-6-50, 4 ♂♂, 1 ♀ (TU 2182).

POLITES THEMISTOCLES (LATREILLE).—The Tawny-edged Skipper is well distributed throughout Louisiana. All specimens thus far have been collected during the summer months in open sunny spots in fields and woods, especially where there are flowers in bloom. The caterpillars feed on grass.

The species has not been recorded from Louisiana previously. The records are: *East Feliciana*: Felixville, VI-8-50, 1 ♂ (TU 2039); *Sabine*: Negreet, VII-7-50, 1 ♀ (TU 2101); *St. Tammany*: Hickory,

VII-15-50, 1 ♀ (TU 2001); *Tangipahoa*: Lee Landing, IX-6-50, 1 ♂, 1 ♀ (TU 2181); Ponchatoula, IX-6-50, 1 ♂ (TU 2182); *Union*: Haile, VI-20-50, 1 ♂ (TU 2067).

POLITES VIBEX BRETTUS (BOISDUVAL AND LECONTE), the Whirlabout.—There is no apparent localization of this species in Louisiana, and although it is not common, it has been taken often in the pine flats of the Florida parishes and in other parts of the state. All specimens were collected while they were feeding on wild flowers. The larvae feed on grasses.

P. vibex brettus has not been recorded from Louisiana previously. The records are: *Evangeline*: 12 miles west of Mamou, X-16-49, 1 ♀ (TU 1576); *Sabine*: Negreet, VI-7-50, 2 ♂♂, 2 ♀♀ (TU 2101); 8 miles west of Negreet, VII-8-50, 1 ♂ (TU 2107); *St. Tammany*: Covington, IX-8-50, 1 ♂ (TU 2180) and IX-8-50, 3 ♂♂ (TU 2196); *Tangipahoa*: Robert, IX-6-50, 2 ♂♂ (TU 2185); *Union*: Haile, VI-20-50, 1 ♀ (TU 2067).

WALLENGRENIA OTHO OTHO (J. E. SMITH), Otho's Skipper.—Thus far in Louisiana this species has been collected mostly in the Florida parishes. The larvae feed on crab grass (*Panicum sanguinale*) according to Klots (1951).

Otho's skipper has not been recorded from Louisiana previously. The records are: *Orleans*: New Orleans, III-22-50, 1 ♂ (TU 1821); *St. Tammany*: Covington, 4 ♂♂, 2 ♀♀ (TU 2196); *Tangipahoa*: Ponchatoula, IX-6-50, 1 ♂ (TU 2182).

POANES VIATOR (EDWARDS), the Broadwinged Skipper.—Although this species apparently is locally very common in Louisiana during the spring and early summer months, only twelve specimens have been collected thus far. All of these were taken together while they were feeding on a roadside strip of daisies. The flight is exceptionally fast. Lindsey, Bell and Williams (1931) stated that the species flies from June to August. Nothing is known of the early stages.

The Louisiana record is: *St. Charles*: Norco, III-10-51, 6 ♂♂, 6 ♀♀ (TU 2301). Previously it had been recorded from Orleans parish by Scudder (1889).

ATRYTONE AROGOS AROGOS (BOISDUVAL AND LECONTE), the Iowa Skipper.—A single specimen has been collected in Louisiana while it was feeding on daisies growing in a garbage dump. Little information is available on the immature stages.

The species has not been recorded from Louisiana previously. The lone record is: *St. Tammany*: Covington, IX-8-50, 1 ♂ (TU 2197).

ATRYTONE DUKESI LINDSEY, Dukes' Skipper.—A single specimen has been taken in Louisiana. The species was described from Mobile, Alabama, and Holland (1931) predicted that it would occur over a wider area along the Gulf, although Klots (1951) made no mention of it west of Alabama. The Louisiana record constitutes a possible westward range extension. Information is lacking concerning the early stages.

The species has not been recorded from Louisiana previously. The lone record is: *West Carroll*: 11½ miles west of Oak Grove, VI-19-50, 1 ♂ (TU 2064).

ATRYTONE RURICOLA METACOMET (HARRIS).—The Dun Skipper apparently is not common in Louisiana, as only two specimens have been taken, and those were in the western and northern part of the state. Almost nothing is known about the immature stages of this skipper.

A. ruricola metacomet has not been recorded from Louisiana previously. The records are: *Sabine*: Negreet, VII-7-50, 1 ♂ (TU 2101); *Union*: Marion, VI-24-50, 1 ♂ (TU 2075).

OLIGORIA MACULATA (EDWARDS), the Twin Spot.—Edwards (1865) described this species from New Orleans, but both Holland (1931) and Lindsey, Bell and Williams (1931) considered it to be most abundant toward the Carolinas. Klots (1951) stated that it strays west to Texas. Indeed, the few specimens collected in Louisiana have all been taken from the eastern part of the state, particularly in the pine flats of the Florida parishes. Very little is known concerning the immature stages, although the larvae presumably feed on grass (Klots, 1951).

The records are: *St. Tammany*: St. Tammany, IV-13-50, 1 ♀ (TU 1903); Covington, IX-8-50, 1 ♂ (TU 2196); Hickory, IX-13-50, 1 ♂ (TU 2198); *Tangipahoa*: Ponchatoula, IX-6-50, 2 ♂♂ (TU 2182).

LEREMA ACCIUS (J. E. SMITH).—The Accius Skipper apparently is not abundant in Louisiana. Thus far it has been taken during the late summer months only, although it has been reported to fly during all months of the year in the southernmost limits of its range (Lindsey, Bell and Williams, 1931). The larvae feed on grasses and Indian corn according to Klots (1951).

The records are: *Pointe Coupee*: McCrea, X-14-49, 1 ♂, 1 ♀ (TU 1567, 1568); *St. Tammany*: Covington, IX-5-50, 1 ♀ (TU 2180) and IX-8-50, 3 ♂♂, 1 ♀ (TU 2196); Folsom, IX-7-50, 1 ♂ (TU 2187); *Tangipahoa*: Ponchatoula, IX-6-50, 1 ♂ (TU 2182). Previously it had been recorded from Madison (Glick, 1939) and Orleans parishes (Edwards, 1865).

AMBLYSCIRTES VIALIS (EDWARDS).—A single specimen of the Roadside Skipper has been taken in Louisiana. Klots (1951) stated that the range is from southern Canada to Florida, and westward to Texas, but Holland (1931) wrote that it was common in the Mississippi valley. Lindsey, Bell and Williams (1931) stated that *vialis* apparently is replaced by another species in the southeastern states. There can be no doubt, however, that *vialis* is an occasional visitor in Louisiana, particularly in the northern parishes. The caterpillars feed on grasses.

A. vialis has not been recorded from Louisiana previously. The record is: *Webster*: Leton, VIII-6-49, 1 ♂ (TU 1449).

AMBLYSIRTES TEXTOR (HUBNER).—The Wovenwinged Skipper is represented in Louisiana by a single specimen. This individual was taken while it was feeding on a blackberry flower. Nothing is known of the immature stages.

A. textor has not been recorded from Louisiana previously. The record is: *Jefferson*: Kenner, III-9-51, 1 ♂ (TU 2297).

LERODEA L'HERMINIERI (LATREILLE), the Fuscous Skipper.—Five specimens of this uncommon skipper have been taken in Louisiana during the summer months. Little is known about the immature stages.

L. l'herminieri has not been recorded from Louisiana previously. The records are: *St. Helena*: Liverpool, IX-7-50, 1 ♂ (TU 2193); *Tangipahoa*: Ponchatoula, IX-6-50, 3 ♂ ♂ (TU 2182); *Union*: Haile, VI-20-50, 1 ♂ (TU 2066).

LERODEA EUFALA (EDWARDS), the Eufala Skipper.—This species also is rare in Louisiana. Only four specimens have been taken in the state and these in late summer and early autumn. The larvae feed on grasses.

The records are: *St. Bernard*: Shell Beach, X-18-49, 2 ♂ ♂, 1 ♀ (TU 1595); *Tangipahoa*: Lee Landing, IX-6-50, 1 ♀ (TU 2182). Previously it had been recorded from Madison parish by Glick (1939).

CALPODES ETHLIUS (STOLL), the Brazilian Skipper.—Although this species apparently is common in Louisiana, only one specimen has been taken during the survey. The flight is very rapid, the skipper rising and falling in a very quick undulating manner.

Jung (1950) reported large numbers of the larvae on canna in New Orleans, and the single adult specimen in the Tulane collection was reared from a pupa found on canna leaves. Dr. Forbes informed the writer (in correspondence) that he observed numerous larvae and adults of *ethlius* in New Orleans on January 1, 1933.

The single record is: *Orleans*: New Orleans, X-17-50, 1 ♀ (TU 2224).

PANOQUINA PANOQUIN (SCUDDER).—The Salt-marsh Skipper has not been taken by the writer in Louisiana, but is included here on the basis of Scudder's (1889) report of it from New Orleans. Nothing is known about the early stages.

PANOQUINA OCOLA (EDWARDS).—The Ocola Skipper is fairly common in Louisiana during the late summer, frequenting the edges of forested areas. Nothing is known about the immature stages.

P. ocala has not been recorded from Louisiana previously. The records are: *Allen*: Oberlin, X-16-49, 1 ♀ (TU 1574); Hampton, X-16-49, 1 ♂ (TU 1579); *Evangeline*: St. Landry, X-14-49, 1 ♀ (TU 1569); Point Blue, X-16-49, 1 ♂ (TU 1579); *Pointe Coupee*: McCrea, X-14-49, 1 ♂, 1 ♀ (TU 1567, 1568); *St. Bernard*: Delacroix Island, X-18-49, 1 ♂ (TU 1592); *St. Charles*: Norco, I-24-50, 1 ♂ (TU 1763); *St. Tammany*: Folsom, IX-7-50, 1 ♀ (TU 2187); *Tangipahoa*: Ponchatoula, IX-6-50, 2 ♂ ♂, 1 ♀ (TU 2182).

SUMMARY

Butterflies and skippers were collected in Louisiana during three years (1948-1951) and these records are coupled with those of other institutional and published records to form a composite list for the state. Before the writer's survey was begun there had been 43 species recorded, and during its progress a local study by Jung (1950) added 17 new state records, bringing the total to 60 by July 1950. With the completion of the present study 38 previously unrecorded species are added, and the state list now totals 98.

An attempt was made to collect in many areas of the state, and during different times of the year. Fifty of the 64 parishes of Louisiana were sampled, and two additional ones are included in the literature. Best represented are the southeastern parishes, New Orleans and vicinity. A total of 1501 adult butterflies and skippers were examined in the course of the study.

Each species on record is listed with observations by the writer and a summary of the collection data arranged by parishes.

From laboratory analyses of the records certain geographic patterns are noted. While most species are found distributed more-or-less evenly throughout the state, some are restricted to particular physiographic or vegetational regions. *Euptychia areolata areolata*, *E. gemma gemma*, *Celastrina argiolus pseudargiolus*, *Eurema daira daira*, *Wallengrenia otho otho* and *Oligoria maculata* appear to inhabit only the Florida Parish pine area, with *E. gemma gemma* occasionally visiting the Upland pine areas. *Euptychia cymela cymela*, *Anaea andria*, *Graphium marcellus marcellus* and *Anthocharis genutia* are more-or-less restricted to upland pine and hardwood areas. *Heliconius charitonius*, *Agraulis vanillae nigrior*, *Euptoieta claudia claudia* and *Papilio cressphontes cressphontes* are restricted almost entirely to the southern parishes.

An analysis of the flying dates leads to the general conclusion that most of the common species fly almost throughout the year in Louisiana, with their peaks of abundance in the hot summer months. Figure 3 summarizes the seasonal distribution of all of the commoner species.

On comparison with published distribution patterns it appears that the Louisiana specimens of *Melitaea nycteis nycteis* constitute a range extension of significance. Since the species is not abundant in Louisiana this must be the southern tip of its range. The collections of *Polites manataaquia manataaquia*, *Hemiargus isolus* and *Atrytone dukesi* assist in defining the ranges of these species.

The 98 species recorded here are not all of the butterflies and skippers expected from the state. More concentrated sampling over a longer period of the year, and a more intense consideration of the immature stages will undoubtedly reveal a greater number of species. Perhaps in due time the writer may be able to fill in the vacancies, however, it is hoped that this paper will stimulate entomologists to initiate further studies of the Lepidoptera of Louisiana.

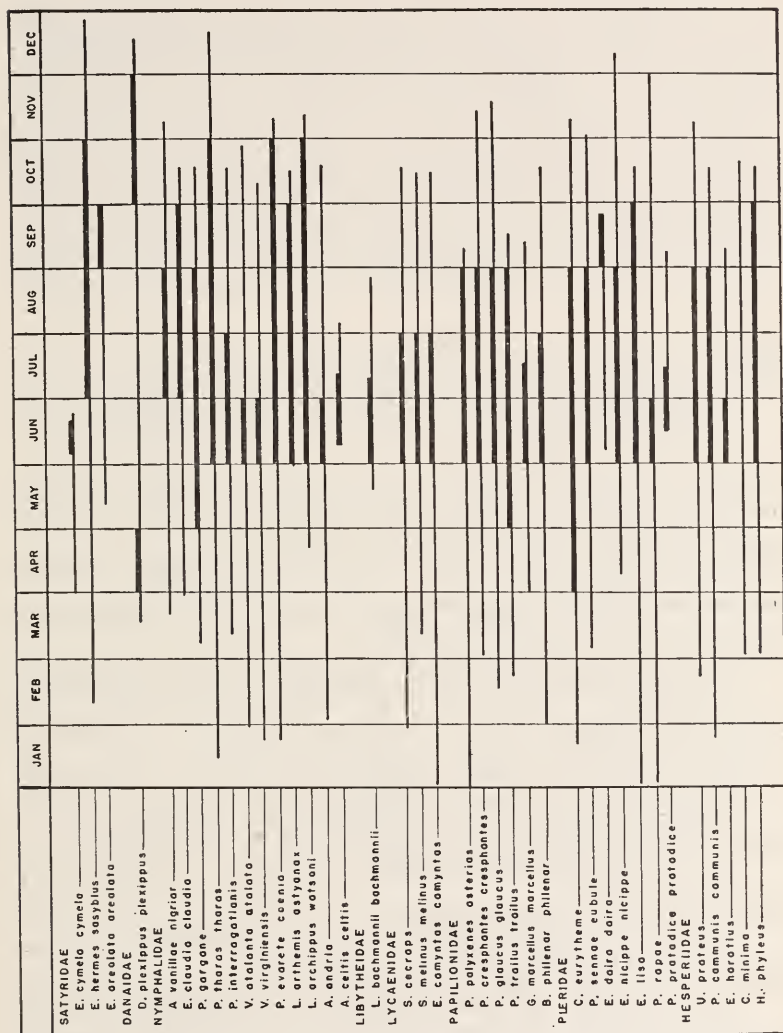


Figure 3. Summary of flying seasons of the commoner species in Louisiana; thickened parts of bars indicate months of greatest abundance.

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TWO NEW SPECIES OF THE GENUS *GRAPTEMYS*

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New Orleans.*

Two distinctive, undescribed populations of turtles were found in Mississippi and Alabama by the Tulane University field crews of 1952 and 1953. The turtles are abundant at the type localities and are the dominant species of turtles present.

Both species are closely related to *Graptemys oculifera* (Baur) and with this species form a unique complex of three allopatric species ranging from the Pearl River in the west to the Alabama river in the east. The three groups of populations are recognized as species because: (a) the degree of difference between the three groups is much greater than that between the subspecies of related species occurring in the central United States; (b) the degree of difference is as great as that occurring between sympatric species of this and related genera; (c) there are no intermediates. These factors suggest that these populations have been reproductively isolated for a long period. It is not possible to conclude that these three forms would not be capable of interbreeding if they were not spatially isolated.

The following abbreviations are used in the descriptions: Cl., carapace length (not along curve); Cw., carapace width; Pl., plastron length; Pw., plastron width; Hw., head width; Ht., height; Aw., alveolar width. All measurements are maximum. The size of individuals is expressed as plastron length.

UMMZ = University of Michigan Museum of Zoology; CNHM = Chicago Natural History Museum.

The illustrations in color were provided through the cooperation of Roger and Isabelle Hunt Conant who had photographed the turtles for inclusion upon one of the color plates in their forthcoming *Field Guide to the Reptiles and Amphibians*. Mr. George P. Meade generously provided the funds for their publication here. The research was aided by a grant from the National Science Foundation.

The collections essential to these descriptions could not have been made without the enthusiastic field work of graduate students. I am especially grateful to A. H. Chaney, Robert Gordon, Donald Tinkle, Robert Webb, Walter Stone, and Howard Suzuki.

GRAPTEMYS FLAVIMACULATA, sp. nov.

Yellow-blotched Sawback

Holotype.—Tulane 14798, a juvenile male, collected from the Pascagoula River, 13 miles S.W. of Lucedale, George Co., Mississippi, 18 Aug. 1952 (figs. 3, 5, 7).

Paratypes.—Tulane 14752, 14754, 14756-766, 14768, 14772, 14774-776, 14778-785, 14788, 14790, 14795, 14799-802, 14804, 14806-809, 14811-812, 14815, 14818, 14821-822, 14825-827, 14829, 14832-833, 14842, 14845-846, 14850, 14852-854, 14857-858, 14862-863, 14865-

871, 14873-875, 14920-921, 14935, 14938; CNHM 69806-808; UMMZ 108567-571, 36 juveniles, 44 males and 3 females collected at the type locality by a Tulane University field crew.

Hypodigm.—A total of 124 preserved specimens, 74 examined by dissection and not retained, and many others observed in the field provided a series of observations for the analysis of variation of this species. The study of these individuals has also provided a basis for determination of some aspects of the behavior and for estimating the population structure.

Diagnosis.—*Graptemys flavimaculata* is a member of a narrow-head complex that includes three species occurring only in Louisiana, Mississippi and Alabama, *Graptemys oculifera* in the Pearl River drainage, *Graptemys flavimaculata* in the Pascagoula River and its tributaries, *Graptemys nigrinoda* in the Black Warrior and Alabama Rivers (fig. 9).

G. flavimaculata differs from *G. nigrinoda* in that: the postorbital mark is rectangular or triangular, is broader than any of the lateral neck lines entering the orbit, and is usually joined to a longitudinal line; the ventral surface of the jaw is dominated by broad yellow lines much wider than the olive-green interspaces; each costal with a large yellow or orange central blotch or crescent; the vertebral spines are high, narrow, laterally compressed; the edge of the carapace of males and juveniles is much less serrate (Table 1).

G. flavimaculata differs from *G. oculifera* in that: the orbital mark is broad and is ordinarily joined to a dorsal longitudinal neck line; the lower jaw is dominated by broad yellow lines; each costal has a large blotch or crescent of yellow.

Description of holotype—Carapace length, 8.05 cm; carapace width at juncture of fourth and fifth marginals, 6.15 cm; carapace width at juncture of seventh and eighth marginals, 6.72 cm; plastron length, 7.43 cm; width of posterior lobe of plastron, 3.63 cm; height (measured in vertical line through spine of second vertebral), 3.70 cm; height at spine of third vertebral, 3.41 cm; head width (measured at anterior edge of tympanum) 1.24 cm; length of symphysis of lower jaw, 0.44 cm; alveolar width of upper jaw, 0.25 cm.

Edge of carapace serrate; each marginal projecting beyond anterior corner of the next posterior one. Each marginal with a wide, yellow bar or semicircle of yellow. Each costal with a broad ring or yellow blotch (figs. 1, 3).

Plane of the plastron 1.40 cm below a plane through the edge of the fifth to the seventh marginals. Yellow color predominant on the plastron, bridge and ventral surface of marginals. Black plastral marks extending along the sutures between each pair of shields (fig. 7).

Neck with 19 longitudinal, yellow lines; those on the ventral surface twice the width of those on the dorsal surface. Longitudinal, interorbital line nearly as wide as widest dorsal neck lines and terminating above postorbital mark. Three yellow lines between the orbits. Two broad, yellow lines entering the orbit below a triangular post-

TABLE 1
A COMPARISON OF *Graptemys oculifera*, *flavimaculata* and *nigrinoda*

	<i>oculifera</i>	<i>flavimaculata</i>	<i>nigrinoda</i>
Carapace margin of adult ♂	slightly serrate	slightly serrate	very serrate
Vertebral projection	laterally compressed; spine-like	laterally compressed; spine-like	broad, rounded knob-like
Postorbital mark	Ovoid, rectangular or rounded; usually not connected with dorsal, longitudinal line; usually not wider than widest neck line	usually rectangular and joined to a dorsal, longitudinal neck line; usually 2 or 3 times wider than widest neck line	a vertical curved bar not wider than neck lines; connected dorsally by diagonal lines to form a Y shaped mark
Neck lines entering orbit	two broad, yellow lines; width equal to width of black area between them	two to four yellow lines; 2 widest much broader than width of olive-green area between them	usually four yellow lines; 2 widest about twice width of narrower lines
Interorbital line	broad; equal to or greater than width of broadest neck lines	narrower than neck lines	narrower than neck lines
Color background of soft parts	black	olive-green	black
Markings, lower jaw	longitudinal yellow lines as wide as black interspaces; black color predominant	longitudinal yellow lines much wider than olive-green interspaces; yellow color predominant	longitudinal lines as wide as interspaces; black color predominant
Markings, forelegs	lines from 2nd and 4th digits equal in width; no or very narrow lines from base of 3rd digit	lines from base of 2nd and 4th digits very broad; line from base of 3rd digit $\frac{1}{2}$ to $\frac{1}{2}$ width of line from 3rd digit	as in <i>oculifera</i>
Markings, costal shields	yellow or orange circle formed on each costal by a broad line (broader than widest neck line)	large yellow blotch or crescentic mark covering most of the surface	yellow or orange semi-circle or circle formed by a narrow line (much narrower than widest neck line)
Color, plastron	yellow or orange	light cream	yellow often tinted with red

orbital mark (figs. 1, 5).

Horny edges of both upper and lower jaws light in color. Ventral surface of lower jaw with two broad, transverse, yellow bands.

Anterior surface of forelegs with wide, yellow lines; those from the base of second and fourth toes are the broadest.

Description of paratypes.—The parotypic series is divided into juveniles, adult males and adult females to insure adequate description.

Juveniles.—The juveniles represent individuals in the first to the tenth seasons of growth (figs. 11, 13). The color pattern of the individuals greater than 9 cm in plastron length is basically the same as that of the smaller juveniles but the contrast between the yellow or orange markings and the background is less.

The head pattern in lateral view consists of two wide, yellow lines extending posteriorly from the orbit along the neck, a triangular or vertically elongated postorbital mark, and a broad yellow line extending the length of the lower jaw. The postorbital mark is, in most individuals, joined to a longitudinal line on the dorsal surface of the head (figs. 1, 11, 13).

The head pattern from the dorsal view consists of a wide yellow line between the orbits extending from a point just above the nostrils to above the center of the postorbital mark; two lines from the upper edge of the orbit that, in most individuals, join the postorbital mark and continue posteriorly onto the neck. The latter lines are interrupted in some individuals. The background color is black (figs. 11, 13, 15).

The lower jaw is dominated by wide yellow lines broadly bordered with black. Of the three or four transverse yellow lines, the most posterior ones join longitudinal lines (figs. 11, 13, 15). The neck has 17-20 wide yellow lines around its circumference at the rear of the skull.

The carapace has bright yellow or orange central splotches on each costal. These are extremely variable in shape but usually cover more than one-third the total area of each shield. In some individuals (14795) they are rounded, in others (14788) they are crescent-like. The upper surface of each marginal has a semicircle of yellow enclosing a darker area having a faint indication of two concentric light lines. Each of the vertebral spines is conspicuously colored black.

The plastron has a pattern of black lines tending to extend along the seams. The background is cream or light.

The anterior surface of the forelimbs has fine yellow lines on a black background. Those extending from the base of the second and fourth toes are the wider.

The jaws have a thin, sharp-edged horny covering. That of the upper overlaps the lower to provide a scissor-like action. The alveolar surfaces are not broadened in the larger turtles, $Hw/Aw = 4.7-5.8$; no correlation with size.

The head is narrower in relation to plastron length in the larger juveniles. $Pl/Hw = 4.1-4.5$ in those 5.0 cm to 5.3 cm in plastron

length; 5.5-6.6 in the larger turtles.

The carapace width decreases in proportion to plastron length in the larger individuals; $Pl/Cw = 0.91-0.99$ in those 5.0 cm to 5.5 cm in plastron length, 0.95-1.1 in the larger ones. The height is reduced in larger turtles; $Pl/Ht = 1.7-1.9$ in those 5.0 cm to 5.5 cm in plastron length; 1.8-2.1 in the larger ones.

The spines of the first four vertebrals are conspicuous in all the juveniles (fig. 11). In those with a plastron length of less than 11 cm the height of the spines of the second vertebral is $2/3$ to $3/4$ the length of the seam between the second and third marginal. The elevations on the first and fourth vertebrals are ridge-like, those of the second and third are distinct spines.

Adult males.—The adult* males in the paratypic series range from 7.10 cm to 9.5 cm in plastron length. The smaller adult males (less than 8 cm in plastron length) have the same color pattern as the juveniles. The larger males (more than 8 cm in plastron length) lose the orange tint in the blotches of the carapace and the lines of the head. The plastral pattern is lightened and poorly defined in the larger individuals.

The spines of the vertebral shields are slightly lower in the large males than in the juveniles and those of the first and third shields are rounded (14850, 14858). The carapace edge of the largest male is less serrate anteriorly than in smaller males; the posterior lateral corners of the fifth and sixth marginals project but slightly beyond the anterior lateral corner of the next posterior marginal (fig. 15).

The height is not reduced with increased length as it is in other species, $Pl/Ht = 1.9-2.2$. The carapace is somewhat narrowed as the male increases in length; $Pl/Cw = 1.0-1.1$.

The head is slightly narrower in relation to plastron length in larger males, $Pl/Hw = 5.6-5.8$ in those 7-8 cm in plastron length; $Pl/Hw = 6.0-6.3$ in those greater than 8 cm in length. There is no consistent broadening of the alveolar surfaces in larger males, $Hw/Aw = 5.1-6.1$.

The third claw of the forefoot is slightly longer than the length of the seam between the second and third marginals.

Adult females.—The adult females retain the color pattern of the juveniles but the blotches on the carapace and the black lines of the plastron are not as distinct. The largest female (14815) has the black background of the carapace lightened by the development of irregular areas of olive-green. The black borders of the yellow marks on the marginals are indistinct. The only remaining vestige of the black lines of the plastron are present on the gular, humeral and anal shields.

The spines of the vertebral shields are much more reduced than in adult males but remain clearly evident on the first four vertebrals (height of spine of second vertebral = $1/4-1/3$ length of seam between first and second marginals). The carapace edge is not serrate except between the eighth to the twelfth marginals.

The smallest mature female (14920) in the paratype series has the following measurements: Pl. 14.0, Cl. 14.9, Cw. 13.0, Ht. 6.5, Hw. 2.1, Aw. 0.43. The largest (14815) has these measurements: Pl. 15.9, Cl. 17.4, Cw. 14.3, Ht. 7.3, Hw. 2.33, Aw. 0.52.

The carapace height is not reduced in comparison with the juveniles and adult males, Pl/Ht = 1.9-2.2. The carapace is slightly broadened in contrast with the adult males, Pl/Cw = 1.1 (in all three individuals).

The head is proportionately broader than in adult males, Pl/Hw = 4.5-4.9 and the alveolar surfaces are wider, Hw/Aw = 4.5-4.9. The third claw of the forefoot is $1/2$ to $2/3$ the length of the seam between the second and the third marginal.

Range.—Specimens are available from three localities; the type locality, the Chickasawhay River and 15 miles from the mouth of the Pascagoula River, Jackson County, Mississippi (AMNH 46774, collected by M. J. Allen, 1930). All specimens have been taken from the Pascagoula River or its tributaries. It is apparent that this species is restricted to this stream system as repeated efforts to collect it from adjacent rivers to the east and west were unsuccessful (fig. 9). Populations undoubtedly occur in all the major tributaries and should be especially abundant in the Escatawpa River.

Habitat.—The Pascagoula River basin, comprising 8,900 square miles, has had the greatest concentration of industry in Mississippi. Two of the tributaries, Tallahala and Sowashee Creeks, have been highly polluted by sewage and waste from wood pulp and chemical industries (Anderson, 1950). This pollution has apparently had no tendency to reduce the *Graptemys* populations and has probably, through contributing to the increase of the mollusc populations, improved the general habitat for *G. flavimaculata*.

The river at the type locality has a sand and clay bottom and many sand bars and beaches. Flood-stranded debris is abundant and much of the shoreline has a stand of dense brush. The debris and brush extending into the water provides shelter for turtles. The river is 75 to 250 feet in width and deep pools are separated by long stretches of shallow water. A moderately rapid current maintains a narrow channel through the shallow areas.

These turtles were most abundant about the tangled roots of trees. Often several turtles were observed lying together in such places. The approach of the boat usually caused them to leave the resting site and swim rapidly toward deep water.

The Chickasawhay River is 30-150 feet wide; the banks have exposed areas of limestone in many places and the bottom is generally rock and sand. Deep, quiet pools are connected by fast-flowing stretches of shallow water. Drift wood and rocks are abundant along the shores. No *G. flavimaculata* were taken in the faster current or the static water but they were abundant in the snags in the slower current.

This species occurs with *Graptemys pulchra*, *Pseudemys floridana*

mobilensis, *Pseudemys scripta elegans* and *Sternotherus carinatus*. It is clearly the dominant turtle species in the Pascagoula and Chickasawhay Rivers.

Bionomics.—*G. flavimaculata* is a comparatively small, rapidly growing turtle adapted to live in moderate current. The smallest sexually mature male studied had a plastron length of 6.67 cm; the smallest mature female had a plastron length of 13.30 cm.

The males may reach sexual maturity in the second growing season. The smallest mature male was in its second growing season when collected and three others ranging in size from 7.47 cm to 8.00 cm were in the third and fourth seasons. The largest male studied had a plastron length of 10.95 cm.

The age at maturity of females could not be determined as the early growth rings were not evident in any mature individual. None of the females larger than 14 cm in length had measurable growth zones.

GRAPTEMYS NIGRINODA, sp. nov.

Black-knobbed Sawback

Holotype.—Tulane 14662, a juvenile female, collected from the Black Warrior River, above Lock 9, 17.5 miles SSW of Tuscaloosa, Tuscaloosa County, Alabama (figs. 4, 6, 8).

Paratypes.—Tulane 14643, 14647-648, 14652-653, 14655-657, 14659, 14664-665, 14682, 14691, 14694, 14697, 14700, 14706, 14708-710, 14714, 14720, 14723, 14725, 14729; CNHM 69809-811, UMMZ 108572-574, 26 juveniles, 5 adult males.

Diagnosis.—*Graptemys nigrinoda* differs from *G. flavimaculata* and *G. oculifera* in that: the yellow postorbital mark is boomerang-shaped and is joined to the mark of the opposite side by a diagonal line; the interorbital line is narrow or indistinct; each costal has a circular or semicircular mark formed by a narrow yellow line; the vertebral spines are flattened, compressed, knob-like; the carapace is very serrate.

Hypodigm.—A total of 117 individuals were available for study from two localities and numerous others were observed in the field. The data derived from field observations and a study of the 117 preserved individuals provide the basis for the information presented.

Description of the holotype.—Maximum carapace length, 8.02 cm; carapace width at juncture of fourth and fifth marginals 6.54 cm; carapace width at juncture of seventh and eighth marginals 6.91 cm; maximum plastron length 7.52 cm; maximum width of posterior lobe of plastron, 3.87 cm; maximum height (measured in vertical line through spine of second vertebral, 3.42 cm; height at spine of third vertebral 3.30 cm; maximum head width (measured at anterior edge of tympanum) 1.32 cm; length of symphysis of lower jaw 0.57 cm; alveolar width of upper jaw 0.28 cm.

Edge of carapace very serrate (fig. 4). General color of carapace dark olive green. Faintly defined, narrow circular or semicircular mark formed by a thin yellow line on each marginal and costal (figs.

2, 4).

Plane of the plastron 1.23 cm below a plane through the edge of the fifth to the seventh marginals. Yellow color predominant on plastron and ventral surfaces of marginals. Branching, black pattern on plastron (fig. 8).

Neck with 25 longitudinal yellow lines; those on the ventral surface not much wider than those on the dorsal surface. Longitudinal inter-orbital line narrower than lateral neck lines. Fine yellow lines between orbits. Four yellow lines entering the orbit laterally; two of these broader than others. Postorbital mark boomerang-shaped and joined to mark of opposite side by a diagonal line (fig. 2).

Ventral surface of lower jaw with a broad, transverse yellow line (fig. 8).

Anterior surface of forelegs with five yellow lines.

Description of the paratypes.—The paratypic series is divided into two groups, juveniles and adult males.

Juveniles.—The juveniles are in their first or second season of growth. The background color of the carapace is dark olive green and that of the soft parts intense black.

The head pattern differs from that of juveniles of *flavimaculata* in that the postorbital yellow mark is a vertically elongated, boomerang-shaped line extending posteriorad on the dorsal surface to join the mark of the opposite side to form a Y. The interorbital, longitudinal stripe is narrow and indistinct in many individuals.

The lower jaw has one broad, yellow transverse line sometimes bordered both anteriorly and posteriorly by narrow yellow lines. Two of the wide, longitudinal neck lines join behind the level of the jaw juncture to form another transverse line. The lower surface of the neck is dominated by black on which the yellow lines appear to be superimposed (figs. 10, 12).

The carapace has a complete circle of a narrow yellow line on each costal. The knob-like vertebral spines are intense black. The upper surface of each marginal has a semicircular mark formed by a narrow yellow line. The ventral surface of each marginal may be yellow with an ocellus of black and yellow rings, or the yellow may be reduced to an irregular blotch on the medial side with the remainder of the marginal covered with alternating black and yellow lines (figs. 2, 8).

The plastron is yellow to bright orange with black lines extending along the seams (fig. 8). The anterior surface of the forelimb has two to five yellow lines. When four or five are present, those from the base of the second and fourth digits are much the wider.

The jaws are as described for *flavimaculata*. The alveolar width is contained 4.0-6.0 times in the head width. There is no relative broadening of the alveolar surface in the larger individuals.

The head is narrower in relation to plastron length in the larger turtles than in the smaller, $Pl/Hw = 4.6-5.6$. The carapace width decreases in proportion to plastron length with size, $Pl/Cw = 0.9-1.0$.



Figures 1-2. 1 (upper), *G. nigrinoda*, sp. nov.; 2 (lower), *G. flavimaculata*, sp. nov. (Photographs and color renditions by Isabelle Hunt Conant).

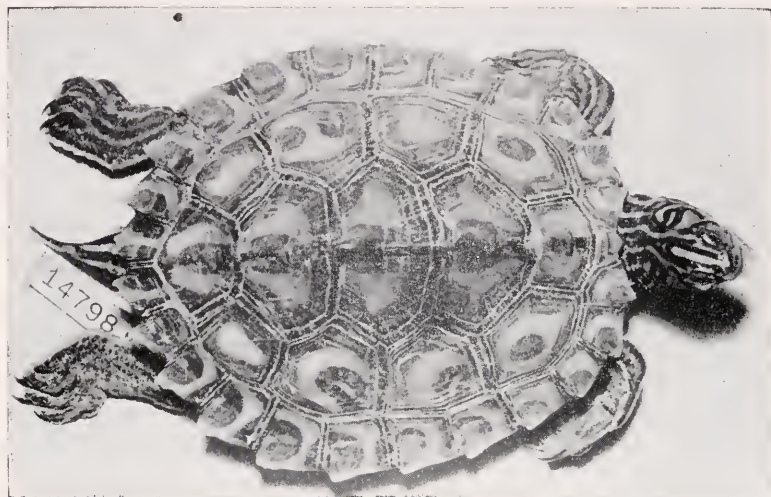


Figure 3. Dorsal view, *G. flavimaculata*, sp. nov. (Photograph by Isabelle Hunt Conant).

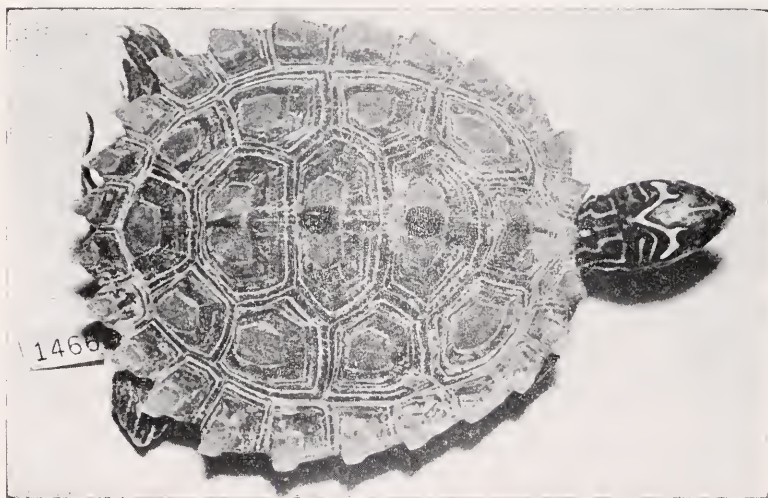


Figure 4. Dorsal view, *G. nigrinoda*, sp. nov. (Photograph by Isabelle Hunt Conant).



Figure 5. Lateral view, *G. flavimaculata*, sp. nov. (Photograph by Isabelle Hunt Conant).

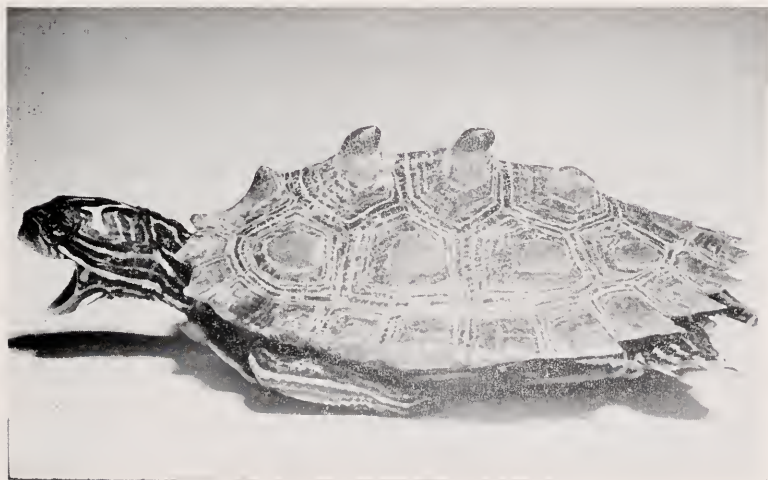


Figure 6. Lateral view, *G. nigrinoda*, sp. nov. (Photograph by Isabelle Hunt Conant).

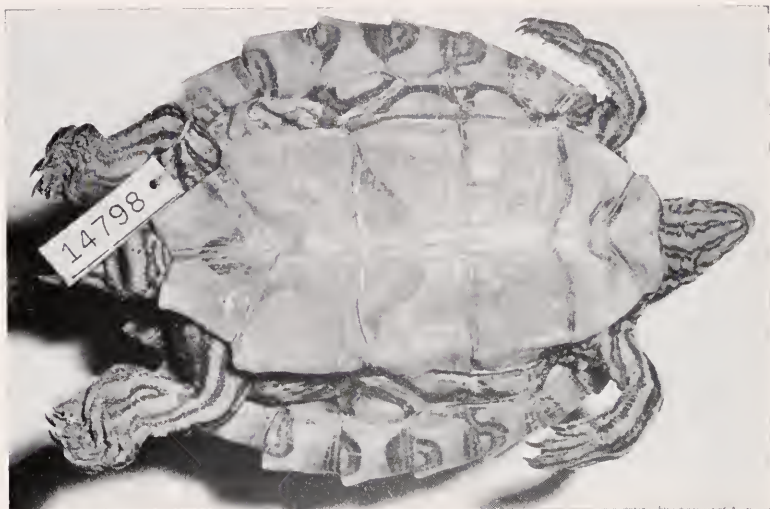


Figure 7. Ventral view, *G. flavimaculata*, sp. nov. (Photograph by Isabelle Hunt Conant).

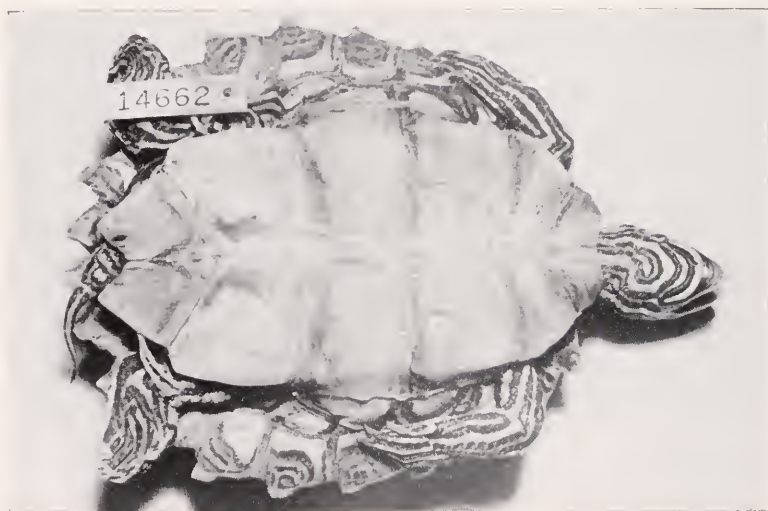


Figure 8. Ventral view, *G. nigrinoda*, sp. nov. (Photograph by Isabelle Hunt Conant).

The height is proportionately reduced in the larger turtles $Pl/Ht = 1.8-2.2$.

The spines of the first four vertebrals are high (height of second equals $2/3$ or more lengths of seam below second and third marginal) and are much broadened and rounded. This is in sharp contrast with *flavimaculata*.

Adult males.—The adult males range from 6.80 cm to 8.00 cm in length. They have the same color pattern as the juveniles but the yellow markings of the carapace and the black markings of the plastron are more obscure. The lines of the head in the largest male (14648) are fainter and the black background is lightened.

The spines of the vertebral shields are worn and eroded in the largest specimen and do not have the broadened, rounded appearance of the spines of juveniles. The carapace edge is less serrate than in the four smaller individuals (fig. 14).

The height is reduced in the largest male in relation to plastron length ($Pl/Ht = 2.0-2.2$ in smaller animals; 2.3 in largest). This is primarily a reflection of the worn spines. The carapace is not narrower in the larger males, $Pl/Cw = 0.9-1.0$; in four smaller ones, $Pl/Cw = 1.0$ in largest.

The head is slightly narrower in relation to plastron length in the larger males; $Pl/Hw = 5.3-5.5$ in those 6.0 cm-7.1 cm in plastron length, $Pl/Hw = 5.5-6.0$ in those greater than 7.5 cm in plastron length. There is a slight broadening of the alveolar surfaces in relation to head width, $Hw/Aw = 5.8$ in smallest, 4.8 in largest.

The third claw of the forefoot is slightly shorter than the length of the seam between the second and third marginal.

Adult females.—No adult females were collected but one was studied with binoculars and a 20 power telescope in the field. This large female retained the distinctive markings of the juveniles. The black background color of the head and the brilliant yellow markings were not reduced.

Range.—Specimens were collected from only two localities, the type locality and the Alabama River 5.5 miles east of Gosport, Monroe County, Alabama. Collecting on the Coosa River and the Mulberry Fork of the Black Warrior River did not yield this species. Its absence from these streams poses the problem of what limiting factors have prevented its movement northward. An attempt to approximate the northernmost occurrence in the Black Warrior was made June 18. A count of basking turtles was made from the juncture of Locust Fork and Mulberry Fork to the Barney Coal Mine during the period from dawn until 1 PM. No *G. nigrinoda* were observed until the river widened approximately three miles above the Barney mine. Basking turtles were common along the entire stretch. There was an apparent correlation between the occurrence of *G. nigrinoda* and the occurrence of *Amyda*. *Graptemys pulchra* is present in Mulberry Fork and Locust Fork.

Habitat.—Generally similar to that of *G. oculifera* and *G. flavimaculata*. All individuals were taken from brush or logs in current or



Figure 9. The distribution of *G. oculifera* (narrow vertical lines), *G. flavimaculata* (horizontal lines), and *G. nigrinoda* (wide vertical lines). The black spots indicate collecting sites; the circles indicate localities where intensive collecting has failed to produce members of this complex.

were shot from basking sites above current. Both the Black Warrior and Alabama Rivers are wider, deeper rivers than the Pascagoula or the Pearl Rivers but they also have sand and clay bottoms and moderate current in those areas where *G. nigrinoda* was collected.

This species occurs in association with *G. pulchra*, *Pseudemys floridana mobilensis*, *Pseudemys scripta elegans*, *Sternotherus carinatus*, and *Amyda* sp.

Bionomics.—The smallest male has a plastron length of 6.80 cm and is in the third season of growth. The largest male observed was 8.76 cm in length and had no growth zones present. No adult females were collected.

DISCUSSION

Other turtle species occurring in the Pearl, Pascagoula and the lower parts of the Tombigbee and Alabama rivers exhibit a gradual coast-wise gradient in most of their characters. The populations of *Pseudemys scripta*, *Pseudemys floridana*, *Kinosternon subrubrum*, *Amyda ferox* and *Graptemys pulchra* of each river system are different in the percent expression of characters but much overlap is evident.

Graptemys pulchra occurs in these same stream systems as well as in the Escambia to the east and the upper reaches of the Alabama where *G. nigrinoda* is absent. However, the populations of the upper Alabama are conspicuously different from those of the lower. This

difference in parts of the Alabama is also reflected in the fact that *Graptemys geographica* occurs in the upper reaches but not in the lower.

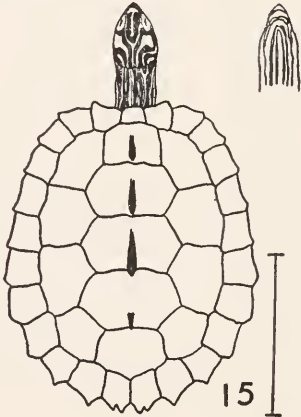
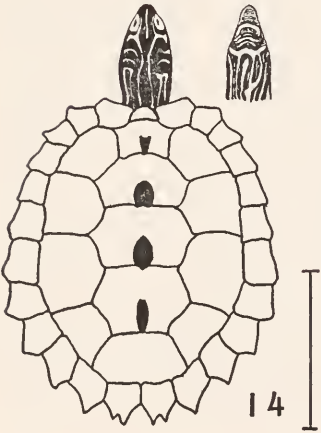
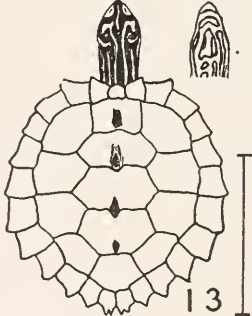
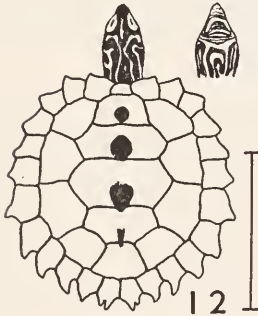
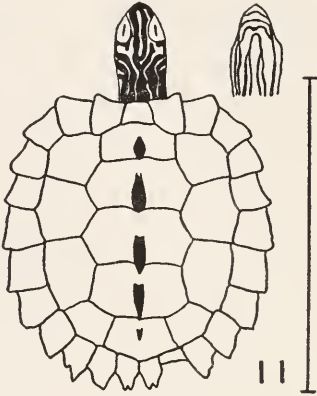
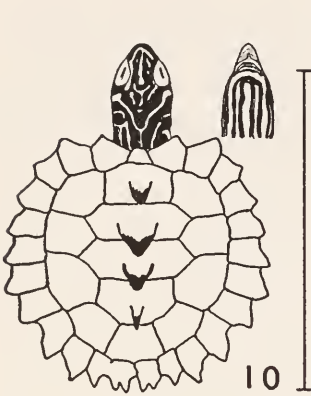
The restriction of *G. nigrinoda* to that part of the river below the fall line may be suggestive of a rather recent, rapid evolution of this complex since the exposure of the Gulf Coast in Pliocene time. There is a correlation between the northern limit of distribution and the isocryme of 15° C (as reported by Hedgpeth, 1953).

The absence of these three forms in river systems east of the Alabama and west of the Pearl is further evidence that the evolutionary history of this complex is substantially different from that of other turtle species of the Gulf Coast (fig. 9). Unfortunately there is but limited information available on the history of these river systems. The extent of the Alabama and Tombigbee systems as contrasted with the Pearl and Pascagoula is suggestive of greater age. Perhaps in this situation rests the explanation of the greater degree of divergence in *G. nigrinoda*, it perhaps being the older of the three forms. The biologist has no precise knowledge of comparative rates of evolution in the turtles but their long fossil record suggests unusually slow response. The relative youth of the Gulf Coast streams implies that rapid evolution has occurred in this complex.

These current-dwelling turtles do not inhabit the extreme head waters and smaller tributaries as do members of the genera *Amyda*, *Pseudemys* and *Kinosternon*. There are no reports of overland movements although such observations are common for other turtles. Their isolation is thus possibly much more complete than is implied by the proximity of the drainage systems. The cohesiveness of the three groups would suggest the designation of a superspecies. This would serve to emphasize the differences between these and the remainder of the genus. Each of the three groups of populations could be designated a semispecies (Mayr, 1942; Cain, 1953).

Although the three forms are basically similar in their osteology and general configuration, the morphological gap between *G. nigrinoda* and *G. flavimaculata* is much greater than that between *G. flavimaculata* and *G. oculifera* (Cagle, 1953b). Particularly striking is the contrast between the flattened carapace and knob-like projections in *G. nigrinoda* and the elevated carapace and laterally compressed spines of the other two species. An alternative taxonomic arrangement would be the recognition of *G. flavimaculata* as a subspecies of *G. oculifera* while retaining *G. nigrinoda* as a separate entity. Such an arrangement would place emphasis on the differences in degree of divergence between the forms but the evolutionary implications of such a grouping can not be justified.

Related species of this genus do not have such striking differentiation in adjacent stream systems. *Graptemys geographica*, *Graptemys pseudogeographica* and *Graptemys kohni* occupy more extensive ranges without developing such gaps or steepening gradients in variation (Cagle, 1953a).



A TENTATIVE KEY TO THE GENUS *GRAPTEMYS*

This key is presented as an aid to identification of the members of this genus. It is not intended to present those characters that are of fundamental significance in establishing the patterns of speciation.

1. Length of symphysis of lower jaw $\frac{1}{4}$
longer than minimum distance be-
tween the orbits and a small triangu-
lar, yellow spot back of orbit sepa-
rated from orbit by 2 to 3 diagonal
yellow lines *Graptemys geographica* (LeSueur)
(Geographic turtle. Mississippi and
St. Lawrence basins. Northern Lou-
isiana north through eastern Oklaho-
ma and Kansas to northern Minne-
sota; eastward through Missouri,
Illinois, Kentucky, Tennessee to Ver-
mont. Northern Mississippi, Ala-
bama.)
- Length of symphysis of lower jaw equal
to or less than minimum distance be-
tween the orbits; or, if symphysis is
longer than minimum distance be-
tween orbits, no triangular spot be-
hind eye but a large, irregular-
shaped greenish or yellowish post-
orbital blotch present 2
2. Each costal with a large yellow-orange
blotch, crescentic mark or ring. 3
Costals without markings as described 5
3. Each costal with a large yellow or
orange blotch or crescentic mark cov-
ering much of the shield. Yellow the
dominant color on the ventral surface
of jaw and neck *Graptemys flavimaculata* n. sp.
(Yellow-blotched sawback. Pasca-
goula River and tributaries, Missis-
sippi.)
- No such markings 4
4. Each costal with one complete circle of
yellow or orange formed by a line
broader than the widest neck line. A
yellow postorbital ovoid, rectangular
or rounded spot not connected with a
dorsal, longitudinal line. Vertebral
spines laterally compressed *Graptemys oculifera* (Baur)

Figures 10-15. Juveniles and males of *G. nigrinoda* and *G. flavimaculata*; scale line = 5 cm. 10, Hatchling, *G. nigrinoda*; 11, Individual in first season of growth, *G. flavimaculata*; 12, Juvenile male, *G. nigrinoda*; 13, Juvenile male, *G. flavimaculata*; 14, Adult male, *G. nigrinoda*; 15, Adult male, *G. flavimaculata*.

(Ringed sawback. Pearl River and tributaries, Louisiana and Mississippi.)

Each costal with a yellow or orange semicircle or circle formed by a line much narrower than the widest neck line. A yellow, vertical curved post-orbital bar connected by a diagonal line with the postorbital bar of the opposite side. Vertebral spines knob-like *Graptemys nigrinoda* n. sp.

(Black-knobbed sawback. Alabama and Black Warrior River systems.)

5. Females never developing a head as wide as $\frac{1}{3}$ the carapace width. Post-orbital mark not a large irregular shaped greenish or yellow blotch 6

Females developing a much broadened head as wide as $\frac{1}{3}$ the carapace width. Postorbital mark an irregular bordered greenish or yellowish blotch or mark absent (see illustrations, Cagle, 1952.) 10

6. Without vertebral spines (each vertebral may be slightly elevated above next posterior one). Maximum plastron length about 16 cm. *Graptemys versa* Stejneger

(Texas map turtle. Colorado River System, Texas.)

With distinct vertebral spines (absent in some individuals greater than 16 cm in plastron length.) 7

7. A postorbital vertical line extending from a dorsal longitudinal line to the base of the orbit and anteriorly under the orbit; vertical line frequently interrupted by a longitudinal line or bar *Graptemys kohni* (Baur)

(Mississippi map turtle. Eastern Texas, Oklahoma, Kansas and Nebraska east to Mississippi River and southern Indiana.)

No postorbital vertical line; a comma-shaped, rectangular or ovoid post-orbital mark. A series of longitudinal neck lines entering orbit below postorbital mark. 8

8. Postorbital spot, oval or elongate, much smaller than orbit, and surrounded by 2 or 3 concentric lines; 3 or 4 conspicuous longitudinal lines entering orbit; these lines alternating with thinner, less conspicuous lines. A total of 6-7 lines entering orbit; a wide yellow band extending the width of the ventral surface of the jaw; no large yellow spot beneath eye -----

-----*Graptemys pseudogeographica sabinensis* Cagle

(Sabine map turtle. Sabine River of western Louisiana and eastern Texas.)

Not as above. ----- 9

9. Postorbital spot not elongate but rectangular; length of rectangle extending dorso-ventrally; maximum of 5 longitudinal lines entering the eye. No wide yellow band extending the width of ventral surface of jaw but a large spot present at symphysis of lower jaw; a large yellow spot beneath eye. -----

-----*Graptemys pseudogeographica ouachitensis* Cagle

(Ouachita map turtle. Louisiana northwestward into eastern Oklahoma, Kansas, Nebraska and eastward through southern Wisconsin, Illinois and southern Indiana to northern Alabama. Eastward in the Ohio River System.)

- Postorbital spot comma-shaped; not rectangular; maximum of 5 longitudinal lines entering the eye; no wide yellow band extending the width of the ventral surface of the jaw; no large spot present on symphysis of lower jaw; no large yellow spot beneath the eye. -----

-----*Graptemys pseudogeographica pseudogeographica* (Gray)

(False map turtle. Eastern Nebraska, southeastern South Dakota eastward through southern Minnesota and Iowa to eastern Illinois.)

10. An irregular bordered yellow bar extending completely across ventral surface of lower jaw; margins of plastral shields not bordered with black -----

-----*Graptemys barbouri* Carr

(Barbour's map turtle. Southwestern Georgia and Panhandle of Florida.)

No bar as described (an elongated blotch or bar may be present); margins of plastral shields bordered with black

----- *Graptemys pulchra* Baur

(Alabama map turtle. Pearl River, Louisiana eastward to Alabama, Coosa and Escambia rivers.)

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THE TAXONOMIC STATUS OF THE MID-GULF COAST
AMPHIUMA

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THE TAXONOMIC STATUS OF THE MID-GULF COAST AMPHIUMA¹

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The identity of the *Amphiuma* of the Gulf Coast has been studied by Ryder (1880), Cope (1886), Brimley (1909), Goin (1938) and Baker (1947). These investigators have drawn different conclusions from the study of similar material. Their conclusions have been based on analyses utilizing either one or several of the following characters: number of toes, color, ratio of total length to body length, number of costal grooves and ratio of body length to limb lengths.

The early investigators, Ryder, Cope and Brimley, had only a small number of individuals available for their studies. The more recent workers, Goin and Baker, considered populations of individuals, but none of the investigators, measured or dealt with ontogenetic variation, allometric growth or sexual dimorphism. Since some authors give only the mean of the ratios and of the costal groove number, it is not possible to evaluate the characters reported. A new approach was required to evaluate the characters previously used and to investigate other differences, if any, between the populations.

Historical—Garden described *Amphiuma means* in 1821. In 1827 Cuvier described a three-toed individual as *Amphiuma tridactylum* and compared it with a two-toed one: "This description of the *Amphiuma* of three digits agrees nearly in everything to the kind with two digits. Its general form is the same; its diameter is one-twentieth of its length; the length of its head is nearly one-fourteenth; its tail is exactly one-fourth. It has similar folds on each side. Its color is the same. Summarizing, it is necessary for descriptive purposes to look closely at its extremities. Then one sees that each of its limbs is divided into three perfectly distinct toes; it is in reality its only exterior character which is readily discernable."

The three-toed individuals were placed in the genus *Mauraenopsis* by Fitzinger (1843). Ryder (1880) studied a series of young *Amphiuma* from Biloxi, Mississippi and reestablished the three-toed salamander in the genus *Amphiuma*. Ryder based his classification solely on the number of digits. He stated "so that in some the number of digits (two) is characteristic of *Amphiuma*, and in others (three) they are characteristic of *Mauraenopsis*." Cope (1886) could not separate his specimens into two-toed and three-toed groups and so he classified all individuals, regardless of the number of toes, as *Amphiuma means*.

Brimley (1909) called the three-toed animal *Amphiuma tridactylum*. Brimley stated that the three-toed specimens differed from the

¹ From a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science of the Graduate School of Tulane University.

two-toed ones in being lighter in color on both the dorsal and ventral surfaces and in being distinctly bicolored; the limbs of the three-toed *Amphiuma* were "more strongly developed." The character used in separating the two forms, prior to 1909, was number of toes. Brimley also reported that he had never seen a two-toed individual which had attained as great a size as the three-toed ones; one three-toed individual examined by Brimley was 736.6 mm in length.

Goin (1938) examined 206 individuals and found that the costal groove count and the ratio of total length to body length may also be used as taxonomic characters. Considering the region where the two ranges meet, he stated "coloration, costal groove count and ratio of total length to body length change more or less gradually, but the two-toed specimens of the east interdigitate with the three-toed specimens of the Mississippi Valley." According to Goin, *Amphiuma means means* is a two-toed, unicolored animal with 57-60 costal grooves and a ratio of total length to body length which averages 1.33. *Amphiuma means tridactylum* is a three-toed, bicolored animal with 60-64 costal grooves and a ratio of total length to body length which averages 1.29. Goin considered the area of intergradation as the region between Lake Pontchartrain in southeastern Louisiana and Liberty County, Florida.

Baker (1947) examined over 280 *Amphiuma* and concluded that "two species of Amphiumae, *Amphiuma means* and *Amphiuma tridactylum*, occur, each occupying a distinct ecological range." Baker found no evidence of intergrades and stated that all known specimens could be designated as one of these species by the "valid species characters of number of toes, body length in total length, length of limbs in body length and coloration."

PROCEDURES

Number of toes and coloration—In the course of this investigation, 537 *Amphiuma* were examined. Two hundred and forty-six of these were two-toed, two hundred and eighty-eight were three-toed, and three individuals had both two- and three-toed limbs (Table 1). All individuals examined are placed into one of six arbitrary geographical series to determine the degree of difference, if any, between the series. Series 1 includes all three-toed *Amphiuma* from the west bank of the Mississippi River westward. The most western locality of an *Amphiuma* examined in this study is nine miles northwest of Saratoga, Hardin County, Texas. Series 2 consists of the individuals from Audubon Park in New Orleans, Louisiana. Series 3 includes all individuals in the alluvial valley east of the Mississippi River. Included in Series 4 are the three-toed *Amphiuma* from the region east of the alluvial valley of the Mississippi River to western Alabama. This series includes individuals from extreme southeastern Louisiana and Mississippi.

Series 5 consists of the two-toed individuals from the same geographical area as Series 4, and Series 6 consists of those individuals from the Atlantic coastal states westward to Liberty County, Florida

TABLE 1.
NUMBER OF TOES

Series	Number with Two Toes	Number with Uncertain Number of Toes	Number with Three Toes	Total Number Examined
1	0	0	33	33
2	0	0	191	191
3	0	0	17	17
4	0	3	47	133
5	83		0	
6	163	0	0	163
Total	246	3	288	537



Figure 1. Distribution of the 537 *Amphiuma* examined in this research. The circular and X-shaped symbols represent three-toed and two-toed individuals respectively.

(figure 1). The individuals from western Alabama to Liberty County, Florida, were not placed into any of the six series because they were too few in number to constitute an additional series. Series 4 and 5 extend as far east as the locality where both the two-toed and the three-toed individuals are found in close association. This arbitrary grouping into series does not mean to imply that the individuals from western Alabama to Liberty County, Florida, are different from those in Series 4 and 5.

Most of the specimens utilized in this study are deposited in the collections of Tulane University (TU); a few were borrowed from the American Museum of Natural History, the United States National Museum, and the University of Florida.

An external morphological study was made on each individual. The following information was recorded: museum catalogue number, date collected, collector, tail length, body length, hind-limb length, fore-limb length, head length, number of toes, sex and coloration. The length of the tail was taken as the distance from the anterior end of the cloacal opening to the tip of the tail. The limbs were pressed posteriorly and horizontally along the body and the lengths were recorded as the distances from the base of the limb to the distal end of the longest digit. In the three-toed individuals, the longest digit is the middle one and the outermost toe is the smallest (when the limbs are pressed posteriorly and horizontally along the body). The measurements were made consistently on the right limbs of the animals unless the right limbs were mutilated. The head length was taken as the straight line distance from the anterior end of the brachial fissure to the tip of the nose. The number of toes on each limb was recorded in a formula arrangement, e.g. 2/2 2/2.

The formula is read from left to right, and the numbers represent, respectively, the number of toes on the right fore-limb, the number of toes on the left fore-limb, the number of toes on the right hind-limb and the number of toes on the left hind-limb. If the individuals were sexed, this was done by dissection. The dorsal, ventral and throat colorations were recorded. Table 2 indicates the throat coloration of the specimens from the six geographical series.

The measurements were made with vernier calipers, except when the structure was greater than 125 mm. In the latter case or if the preserved animal were coiled, a string was used and transferred to a ruler calibrated in millimeters. The measurements were recorded to the nearest millimeter. All of the measurements were made on preserved specimens. There is undoubtedly some differential shrinkage between the various body parts, resulting from the preservation, but this possible error is likely to be minimized since all of the individuals examined were preserved by comparable methods.

Only those individuals were measured whose parts were not mutilated. Mutilation could usually be detected by the presence of scar tissue. Frequently, *Amphiuma* have part of a limb or an entire limb missing. Obviously, it is easier to detect a mutilation which has

TABLE 2.
THROAT COLORATION

Series	Number without Throat Patch	Number with Uncertain Throat Color	Number with Throat Patch	Total Number Examined
1	0	0	33	33
2	0	0	191	191
3	0	0	17	17
4	0	3	47	133
5	83		0	
6	163	0	0	163
Total	246	3	288	537

occurred recently in the life of an animal than it is to determine one which occurred very early in the life of the individual. It is unusual to find all four limbs of an animal mutilated. The hind-limbs are normally longer than the fore-limbs, except in individuals less than a hundred millimeters in length. One can usually confirm the opinion of whether or not a digital mutilation has occurred by comparing the measurements of all four limbs.

Body proportions—Heretofore, three assumptions have been made by some workers who have considered body proportions as taxonomic characters in *Amphiuma*. These assumptions include absence of sexual dimorphism, high correlation between the dimensions of the body parts, no ontogenetic variation. The latter is illustrated by Baker's use of simple ratios, implying that body proportions do not change with an increase in age (body length).

If these assumptions represent the facts, then the previous work is valid, but if one or more of the assumptions are incorrect, the results may require some qualification. Statistical methods can often be used to give quantitative estimates of these assumptions. The preliminary procedure was to determine the presence or absence of sexual dimorphism, the degree of correlation between the body parts, and whether or not ontogenetic variation was present.

To determine the presence or absence of sexual dimorphism, four groups of graphs were set up, each group being composed of six graphs representing the six geographical series. The four groups represent the following four body proportions: head length to body length, fore-limb length to body length, hind-limb length to body length and tail length to body length. For each graph the horizontal scale represents the body length in millimeters and the vertical scale represents the other body part. The presence or absence of important sexual dimorphism can be estimated by inspection. An inspection of the scattergrams indicates that the males and females do not fall

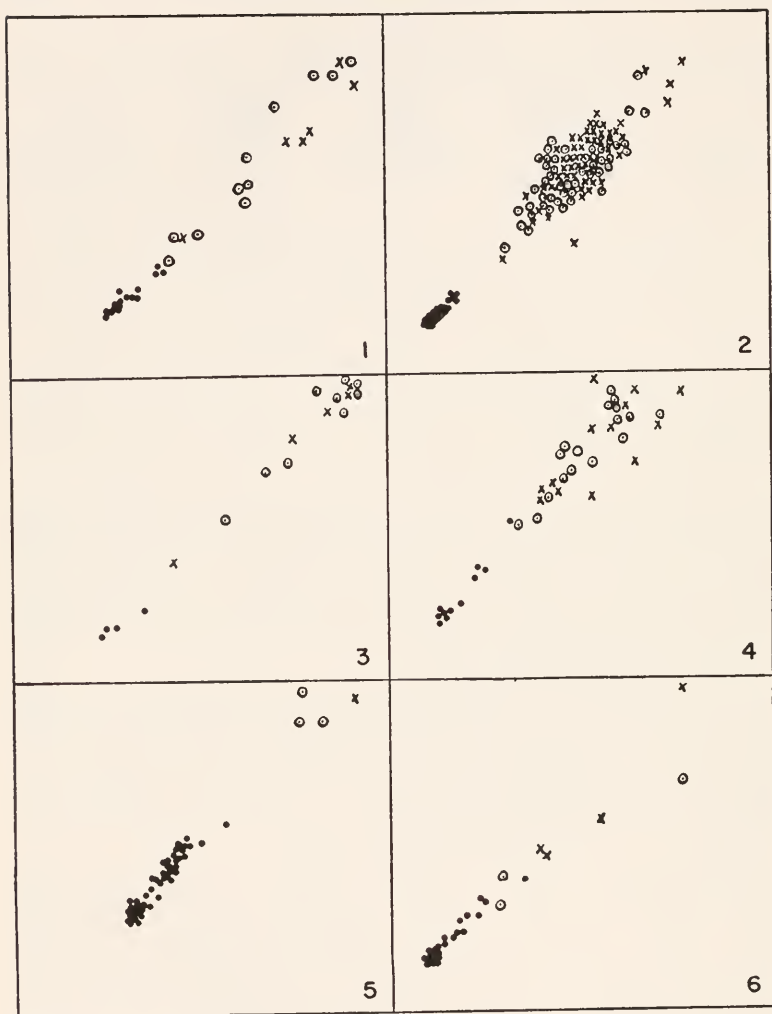


Figure 2. Scattergrams showing the relationship of head length to body length for each of the six series. The three symbols, X, circle with dot and plain dot, identify respectively male, female and unsexed individuals.

into two separate groups in any of the series; therefore, if sexual dimorphism exists it is negligible (figures 2-5).

Obviously, there is a definite relationship of head length, fore-limb length, hind-limb length and tail length to body length so the problem is concerned with the degree of correlation and the nature of the correlation (*e.g.*, simple and linear). The degree of correlation of

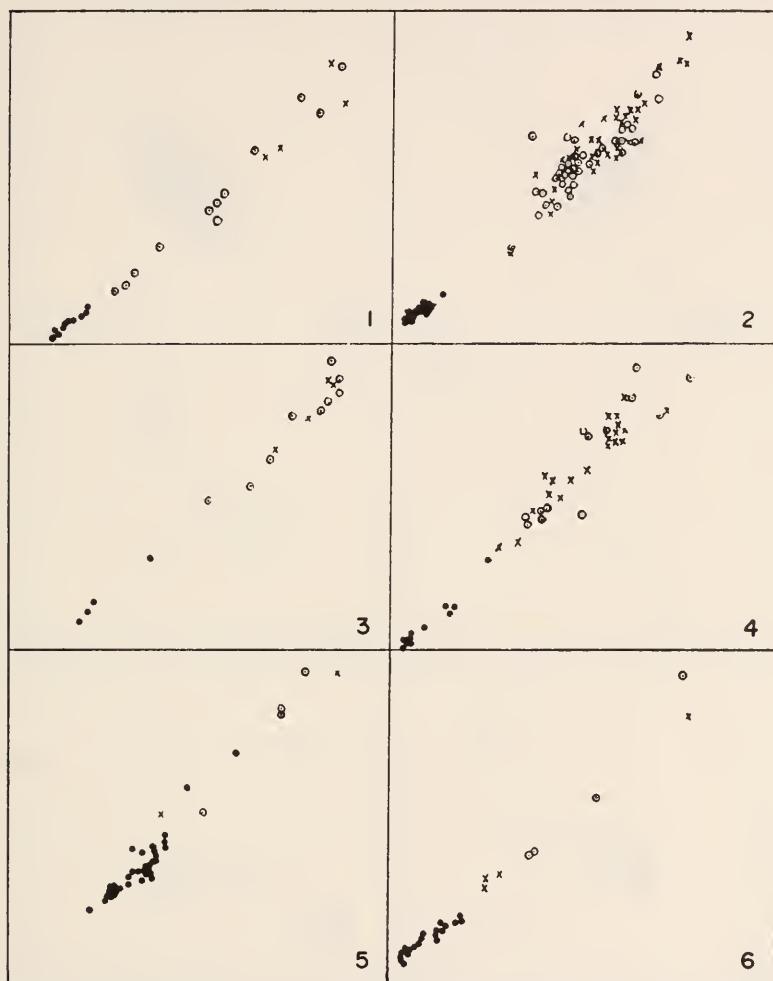


Figure 3. Scattergrams showing the relationship of fore-limb length to body length for each of the six series. Symbols as in fig. 2.

the various body parts with the body length was determined by calculating the correlation coefficients (Tables 3-6). The method used was Pearson's product-moment method using grouped data cross-tabulated. Twenty-four correlation tables were constructed. In constructing the correlation tables, the body length was considered the independent variable and the other body part length the dependent variable (Peatman, 1947).

Ontogenetic variation—To determine whether or not body pro-

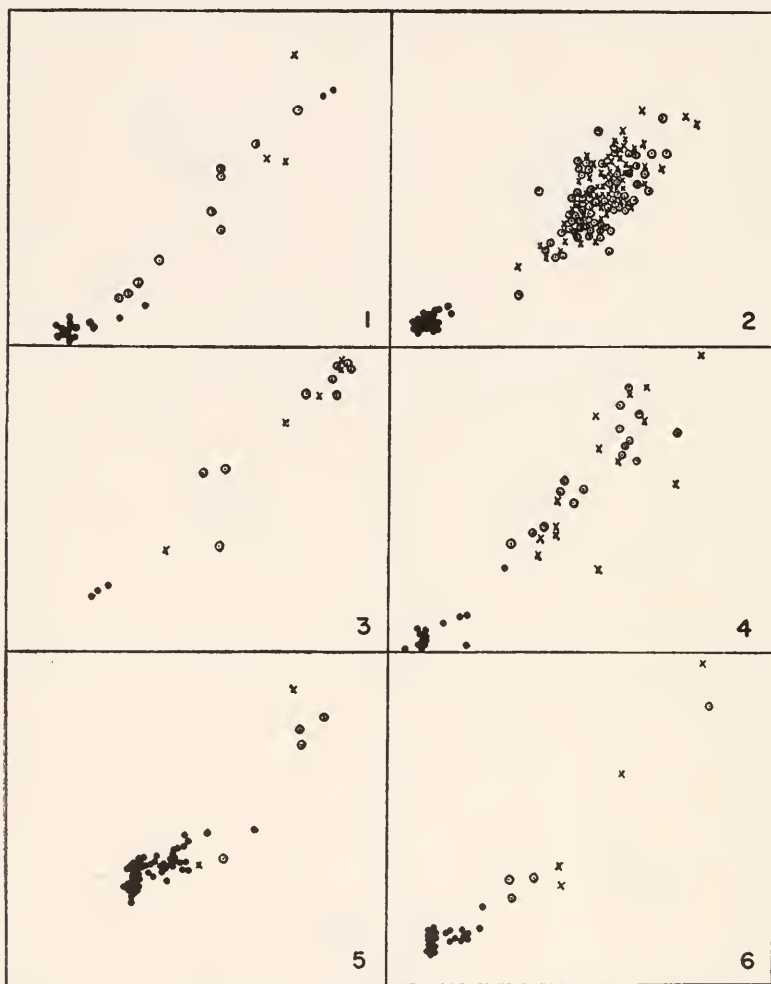


Figure 4. Scattergrams showing the relationship of hind-limb length to body length for each of the six series. Symbols as in fig. 2.

portions remain constant as the animal increases in age (length), the regression lines for the four body parts of each of the six series were calculated. The correlations in ontogenetic series are nearly always high, but inspection of the scattergrams indicate that linearity may be assumed for practical purposes.

The fact that the line is linear for the four body proportions of each of the six series was established by the product-moment correlation coefficients. Thus, the regression equation for the straight line is:

$$X = a + aB$$



Figure 5. Scattergrams showing the relationship of tail length to body length for each of the six series. Symbols as in fig. 2.

where X is equal to either head length, fore-limb length, hind-limb length or tail length; a and b are the regression constants and B is the body length corresponding to a particular X length. In order to determine X for any particular body length, B , the regression constants must be calculated.

The three methods suggested by Klauber (1943) for calculating the regression constants are: (1) analytical methods, (2) method of least squares and (3) the graphical method. Of these, the latter was

TABLE 3.
RELATIONSHIP OF HEAD LENGTH TO BODY LENGTH

Series	1	2	3	4	5	6
Total number of individuals	33	191	17	47	84	163
Body length range, mm	63.5-566.8	43.2-535	51.5-504.5	73.1-563.3	63-442.1	45.1-600
Correlation coefficient, r	0.981	0.936	0.985	0.968	0.919	0.989
	± 0.0044	± 0.0061	± 0.020	± 0.0063	± 0.011	± 0.0012
Regression constants	a 0.82	a 1.034	a 0.262	a 0.605	a 1.650	a 1.830
	b 0.125	b 0.119	b 0.116	b 0.109	b 0.096	b 0.090
Restricted number of specimens	13	68	12	21	5	8
Body length range, mm	330.6-566.8	350.8-535	341.6-504.1	353.3-563.3	285-442.1	249.1-600
Standard body length, mm ..	400	400	400	400	400	400
Standardized head length range, mm	39.3-59.7	35.6-51.2	40.5-51.4	34.3-52.8	40.1-45.8	38.5-49.5
Mean head length equated to standard body length, mm	47.54	43.1	44.8	45.02	44.0	41.3
Standard error of mean, mm	± 1.38	± 0.233	± 0.92	± 0.86	± 0.95	± 1.40
Standard deviation, mm	4.97	4.00	3.05	3.86	1.90	3.71

TABLE 4.
RELATIONSHIP OF FORE-LIMB LENGTH TO BODY LENGTH

Series	1	2	3	4	5	6
Total number of individuals	33	191	17	47	84	163
Body length range, mm	63.5-566.8	43.2-535	51.5-504.5	73.1-563.3	63-442.1	45.1-600
Correlation coefficient, <i>r</i>	0.962	0.919	0.595	0.929	0.901	0.968
Regression constants	± 0.089	± 0.0074	± 0.104	± 0.013	± 0.017	± 0.0034
	a 1.404	a 1.68	a 1.72	a 0.329	a 0.526	a 1.34
	b 0.0234	b 0.0297	b 0.0261	b 0.0276	b 0.021	b 0.0207
Restricted number of specimens	13	68	12	21	5	8
Body length range, mm	330.6-566.8	350.8-535	341.6-504.1	353.3-563.3	285-422.1	249.1-600
Standard body length, mm ..	400	400	400	400	400	400
Standardized limb length range, mm	9.3-14.2	9.1-13.5	10.1-13.0	7.0-13.2	6.2-8.9	6.8-10.9
Mean fore limb length equated to standard body length, mm	10.90	10.90	12.09	11.25	7.99	8.50
Standard error of mean, mm	± 0.257	± 0.164	± 0.250	± 0.427	± 0.121	± 0.576
Standard deviation, mm	0.894	1.35	0.83	1.86	0.767	1.41

TABLE 5.
RELATIONSHIP OF HIND-LIMB LENGTH TO BODY LENGTH

Series	1	2	3	4	5	6
Total number of individuals	33	191	17	47	84	163
Body length range, mm	63.5-566.8	43.2-535	51.5-504.5	73.1-563.3	63-442.1	45.1-600
Correlation coefficient, r	0.979	0.943	0.926	0.952	0.909	0.949
	± 0.0049	± 0.0055	± 0.036	± 0.0093	± 0.013	± 0.0078
Regression constants	a 0.18 b 0.0422	a 1.033 b 0.0417	a 0.72 b 0.0431	a 1.224 b 0.0368	a 0.0351 b 0.0319	a 1.572 b 0.0237
Restricted number of specimens	13	68	12	21	5	8
Body length range, mm	330.6-566.8	350.8-535	341.6-504.1	353.3-563.3	285-442.1	249.1-600
Standard body length, mm	400	400	400	400	400	400
Standardized limb length, range, mm	15.2-18.9	13.1-20.1	14.7-18.8	11.8-23.8	9.8-14.2	9.5-14.0
Mean hind limb length equated to standard body length, mm	17.27	16.49	18.38	17.35	12.75	11.70
Standard error of mean, mm	± 0.148	± 0.034	± 0.139	± 0.445	± 0.316	± 0.596
Standard deviation, mm	1.33	1.53	1.24	2.91	1.26	1.73

TABLE 6.
RELATION OF TAIL LENGTH TO BODY LENGTH

Series	1	2	3	4	5	6
Total number of specimens ..	33	191	17	47	84	163
Body length range, mm	63.5-566.8	43.2-535	51.5-504.1	73.1-563.3	63-442.1	45.1-588.3
Correlation coefficient, <i>r</i>	0.924	0.998	0.981	0.931	0.960	0.860
Regression constants	± 0.017	± 0.0020	± 0.0062	± 0.013	± 0.0057	± 0.014
	a 2.976	a 4.005	a 3.173	a 4.209	a 2.775	a 5.53
	b 0.338	b 0.343	b 0.353	b 0.362	b 0.380	b 0.389
Restricted number of specimens	13	68	12	21	5	8
Body length range, mm	330.6-566.8	350.8-535	341.6-504.1	353.3-563.3	285-442.1	294.3-588.3
Standard body length, mm ..	400	400	400	400	400	400
Standardized tail length range, mm	112.8-166.6	99.8-149.8	127.9-160.0	105.5-137.4	132.4-169.0	129.7-170.2
Mean tail length equated to standard body length, mm	138.5	127.05	140.2	137.2	145.9	148.95
Standard error of mean, mm	± 4.42	± 1.48	± 2.32	± 4.20	± 4.10	± 5.78
Standard deviation, mm	15.30	12.17	7.70	18.70	8.20	14.16

chosen, the reason being that the same graphs used to determine sexual dimorphism could be used to determine the regression constants.

After obtaining a and b for each of the four body proportions for each of the six series, these constants were substituted in their respective regression equations.

From a study of the regression lines, it was determined that the body proportions do not remain constant throughout life. The reason for the foregoing statement is that a is not equal to zero (the regression line does not pass through the origin) (Klauber, 1943). However, it should be mentioned that in some cases a is almost equal to zero; although, additional collections may or may not reduce a to zero. If the proportion remains constant throughout life, the relationship of the head length to the body length should be the same in the adults as it is in the juveniles. If a juvenile with a body length of 50 mm is substituted in the regression equation ($H = 1.034 + 0.119B$), the value of H is equal to 6.984 mm. If an adult body length of 600 mm is substituted in the regression equation, H is equal to 72.434 mm. The juvenile head length is 14 percent of its body length; the adult head length is only 12 percent of its body length. This indicates that the juveniles have proportionately larger heads than the adults; therefore, the proportionality does not remain constant with an increase in body length.

Standardization—Since there were insufficient numbers of individuals of a single body length in each series, a second method suggested by Klauber was utilized to eliminate ontogenetic variation. This method requires the conversion of the head length, fore-limb length, hind-limb length, and tail length of the individual to a standard body length. In using this method, the assumption was made that any specimen in growing to (or returning to) the standard body length does so by maintaining a constant percentage deviation from the regression line (Klauber, 1941). The standard body length was arbitrarily chosen as 400 mm. In determining the standard body size, the writer was guided by the known biology of *Amphiuma* so that the chosen body length would be within the adult (sexually mature) body length range of the individuals of each of the six series. The females of the Audubon Park population become sexually mature when they attain a body length of 330 mm but the individuals of the Audubon Park population do not attain a size as large as that of *Amphiuma* collected from the surrounding areas (Cagle, 1948). The 400 mm body length should include the sexually mature individuals from all geographical series.

The body length range for the restricted number of specimens was chosen to include the greatest number of individuals, the limiting factor being the exclusion of individuals less than 249 mm in body length or greater than 600 mm in body length (Tables 3-6). The statistical accuracy sacrificed by limiting the study to fewer specimens (by taking a narrow range) is more than compensated for by the elimination of possible errors in translating the specimens

over too great a distance along their regression lines (Klauber, 1938).

The actual measurements of the body parts of each individual within the restricted ranges were converted to the measurement they would probably have at 400 mm body length by substituting the actual measurements in a standardization formula (Klauber, 1941).

A survey of the available material indicated that a moderate number of individuals (all sizes included) were available in Series 1 through 4, but the number in the restricted size range of Series 5 and 6 was very small. The range could not be widened because the millimeter spread on either side of the mid-point could not exceed 200 mm (Klauber, 1938). Klauber has used as few as five individuals in his snake studies.

In order to determine the standardized body parts for each individual of each series, the individuals from the restricted ranges of Series 1 through 6 were standardized by substituting the actual length of the part and the body length in a standardization formula. The estimated head length that the *Amphiuma* would have at the standard body length of 400 mm is 34.33 mm. Standardized lengths of the body parts, computed for the restricted number of specimens, were gathered into an array (separate for each geographical series) and their statistics computed (Tables 3-6).

Graphical relationships—Bar graphs were constructed to show the relationship of the range, standardized mean, standard error of the mean and the standard deviation of the four body parts for each of the six series. The horizontal axis was calibrated to include the range of the standardized measurements. For each series (geographical locality) the range of variation is shown by a horizontal line and the mean (M) by a short vertical line. The blackened part of each bar comprises two standard errors of the mean ($2\sigma_M$) on either side of M . One-half of each black bar plus the white bar at either end outline one standard deviation (σ) on either side of M . Standard deviation indicates dispersion and two standard errors of the mean indicates reliability (Hubbs and Hubbs, 1953).

RESULTS

Number of toes and coloration—The division of the 537 individuals into the six geographical series shows the Audubon Park individuals (Series 2) to be the most numerically representative of any of the series. Series 6, 5, 4, 1, and 3 follow, respectively, in decreasing numbers. The division of the individuals into size groups of 50 mm to determine the adequacy of the various age groups of each series, yielded the following information: of the three-toed groups, Series 1 was not represented in the size groups of less than 50 mm, of 250-300 mm, and of 350-400 mm; Series 2 was not represented in the size groups of 100-150 mm and 550-600 mm; Series 3 was not represented in the size groups of less than 50 mm, 100-150 mm, 200-250 mm, and 550-600 mm; Series 4 was not represented in the size group of less than 50 mm. The groups not represented

in the two-toed populations by Series 5 are size groups of less than 50 mm, 300-350 mm, 450-500 mm, 500-550 mm, 550-600 mm; by Series 6, 300-350 mm, 450-500 mm, and 500-550 mm (figures 6 and 7).

An inspection of the map showing the geographical distribution of the individuals examined in this research indicates that the two-toed and three-toed individuals occur together in the region where the alluvial valley of the Mississippi River meets the East Gulf Coastal Plain (figure 1). Within this region the proximity of the three-toed *Amphiuma* to the two-toed *Amphiuma* varies. A collection made in Amite, Louisiana, June 8, 1948, consisted of 42 *Amphiuma* taken from the same mud hole; of these, forty-one individuals had two toes on all four limbs and one individual had three toes on all four limbs. There is reason to believe that these individuals are from the same brood. All except one individual had a body length of approximately 214 mm. In the same region individuals with two toes on all four limbs and individuals with three toes on all four limbs have been collected together, either in the same drainage ditches, in adjacent drainage ditches or within a few miles (less

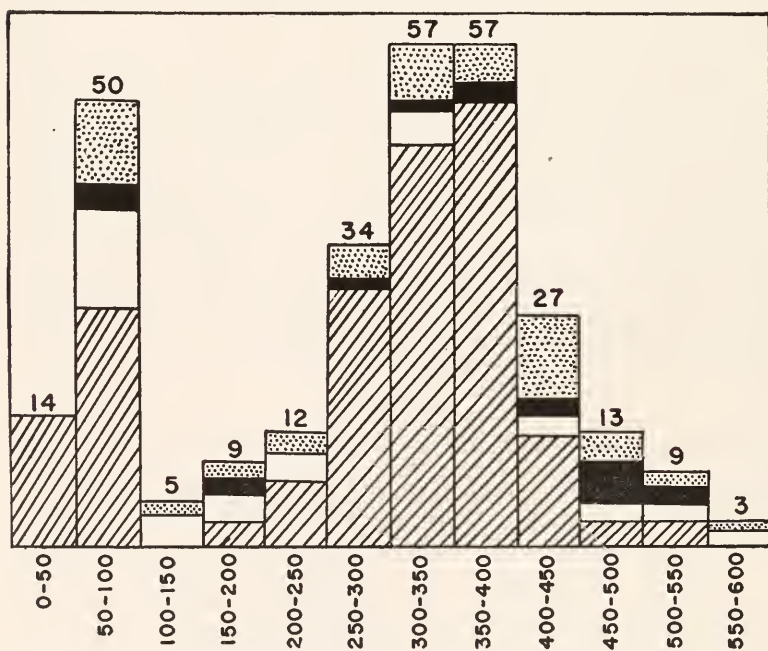


Figure 6. The distribution of body lengths of 290 specimens: Audubon Park (cross-hatched), west of the Mississippi River (clear), eastern alluvial valley (shaded), and Series 4 (stippled). The total number of individuals composing each 50 mm size group is given at the top of each bar of the histogram.

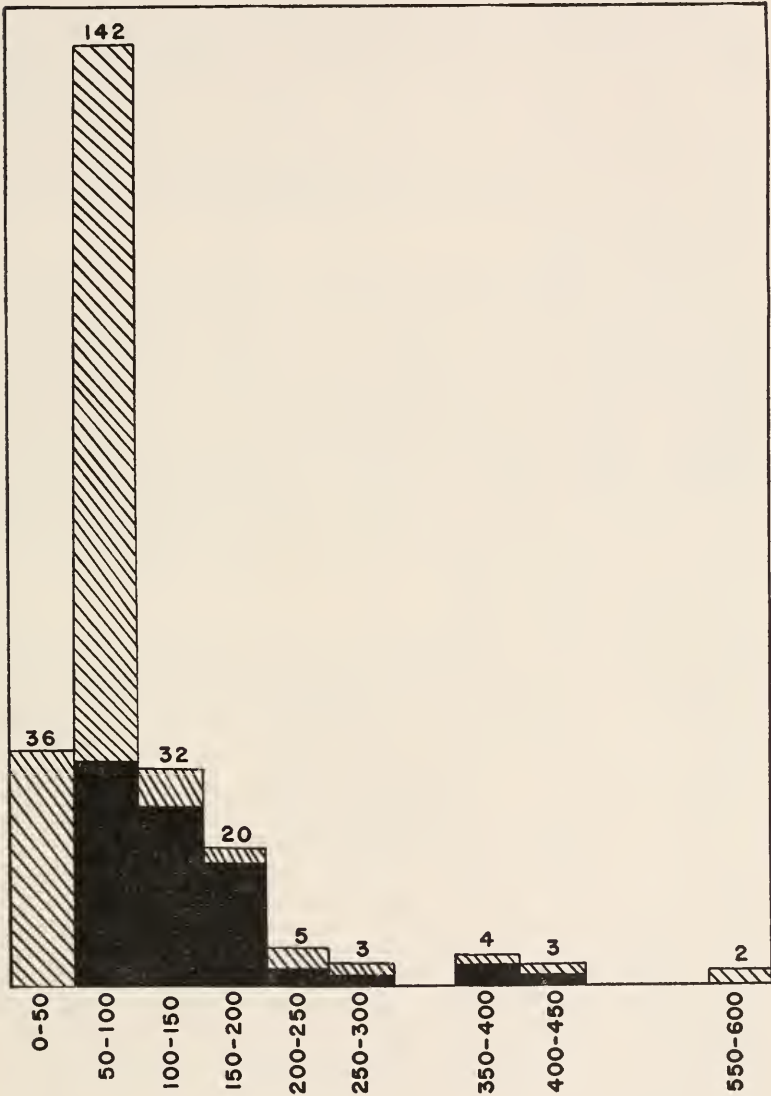


Figure 7. The distribution of body lengths of 83 specimens from Series 5 (shaded) and 163 specimens from the Atlantic coastal states (cross-hatched). The number of individuals comprising each 50 mm size group is given at the top of each bar of the histogram.

than five) of each other.

Three individuals with both two-toed and three-toed limbs on the same individual have been collected within this same geographical area. One of these was collected in Mandeville, Louisiana, in August, 1924, and the other two individuals were collected three miles north of the town of Pearl River, Louisiana. Both of these individuals were collected within the critical area (Series 4 and 5). The one from Mandeville (TU 2207) has a body length of 235.5 mm. The ones collected north of Pearl River in January, 1949 (TU 4777), and January, 1950 (TU 11414), have body lengths of 356 mm and 433 mm respectively.

Courtship activity between a two-toed and a three-toed *Amphiuma* has never been reported. The males of the Audubon Park series are reproductively active from mid-January to mid-May (Cagle, 1948). It is possible that in the region where the alluvial valley of the Mississippi River meets the East Gulf Coastal Plain, the two-toed and three-toed *Amphiuma* are reproductively active at the same time. The reason for the foregoing statement is that a two-toed male *Amphiuma* collected one mile north of Covington, Louisiana, March 6, 1950, was in a reproductive condition. The cloaca of this male was red, swollen and partially everted. The animal had more than ten well defined teeth prints and cuts on its body. These teeth marks and cuts may indicate fighting between the males during the reproductive season (Cagle, 1948).

All individuals examined could be placed into one of the two groups on the basis of number of toes except the three peculiar individuals, or 0.56 percent of the population. The toe formula for the individual from Mandeville is $2/2 \ 3/3$; for the two Pearl River specimens, the formulae are $2/2 \ 3/2$ and $3/2 \ 2/3$. All individuals of the six geographical series can be definitely separated into two-toed groups and three-toed groups on the basis of color, with the exception of the same three individuals which cannot be separated into one of two groups on the basis of the number of toes.

Within the three-toed group there are various degrees of ventral pigmentation, but the overall coloration is never so dark as that of the two-toed individuals. Whether this variation in the ventral coloration within the three-toed group is due to the effects of preservation, ecology, or inheritance has not been determined. The percentage of individuals of two of the three-toed series with ventral pigmentation is as follows: 7.8 percent for the Audubon Park individuals and 19.1 percent for those examined in Series 4. The individuals from the eastern alluvial valley usually have a mottled ventral surface.

Characteristically, the three-toed individuals have a black throat patch. The two-toed individual has no throat patch. Two of the three individuals, which cannot be separated into either the two-toed or the three-toed groups on the basis of a consistent number of toes and coloration, do not have a characteristic black throat patch, but

one of the individuals does have an indication of a throat patch.

Body proportions—Although the ontogenetic spread is comparatively satisfactory for the six series, the frequencies of all size groups should be increased, with the possible exceptions of the eastern two-toed juveniles (50-100 mm) and the Audubon Park adults (300-400 mm).

The correlation coefficients (r) are all high except that for fore-limb length to body length of Series 3 (0.595). No explanation is attempted for this low correlation coefficient.

The values for standard deviation (σ) are calculated on the assumption of normal distribution which is not likely to be realized in small samples. There are reasons for distrusting the reliability of the difference that is indicated by the graphical method when the samples include fewer than thirty specimens. Consequently, the limitation of the graphs (figures 8-11) is realized. The graphical analysis indicates why a broad overlap of the dark bars indicates low reliability of the observed difference between two samples and why any considerable separation of these bars indicates a high reliability. The plotting of one standard deviation on either side of the mean indicates an 84 percent separation.

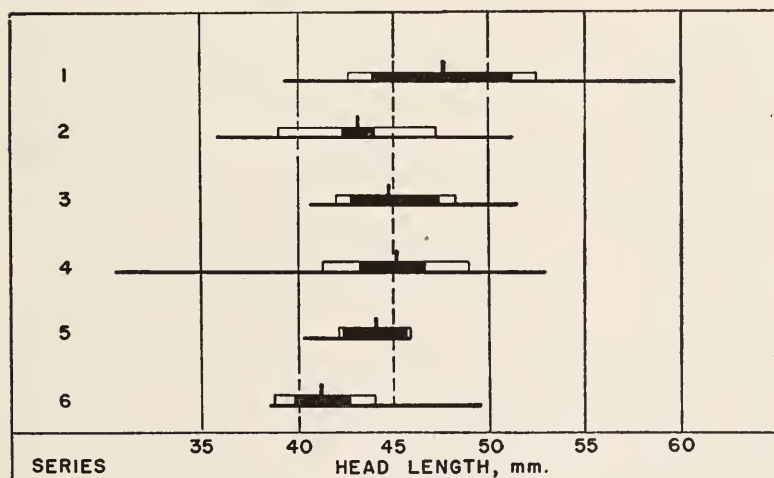


Figure 8. Bar graphs showing the relationship of the range, mean, standard deviation and standard error of the mean for head length for each of the six series. For each locality the range of variation is shown by a horizontal line; the mean (M), by a short vertical line. The blackened part of each bar comprises 2 standard errors of the mean ($2\sigma M$) on either side of M . One-half of each bar plus the white bar at either end outline 1 standard deviation (σ) on either side of M .

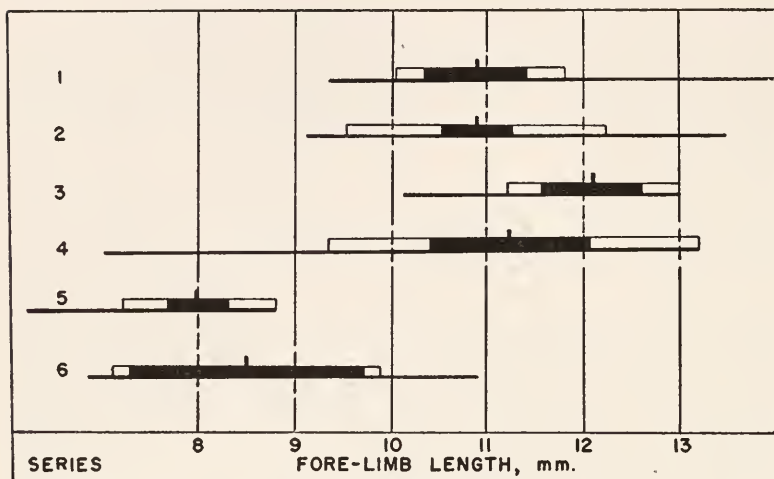


Figure 9. Bar graphs showing the relationship of the range, mean, standard deviation and standard error of the mean for fore-limb length. Arrangement as in fig. 8.

DISCUSSIONS AND CONCLUSIONS

Number of toes and coloration—The separation of *Amphiuma* into three groups on the basis of number of toes and coloration gives rise to the question as to whether or not the smallest of the three groups, comprising 0.56 percent of the population, is an intergrade group. If the coloration of these three individuals is due to either ecology or to methods of preserving the animals, and if the variation in the number of toes is due to either mutilation or to the inheritance of the monodactyly or polydactyly type, then *Amphiuma* can be completely separated into two groups, indicating no intergradation.

Since other individuals occurring within the same ecological area do not have the same coloration as these three individuals, indicates that ecology *per se* is not the causative factor in producing this coloration, unless the ecological factor producing it is extremely localized. The latter assumption is unlikely; for, if *Amphiuma* is so susceptible to these extremely localized conditions, a greater degree of natural variation would be expected among the remaining individuals than has been found. It is interesting that the type of coloration shown by these three individuals, which may be a blending resulting from the interbreeding of a bicolored individual with a unicolored individual, is found only in the region where the ranges of the two-toed and the three-toed individuals meet and overlap.

The fact that these three animals have no apparent scar tissue and that the measurements of the left limbs are the same as those of their corresponding right limbs constitutes evidence against the occurrence of mutilation. It is true that monodactyly and polydactyly

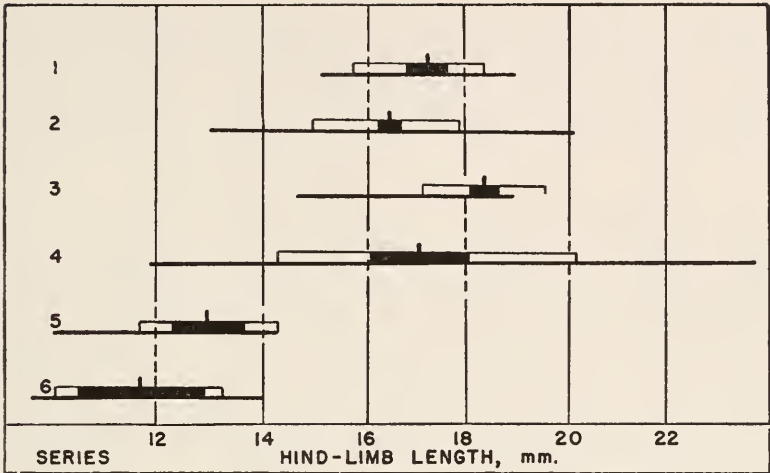


Figure 10. Bar graphs showing the relationship of the range, mean, standard deviation and standard error of the mean for hind-limb length. Arrangement as in fig. 8.

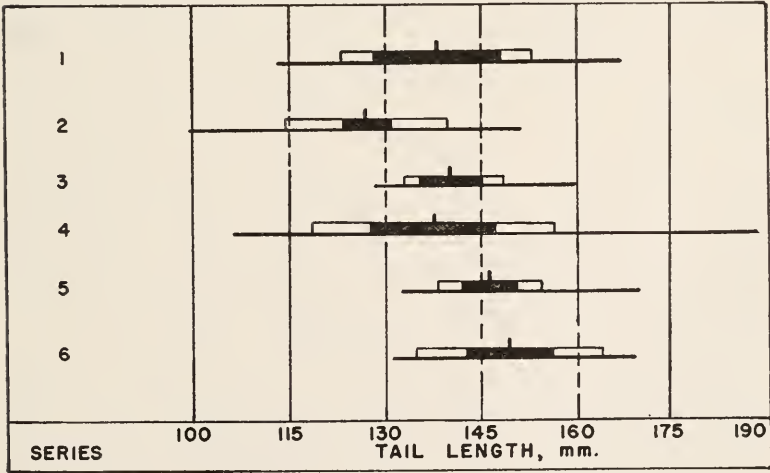


Figure 11. Bar graphs showing the relationship of the range, mean, standard deviation and standard error of the mean for tail length. Arrangement as in fig. 8.

occur in *Amphiuma*, but it is not evident that either one of these conditions expresses itself in any of the three individuals. Polydactyly has been observed only in individuals in the three-toed series, which series were designated by number of toes, coloration (general body color and the presence of throat patch), and geographical location. TU 4777 would have to be considered a three-toed individual because of the presence of the throat patch. The toe formula $2/2 \ 2/3$ must then be a result of inheritance (didactyly) as there is no evidence of mutilation. TU 2207 and TU 11414 because of the absence of a throat patch would be considered two-toed individuals. The toe formulae, $2/2 \ 3/3$ and $3/2 \ 2/3$, respectively, for TU 2207 and TU 11414 must be explained also by inheritance (polydactyly); however, polydactyly has not been observed in two-toed individuals (concerning geographical ranges) in this collection. In spite of the assumption of the presence of polydactyly, and the fact that the throat patch separates the three individuals into two groups, the uniform coloration of the three individuals and the almost identical general coloration of two of the individuals, TU 4777 with the throat patch and TU 11414 without the throat patch, prevents these three individuals from being separated into one of two groups.

Basically, the taxonomic position of the Mid-Gulf Coast *Amphiuma* resolves itself into the taxonomic position of these three individuals; that is, whether or not the three can be separated into one of two groups, a two-toed or a three-toed group, or whether all three should be placed into a third group, an intergrade group. The question is whether these three intermediates are true subspecies or hybrids.

With the exception of three specimens, all two-toed specimens have one toe pattern and all three-toed specimens have another. Since the two tables (1 and 2) are generally concordant and the forms (consistent with respect to two different characters, number of toes and pattern) are also sympatric in southeastern Louisiana (at least), and, in some cases, in the same pond, we are probably dealing with two separate species. It is difficult to conceive of two characters as different as number of toes and pattern that would result from a single genic element. If we were dealing with true subspecies and an area of intergradation, we should expect to find an almost complete mixture of characters in the intergrading area; that is, two-toed individuals with all variations in pattern and three-toed individuals with the same diversity. Intergradation is indicated in only three specimens out of 131 from the critical area (Series 4 and 5).

On the basis of this investigation the writer considers the three individuals to be hybrids. If there were a high proportion of mixed individuals in the critical area, the case for intergradation and a subspecific relationship would be greatly strengthened, particularly if the characters typifying the two groups were well jumbled in the intermediates. More individuals need to be collected from the critical area (Series 4 and 5).

Body proportions—The indication of species separation is further

reinforced by the fact that three-toed individuals, as a group, differ from the two-toed in proportionate limb length, and that the difference exceeds the within-group divergence (Tables 3 and 4). This is probably one of the most valuable parts of the investigation. It is not as important to note that head and tail portionalities are similar as to note that the latter reinforce and substantiate the fundamental toe and color pattern differences.

SUMMARY

Amphiuma has been separated into two species, *Amphiuma means* and *Amphiuma tridactylum*, by Baker on the basis of number of toes, color and the ratios of total length to body length and body length to limb lengths. In deriving the mean ratios, Baker did not recognize the influence of ontogenetic variation, allometric growth or sexual dimorphism.

This writer's research was concerned with the evaluation of the three assumptions above and an attempt to determine the real differences between the two-toed groups and the three-toed groups.

Heretofore, *Amphiuma* has been separated into a maximum of three groups to be compared with each other. Goin divided *Amphiuma* into a three-toed group, a two-toed group and an intergrade group and compared these groups. The author divided 537 *Amphiuma* into six series on the basis of geographical distribution. Series 1 is composed of individuals collected west of the Mississippi River; Series 2 consists of individuals from Audubon Park; Series 3 includes those individuals within the alluvial valley east of the Mississippi River; Series 4 (three-toed) and Series 5 (two-toed) includes those *Amphiuma* within the region where the alluvial valley of the Mississippi River meets the East Gulf Coastal Plain; Series 6 is composed of individuals from the Atlantic coastal states.

The reason for this division of *Amphiuma* into series was to determine the range of variation within the three-toed series and within the two-toed series so that the differences between two-toed and three-toed *Amphiuma* could be interpreted more accurately. The Audubon Park series was separated from all other series because it is geographically isolated and the individuals of this series do not reach a size as large as those from the surrounding areas. Since it was not known whether or not the three-toed *Amphiuma* within the eastern alluvial valley of the Mississippi River were genetically similar to those west of the Mississippi, these two series were separated. Series 5 was separated from Series 6 in order to determine if there was any difference between these two two-toed groups and to determine if there was a closer relationship between Series 5 and Series 6 than between Series 4 and Series 5.

The characters used in determining the differences and/or similarities between the series are number of toes, coloration, body proportions of head length to body length, fore-limb length to body length, hind-limb length to body length and tail length to body length. The two-toed and the three-toed *Amphiuma* cannot be completely

separated into two groups by any one of the above characters. The best separation is obtained on the basis of number of toes and throat coloration.

Intergradation is indicated in only three specimens out of 131 from the critical area (Series 4 and 5). On the basis of this investigation the three individuals are considered hybrids. The indication of species separation is further reinforced by the fact that three-toed individuals, as a group, differ from the two-toed in proportionate limb length, and that the difference exceeds the within-group divergence.

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